The influence of the physical environment, topography and time on the inshore distribution of invertebrate larvae: a multi-taxon approach

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Abstract

Coastal hydrodynamics regulate population dynamics through the distribution and dispersal of the meroplankton of many benthic invertebrates. I examined the hydrodynamics at four different sites on the south-east coast of South Africa and coupled them with larval sampling done at high temporal and spatial resolution. Day and night sampling was done at all four sites and a continuous 24 hour study was done in one site, both forms of sampling were carried out in autumn and spring. Samples were taken at two stations, 900 metres offshore and 300 metres apart, within each site. Water properties measured were depth, temperature and current velocity and direction. Plankton samples were collected using a plankton pump at various depths, from the surface, bottom and either side of the thermocline when present. A wide range of taxa (mostly bryozoans, bivalves, barnacles and decapods) was examined. 2-way ANOVAs were used to test the effects of time and depth on each taxon. In addition, multiple regression analyses were performed on each taxon to investigate the effects of hydrodynamics on the distribution of larvae. Bryozoan larvae proved to be positively phototactic whilst bivalve veligers, barnacle larvae and decapod zoeae performed diel vertical migration. Turbulence and temperature had an effect on the vertical distribution/migration of decapod zoeae. These results highlight the role of taxon-specific responses to flow and the potential differential effects on larval retention and ultimately connectivity of benthic populations.

Contents

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CHAPTER ONE

GENERAL INTRODUCTION

Differences in the physical characteristics of air and water lead to the clear, dichotomous separation between the terrestrial and marine realms (Shanks & Eckert, 2005) with consequences for their respective ecologies (Carr *et al.*, 2003). Organisms in the aquatic environment tend to be easily suspended in the water column due to water density and viscosity (Shanks & Eckert, 2005). Consequently, the aquatic environment provides a wide variety of means of dispersal for early life stages of aquatic organisms, including planktonic larvae (Cowen & Sponaugle, 2009).

Inshore communities include intertidal species that inhabit the zone between low and high tide, and those found below the low tide zone (Rawlinson *et al.*, 2004), the majority of which have a planktonic larval phase. While holoplankton reside in the water column throughout the life cycle (Bullard & Hay, 2002), meroplankton comprise the larvae of benthic adults (Mileikovsky, 1971; Pineda, 1994; Roughgarden *et al.*, 1994; Wendt & Woollacott, 1999; Shanks *et al.*, 2000; Dobrestov & Miron, 2001; Pineda *et al.*, 2010). Long evolutionary debates have questioned whether the benthic adult form has evolved from the planktonic larvae or vice versa. Two main theories are key subjects of the discussion, with the Intercalation Theory suggesting that the larval stages became "intercalated" in the ancestral holobenthic life cycle, whilst the Additional Theory suggests that an ancestor adult was holopelagic and the new sexually mature benthic stage was added to the life cycle and the pelagic stage retained as a larva (Nielsen, 2009). Pechenik (1999) suggests that benthic adults preceded the larvae, followed by the release of pelagic larvae which had the advantage of not having to compete with the adults for space or food. Jägersten (1972) strongly considers the pelagic larva as the original feature. Regardless of the "order of appearance", the pelagic larval phase is indeed the dominant dispersal stage for most coastal marine species (Cowen & Sponaugle, 2009).

Advantages of having dispersing propagules include improved gene flow, the ability to colonise of new habitats easily, a wide distribution of offspring, increased population connectivity and the elimination of competition between larvae and conspecific adults (Roughgarden *et al.*, 1994; Pechenik, 1999; Metaxas & Saunder,

2009; Robins *et al.*, 2013). For a successful life cycle, larvae are released so as to disperse, return to adult grounds and find a suitable habitat to settle and be fecund (Pineda, 1994; Abelson & Denny, 1997; Wendt & Woollacott, 1999). The time between spawning and settlement is variable and taxon-specific and can last for hours to months (Pineda, 1994; Metaxas & Saunder, 2009). During this period in the water column, larvae can disperse over 10's or even 1000's of kilometres from the parent population (Shanks, 1983; Shanks & Shearman, 2009). This dispersal phase is dependent on environmental factors, such as wind-driven circulation of currents, tides, fronts and temperature (Zaret & Suffern, 1976; Cronin & Forward Jr, 1986; Shanks, 1986; Pineda, 1994; Roughgarden *et al.*, 1994; Abelson & Denny, 1997; Dobrestov & Miron, 2001; Almeida & Queiroga, 2003; Shanks & Eckert, 2005; Marta-Almeida *et al.*, 2006; Queiroga *et al.*, 2006; Aiken *et al.*, 2007; Queiroga *et al.*, 2007; Cowen & Sponaugle, 2009).

Circulation of the ocean currents are among the most important physical processes that control the supply of larvae to adult habitats (Dobrestov & Miron, 2001; Queiroga *et al.*, 2006). Such dependence of larvae on oceanic flow (Yeung & McGowan, 1991; Graham & Sebens, 1996; McQuaid & Phillips, 2000; Shanks *et al.*, 2003a; b; Kinlan *et al.*, 2005; Aiken *et al.*, 2007; Mitarai *et al.*, 2008; Pattrick & Strydom, 2008) is the cornerstone of larval dispersal, marine community structure and overall population connectivity (Connell, 1985; Shanks & Brink, 2005) as the success of any population depends on how many larvae settle back to the parent community and/or new habitats and reproduce (Pineda, 1994; Pineda *et al.*, 2007).

Despite its importance, the spatio-temporal scales and predictability of larval dispersal and how it is regulated by physical circulation is however still poorly understood (Butman *et al.*, 1994; Gilg & Hilbish, 2003; Pernet *et al.*, 2003; Baums *et al.*, 2006; Knights *et al.*, 2006; Cowen *et al.*, 2007; Pineda *et al.*, 2007), especially for marine invertebrates (Manuel *et al.*, 1996). Meroplankton are minute (<2mm) and are very weak swimmers (~0.1 – 15mm.s^{-1}) and therefore are unable to swim against fast flowing horizontal currents (Chia *et al.*, 1984; Metaxas, 2001). Vertical current velocities, however, are much slower and are often of the order of ~1 –

2mm.s^{-1}, allowing larvae to influence their horizontal distribution and dispersal by swimming against weak vertical current flows (Metaxas, 2001).

The capacity of larvae to disperse is taxon-specific (Scheltema, 1988), depending on the embryonic development and whether the larvae are feeding or non-feeding (Strathmann, 1985; 1986; Scheltema, 1988; Pringle *et al.*, 2014). Planktotrophic larvae (feeding larvae) have a longer planktonic period, with the most extreme examples of teleplanic larvae (Scheltema, 1986), whilst the dispersal distance for lecithotrophic larvae (non-feeding larvae) is potentially limited, since the planktonic period is short and usually larvae are nearly competent to settle when released (Strathmann, 1986; Graham & Sebens, 1996; Shanks & Shearman, 2009). Feeding larvae have an advantage of having a prolonged period to select a site for the sedentary life form (Strathmann, 1985), increase genetic mixing, escaping temporal fluctuations, eliminating competition between conspecific adults and increasing population connectivity through habiting new sites (Roughgarden *et al.*, 1994; Pechenik, 1999).

Upwelling, downwelling, wind-driven turbulence, temperature, salinity, food concentration, current magnitude and direction all vary across a variety of spatio-temporal scales and can influence the vertical and horizontal distribution of invertebrate larvae in the water column (Shanks, 1985; Peters & Marrasé, 2000; Dobrestov & Miron, 2001; Marta-Almeida *et al.*, 2006; dos Santos *et al.*, 2008; Miller & Morgan, 2013). The influence of hydrodynamics varies with ontogenetic changes within a single taxon (Cragg, 1980; Gallager *et al.*, 1996; Manuel & O'Dor, 1997; DiBacco *et al.*, 2001; Dobrestov & Miron, 2001) as well as among different taxa (Zaret & Suffern, 1976). Some organisms tend to follow a day/night depth preference (Webb & Wooldridge, 1990; Armengol & Miracle, 2000; Marta-Almeida *et al.*, 2006). Current velocities and directions often differ with depth through the water column (Shanks, 1985) and might have different results in larvae found at different depths within the water column (Lloyd, 2011).

Strong alongshore winds drive offshore transport of the surface Ekman layer thereby forcing upwelling of cold, nutrient-rich bottom waters (Kirincich *et al.*, 2005). Benthic organisms find coastal areas that experience upwelling favourable for reproduction

and growth since food and nutrients are often abundant (Marta-Almeida *et al.*, 2006). These high-energy environments pose a major threat to dispersal as they forcefully remove planktonic larvae offshore (Garland *et al.*, 2002; Marta-Almeida *et al.*, 2006), limiting the numbers of potential recruits to coastal communities (Gaines & Roughgarden, 1985). Some invertebrate larvae actively change their vertical distribution by swimming against vertical flow (Tommasi *et al.*, 2014), and in upwelling systems, this might control their advection towards or away from the coast.

Turbulence can be defined as the natural mixing of a body of water generated by unstable excess of physical energy at larger scales, transferred to smaller and smaller scales through a cascading of instability (Sanford, 1997). The degree of vertical mixing and the swimming ability of larvae determine vertical larval distribution within the water column (Pearce *et al.*, 1998). Turbulence is one of the major factors that structure marine communities (Margalef, 1978; Peters & Marrasé, 2000) and can either be shear or buoyancy generated with the former resulting from large eddies and is predominant in the open ocean, while the latter is a result of wind driven upwelling and downwelling in the coastal ocean (Sanford, 1997). Larval responses to turbulence are species-specific with a specific range of turbulence that each species responds to (Fuchs & DiBacco, 2011).

Temperature affects the survival, growth and behaviour of aquatic organisms and every species has a normal/favourable temperature range, the range at which metabolism is at its peak and growth at its maximum (Goss & Bunting, 1976; Pörtner & Knust, 2007; Farrell *et al.*, 2008). Larvae of different taxa have shown vertical distribution that is influenced strongly by vertical discontinuities of temperature and salinity (Boudreau *et al.*, 1992; Gallager *et al.*, 1996; Manuel *et al.*, 1996). Thermal variability have been shown to affect growth, settlement and mortality (e.g. Boudreau *et al.*, 1992; Pörtner & Knust, 2007; Farrell *et al.*, 2008)

Aims and objectives

The aim of this study was to examine fine scale larval vertical distribution/migration in the water column of nearshore waters. The physical properties of the water column were considered the main predictors of larval distribution within the water column. Four study sites, two within bays and two on the open coast were used to investigate this phenomenon on the assumption that local hydrodynamics would be influenced by coastal topography, with consequences for larval distribution and, possibly, swimming behaviour. Larvae from different taxa were examined, including slow swimming bivalve veligers, barnacle nauplii and cyprids and fast swimming decapod zoeae. Sampling was done at discrete intervals, during the day and night at all four sites. Subsequently, finer scale sampling was done in one of the embayments, Algoa Bay, where 24 hour continuous sampling was done twice, to clearly determine whether there was fine time scale diel vertical migration in a shallow water column.

Additionally, an investigation of the coastal hydrodynamics that could affect larval distribution was undertaken. Due to the enclosure of bays, I assumed that the hydrodynamic characteristics of the bay would differ from those of the open coast, due to moderation of the effects of the wind on water circulation.

Ultimately, I wished to determine whether larvae act as passive particles or if they are able to control their position in the water column actively.

CHAPTER TWO

DAY AND NIGHT COMPARISON IN THE DISTRIBUTION OF MEROPLANKTON IN TWO EMBAYMENTS AND TWO OPEN COASTS

2.1 Introduction

Topography greatly influences species composition of marine communities (McQuaid & Branch, 1984; 1985). The abundance and distribution of flora and fauna differ between embayments and open coasts (Seapy & Littler, 1978; McQuaid & Branch, 1984; 1985; Bustamante & Branch, 1996; Davis *et al*., 2002), this being closely linked to differences in wave exposure. Open coasts receive intensive wave exposure whilst bays receive reduced wave shock (Seapy & Littler, 1978; Bustamante & Branch, 1996). Embayments generally have reduced flow speeds as compared to open coasts (Leonard *et al*., 1998). In some regions, bays are also usually characterised by an upwelling shadow (Graham, 1993), which is the result of upwelling on the open coast and increases residence time of water masses within an embayment (Graham *et al*., 1992; Graham, 1993).

A similar, but also independent factor is a change in temperature (Bakun, 1990). Temperature gradients also differ between embayments and the open coasts as the former present shallower depth profiles than the latter and consequently less thermal difference (Price *et al*., 1986). High wind speeds easily mix the water column resulting in a lack of thermal stratification and therefore no thermocline (Price *et al*., 1986; Noh & Kim, 1999; Gentemann *et al*., 2003), especially in these shallow waters. The differences in water temperature found between day and night, are mostly due to solar heating during the day (Price *et al*., 1986; Gentemann *et al*., 2003). A big difference in temperature change from the surface to the bottom of the water column is likely to occur at the open coast and would result in the formation or presence of a thermocline (Boudreau *et al*., 1992). Additionally, the sea presents a mesopelagic sound-scattering layer which moves regularly, following a diel cycle (Plueddemann & Pinkel, 1989; McManus *et al*., 2008). This layer moves closer to the surface at sunset and sinks to deeper layers of the water column at sunrise (Plueddemann & Pinkel, 1989). Since the movement of such layer could be influenced, if not triggered, by light, it might affect biological processes such as photosynthesis and therefore indirectly larval feeding.

To perform vertical migration, meroplankton respond to several cues provided by tidal state, lunar phase and time of day (Manuel & O'Dor, 1997; DiBacco *et al*., 2001). Even with clear and regular cues, it is uncertain whether larvae actively regulate their depth or passively drift within the water column (Metaxas & Saunders, 2009). Most studies have either focused on a single species (e.g. Clarke, 1934; Gaines & Roughgarden, 1985; Webb & Wooldridge, 1990; McQuaid & Phillips, 2000; Almeida & Queiroga, 2003; Fuchs *et al*., 2004; Marta-Almeida *et al*., 2006; Queiroga *et al*., 2006; Fuchs & DiBacco, 2011), or a single taxonomic group (e.g. Incze *et al*., 2001; Tapia & Pineda, 2007; dos Santos *et al*., 2008; North *et al*., 2008; Fuchs *et al*., 2010), or commercial species (e.g. Marshall & McQuaid, 1993; McCulloch & Shanks, 2003; Bownes & McQuaid, 2006) to address behavioural activity or passiveness of larvae in the water column.

On the other hand, many researchers examining larval behaviour in the water column have focused their work on a single site, either an embayment (e.g. Webb & Wooldridge, 1990; McCulloch & Shanks, 2003; Pattrick & Strydom, 2008), or an open coast (e.g. Marta-Almeida *et al*., 2006; Tapia & Pineda, 2007; dos Santos *et al*., 2008), or even in the deep open sea (e.g. Cisewski *et al*., 2010). Patterns of vertical migration however, may differ, not only depending on the taxonomic group, but also on nearshore topography and associated hydrodynamics.

The research presented in this chapter targeted multiple sites, representative of bay and open coast. Unlike some of the studies mentioned above, this study also focused on a wide range of taxa, from slow swimming bivalve veligers (0.11 cm/s for *Mytilus edulis*, Chia *et al*., 1984); bryozoan larvae (0.19 cm/s for *Membranipora* sp., Chia *et al*., 1984); barnacle larvae (0.45 cm/s for *Balanus* sp.) and even fast swimming decapod zoeae (1.38 cm/s for brachyuran zoeae, 1.65 cm/s for porcelanid zoeae and 1.85 for anomuran, *Eupagurus* sp. last larva) (Mileikovsky, 1973; Chia *et al*., 1984).

The aim of this study was to examine the possible patterns in the day and night hydrographic structure and water currents and links between these and the vertical distribution of meroplankton larvae in bays and open coasts on the south-eastern coast of South Africa.

2.2 Materials and methods

2.2.1 Study sites

Four different study sites (Figure 2.1) were selected along the south east coast of South Africa. Two sites were located in embayments (Algoa Bay: 33° 55′ S and 25° 37′ E; St. Francis Bay: 34° 10′ S and 24° 50′ E) and two on the open coast (Skoenmakerskop: 34° 05′ S and 25° 53′ E; Cape St. Francis: 34° 13′ S and 24° 49′ E). At the sampling stations, both bay sites were shallow (maximum depths ~14m for Algoa Bay and ~13m for St. Francis Bay), whilst the open coast sites were deeper (maximum depths ~50m for Skoenmakerskop and ~60m for Cape St. Francis).

Stations were marked using a Global Positioning System (GPS). At each site, one replicated sampling station (900 metres from the shore and 300 metres apart) was marked, providing a total of 8 different stations for the region considered during this study. Physical properties of water and zooplankton samples were collected from a research vessel, Ukwabelana.

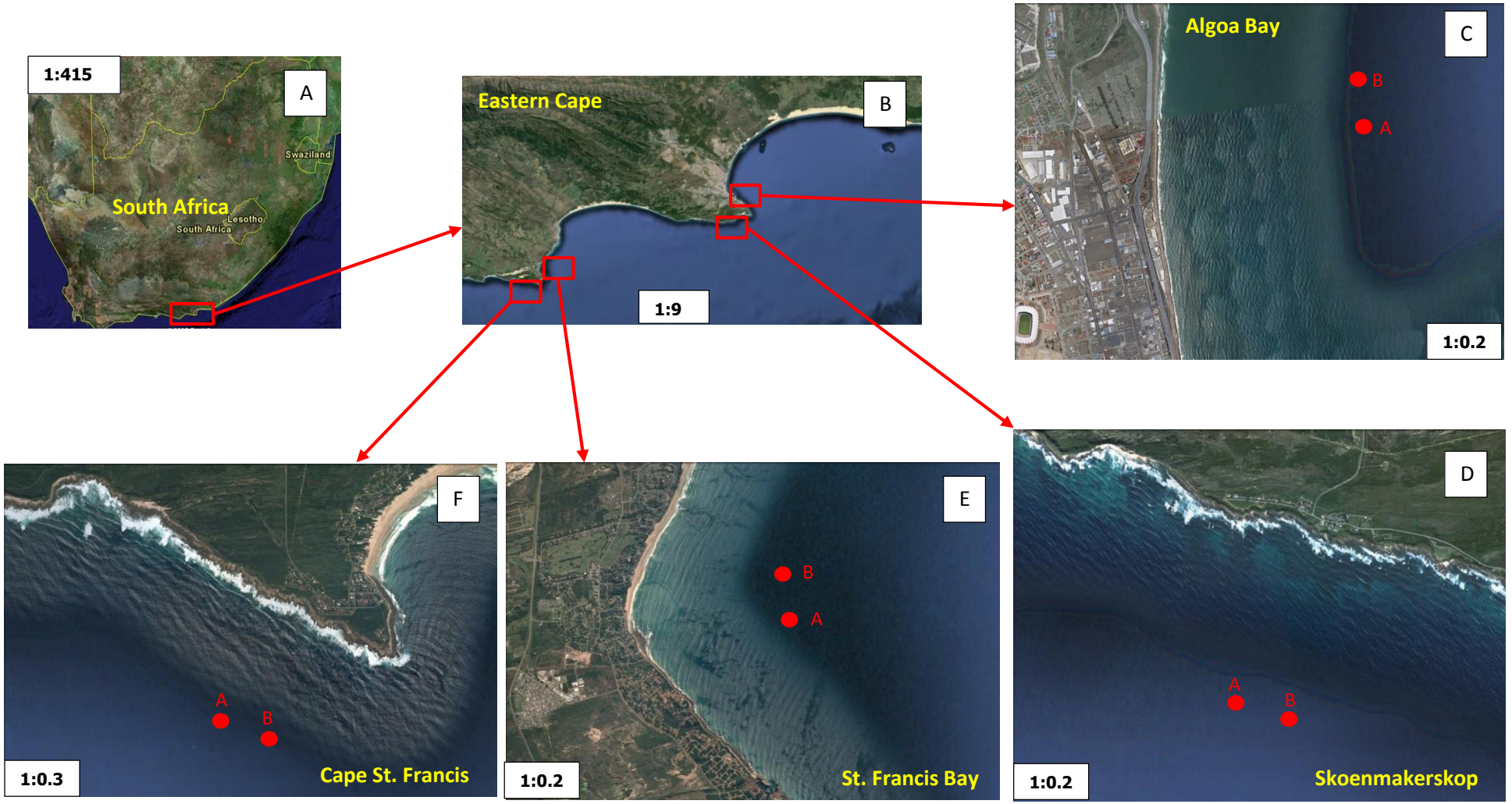


Figure 2.1: Map of the study area and sites. Map of South Africa (A), Eastern Cape (B), Algoa Bay (C), Skoenmakerskop (D), St. Francis Bay (E), and Cape St. Francis (F). The two red dots on each of the maps indicate the sampling stations.

2.2.2 Physical observations

The physical characteristics of the water column were measured during sampling, both during day and night times. The physical data were collected concurrently with the collection of biological data. A CTD Seabird SBE-19 and/or an YSI Incorporated 650-MDS CTD were deployed at each station to get vertical profiles of temperature, conductivity, salinity and depth. When the two instruments were deployed, they were calibrated against each other to make the dataset consistent. Concurrently, an Acoustic Doppler Current Profiler (ADCP Workhorse Monitor Teledyne) was deployed at each station to obtain vertical profiles of current magnitude and direction. Zonal (East-West) and meridional (North-South) currents were measured by the instrument every 3-5 seconds and were averaged every 7-10 minutes. On arrival at each station, the ADCP was deployed from the boat facing down through the water column for about 1 hour or until sampling of zooplankton was completed. The ADCP was then recovered before the next deployment on the other station. The ADCP data was averaged every 7-10 minutes after removing values which did not pass the quality control pertaining to the percentage of good data, which takes into account mainly the amplitude of the acoustic signal. Due to the measurements being instantaneous, removing tidal flows was not possible, but in any event, tidal signatures in currents were absent when long time moored ADCPs data were analysed (Schumann, *et al.*, 2005; Weidberg *et al.*, 2015). Wind data (velocity and direction) for Algoa Bay and Skoenmakerskop were obtained from a meteorological station situated at Algoa Bay, Port Elizabeth, and wind data (speed and direction) for both St. Francis Bay and Cape St. Francis were obtained from a meteorological station situated at St. Francis Bay. The meteorological stations in the two places collected wind data from different heights (35 metres in St. Francis and 9 metres in Algoa Bay) so these were corrected or adjusted to a single height (9 metres). Wind speed and direction data were used to calculate turbulence (W kg^{-1}) as done by Pringle (2007), without the removal of a tidal effect as this had no effect on turbulence in this system (Weidberg *et al.*, 2015). This turbulence proxy calculated from wind data fits well with our open ocean systems as turbulence generated from tidal effects is minimal, in contrast to the situation in lab mesocosms and shallow estuaries (Weidberg *et al.*, 2015). An upwelling index (m^3 km^{-1} s^{-1}) was calculated

using the equation below (Bakun, 1973; Pringle, 2007; Oakey, 1985; Llope *et al.*, 2006):

$$Q_y = \frac{\mathcal{T}x}{f.\rho w} = \frac{\rho a.Cd.vx.\,|v\,|}{f.\rho w}$$

where Q_y is the upwelling index, $\mathcal{T}x$ represents the wind stress along the x-axis, ρa being the density of the air (1.22 kg.m^{-3} constant), Cd is an empirical dimensionless drag coefficient considered a constant at 0.0014, vx is the east-west component of the wind, that induces upwelling, and $|v|$ is the module of the wind. $f = 2\Omega \sin \Phi$ is the Coriolis parameter, approximately 9.96 10^{-5}s^{-1} at mid-latitudes, and ρw is the seawater density (1025 kg.m^{-3}).

2.2.3 Biological data

Plankton samples were collected from each station using a KC Denmark Plankton Pump Model 23.570, provided with a flowmeter and a cod end of 75µm mesh size. The mesh size was fine enough to retain all decapod larvae (zoea to megalopae), barnacle larvae (nauplii stages I-VI to cyprids) and bivalve larvae (including D-larvae). The volume of water (m^3) was obtained from the flowmeter readings by applying the corresponding calibration factor found on the pump manual (KC Denmark Plankton Pump Model 23.570 technical manual). Due to logistic constraints, during the second sampling season, sampling at Skoenmakerskop was done in November 2013 instead of either September or October.

2.2.4 Sampling protocol

Sampling at each site was done on different days due to time limitations and weather conditions. In the March-April sampling season, sampling was done on the 06th March 2013 at Algoa Bay, 21st March 2013 at Skoenmakerskop, 05th April 2013 at Cape St. Francis and on the 15th April 2013 in St. Francis Bay. The next sampling season was done on the 23rd September 2013 at Algoa Bay, 03rd and 04th October 2013 at St. Francis Bay and Cape St. Francis respectively and on the 03rd November 2013 in Skoenmakerskop. Wave height and periodicity and the wind speed were the determining factors for a successful sampling day and these conditions were monitored for convenience on the Windguru website for each site (www.windguru.com).

Sampling was done at depth intervals determined by the specific maximum depth at the site. At Algoa Bay, which had a maximum depth of about 14 metres, samples were taken at intervals of 4 metres (i.e. 0, 4, 8, and 12 metres). At St. Francis Bay, the maximum depth was about 12-13 metres. Samples were taken at 0, 5-5.5 and 10-11 metres. The open coast sites were much deeper than the bays, with maximum depths of about 50 metres at Skoenmakerskop and 60 metres at Cape St. Francis. At the open coast deep sites, the presence of a thermocline was often recorded and thus the biological sampling included the depth on either side of the thermocline or within the thermocline layer. Samples at Skoenmakerskop were therefore taken at depths of 0, 10, 20 and 30 metres (intervals of 10 metres), and the thermocline was generally around 15 - 20 metres. At Cape St. Francis, samples were taken at depths of 0, 12, 20, 32 and 42 metres, and the thermocline was found generally at about 20 metres. The space left below the plankton pump's last sampling depth was a precautionary measure for the safety of the pump as it could hit the bottom.

Sampling was done at all depths within a station and the boat was then driven to the other station. The pump was deployed at each depth for 7-10 minutes and hauled back on board. Contents from the cod end were washed off into a sieve with the same mesh size as the cod end (75µm) using pressurised sea water (from the outside of the cod end to avoid potential addition of larvae) from a pump on the boat. Contents from the sieve were then washed off using 70% or 100% ethanol into 250 ml jars. Zooplankton samples were stored in 250ml jars and preserved using 70% or 100% ethanol. Samples were then transported back to the laboratory at the end of each sampling event.

Species identification and counting was done in the laboratory. No aliquots were made as the whole sample was processed and analysed. Zooplankton samples were transferred in small amounts onto a counting plate using a pipette and then each small amount extracted was viewed under a dissecting microscope. Identification of each taxon and stage of development was done using the guides and identification keys compiled by Sandison and Day (1954); Provenzano (1978); Booth (1983);

Brown and Roughgarden (1985); Achituv (1986); Lago (1987; 1993); Shenoy and Sankolli (1993); Kado and Kim (1996); dos Santos and González-Gordillo (2004).

2.2.5 Statistical analysis

For the analysis of variance (ANOVA) only taxa that reached at least 10 individuals per cubic metre (ind/m^3) at any given depth per station were analysed, following Weidberg *et al*. (2014).

For the day-night cruises, at the 2 bay and 2 open coast sites, separate 2-way analyses of variance (hereafter, ANOVA) were used to analyse the data of each site and sampling period independently for each taxon. Due to the lack of overlapping/common taxa among different sites, reaching the minimum analysis threshold of 10 ind/m^3, site comparison was not done even though topographic comparison among sites was one of the questions. All statistical analyses were performed using Statistica 12. The independent factors were Day/Night and Depth. Possible changes in the position of larvae in the water column in relation to day and night were also investigated by looking at the significance of the interaction between Day/Night and Depth. Such significance could be an indication of vertical migration, when larvae may be found at a given depth during the day and either sink or ascend at night. The dependent variable was the log transformed [$\log_{10}(X+1)$] abundance of each taxon. If there was a significant effect of any factor and/or the interaction on larval abundances, post hoc Fisher LSD contrast tests were subsequently performed. The levels of significance in the ANOVA tables are represented by asterisks with $p \leq 0.05$ = *; $p \leq 0.01$ = **; $p \leq 0.001$ = ***; $p \leq 0.0001$= ****; and non-significant (n.s).

Statistical Analysis for Macroecology (SAM v4.0) software package was used to analyse the multivariate structure of larval abundance considering the possible effects of the physical characteristics of the water column. The physical variables tested against the larval abundance were upwelling index, averaged over 4 days, the typical period at which Ekman transport develops with winds (García-Reyes & Largier, 2010); turbulence, averaged over 12 hours (which proved to be the best time lag to have an effect on plankton dynamics as multiple time periods were tested); zonal flow (west or east current direction); meridional flow (north or south

current direction) and temperature. Both upwelling index and wind driven turbulence were averaged over those time scales because they reflect the periods at which these variable significantly affect water movements (Dever, 1997; Ganachaud & Mercier, 2002; Pringle, 2007). Each of these predictors was introduced in a multiple linear regression for each taxon. To avoid multicollinearity, models which contain predictors that were significantly correlated were not taken into account. Due to the repeated nature of the analysis over each taxon, Bonferroni corrections were applied to prevent Type I error.

2.3 Results

2.3.1 Physical results

Different temperature ranges were found in each of the four sites during the March-April as well as the September-October 2013 sampling seasons. (Figures 2.2, 2.3, 2.4, 2.5).

There was little change in temperature from the surface to the bottom in bays during the March sampling (Table 2.1). This shows that there was no thermocline found in both bays. There was however a thermocline on both sites on the open coasts (Table 2.1). During the day, at Skoenmakerskop, the temperature decreased from 17.8°C (at 8 metres) to 15.4°C (at 20 metres) at station A and 17.4°C (at 8 metres) to 13.9°C at station B (at 20 metres). At night, the temperature dropped from 17.9°C (at 16 metres) to 14.8°C (at 24 metres) at both stations. At Cape St. Francis, the temperature changed from 15.8°C (surface) to 11.0°C (at 12 metres) at both stations during the day. At night, a drastic change in temperature was found between the sampling depth of 6 metres (16.0°C) and 12 metres (11.5°C) at both stations.

As for the March-April 2013 sampling season, during the September-October 2013 sampling, there was no thermocline in either bay, while it was clear at both the open coast sites (Table 2.2). During the day at Skoenmakerskop, the temperature decrease from 21°C (surface) to 17°C (at 10 metres) at station A and 20°C (surface) to 18°C (at 10 metres) at station B. At night, the temperature changed from 16°C

(at 10 metres) to 14°C (at 20 metres) in both stations. Cape St. Francis had a temperature drop from 15.8°C (surface) to 11.0°C (at 12 metres) during the day at both stations. At night, the temperature dropped from 16.5°C (surface) to 11.5°C (at 12 metres) in both stations.

Table 2.1: Water temperature for each site at each station during the day and night sampling times during the March-April 2013 sampling season. Each depth represents the exact depth sampled. Depths 1 to 5 on the table represent the depths that were sampled and the exact sampling depth values are given in the methodology section.

	Temperature (°C)																			
	Day										Night									
	Station A					Station B					Station A					Station B				
	Depth					Depth					Depth					Depth				
Site	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Algoa Bay	22.0	21.5	21.2	21.1		21.7	21.6	21.3	21.0		21.7	21.7	21.6	21.1		21.5	21.5	21.5	21.0	
St. Francis Bay	18.0	17.9	17.7			18.4	18.0	17.7			18.8	18.2	17.4			18.3	18.2	17.6		
Skoenmakerskop	18.8	17.8	15.4	13.1		18.3	17.4	13.9	10.6	9.8	18.3	18.3	17.9	14.8	12.0	18.3	18.3	17.8	14.8	12.3
Cape St. Francis	15.8	11.0	10.5	9.0	8.9	15.8	11.0	10.5	9.0	8.9	16.5	16.0	11.5	8.9	8.9	16.5	16.0	11.5	8.9	8.9

Table 2.2: Water temperatures for each site at each station during the day and night sampling times during the September-October 2013 sampling season. Each depth represents the exact depth sampled at each site. Depths 1 to 5 on the table represent the depths that were sampled and the exact sampling depth values are given in the methodology section.

	Temperature (°C)																			
	Day										Night									
	Station A					Station B					Station A					Station B				
	Depth					Depth					Depth					Depth				
Site	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Algoa Bay	18.0	17.8	17.8	17.8		18.1	18.0	17.8	17.7		18.0	18.1	18.0	17.8		17.9	18.0	18.0	18.0	
St. Francis Bay	19.2	18.3	17.9			18.8	18.4	17.9			18.7	18.7	18.2			18.7	18.7	18.5		
Skoenmakerskop	21.0	17.0	15.0	13.0		20.0	18.0	15.0	12.0		16.0	16.0	14.0	12.0		16.0	16.0	14.0	12.0	
Cape St. Francis	15.8	11.0	10.5	9.0	8.9	15.8	11.0	10.5	9.0	8.9	16.5	11.5	9.2	8.9	8.9	16.5	11.5	9.2	8.9	8.9

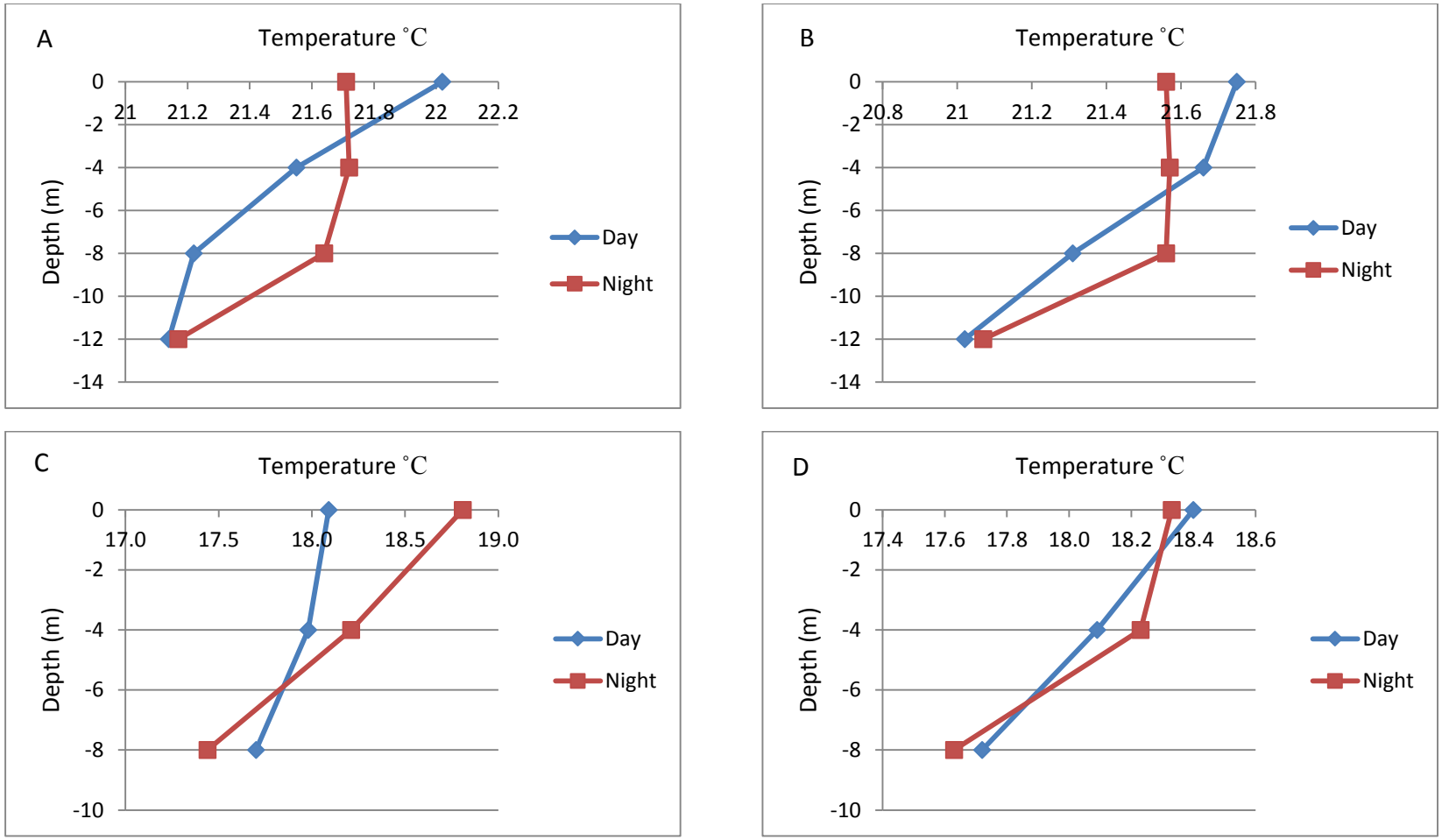


Figure 2.2: Temperature-depth profiles at Algoa Bay for stations A and B (graph A and B respectively) on 6 March 2013 and at St. Francis Bay for stations A and B (graph C and D respectively) on 15 April 2013 during the day and night sampling times. Different scales were used to maximise within-station state.

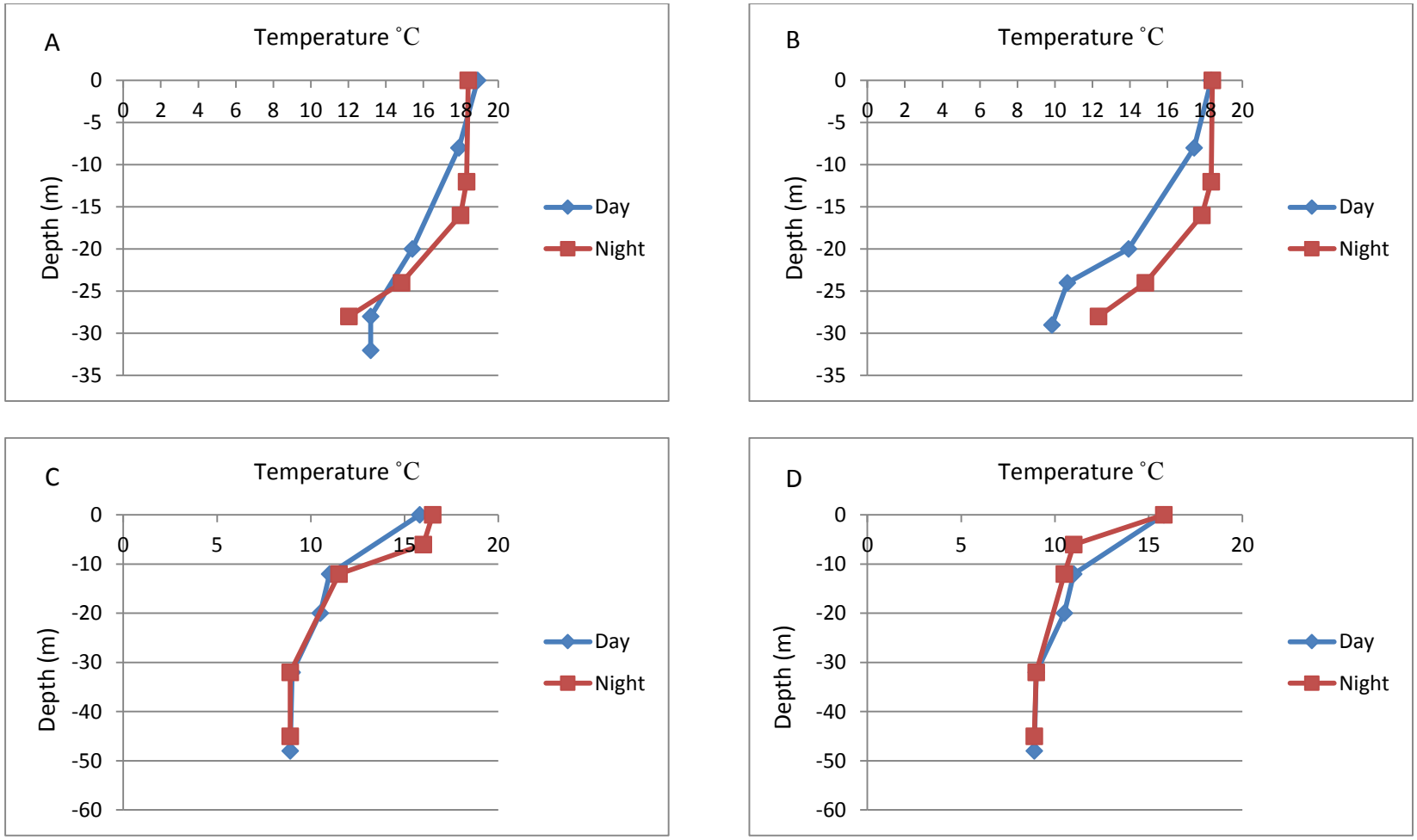


Figure 2.3: Temperature-depth profiles at Skoenmakerskop for stations A and B (graph A and B respectively) on 21 March 2013 and Cape St. Francis for stations A and B (graph C and D respectively) on 5 April 2013 during the day and night sampling times. Different scales were used to maximise within-site state.

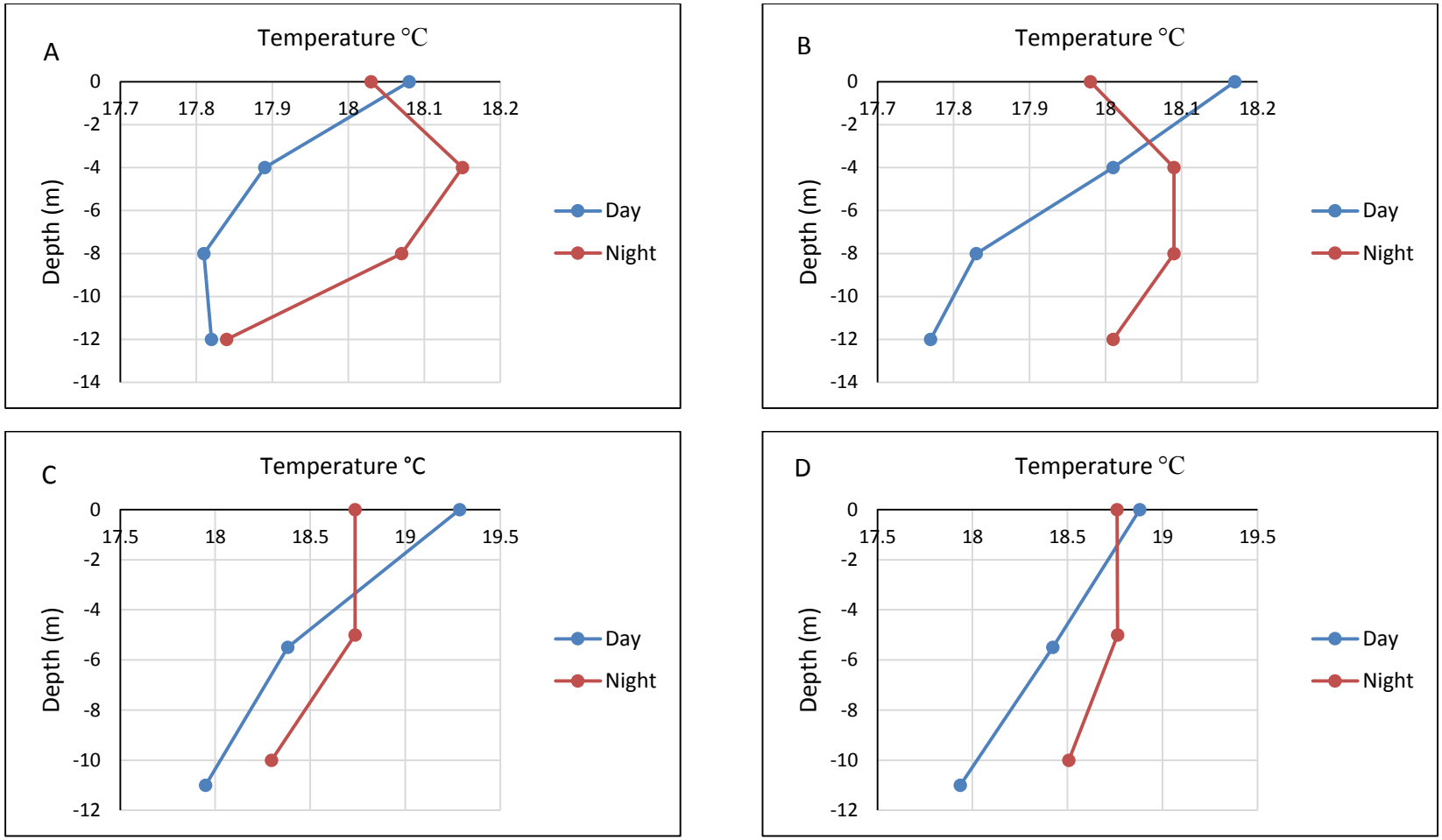


Figure 2.4: Temperature-depth profiles at Algoa Bay for stations A and B (graph A and B respectively) on 23 September 2013 and at St. Francis Bay for stations A and B (graph C and D respectively) on 3 October 2013 during the day and night sampling times. Different scales were used to maximise within-site state.

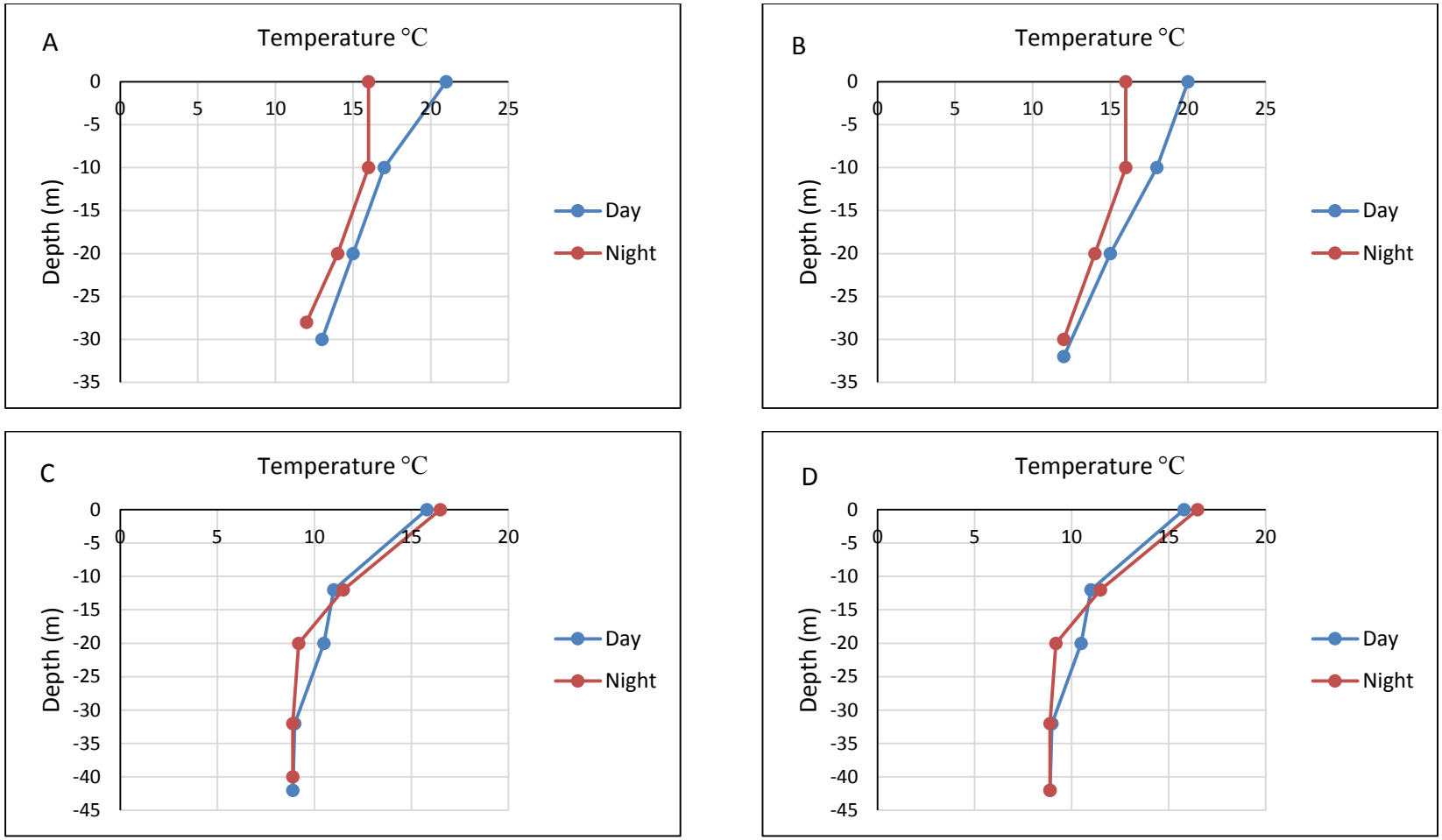


Figure 2.5: Temperature-depth profiles at Skoenmakerskop for stations A and B (graph A and B respectively) on 3 November 2013 and Cape St. Francis for stations A and B (graph C and D respectively) on 4 October 2013 during the day and night sampling times. Different scales were used to maximise within-site state.

2.3.2 Biological data

A wide range of taxa was found in the March-April and September-October 2013 (Table 2.3) samples, from bivalves (slow/passive swimmers; Chia *et al.*, 1984) to barnacles (nauplii to cyprids) and different decapod taxa (fast/very active swimmers; Chia *et al.*, 1984). Some taxa or ontogenetic stages were however not consistently found in all the sites and during both seasons (Tables 2.3). Throughout the thesis, wherever there is a mention of brachyurans, pinnotherids and sesarmids are excluded even though they are brachyurans, and similarly the group anomura group, excludes porcelanids, even though they are anomurans as all these groups were analysed separately. The Level of significance in the ANOVA tables is represented by asterisks with $p \leq 0.05$ = *; $p \leq 0.01$ = **; $p \leq 0.001$ = ***; $p \leq 0.0001$= ****; and non-significant (n.s).

Table 2.3: Different taxa/groups and larval stages found during sampling in March-April and September-October 2013. X indicates the presence of taxon and/or larval stage at that site.

Species/Taxa/Group	March-April 2013				September-October 2013			
	Algoa Bay	St. Francis Bay	Skoenmakerskop	Cape St. Francis	Algoa Bay	St. Francis Bay	Skoenmakerskop	Cape St. Francis
BRYOZOANS								
Bryozoan larvae	X	X	X	X		X		X
BIVALVES								
Perna perna	X		X	X	X	X	X	X
Mytilus galloprovincialis	X	X	X	X	X	X		X
Choromytilus meridionalis	X		X			X		
Oysters	X	X	X	X	X	X	X	X
Hiatella spp.	X	X	X	X	X	X	X	X
D-larvae	X	X	X	X	X	X		
Bivalve sp. A	X	X	X	X	X	X	X	X
Bivalve sp. B	X	X	X	X	X	X	X	X
Other mussels	X	X	X	X	X	X	X	X
BARNACLES								
Balanid nauplii (early stages)	X	X	X	X	X	X	X	X
Balanid nauplii (late stages)	X	X	X	X	X	X	X	X
Chthamalid nauplii (early stages)	X		X	X				X
Chthamalus spp. nauplii (late stages)	X							

Octomeris angulosa nauplii (late stages)	X		X					
Chthamalid cyprids	X	X	X	X	X	X	X	X
Cyprid sp. A	X	X	X	X	X	X	X	X
Cyprid sp. B	X		X	X	X	X	X	X
DECAPODS								
Sesarmid zoeae	X				X		X	
Brachyuran zoeae	X	X	X	X	X	X	X	X
Brachyuran megalopae	X	X			X	X	X	X
Pinnotherid zoeae	X	X	X	X	X	X	X	X
Porcelanid zoeae	X	X	X	X	X	X	X	X
Anomuran zoeae	X	X	X	X	X	X	X	X

Bryozoans

Bryozoan larvae reached the analysis threshold only in the March-April sampling season and only the data from that season were therefore analysed. There was a significant effect of the interaction between Depth and Day/Night indicating a change in depth preference between day and night (Table 2.4). During the day, larval abundance was higher on the surface than at the other depths (Figure 2.6). At 4 metres, larvae were also in higher abundances compared to depths 8 and 12 metres. This abundance pattern was also found during the night. The only difference was that the higher abundances were found amongst three depths (0, 4 and 8 metres) at night. At 12 metres, abundances were significantly lower. This shows that bryozoan larvae found at Algoa Bay preferred the shallow depths during both sampling times, day and night in March 2013.

At St. Francis Bay, the pattern was similar to Algoa Bay. Larvae were most abundant at the surface during the day. The abundance on the surface was statistically higher than at the other lower depths (4 and 8 metres), but at night abundance was homogenous throughout the water column (Figure 2.7).

At Skoenmakerskop, which is the only open coast where bryozoan larvae were found, only Depth had a significant effect on the abundance (Table 2.6). Figure 2.8 clearly shows that the significantly higher abundance of this taxon were found on the surface.

Table 2.4: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of bryozoans throughout the water column on 6 March 2013 at Algoa Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	Df	MS	F	p
Depth	4.82271	3	1.60757	44.8833	****
Day/Night	0.05240	1	0.05240	1.4631	n.s
Depth*Day/Night	1.18773	3	0.39591	11.0538	**
Error	0.28653	8	0.03582		

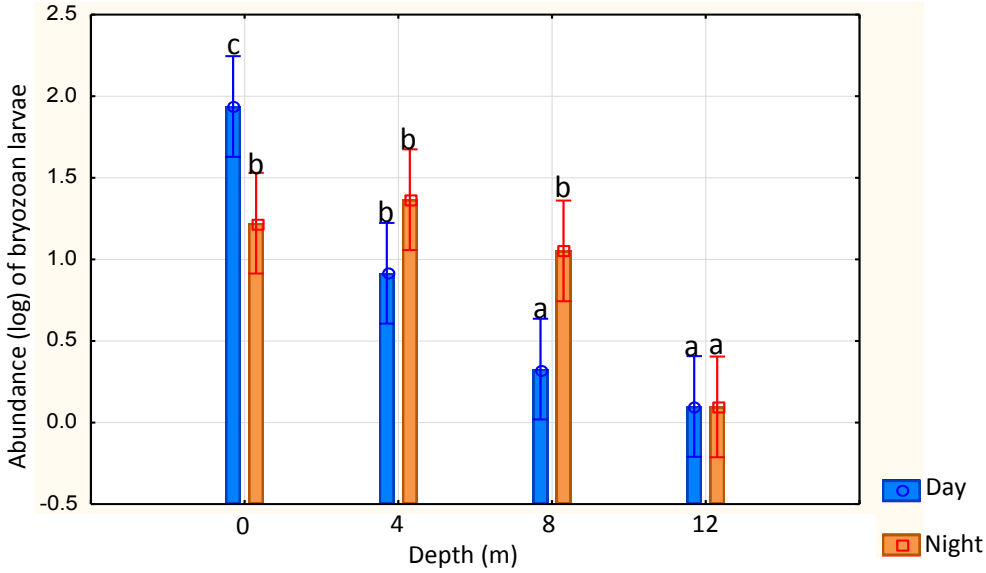


Figure 2.6: Abundance of bryozoan larvae with the significant interaction of Day/Night and Depth at Algoa Bay on 6 March 2013. Error bars indicate standard errors. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night.

Table 2.5: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of bryozoans throughout the water column on 15 April 2013 at St. Francis Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	1.279710	2	0.639855	6.62077	*
Day/Night	1.832365	1	1.832365	18.96004	**
Depth*Day/Night	2.160902	2	1.080451	11.17975	**
Error	0.579861	6	0.096644		

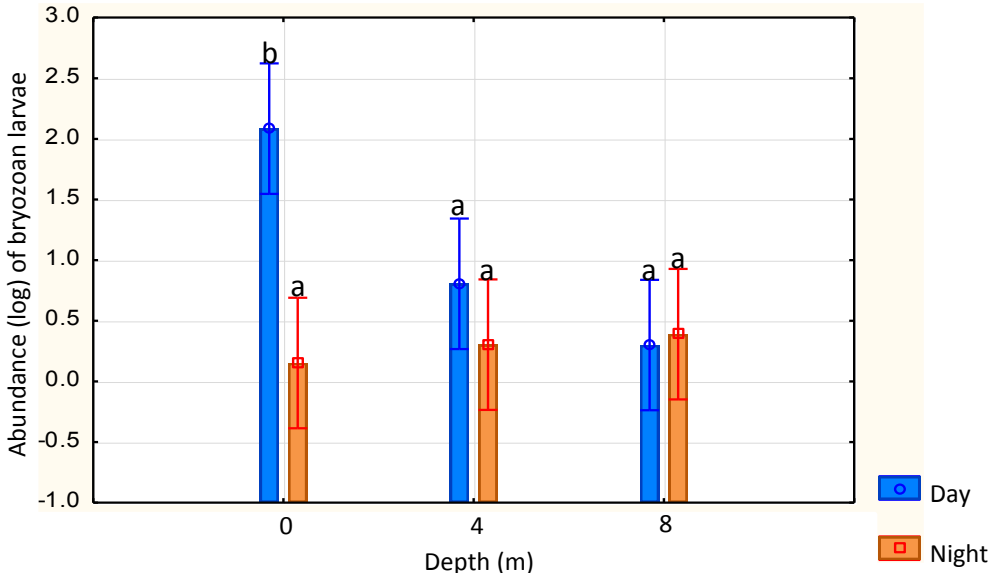


Figure 2.7: Abundance of bryozoan larvae with the significant interaction of Day/Night and Depth at St. Francis Bay on 15 April 2013. Error bars indicate standard errors. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night.

Table 2.6: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of bryozoans throughout the water column on 21 March 2013 at Skoenmakerskop. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	4.231021	4	1.057755	18.14991	****
Day/Night	0.150852	1	0.150852	2.58846	n.s
Depth*Day/Night	0.227344	4	0.056836	0.97524	n.s
Error	0.582788	10	0.058279		

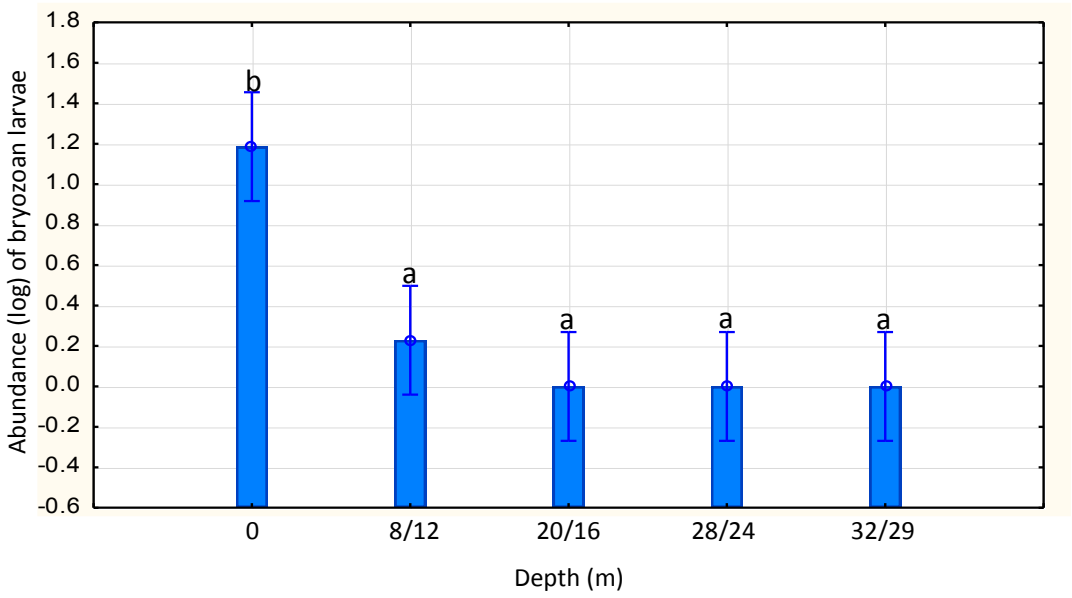


Figure 2.8: Abundance of bryozoan larvae with change in depth over a day and night sampling period at Skoenmakerskop on 21 March 2013. Error bars indicate standard errors Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of Depth. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

BIVALVES

D-larvae

About 95 µm in length, flat on one side and round on the other, shaped like the letter D, this is a group of early bivalve veligers (D-larvae; Siddal, 1980). At that size and stage, it was not possible to identify these larvae to any taxonomic resolution beyond class. This group of organisms reached the minimum threshold of 10 ind/m^3 only at St. Francis Bay in the September-October sampling season. The 2-way ANOVA revealed a significant effect only for Day/Night (Table 2.7), with significantly higher abundance of D-larvae during the day (Figure 2.9).

Table 2.7: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of D-larvae throughout the water column on 3 October 2013 at St. Francis Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	0.083444	2	0.041722	0.38635	n.s
Day/Night	1.074634	1	1.074634	9.95130	**
Depth*Day/Night	0.114347	2	0.057173	0.52944	n.s
Error	0.647936	6	0.107989		

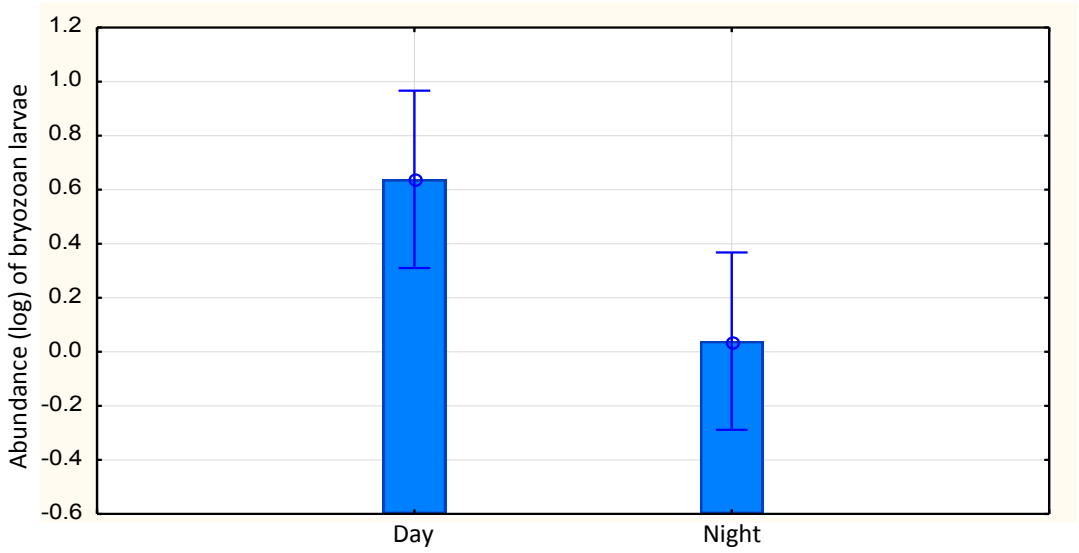


Figure 2.9: Abundance of D-larvae larvae during a day and night sampling period at St. Francis Bay on 3 October 2013. Error bars indicate standard errors.

Oyster veligers

Oyster veligers were found during both sampling seasons on the open coasts, but not in the bays. During the March-April sampling, Depth and Day/Night had a significant effect on the abundance of oyster veligers (Table 2.8, Skoenmakerskop and 2.9, Cape St Francis). Although there was a significant effect of depth, the post hoc test did not succeed in the identification of groups; veligers were therefore homogenously distributed throughout the water column (Figure 2.10 and 2.12). Oyster veligers were, however, found at significantly higher abundances at night (Figure 2.11 and 2.13).

The interaction of Depth and Day/Night had a significant effect on the abundance of oyster veligers on the September-October sampling season at Skoenmakerskop (Table 2.10). During the day, abundance did not differ significantly among depths (Figure 2.14). Oyster veligers were however found at significantly higher abundances at the surface compared to the bottom depth (28 metres) at night (Figure 2.14).

Table 2.8: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of oysters throughout the water column in 21 March 2013 at Skoenmakerskop. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	4.45931	4	1.11483	4.6968	*
Day/Night	1.71904	1	1.71904	7.2424	*
Depth*Day/Night	0.99397	4	0.24849	1.0469	n.s
Error	2.37357	10	0.23736		

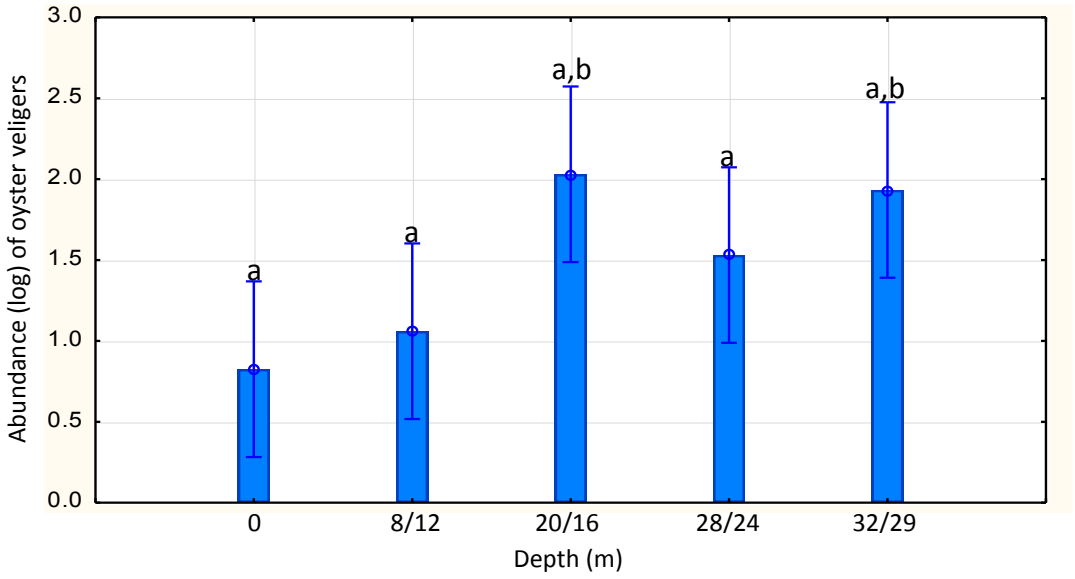


Figure 2.10: Abundance of oyster veligers with change in depth over a day and night sampling period at Skoenmakerskop on 21 March 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of Depth. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

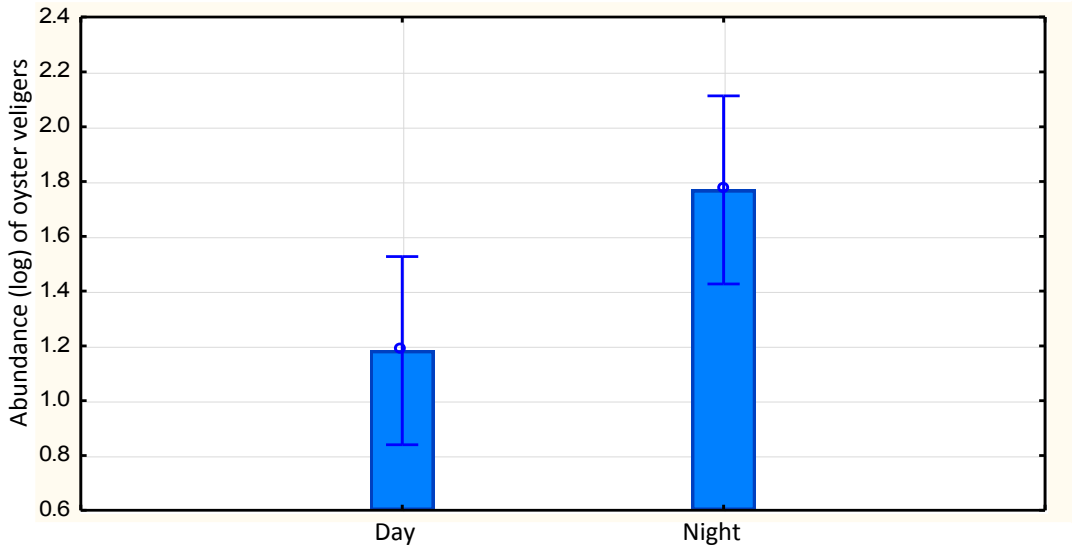


Figure 2.11: Abundance of oyster veligers during a day and night sampling period at Skoenmakerskop on 21 March 2013. Error bars indicate standard error.

Table 2.9: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of oyster veligers throughout the water column in 5 April 2013 at Cape St. Francis. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	2.22127	4	0.55532	3.9010	*
Day/Night	0.92483	1	0.92483	6.4968	*
Depth*Day/Night	0.35656	4	0.08914	0.6262	n.s
Error	1.42353	10	0.14235		

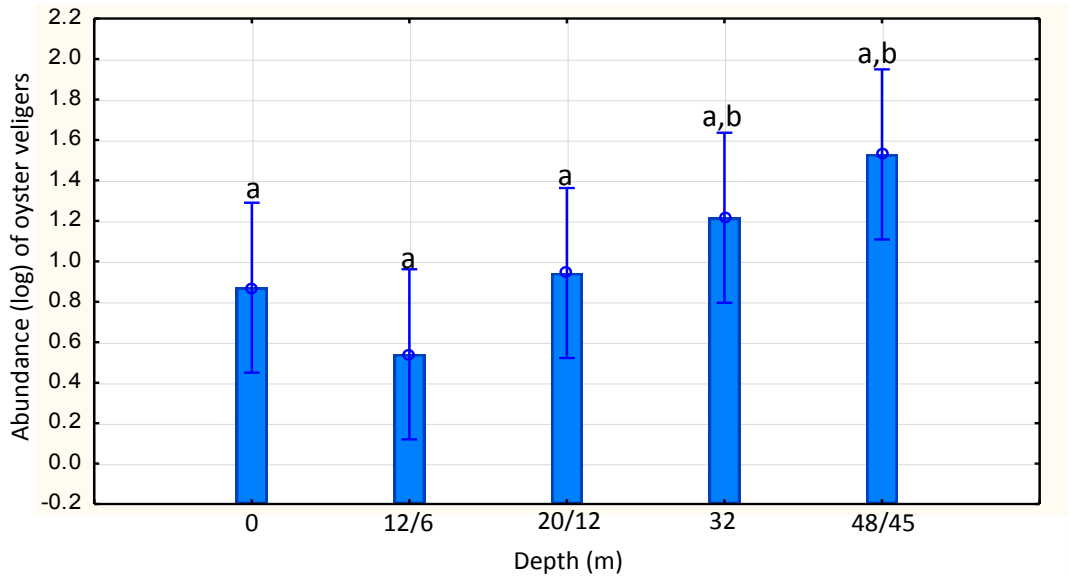


Figure 2.12: Abundance of oyster veligers with change in depth over a day and night sampling period at Cape St. Francis on 5 April 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of Depth. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

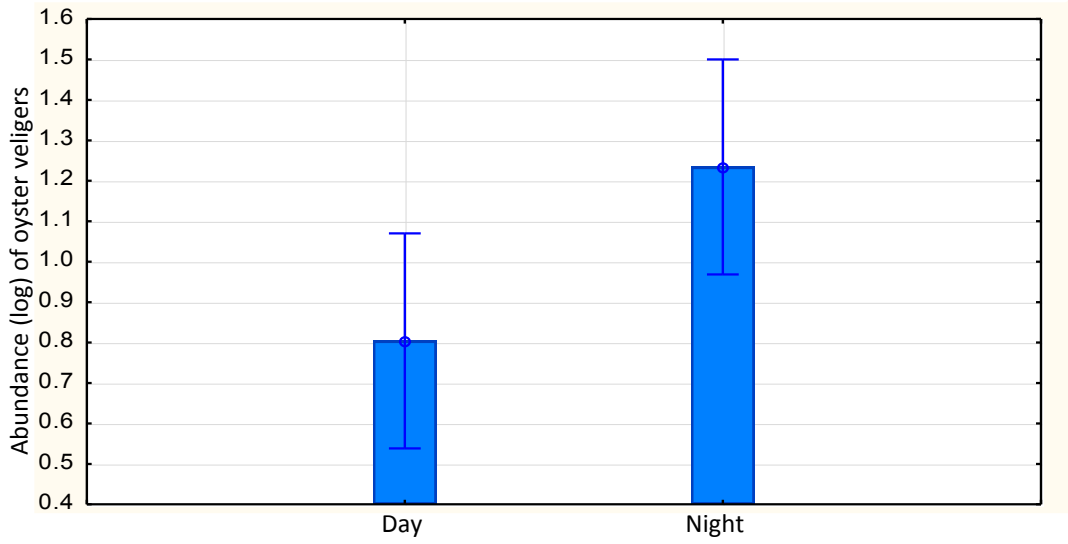


Figure 2.13: Abundance of oyster veligers during a day and night sampling period at Cape St. Francis on 5 April 2013. Error bars indicate standard error.

Table 2.10: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of oyster veligers throughout the water column in 3 November 2013 at Skoenmakerskop. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	Df	MS	F	p
Depth	0.655103	3	0.218368	2.01015	n.s
Day/Night	0.576206	1	0.576206	5.30419	*
Depth*Day/Night	2.118163	3	0.706054	6.49949	**
Error	0.869059	8	0.108632		

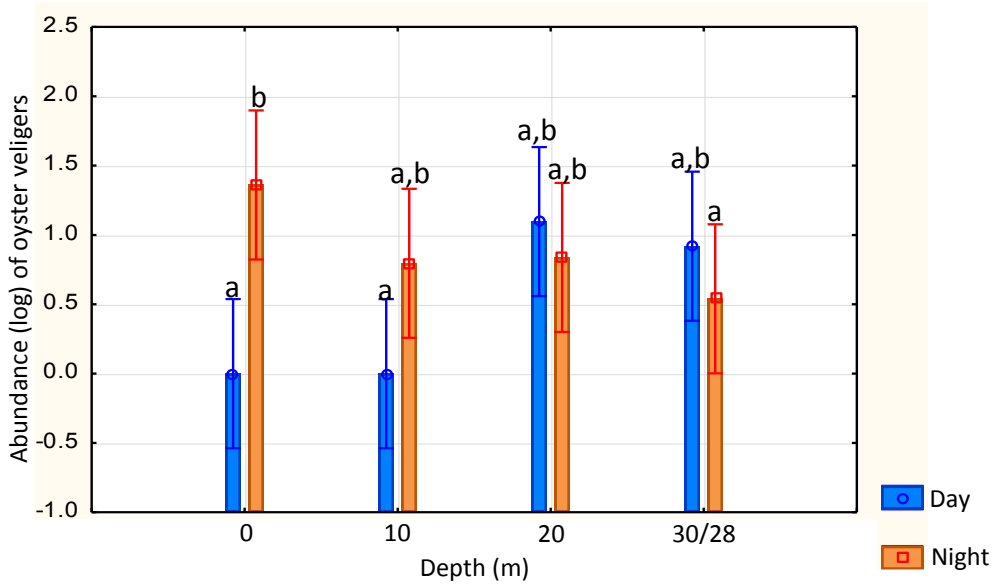
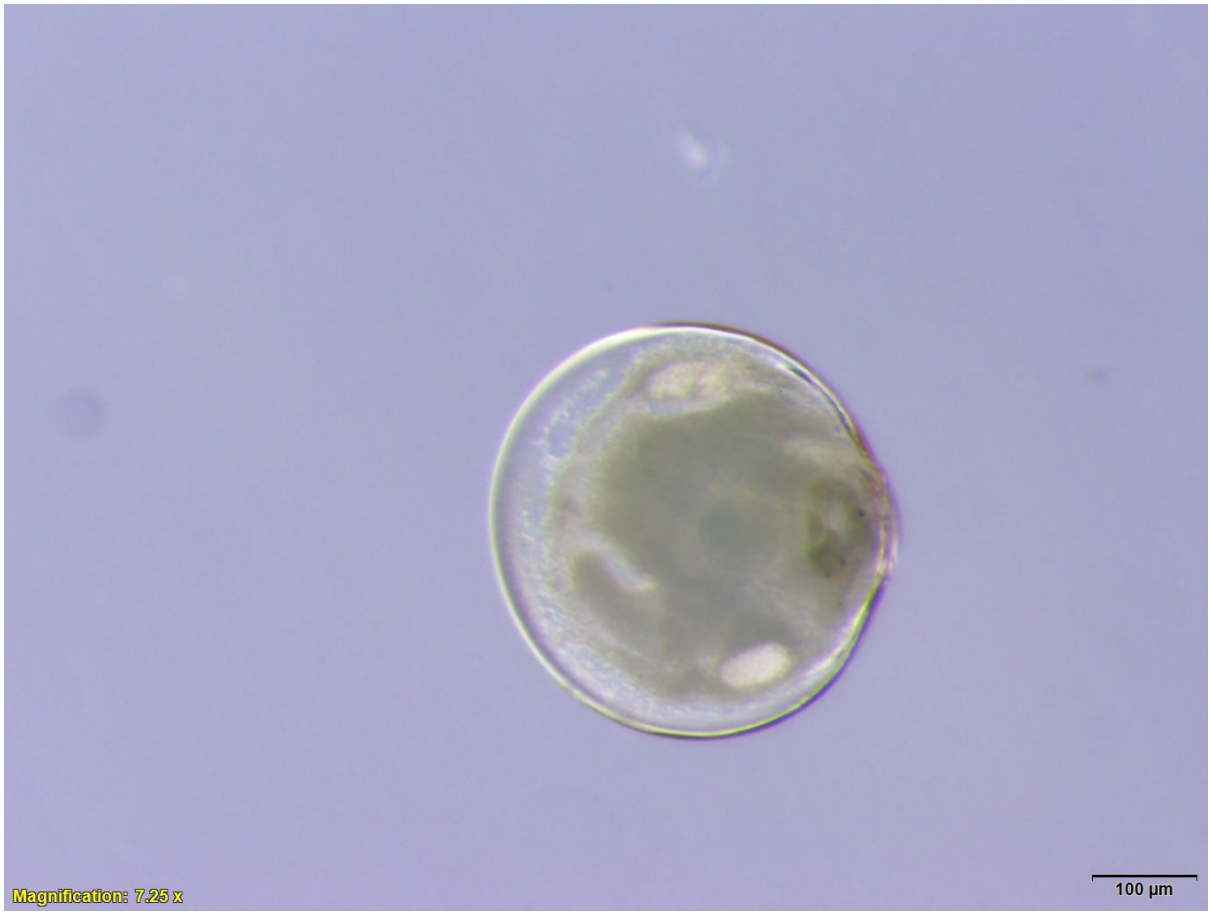


Figure 2.14: Abundance of oyster veligers with the significant interaction of Day/Night and Depth at Skoenmakerskop on 3 November 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Bivalve sp. A veligers



Picture 2.1: Bivalve sp. A. Photo by Paula Pattrick.

An unidentified, morphologically distinct bivalve group (Bivalve sp. A) was often found in the samples (Picture 2.1). The veligers were more rounded and looked transparent. These veligers reached the minimum threshold for analysis at St. Francis Bay and Skoenmakerskop in both sampling seasons.

Day/Night alone had a significant effect on the abundance of Bivalve sp. A veligers at St. Francis Bay, 15 April 2013 (Table 2.11) and figure 2.15 shows that the significantly higher abundances were found at night rather than during the day. On 21 March 2013, at Skoenmakerskop the interaction of Depth and Day/Night had a significant effect (Table 2.12). There was, however, no clear pattern (Figure 2.16).

In the 2nd sampling season (October/November), at St. Francis Bay, Bivalve sp. A veligers were found in significantly higher abundances on the surface and at mid-

depths (5.5/5 metres) at night than during the day whilst there were no differences in abundance between day and night at the bottom (11/10 metres) (Figure 2.17). At Skoenmakerskop, abundance was homogenous during the day with significantly higher abundances at shallow depths (0 and 10 metres) at night (Table 2.14; Figure 2.18).

Table 2.11: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Bivalve sp. A throughout the water column in 15 April 2013 at St. Francis Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	P
Depth	0.218220	2	0.109110	3.45299	n.s
Day/Night	0.753398	1	0.753398	23.84271	**
Depth*Day/Night	0.218220	2	0.109110	3.45299	n.s
Error	0.189592	6	0.031599		

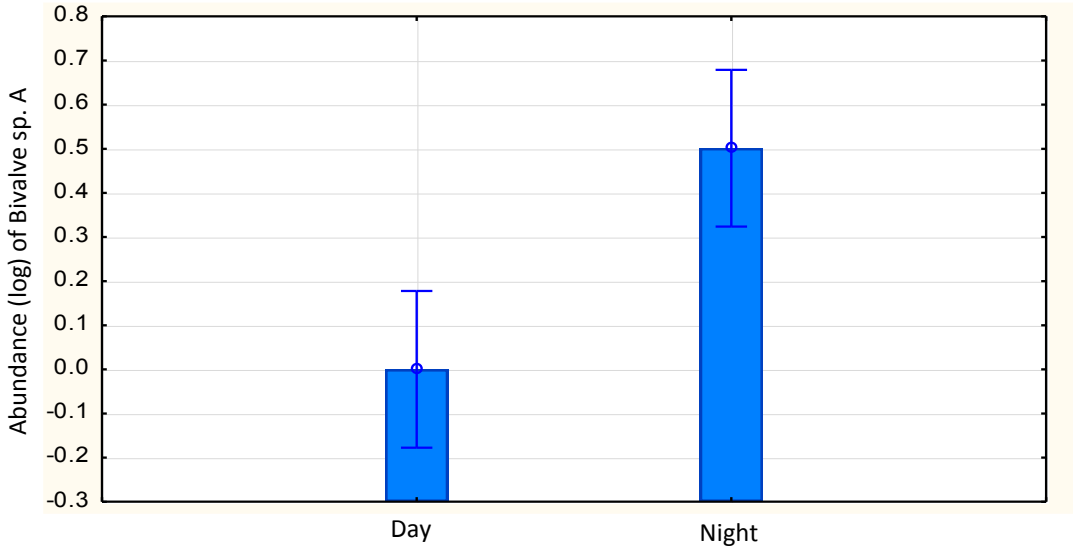


Figure 2.15: Abundance of Bivalve sp. A during a day and night sampling period at St. Francis Bay on 15 April 2013. Error bars indicate standard error.

Table 2.12: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Bivalve sp. A throughout the water column in 21 March 2013 at Skoenmakerskop. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	P
Depth	0.526670	4	0.131668	1.18042	n.s
Day/Night	0.041835	1	0.041835	0.37506	n.s
Depth*Day/Night	1.607453	4	0.401863	3.60276	*
Error	1.115430	10	0.111543		

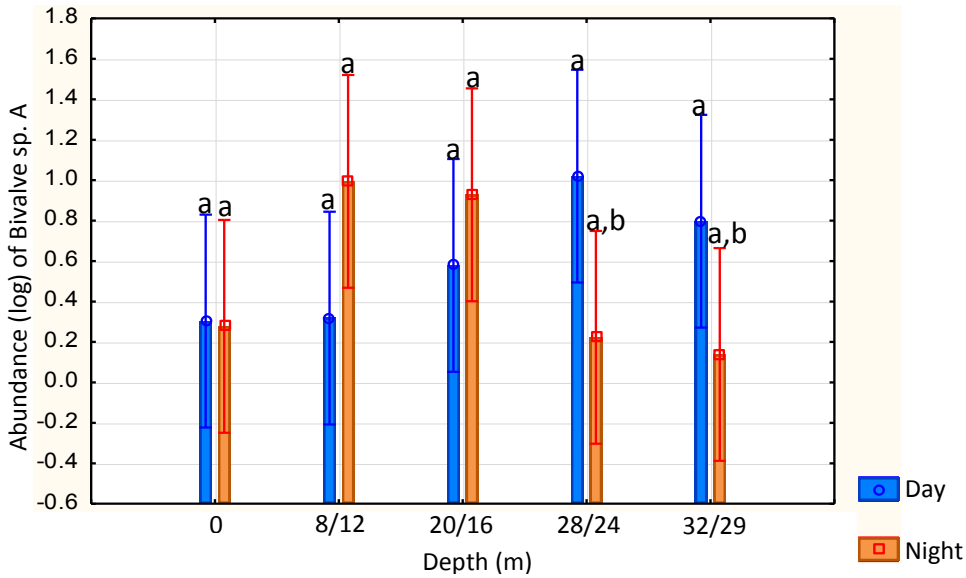


Figure 2.16: Abundance of Bivalve sp. A with the significant interaction of Day/Night and Depth at Skoenmakerskop on 21 March 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Table 2.13: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Bivalve sp. A throughout the water column in 3 October 2013 at St. Francis Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	Df	MS	F	P
Depth	0.448725	2	0.224363	4.5459	n.s
Day/Night	0.777489	1	0.777489	15.7531	**
Depth*Day/Night	0.860029	2	0.430014	8.7127	**
Error	0.296128	6	0.049355		

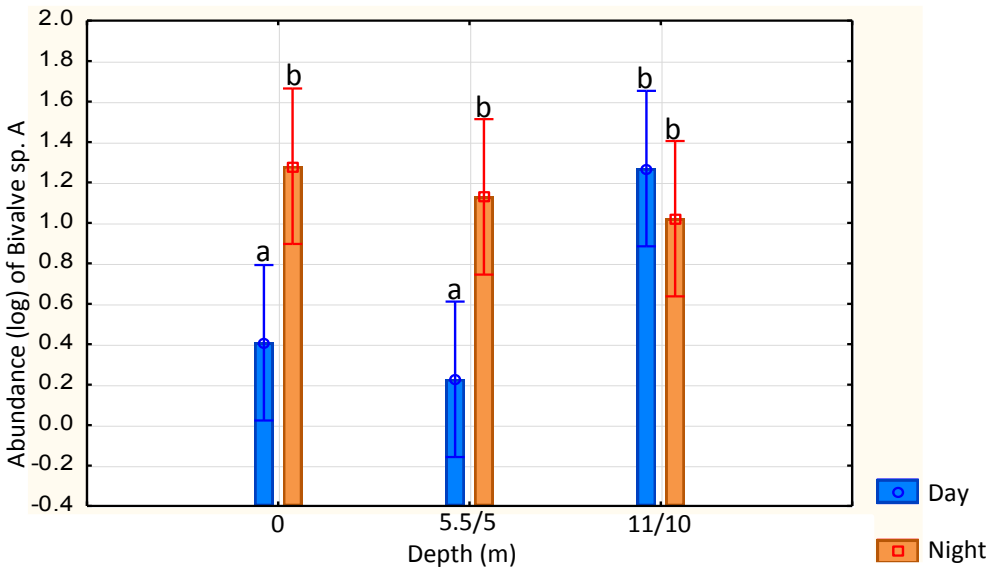


Figure 2.17: Abundance of Bivalve sp. A with the significant interaction of Day/Night and Depth at St. Francis Bay on 3 October 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Table 2.14: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Bivalve sp. A throughout the water column in 3 November 2013 at Skoenmakerskop. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	1.59401	3	0.53134	11.6830	**
Day/Night	0.16229	1	0.16229	3.5684	n.s
Depth*Day/Night	0.91734	3	0.30578	6.7235	**
Error	0.36384	8	0.04548		

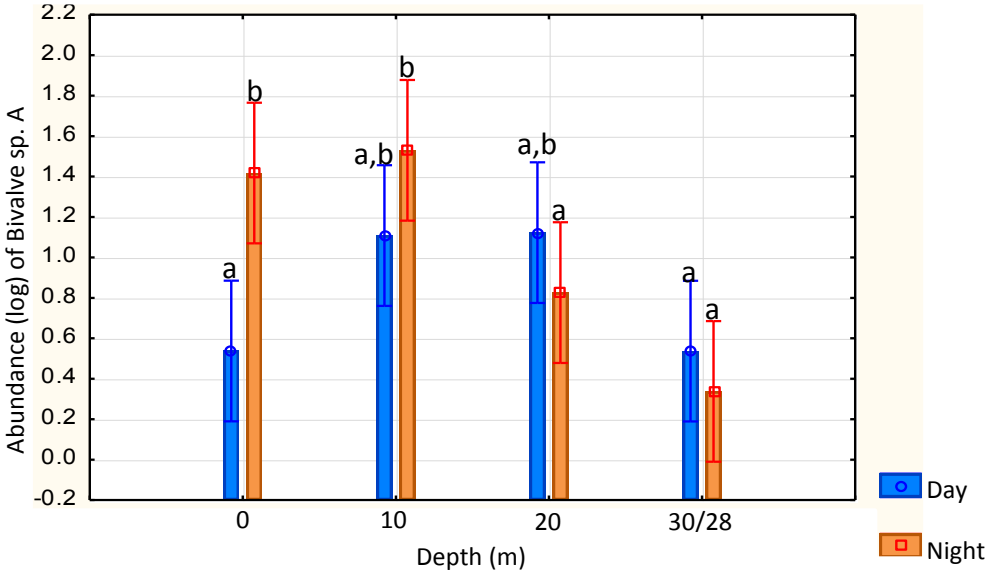
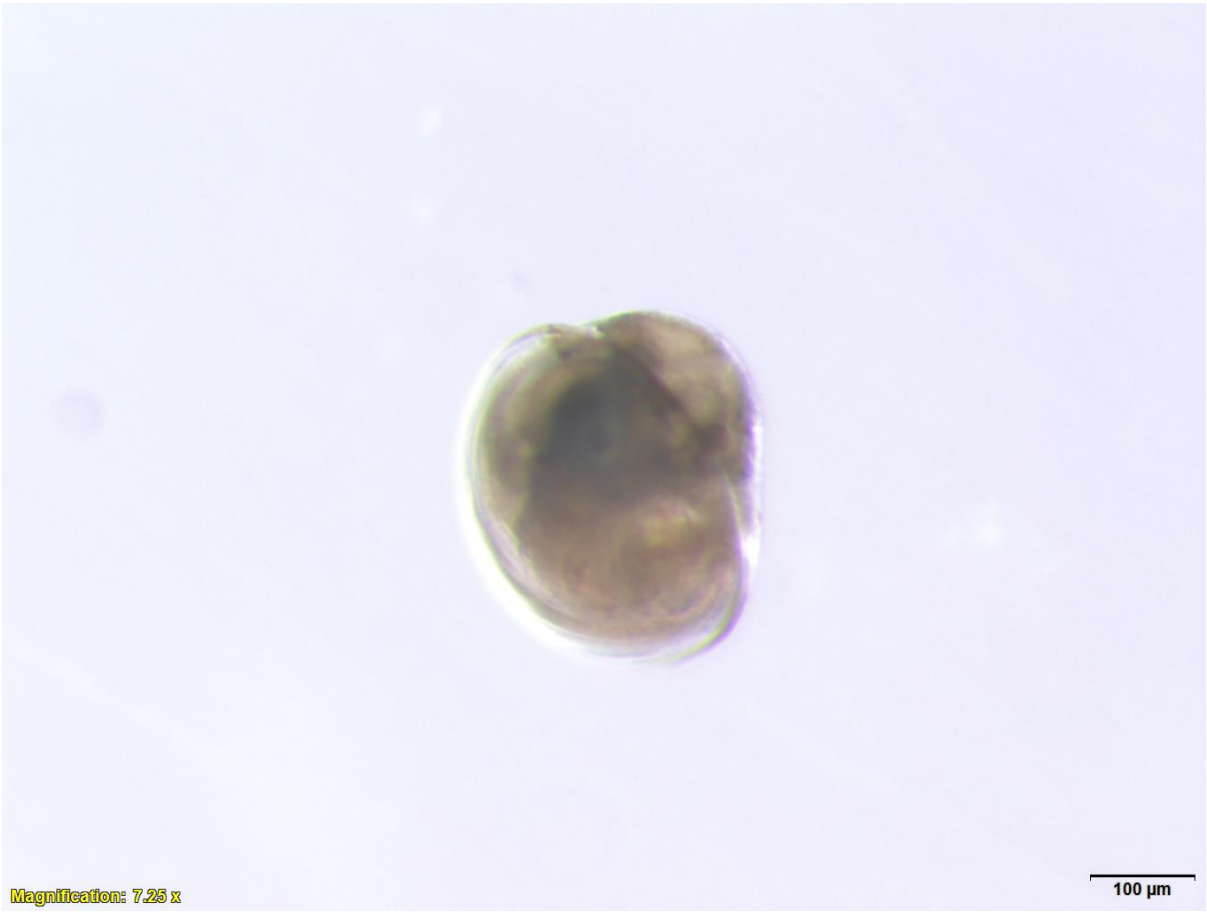


Figure 2.18: Abundance of Bivalve sp. A with the significant interaction of Day/Night and Depth at Skoenmakerskop on 3 November 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Bivalve sp. B veligers



Picture 2.2: Bivalve sp. B. Photo by Paula Pattrick.

Another morphologically different bivalve species (Bivalve sp. B) was found (Picture 2.2). It had an umbo region protruding outwards. This species reached the threshold for analysis on the 1st sampling season at Skoenmakerskop. Day/Night had a

significant effect on abundance of Bivalve sp. B at Skoenmakerskop (Table 2.15), with significantly higher abundances at night (Figure 2.19).

Table 2.15: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Bivalve sp. B throughout the water column in 21 March 2013 at Skoenmakerskop. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	P
Depth	0.987337	4	0.246834	1.72167	n.s
Day/Night	1.570629	1	1.570629	10.95514	**
Depth*Day/Night	0.368662	4	0.092165	0.64285	n.s
Error	1.433692	10	0.143369		

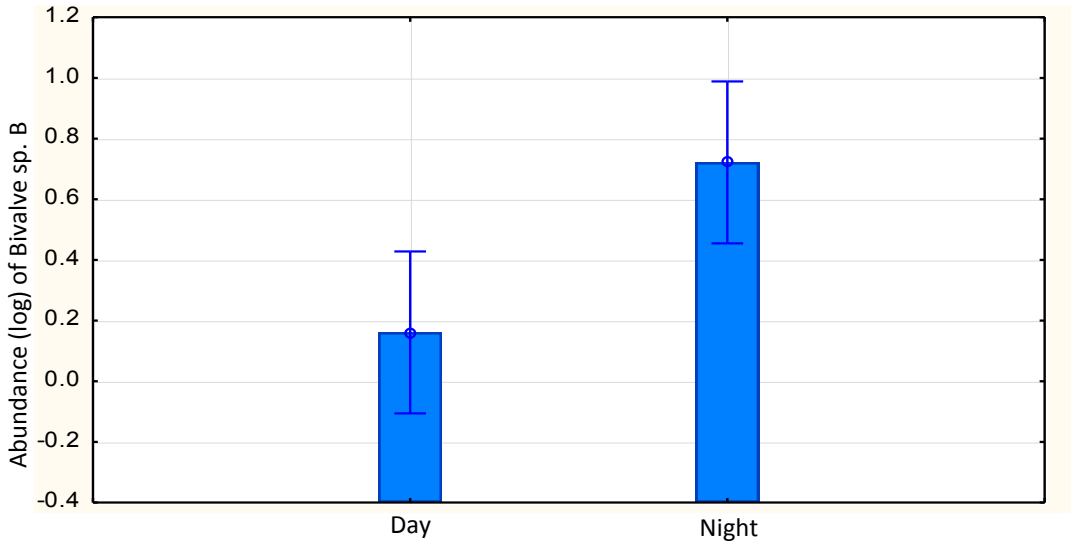


Figure 2.19: Abundance of Bivalves sp. B during a day and night sampling period at Skoenmakerskop on 21 March 2013. Error bars indicate standard error.

BARNACLES

Balanid nauplii (early stages)

Nauplii were divided into two ontogenetic stages (early and late). The early nauplii comprised stages 1-3 and the late nauplii stages 4-6 (Sandison & Day, 1954). The easily observed morphological difference between the early and late stages included the development of two posterior shield spines in the late stages.

In both sampling seasons, the early stages reached the analysis threshold only on the open coasts and not in the bays. In the 1st sampling season (March/April), Depth had a significant effect on the abundance of early Balanid nauplii at Skoenmakerskop (Table 2.16) and the interaction of Depth and Day/Night had a significant effect at Cape St. Francis (Table 2.17). Figure 2.20 shows that the early nauplii were found at significantly higher abundances at the mid-depths (8, 20 and 28 metres during the day and 12, 16 and 24 during the night) at Skoenmakerskop. At Cape St. Francis, significantly higher abundances were found at 12 metres during the day (Figure 2.21).

In October/November, the interaction between Day/Night and Depth had a significant effect on the abundance of the early stages of the Balanid nauplii at both Skoenmakerskop and Cape St. Francis (Table 2.18 and 2.19 respectively). The abundances at Skoenmakerskop were homogenous through the water column during the day with a preference of the surface layer at night (Figure 2.22). The pattern was similar at Cape St. Francis, with abundance being homogenous during the day but with less clear patterns than for Skoenmakerskop at night (Figure 2.23).

Table 2.16: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Balanid nauplii (early stages) throughout the water column in 21 March 2013 at Skoenmakerskop. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	P
Depth	10.91095	4	2.72774	13.8697	***
Day/Night	0.61879	1	0.61879	3.1464	n.s
Depth*Day/Night	1.38339	4	0.34585	1.7585	n.s
Error	1.96669	10	0.19667		

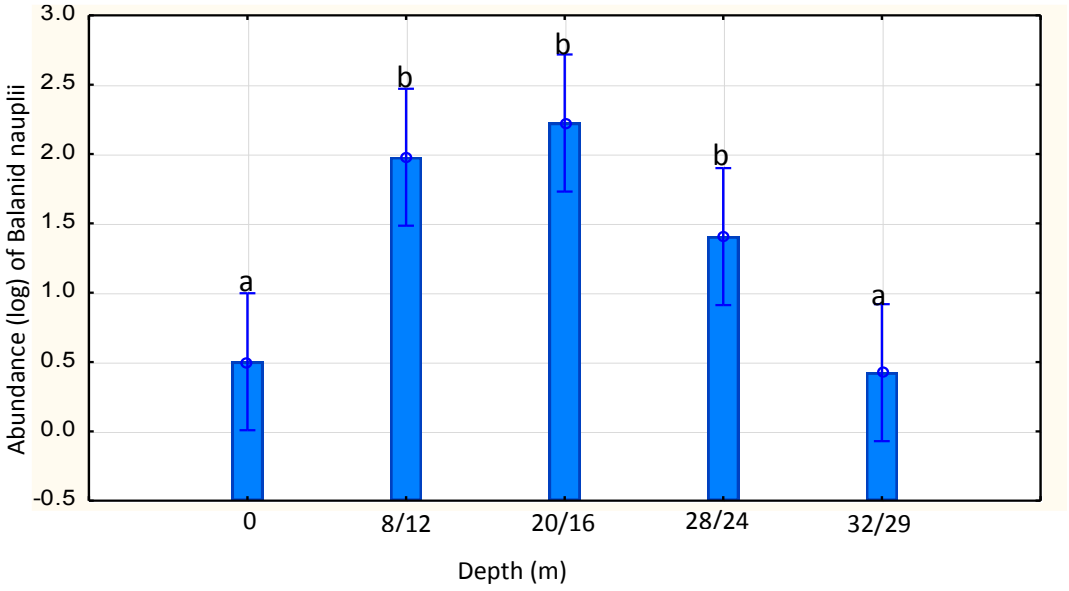


Figure 2.20: Abundance of Balanid nauplii (early stages) with change in depth over a day and night sampling period at Skoenmakerskop on 21 March 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of Depth. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Table 2.17: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Balanid nauplii (early stages) throughout the water column in 5 April 2013 at Cape St. Francis. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	P
Depth	9.304321	4	2.326080	42.6673	****
Day/Night	0.396075	1	0.396075	7.2652	*
Depth*Day/Night	3.450958	4	0.862740	15.8252	***
Error	0.545167	10	0.054517		

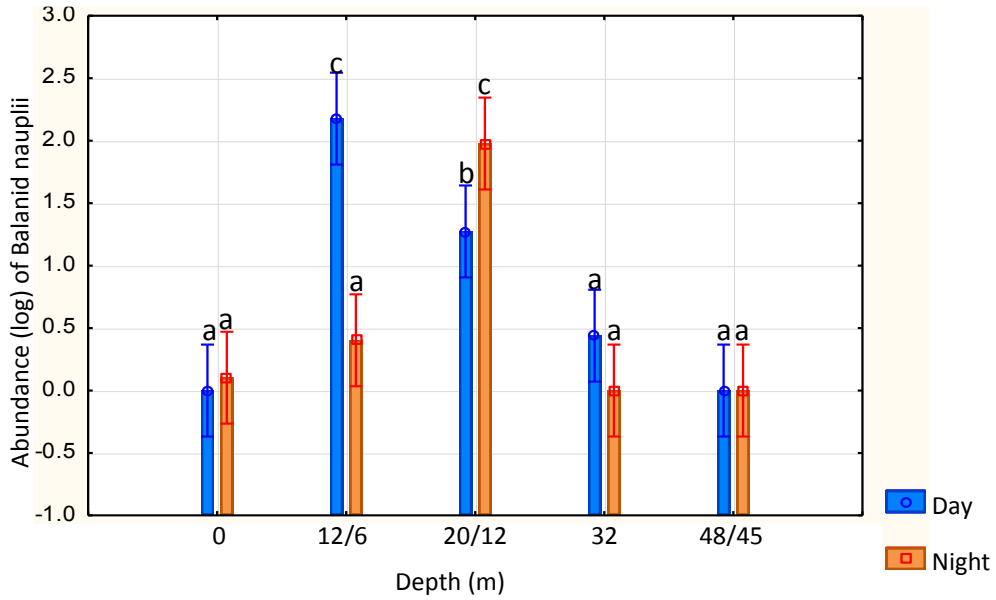


Figure 2.21: Abundance of Balanid nauplii (early stages) with the significant interaction of Day/Night and Depth at Cape St. Francis on 5 April 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Table 2.18: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Balanid nauplii (early stages) throughout the water column in 3 November 2013 at Skoenmakerskop. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	1.44291	3	0.48097	6.3878	**
Day/Night	1.75613	1	1.75613	23.3234	***
Depth*Day/Night	2.38734	3	0.79578	10.5688	**
Error	0.60236	8	0.07529		

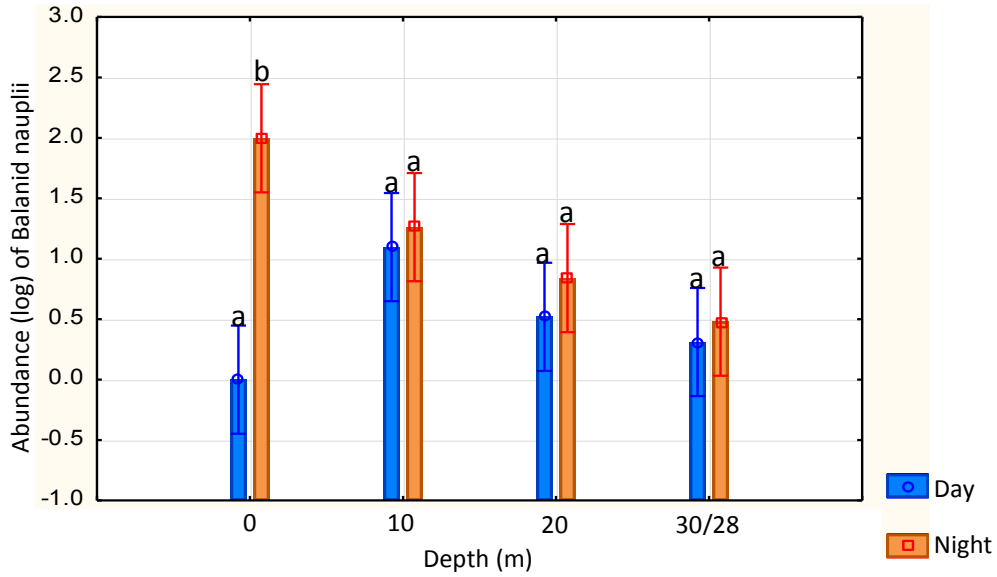


Figure 2.22: Abundance of Balanid nauplii (early stages) with the significant interaction of Day/Night and Depth at Skoenmakerskop on 3 November 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Table 2.19: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Balanid nauplii (early stages) throughout the water column in 4 October 2013 at Cape St. Francis. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	2.09761	4	0.52440	2.4032	n.s
Day/Night	0.24762	1	0.24762	1.1348	n.s
Depth*Day/Night	4.79266	4	1.19817	5.4909	**
Error	2.18210	10	0.21821		

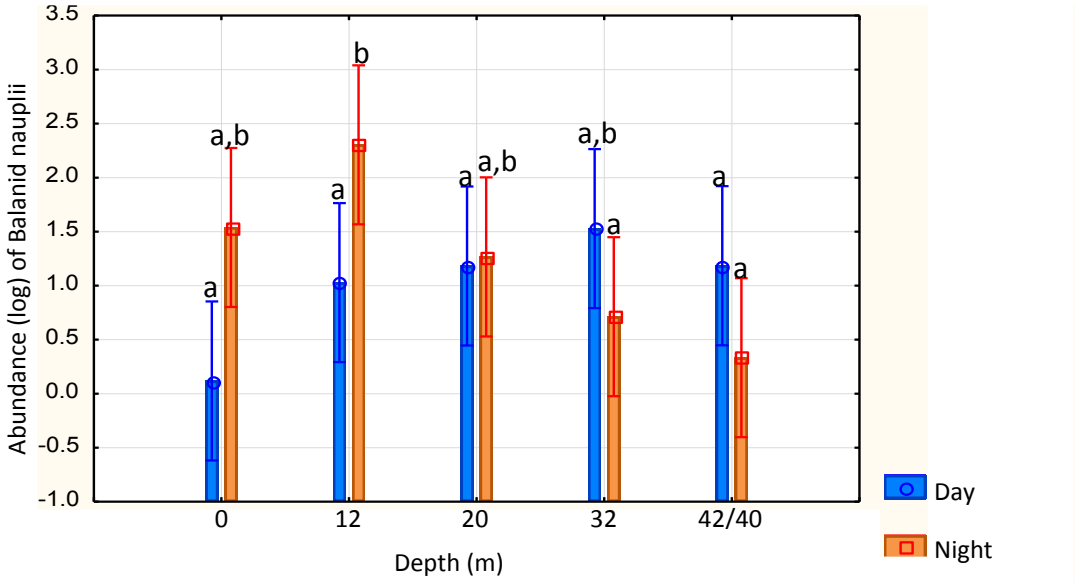


Figure 2.23: Abundance of Balanid nauplii (early stages) with the significant interaction of Day/Night and Depth at Cape St. Francis on 4 October 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Balanid nauplii (late stages)

The late stages were nauplii stages 4-6. These had developed two posterior shield spines, which is what made them distinct from the early stages (Sandison & Day, 1954).

Depth and Day/Night each had a significant effect on the abundance of late Balanid nauplii at St. Francis Bay in the March-April 2013 sampling season (Table 2.20). There was no clear depth preference for the late nauplii (Figure 2.24), but significantly higher abundances were found at night than during the day (Figure 2.25). At Skoenmakerskop, Depth and Day/Night had also significant effects on the abundances of larvae (Table 2.21). Nauplii seemed to avoid the surface layer and were found in significantly higher abundances at depths of 8, 20, and 28 metres during the day and 12, 16, and 24 at the night (Figure 2.26). Significantly higher abundances of nauplii were found at night than during the day (Figure 2.27). At Algoa Bay and Cape St. Francis, the interaction of Depth and Day/Night had a significant effect on the abundance of late nauplii (Tables 2.22 and 2.23). In the bay site (Algoa Bay), the abundance of nauplii was homogeneous through the water column (Figure 2.28). On the open coast however, there was some depth preference. During the day, nauplii avoided the surface and bottom layers (48 metres). The statistically highest abundances were found at 12 and 20 metres. During the night, nauplii were mostly at 12 metres (Figure 2.29).

In the 2nd sampling season (October/November) the interaction of Depth and Day/Night had a significant effect on the abundance of late nauplii in both the open coasts (Tables 2.24 and 2.25). At Skoenmakerskop, the nauplii performed vertical migration (Figure 2.30). During the day, the highest abundances were found at 10 and 20 metres. During the night though, in addition to 10 and 20 metres, highest abundance was also found at the surface. This pattern was less clear at Cape St. Francis (Figure 2.31).

Table 2.20: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Balanid nauplii (late stages) throughout the water column in 15 April 2013 at St. Francis Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	2.98259	2	1.49129	5.0280	*
Day/Night	6.20704	1	6.20704	20.9274	**
Depth*Day/Night	1.32512	2	0.66256	2.2339	n.s
Error	1.77959	6	0.29660		

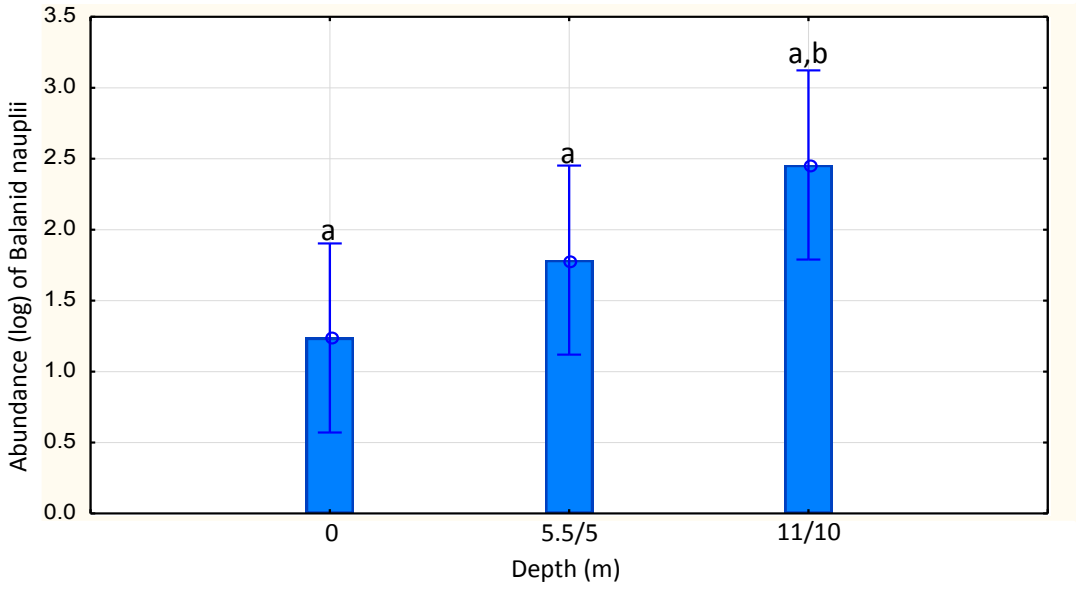


Figure 2.24: Abundance of Balanid nauplii (late stages) with change in depth over a day and night sampling period at St. Francis Bay on 15 April 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of Depth. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

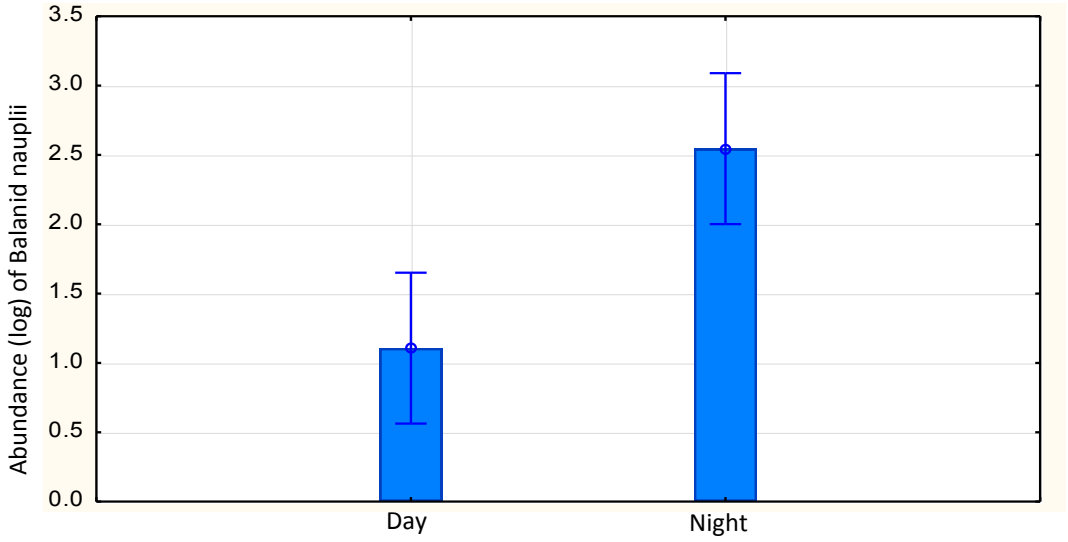


Figure 2.25: Abundance of Balanid nauplii (late stages) during a day and night sampling period at St. Francis Bay on 15 April 2013. Error bars indicate standard error.

Table 2.21: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Balanid nauplii (late stages) throughout the water column in 21 March 2013 at Skoenmakerskop. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	Df	MS	F	p
Depth	5.28681	4	1.32170	14.3927	***
Day/Night	0.57740	1	0.57740	6.2876	*
Depth*Day/Night	0.48853	4	0.12213	1.3300	n.s
Error	0.91831	10	0.09183		

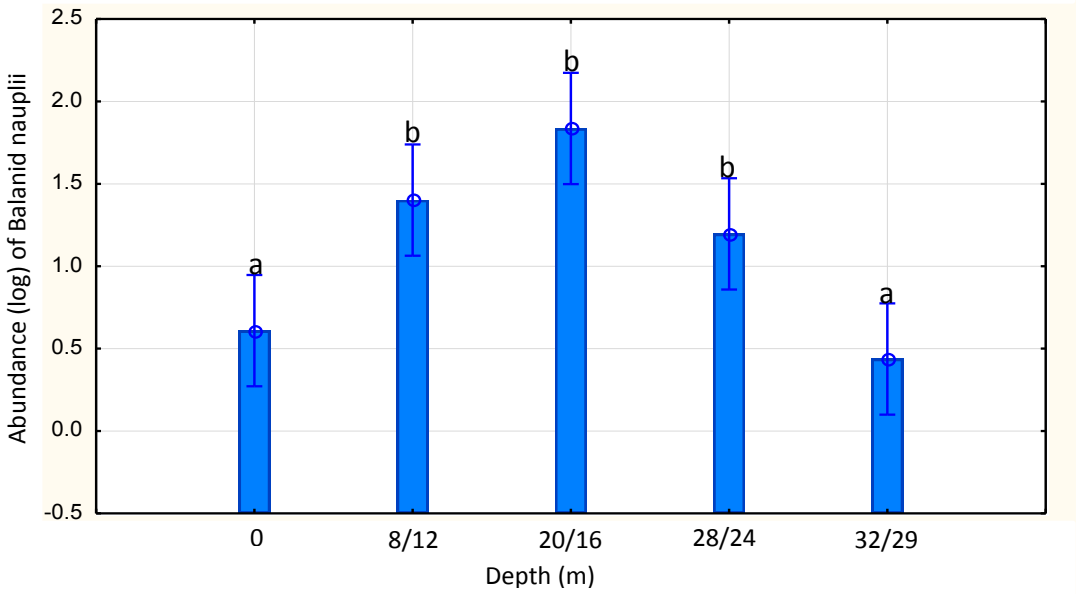


Figure 2.26: Abundance of Balanid nauplii (late stages) with change in depth over a day and night sampling period at Skoenmakerskop on 21 March 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of Depth. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

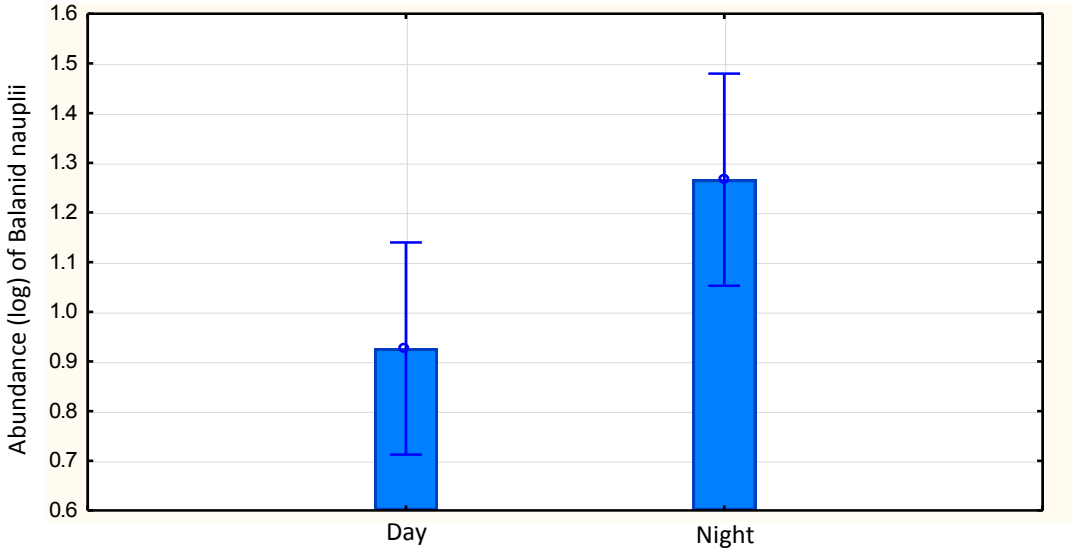


Figure 2.27: Abundance of Balanid nauplii (late stages) during a day and night sampling period at Skoenmakerskop on 21 March 2013. Error bars indicate standard error.

Table 2.22: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Balanid nauplii (late stages) throughout the water column in 6 March 2013 at Algoa Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	Df	MS	F	p
Depth	0.33532	3	0.11177	0.53218	n.s
Day/Night	0.01300	1	0.01300	0.06190	n.s
Depth*Day/Night	3.18204	3	1.06068	5.05009	*
Error	1.68025	8	0.21003		

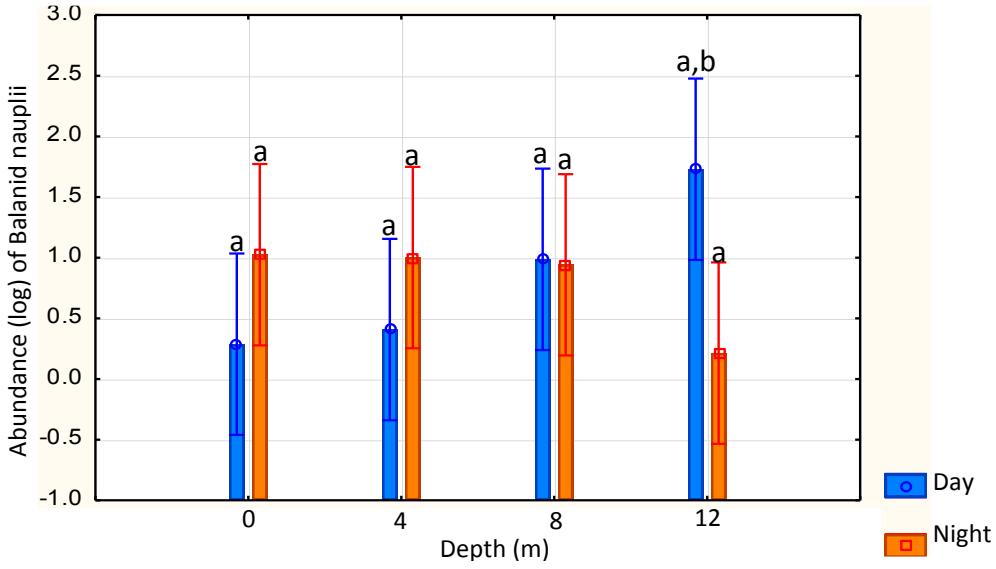


Figure 2.28: Abundance of Balanid nauplii (late stages) with the significant interaction of Day/Night and Depth at Algoa Bay on 6 March 2013. Error bars indicate standard errors. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night.

Table 2.23: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Balanid nauplii (late stages) throughout the water column in 5 April 2013 at Cape St. Francis. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	6.828361	4	1.707090	47.8901	****
Day/Night	0.445603	1	0.445603	12.5008	**
Depth*Day/Night	1.736457	4	0.434114	12.1785	***
Error	0.356460	10	0.035646		

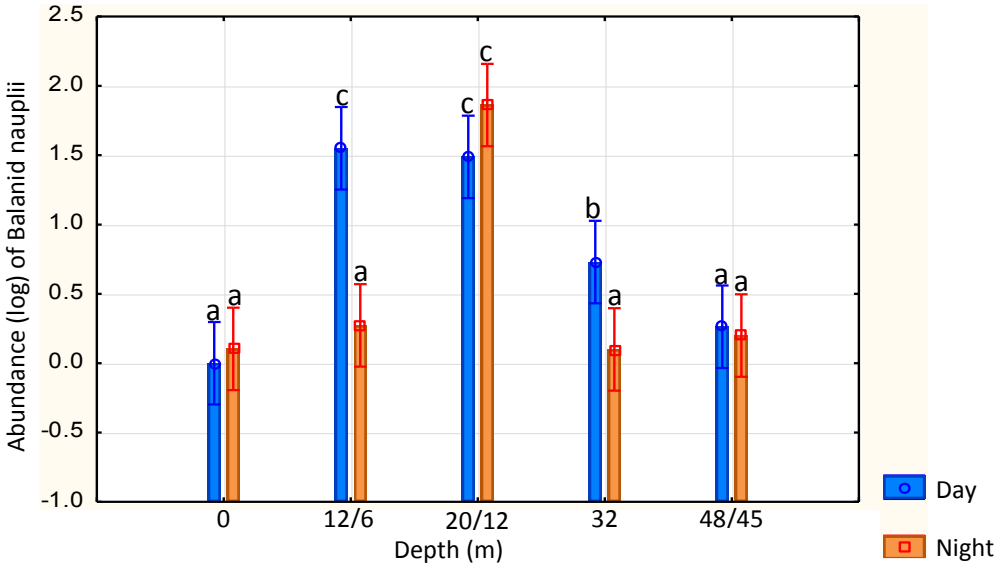


Figure 2.29: Abundance of Balanid nauplii (late stages) with the significant interaction of Day/Night and Depth at Cape St. Francis on 5 April 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Table 2.24: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Balanid nauplii (late stages) throughout the water column in 3 November 2013 at Skoenmakerskop. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	3.23553	3	1.07851	22.1878	***
Day/Night	0.51370	1	0.51370	10.5682	**
Depth*Day/Night	3.37955	3	1.12652	23.1754	***
Error	0.38887	8	0.04861		

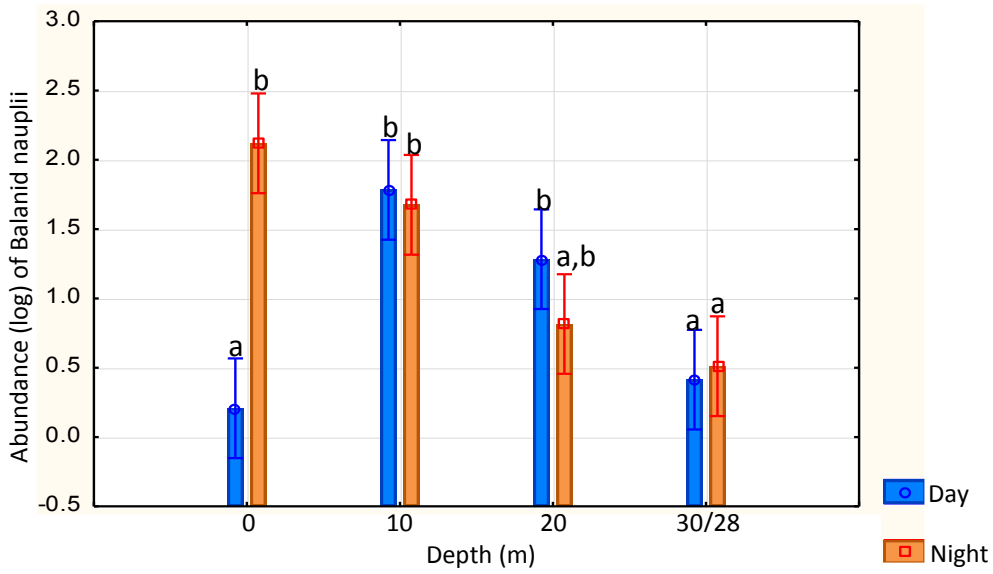


Figure 2.30: Abundance of Balanid nauplii (late stages) with the significant interaction of Day/Night and Depth at Skoenmakerskop on 3 November 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Table 2.25: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Balanid nauplii (late stages) throughout the water column in 4 October 2013 at Cape St. Francis. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	1.84082	4	0.46020	2.3468	n.s
Day/Night	0.11594	1	0.11594	0.5912	n.s
Depth*Day/Night	4.73407	4	1.18352	6.0352	**
Error	1.96102	10	0.19610		

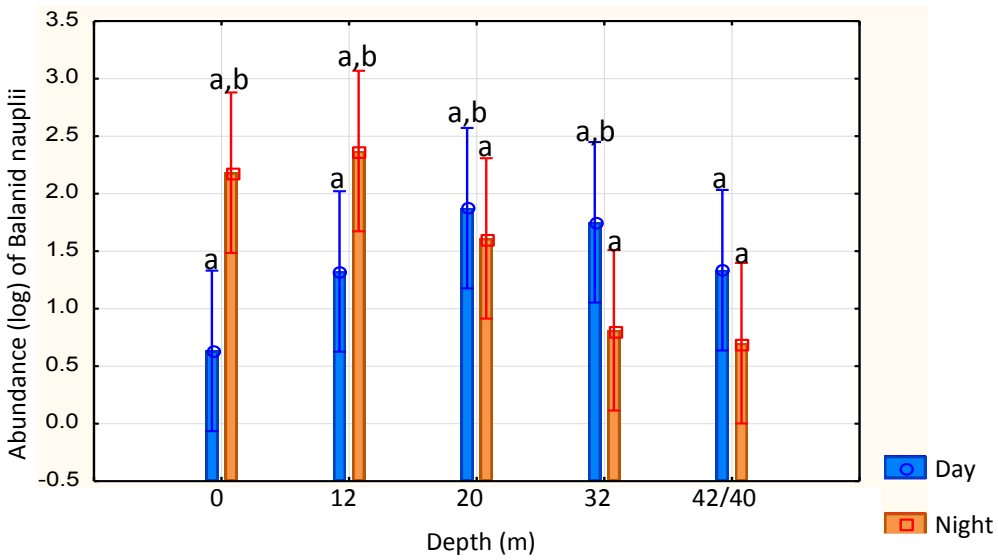
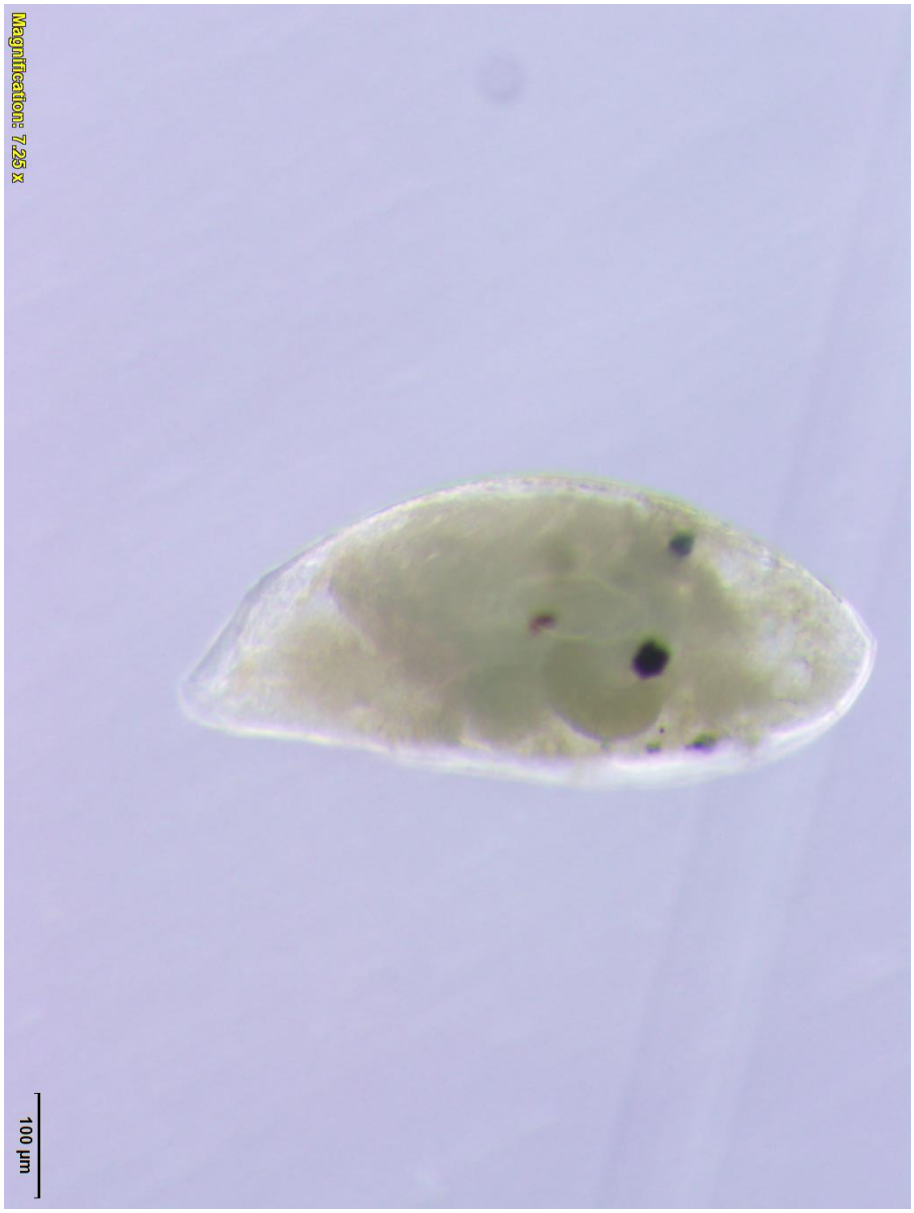


Figure 2.31: Abundance of Balanid nauplii (late stages) with the significant interaction of Day/Night and Depth at Cape St. Francis on 4 October 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Cyprid sp. A



Picture 2.3: Cyprid sp. A. Photo by Paula Pattrick.

Morphological differences allowed the separation of two types of balanid cyprids (Cyprid sp. A and Cyprid sp. B). Cyprid sp. A (Picture 2.3) was more pointed anteriorly whilst Cyprid sp. B (Picture 2.4) was more rounded. Cyprid sp. A was also visibly smaller than Cyprid sp. B, though this was not quantified.

In the 1st sampling season (March/April), Day/Night had a significant effect on the abundance of Cyprid sp. A (Table 2.26) at Cape St. Francis, with significantly higher abundances during the day than during the night (Figure 2.32).

In the 2nd sampling season, at all sites, the abundance of these cyprids reached the threshold for analysis. At Algoa Bay, Day/Night had a significant effect on the abundance of Cyprid sp. A with significantly higher abundances at night than during the day (Table 2.27 and Figure 2.33). On the adjacent open coast, Skoenmakerskop, Depth had a significant effect on the abundance of Cyprid sp. A (Table 2.28). Figure 2.34 shows that the cyprids avoided the surface, and were more abundant at depths of 10, 20 and 30 metres in the day, and 28 metres at night. The interaction of Depth and Day/Night was significant at St. Francis Bay, but there was no clear pattern showed by the post hoc grouping as the abundances were homogenous through depths and for both day and night (Table 2.30; Figure 2.37). On the other open coast site, Cape St. Francis, Depth and Day/Night, independently, had a significant effect on the abundance of Cyprid sp. A (Table 2.29). Abundances were highest at 20, 30 and 42 metres, during the day, and at 40 metres at night (Figures 2.35).The highest abundances were also found during the night (Figure 2.36).

Table 2.26: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$\log_{10}(X+1)$ transformed] of Cyprid sp. A. throughout the water column in 5 April 2013 at Cape St. Francis. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	Df	MS	F	P
Depth	0.63340	4	0.15835	1.6891	n.s
Day/Night	0.72740	1	0.72740	7.7592	**
Depth*Day/Night	0.52509	4	0.13127	1.4003	n.s
Error	0.93746	10	0.09375		

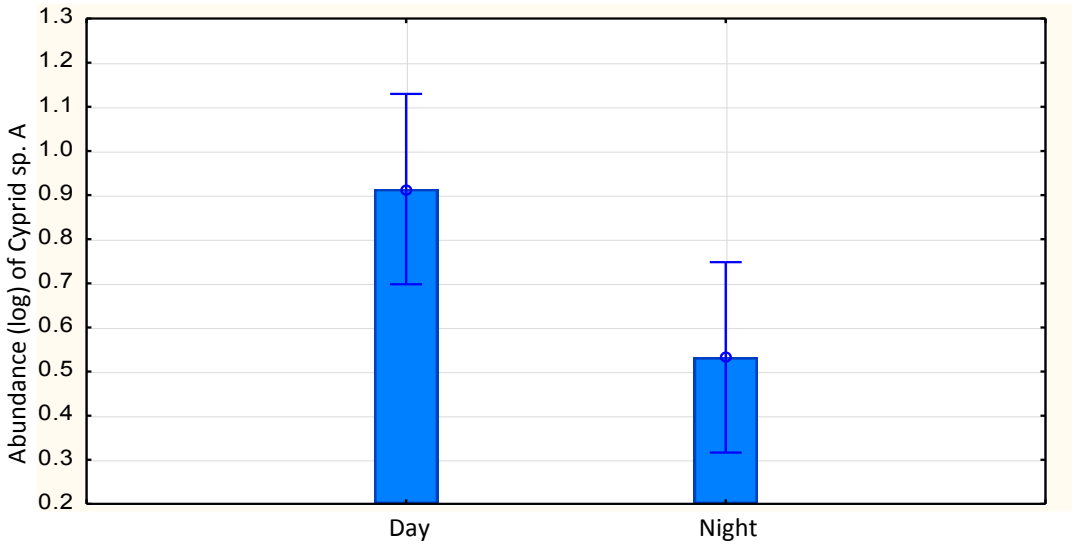


Figure 2.32: Abundance of Cyprid sp. A during a day and night sampling period at Cape St. Francis on 5 April 2013. Error bars indicate standard error.

Table 2.27: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$\log_{10}(X+1)$ transformed] of Cyprid sp. A. throughout the water column in 23 September 2013 at Algoa Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	2.71408	3	0.90469	1.84427	n.s
Day/Night	3.32231	1	3.32231	6.77271	*
Depth*Day/Night	0.76583	3	0.25528	0.52039	n.s
Error	3.92435	8	0.49054		

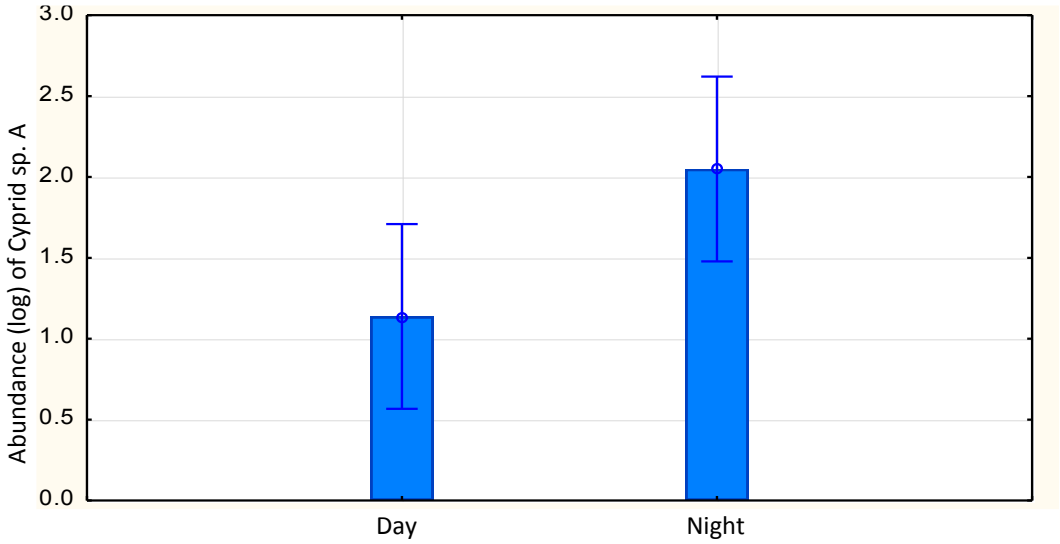


Figure 2.33: Abundance of Cyprid sp. A during a day and night sampling period at Algoa Bay on 23 September 2013. Error bars indicate standard error.

Table 2.28: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Cyprid sp. A. throughout the water column in 3 November 2013 at Skoenmakerskop. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	1.302076	3	0.434025	6.01189	**
Day/Night	0.032117	1	0.032117	0.44486	n.s
Depth*Day/Night	0.098005	3	0.032668	0.45250	n.s
Error	0.577556	8	0.072194		

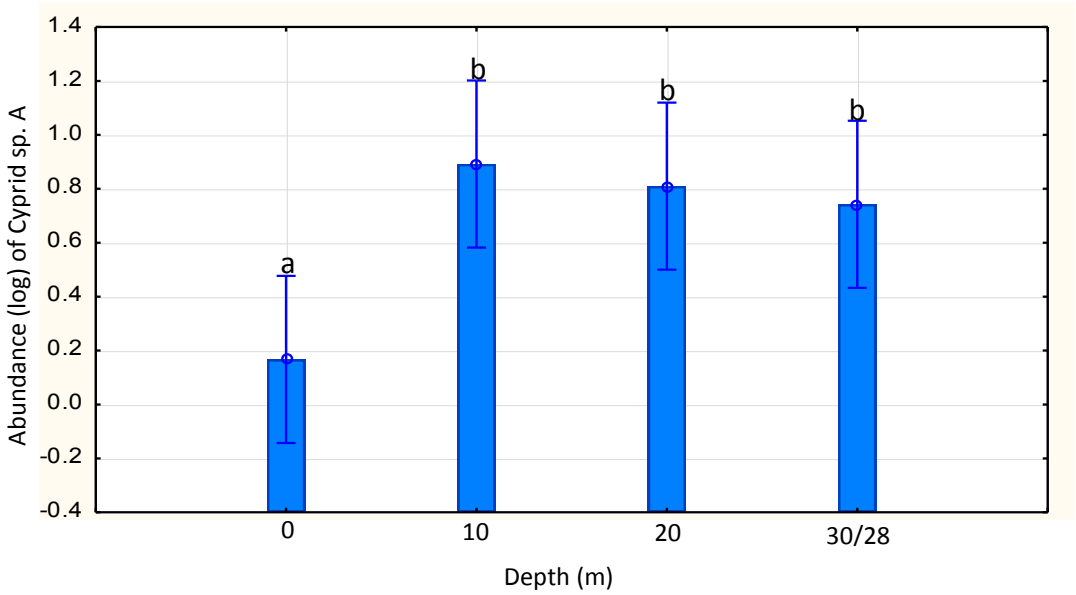


Figure 2.34: Abundance of Cyprid sp. A with change in depth over a day and night sampling period at Skoenmakerskop on 3 November 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of Depth. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Table 2.29: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Cyprid sp. A. throughout the water column in 4 October 2013 at Cape St. Francis. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	1.81995	4	0.45499	6.5637	**
Day/Night	3.87329	1	3.87329	55.8768	****
Depth*Day/Night	0.16774	4	0.04194	0.6050	n.s
Error	0.69318	10	0.06932		

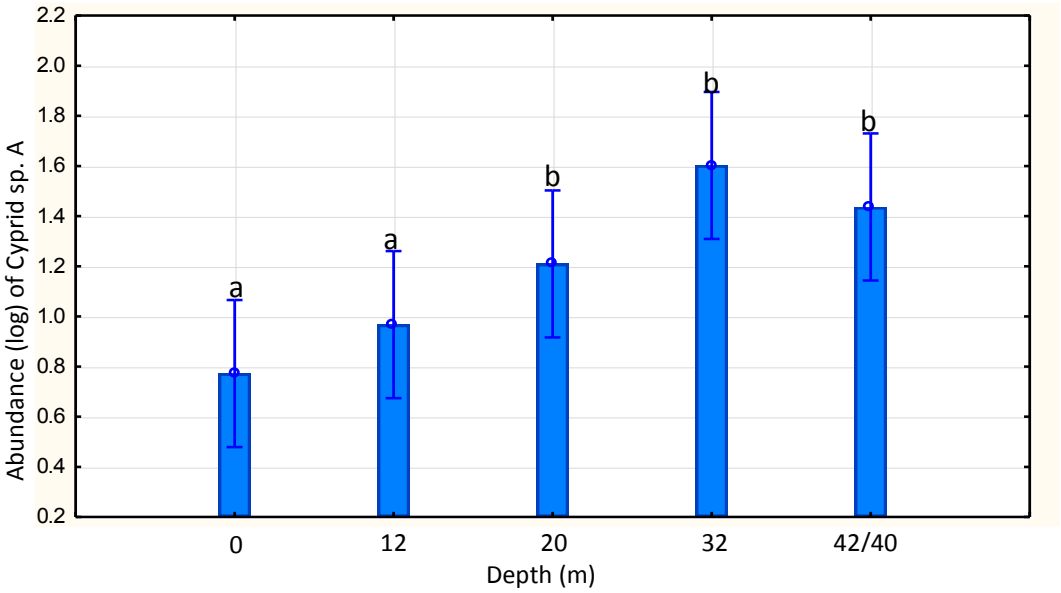


Figure 2.35: Abundance of Cyprid sp. A with change in depth over a day and night sampling period at Cape St. Francis on 4 October 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of Depth. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

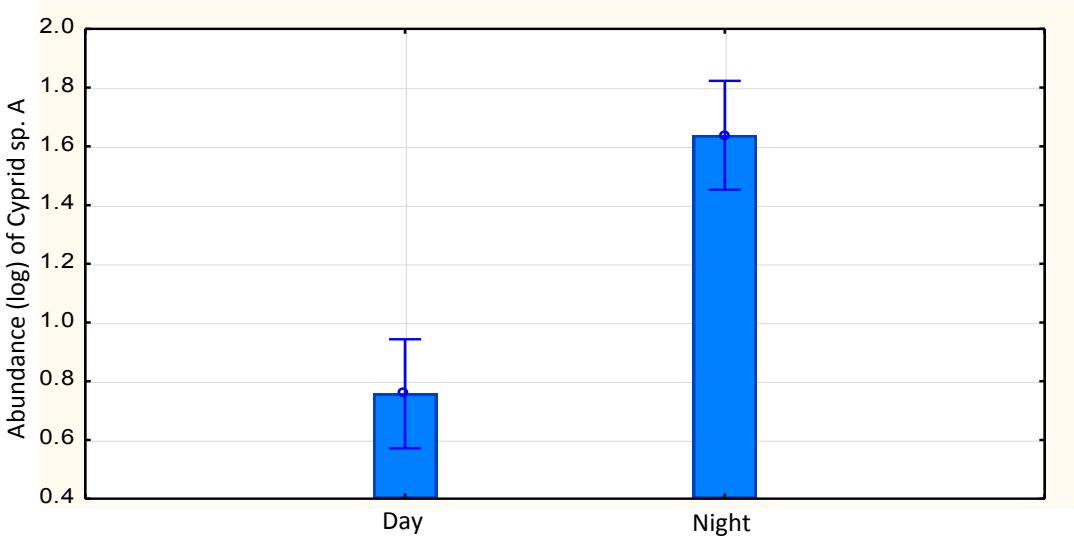


Figure 2.36: Abundance of Cyprid sp. A during a day and night sampling period at Cape St. Francis on 4 October 2013. Error bars indicate standard error.

Table 2.30: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Cyprid sp. A. throughout the water column in 3 October 2013 at St. Francis Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	0.69827	2	0.34914	4.0349	n.s
Day/Night	1.11693	1	1.11693	12.9081	**
Depth*Day/Night	0.90728	2	0.45364	5.2426	*
Error	0.51918	6	0.08653		

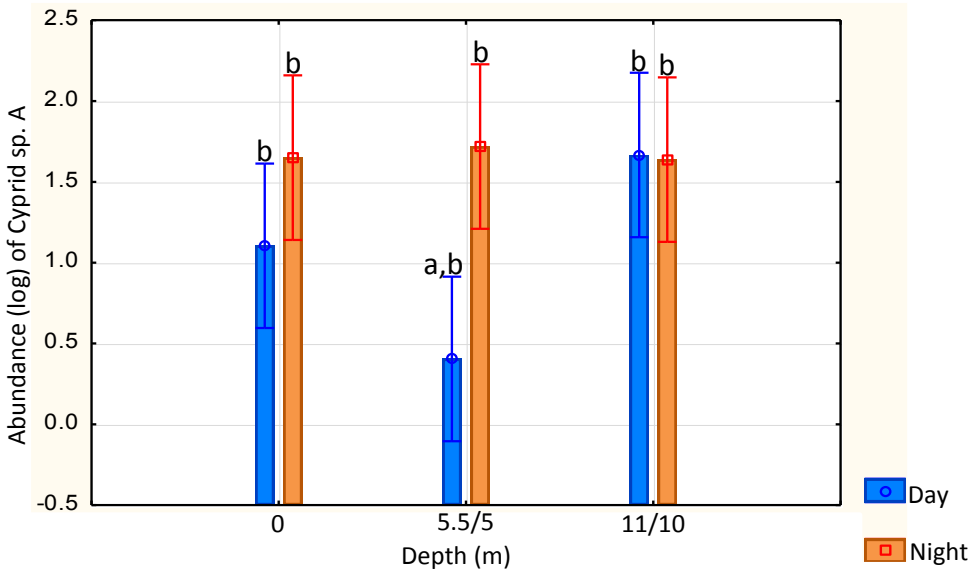
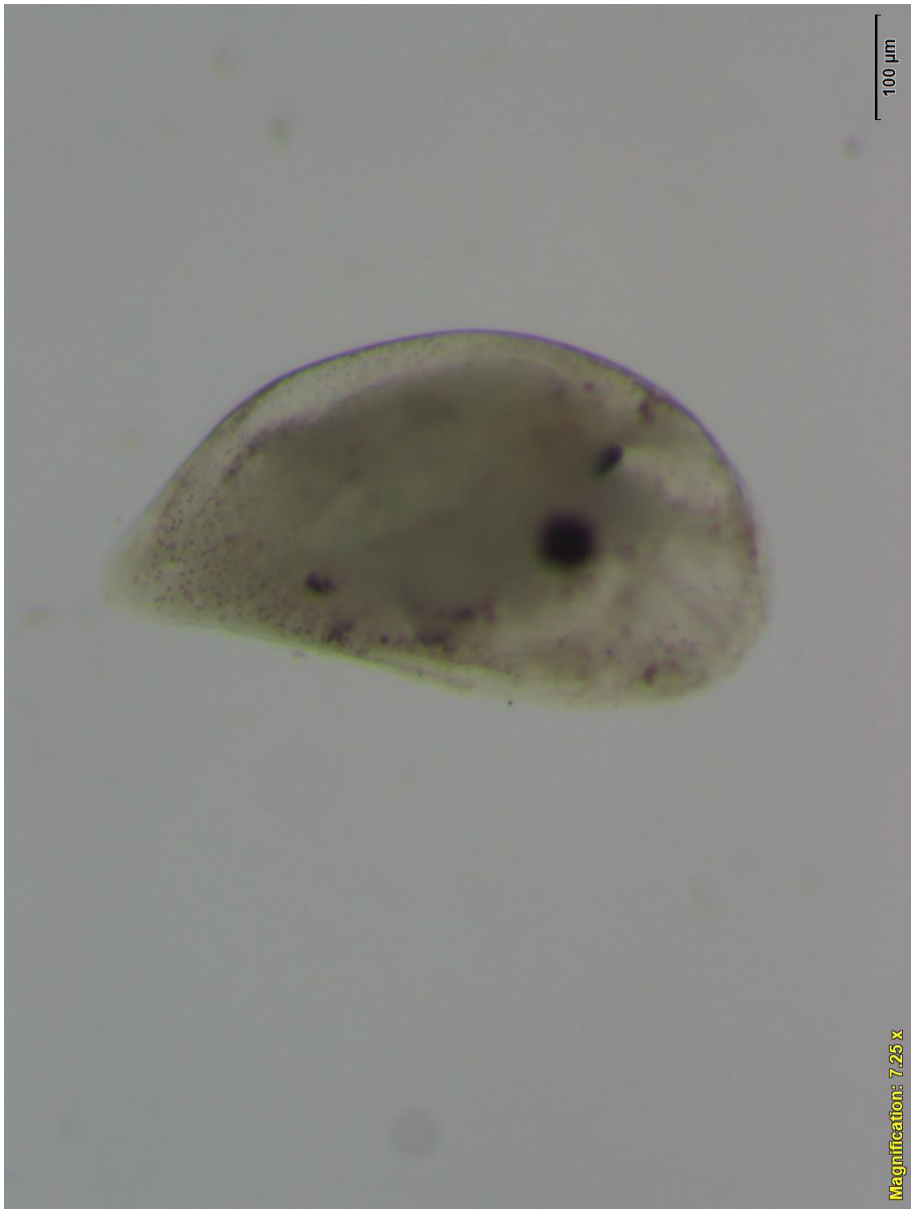


Figure 2.37: Abundance of Cyprid sp. A with the significant interaction of Day/Night and Depth at St. Francis Bay on 3 October 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Cyprid sp. B



Picture 2.4: Cyprid sp. B. Photo by Paula Pattrick.

Cyprid sp. B was found at abundances that reached the threshold for analysis only at Algoa Bay, in the March-April 2013 season. Depth and Day/Night both had significant effects (Table 2.31). The highest abundance of Cyprid sp. B was found at 12 metres (Figure 2.38). This coincided with significantly higher abundances found during the day (Figure 2.39) than during the night, suggesting that Cyprid sp. B were mostly at the bottom layers during the day.

Table 2.31: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of Cyprid sp. B. throughout the water column in 6 March 2013 at Algoa Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	P
Depth	0.788486	3	0.262829	3.82794	*
Day/Night	0.539939	1	0.539939	7.86388	*
Depth*Day/Night	0.102726	3	0.034242	0.49871	n.s
Error	0.549285	8	0.068661		

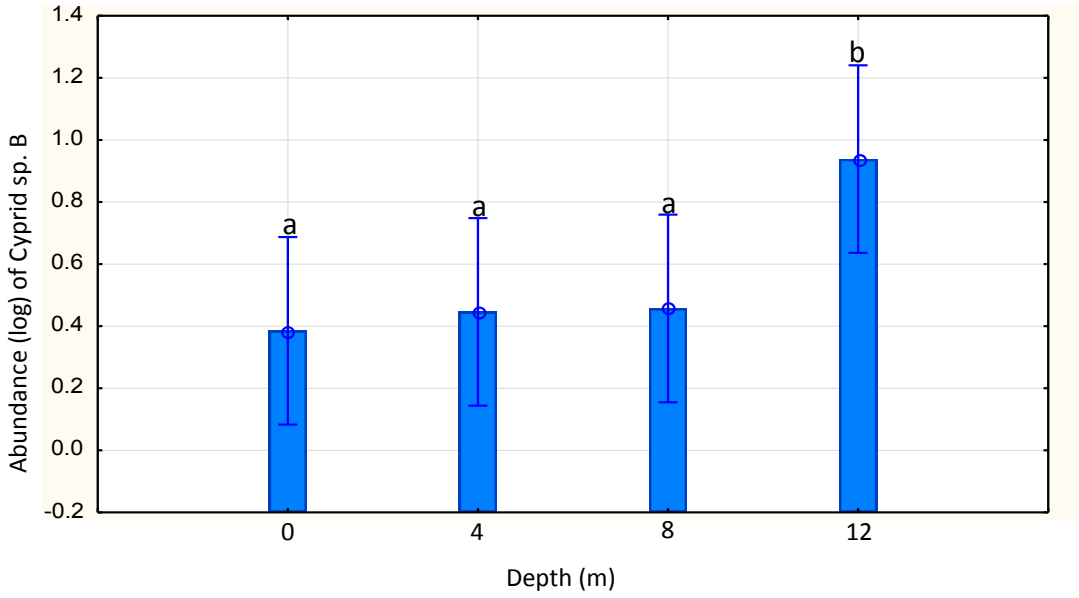


Figure 2.38: Abundance of Cyprid sp. B with change in depth over a day and night sampling period at Algoa Bay on 6 March 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of Depth.

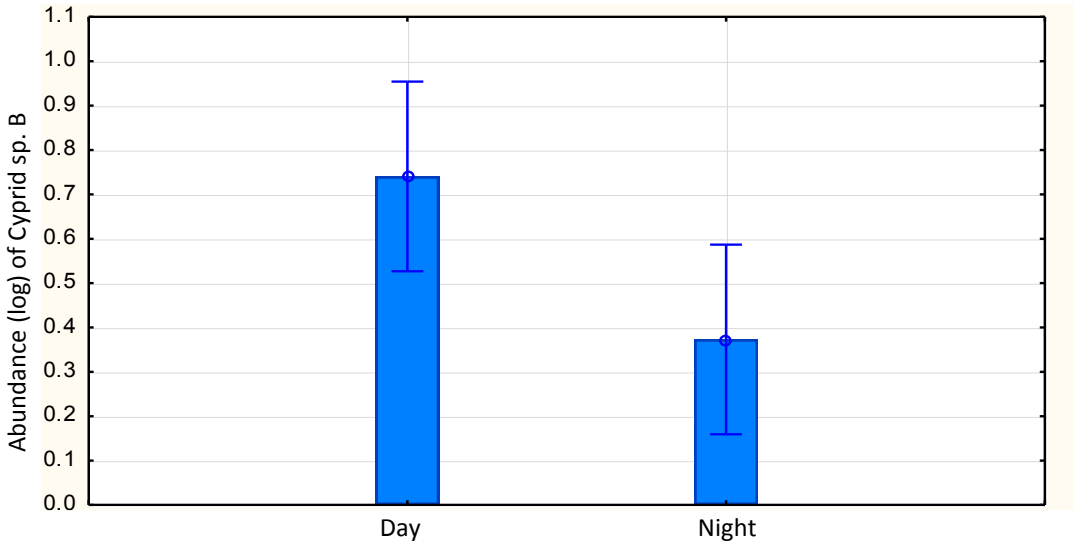


Figure 2.39: Abundance of Cyprid sp. B during a day and night sampling period at Algoa Bay on 6 March 2013. Error bars indicate standard error.

DECAPODS

Brachyuran zoeae

Brachyuran zoeae reached the threshold for analysis in both seasons. In the March-April season, only Cape St. Francis did not have brachyuran zoeae reaching the analysis threshold, and in the September-October season all sites had brachyuran zoeae reaching the threshold analysis value.

In the 1st sampling season (March/April), Day/Night had a significant effect on the abundance of brachyuran zoeae in both bays (Tables 2.32; Algoa Bay and 2.33; St Francis Bay) and significantly higher abundances were found during the night than the day, in both bays (Figures 2.40 and 2.41). The interaction of Depth and Day/Night had a significant effect on the abundance of brachyuran zoeae at Skoenmakerskop (Table 2.34). Even though during the day the pattern was not clear as the abundance was homogenous throughout the water column, at night zoeae were found at significantly higher abundances in the surface layer (Figure 2.42).

During the 2nd sampling season (October/November), a significant effect of Day/Night was found in both bays, while on the open coast, the interaction was significant (Tables 2.35 – 2.38). Statistically, higher abundances were found at night than during the day, in both bays (Figures 2.43 and 2.44). At Skoenmakerskop, during the day, the zoeae avoided the surface, preferring deeper layers and at night the higher abundances were found at the surface (Figure 2.45), suggesting diel migration. At Cape St. Francis, such patterns were not clear, with homogenous abundances through the water column during the day. At night however, there was preference for the surface (Figure 2.46).

Table 2.32: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of brachyuran zoeae throughout the water column in 6 March 2013 at Algoa Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	0.536591	3	0.178864	1.33327	n.s
Day/Night	1.880071	1	1.880071	14.01426	**
Depth*Day/Night	0.709660	3	0.236553	1.76330	n.s
Error	1.073233	8	0.134154		

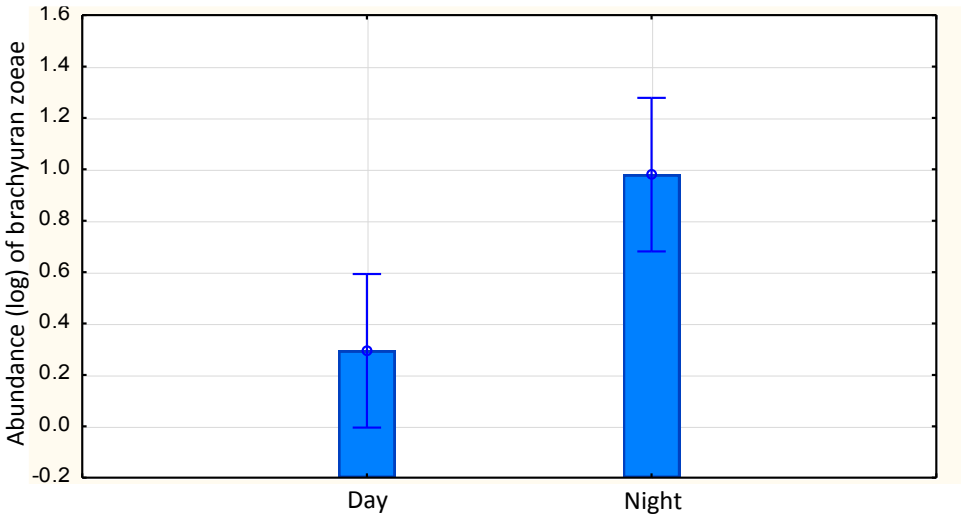


Figure 2.40: Abundance of brachyuran zoeae during a day and night sampling period at Algoa Bay on 6 March 2013. Error bars indicate standard error.

Table 2.33: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of brachyuran zoeae throughout the water column in 15 April 2013 at St. Francis Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	0.17805	2	0.08902	0.9049	n.s
Day/Night	2.78945	1	2.78945	28.3546	***
Depth*Day/Night	0.36892	2	0.18446	1.8751	n.s
Error	0.59026	6	0.09838		

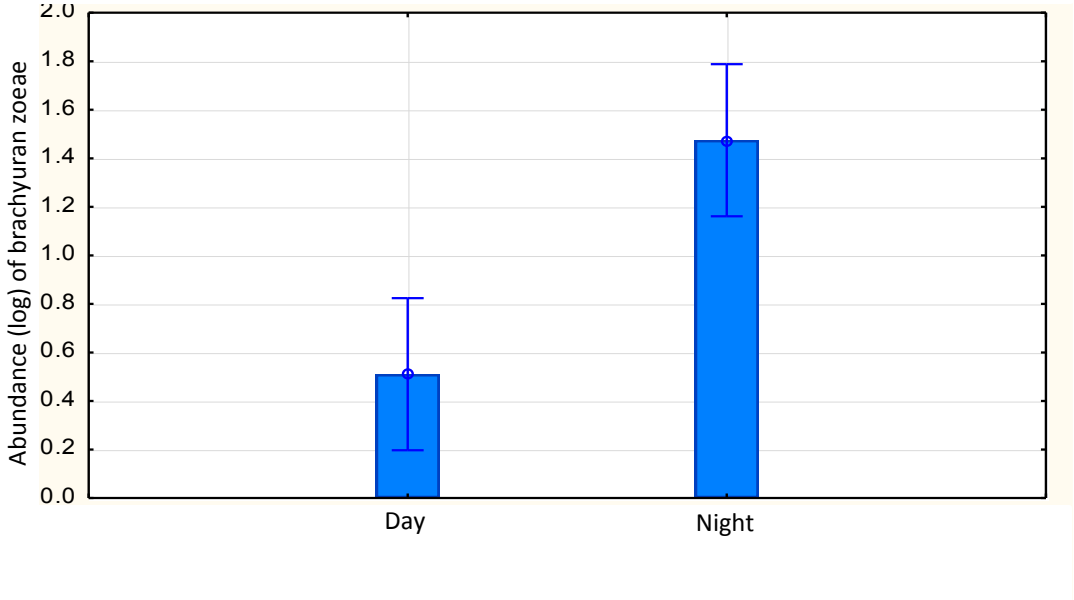


Figure 2.41: Abundance of brachyuran zoeae during a day and night sampling period at St. Francis Bay on 15 April 2013. Error bars indicate standard error.

Table 2.34: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of brachyuran zoeae throughout the water column in 21 March 2013 at Skoenmakerskop. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	0.582975	4	0.145744	3.6020	*
Day/Night	0.034380	1	0.034380	0.8497	n.s
Depth*Day/Night	1.558494	4	0.389623	9.6294	***
Error	0.404618	10	0.040462		

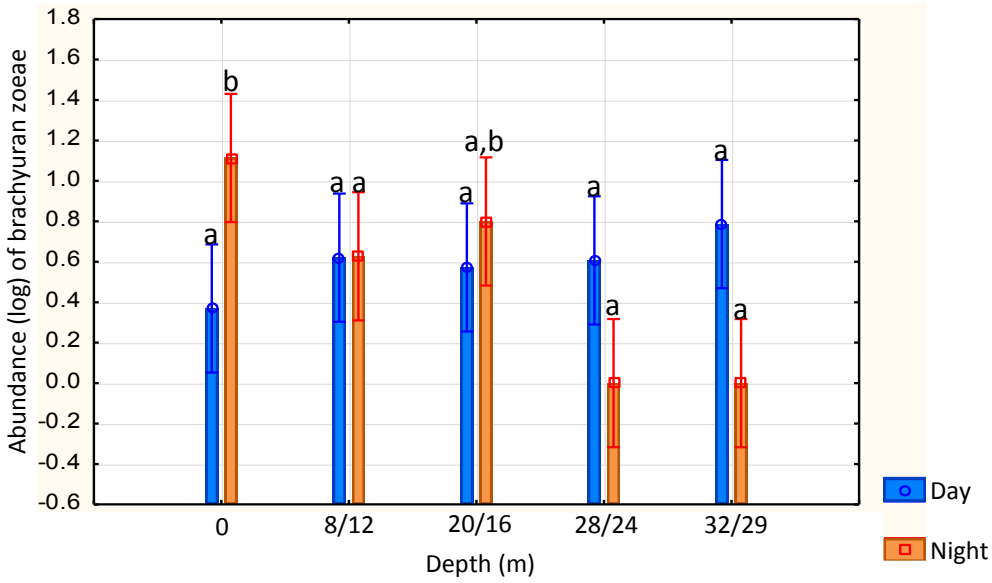


Figure 2.42: Abundance of brachyuran zoeae with the significant interaction of Day/Night and Depth at Skoenmakerskop on 21 March 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Table 2.35: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of brachyuran zoeae throughout the water column in 23 September 2013 at Algoa Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	3.64181	3	1.21394	3.21950	n.s
Day/Night	3.05526	1	3.05526	8.10291	*
Depth*Day/Night	1.22820	3	0.40940	1.08578	n.s
Error	3.01646	8	0.37706		

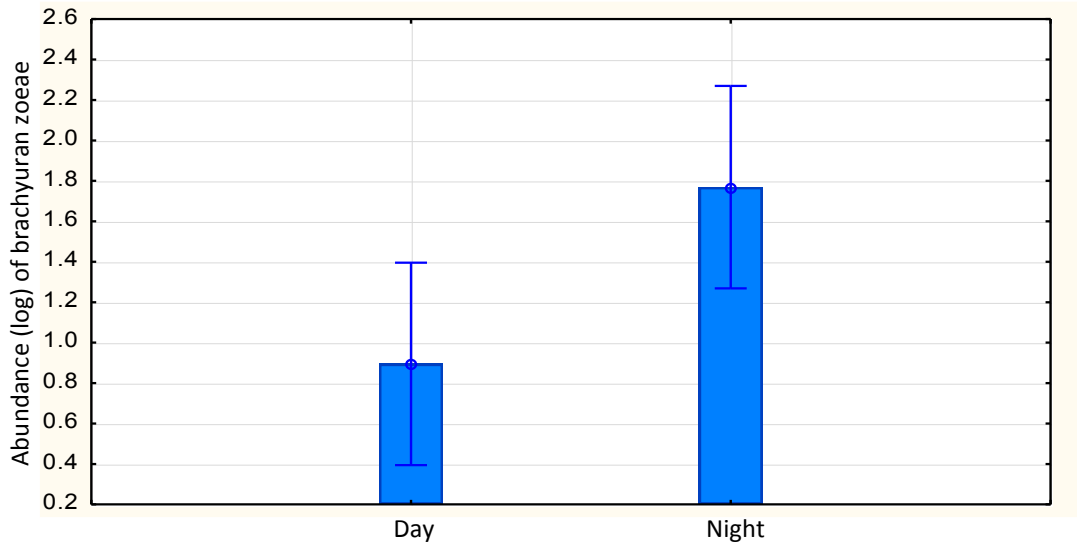


Figure 2.43: Abundance of brachyuran zoeae during a day and night sampling period at Algoa Bay on 23 September 2013. Error bars indicate standard error.

Table 2.36: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of brachyuran zoeae throughout the water column in 3 October 2013 at St. Francis Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	0.201818	2	0.100909	1.14607	n.s
Day/Night	1.586096	1	1.586096	18.01397	**
Depth*Day/Night	0.407635	2	0.203818	2.31484	n.s
Error	0.528289	6	0.088048		

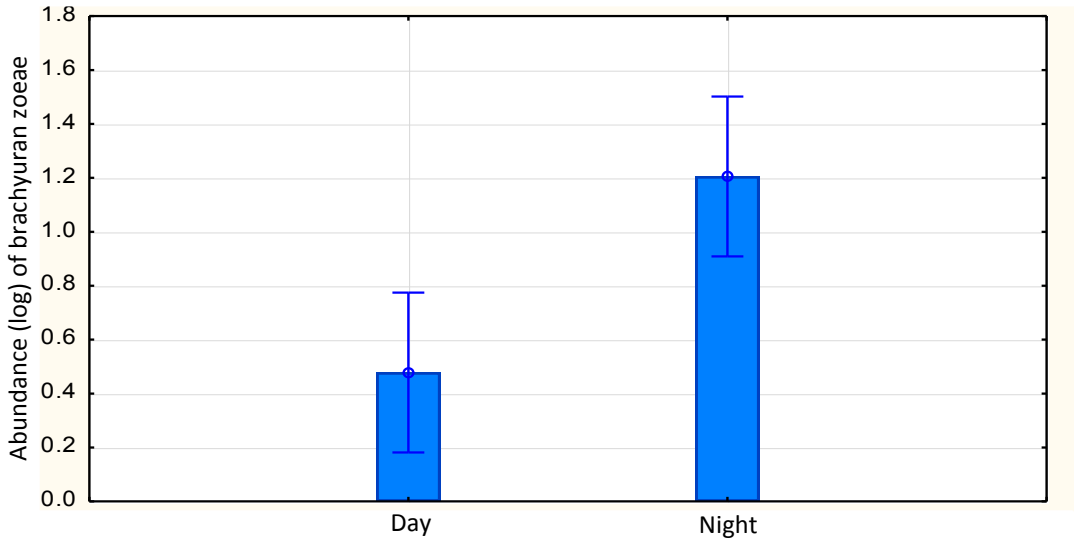


Figure 2.44: Abundance of brachyuran zoeae during a day and night sampling period at St. Francis Bay on 2 October 2013. Error bars indicate standard error.

Table 2.37: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of brachyuran zoeae throughout the water column in 3 November 2013 at Skoenmakerskop. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	0.42339	3	0.14113	5.8740	*
Day/Night	0.05244	1	0.05244	2.1826	n.s
Depth*Day/Night	2.41252	3	0.80417	33.4708	****
Error	0.19221	8	0.02403		

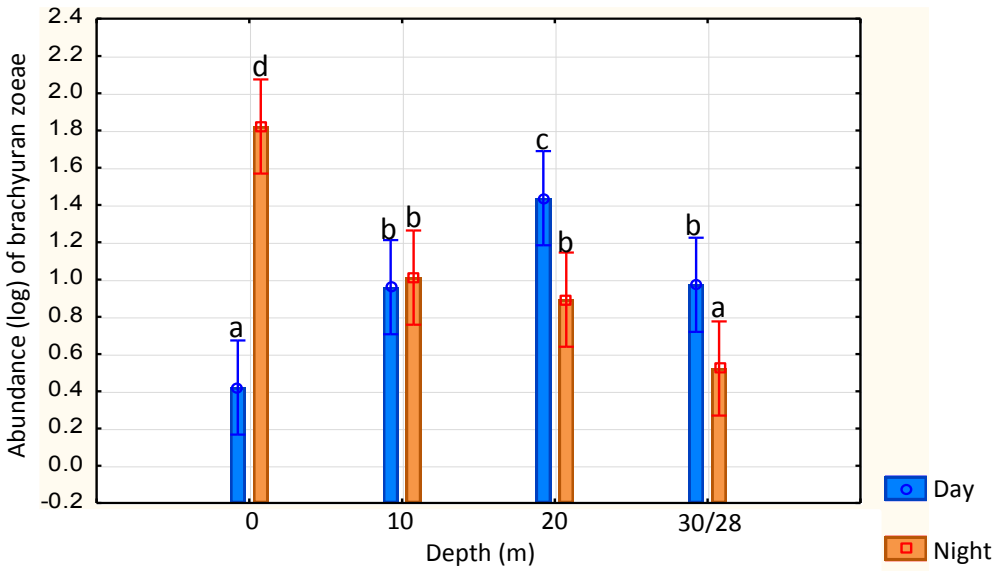


Figure 2.45: Abundance of brachyuran zoeae with the significant interaction of Day/Night and Depth at Skoenmakerskop on 3 November 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Table 2.38: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of brachyuran zoeae throughout the water column in 4 October 2013 at Cape St. Francis. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	0.299823	4	0.074956	1.24867	n.s
Day/Night	0.880385	1	0.880385	14.66612	**
Depth*Day/Night	1.211519	4	0.302880	5.04560	**
Error	0.600285	10	0.060028		

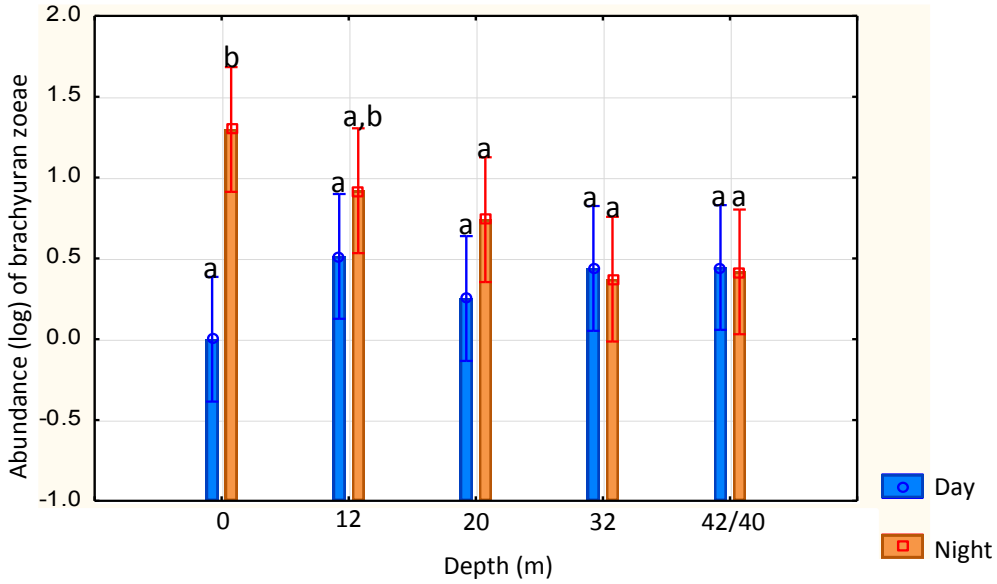


Figure 2.46: Abundance of brachyuran zoeae with the significant interaction of Day/Night and Depth at Cape St. Francis on 4 October 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects on the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Pinnotherid zoeae

Pinnotherid zoeae were another taxon of decapods that was commonly found during sampling. In the bays, this group reached the analysis threshold for both seasons.

Day/Night had a significant effect on the abundance of pinnotherid zoeae in both bays and in both sampling seasons (Tables 2.39, March, Algoa Bay; 2.40, April, St Francis Bay; 2.41, September, Algoa Bay and 2.42, October, St Francis Bay). The histogram bar graphs indicate that the zoeae were found in higher abundances at night than during the day, at both sites during both sampling seasons (Figures 2.47, 2.48, 2.49, and 2.50).

Table 2.39: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of pinnotherid zoeae throughout the water column in 6 March 2013 at Algoa Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	Df	MS	F	p
Depth	0.20430	3	0.06810	0.43315	n.s
Day/Night	2.17596	1	2.17596	13.83990	**
Depth*Day/Night	0.34025	3	0.11342	0.72137	n.s
Error	1.25779	8	0.15722		

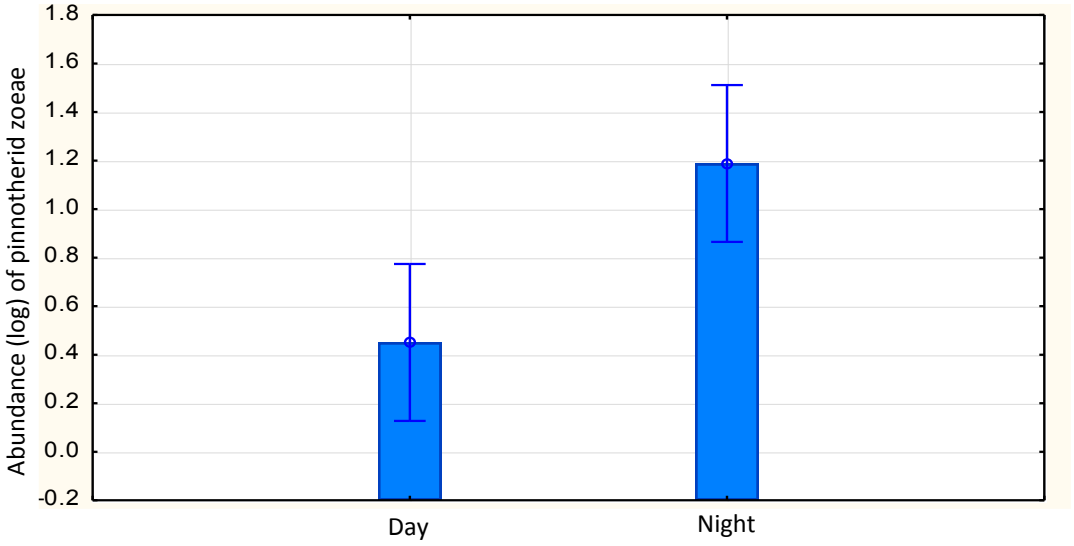


Figure 2.47: Abundance of pinnotherid zoeae during a day and night sampling period at Algoa Bay on 6 March 2013. Error bars indicate standard error.

Table 2.40: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of pinnotherid zoeae throughout the water column in 15 April 2013 at St. Francis Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	0.190266	2	0.095133	0.27210	n.s
Day/Night	2.230930	1	2.230930	6.38093	*
Depth*Day/Night	0.351366	2	0.175683	0.50249	n.s
Error	2.097746	6	0.349624		

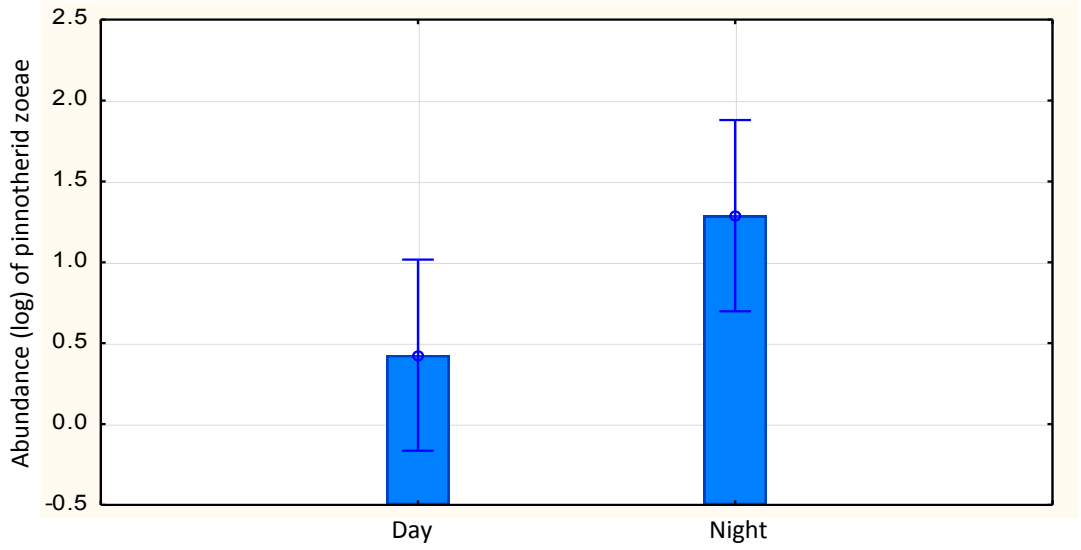


Figure 2.48: Abundance of pinnotherid zoeae during a day and night sampling period at St. Francis Bay on 15 April 2013. Error bars indicate standard error.

Table 2.41: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of pinnotherid zoeae throughout the water column in 23 September 2013 at Algoa Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	4.50734	3	1.50245	3.9255	n.s
Day/Night	2.58859	1	2.58859	6.7634	*
Depth*Day/Night	0.93088	3	0.31029	0.8107	n.s
Error	3.06191	8	0.38274		

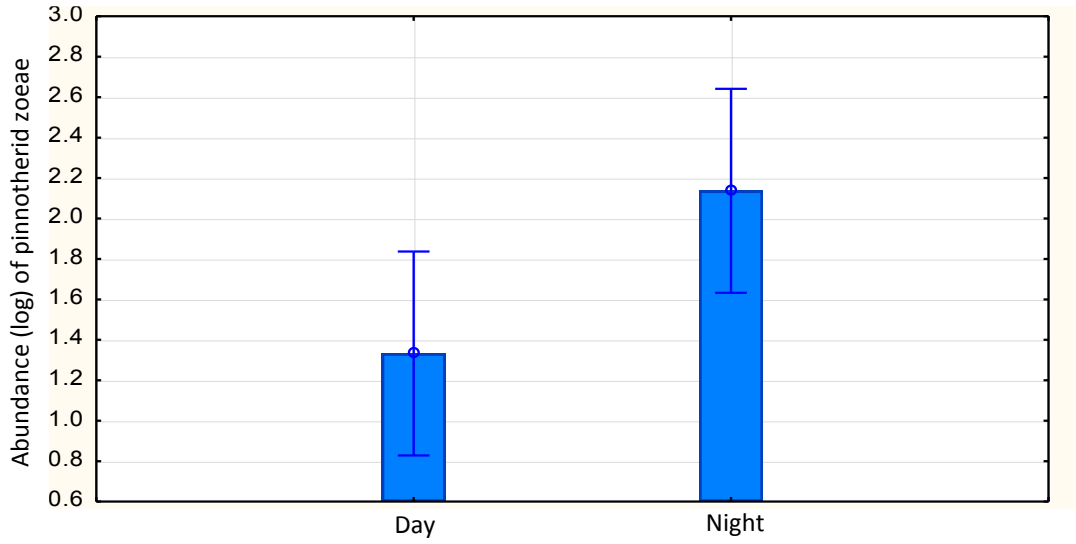


Figure 2.49: Abundance of pinnotherid zoeae during a day and night sampling period at Algoa Bay on 23 September 2013. Error bars indicate standard error.

Table 2.42: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of pinnotherid zoeae throughout the water column in 3 October 2013 at St. Francis Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	0.62723	2	0.31362	2.18336	n.s
Day/Night	2.96485	1	2.96485	20.64084	**
Depth*Day/Night	0.62108	2	0.31054	2.16195	n.s
Error	0.86184	6	0.14364		

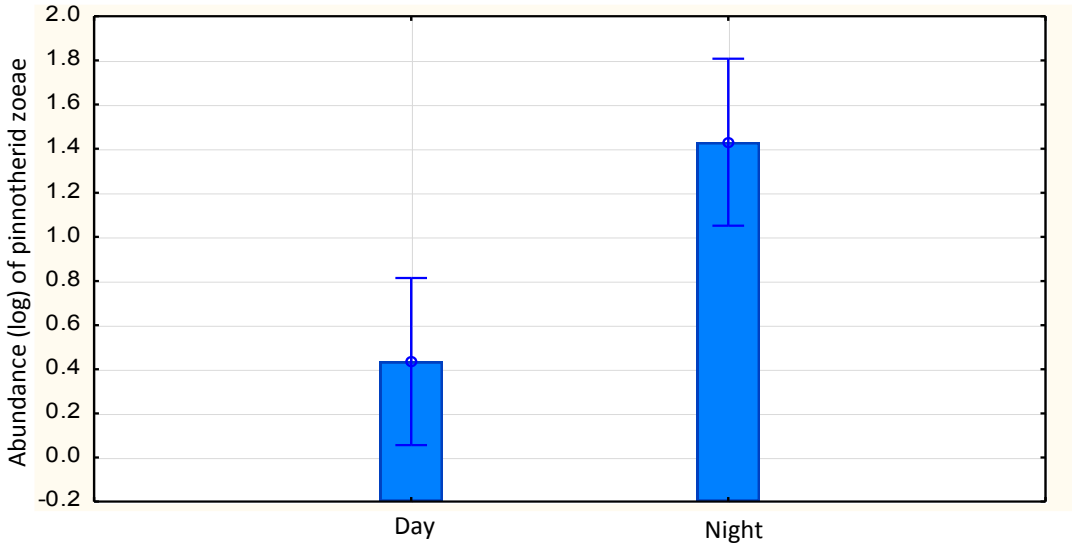


Figure 2.50: Abundance of pinnotherid zoeae during a day and night sampling period at St. Francis Bay on 3 October 2013. Error bars indicate standard error.

Porcelanid zoeae

Porcelanid zoeae were identified in the samples, reaching the threshold for analysis at Algoa Bay and Cape St. Francis in both sampling seasons.

At Algoa Bay, Day/Night had a significant effect in the 1st sampling season (March, Table 2.43). The statistically significant highest abundance was found at night (Figure 2.51). In the open coast, Cape St. Francis, the interaction of Depth and Day/Night had a significant effect (Table 2.44). Significantly higher abundances were found at 12 metres during the day, whilst at night, abundances were homogenous through the water column (Figure 2.52).

Higher abundances were again found at night at Algoa Bay in the 2nd sampling season (September) where Day/Night had a significant effect (Table 2.45, Figure 2.53). At Cape St. Francis, the interaction had a significant effect on the abundance of porcelanid zoeae, but the post hoc grouping could not reveal a clear pattern (Table 2.46, Figure 2.54).

Table 2.43: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$\log_{10}(X+1)$ transformed] of porcelanid zoeae throughout the water column in 6 March 2013 at Algoa Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	P
Depth	0.522475	3	0.174158	0.79350	n.s
Day/Night	2.843122	1	2.843122	12.95392	**
Depth*Day/Night	0.338300	3	0.112767	0.51379	n.s
Error	1.755838	8	0.219480		

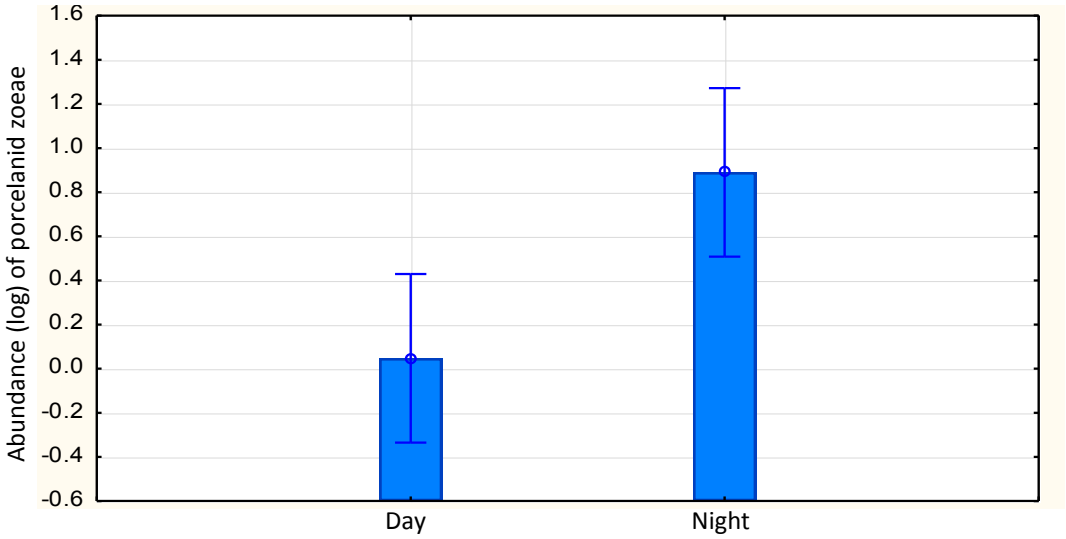


Figure 2.51: Abundance of pinnotherid zoeae during a day and night sampling period at Algoa Bay on 6 March 2013. Error bars indicate standard error.

Table 2.44: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$\log_{10}(X+1)$ transformed] of porcelanid zoeae throughout the water column in 5 April 2013 at Cape St. Francis. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	1.203381	4	0.300845	16.60766	***
Day/Night	0.079713	1	0.079713	4.40040	n.s
Depth*Day/Night	0.406200	4	0.101550	5.60589	**
Error	0.181149	10	0.018115		

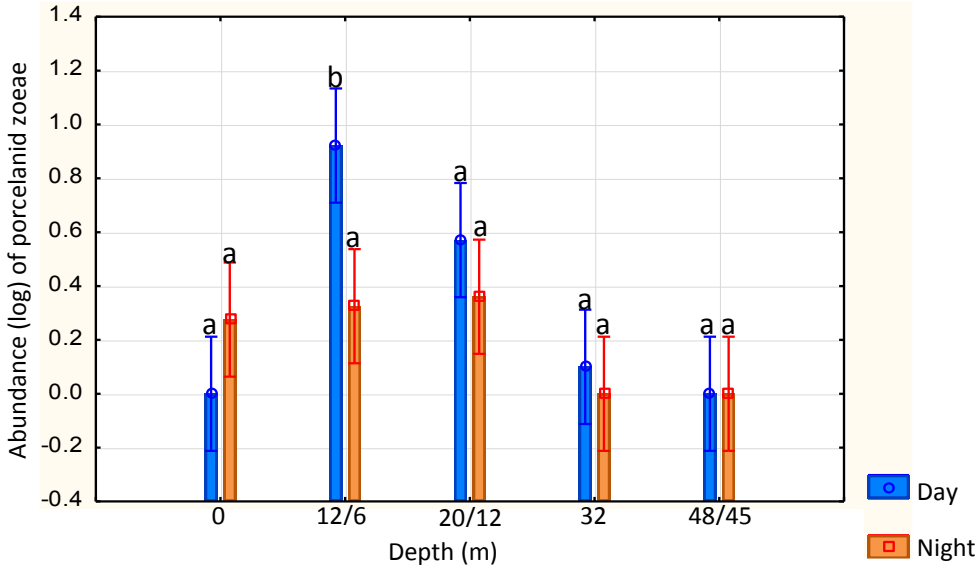


Figure 2.52: Abundance of porcelanid zoeae with the significant interaction of Day/Night and Depth at Cape St. Francis on 5 April 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Table 2.45: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of porcelanid zoeae throughout the water column in 23 September 2013 at Algoa Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	1.152178	3	0.384059	3.25005	n.s
Day/Night	2.199178	1	2.199178	18.61026	**
Depth*Day/Night	0.231837	3	0.077279	0.65396	n.s
Error	0.945362	8	0.118170		

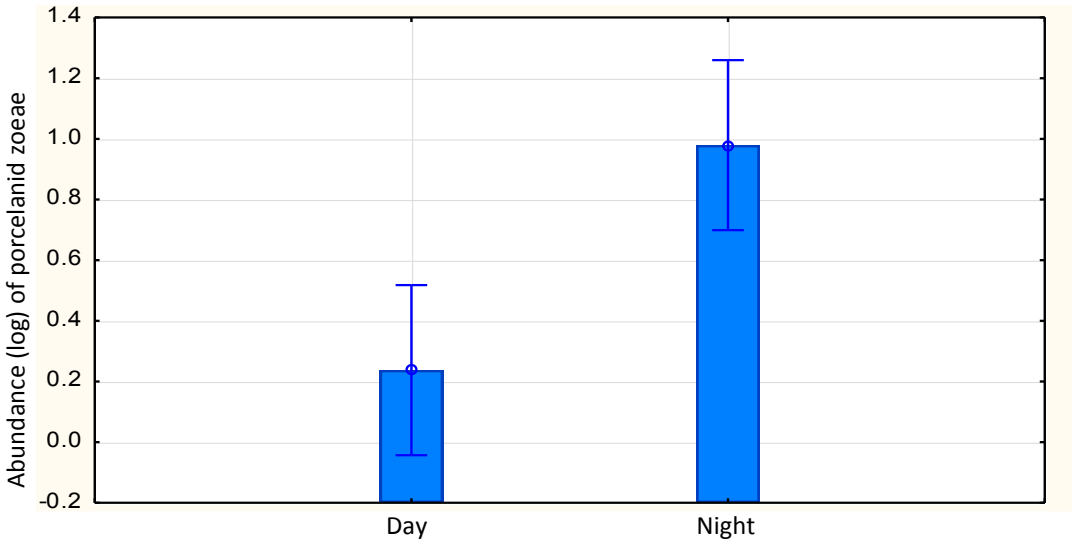


Figure 2.53: Abundance of porcelanid zoeae during a day and night sampling period at Algoa Bay on 23 September 2013. Error bars indicate standard error.

Table 2.46: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$\log_{10}(X+1)$ transformed] of porcelanid zoeae throughout the water column in 4 October 2013 at Cape St. Francis. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	0.987542	4	0.246886	3.0157	n.s
Day/Night	0.208496	1	0.208496	2.5468	n.s
Depth*Day/Night	1.352667	4	0.338167	4.1307	*
Error	0.818670	10	0.081867		

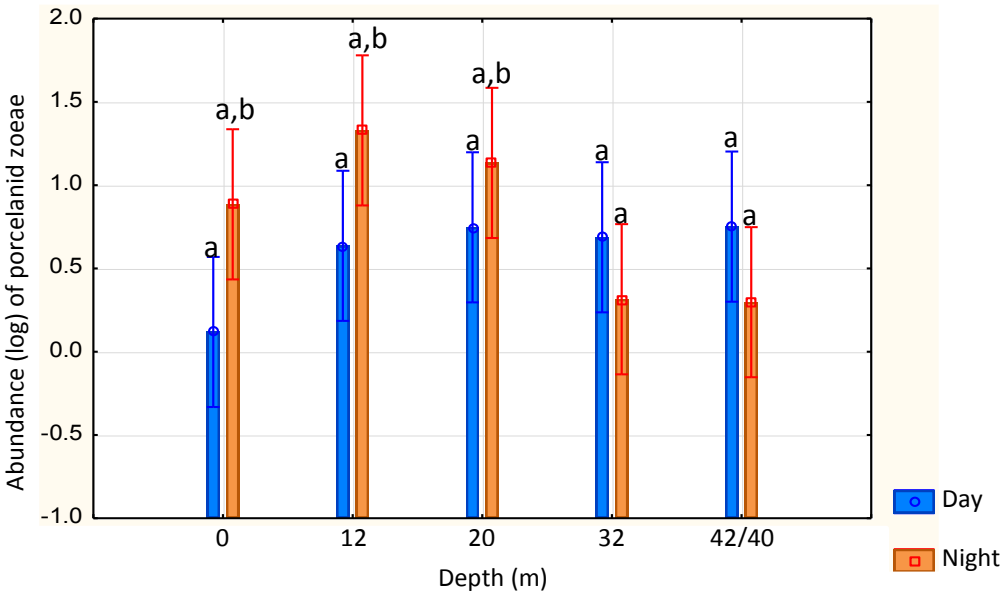


Figure 2.54: Abundance of porcelanid zoeae with the significant interaction of Day/Night and Depth at Cape St. Francis on 3 October 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Anomuran zoeae

At St. Francis Bay, Skoenmakerskop and Cape St. Francis, anomuran zoeae were present in significant amounts during the 1st season (March/April). For these 3 sites, the interaction of Depth and Day/Night had a significant effect on the abundance of anomuran zoeae (Tables 2.47, 2.48, and 2.49). There was a clear trend noticeable with this taxon. In all the sites, the zoeae avoided the surface and preferred a deeper, but not always bottom layer (4 and 8 metres at St. Francis Bay; 8 metres at Skoenmakerskop; 12 and 20 metres at Cape St. Francis) during the day, however, larvae were homogenously distributed through the water column at night (Figures 2.55, 2.56, and 2.57).

In the 2nd sampling season (September/November), this taxon reached the minimum analysis threshold at Algoa Bay and Skoenmakerskop. Day/Night had a significant

effect on the abundance of the zoeae in Algoa Bay with statistically higher abundances found at night (Table 2.50, Figure 2.58). As for the 1st sampling season in the three sites, the trend continued at Skoenmakerskop in the 2nd sampling season with the significant effect of the interaction Day/Night and Depth on the abundance of anomuran zoeae (Table 2.51). Zoeae avoided the surface and were found in significantly higher abundances on the deeper layers (10, 20 and 30 metres) during the day while they were homogenously distributed through the water column at night (Figure 2.59).

Table 2.47: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of anomuran zoeae throughout the water column in 15 April 2013 at St. Francis Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	0.11421	2	0.05711	1.1952	n.s
Day/Night	0.53234	1	0.53234	11.1415	**
Depth*Day/Night	0.48820	2	0.24410	5.1089	*
Error	0.28668	6	0.04778		

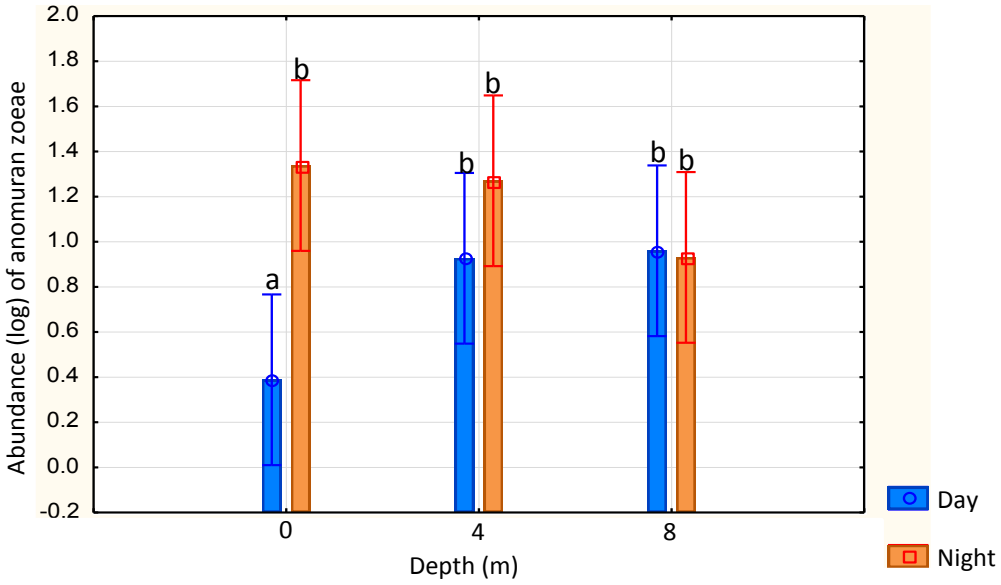


Figure 2.55: Abundance of anomuran zoeae with the significant interaction of Day/Night and Depth at St. Francis Bay on 15 April 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects the interaction of Depth and Day/Night.

Table 2.48: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of anomuran zoeae throughout the water column in 21 March 2013 at Skoenmakerskop. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	1.70731	4	0.42683	10.8919	***
Day/Night	0.05719	1	0.05719	1.4594	n.s
Depth*Day/Night	0.86845	4	0.21711	5.5404	**
Error	0.39188	10	0.03919		

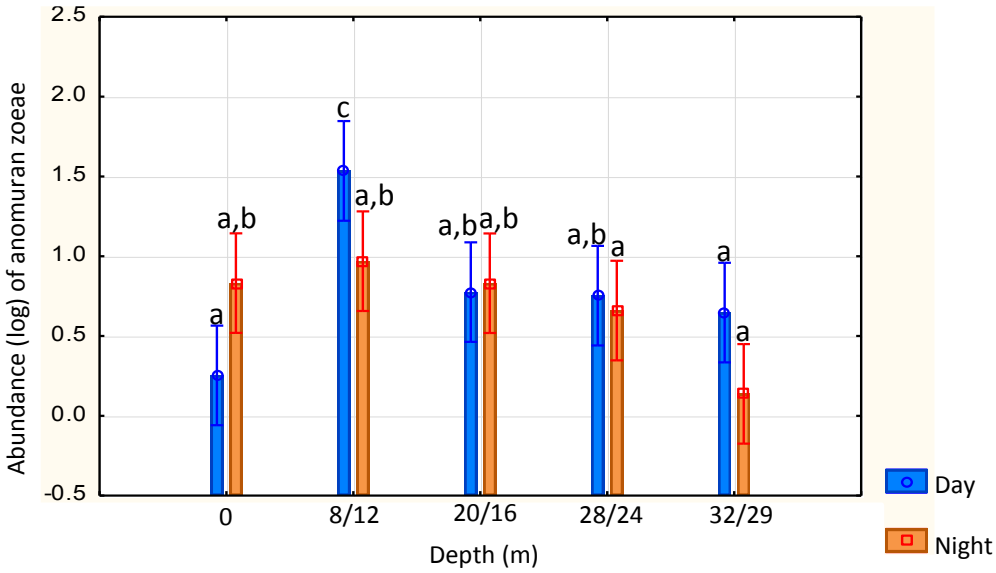


Figure 2.56: Abundance of anomuran zoeae with the significant interaction of Day/Night and depth at Skoenmakerskop on 21 March 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Table 2.49: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$\log_{10}(X+1)$ transformed] of anomuran zoeae throughout the water column in 5 April 2013 at Cape St. Francis. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	1.751984	4	0.437996	11.66354	***
Day/Night	0.479795	1	0.479795	12.77662	**
Depth*Day/Night	0.563080	4	0.140770	3.74861	*
Error	0.375526	10	0.037553		

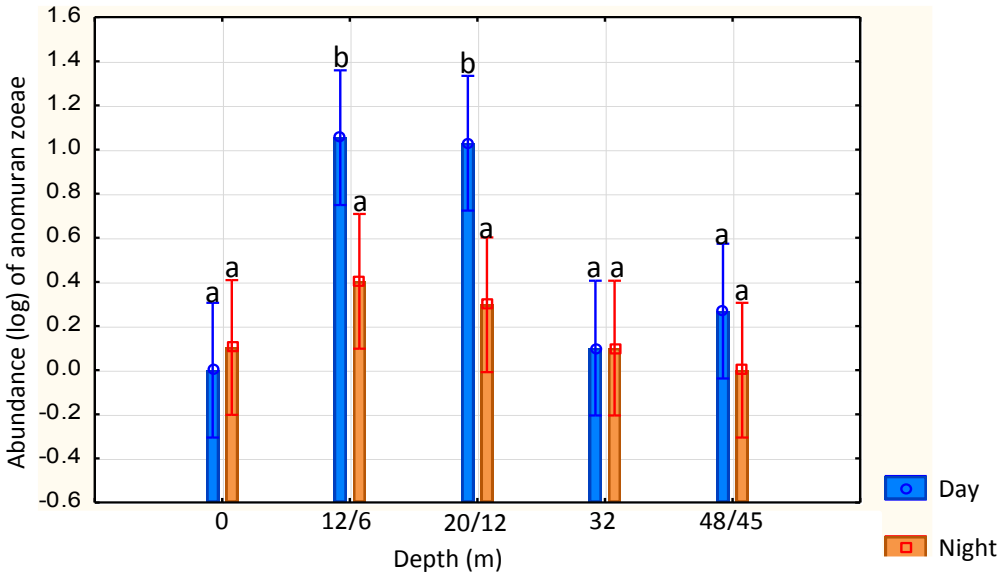


Figure 2.57: Abundance of anomuran zoeae with the significant interaction of Day/Night and Depth at Cape St. Francis on 5 April 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Table 2.50: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of anomuran zoeae throughout the water column in 23 September 2013 at Algoa Bay. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	2.68061	3	0.89354	1.87520	n.s
Day/Night	7.88779	1	7.88779	16.55353	**
Depth*Day/Night	1.96535	3	0.65512	1.37485	n.s
Error	3.81202	8	0.47650		

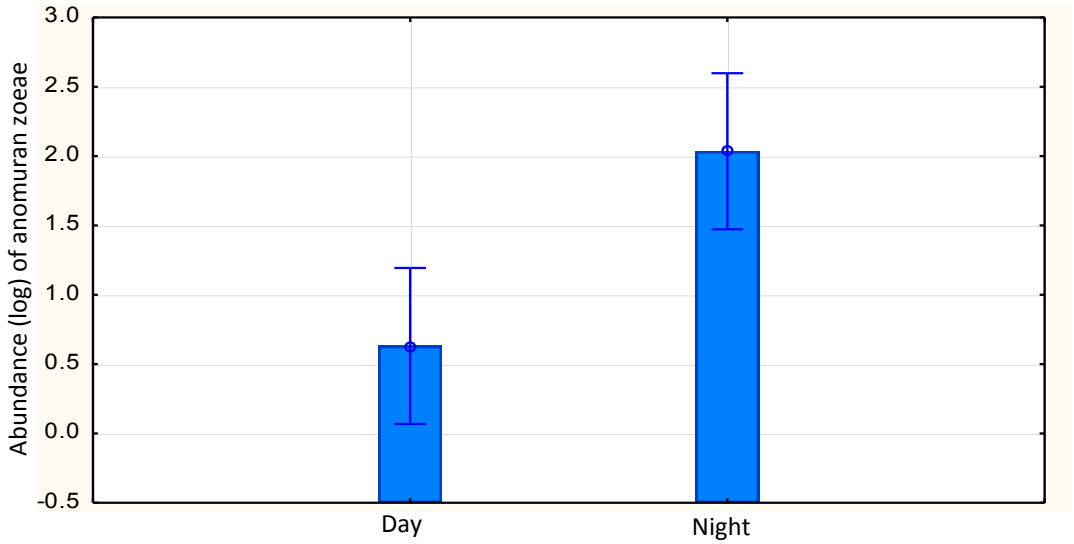


Figure 2.58: Abundance of anomuran zoeae during a day and night sampling period at Algoa Bay on 23 September 2013. Error bars indicate standard error.

Table 2.51: Analysis of Variance (ANOVA) examining the effects of Day/Night and Depth on the abundance [$log_{10}(X+1)$ transformed] of anomuran zoeae throughout the water column in 3 November 2013 at Skoenmakerskop. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Depth	0.56536	3	0.18845	7.9505	**
Day/Night	0.18132	1	0.18132	7.6497	*
Depth*Day/Night	1.67269	3	0.55756	23.5226	***
Error	0.18963	8	0.02370		

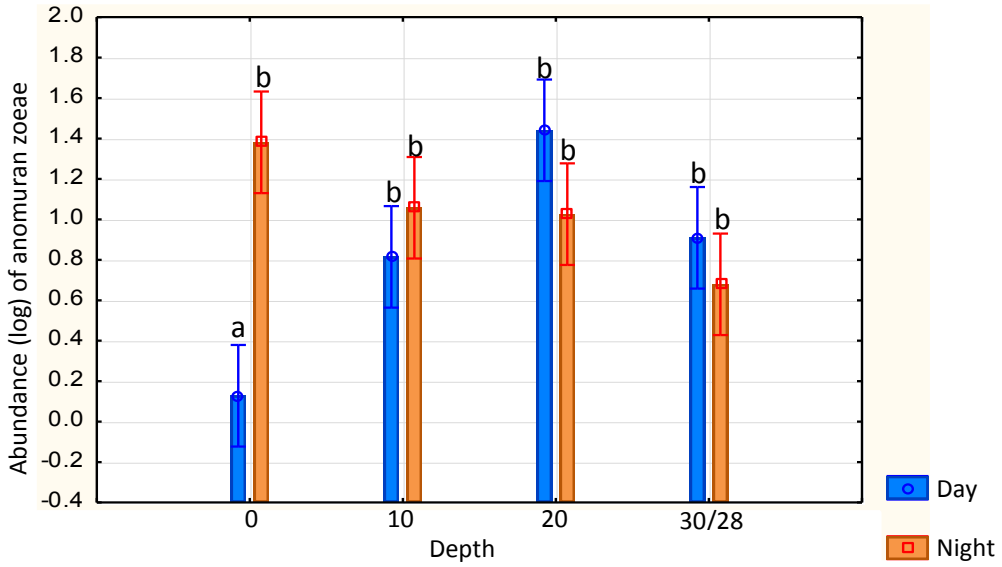


Figure 2.59: Abundance of anomuran zoeae with the significant interaction of Day/Night and Depth at Skoenmakerskop on 3 November 2013. Error bars indicate standard error. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Depth and Day/Night. The paired numbers are the depths that were sampled at different times (day and night). The 1st numbers on the X-axis indicate the day sampling depths and the 2nd are the depths sampled at night.

Overview

The different taxa revealed a general trend. Mostly, when there was a significant effect of the interaction between time and depth, the larvae tend to avoid the surface during the day. This is shown by slow swimming veligers of oysters and Bivalve sp. A (Figures 2.14 and 2.17 respectively). This was followed by an ascent at night, with the oyster and Bivalve sp. A veligers occupying the surface layer during the night (Figures 2.14 and 2.18). Barnacles also showed this trend, with early and late stages of balanid nauplii avoiding the surface layer (but also the deepest bottom layer) during the day (Figures 2.21 and 2.29 respectively) and moving towards the surface at night (Figures 2.22 and 2.30 respectively). This was not only seen in the rather slower swimmers but also for fast swimming decapods. Decapods seemed to avoid the surface during the day (Figures 2.45, 2.52, 2.55, 2.56, 2.57, and 2.59) and ascend to the surface at night (Figures 2.42, 2.45, 2.46, and 2.59). Such patterns of diurnal avoidance of the surface layers and night ascent from the deeper layers were particularly common at the open coast sites. The avoidance of the surface and bottom layers, inhabiting mid-layers might be a result of the thermocline acting as a barrier/accumulation zone for decapods, even though a study by dos Santos and co-workers (2008) indicated that the thermocline does not trap fast swimming decapod larvae.

MULTIPLE REGRESSION ANALYSIS

The data from all sites in the March-April 2013 sampling season were pooled for this analysis. Only taxa that were common throughout all four sites were analysed. Those common taxa also had to meet the minimum analysis threshold of 10 individuals per cubic meter in at least one sample at a station (Weidberg *et al.*, 2014). Only late stages of balanid nauplii; Cyprid sp. A and anomuran zoeae were common amongst all four sites and reached the analysis threshold. There were 23 models that were created and tested against each taxon. With Bonferroni correction applied, the new alpha value was $p \leq 0.002$. With all the models being tested on each taxon independently, there was no significant effect from any model on any taxon.

When all sites were pooled together in the September-October 2013 sampling season, Bivalve sp. A; late stages of Balanid nauplii; Cyprid sp. A; brachyuran zoeae and anomuran zoeae were common amongst the sites and reached the analysis threshold. Only 11 models could be formed and tested on each taxon independently. After Bonferroni correction applied, the alpha value was $p \leq 0.004$. Table 2.52 shows the models that had significant effects.

Table 2.52: Multiple linear regression analyses for the common taxa amongst the four sites in the September-October 2013 sampling season. For each variable/model the sign of the correlation, the level of significance and the total variance explained are shown. The + and – signs indicate the relation between the model and the taxon. AIC indicates the Akaike Information Criterion.

Species/Taxa/Group	Variables/Models	p-value	R^2	AIC
BIVALVES				
Bivalve sp. A	1. Upwelling, -	0.001	0.154	583.536
BARNACLES				
Cyprid sp. A	1. Upwelling, - Turbulence, +	<0.001	0.226	778.595
	2. Upwelling, -	0.002	0.142	782.904
DECAPODS				
Brachyuran zoeae	1. Upwelling, - Turbulence, +	<0.001	0.22	704.617
	2. Upwelling, -	0.001	0.161	707.064
Anomuran zoeae	1. Upwelling, - Turbulence, +	<0.001	0.381	808.506
	2. Turbulence, +	<0.001	0.281	815.804
	3. Upwelling, -	0.004	0.125	828.403

2.4 Discussion

2.4.1 Physical characteristics

The two bays considered in this study are very shallow, neither exceeding depths of 15 metres. The temperatures in both bays did not vary from the surface to the bottom. At all stations, in both bays, there was not even a single degree of temperature change from the surface to the bottom. This suggests that neither bay presented thermal stratification, regardless of time of day or season. The sites on the open coast were deeper than the bay sites and, as a result, some thermal stratification was observed at Skoenmakerskop and Cape St. Francis. The only difference between the capes was the depth at which the thermocline was found. At Skoenmakerskop for example, the thermocline was found between sampling depths of 8 and 20 metres during the day and between 16 and 24 metres at night in the March-April sampling season. In comparison at Cape St. Francis, the thermocline was shallower, lying between the surface and 12 metres during the day and between 6 and 12 metres at night.

In the September-October sampling season, during the day, the thermocline was found at similar depths for both capes (between surface and 12 metres). During the night at Cape St. Francis it remained the same, Skoenmakerskop had a thermocline in-between 10 and 20 metres of depth.

Another important result was the difference in upwelling between the two seasons. March-April had a higher upwelling index than the September-October season.

Schumann *et al*. (1988) noted that, on the south-east coast of South Africa, upwelling occurs at capes including Cape Recife at the western end of Algoa Bay. Upwelling originates from open coasts as compared to embayments, which are considered to lie in upwelling shadows (Tracey, 1990; Rosenfeld *et al*., 1994; Graham & Largier, 1997). This upwelling on the open coasts might be due to the prevailing winds. Bays usually have no thermal stratification, irrespective of season (Graham & Largier, 1997). The only thermal stratification found in bays might be a result of them lying within upwelling shadows (Rosenfeld *et al*., 1994).

2.4.2 Biological data

Bryozoans

Bryozoan larvae were found in high abundances at the surface at Algoa Bay, St. Francis Bay and Skoenmakerskop during the day (Figures 2.6, 2.7 and 2.8 respectively). At night, larvae did not show any migration to the bottom, but remained at/close to the surface. The same results were found for the bryozoan species, *Bugula neritina* by Pires and Woollacott (1997); and *B. neritina*, *B. simplex*, *B. stolonifera* by and Wendt and Woollacott (1999). Bryozoan larvae of the above mentioned species are positively phototactic during their early development and later become negatively phototactic (Pires & Woollacott, 1997; Wendt & Woollacott, 1999). This means that early stages of bryozoan larvae prefer to be close to the surface during the day due to light attraction. During early developmental stages, larvae might not be good swimmers so the sea breeze might assist in nearshore retention for surface dwellers. Later stages are better swimmers and therefore can inhabit bottom layers and swim to maintain their nearshore position (Pineda, 1999). Light cues are useful in position regulation, facilitate dispersal of the larvae and finding suitable sites for metamorphosis (Pires & Woollacott, 1997; Wendt & Woollacott, 1999). Such counterintuitive diurnal permanence at the surface could be explained by the fact that bryozoans are transparent in colour and that might serve as an advantage in the water column, as it might be difficult for predators to visually note them (Wendt & Woollacott, 1999).

Bivalves

Even the slow swimming bivalves (0.11 cm/s, Chia *et al*., 1984) do perform some vertical migration, as seen with Bivalve sp. A. Even though some taxa were homogenously distributed through the water column, there was a pattern for others. During the day, they were found in high abundances at the bottom layers or away from the surface with an ascent at night to the surface layer, especially for oysters and Bivalve sp. A in October (Figures 2.14, 2.17 and 2.18). In October, upwelling had a significant negative effect on the abundance of Bivalve sp. A, with higher abundances during downwelling. Downelling often provides an indication of relaxation of offshore winds (Gaines & Roughgarden, 1985), with potential links to

larval retention. Similar results of larval retention due to downwelling have been observed in other regions (Shanks & Brink, 2005) on the bivalve veligers of *Spisula solidissima* and *Ensis directus* which avoid the surface in upwelling waters by remaining below the thermocline. Larvae of Mytilidae have also been found associated to the bottom in upwelling waters (Ma *et al*., 2006). Shanks *et al*. (2003a) found the same results with a group of bivalves, they remained close to the bottom in upwelling conditions. Offshore transport of larvae during upwelling was ruled out as veligers of *Tellina* spp. and *Mulinia lateralis* did not behave as passive particles, but controlled their vertical distribution and remained close to shore (Shanks & Brink, 2005). Bivalves might use the same strategy observed in gastropods, to retract the velum and sink to the bottom in turbulent waters (Fuchs *et al*., 2004).

Barnacles

Even though no clear pattern was observed in the abundance of cyprids, nauplii showed vertical migration, especially at the capes in October. When the interaction of Depth and Day/Night had a significant effect on the Balanid nauplii, they were shown to avoid the surface during the day, with high abundances at the lower depths (Figures 2.21, 2.29 and 2.30). At night however, they were found in higher abundances at the surface (Figures 2.22 and 2.30). Barnacle nauplii have been found to be able to swim against the vertical flow, thus changing their vertical positioning in the water column (Weidberg *et al*., 2013). This change in vertical positioning of nauplii is presumably performed to enhance onshore retention (Weidberg *et al*., 2013). As seen in table 2.53, the abundance of barnacle Cyprid sp. A, positively correlated with turbulence and negatively correlated with upwelling. As noted by Fuchs and DiBacco (2011), larvae respond to turbulence by either swimming up or sinking down the water column. Fuchs *et al*. (2010) found the same results as the Cyprid sp. A, when they studied *Crepidula* spp. and *Anachis* spp. Activity seems to be triggered by turbulence, with an upward swimming response under turbulent conditions which may favour retention of larvae in proximity to the shore (Fuchs *et al*., 2010; Fuchs and DiBacco, 2011). A positive response to turbulence in zooplankton is advantageous since it increases feeding opportunities for zooplankton (Rothschild & Osborn, 1988; Alcaraz, 1997) as the gut content of

bivalve larvae was found to increase with an increase in turbulence (Raby *et al*., 1994). Turbulence increases predator-prey encounters (Rothschild & Osborn, 1988).

Decapods

Whenever the interaction of Depth and Day/Night was non-significant for this order and the factor Day/Night had a significant effect, the higher abundances of zoeae occurred at night (Figures 2.40, 2.41, 2.43 and 2.44 for brachyuran zoeae; 2.47, 2.48, 2.49 and 2.50 for pinnotherid zoeae; 2.51, 2.53 for porcelanid zoeae; and 2.58 for anomuran zoeae). Taxa in this order proved that vertical migration of larvae does occur regularly in the water column. Even though the distribution may have been evenly distributed throughout the water column during the day, at night surface preference was seen (Figures 2.42 and 2.46). On occasions, the distribution was evenly distributed throughout the water column at night, during the day though, zoeae avoided the surface layer (Figures 2.52, 2.55, 2.56 and 2.57). Clear diel vertical migration was also detected, as shown in figures 2.45 and 2.59. This consistent trend confirms patterns observed in other studies on individual groups of decapod larvae. Zoeae of *Carcinus maenas,* studied in the Portuguese coastal upwelling system (Marta-Almeida *et al*., 2006; dos Santos *et al*., 2008) were found closer to the surface at night and closer to the bottom during the day. Shanks and Eckert (2005) found the same results with crustacean larvae in general. They were found to inhabit the surface layer over night and to sink to the bottom during the day. The supply of megalopae of the littoral crab, *Carcinus maenas,* to the estuaries on the Portuguese west and north coast and in the western Iberia upwelling ecosystem was aided by onshore advection following downwelling winds (Almeida & Queiroga, 2003; Queiroga *et al*., 2006; Queiroga *et al*., 2007). This could be an indication that these larvae preferred downwelling events for onshore retention, as shown in this study by a negative correlation between upwelling and zoeae. The negative correlation between upwelling and the zoeae was visible in the September-October sampling season, which had stronger downwelling than the March-April season. Criales *et al.* (2013) found a positive response to turbulent kinetic energy (TKE) in the pink shrimp, *Farfantepenaeus duorarum,* to a given amount of TKE over a 10 minute period. Turbulent kinetic energy is the resultant energy driven by

turbulence and/or water flow (Criales *et al.*, 2013). Larvae of this shrimp started swimming at a given amount of turbulence (1.1 – 3.5 cm^2/s^2). This study also showed a positive correlation between decapod zoeae and turbulence. This positive response to turbulence might be a behaviour to increase feeding ability as turbulence increases the encounter rate between zooplankton and their food (Rothschild & Osborn, 1988; Alcaraz, 1997).

Regardless of offshore flow due to Ekman transport, many taxa might have shown that swimming might greatly influence their spatial distribution. Although the patterns of vertical distribution may differ among taxa, there is however a general pattern of a preference for deeper layers during the day, with an ascent at dusk to inhabit the surface layers overnight. As other authors have stated, a bottom dwelling habit during the day is a strategy to avoid being seen by predators with the ascent at night making it hard for predators to visibly identify the plankton (Raby *et al.*, 1994). Only bryozoan larvae remained at the surface layer even during the day. Bryozoans are said to be positively phototactic, at least for some part of their life stages. As the larvae are transparent, they are not visible in the water column and therefore are still safe from predators in the water column during the day. Light cues are said to be a determinant for bryozoan larvae to undergo metamorphosis.

CHAPTER THREE

MEROPLANKTON DISTRIBUTION IN RELATION TO PHYSICAL WATER COLUMN STRUCTURE OVER A 24 HOUR PERIOD

3.1. Introduction

Sunlight (UV radiation) is a fundamental ecological factor in aquatic ecosystems, playing a vital role in short-term/daily changes in the vertical distribution of species in the water column (Williamson *et al.*, 1994; Cabrera *et al.*, 1997). UV radiation enhances surface accumulation by some species and sinking by others. For instance, among many existing examples, an increase in chlorophyll a on the surface due to sunlight correlated with a bloom in the population of *Ankyra judayi* (Chlorophyta) on the surface (Cabrera *et al.*, 1997). Inversely, high UV-B radiation inhibited surface dwelling by cladoceran species, *Chydorus sphaericus*, and the rotifer species, *Lepadella ovalis* (Cabrera *et al.*, 1997). High levels of UV-B radiation have also shown to prevent some zooplankton species from inhabiting the surface waters (Williamson *et al.*, 1994).

Light plays a major role in diel vertical migration of zooplankton, as daily migrations do occur with the shift from day to night times (Clarke, 1934; Forward *et al.*, 1984). Herbivorous and omnivorous copepods have been found to prefer the surface layer during the day as light favoured the proliferation of phytoplankton while non-herbivorous copepods preferred the aphotic layers of the water column (Martynova & Gordeeva, 2010). Zoeae of the crab *Rhithropanopeus harrisii* proved to be negatively phototactic, exhibiting positive geotaxis during the day and negative geotaxis in the absence of light (Forward *et al.*, 1984). When the surface layer froze, the krill species *Meganyctiphanes norvegica* preferred to inhabit the subneustonic layer, just below the ice where the light intensity is much higher than through the rest of the unfrozen water column below (Vestheim *et al.*, 2014).

To increase the understanding of the vertical resolution of movement of marine larvae through the water column, measurements from discrete depths (e.g. Shanks, 1986) rather than fine scale or high resolution vertical sampling (dos Santos *et al.*, 2008, Kunze *et al.*, 2013) have been implemented.

The detection of variability in larval abundance largely depends on the methodology applied, which influences the spatio-temporal resolution of observation. Some researchers have focused on larval dispersal, distribution, supply and attachment over a single season, which was spread over different days or months (e.g. Shanks,

1986; Dobrestov & Miron, 2001; Shanks *et al*., 2003a; Shanks & Brink, 2005; dos Santos *et al*., 2008; Kunze *et al*., 2013). The research presented in this chapter was carried out in two seasons, autumn (March 2013) and spring (October 2013). Such an approach has been previously used in a series of studies investigating larval distribution and dispersal (e.g. Di Bacco *et al*., 2001; Knights *et al*., 2006; Queiroga *et al*., 2006; Fuchs *et al*., 2010).

The approach used to collect samples for this study was (similar to that of Kunze and co-workers 2013) aimed at resolving potential small scale variability in the distribution of benthic invertebrate larvae. This was achieved using a plankton pump deployed in at discrete depths over a 24h period, in order to observe possible fine scale patterns of ascent and descent of different taxa in the water column.

3.2 Materials and methods

3.2.1 Study site

Algoa Bay (33° 55' S and 25° 37' E), located on the south east coast of South Africa was the selected site for the study (Figure 3.1). The bay faces eastward and is about 80km wide with a maximum depth of about 72m (Harry, 1978; Schumann *et al*., 2005).

Two sampling stations, 1A (33° 55', 688' S and 25° 37, 709' E) and 1B (33° 55, 493' S and 25° 37, 693' E) were selected and marked using a Global Positioning System (GPS). The distance of both stations from the shore was 900 metres and the stations were about 300 metres apart (Figure 3.1C). Physical properties of the water column and zooplankton samples were collected from the 12 metre long research vessel, the RV Ukwabelana.

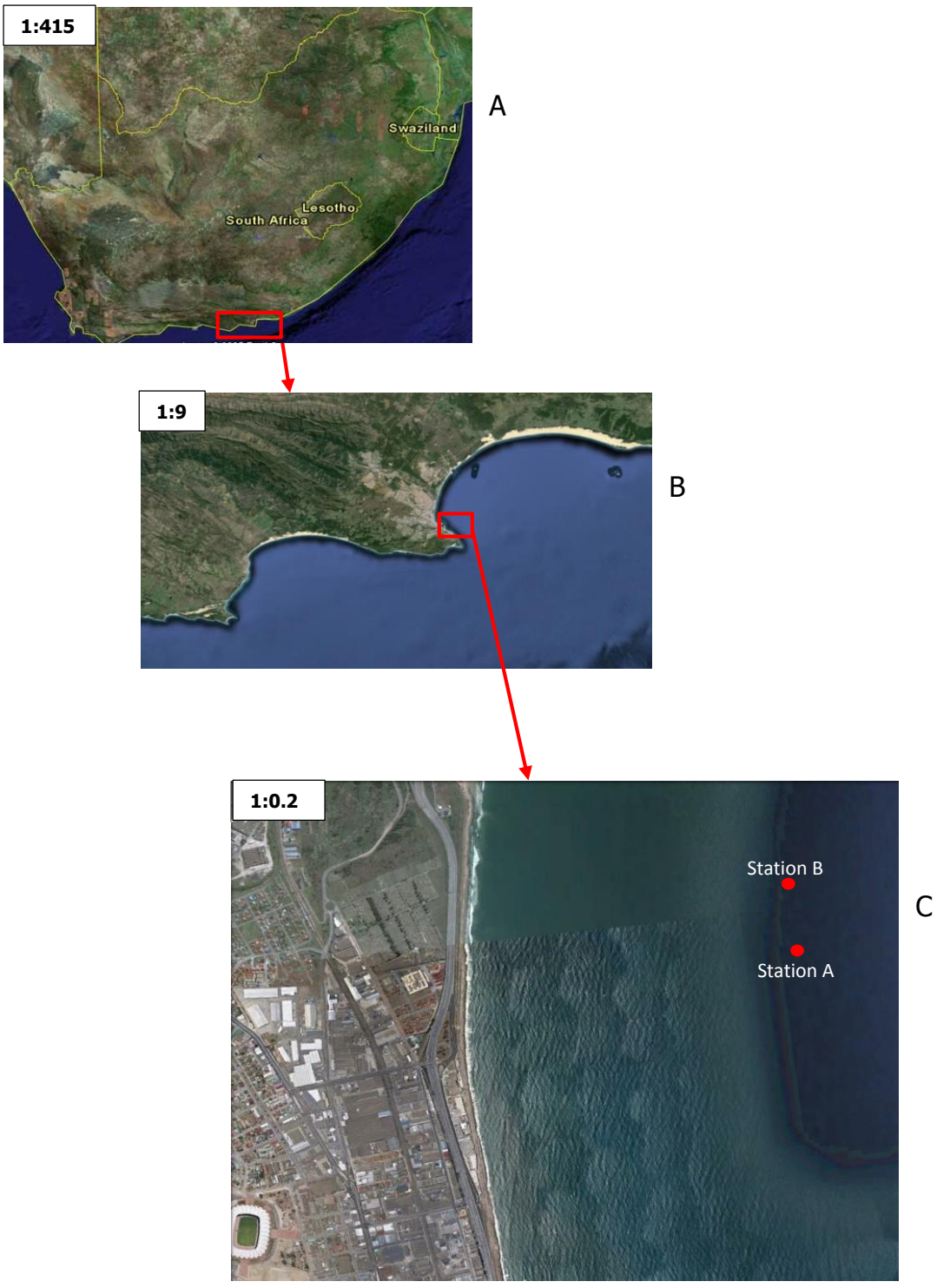


Figure 3.1: Map of South Africa (A), showing Port Elizabeth (B) with a portion of Algoa Bay bordered by the red rectangle. Two sampling stations (red dots) shown in Algoa Bay, Port Elizabeth (C).

3.2.2 Data collection

Collection of physical and biological data was done using the protocol described in detail in chapter 2, with the difference that data were collected over a single 24 hour period in Algoa Bay alone. Current velocity and direction were measured using an Acoustic Doppler Current Profiler (ADCP) that was submerged on arrival at each station and hauled back on board when sampling of biological data was complete. For the water temperature, the YSI CTD and/or the Seabird CTD was lowered to the sea floor after a 5 minute acclimation period in the sub-surface layer of the water column and pulled back on board on the arrival at each station. For biological data, sampling was done first at station A, where the pump used for chapter 2 was deployed for 7-10 minutes at each depth and hauled back on board and cleaned as described. To compare the results with those in chapter 2 for Algoa Bay, the same 4 depths were sampled (0, 4, 8 and 12 metres). After all depths were sampled at station A, the vessel moved to station B, to repeat sampling following the same protocol. Sampling required approximately 45 minutes at each station, with an additional 10 - 15 minutes to relocate between stations, so that the intervals between samples at each station were approximately 60 minutes. The alternate sampling of stations continued throughout the 24 hour period for a total of seven sampling cycles at each station. The full 24 hour study was done on 2-3 March 2013 and repeated again on 9-10 October 2013. In March, sampling started at 08:30 on the 2nd March and ended at 09:06 of the 3rd March and again, it started at 07:20 of the 9th October and ended at 08:09 of the 10th October. All samples were preserved in 100% ethanol. The processing of samples in the laboratory and larval identification followed the procedure described in the previous chapter.

3.2.3 Data Analysis

Only taxa that reached a minimum threshold concentration of at least 10 individuals per cubic meter (ind/m^3) of water were analysed. A 2-way Analysis of Variance (ANOVA) test and a post hoc test were run using Statistica 12. The effects of time and depth on the abundance of larvae were analysed for each taxon separately using a 2-way ANOVA, using factors Cycle (number of times a given station was

sampled over a 24 hour period) and Depth as fixed, orthogonal predictors. The interaction of Cycle and Depth (Cycle*Depth) was considered to reflect changes in vertical position with time pointing to potential larval vertical migrations. To avoid heterogeneity of variances, the log-transformed [$\log_{10}(X+1)$] abundance of each taxon was used as the dependant variable. If any factor and/or interaction was statistically significant, post hoc Fisher LSD tests were subsequently performed. In addition, a power analysis was done to examine the validity and reliability of the results. Due to the high number of replicates, the factors Cycle and Depth had high power. For the interaction of Cycle and Depth, there were however only two replicates, being two stations present, A and B. The number of replicates was therefore not enough for the power of analysis to be strong (less than 0.8). This means that wherever there was no significant effect of Cycle or Depth on the results, there was indeed no effect of those factors on the abundance of larvae. For the interaction of Cycle and Depth however, non-significant results may simply reflect a lack of statistical power.

Statistical Analysis for Macroecology (SAM v4.0) software was used to analyse the relationship between larval abundance and the physical characteristics of the water column. The physical variables used as predictors of depth-integrated larval abundances were upwelling index, averaged over 4 days; turbulence, averaged over 12 hours; zonal flow (west or east current direction); meridional flow (north or south current direction) and temperature. Due to the shape of the bay, north and west were onshore directions whilst south and east were offshore. Each of these predictors was introduced in a multiple linear regression for each taxon. To avoid multicolinearity, when predictors were significantly correlated to each other, the whole model was excluded. Contour profiles of the physical variables and larval abundances at each station were created using Surfer 8 software.

3.3 Results

3.3.1 Physical data

Contour profiles of flow were done to explore the structure of currents at both stations, in March and October 2013 (Figures 3.2 and 3.3). Currents did not show any vertical stratification in March. In March, from 8:30 until about 17:33 at station A, the flow was predominantly eastwards (offshore) with a velocity ranging from 0.5 – 17.2 cm/s. The same was true at station B, predominantly eastwards (offshore) flow ranging from 0.4 – 14.9 cm/s between from 09:43 and 16:29. The eastward (offshore) current persisted throughout the night but at slower speeds for both stations. The velocity range was 0.1 – 4.9 cm/s and 0.4 – 3.9 cm/s for stations A and B, respectively. During the day, the meridional (north-south) flow was mostly northward (onshore) at both stations. The velocity range was 0.1 – 6.2 cm/s and 0.3 – 5.9 cm/s for stations A and B, respectively. At night the stations were mostly dominated by a southward (offshore) flow with a velocity range of 0.3 – 5.0 cm/s and 0.2 – 7.3 cm/s at stations A and B respectively.

In October, there was clear vertical stratification at both stations in both zonal and meridional flow during the day. From the surface to about 6 metre depth, flow was offshore and below that to the bottom, the currents flowed onshore, exhibiting a typical upwelling pattern (Kirincich *et al.*, 2005; Marta-Almeida *et al.*, 2006). The surface offshore flow had a maximum velocity of 8.3 cm/s and 9.3 cm/s at stations A and B respectively, whilst the onshore flow had maximum velocities of 5.1 cm/s and 3.5 cm/s respectively. At night, the currents became homogenous and flowed onshore at both stations. The velocity ranges were 0.2 – 3.7 cm/s and 0.5 – 5.1 cm/s for stations A and B respectively in the west-east direction (zonal flow) and 0.6 – 8.8 cm/s and 0.7 – 9.8 cm/s respectively in the north-south direction (meridional flow).

Temperature data indicated no vertical stratification and the absence of any thermocline (data not shown). Mean water temperatures (±SD) were 20.4°C (± 0.2) in March and 19.4°C (± 0.9) in October.

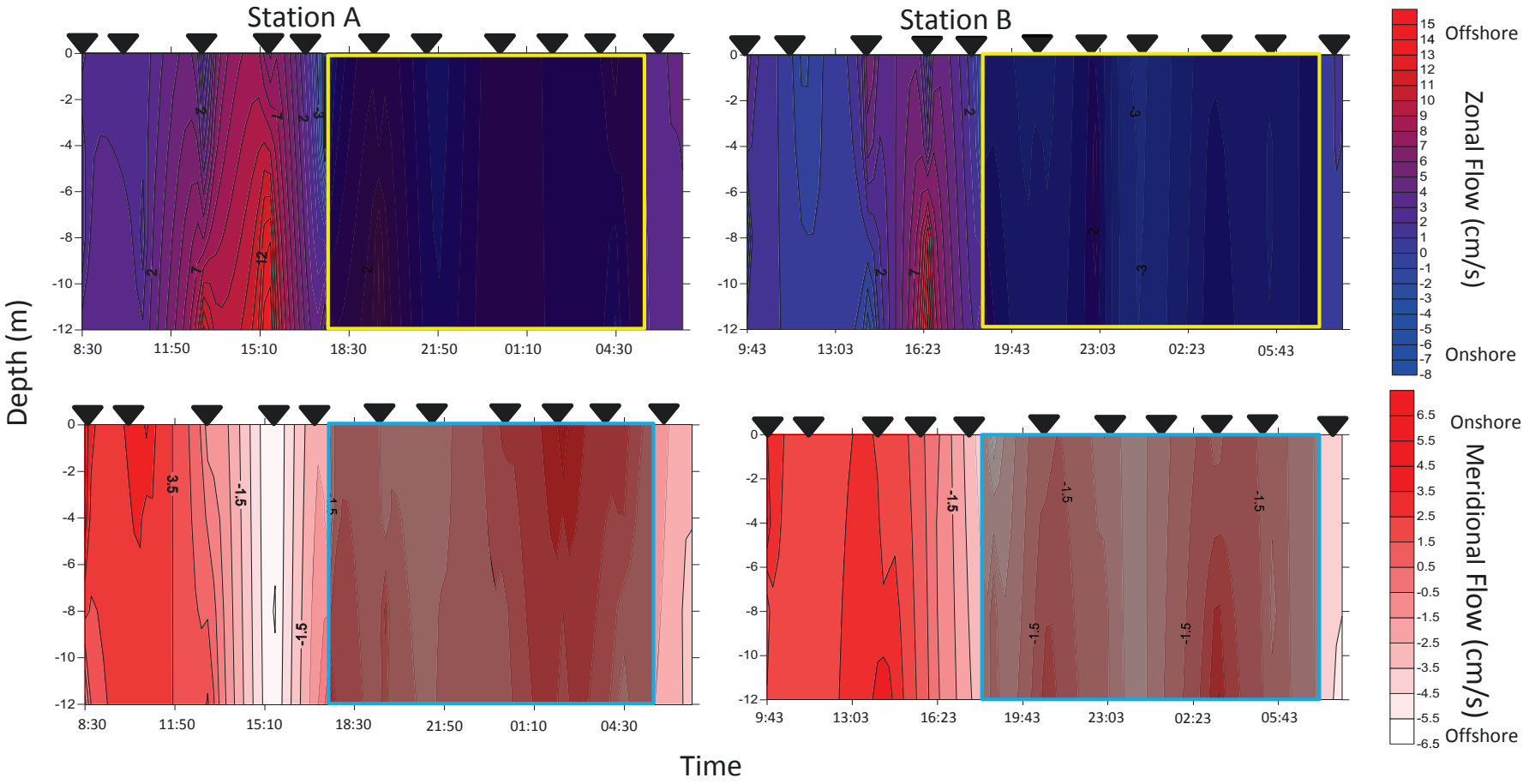


Figure 3.2: Contour profiles of current direction and velocity at different depths at stations A and B on 02-03 March 2013 during a 24 hour sampling period. The sections outlined in yellow (zonal flow) and blue (meridional flow) represent night time (i.e. sunset till sunrise) and the inverted triangles show the exact sampling times. Flow magnitude and direction are given on the scale bar on the right of each profile.

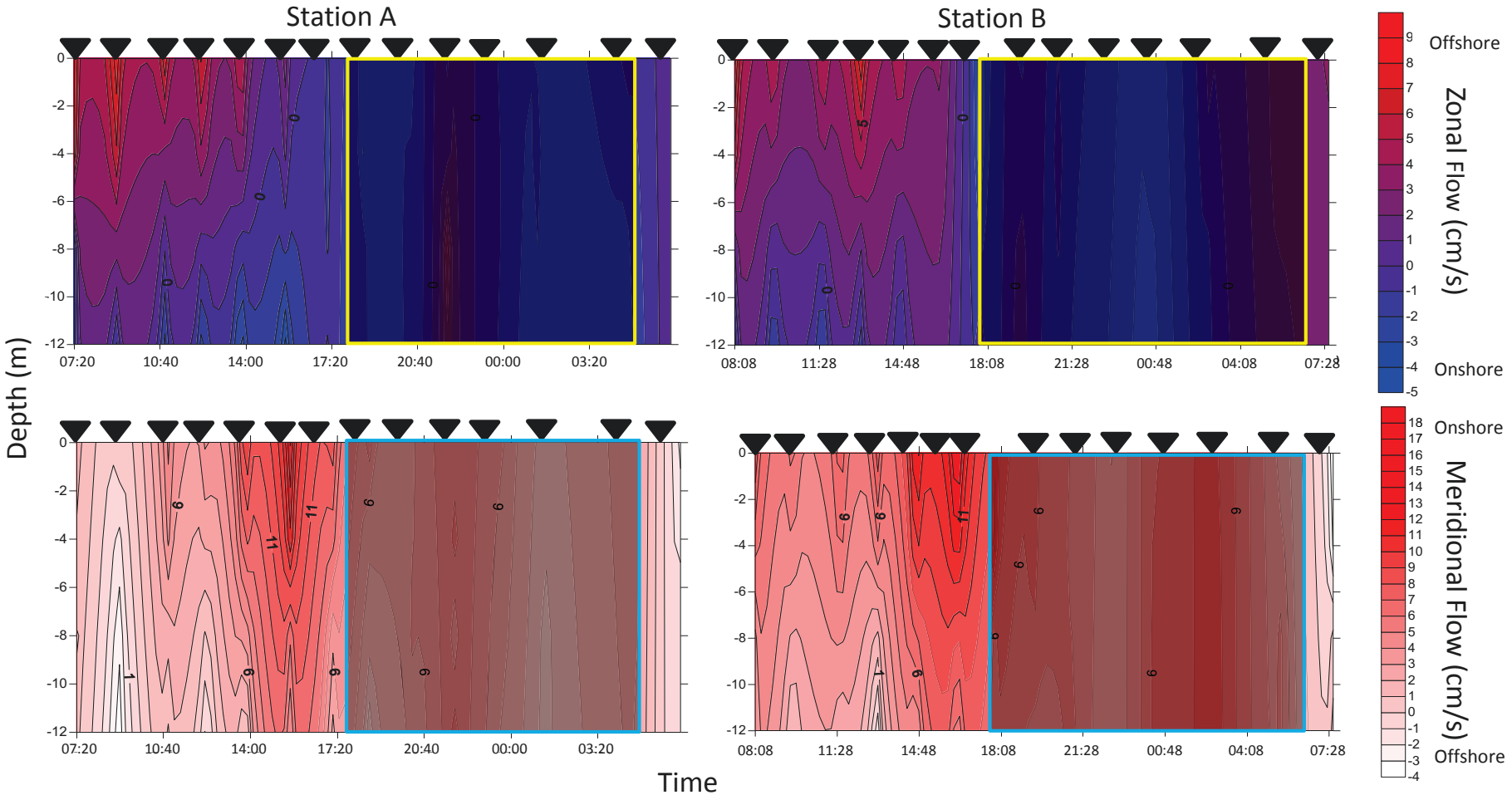


Figure 3.3: Contour profiles showing current direction and velocity at different depths at stations A and B on 09-10 October 2013 during a 24 hour sampling period. The sections outlined in yellow (zonal flow) and blue (meridional flow) represent night time (i.e. sunset till sunrise) and the inverted triangles show the exact sampling times. Flow magnitude and direction are given on the scale bar on the right of each profile.

3.3.2 Biological data

A number of different taxa were found, mostly at low abundances and at just one of the stations (Table 3.1). Analysis was done for those taxa that, for each cruise, reached a minimum abundance threshold of 10 individuals/m^3 in at least 1 sample and that were found in more than 50% of the samples (Weidberg *et al.*, 2013). The mussel *Perna perna* did not reach the minimum threshold in October, but was still analysed due to the general ecological importance of this species on this coast. No environmental predictor had a significant effect on bivalves or barnacles in March, but turbulence and temperature did have an effect on decapods. In October, only zonal flow had an effect on Bivalve sp. B and no other taxa or species was affected by the environmental predictors.

Table 3.1: Taxa and larval stages found during two different sampling seasons (March and October 2013). X indicates the presence of the taxon and/or larval stage in that sampling season.

Species/Taxa/Group	March 2013	October 2013
BRYOZOANS		
Bryozoan larvae		X
BIVALVES		
Perna perna	X	X
Mytilus galloprovincialis	X	X
Choromytilus meridionalis	X	X
Oysters	X	X
Hiatella spp.	X	X
D-larvae	X	X

Bivalve sp. A	X	X
Bivalve sp. B	X	X
Other mussels	X	X
BARNACLES		
Balanid nauplii (early stages)	X	X
Balanid nauplii (late stages)	X	X
Chthamalus dentatus nauplii (early stages)	X	X
Chthamalus dentatus nauplii (late stages)		X
Chthamalus dentatus cyprids	X	X
Cyprid sp. A	X	X
Cyprid sp. B	X	X
DECAPODS		
Sesarmid zoeae	X	
Brachyuran zoeae	X	X
Brachyuran megalopae	X	
Pinnotherid zoeae	X	X
Porcelanid zoeae	X	X
Anomuran zoeae	X	X

The results of the ANOVA shown in the next subsections differed among taxa and between sampling occasions. Level of significance in the ANOVA tables is represented by stars with $p \leq 0.05$ = *; $p \leq 0.01$ = **; $p \leq 0.001$ = ***; $p \leq 0.0001$= ****; and non-significant (n.s).

BIVALVES

D-larvae

D-larvae were a group of very minute (~ 95µm in length), early stage bivalves. At that size, they cannot be taxonomically identified (Siddall, 1980). They have a shape which looks like the capital letter, D, rounded on one side and flat on the other side (Siddall, 1980). Due to low abundances in March, D-larvae were not analysed for that season. Two-way ANOVA revealed that the abundance of D-larvae was significantly affected by Cycle and Depth during October. For most of the day, they were homogenously distributed throughout the water column, but at 10:49-12:07 and 13:47-15:10 they were mostly far below the surface, at 12m depth (Figures 3.4 and 3.5). During the night, larvae were again found throughout the water column and did not clearly prefer a particular depth, but at 01:18-04:25 they were found mostly at the surface (Figure 3.4).

Table 3.2: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance of D-larvae [$\log_{10}(X+1)$] throughout the water column on 09-10 October 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	P
Cycle	1.804385	13	0.138799	4.12895	****
Depth	0.351190	3	0.117063	3.48237	*
Cycle*Depth	2.139529	39	0.054860	1.63195	*
Error	1.848880	55	0.033616		

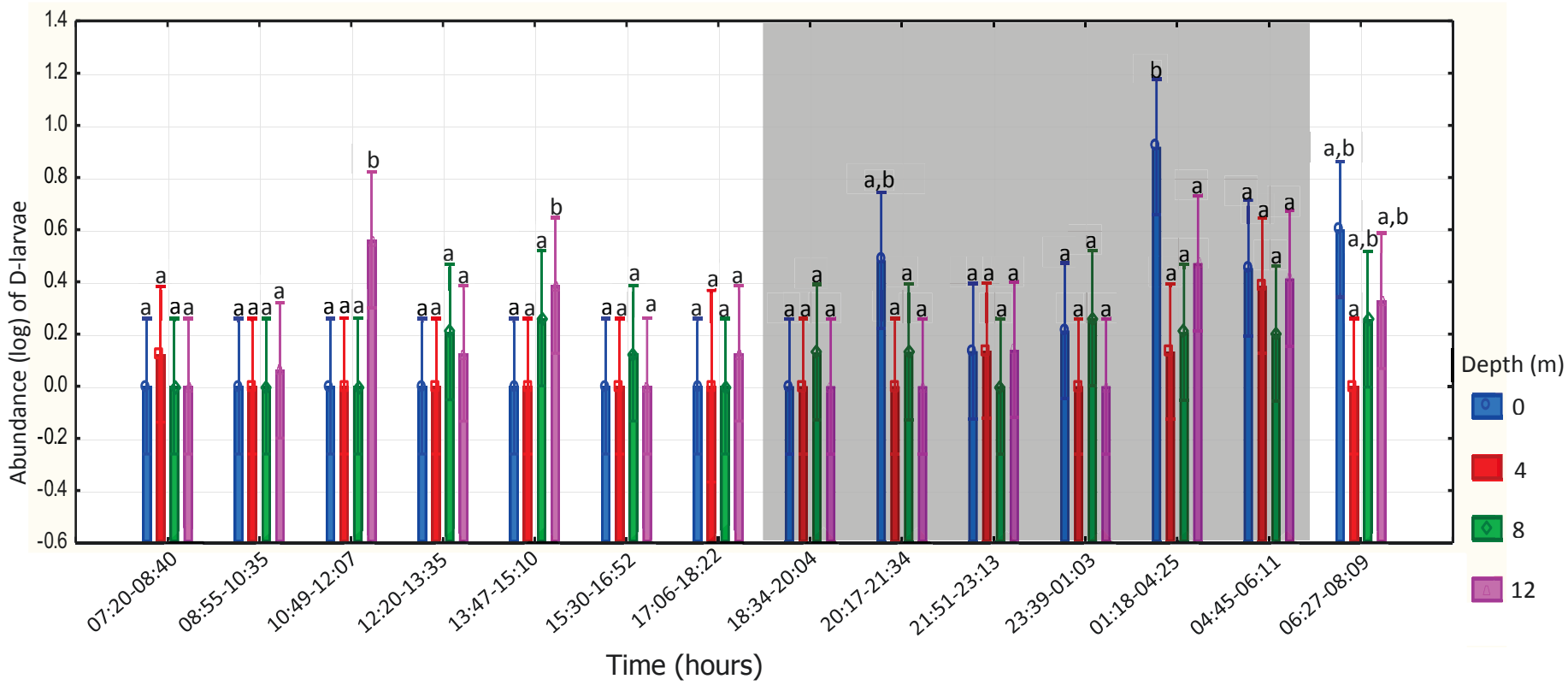


Figure 3.4: Abundance [$\log_{10}(X+1)$] of D-larvae over a 24-hour sampling period on 09-10 October 2013 in relation to time and depth. Error bars show standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of the interaction of Cycle and Depth.

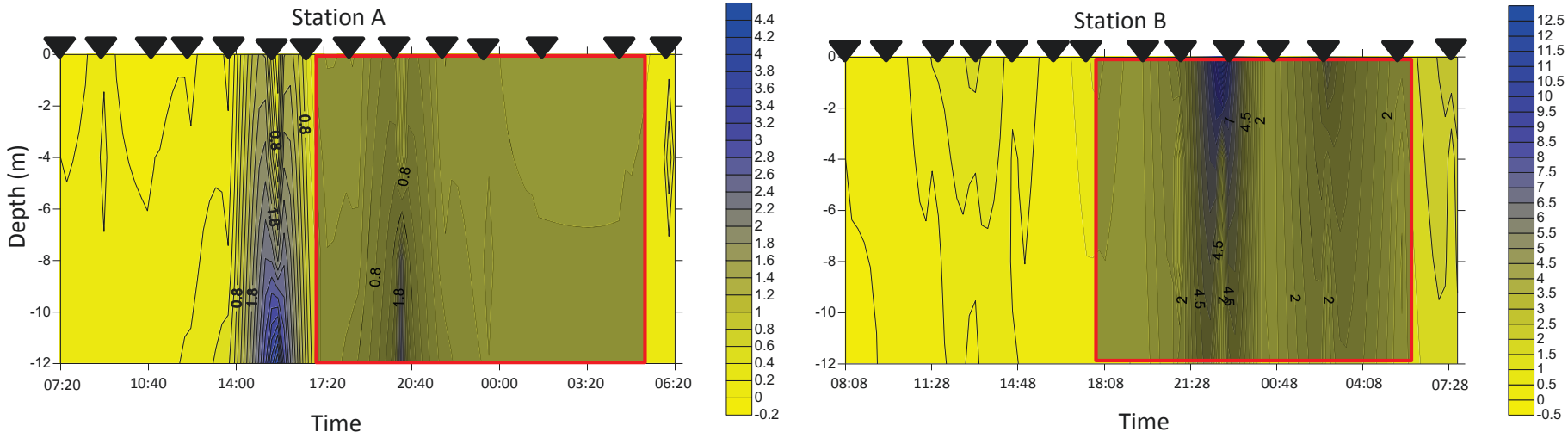


Figure 3.5: Abundance contours of D-larvae on station A and B on 09-10 October 2013. The sections outlined in red indicate night-time sampling. The triangles on top of each profile show the exact time the samples were taken. Abundance (individuals/m^3) is given on the scale bar on the right of each profile.

Perna perna

In March 2013, Cycle had an effect on the abundance of *Perna perna* (Table 3.3). The highest abundances of *P. perna* were found during the day (Figure 3.6). At night they were found in low abundances. Day and night depth preference was not clearly distinct.

Cycle and Depth, independently, had significant effects on the abundance of *P. perna* in October, while their interaction was non-significant. For depth, the abundance of this species was generally homogenous with a peak in abundance found at 06:27-08:09 on October 10, at the end of the 24 hour cycle (Figure 3.7). The depth-abundance graph (Figure 3.8) showed that larvae were found at significantly higher abundances at the surface and at 8 metres than at 4 metres.

Table 3.3: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$\log_{10}(X+1)$] of *Perna perna* throughout the water column on 02-03 March 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	P
Cycle	1.121415	10	0.112142	3.01211	**
Depth	0.197059	3	0.065686	1.76433	n.s
Cycle*Depth	0.882899	30	0.029430	0.79049	n.s
Error	1.638129	44	0.037230		

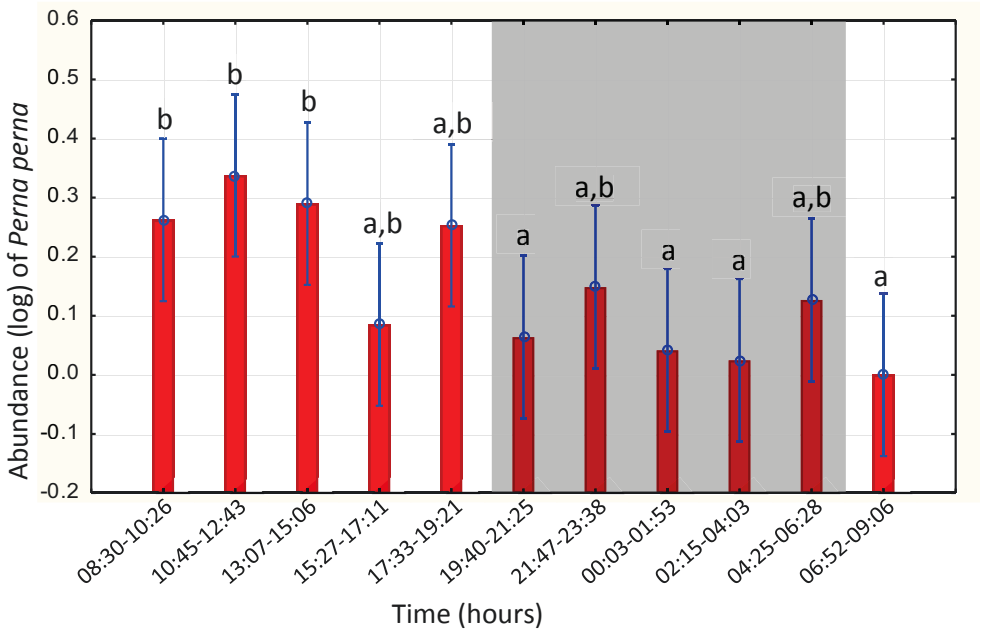


Figure 3.6: The abundance [$\log_{10}(X+1)$] of *Perna perna* over a 24 hour sampling period on 02-03 March 2013. Error bars indicate standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of Cycle.

Table 3.4: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$\log_{10}(X+1)$] of *Perna perna* throughout the water column on 09-10 October 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	P
Cycle	0.864940	13	0.066534	2.67329	**
Depth	0.329580	3	0.109860	4.41410	**
Cycle*Depth	1.176989	39	0.030179	1.21258	n.s
Error	1.368862	55	0.024888		

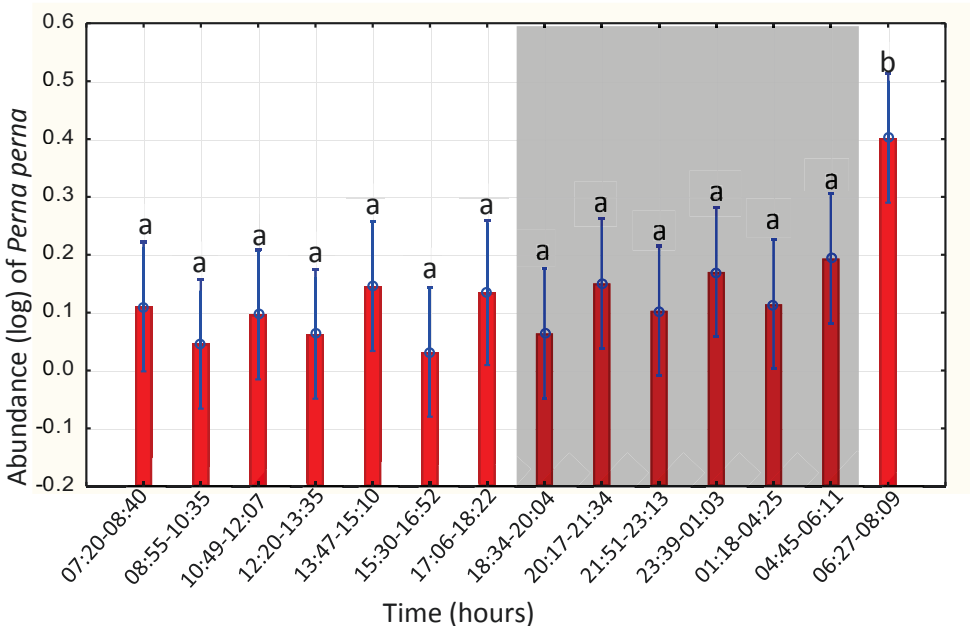


Figure 3.7: Abundance [$\log_{10}(X+1)$] of *Perna perna* over a 24 hour sampling period on 09-10 October 2013. Error bars show standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of Cycle.

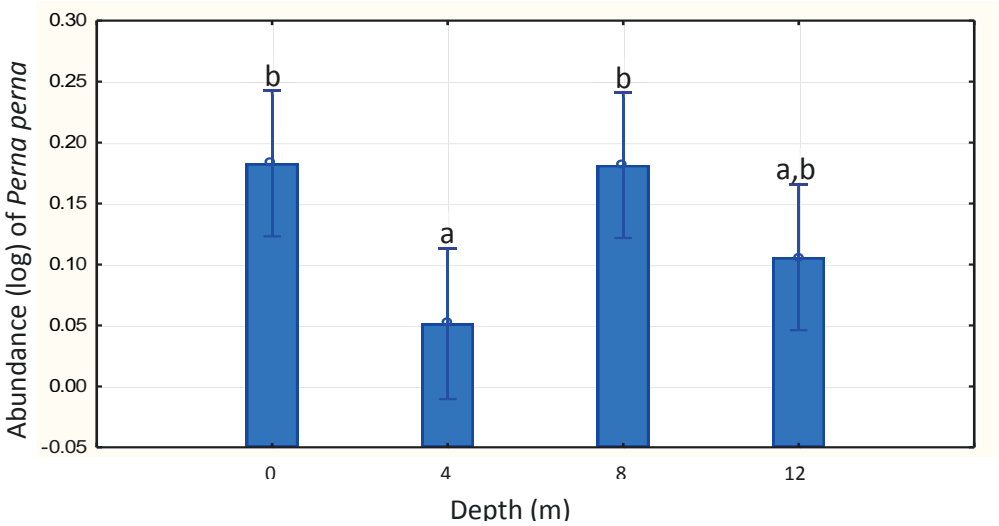


Figure 3.8: Abundance [$\log_{10}(X+1)$] of *Perna perna* at different depths on 09-10 October 2013. Error bars show standard errors. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of Depth.

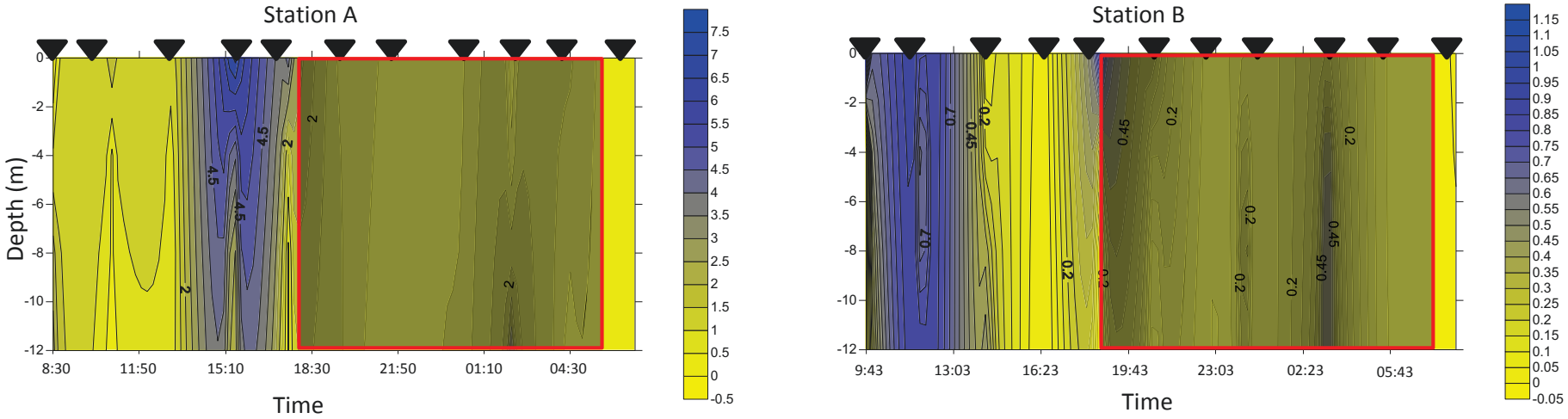


Figure 3.9: Abundance contours of *Perna perna* on stations A and B on 02-03 March 2013. The sections outlined in red indicate night-time sampling. The triangles on top of each profile show the exact time the samples were taken. Abundance (individuals/m^3) is given on the scale bar on the right of each profile.

Intertidal bivalves

P. perna, Mytilus galloprovincialis, Choromytilus meridionalis, and oysters are intertidal bivalves found along the coast of South Africa. Since these species were found at low abundances in October (not reaching the minimum threshold of 10 ind/m^3 except *P. perna*), they were grouped together (including *P. perna*) as intertidal bivalves and then analysed. The interaction of Cycle and Depth had a significant effect on the abundances of these bivalves. The plots (Figure 3.10 and 3.11), however, indicate no clear pattern in the change of depth over time for this group. Abundance was homogenous throughout the day and night except in the last sampling hours at night where this group was found in high abundance at 12 metres depth.

Table 3.5: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$\log_{10}(X+1)$] of intertidal bivalves throughout the water column on 09-10 October 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	P
Cycle	2.226548	13	0.171273	4.2901	****
Depth	0.253794	3	0.084598	2.1191	n.s
Cycle*Depth	2.594214	39	0.066518	1.6662	*
Error	2.235657	56	0.039922		

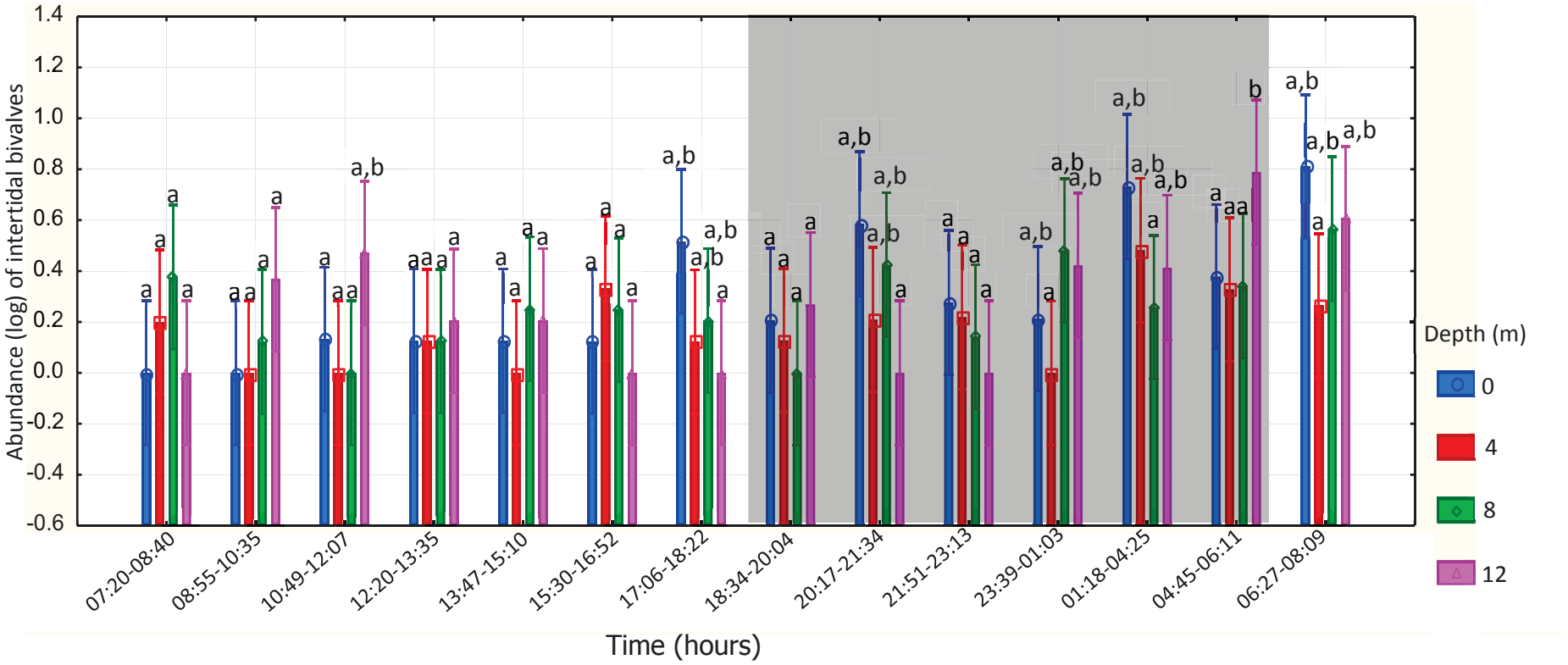


Figure 3.10: Abundance [$\log_{10}(X+1)$] of intertidal bivalves over a 24-hour sampling period on 09-10 October 2013 in relation to time and depth. Error bars show standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of the interaction of Cycle and Depth.

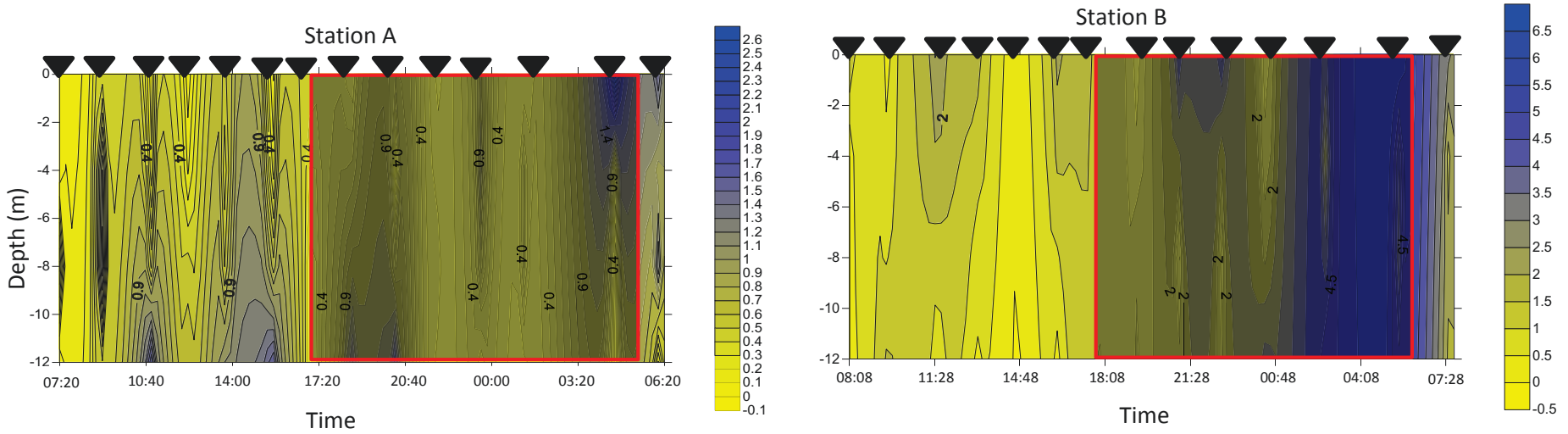


Figure 3.11: Abundance contours of intertidal bivalves on station A and B on 09-10 October 2013. The sections outlined in red indicate night-time sampling. The triangles on top of each profile show the exact time the samples were taken. Abundance (individuals/m^3) is given on the scale bar on the right of each profile.

Hiatella spp.

Hiatella spp. belong to Bivalvia. These reached the analysis threshold only in October 2013. A 2-way ANOVA showed that the interaction of Cycle and Depth was significant (Table 3.6). *Hiatella* spp. veligers avoided the surface at 07:20-08:40 and 10:49-12:07 and mostly occurred at 8 and 12 metres (Figure 3.12). At night, these veligers were found throughout the water column (Figure 3.12 and 3.13).

Table 3.6: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$\log_{10}(X+1)$] of *Hiatella* spp. throughout the water column on 09-10 October 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	P
Cycle	4.87245	13	0.37480	3.8096	***
Depth	0.28652	3	0.09551	0.9708	n.s
Cycle*Depth	6.81966	39	0.17486	1.7774	*
Error	5.41107	55	0.09838		

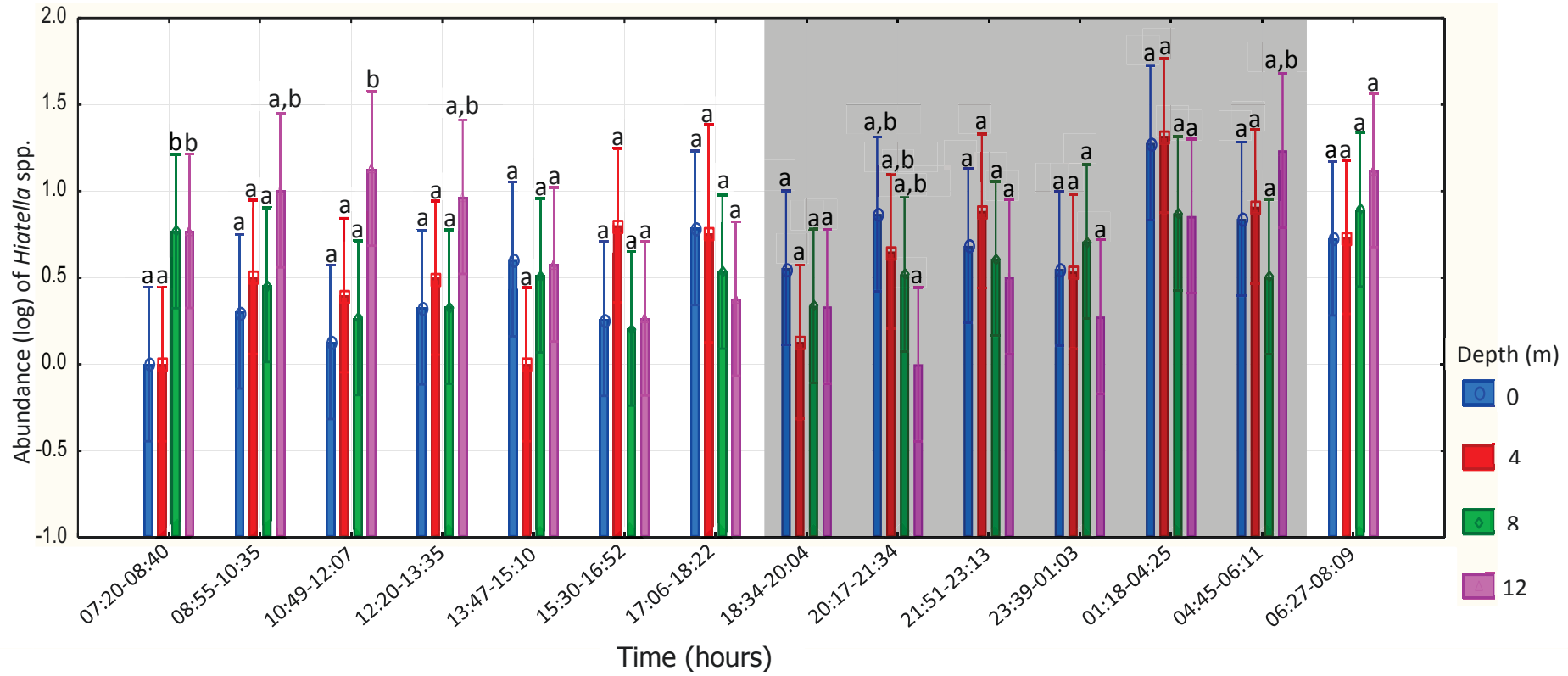


Figure 3.12: Abundance [$\log_{10}(X+1)$] of *Hiatella* spp. veligers in relation to time and depth over a 24-hour sampling period on 09-10 October 2013. Error bars show standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of the interaction of Cycle and Depth.

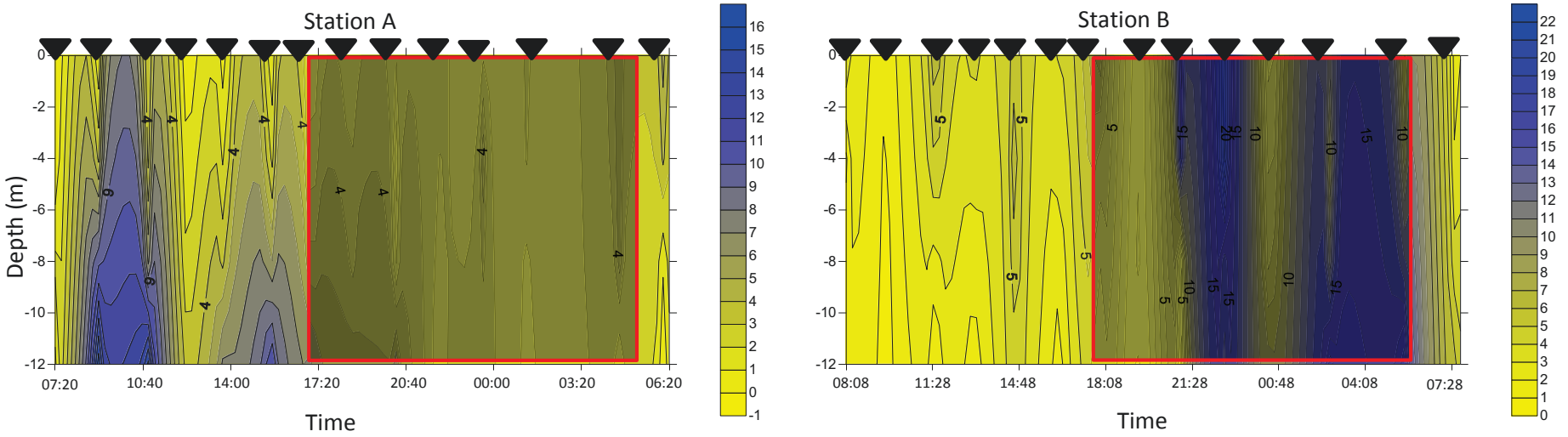


Figure 3.13: Abundance contours of *Hiatella* spp. on station A and B on 09-10 October 2013. The sections outlined in red indicate night-time sampling. The triangles on top of each profile show the exact time the samples were taken. Abundance (individuals/m^3) is given on the scale bar on the right of each profile.

Bivalve sp. A veligers

A distinctive, but unidentified species of bivalve (Bivalve sp. A, picture 2.1, chapter 2) was often collected at high abundances. This species of bivalve was morphologically different from the other species, being more rounded and transparent. Two-way ANOVA revealed a significant effect of the interaction between Cycle and Depth on the abundance of this species. Between 13:47 and 15:10, more larvae were found at 8 and 12 metres than at 0 and 4 metres (Figures 3.14 and 3.15). From 20:17-21:34, the highest abundance was observed at 0-8 metres of depth (Figure 3.14). These results suggest an ascent of the larvae at night.

Table 3.7: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$log_{10}(X+1)$] of Bivalve sp. A throughout the water column on 09-10 October 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Cycle	5.83301	13	0.44869	4.4629	****
Depth	0.45833	3	0.15278	1.5196	n.s
Cycle*Depth	7.79565	39	0.19989	1.9882	**
Error	5.52955	55	0.10054		

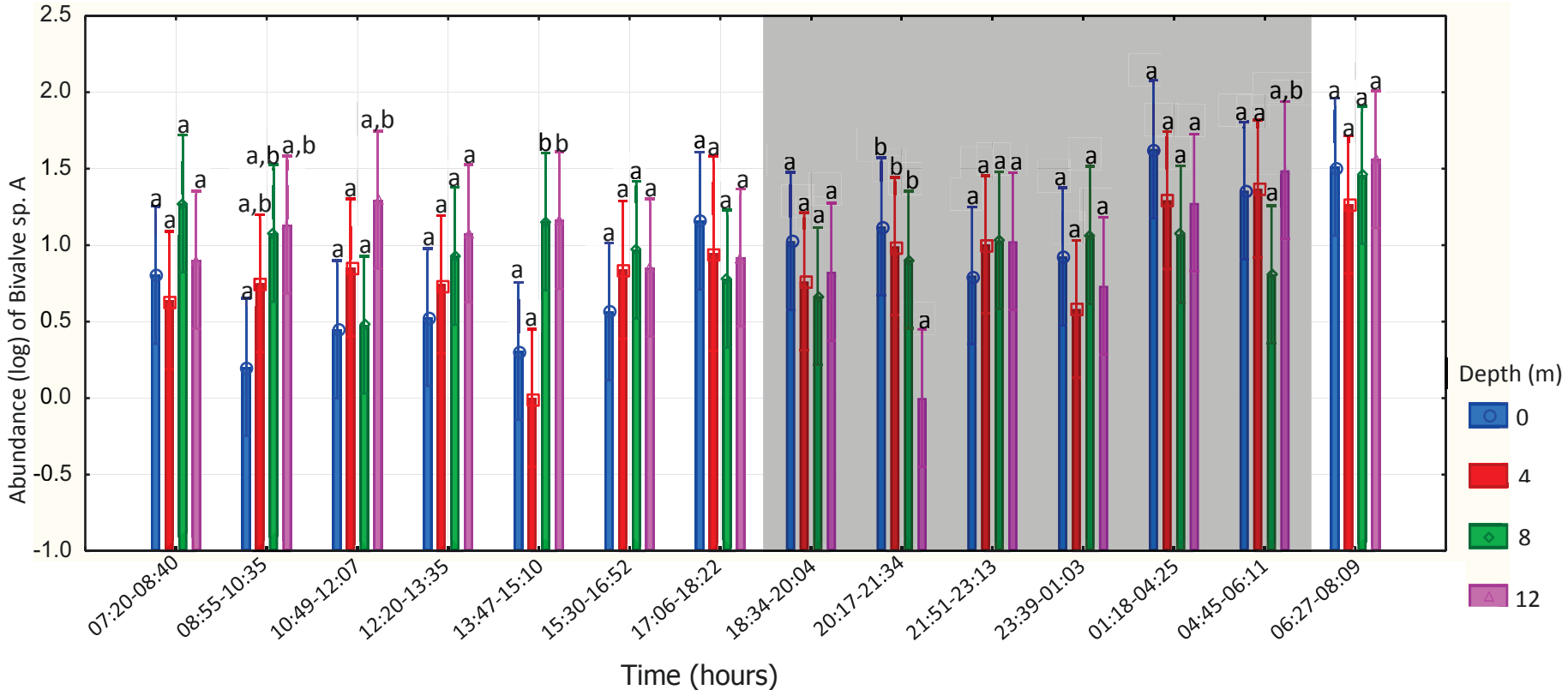


Figure 3.14: Abundance [$\log_{10}(X+1)$] of Bivalve sp. A in relation to cycle and time over a 24-hour sampling period on 09-10 October 2013. Error bars indicate standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of the interaction of Cycle and Depth.

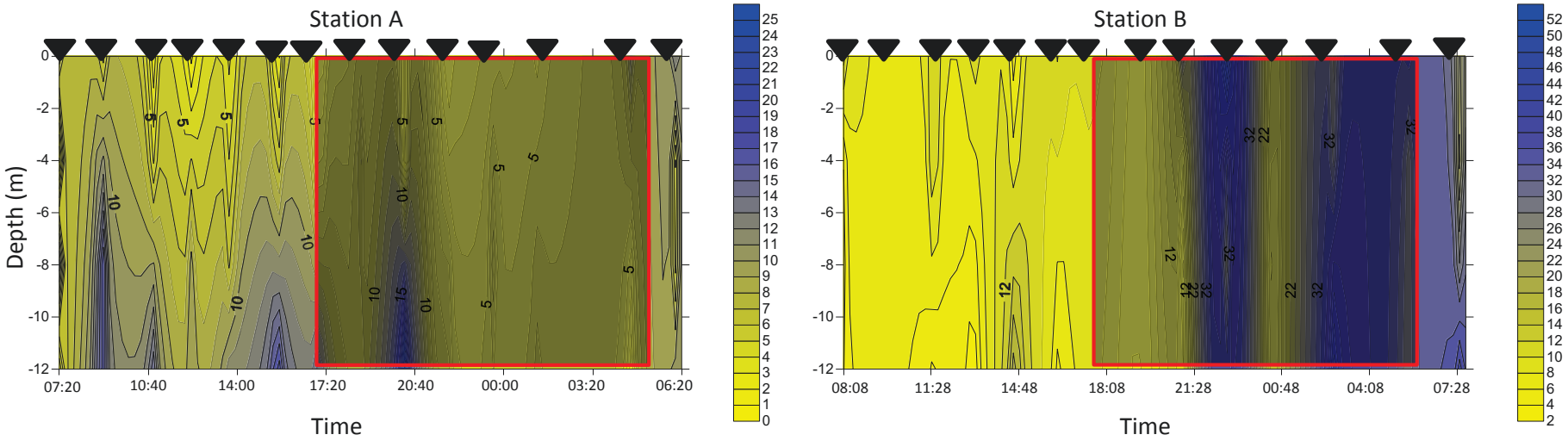


Figure 3.15: Abundance contours of Bivalve sp. A on station A and B on 09-10 October 2013. The sections outlined in red indicate night-time sampling. The triangles on top of each profile show the exact time the samples were taken. Abundance (individuals/m^3) is given on the scale bar on the right of each profile.

Bivalve sp. B veligers

Another species of unidentified bivalve (Bivalve sp. B, picture 2.2, chapter 2) with an outward region protruding from the umbo was regularly collected. This species of bivalve was found in both March and October. The 2-way ANOVA for the abundance in March revealed a significant effect of Depth (Table 3.8). There was, however, no clear pattern in the post-hoc results (Figure 3.16).

In October, the interaction of Cycle and Depth had a significant effect on the abundance of this species (Table 3.9). From 08:55 to 13:35, the abundance was statistically higher at 12 metres than the shallower depths (0, 4 and 8 metres). At night, there was no depth preference by the larvae (Figure 3.17 and 3.18, bottom). When the abundance of Bivalve sp. B was tested against the environmental conditions (upwelling, turbulence, zonal flow, meridional flow, and temperature), all were non-significant except zonal flow, which had a significant negative effect (Table 3.21).

Table 3.8: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$\log_{10}(X+1)$] of Bivalve sp. B throughout the water column on 02-03 March 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	Df	MS	F	p
Cycle	0.809933	10	0.080993	1.35521	n.s
Depth	0.614594	3	0.204865	3.42787	*
Cycle*Depth	2.269471	30	0.075649	1.26579	n.s
Error	2.629636	44	0.059764		

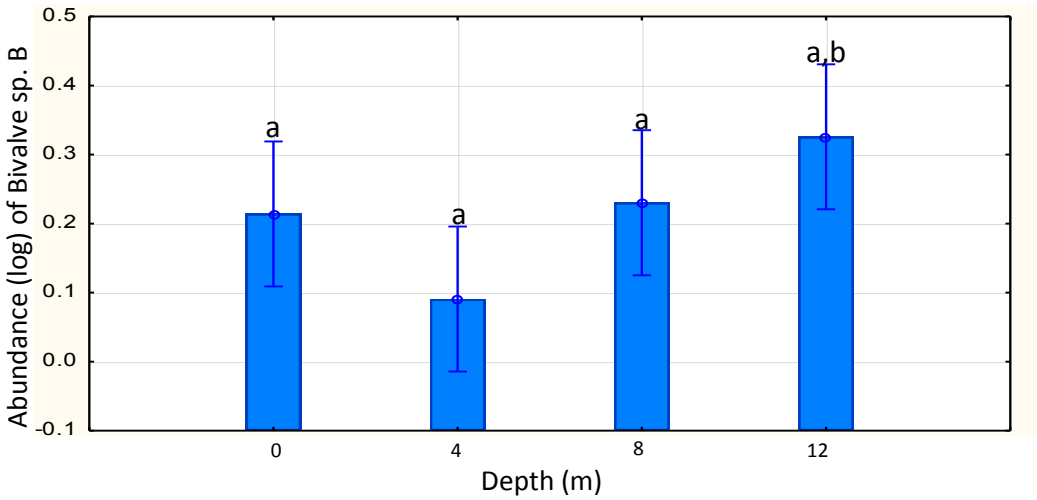


Figure 3.16: Abundance [$log_{10}(X+1)$] of Bivalve sp. B at different depths of the water column. Error bars indicate standard errors. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of depth.

Table 3.9: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$log_{10}(X+1)$] of Bivalve sp. B throughout the water column on 09-10 October 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Cycle	2.79358	13	0.21489	3.6990	***
Depth	2.13507	3	0.71169	12.2506	****
Cycle*Depth	4.16636	39	0.10683	1.8389	**
Error	3.19519	55	0.05809		

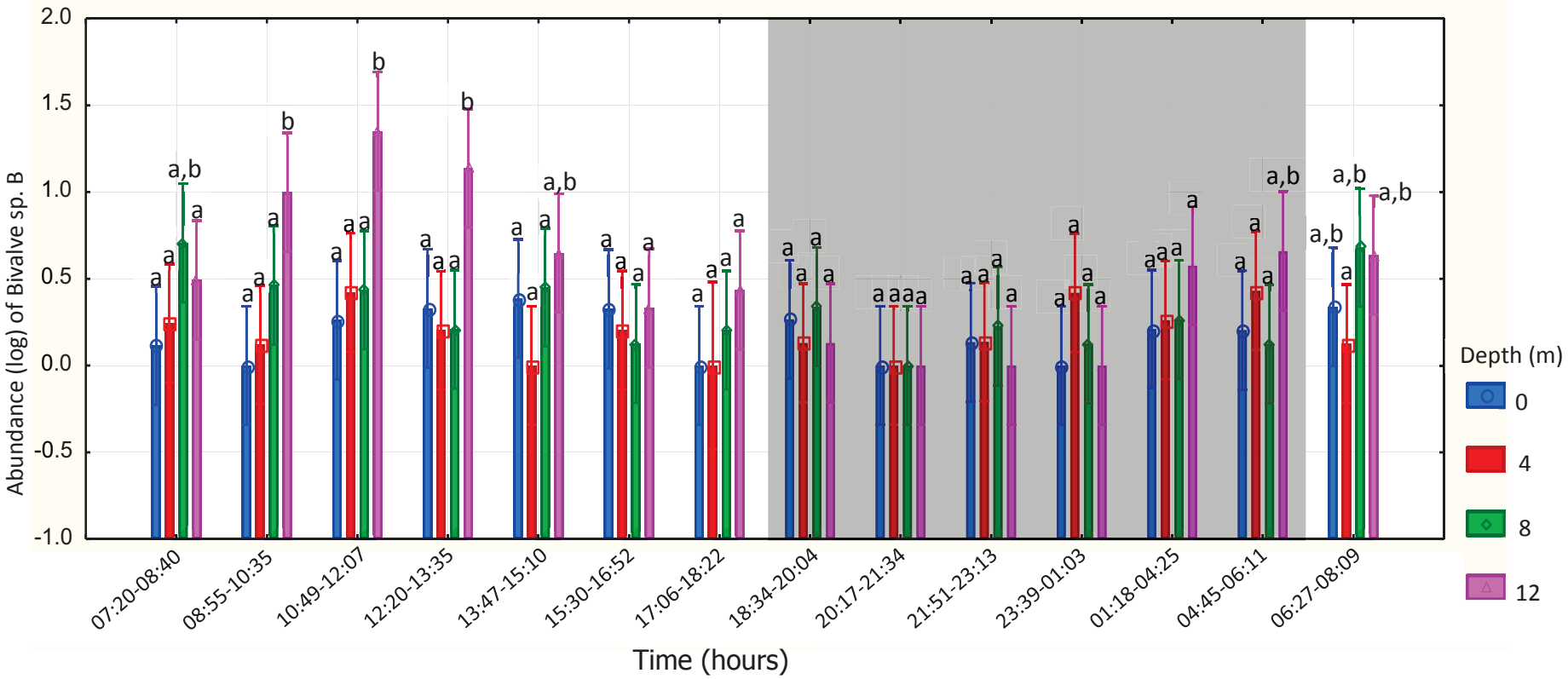


Figure 3.17: Abundance [$\log_{10}(X+1)$] of Bivalve sp. B in relation to cycle and depth over a 24-hour sampling period on 09-10 October 2013. Error bars indicate standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Cycle and Depth.

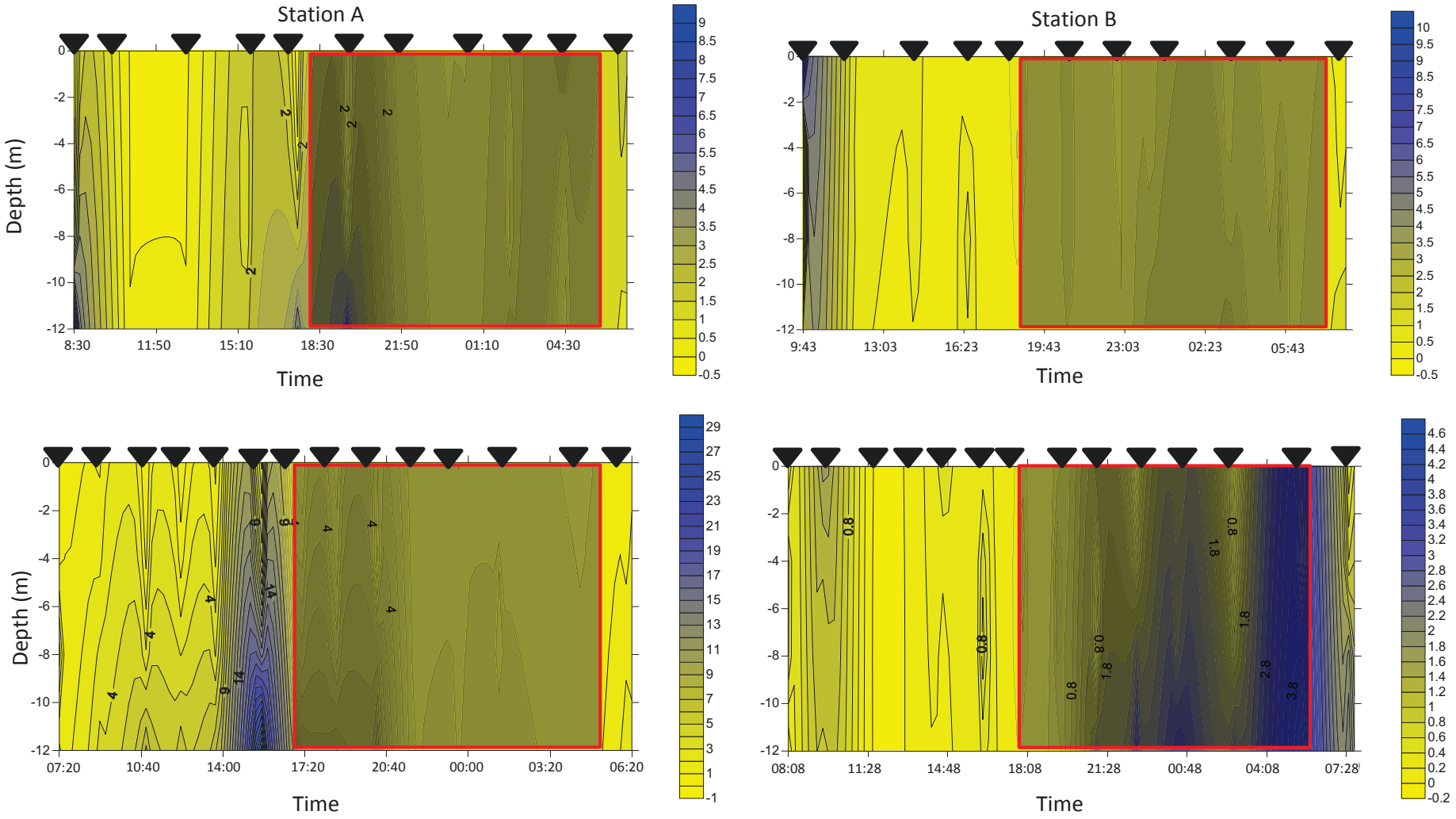


Figure 3.18: Abundance contours of Bivalve sp. B on station A and B (top March and bottom October 2013). The sections outlined in red indicate night-time sampling. The triangles on top of each profile show the exact time the samples were taken. Abundance (individuals/m^3) is given on the scale bar on the right of each profile.

Other mussels

All the other mussels that could not be identified (due to the mussels being broken) or not fit into any of the categories identified were grouped together. The 2-way ANOVA showed that Cycle and Depth each had a significant effect on this group in October. The post hoc grouping did not show any pattern for the abundance of this group in relation to depth (Figure 3.20), although Figure 3.21 shows the abundance tended to be greater at the deeper layer during the day and homogenously distributed through the water column at night.

Table 3.10: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$\log_{10}(X+1)$] of other mussels, unidentified group, throughout the water column on 09-10 October 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	Df	MS	F	P
Cycle	1.742654	13	0.134050	2.9845	**
Depth	0.402200	3	0.134067	2.9849	*
Cycle*Depth	2.703176	39	0.069312	1.5432	n.s
Error	2.470364	55	0.044916		

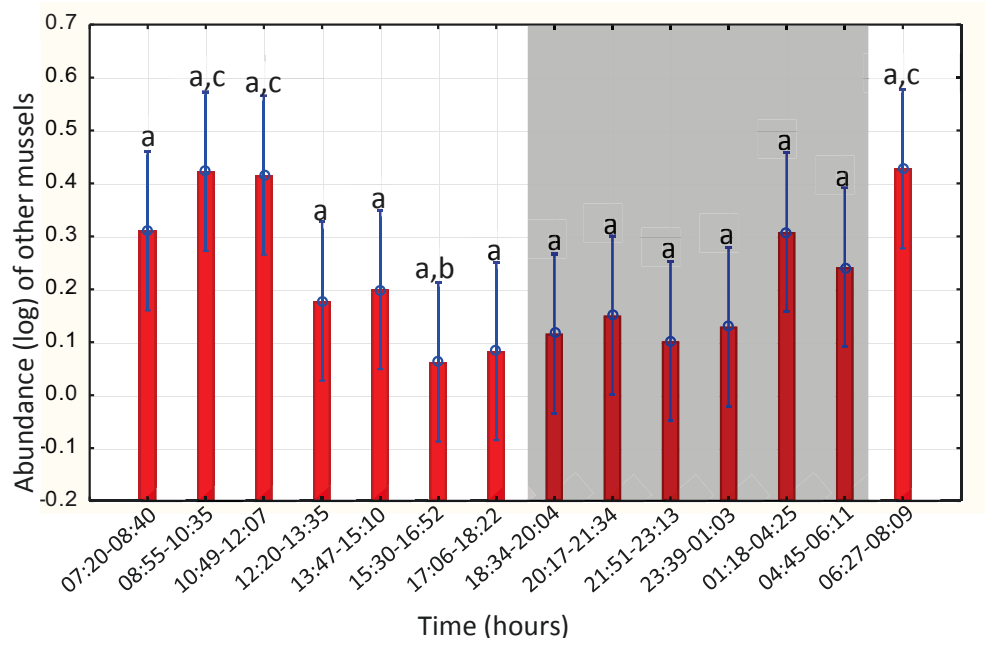


Figure 3.19: The abundance [$\log_{10}(X+1)$] of other mussels (unidentified group) over a 24 hour sampling period on 09-10 October 2013. Error bars indicate standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of Cycle.

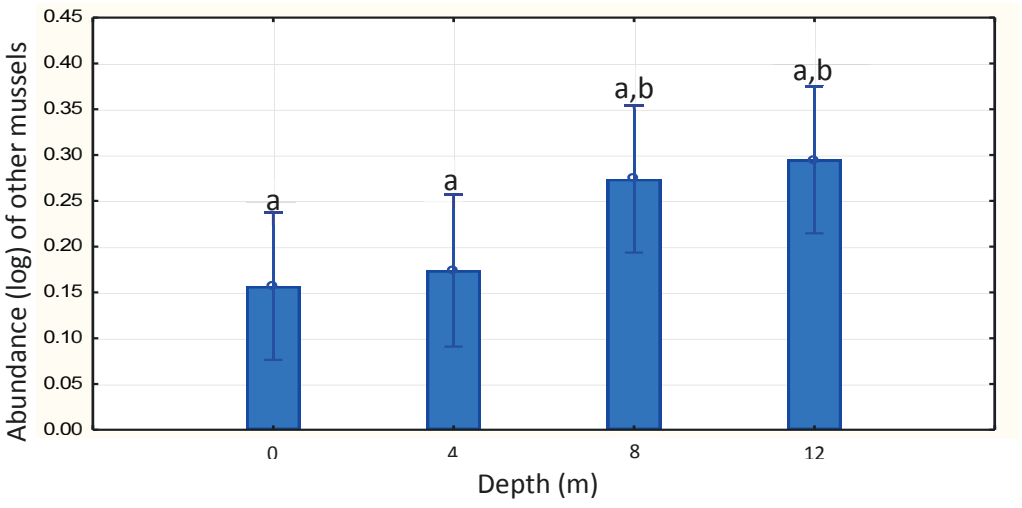


Figure 3.20: Abundance [$\log_{10}(X+1)$] of other mussels (unidentified group) at different depths of the water column on 09-10 October 2013. Error bars indicate standard errors. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of Depth.

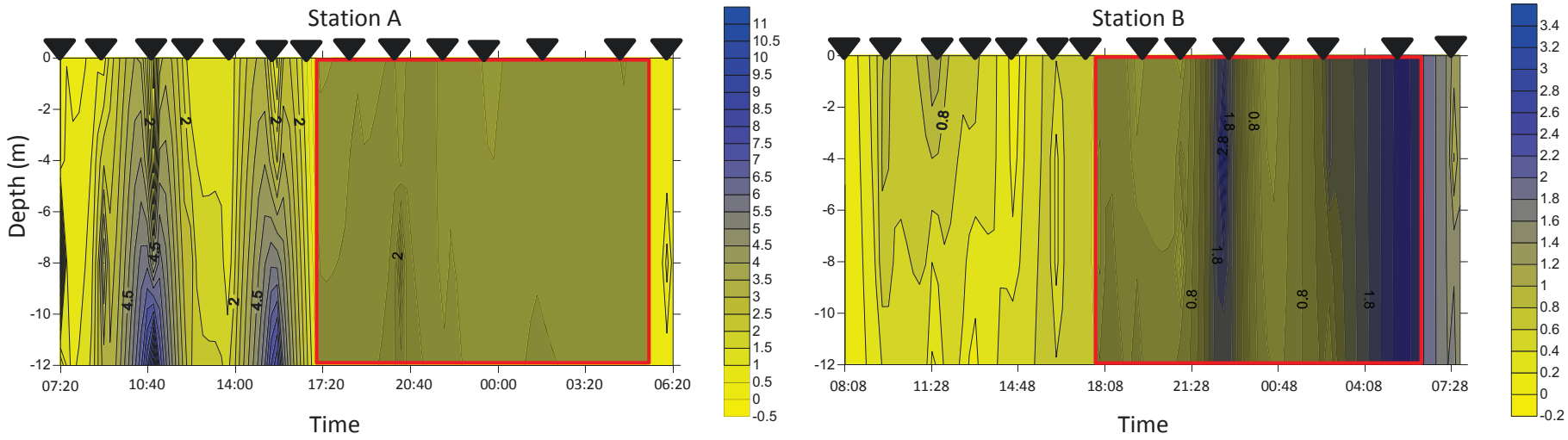


Figure 3.21: Abundance contours of other mussels on station A and B on 09-10 October 2013. The sections outlined in red indicate night-time sampling. The triangles on top of each profile show the exact time the samples were taken. Abundance (individuals/m^3) is given on the scale bar on the right of each profile.

BARNACLES

Cyprid sp. A

The last larval stage of a barnacle's life cycle is the cyprid stage (Sandison & Day, 1954). Two morphologically different types of cyprids were observed and were classified as Cyprid sp. A and Cyprid sp. B. Cyprid sp. A was more pointed anteriorly than Cyprid sp. B, which was more round anteriorly (picture 2.3 and 2.4 respectively, chapter 2). Cyprid sp. A appeared to be smaller than Cyprid sp. B though these differences were not quantified.

The 2-way ANOVA (Table 3.11) revealed that Cycle and Depth, independently had a significant effects on the abundance of Cyprid sp. A in October. From 10:49 to 13:35, the abundance was statistically higher than at the other times (Figure 3.22). Cyprid sp. A abundances were statistically higher at 12 metres than at the other depths, particularly during the day. Figure 3.24 shows the abundance was greater at deeper layers during the day and homogenously distributed at night.

Table 3.11: Analysis of Variance (ANOVA) on the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$\log_{10}(X+1)$] of Cyprid sp. A, unidentified group, throughout the water column on 09-10 October 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	P
Cycle	10.13231	13	0.77941	5.7007	****
Depth	7.00710	3	2.33570	17.0838	****
Cycle*Depth	5.56257	39	0.14263	1.0432	n.s
Error	7.65634	56	0.13672		

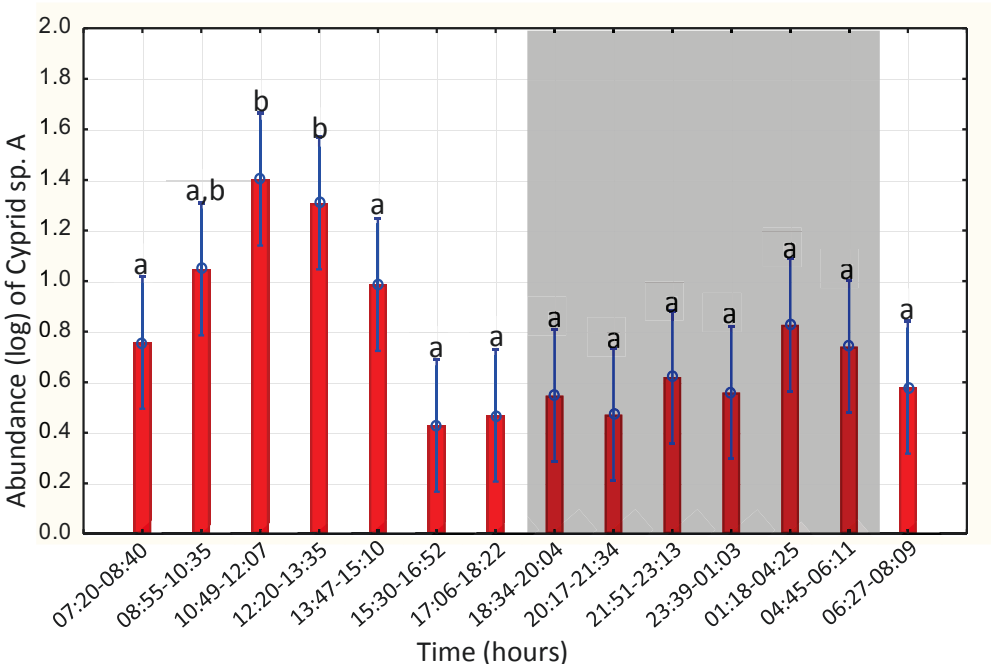


Figure 3.22: Abundance [$\log_{10}(X+1)$] of Cyprid sp. A over a 24 hour sampling period on 09-10 October 2013. Error bars indicate standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of Cycle.

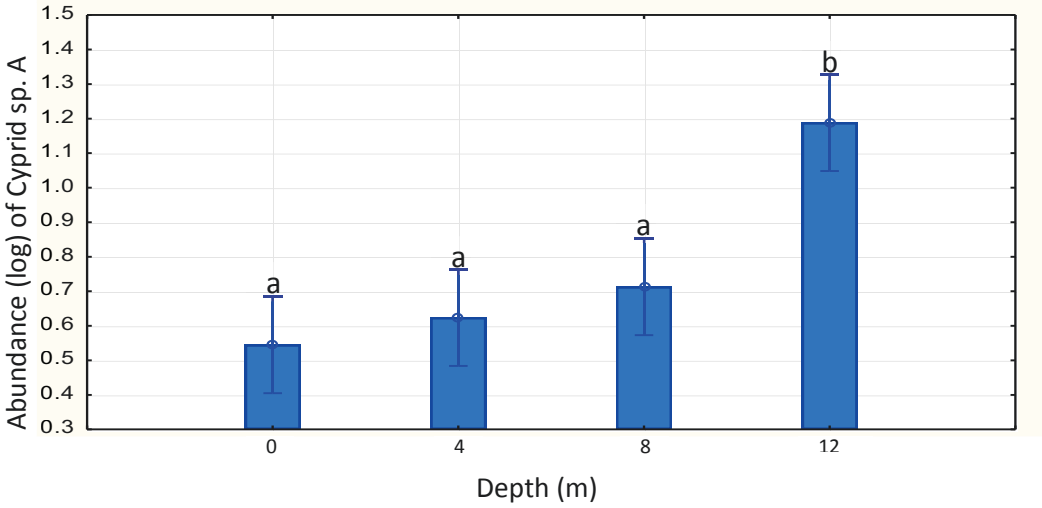


Figure 3.23: Abundance [$\log_{10}(X+1)$] of Cyprid sp. A at different depths of the water column on 09-10 October 2013. Error bars showing standard errors. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of Depth.

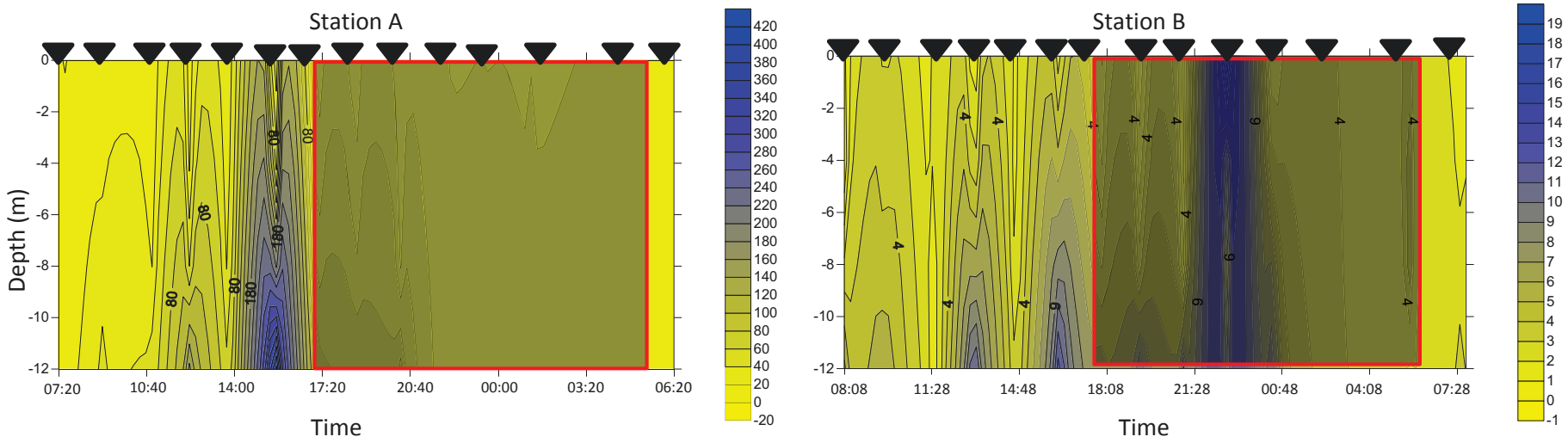


Figure 3.24: Abundance contours of Cyprid sp. A on station A and B on 09-10 October 2013. The sections outlined in red indicate night-time sampling. The triangles on top of each profile show the exact time the samples were taken. Abundance (individuals/m^3) is given on the scale bar on the right of each profile.

Cyprid sp. B

The 2-way ANOVA revealed that Cycle had a significant effect on the abundance of Cyprid sp. B in March (Table 3.12). The statistically higher abundances were visible from 17:33, up until 23:38 (Figure 3.25). The effect of depth was non-significant and Figure 3.26 shows no clear distribution pattern in the abundance of Cyprid sp. B.

Table 3.12: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$\log_{10}(X+1)$] of Cyprid sp. B, unidentified group, throughout the water column on 02-03 March 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Cycle	2.67310	10	0.26731	4.1074	***
Depth	0.42244	3	0.14081	2.1637	n.s
Cycle*Depth	1.31912	30	0.04397	0.6756	n.s
Error	2.86350	44	0.06508		

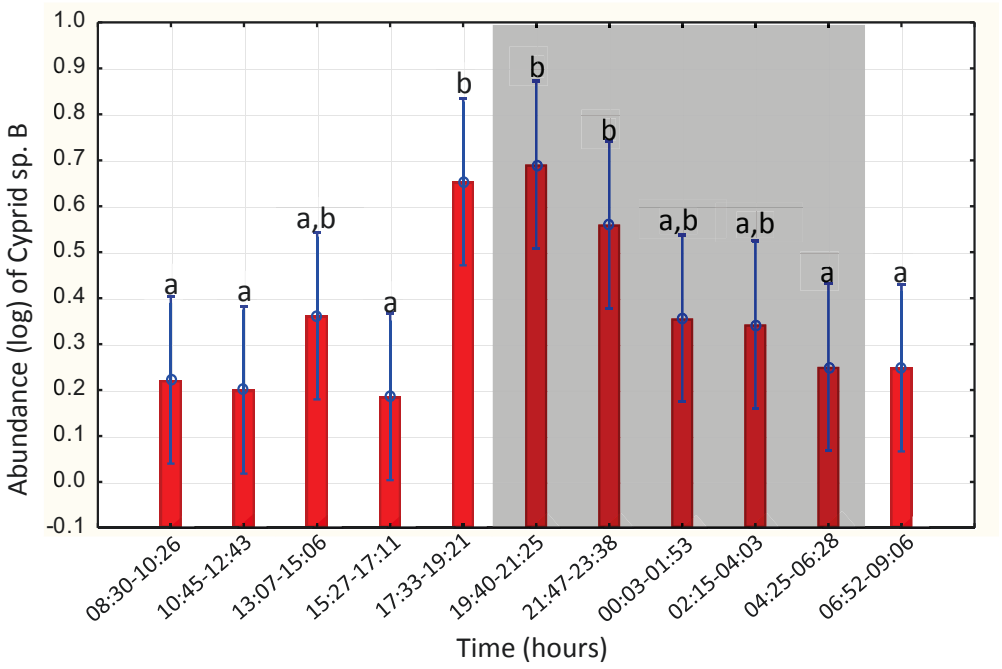


Figure 3.25: Abundance [$\log_{10}(X+1)$] of Cyprid sp. B over a 24 hour sampling period on 02-03 March 2013. Error bars show standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of Cycle.

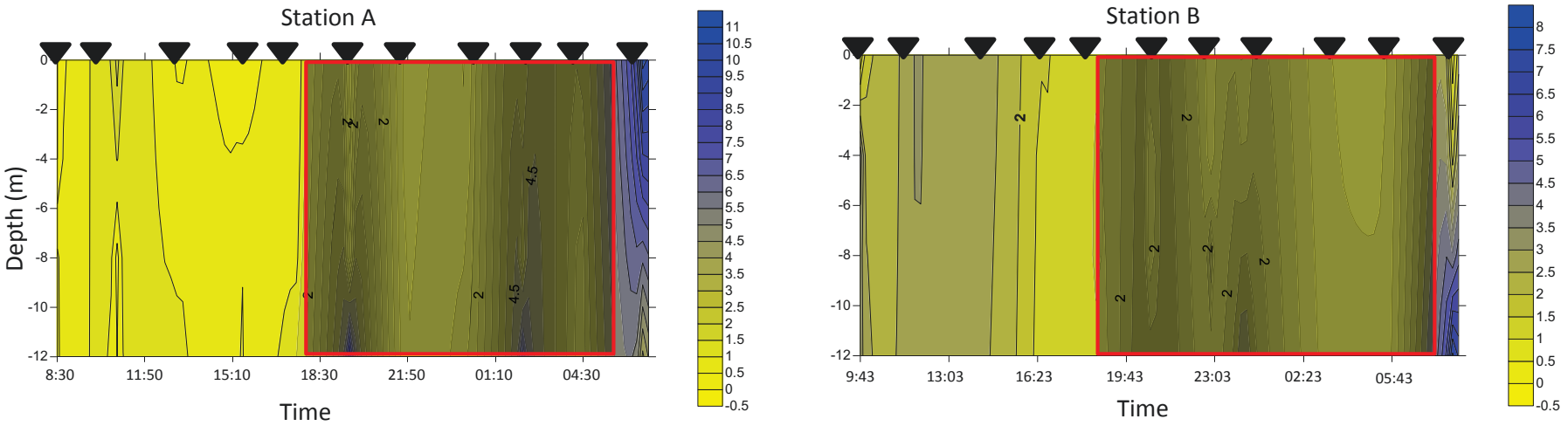


Figure 3.26: Abundance contours of Cyprid sp. B on station A and B 02-03 March 2013. The sections outlined in red indicate night-time sampling. The triangles on top of each profile show the exact time the samples were taken. Abundance (individuals/m^3) is given on the scale bar on the right of each profile.

DECAPODS

Brachyuran zoeae

Brachyuran zoeae were also found in the water column during March and October. Only Depth had a significant effect on brachyuran zoeae in March (Table 3.13). The abundance of brachyuran zoeae was greater at the surface than at the other depths (4, 8 and 12 metres, Figure 3.27). When this group was tested against the environmental variables, both temperature and turbulence had a positive effect (Table 3.20) on the abundance of zoeae.

In October, the results of the ANOVA showed that the interaction of Cycle and Depth had a significant effect on the abundance of brachyuran zoeae (Table 3.14), suggesting that larvae changed their position in the water column over time. Figure 3.28 shows that larvae descended in the early morning, remained at the bottom during the day, ascended at dusk, and inhabited the surface at night. At 07:20-08:40, the larvae were found in high abundances at 4 and 12 metres. At 10:49-12:07, higher abundances were found at 8 and 12 metres. From 12:20-15:10 significantly higher abundances were found at 12 metres. Later on, from 15:30-16:52, there was an ascent with high abundances at 12 and 8 metres. At 17:06-18:22 (dusk), the higher abundances were at 8 and 4 metres. Overnight, from 20:17 to 06:11, the higher abundances of larvae was always visible on the surface. Contour profiles of larval abundance show the abundance at the bottom during the day and on the surface during the night (Figures 3.29).

Table 3.13: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$log_{10}(X+1)$] of brachyuran zoeae throughout the water column on 02-03 March 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	P
Cycle	0.880094	10	0.088009	1.64042	n.s
Depth	1.742314	3	0.580771	10.82510	****
Cycle*Depth	1.503876	30	0.050129	0.93437	n.s
Error	2.360620	44	0.053650		

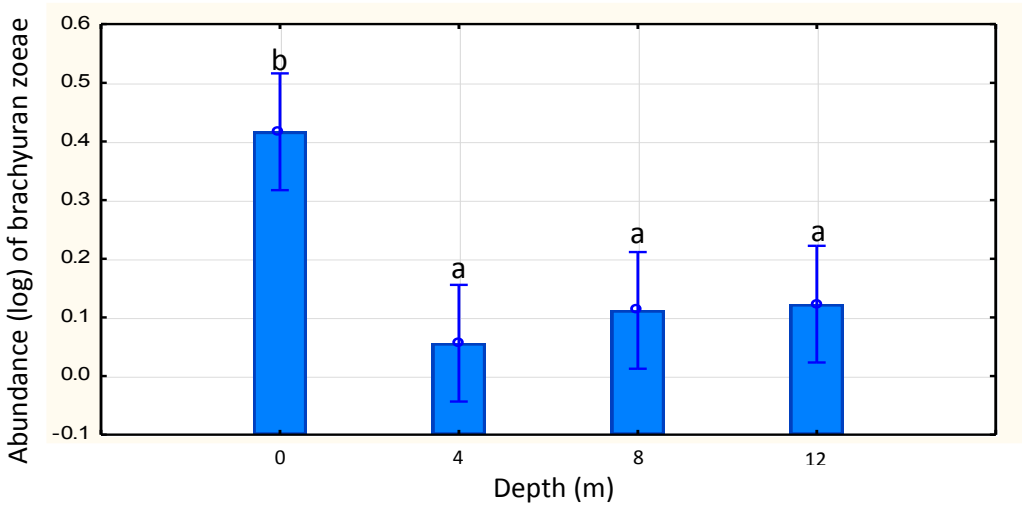


Figure 3.27: Abundance [$log_{10}(X+1)$] of brachyuran zoeae at different depths of the water column on 02-03 March 2013. Error bars showing standard errors. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effect of Depth.

Table 3.14: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$\log_{10}(X+1)$] of brachyuran zoeae throughout the water column on 09-10 October 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	P
Cycle	4.3882	13	0.3376	3.236	***
Depth	0.9999	3	0.3333	3.195	*
Cycle*Depth	19.2971	39	0.4948	4.744	****
Error	5.8410	56	0.1043		

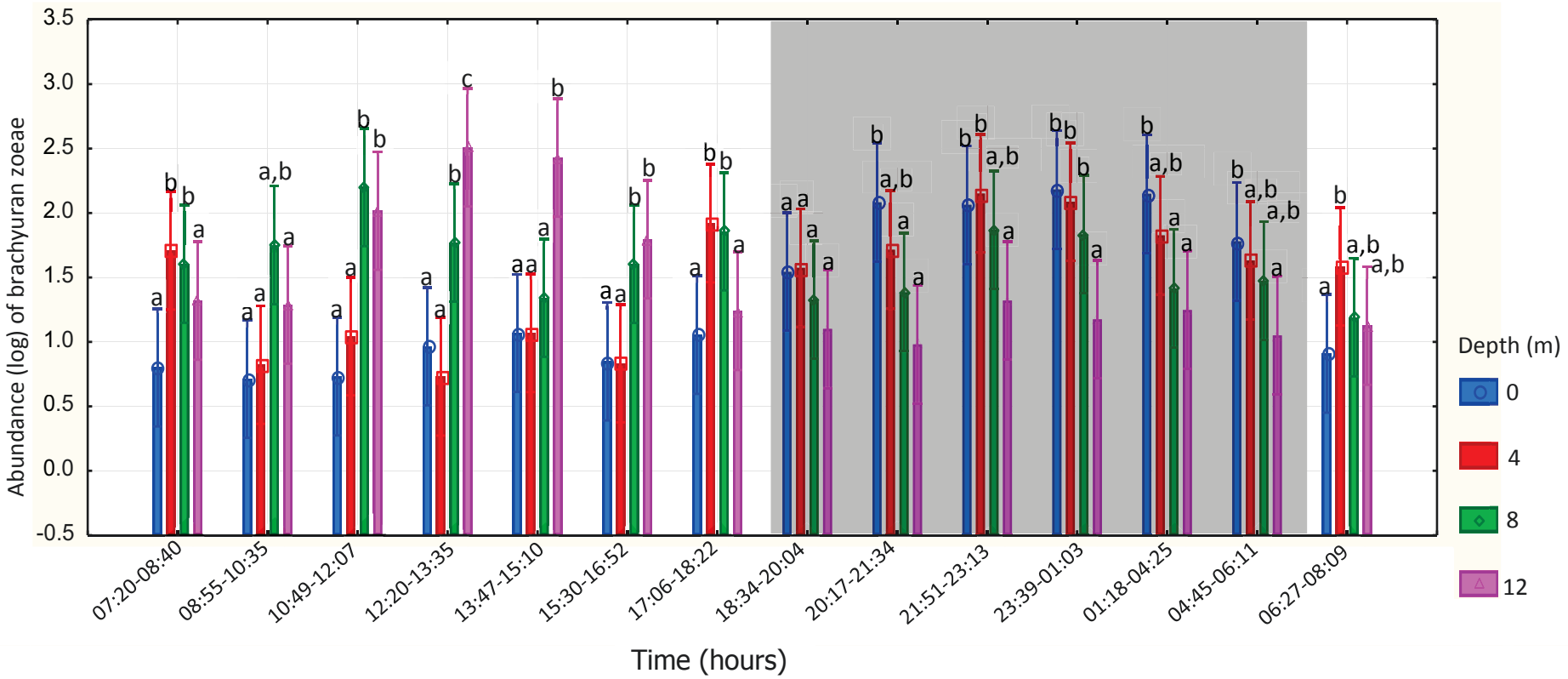


Figure 3.28: Abundance [$\log_{10}(X+1)$] of brachyuran zoeae over a 24-hour sampling period on 09-10 October 2013. Error bars indicate standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Cycle and Depth.

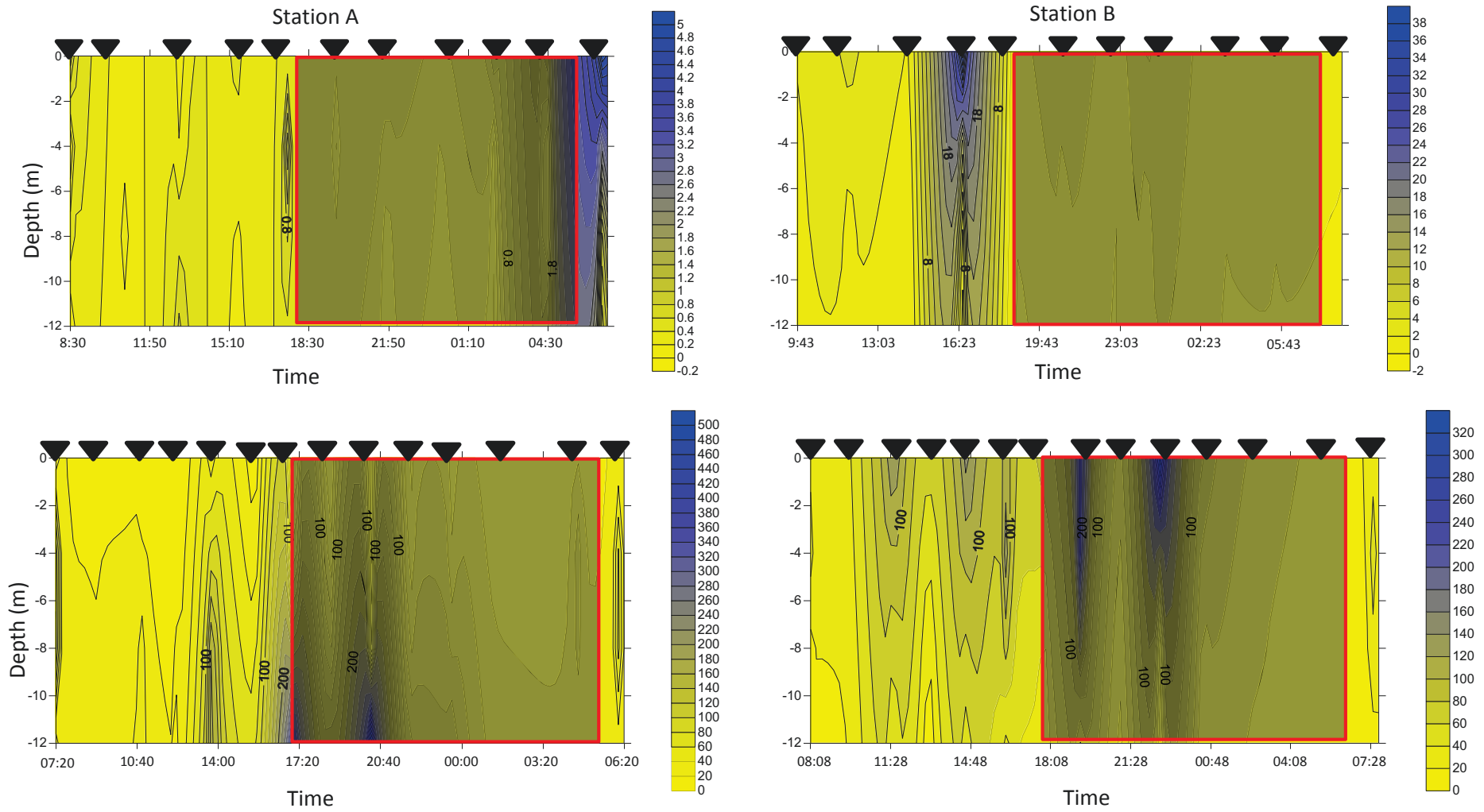


Figure 3.29: Abundance contours of brachyuran zoeae on station A and B (top, March and bottom, October 2013). The sections outlined in red indicate night-time sampling. The triangles on top of each profile show the exact time the samples were taken. Abundance (individuals/m^3) is given on the scale bar on the right of each profile.

Pinnotherid zoeae

Pinnotherid zoeae were found in both March and October 2013. Results of the 2-way ANOVA showed that Cycle and Depth independently had significant effects on the abundance of pinnotherid zoeae (Table 3.15) in March. The abundance was evenly distributed through the water column through the 24 hour sampling period in March, except for a peak at 10:45-12:43, when the abundance was statistically higher than at other times (Figure 3.30). Pinnotherid zoeae were also found at statistically higher abundances at the surface than at the deeper layers (Figure 3.31). Temperature and turbulence also had a positive effect on this group of organisms (Table 3.20), indicating that higher temperature was related to higher abundance (Figure 3.39D) and higher turbulence was related to higher abundance (Figure 3.39C).

The interaction of Cycle and Depth had a significant effect on pinnotherid zoeae abundance in October (Table 3.16). From 08:55 to 15:10 significantly higher abundances of larvae were never found on the surface. At 08:55-10:35 the abundances were significantly higher at 8 metres; at 10:49-12:07 they were higher at 4, 8 and 12 metres; at 12:20-13:35 they were higher at 8 and 12 metres; and at 13:47-15: at 12 metres. At dusk (17:06-18:22), the highest abundance of larvae was found at 4 metres. During some hours of the night, at 20:17-21:34 and at 01:18-04:25, the highest abundances of larvae were found at the surface (Figure 3.32). Contour profiles also show the depth positions of the high abundances of larvae through a water column (Figures 3.33).

Table 3.15: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$log_{10}(X+1)$] of pinnotherid zoeae throughout the water column on 02-03 March 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Cycle	1.39793	10	0.13979	2.1943	*
Depth	0.96884	3	0.32295	5.0693	**
Cycle*Depth	2.18526	30	0.07284	1.1434	n.s
Error	2.80308	44	0.06371		

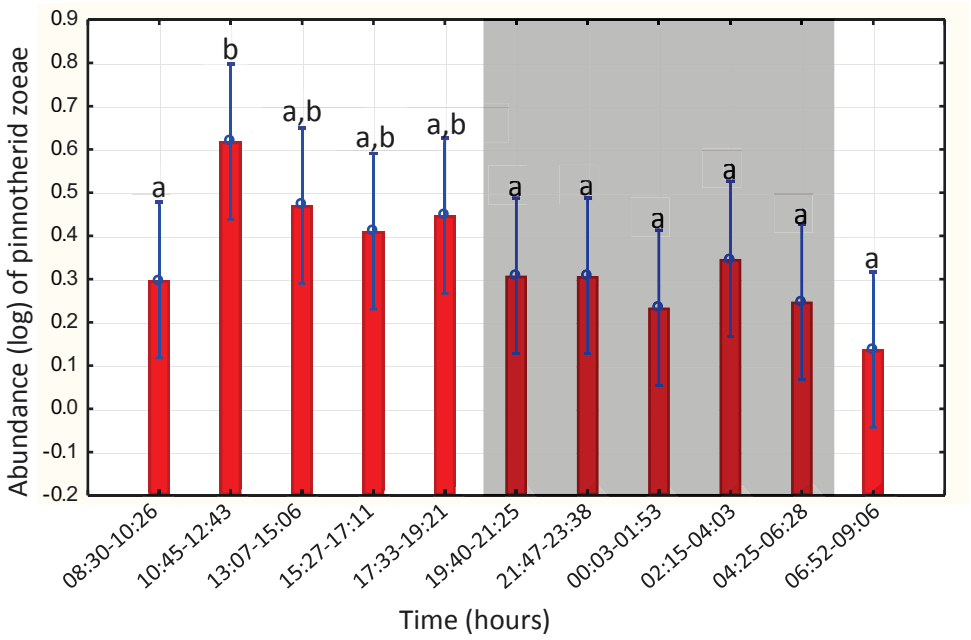


Figure 3.30: Abundance [$log_{10}(X+1)$] of pinnotherid zoeae over a 24 hour sampling period on 02-03 March 2013. Error bars show standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of Cycle.

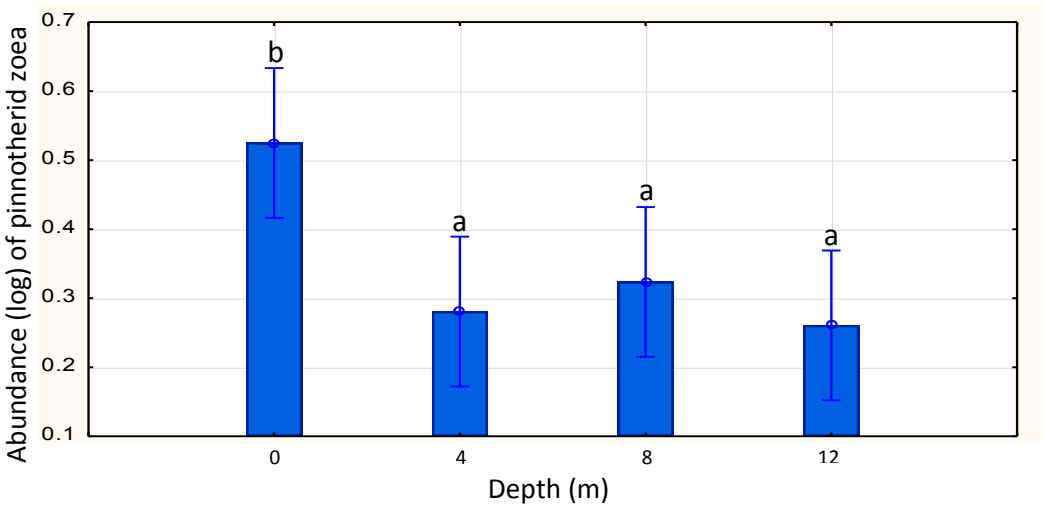


Figure 3.31: Abundance [$log_{10}(X+1)$] of pinnotherid zoeae at different depths of the water column on 02-03 March 2013. Error bars showing standard errors. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of Depth.

Table 3.16: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$log_{10}(X+1)$] of pinnotherid zoeae throughout the water column on 09-10 October 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Cycle	3.01204	13	0.23170	2.6553	**
Depth	0.67963	3	0.22654	2.5962	n.s
Cycle*Depth	12.54026	39	0.32155	3.6850	****
Error	4.88646	56	0.08726		

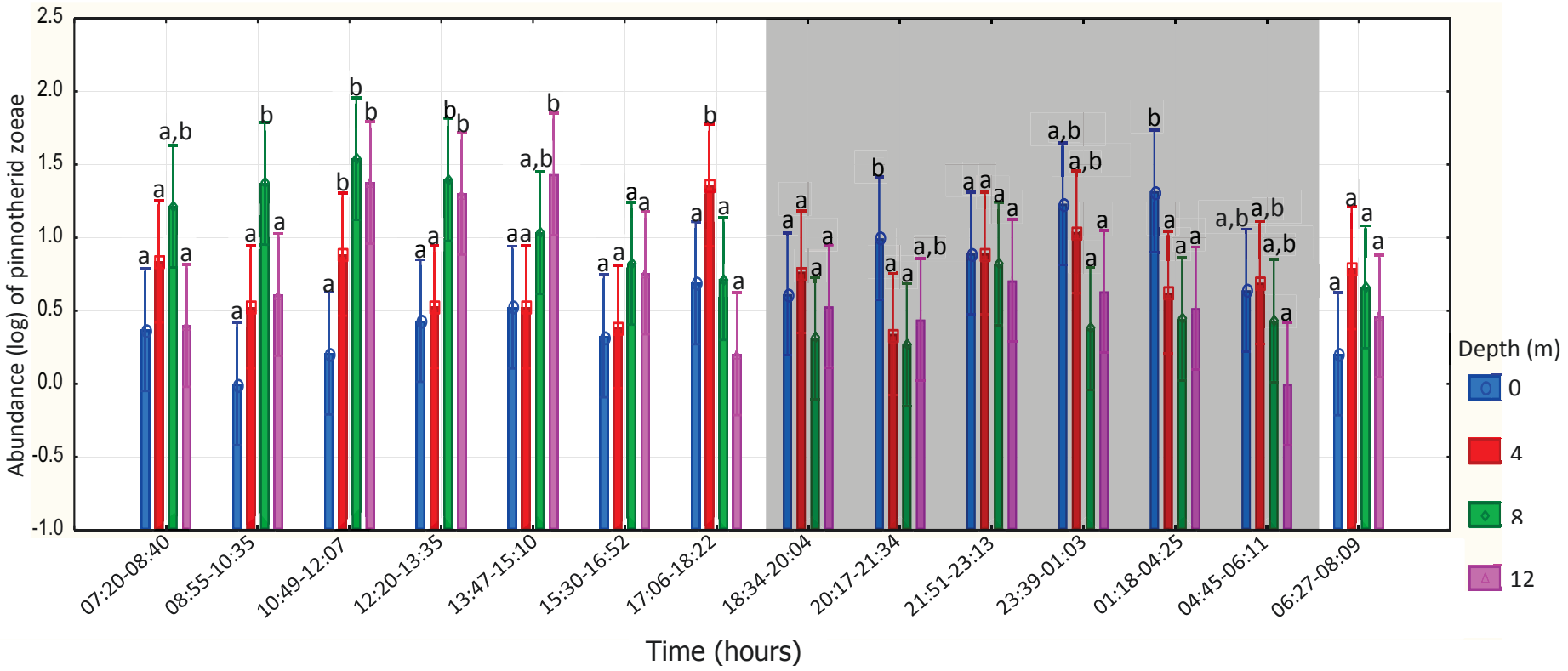


Figure 3.32: Abundance [$\log_{10}(X+1)$] of pinnotherid zoeae over a 24-hour sampling period on 09-10 October 2013. Error bars indicate standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Cycle and Depth.

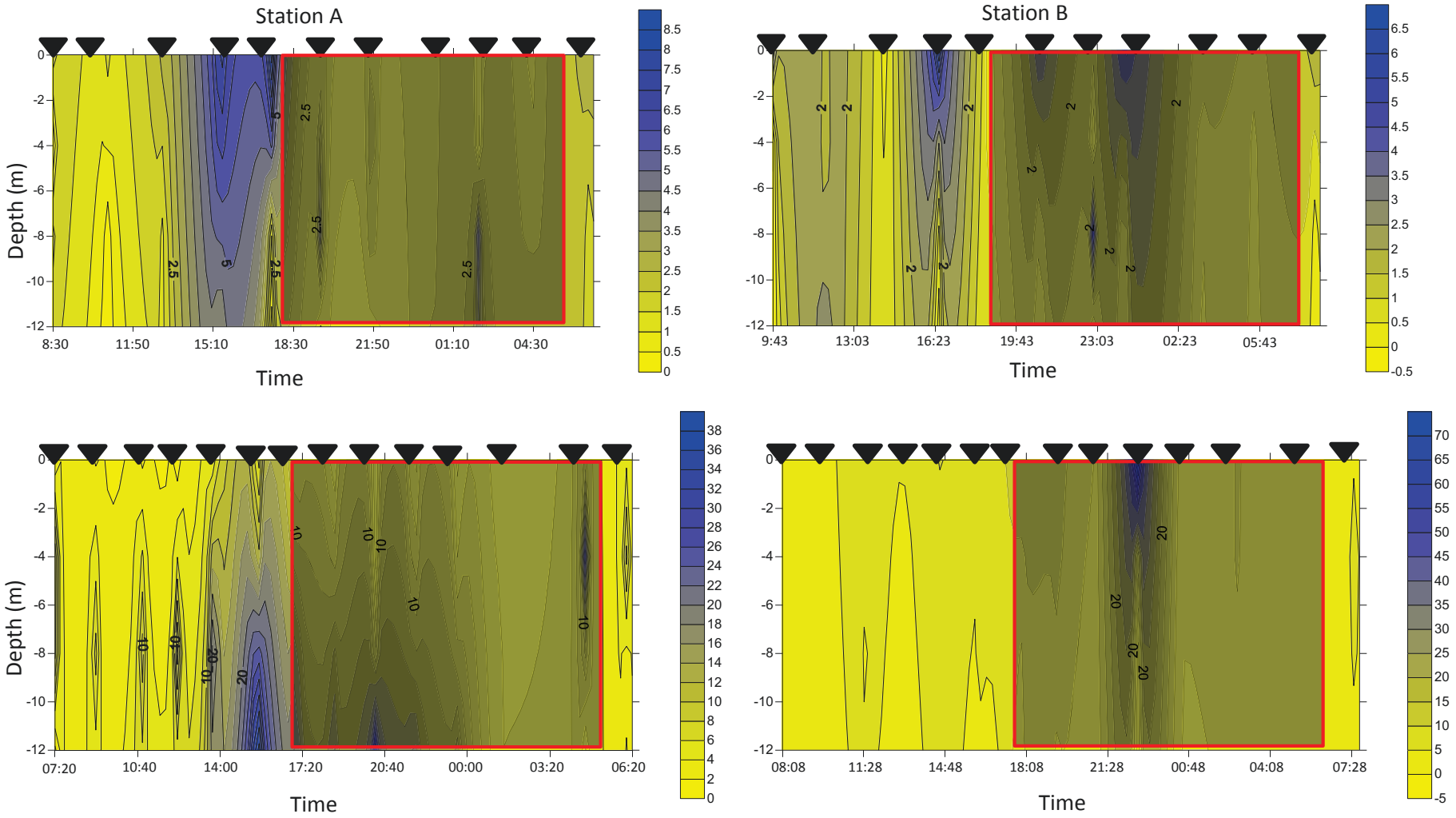


Figure 3.33: Abundance contours of pinnotherid zoeae on station A and B (top, March and bottom, October 2013). The sections outlined in red indicate night-time sampling. The triangles on top of each profile show the exact time the samples were taken. Abundance (individuals/m^3) is given on the scale bar on the right of each profile.

Porcelanid zoeae

Porcelanid zoeae were found in the samples and they reached the minimum abundance threshold for analysis in October 2013. Results of the 2-way ANOVA showed a significant effect of the interaction of Cycle and Depth on their abundance (Table 3.17). During the day, high abundances of porcelanid zoeae were not found at the surface. At 10:49-12:07 the highest abundance was at 8 metres; at 12:20-13:35 abundances were significantly higher at 8 and 12 metres and from 13:47 to 16:52 the higher abundances were at 12 metres (Figure 3.34). Figure 3.35 shows the abundance at the bottom layer at dusk and at the surface layer during the night.

Table 3.17: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$\log_{10}(X+1)$] of porcelanid zoeae throughout the water column on 09-10 October 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Cycle	3.25045	13	0.25003	1.7706	n.s
Depth	0.52146	3	0.17382	1.2309	n.s
Cycle*Depth	16.25706	39	0.41685	2.9519	****
Error	7.90783	56	0.14121		

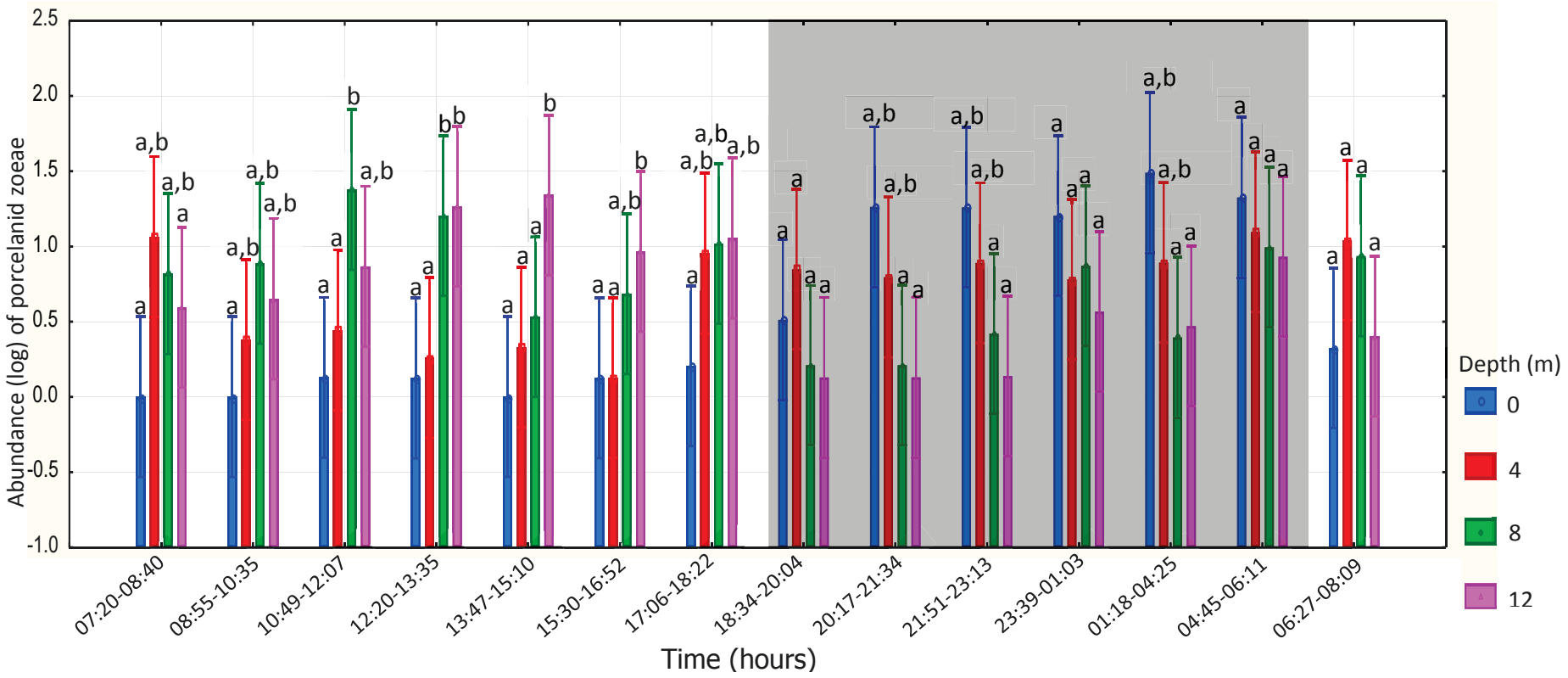


Figure 3.34: Abundance [$\log_{10}(X+1)$] of porcelanid zoeae over a 24-hour sampling period on 09-10 October 2013. Error bars indicate standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Cycle and Depth.

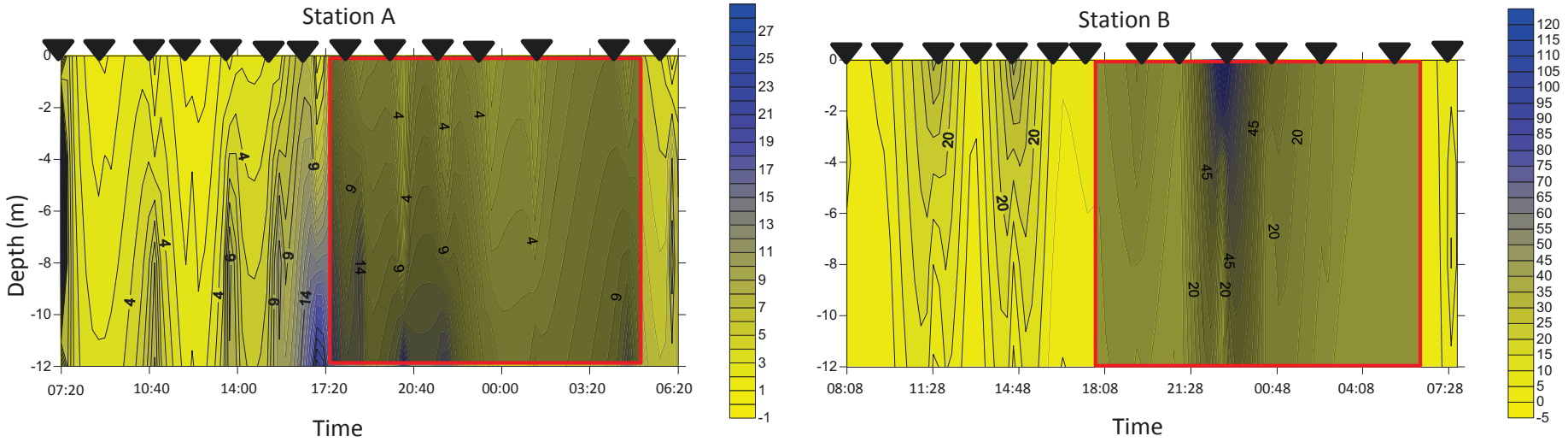


Figure 3.35: Abundance contours of porcelanid zoeae on station A and B on 09-10 October 2013. The sections outlined in red indicate night-time sampling. The triangles on top of each profile show the exact time the samples were taken. Abundance (individuals/m^3) is given on the scale bar on the right of each profile.

Anomuran zoeae

For anomuran zoeae, the interaction of Cycle and Depth had a significant effect both seasons (2-way ANOVA, Table 3.18). In March, despite the significant interaction between cycle and depth, there was no significant difference of the preferred depths by the zoeae, (based on the Fischer LSD post-hoc test), suggesting that abundance was homogenous through the water column during the day. From 00:03 until 04:03 higher abundances of larvae were found on the surface (Figure 3.36). Of the environmental predictors, turbulence had a positive significant effect on the abundance of this taxon (Table 3.20).

In October, higher abundances of anomuran zoeae were found at 4, 8 and 12 metres from 15:30 to 18:22 (Figure 3.37). Contour profiles of anomuran zoeae abundances with depth revealed that the zoeae were found at the bottom layers during the day and at the surface at night (Figures 3.38).

Table 3.18: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$\log_{10}(X+1)$] of anomuran zoeae throughout the water column on 02-03 March 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Cycle	3.23879	10	0.32388	5.1522	****
Depth	2.09550	3	0.69850	11.1116	****
Cycle*Depth	3.41022	30	0.11367	1.8083	*
Error	2.76594	44	0.06286		

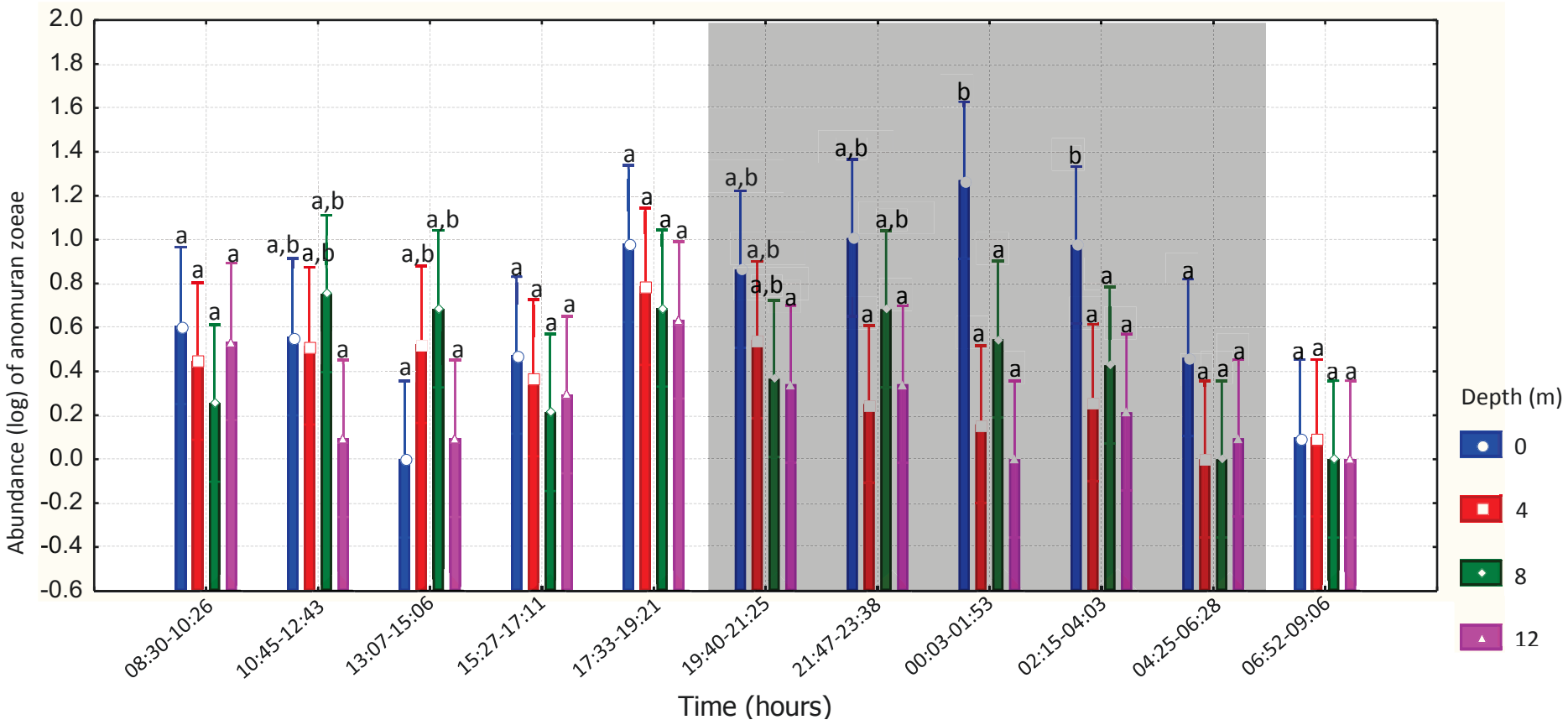


Figure 3.36: Abundance [$\log_{10}(X+1)$] of anomuran zoeae over a 24-hour sampling period on 02-03 March 2013. Error bars indicate standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Cycle and Depth.

Table 3.19: Analysis of Variance (ANOVA) examining the effects of Cycle and Depth (0, 4, 8, 12m) on the abundance [$\log_{10}(X+1)$] of anomuran zoeae throughout the water column on 09-10 October 2013. SS - Sum of Squares; df – degree of freedom; MS – mean squares; F – F-ratio and p – p-value.

Effects	SS	df	MS	F	p
Cycle	12.8384	13	0.9876	6.818	****
Depth	2.9907	3	0.9969	6.882	***
Cycle*Depth	11.4964	39	0.2948	2.035	**
Error	8.1115	56	0.1448		

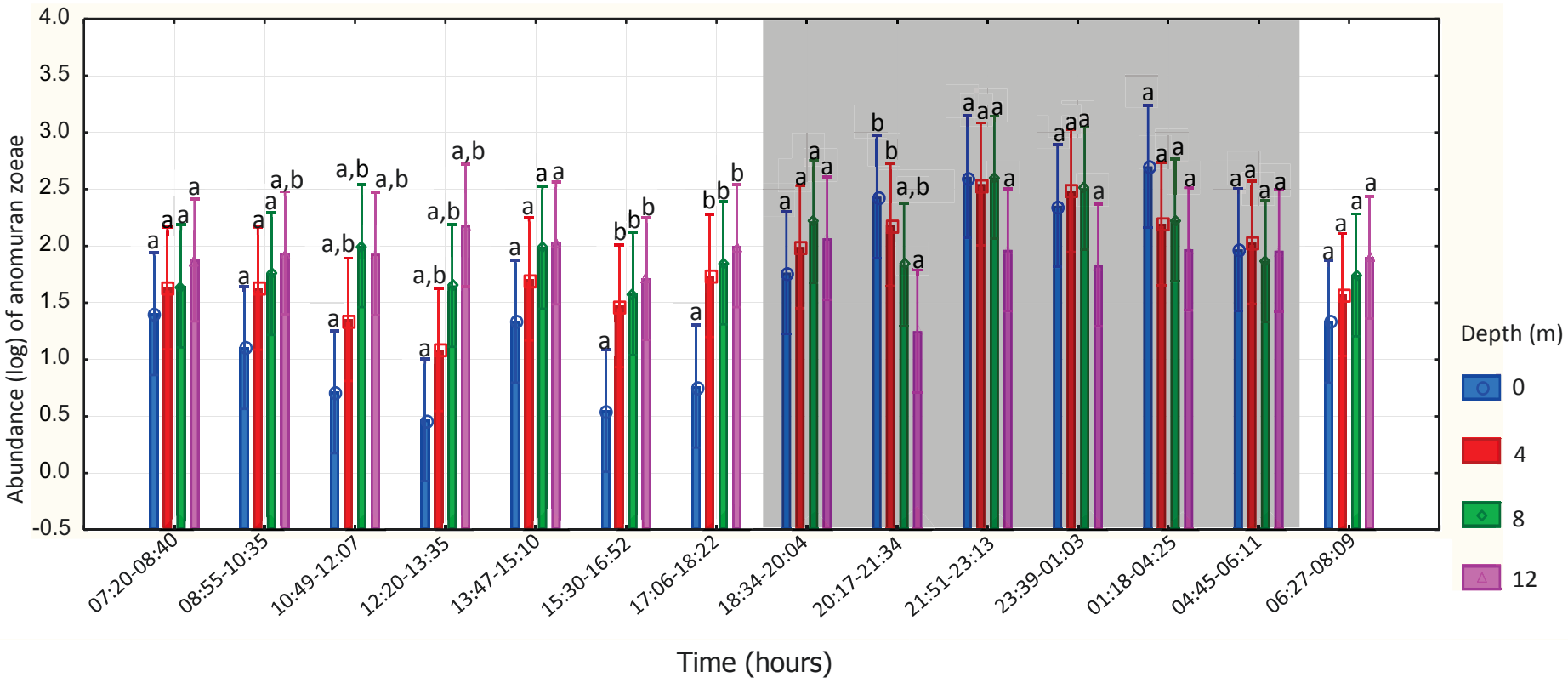


Figure 3.37: Abundance [$\log_{10}(X+1)$] of anomuran zoeae over a 24-hour sampling period on 09-10 October 2013. Error bars indicate standard errors. The shaded area indicates night-time sampling. Letters above the histogram bars indicate homogenous groups identified by post hoc tests performed on the effects of the interaction of Cycle and Depth.

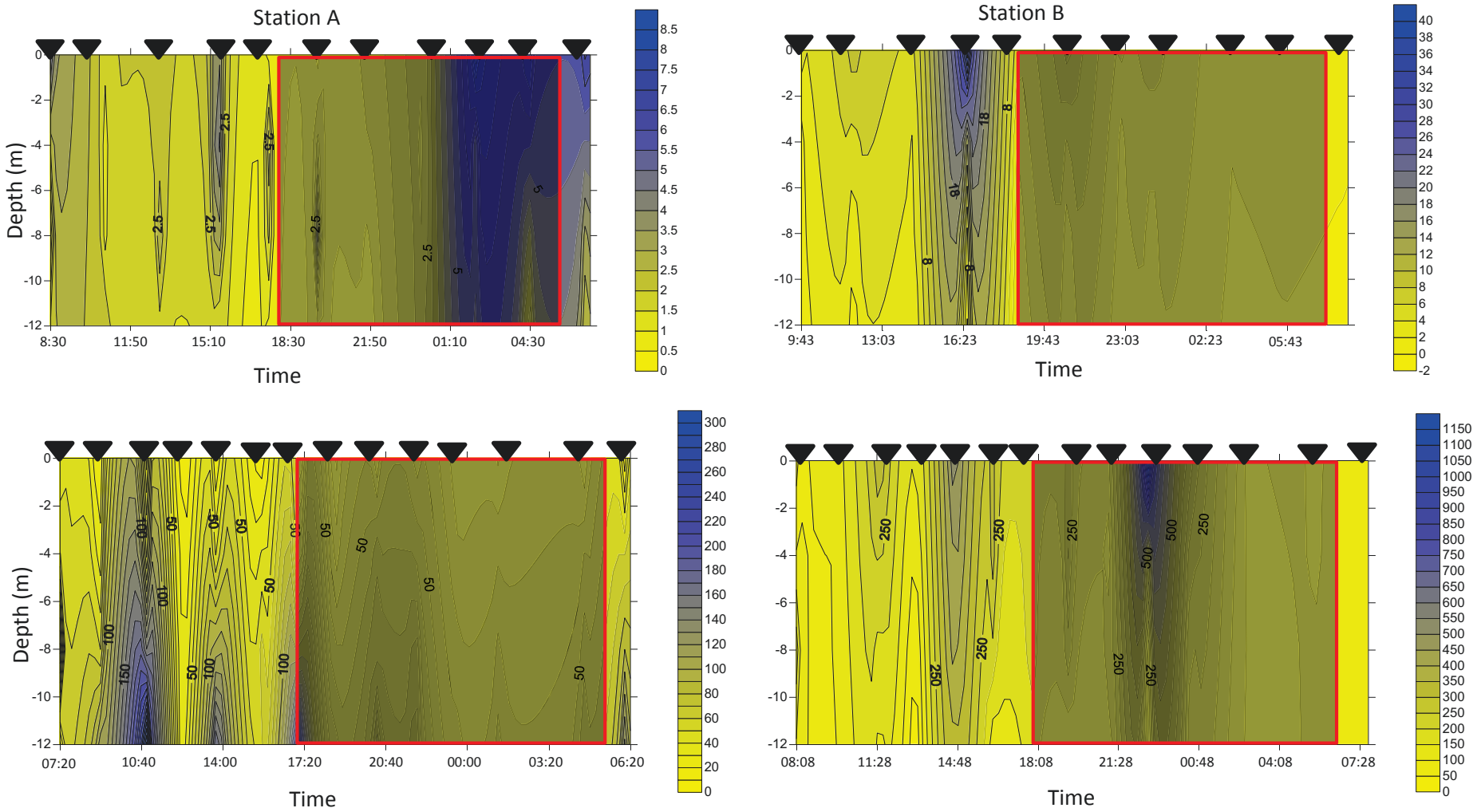


Figure 3.38: Abundance contours of anomuran zoeae on station A and B (top, March and bottom, September). The sections outlined in red indicate night-time sampling. The triangles on top of each profile show the exact time the samples were taken. Abundance (individuals/m^3) is given on the scale bar on the right of each profile.

Overview

In general terms, whenever the interaction between Cycle and Depth was significant, larvae were closer to the bottom during the day and to the surface during the night. These diel vertical patterns tended to occur in October especially for decapod zoeae (Figures 3.19, 3.22, 3.23, and 3.25) but, although less clear, also for some of the bivalve taxa (D-larvae veligers, intertidal bivalve veligers, *Hiatella* spp. veligers, Bivalve sp. A and B). In contrast, in March no bivalve veligers showed variations in vertical positioning with time (Figures 3.5 and 3.6, 3.11, and 3.13) and only anomuran zoeae presented a weak diel vertical migration pattern (Figure 3.24).

MULTIPLE REGRESSION ANALYSES

For this analysis some models were tested for each taxon independently and each season was analysed independently. In March, due to correlations among some predictors, which led to models being excluded, there were 9 models that could be tested on each taxon, as compared to the 8 that were possible in October. After Bonferroni correction, the new alpha level in March was $p \leq 0.005$ and in October it was $p \leq 0.006$. In October, after Bonferroni correction, there was no model that had a significant effect on decapod larvae (Table 3.21). In contrast, in March, turbulence and temperature had significant effects on the abundance of decapod larvae (Table 3.20).

The abundances of decapod zoeae increased with turbulence and temperature (Table 3.20, Figures 3.26 and 3.27). In October, environmental predictors only explained larval abundance patterns in the case of Bivalve B: high abundances of this species were associated with westward, onshore flow (Table 3.21, Figure 3.28). In all cases, coefficients of determination were extremely low (R^2 always less than 0.16, Figures 3.39 to 3.41).

Table 3.20: Multiple regression table with the taxon being tested against the models formed with the physical characteristics of the water column over a 24 hour period on 02-03 March 2013. The significance level was adjusted using Bonferroni correction. The significance level (p*≤0.05; p**≤0.01; p***≤0.001; p****≤0.0001) and the sign of the correlations are shown. upw – upwelling; Ɛ – turbulence; zf – zonal flow; mf – meridional flow; temp – temperature. A + sign shows a positive correlation between the environmental predictor and the abundance of the taxon.

Species	upw	Ɛ	zf	mf	temp	upw*zf	Ɛ*zf	zf*mf	zf*temp
BIVALVES									
Perna perna	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
Bivalve sp. B	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
BARNACLES									
Cyprid sp. B	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
DECAPODS									
Brachyuran zoeae	n.s	***, +	n.s	n.s	***, +	n.s	n.s	n.s	n.s
Pinnotherid zoeae	n.s	***, +	n.s	n.s	***, +	n.s	n.s	n.s	n.s
Anomuran zoeae	n.s	***, +	n.s	n.s	***, +	n.s	n.s	n.s	n.s

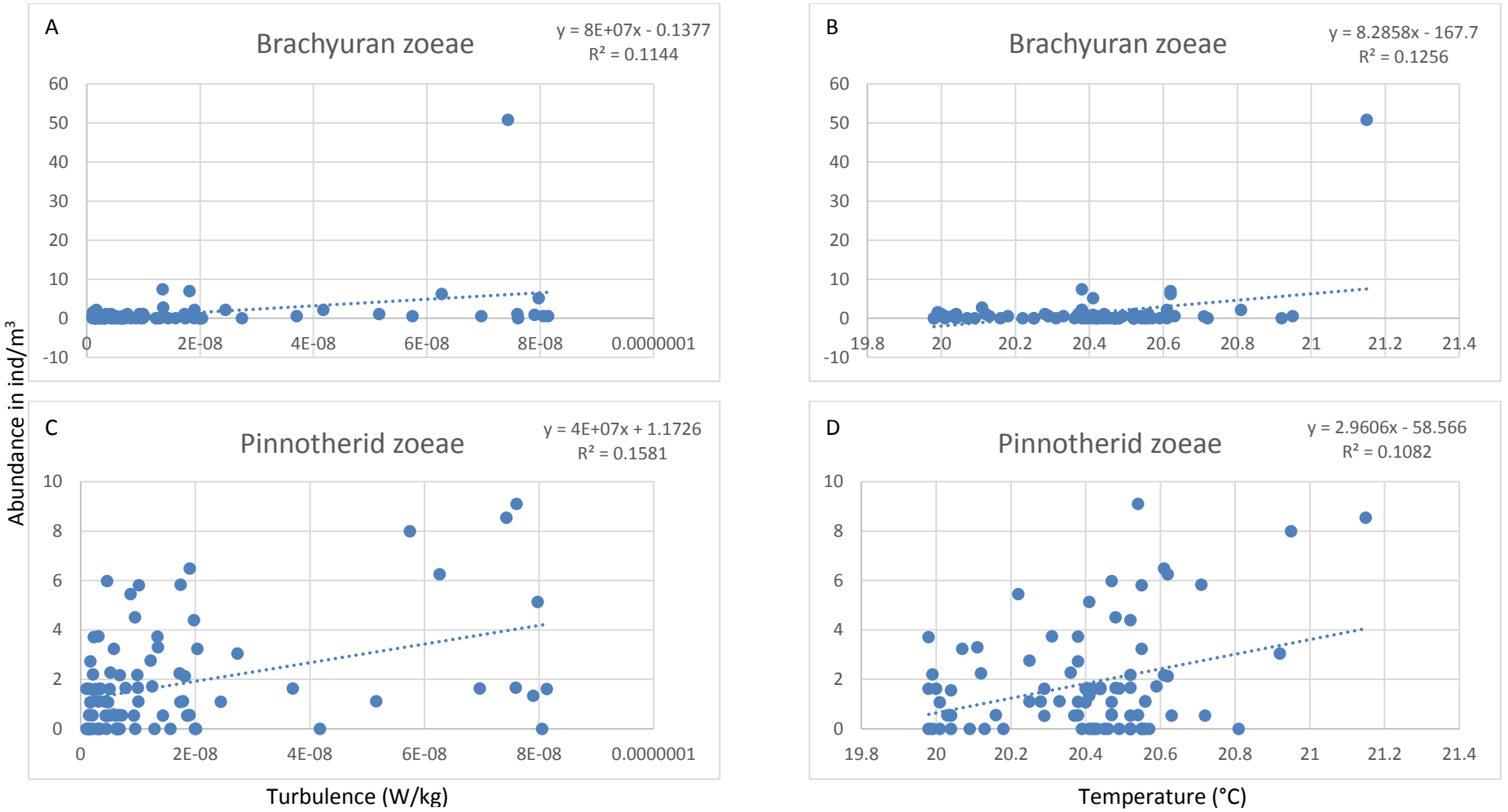


Figure 3.39: Effects of turbulence on the abundance (ind/m^3) of brachyuran zoeae (graph A) and pinnotherid zoeae (graph C) and the effects of temperature on the abundance (ind/m^3) of brachyuran zoeae (graph B) and pinnotherid zoeae (graph D) on 02-03 March 2013.

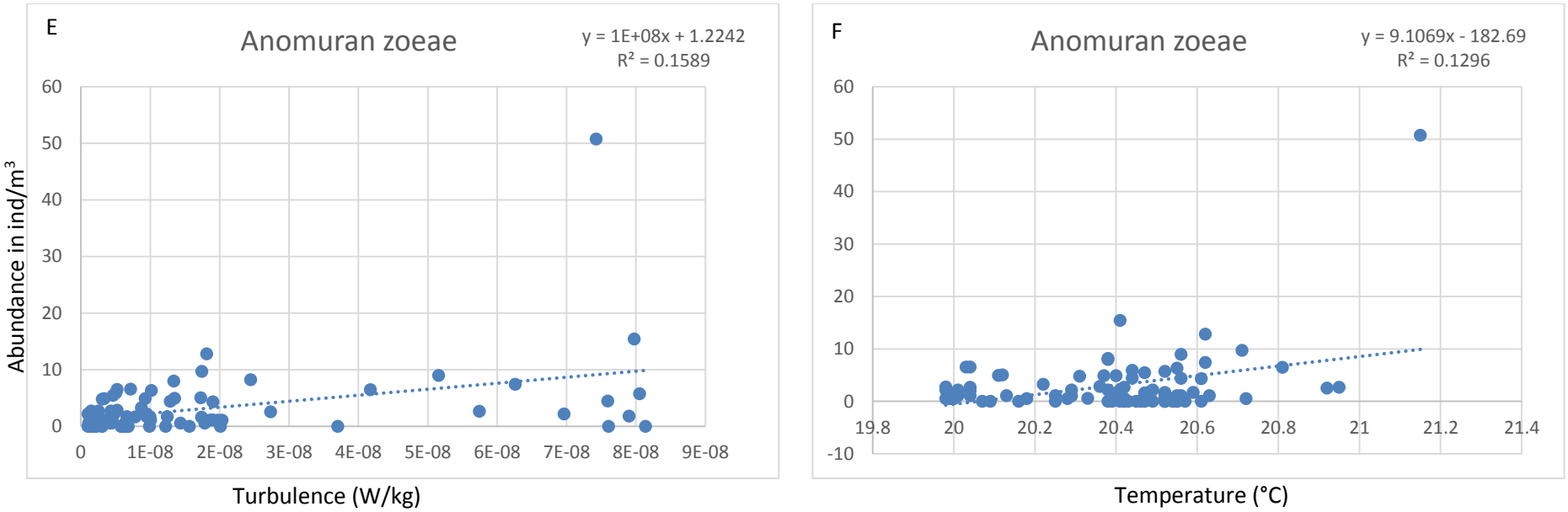


Figure 3.40: Effects of turbulence on the abundance (ind/m^3) of anomuran zoeae (graph E) and the effects of temperature on the abundance (ind/m^3) of anomuran zoeae (graph F).

Table 3.21: Multiple regression table with the taxon being tested against the models formed with the physical characteristics of the water column over a 24 hour period on 09-10 October 2013. The significance level was adjusted using Bonferroni correction. The significance level (p*≤0.05; p**≤0.01; p***≤0.001; p****≤0.0001) and the sign of the correlations are shown. upw – upwelling; Ɛ – turbulence; zf – zonal flow; mf – meridional flow; temp – temperature. A – sign indicates a negative correlation between the environmental predictor and the taxa.

Species	upw	Ɛ	zf	mf	temp	upw*zf	Ɛ*zf	Ɛ*mf
BIVALVES								
Perna perna	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
Mytilus galloprovincialis	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
Choromytilus meridionalis	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
Oysters	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
Intertidal bivalves	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
Hiatella spp.	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
D-larvae	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
Bivalve sp. A	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
Bivalve sp. B	n.s	**, -	n.s	n.s	n.s	n.s	n.s	n.s
Other mussels	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
BARNACLES								
Cyprid sp. A	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
DECAPODS								
Brachyuran zoeae	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
Pinnotherid zoeae	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
Porcelanid zoeae	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
Anomuran zoeae	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s

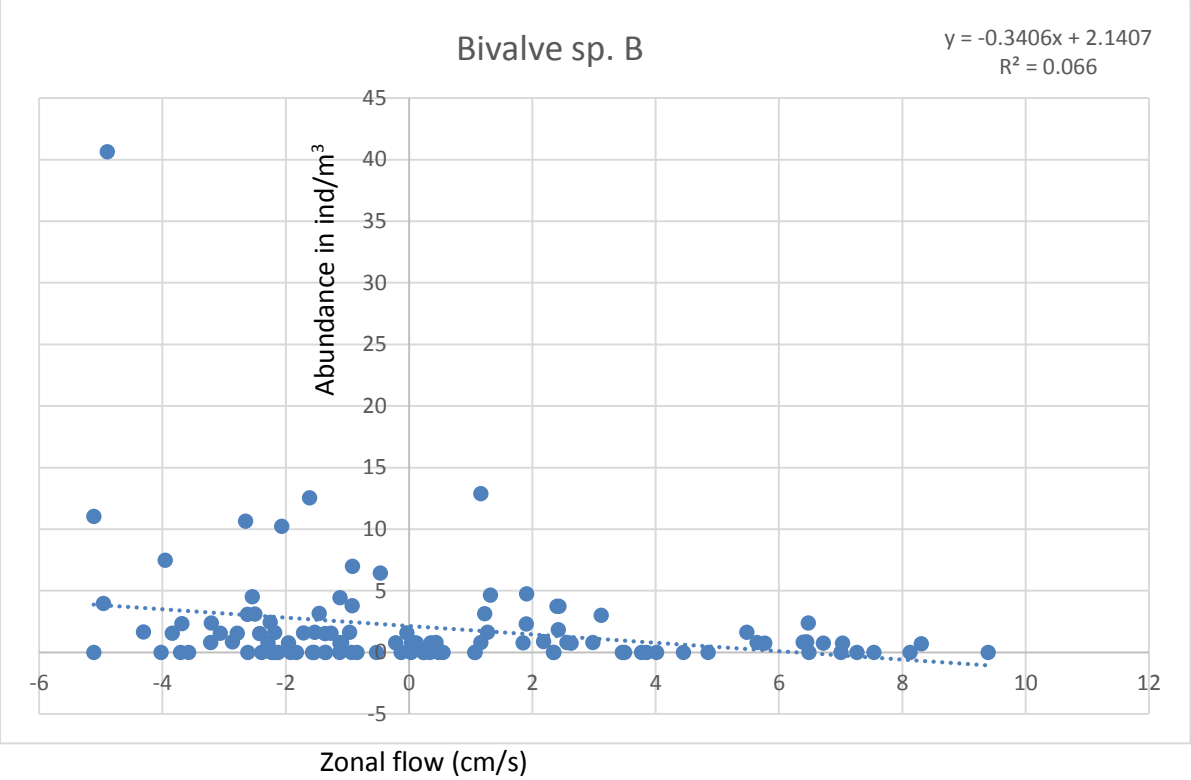


Figure 3.41: The effect of zonal flow (west to east direction of the current) on the abundance (ind/m^3) of Bivalve sp. B throughout the water column over a 24 hour sampling period on the 09-10 October 2013.

3.4 Discussion

3.4.1 Physical characteristics

In March, zonal currents were mostly homogenous, moving towards the shore (West) whereas the meridional flow was mostly offshore (South). In October, waters were more stratified so that currents moved in opposite directions at different depths, specifically for the zonal flow during the day. It is possible that the stratified water column in October was caused by easterly winds that are more prevalent in austral summer and lead to upwelling (Schumann & Martin, 1991).

The current data suggest that there was offshore flow in shallower depths, and onshore flow in deeper waters, a pattern typical of upwelling (Marta Almeida *et al*., 2006). At night, the currents were mostly homogenous, flowing in the east to west, or onshore direction.

These circulation patterns in October are consistent with upwelling driven by diurnal sea-land breezes (Rosenfeld *et al*., 1994; Goschen & Schumann, 1995; Garland *et al*., 2002; Kirincich *et al*., 2005; Marta Almeida *et al*., 2006; Woodson *et al*., 2007). Sampling was however done in a very shallow bay and very close to the coast where upwelling effects may be concealed by the presence of the coastal boundary layer (Wolanski & Hamner, 1988; Largier, 2003). Moreover, many bays are usually isolated from the upwelling which occurs at the open coast, forming a so-called upwelling shadow (Graham *et al*., 1992; Graham & Largier, 1997; Morgan & Fisher, 2010). Despite these observations, Kirincich *et al*. (2009) found that very shallow coastal waters without any thermal stratification, like the ones sampled in Algoa Bay, were stratified in terms of flow direction and magnitude, thus still responding to upwelling. In fact, very nearshore waters in Algoa Bay have been affected by upwelling events which originated in Cape Recife at its western boundary (Goschen & Schumann, 1995). Such upwelling events cause an influx of cold waters and are responsible for temperature changes within the bay, with cold water influxes leading to thermoclines in the shallow embayments (Goschen & Schumann, 1995). This type of coastal circulation affect alongshore currents by altering current patterns and creating eddies and fronts (Wolanski & Hamner, 1988), and consequently affect larval distribution and settlement (McCulloch & Shanks, 2003).

3.4.2 Biological data

Bivalves

D-larvae, veligers of intertidal bivalves, *Hiatella* spp. and Bivalve sp. A and B, changed vertical position with time, showing vertical migration patterns in October. This highlights the fact that even larvae as small as bivalve veligers have the ability to maintain some control of their depth. Offshore zonal flow during the day in October (Figure 3.3) might be the reason for avoidance of the surface by larvae, which would enhance their onshore retention. The mud snail, *Ilyanassa obsoleta* showed nearshore retention and settling on the sediment due to sinking and inhabiting the deeper layers of the water column (Fuchs *et al.*, 2004). Similar mechanisms have been observed in the larval transport of the crab, *Carcinus maenas*, which, in upwelling systems, spend most of the time in the deeper onshore flow, enhancing onshore retention (Marta Almeida *et al.*, 2006). Upwelling waters tend to bring food particles and nutrient from deeper offshore layers to the surface (Peters & Marrasé, 2000; Marta-Almeida *et al.*, 2006) which could influence the ascent of larvae to the surface to feed (Clarke, 1934; Raby *et al.*, 1994; Vestheim *et al.*, 2014). Calanoid copepods as well as scallop larvae have been found to dwell near the bottom during the day and to use night ascension to avoid predators (Zaret & Suffern, 1976; Manuel & O'Dor, 1997). Not all bivalve larvae migrated to the surface at night in October, as *Hiatella* veligers stayed at the bottom during the day and were homogeneously distributed throughout the column during the night (Figure 3.12). Note that at night, the currents throughout the water column were moving onshore (Figure 3.3), thereby keeping larvae close to the shore regardless of depth. This mechanism has been confirmed by other studies (e.g. Fuchs *et al.*, 2004; Marta-Almeida *et al.*, 2006).

Barnacles

Barnacle cyprids did not show any vertical migration pattern. In fact, species A and B showed different distributions, with Cyprid sp. A positioned at the bottom during the day in October (Figures 3.22, 3.23 and 3.24), whilst Cyprid sp. B appeared in higher

abundances only at night regardless of depth (Figures 3.25 and 3.26). Vertical migrations in cyprids are not the common and usually they are found at fixed depths (neuston layer) or upper 20 metres (dos Santos *et al*., 2007). Cyprids of *Chthamalus montagui*, *Pollicipes pollicipes* and *Balanus perforatus* were found to be mostly restricted to the neuston layer whilst *C. stellatus* cyprids were mostly found to inhabit the upper 20 metres of the water column at night (dos Santos *et al*., 2007). This mechanism could favour the onshore transport of cyprids for settlement at the shore (dos Santos *et al*., 2007).

Decapods

Brachyuran and pinnotherid zoeae presented very similar patterns. In March they were associated with warmer surface waters during the day, but no diel vertical migration pattern was evident (Figures 3.18, 3.20 and 3.21). Temperature of the water column during the day was higher near the surface, and decreased with depth, as noted by other researchers (Price *et al*., 1986). Wind-driven turbulence acts the same way as temperature. Since it is wind-driven, surface waters are more turbulent than deeper layers in the water column (Pringle, 2007). The positive effect of turbulence and temperature on larval abundance (Table 3.20) might explain the preference for the surface in decapod larvae. Turbulence increases predator-prey encounter rates (Peters & Marrasé, 2000). To enhance recruitment, larvae should actively position themselves so as to be retained near the shore (Connell, 1985; Roughgarden *et al*., 1994; Manuel *et al*., 1996; Manuel & O'Dor, 1997; Shanks & Brink, 2005; Metaxas & Saunder, 2009; Tommasi *et al*., 2014). During the day, at a given time period, the currents in March had an offshore flow at the bottom whilst at the surface there was onshore flow. Brachyuran and pinnotherid zoeae were on the surface, likely enhancing onshore retention by avoiding the offshore flow at the bottom layers. In October, diel vertical migration was evident for these two taxa as well as for porcelanids and anomurans (Figures 3.34 and 3.37), and was much clearer than for bivalve veligers. Marta-Almeida *et al*. (2006) examined the zoeae of the littoral crab, *Carcinus maenas*, and argued that descent during the day and ascent at night enhances onshore retention. In October, there was stratification

during the day in the zonal currents. Such water stratification seemed to have favoured behavioural shifts in the vertical axis for decapods as they migrated to enhance onshore retention. Different patterns of larval distribution in relation to the time of the year could however be due to a shift in species composition: species in the group of brachyuran zoeae found in March may have differed from the species found in October.

Behavioural shifts in vertical migration

The results show that, for a wide range of larvae, behaviour in the vertical axis can differ depending on taxonomy and change depending on whether hydrographic conditions are suitable for active diel positioning (October) or not (March). Thus, for most of the larvae, the interaction of Cycle and Depth had a significant effect in October but not in March. Diel vertical migration is a phenomenon carried out by larvae to increase their survival rate and it can involve some level of plasticity, mainly in response to spatio-temporal changes in the availability of food and/or variability in environmental parameters. A study by Vestheim *et al*. (2014) and Cisewski *et al*. (2010) on ice forming surface layers of water showed that species perform diel vertical migration, but only when there is a need to. When food is abundant throughout the water column species tend to perform diel vertical migration, as proven by the krill species *Meganyctiphanes norvegica* (Vestheim *et al*., 2014). In the polar systems however, the melting of ice results in phytoplankton blooms in the upper layers of the water column causing the Antarctic krill, *Euphausia superba*, to remain close to the surface as to maximise feeding opportunities given the limited duration of the spring/summer season (Cisewski *et al*., 2010). These studies generally show that diel vertical migration is performed to increase their feeding opportunities and therefore survival.

A response to environmental predictors was particularly evident on the fast swimming decapod (1.5 cm/s for pinnotherid zoeae; 2.0 cm/s for anomuran zoeae) larvae compared to slower (0.11 cm/s for *Mytilus galloprovincialis*) bivalve veligers (Chia *et al*., 1984). Results found in this research were similar to a study done by

dos Santos *et al*. (2008), who showed that decapod zoeae were more abundant than megalopae in the water column. Decapods responded positively to temperature and turbulence. Responses to turbulence are species specific as some species sink and others swim in turbulent waters. There is a specific range of turbulence to which each species responds (Fuchs & DiBacco, 2011). For example, the mud snail, *Ilyanassa obsoleta,* retracts its velum and sinks in turbulence above a kinetic energy dissipation rate, of $\varepsilon \approx 4.0 \times 10^{-1}$ cm^2 s^{-3} (Fuchs *et al*., 2004). Copepodites of *Eucalanus bungi* and *Neocalanus cristatus* were also found to avoid turbulent waters by Mackas *et al*. (1993). Larvae of the slipper limpets, *Crepidula* spp. and the dove snails, *Anachis* spp. sink in calmer waters and swim upward in turbulence above threshold levels (Fuchs *et al*., 2010).

Overall, this study shows that planktonic invertebrate larvae, which are generally small and relatively slow swimmers still have the ability to maintain their distribution in the water column. Turbulence and temperature may act as cues for larvae to undertake migration either up or down a water column. Migration of species in the water column is resultant of a need to maximise each taxon's advantages, be it feeding, predator avoidance or onshore retention. Measurements of light levels, salinity and chlorophyll or fluorescence down a water column might be needed in future studies so as to find whether the vertical distribution and migration of larvae is also due to light.

CHAPTER FOUR

GENERAL DISCUSSION
&
CONCLUSIONS

The westerly and easterly components of winds on the south coast of South Africa show seasonal variations peaking in spring, with maximum averages of 4 - 4.7 m/s, with open coasts receiving stronger winds than bays because of the effects of topography (Schumann & Martin, 1991). Wind can be a major factor in determining current velocity and direction, upwelling and turbulence. Local topography can further strongly influence the strength of upwelling (Figueroa & Moffat, 2000). Given that strong winds mostly occur in spring, I expected more upwelling, but in contrary, there was more downwelling noted on the sampling days in the spring season, which influence the abundance of decapod zoeae, characterised then by diel vertical migration.

Vertical migration is a common behavioural mechanism observed in most plankton (Raby *et al.*, 1994; Garland *et al.*, 2002; Lie *et al.*, 2012). In top zooplankton predators such as chaetognaths, vertical migration is related to the search for food (Cisewski *et al.*, 2010; Lie *et al.*, 2012). Alternatively and contrastingly, diel migration by plankton can also be used for the avoidance of predators (Garland *et al.*, 2002).

Generally, there was temporal variation in diel vertical migration, with more taxa performing diel vertical migration in spring. Temporal variation of diel vertical migration is common in zooplankton (Cisewski *et al.*, 2010; Vestheim *et al.*, 2014). A certain amount of downwelling might have been the cue for larvae to undertake diel vertical migrations, as upwelling had negatively influenced the abundance of bivalves and Cyprid sp. A as well as brachyuran and anomuran zoeae. Acknowledging the physical dynamics of upwelling (Beckley, 1983), the negative relation with larval abundance was expected, whereby larvae avoid being transported offshore by surface currents. Offshore flowing layers tend to transport larvae away from the coast, while subsurface larvae are transported onshore by the subsurface flow (Ma *et al.*, 2006). During upwelling and downwelling events, larvae do not act as passive particles but control their vertical positioning, as Shanks and Brink (2005) found with two bivalve species, *Tellina* spp. and *Mulinia lateralis*. Bivalve veligers tend to avoid offshore surface layer of water and control retention by sinking under upwelling conditions (Shanks *et al.*, 2003a; Shanks & Brink, 2005; Ma *et al.*, 2006).

Seasonal variations in water temperature are also evident on the south coast of South Africa, with clear thermocline formation during summer, but mostly isothermal water column during the rest of the year (Beckley, 1983). Temperature changes can act as a cue for diel vertical migration and vertical discontinuities in temperature can be a barrier to larval vertical migration, at least on the open coasts (where the thermocline has a clear presence). One of the shortcomings to this study was CTD problems, which at times was replaced with a diving computer as the CTD was not working. Temperature was positively correlated with the abundance of decapod larvae, at least for the 24 hour study and temperature is known to have an influence on the abundance and behaviour of many meroplankton. A positive correlation between larvae and temperature was also observed by Herbing (2002) when an increase in temperature resulted in an increase in swimming activity of fish larvae.

Shallow water columns are easily influenced by wind-induced turbulence. In turbulent waters, there should be less temperature variation between the surface and bottom (Beckley, 1983), food should be evenly distributed (Rothschild & Osborn, 1988), and most importantly, so should larvae. The abundance and distribution of decapod larvae were positively correlated with turbulence and results from this study indicated that even in shallow embayments, with turbulence, vertical migration of larvae was present. Turbulence is a cue for positive (Fuchs *et al.*, 2004; 2010; 2013) or negative (Fuchs & DiBacco, 2011) behavioural responses, depending on the species, ontogenetic stage and strength of turbulence.

This thesis gives a contribution to the understanding of the distribution of larvae in the nearshore water column under different physical conditions. It shows that diel vertical migration is a phenomenon performed by meroplankton. This behaviour however, differed among taxa, among species and among different ontogenetic stages within a species. With that said, clear patterns might have been missed for some groups due to lack of taxonomic resolution in some taxa and low numbers for different ontogenetic stages. Such behavioural responses however, were controlled by the strength of the physical forcing. The strength of the physical forcing can in fact induce a sinking or swimming response so to avoid offshore transport.

Ultimately, connectivity is amongst the most important drivers of population dynamics and through this study, I suggest a gradient of behavioural potentials, regulated by localised and variable strengths of the physical environment, could mediate transport and delivery to the final adult destination.

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