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Nearshore vertical distribution of barnacle cyprids: temporal patterns and hydrographic variability

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A thesis submitted in partial satisfaction of the requirements for the degree of

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ABSTRACT

Most benthic organisms living in the intertidal zone have planktonic larvae that reside temporarily in the water column before settling in their adult habitats. Larvae aggregate in offshore larval pools, and transport horizontally and vertically in the water to remain in the nearshore and during their pelagic life. While some horizontal transport of larvae can be attributed to advection, behavioral responses, like vertical swimming and buoyancy control, allow larvae to position themselves at depths where flow direction can be exploited. Thus, knowledge on how vertical larval distribution relates to physical processes can be fundamental to better understand larval transport. These larvae must then return to shore to successfully metamorphose and complete their life cycle. Recent work at our study site in Bird Rock (La Jolla), California, USA suggests that late-stage barnacle larvae (cyprids) accumulate at a mid-depth in a shallow (4m) station when offshore waters are stratified. However, it remains unknown how the water column structure (e.g., temperature) varies at this site, and the consequences to the vertical distribution and abundance of larvae. This study conducted repeated hourly larval collections at 1m-depth intervals at a 4m-deep station ~300m from shore. Sampling was conducted over 5, 24-hour cruises during the summers of 2017 and 2018. Larval vertical distributions were characterized and compared to hydrographic (thermal stratification, thermocline depth) and hydrodynamic (currents) variables collected at three stations (4m, 5m and 8m depths). Vertical distribution patterns of barnacle cyprids showed that they remained

closer to the bottom during the day and migrated slightly shallower at night, despite varied physical conditions between cruises. Additionally, our results showed that higher thermal stratification allowed the thermocline to penetrate closer to shore, and more larvae to accumulate at 4m-deep. This study supports previous work suggesting that thermal stratification is a key factor in nearshore accumulation and suggests that larval behavior can be better exercised when thermal stratification is high, all of which have important implications on barnacle settlement and recruitment to the intertidal.

CHAPTER 1: Introduction

1.1 Larval Transport

The dispersal and transport of planktonic larvae in the water column determines population connectivity of marine organisms (Scheltema 1971, Cowen et al. 2000, Cowen et al. 2007, Pineda et al. 2007). Larval transport refers to the mean horizontal translocation of larvae between points along a specified one-dimensional axis per unit time (Pineda and Reyns 2018) and for most benthic invertebrates, this process is important for establishing distribution patterns, and setting community structure (Gaines and Roughgarden 1985, Roughgarden et al. 1988, Wieters et al. 2008, Aiken and Navarrete 2014). The interplay between biotic and abiotic factors, along with behavior, influences the development and survival of larvae and facilitates their dispersal in the pelagic system (Cowen and Sponaugle 2009, Bonicelli et al. 2016, Pineda and Reyns 2018).

Transport of larvae depends on the physical properties of their surrounding waters (Emlet and Strathmann 1985), particularly for nearshore organisms, where the hydrodynamics vary significantly (Arthur 1955, Winant 1974, Pineda 1994, Kaplan et al. 2003). Physical processes such as wind-driven circulation (Tapia et al. 2004, Reyns et al. 2007) and internal tidal bores (Pineda 1999) generate advection and larval transport (Shanks et al. 2003, Pineda et al. 2009). Horizontal transport of larvae is generally attributed to advection; however, recent studies argue that competent behavior, like vertical swimming or buoyancy control, allows larvae to position themselves at depths

where flow can be exploited to travel towards shore (reviewed in: Pineda 1994, Metaxas 2001, 2006, Pineda and Reyns 2018). Additionally, relevant processes like Ekman transport and diurnal wind-cycles have been observed to alter current velocities vertically in the water column, allowing larvae at different depths to be advected differently (McEdward 1995, Kaplan et al. 2003, Rivera et al. 2013).

1.2 Distribution Constraints due to Physical Processes

Physical oceanographic, including water stratification, fluctuate at different scales. Long-term variations happen inter-annually due to events such as the El Niño Southern Oscillation (ENSO) (Pineda et al. 2018), upwelling and downwelling (Ramp et al. 1997, Lluch-Cota et al. 2001); and monthly due to seasonal variations in solar radiation and precipitation (Pfister 1997, Williams and Williams 1997). Shorter-scale changes on the order of days are attributed to internal tides and diurnal wind cycles (Winant and Bratkovich 1981, Pineda 1991, Kaplan et al. 2003). Many studies have examined the relevance of large-scale processes on larval advection and transport (Pineda 2000), but recent findings (Carr et al. 2008, Bonicelli et al. 2016, Hagerty et al. 2018) suggest that local small-scale hydrographic conditions are as important for horizontal transport and vertical migration.

Most intertidal benthic invertebrates inhabit nearshore waters during their larval stage and rely on shoreward transport to successfully complete their lifecycle (Pineda 1999, 2000; Pineda et al. 2009; Tapia et al. 2010; Bonicelli et

al. 2016; Hagerty et al. 2018). The presence of shallow depths and a shoreline barrier in nearshore environments causes the hydrographic conditions to differ from those of deeper waters (Pineda 2000). Nearshore environments such as estuaries and lagoons are known to have strong cross-shore currents; however, open coastlines modify tidal currents to be more energetic in the alongshore direction than the cross-shore direction (Pineda 2000, Lentz and Fewings 2012). Tidal fronts and internal tidal bores, which have been previously associated with larval transport (Shanks et al. 1983, Pineda 1999, Woodson et al. 2012) also occur in shallow waters (Clancy and Epifanio 1989, Pineda 1999). Since the flows in open coastlines are dynamic (Hickey 1979), larvae have to adjust their vertical position in the water column to exploit shoreward currents and successfully complete their life cycle in the intertidal (McEdward 1995, Tapia et al. 2010, Hagerty et al. 2018). So, successful development, and dispersal and survival of pelagic larvae is determined by the interaction of physical and biological factors, such as their behavior in the water column (Barnes 1956, McEdward 1995).

Planktonic larvae tend to be weak swimmers unable to move against horizontal currents (Chia et al. 1984), but most larvae are capable of, and display, vertical migration (Shanks 1986, Lloyd et al. 2012, Bonicelli et al. 2016). Some larvae are able to regulate their vertical position by either adjusting their buoyancy or swimming vertically (DiBacco et al. 2011, Daigle and Metaxas 2011, Civelek et al. 2013, Bonicelli et al. 2016) as a response to physical cues like changes in temperature and salinity (Carriker 1951, Brinton

1967), which allow them to cross density gradients (Boudreau et al. 1992, Daigle and Metaxas 2011, Civelek et al. 2013) to control the direction in which they are advected (Rivera et al. 2013). Larvae have been observed to migrate below the thermocline to avoid being transported offshore during upwelling events (Shanks et al. 2003, Shanks and Brink 2005), and to exhibit ontogenetic vertical distribution regardless of seasonal variations in temperature and stratification (Hagerty et al. 2018). The responses of larvae to physical processes in the water column are particularly important in the understanding of population dynamics and connectivity of coastal benthic organisms; it determines the chances of successful shoreward transport and recruitment of intertidal species (Cowen et al. 2006, Metaxas and Saunders 2009, Shanks and Shearman 2009).

Changes in vertical distribution between the surface and bottom of the water column occurs in zooplankton (Cohen and Forward 2009), and crustacean larvae in particular have been recognized as proficient vertical swimmers (reviewed in: Epifanio and Cohen 2016). Their ability to move vertically during diel cycles allows them to evade visual predators and reduce energy consumption by remaining in colder waters (Thorson 1964, Zaret and Suffern 1976, Forward and Rittschof 2000), which is relevant to non-feeding cyprids who are constrained by their lipid reserves. Likewise, it allows larvae to regulate their exposure to different current velocities and influence the direction in which they are advected in waters with daily significant stratification changes (i.e. nearshore open coastlines) (Pineda 1999, Kaplan et

al. 2003, Pineda et al. 2009, Tapia et al. 2010, Bonicelli et al. 2016). Kaplan et al. (2003) found daily temperature variations to rival annual changes in temperature off the coast of Chile during the austral summer. Similarly, Winant (1974) found diurnal temperature changes off the Scripps Pier in La Jolla, CA, USA to vary significantly with depth at shallow stations. Environments where thermal gradients changes are so dynamic can be expected to influence larval behavior on a short-term or daily basis, which is why examining vertical distribution patterns with high temporal resolution can help understand larval retention and dispersal, in addition to providing insight as to how larvae interact with their physical environment.

1.3 Study Species

This research examines barnacle larvae, specifically that of *Chthamalus fissus*. *C. fissus* distribution ranges from San Francisco to Baja California (Miller et al. 1989). Barnacle larvae live ~ 2-5 weeks in the plankton and includes 7 stages– 6 naupliar and one non-feeding cyprid (Walley 1969). Barnacle cyprids must locate suitable benthic habitats on which to attach and metamorphose into a juvenile to successfully complete their lifecycle (Walley 1969). The mechanisms and behaviors involved in the shoreward transport of cyprids is still debated; however, their shoreward transport has been associated with physical processes like internal tidal bores, wave height, currents and stratification (Pineda 1999, Jeffrey and Underwood 2000, Shanks et al. 2010, Pfaff et al. 2015, Pineda and Reyns 2018). Cyprids have also been observed to

swim vertically in a downwelling flume (DiBacco et al. 2011), suggesting that these larvae can competently behave to regulate their cross-shore transport. Cyprids have a well-developed brain and sensory organs that exceeds the capabilities of naupliar larvae (Anil et al. 2010), increasing their ability to respond to physical processes.

Studies on barnacle larvae show that earlier nauplii stages are advected offshore and remain shallower in the water column, while cyprids predominate closer to shore and occupy deeper waters (Bonicelli et al. 2016, Hagerty et al. 2018). Water stratification can also influence *C. fissus* barnacle settlement (Pineda and Lopez 2002). However, studies looking at their vertical position showed no relationship between stratification and vertical distribution (Hagerty et al. 2018). Still, stratification is thought to increase larval retention and facilitate the exploitation of sheared flows (Pineda and Reyns 2018). Even though cyprids were predominantly found near the bottom (Rivera et al. 2013, Hagerty et al. 2018), studies have found barnacle onshore transport to occur during wind relaxation events and internal tidal waves (Farrel et al. 1991, Pfaff et al. 2015). Relaxation may promote higher stratification and promote the propagation of internal tidal motions, which could explain why peaks in barnacle settlement have been associated with higher stratification (Pineda and Lopez 2002, Pfaff et al. 2015).

A study by Bonicelli et al. (2016) observed no diel vertical migration on *Chthalamid* cyprids, still, cyprids seemed to remain deeper in the water column during the daytime. These results come from single vertical tows

conducted for both day and night at 10 different stations, making it hard to infer if cyprids migrate vertically during short time scales or as a response to small-scale physical processes while aggregated in a specific location. *C. fissus* larvae have been observed to reach the intertidal of Bird Rock, La Jolla on a daily basis throughout the year, usually in higher concentrations during the summer months (Hargenrader 2018). Despite the flux being constant, settlement of barnacles at the site also vary at the scale of days (based on settlement plate data collected), which suggests small temporal scale processes must influence the onshore transport of barnacle larvae. This study focuses on how larval vertical distribution changes at an hourly temporal resolution.

How biological and physical variations influence the vertical distribution of barnacle larvae over a 24-hour period is not yet fully resolved. Understanding these processes, and how they contribute to larval transport will help better explain dispersal of barnacle larvae (Bonicelli et al. 2016, Hagerty et al. 2018), how behavior interacts with nearshore physical processes (Pineda 1990, Pfaff et al. 2015), and how behavior ultimately impacts settlement and recruitment (Pineda 1994, Pineda and Lopez 2002). Combining the outcomes of my research with previous observations will help expand the understanding of barnacle life-history processes and their population dynamics in Southern California. Additionally, the life cycle of barnacles relates to that of most marine invertebrates and fishes, so findings from this study could be used to help model the population dynamics of other species.

1.4 Study Site

This study was conducted off the coast of Bird Rock, La Jolla, California within the South La Jolla State Marine Reserve - a marine protected area (MPA). This region hosts large numbers of adult barnacles and receives an annual flux of barnacle larvae (Pineda 1994, Pineda and Lopez 2002, Hagerty et al. 2018, Hargenrader 2018) making it a good location for the study of larval transport. Additionally, various studies centered on settlement, recruitment and dispersal of larvae, specifically barnacles, have been conducted a few kilometers north of this site (Shanks 1986, Pineda 1994, Tapia and Pineda 2007, Tapia et al. 2010). Thus, we can compare our results with those of other researchers to provide greater understanding of barnacle population dynamics.

More recently, a study conducted off Bird Rock for a two-year period examined the cross-shore (100's of meters) and vertical distribution of barnacle larvae (10's of meters) (Hagerty et al. 2018). Hagerty et al. (2018) found ontogenetic patterns for *C. fissus* larvae both horizontally and vertically regardless of sampling season. The ontogenetic vertical distribution of larvae showed no correlation to the hydrodynamic and hydrographic conditions of the water column; however, the increased stratification correlated with increased cyprid density at sites closest to the intertidal adult habitat. Thermal fluctuations at tidal frequencies can be significant around this area, with large vertical differences exceeding 1°C per meter (Cairns and La Fond 1966, Hagerty et al. 2018, Sinnett and Feddersen 2019). These variations tend to be

highest during summer and significantly influence the stratification profiles (Arthur 1954, Cairns and La Fond 1966, Hagerty et al. 2018). Pineda et al. (2018) also found *C. fissus* recruitment to be highest during the summer. Still, the gaps in knowledge on how daily physical variations in nearshore waters impact behavior, vertical migration and overall larval dispersal remains.

1.5 Significance

Larval transport is a crucial aspect of population connectivity, so studying its mechanisms is fundamental in our modelling of population dynamics, and improves conservation practices (Shanks et al. 2003), and the management of fisheries around the world (Reyns et al. 2007, Cowen and Sponaugle 2009). Knowledge on the dispersal and vertical migration of barnacle cyprids can be applied to understand larval transport for other benthic species with pelagic larvae. Additionally, looking at how vertical distribution varies at hourly intervals will allow to us to better depict diel patterns, and how these relate to physical processes in the water column. Finally, my study is amongst the first to address nearshore waters near the adult habitat, a critical yet understudied domain.

Our findings will help elucidate how cyprids aggregate in higher concentrations close to shore and the conditions that promote this behavior. Additionally, since most benthic organisms living in the intertidal zone have planktonic larvae that must return to shore to successfully metamorphose and complete their life cycle (Pineda, 2000), the results of this study can be applied

to better understand how other species susceptible to similar forcings regulate their offshore dispersal and transport to shore.

1.6 Objectives and Research Questions

The importance of larval transport and its implications on population dynamics have been extensively studied off the coasts of La Jolla, San Diego, CA (Shanks 1986, Pineda 1994, Tapia and Pineda 2007, Tapia et al. 2010, Hagerty et al. 2018). Research on barnacle larvae in this area has shown that barnacle larvae exhibit specific horizontal and vertical patterns, and that thermal stratification in the water column is a driver for cyprid accumulation in shallow nearshore waters (Hagerty et al. 2018). This study aimed to further our understanding of the role thermal stratification plays during larval transport, by using high frequency sampling to address the following questions:

I. How does the vertical distribution of *C. fissus* cyprids change during a diel cycle?
II. Is there a relationship between hydrodynamic and hydrographic conditions (temperature and currents) and the vertical distribution of cyprids?
III. How do changes in the depth of the thermocline influence the vertical position of cyprids throughout a 24h period?

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CHAPTER 2:

Nearshore vertical distribution of barnacle cyprids: temporal patterns and hydrographic variability

2.1 Abstract

The vertical distribution and concentration of barnacle cyprids were measured in a nearshore, shallow region off Bird Rock, La Jolla, California, USA. We collected high-resolution physical measurements at 3 stations within 1 km from shore, and high-frequency measurements of barnacle larvae at a 4m-deep station ~300 m from shore. Larvae were sampled hourly for overnight periods that ranged between 13 to 24-hours, during five cruises during the summers of 2017 and 2018. Larval samples were collected using a semi vortex pump from distinct 1m depth intervals (0-1m, 1-2m, 2-3m, 3m-bottom), and by filtering water through a 118 μm mesh net. Barnacle cyprids of *Chthamalus fissus* predominated in all samples. Distinct differences were observed in the vertical distributions of *C. fissus* cyprids between day and night, as cyprids were found deeper in the water column during the day. Results also showed that increases in stratification yielded higher cyprid concentrations at 4m, and that as stratification at 4m increased, so did the depth of the thermocline. Additionally, we found that the vertical distribution of cyprids was correlated to stratification and the depth of the thermocline. As the thermocline deepened at the 4m site, cyprids were distributed more evenly through the water column. These results suggest that stratification has a significant role on nearshore larval transport, by allowing the thermocline to penetrate closer to shore, and more cyprids to accumulate at 4m and thus increase

their chances of successful settlement and recruitment to the nearshore intertidal adult habitat.

2.2 Introduction

Most benthic marine organisms settling in the intertidal zone have planktonic larvae that reside temporarily (days to weeks) in the water-column before returning to shore to complete their life cycle. Therefore, the extent of settlement and recruitment of benthic organisms relies, in part, on successful larval transport. Larval transport, defined as the mean horizontal translocation of larvae between points along a specified one-dimensional axis per unit time (Pineda and Reyns 2018) is a critical component of larval dispersal, defined as the spread of larvae from spawning to settlement site (Pineda 2000). Studying the mechanisms of larval transport is fundamental to conserve marine species, manage fisheries, improve modeling of population dynamics (Cowen and Sponaugle 2009), and understand population connectivity (Pineda et al. 2007).

The physical processes and biological mechanisms driving larval transport have been extensively studied, and yet remain poorly understood in the nearshore (reviewed in Pineda and Reyns 2018). This is partly because studies on intertidal species suggest that larval transport and dispersal of these populations can be episodic, and occurs at smaller spatial scales than previously anticipated, with larvae often remaining within the nearshore close to settlement sites (Shanks et al. 2003, Tapia and Pineda 2007, Hagerty et al. 2018). The generally poor horizontal swimming capabilities of larvae (Chia et

al. 1984) makes them susceptible to be swept away due to the advective nature of coastlines (Lentz 1995). However, larval behavioral responses are key to regulating dispersal and improving chances of returning to a settling site. These behaviors include altering vertical distribution through vertical swimming and buoyancy control (DiBacco et al. 2011, Daigle and Metaxas 2011), and allow larvae to exploit vertically sheared flows and ultimately control horizontal transport (e.g., Wiedberg et al. 2019).

Understanding the extent of this behavior in the nearshore is challenging because conditions can be unpredictable and highly variable (Winant and Bratkovich 1981, Kaplan et al. 2003, Bonicelli et al. 2016, Morgan et al. 2018). Physical processes in shallow coastal waters are affected by bathymetry, topographic features (Lerczak et al. 2003), internal tides (Woodson 2018, Wiedberg et al. 2019), and wind-driven processes (i.e. wind-driven currents and waves) (Huyer et al. 1988, Griffin and Middleton 1991, Middleton and Ramsden 1996), and other meso- and large-scale physical processes that impact the water column from scales of seconds to days to seasons (e.g., Sinnett and Fedderson 2019), all of which affect larval transport and dispersal (Pineda et al. 2007). Moreover, alongshore flow tends to dominate in these shallow environments with implications on cross-shore flow through Ekman processes that cause variation in flow direction through the water column (Lentz and Fewings 2012). Thus, larvae occupying different depths will be advected in different directions (McEdward 1995). Alongshore currents can impact the vertical distribution and cross-shore transport of larvae

nearshore at hourly time scales (MacTavish et al. 2016), underlining the importance that small temporal scale processes play in larval transport. Therefore, it can be expected that hourly changes in the vertical profile of the water column can alter flow dynamics at different depths (Walter et al. 2012, 2014) and that these may impact larval transport. However, there is still a gap in knowledge on how dynamic changes in the hydrographic and hydrodynamic conditions of the water column impacts the vertical distribution of larvae in shallow waters.

Since studies have mostly looked at fish larvae in deeper waters (~200m) where the vertical profile is driven by large-scale oceanographic processes (Gray 1996, Rodriguez et al. 2006), the degree to which larvae are able to regulate transport under a rapidly changing environment in the nearshore is largely unknown. Still, vertical migration has been observed to change under varying physical conditions. For instance, a laboratory study on sea scallop larvae found larvae near the bottom during stratified conditions (Daigle and Metaxas 2011), and Lloyd et al. (2012) found gastropod, bivalve and polychaete larval abundances to be highest below the thermocline. This is important because fish larvae and other zooplankton have been associated with the thermocline depth (Haney 1988, Harris 1988, Gray and Kingsford 2003). These findings suggest that larvae respond and exhibit behaviors in response to water-column dynamics. Thus, it is possible that changes in the thermocline depth could potentially act as a barrier to vertical distribution (Metaxas 2001, Lloyd et al. 2012) and impact larval transport (Pineda and Lopez 2002, Gray

and Kingsford 2003). Furthermore, recent findings suggest that increases in thermal stratification within the nearshore results in larval accumulation closer to shore and limits offshore dispersal (Hagerty et al. 2018). It is possible that higher stratification promotes the development of fronts, tidal bores, or other internal motions that aid onshore larval transport (Pineda 1999, Shanks et al. 2003, Wiedberg et al. 2019). In shallow waters, these internal motions tend to result from tidal flows interacting with bathymetric features, and can travel towards shore along the thermocline (Pond and Pickard 1983, Holloway 1987). The extent of how larvae can exploit onshore flow by altering their vertical position may have profound consequences on successful recruitment of benthic populations and should be characterized at fine temporal resolutions to be better understood.

Barnacles are a great model species because they have a typical marine invertebrate lifecycle, and are very abundant, and knowledge on the vertical migration of their larvae can help to understand larval transport of other benthic species with pelagic larvae. These benthic organisms have seven larval stages: six naupliar stages that develop further from shore than the final non-feeding cyprid larval stage, which resides in nearshore waters (Tapia and Pineda 2007, Bonicelli et al. 2016, Hagerty et al. 2018). Barnacle larvae exhibit ontogenetic differences in vertical distribution (Tapia et al. 2010, Hagerty et al. 2018), may move below the thermocline during upwelling conditions to exploit shoreward transport (Shanks et al. 2003, Shanks and Brink 2005), and may display changes in vertical position during diel cycles

(dos Santos et al. 2007) and in laboratory conditions in response to downwelling flows (DiBacco et al. 2011). More recently, a study found that cyprids aggregate in high concentrations in shallow nearshore waters when offshore waters are more stratified (Hagerty et al. 2018), underlining that both physical processes and behavior are key to cyprid onshore transport. Further, thermal stratification decreased with the shallowing bathymetry of their study site and was hypothesized to result in barnacle cyprid aggregations nearshore (280m) at shallow depths (4m) (Hagerty et al. 2018). We propose that a breakdown in thermal stratification at the nearshore station, 280m from shore, arrests onshore flow associated with internal motions, and results in larval retention.

Studying how barnacle larvae alter their vertical position at fine time scales will allow us to better understand the mechanisms impacting larval transport in shallow, nearshore waters. The objective of the present study was to measure how the vertical distribution of cyprid larvae changes over a 24-hour period, in relation to changes in hydrodynamic and hydrographic conditions using a fine temporal-scale (minutes to hours) sampling resolution. Because cyprids have been observed to alter their vertical distributions (dos Santos et al. 2007, Tapia et al. 2010, Hagerty et al. 2018), we predicted that cyprid larvae would alter their vertical position in response to thermal stratification and changes in thermocline depth to exploit onshore transport and limit offshore dispersal. This study aimed to provide insight on how behavior

and distribution is driven by dynamic conditions at a relatively shallow, nearshore site.

2.3 Materials and Methods

2.4.1 Study site

This study was conducted offshore of Bird Rock, La Jolla, California, USA (Fig. 2.1) within the South La Jolla State Marine Reserve, a marine protected area (MPA). This region hosts large populations of adult barnacles, especially those of the dominant species *Chthamalus fissus,* and larval recruitment occurs throughout the year (Hoffman 1989, Pineda 1991, Pineda 1999, Pineda and López 2002, Tapia et al. 2010, Hagerty et al. 2018, Pineda et al. 2018). Sampling occurred at the same 4m deep station sampled by Hagerty et al. (2018) where cyprid accumulation was observed when offshore waters were stratified. The purpose of this follow-up study was to examine high-frequency (hourly) variations of cyprid vertical distribution with respect to hydrodynamic and hydrographic conditions in the water column, to better understand the processes contributing to larval transport at this relatively shallow, and nearshore location. Sampling was conducted during June and July (hereafter summer) 2017 and 2018, corresponding to periods of high barnacle settlement (Pineda 1994, Pineda et al. 2018) and thermal stratification (Winant and Bratkovich 1981, Hagerty et al. 2018).

2.4.2 Plankton Sampling

Samples were taken from a 7.6m boat anchored at a fixed, shallow (average 4m deep over a tidal cycle) nearshore station (Fig. 2.1) during 5 cruises: Cruises 1 and 2 were conducted July 16-17 and July 25-16, 2017, respectively, while Cruises 3, 4 and 5 were conducted June 7-8, June 21-22 and July 16-17, 2018, respectively. Plankton were sampled hourly using a Dominator submersible semivortex pump (Ebara 50DWXU6.4S) to filter $2m^3$ of seawater from distinct 1m depth intervals extending from the surface to the bottom (0-1m, 1-2m, 2-3m and 3m- to the seafloor bottom [~4m]). Seawater was filtered using a 118-μm mesh net to collect all stages of barnacle larvae, and samples were immediately preserved in 100% ethanol. Due to equipment failure during some cruises, the number of sampling hours differed for each cruise (Cruise 1= 13 hours; Cruise 2= 14 hours; Cruise 3= 23 hours; Cruise 4= 19 hours; and Cruise 5= 24 hours); however, all cruises were sampled during the night (Table 2.1). Plankton samples were quantitatively subsampled using a Folsom plankton splitter, and larvae were enumerated and identified using a dissecting microscope (Olympus SZX2-ILLD). Barnacle cyprids were identified to species based on preexisting morphological descriptions (Lewis 1975, Branscomb and Vedder 1982, Brown and Roughgarden 1985, Miller et al. 1989, Miller and Roughgarden 1994, Shanks 2001, Hagerty et al. 2019). Six total species of barnacle larvae were identified, including *C. fissus* (92% of counted individuals), *Pollicipes polymerus* (7%), with 1% of the cyprids comprised of *Balanus glandula, Balanus trigonus, Tetraclita rubescens,* and *Megabalanus californicus*. Only two individual cyprids remained unidentified.

Given the low concentration of other species, *C. fissus* cyprids will hereafter be the focus of this study.

2.4.3 Hydrographic and Hydrodynamic Measurements

A SonTek CastAway-CTD was used to record temperature and depth profiles every ~7 minutes throughout the plankton sampling period. Since stratification in this region is primarily driven by thermal variation (Hagerty 2017), salinity measurements collected from the CTD casts were not used. Two temperature moorings were deployed to provide longer temporal scale context of offshore thermal stratification during periods of plankton sampling: one mooring at the 5m-deep station (~300m from shore) and one at the 8m-deep station (~600m from shore) during both years (Fig 2.1). SBE-56 thermistors were deployed at 1-m depth intervals on both moorings, such that the 5m and 8m moorings had 4 and 6 instruments, respectively, programmed to record temperature every 5 seconds. Finally, a 1Mhz Nortek Aquadopp acoustic Doppler current profiler (ADCP) was deployed near the 4m deep station at roughly 5m depth (adjacent to 5m temperature mooring) to measure current velocities every 90 seconds in 0.5m depth intervals (Fig 2.1). Current directions were rotated to align with the coastline and separated into cross-shore (positive onshore) and alongshore (positive southward) components. The average current velocity was calculated for both summer 2017 and 2018.

2.4.4 Contour Profiles

To visualize the hydrographic conditions at each station, contour profiles were created from the temperature data using the contourf function in MATLAB R2019a with specified contour levels of 25 for the CTD data, and 5 for the thermistor data. Similarly, current velocity contours were created with 5 contour levels for hourly averages of the alongshore and cross-shore currents. The vertical distribution of *C. fissus* cyprid concentrations (standardized as no. larvae m^{-3} for Cruises 1, 2, and 4, or as no. larvae m^{-3} *10^{-1} for Cruises 3 and 5 when larval concentrations were high) were overlaid on the contour plots to examine patterns and relationships between the physical conditions of the water column and vertical position of cyprids

2.4.5 Larval Distribution

The vertical distribution for *C. fissus* cyprids was determined by calculating their Mean Depth Distribution (MDD, Tapia et al. 2010) for every hour of sampling using the following equation:

$$\text{MDD} = \frac{\sum(\text{no. larvae m}^{-3} \text{ in sample interval} \times \text{mean depth of sample interval})}{\sum(\text{no. larvae m}^{-3} \text{ of sample interval})}$$

To account for the variability of vertical larval distributions per hour, the variance corresponding to the MDD (VDD) was calculated for every hour of sampling using the equation:

$$\text{VDD} = \frac{\sum \text{no. larvae m}^{-3} \text{ in sample interval} \times (\text{depth}_i - \text{MDD})^2}{\sum (\text{no. larvae m}^{-3} \text{ of sample interval})}$$

To resolve diel vertical distribution patterns, sampling hours were separated into day and night based on the hours of civil twilight, defined as the time when the geometric center of the sun is 6 degrees below the horizon. Hence, civil twilight sunrise begins when the sun is 6 degrees below the horizon and civil twilight sunset ends when the sun is 6 degrees below the horizon (National Weather Service, NOAA). We used separate one-way analysis of variance (ANOVA) tests to determine if there were day-night differences (all cruises combined) in the *C. fissus* cyprid MDD, VDD, and depth of maximum concentration. ANOVA assumptions of normality and homogeneity of variance were met.

2.4.6 Hydrographic and Hydrodynamic Relationships

Thermal stratification was defined as the change in temperature m^{-1} ($\Delta°Cm^{-1}$) and calculated as follows for the hourly average temperature:

$$\text{Thermal Stratification} = \frac{(\text{temperature at surface} - \text{temperature at bottom})}{(\text{depth of bottom temperature} - \text{depth of surface temperature})}$$

Thermal stratification values were categorized as stratified when $\Delta°Cm^{-1} \geq 0.1$ (Sinnett and Feddersen 2019). Thermocline depth was calculated as the depth where the maximum change in temperature occurred and was

ignored when the water column was considered unstratified. Two one-way ANOVA's were performed to test whether thermocline depth and thermal stratification varied between day and night periods, and the relationships between the MDD of *C. fissus* cyprids with thermal stratification and thermocline depth were investigated using correlation analysis.

2.4 Results

2.4.1 General conditions: thermal stratification and larval concentrations

Thermal stratification for the mooring data (8m and 5m station) and the CTD data (4m station) were calculated and averaged. Mean thermal stratification was greater at the 8m deep station and decreased with decreasing distance from shore (Table 2.1). Lowest thermal stratification values were generally at the 4m deep station, with the exception of Cruises 3 and 5 when thermal stratification at the 4m deep station slightly increased in comparison to the 5m deep station (Table 2.1). These two cruises also corresponded to the dates with the highest offshore (8m deep station) thermal stratification with values exceeding 0.5 $\Delta°Cm^{-1}$, and the largest *C. fissus* cyprid concentrations (Table 2.1). In contrast, Cruise 4 had the lowest mean thermal stratification of all sampling dates, with minimal stratification offshore (< 0.3 $\Delta°Cm^{-1}$) and unstratified conditions at the 5m- and 4m-deep stations, and the lowest cyprid concentrations (Table 2.1). Thermocline depth varied hourly for all cruises and showed no distinct patterns between day and night (Appendix A, B).

2.4.2 Temperature, currents, and cyprid distributions

Cruises during the summer of 2017 (Cruises 1 and 2) had overall warmer temperatures than those during summer 2018 (Cruises 3-5; Fig. 2.2, Appendix C: Figs. C1- C3). At the 4m deep plankton station, temperatures during Cruises 1 and 2 were similar, between ~ 22.5 °C to 24°C, while Cruises 3, 4 and 5 had cooler temperatures ranging between 19°C to 24°C. The minimum temperature recorded was 18.6°C during Cruise 3 and the highest temperature was 24.2°C for Cruise 2 (Fig. 2.2). The coolest temperatures occurred at the 8 m station in all cruises.

Depth-averaged currents during the summer of 2018 were stronger in both the cross-shore and alongshore directions than those during summer 2017. The average (± standard error) cross-shore current velocity was -0.0049 ms^{-1} ± (0.0001) for the summer of 2017 and -0.0149 ms^{-1} (± 0.0001) for the summer of 2018. The average (± standard error) alongshore current velocity was -0.0064 ms^{-1} (±0.0003) for the summer of 2017 and -0.0134 ms^{-1} (± 0.0003) for the summer of 2018. Thus, mean alongshore and cross-shore currents in both years were northward and offshore (westward). However, higher-frequency temperature and current variations occurred during each cruise (see below) that are not reflected by these mean calculations.

Cruise 1 –

The water column at the 8m and 5m deep stations was more stratified than at the 4m deep station (Fig. 2.3; Table 2.1), and temperature range was 16.7-22.7°C (Fig. 2.3A; Table 2.1). In general, when currents were northward,

cross-shore currents were minimal or onshore (Fig. 2.3C, D). Current reversals in the alongshore direction occurred twice (from northward to southward, and back to northward) during the sampling period (Fig. 2.3D). Northward currents corresponded to periods when warmer waters were observed at the 5m deep station (Fig. 2.3B). Although the 4m deep station (where larval sampling took place) only varied by ~1°C throughout sampling (Fig. 2.2A, 2.3E), 69% of the sampling time was considered stratified ($\Delta°Cm^{-1} > 0.1$). Average (± standard error) concentrations of *C. fissus* cyprids ranged from 4 to 536 (± 2.10) no. larvae m^{-3} (Table 2.1, Fig. 2.3E). Highest larval concentrations were mostly found between 2-3 meters depth and coincided with periods when currents were predominately northward (Fig. 2.3D, E).

Cruise 2 –

The water column at the 8m and 5m deep stations was more stratified than at the 4m deep station (Fig. 2.4A, B, E; Table 2.1), and temperature range was 19.4-23.7°C (Fig. 2.4A; Table 2.1). During this cruise, northward currents were associated with minimal cross-shore currents, and halfway through larval sampling there was a period of strong current reversals (Fig 2.4C, D). These reversals penetrated much of the water column and reversed from northward with minimal cross-shore currents and slightly onshore currents, to southward and offshore flow, and back to northward with a reduction in the cross-shore currents by the end of larval sampling. Temperatures at the 4m deep station varied between ~1-2 °C (Fig. 2.2B, 2.4E), and for 86% of the larval sampling

time, the water was considered stratified. The appearance of warmer waters at the 5m deep station and incoming cooler ones at 4m deep station at about ~ 1am PST (Fig. 2.4B, D, E) coincided with the predominately southward current reversal. Average (± standard error) concentrations of *C. fissus* cyprids ranged from 8 to 288 (± 7.44) no. larvae m^{-3} (Table 2.1, Fig. 2.4E). Although larvae were found throughout the water column during all hours sampled, concentrations were highest in the bottom depth bins sampled (between 2-3 and 3-4 meters, Fig. 2.4E), and to some extent, increases in larval concentration, and a slightly shallower distribution, corresponded to the alongshore current reversals (Fig. 2.4D, E).

Cruise 3 –

In general, temperatures for this cruise were colder than 2017 and vertical temperature differences were larger (~4 to 5°C) (Fig. 2.2C; 2.5A, B, E). The water column at the 8m- and 4m- deep stations was more stratified that at the 5m deep station (Fig. 2.5A, B, E; Table 2.1), and temperature range was 15.8-20.8°C (Fig. 2.5A; Table 2.1). Cross-shore currents were mostly offshore and alongshore currents were minimal and mostly northward throughout larval sampling (Fig. 2.5C, D).

Stratification at the 4m deep station was the highest recorded of all cruises for this station; and the water column was stratified 96% of the larval sampling time (Fig. 2.5E; Table 2.1). Average (± standard error) concentrations of *C. fissus* cyprids ranged between 0 to 6433 (± 98.6) no.

larvae m^{-3} (Table 2.1, Fig. 2.5E). The highest concentrations occurred in the 3-4m depth bins at the beginning of larval sampling (13:00-15:00 PST), after which concentrations shallowed (18:00-20:00 PST) with maximum concentrations within the 2-3m depth bin (Fig. 2.5E). Although this increase in cyprid concentrations closer to the surface corresponded to a period of warming water in the top half of the water column (Fig. 2.2C and 2.5E), it appears that larvae were closer to the bottom at the start of sampling, but moved shallower at the onset of warm surface waters, then remained mid-depth after waters cooled (Fig 2.5E). Larval distributions displayed no clear pattern with currents (Fig 2.5C, D, E).

Cruise 4 –

Although this cruise had the lowest stratification of all cruises, the water column at the 8m and 5m deep stations remained more stratified than at the 4m deep station (Fig. 2.6A, B, E; Table 2.1). Temperatures for this cruise were generally cool (Fig. 2.2) with a temperature range of 18.1-20.5°C (Fig. 2.6A; Table 2.1). Cross-shore currents were mainly offshore, while alongshore currents were minimal at the start of larval sampling and then became more northward (Fig. 2.6D, E). At the 5m station, cooler waters at ~5am PST corresponded with stronger northward currents (Fig. 2.6B, D). Temperatures at the 5m and 4m deep stations changed little for the majority of sampling, and at the 4m deep station waters were only stratified 21% of the larval sampling time. Average (± standard error) concentrations of *C. fissus* cyprids ranged

from 0 to 280 (± 5.88) no. larvae m^{-3} (Table 2.1). Concentrations were generally higher between 2-3m and there was an overall decrease of cyprids at night. Increases in cyprid concentrations at bottom and mid-depths occurred when waters were cooler and alongshore currents were northward and cross-shore currents were minimal (Fig 2.6C, D, E).

Cruise 5–

The water column at the 8m- and 4m-deep stations was more stratified that at the 5m deep station (Fig. 2.7A, B, E; Table 2.1), with a temperature range of 18.3-23.3°C (Fig. 2.7A; Table 2.1). In general, alongshore currents were flowing northward with slight reversals near the surface, and cross-shore currents were mostly offshore except at the beginning and end of larval sampling where bottom water was onshore (Fig. 2.7C, D). Temperature at the 4m deep station varied ~2°C (Fig. 2.2E; 2.7E), and the water remained stratified for the entire duration of plankton sampling. Average (± standard error) concentrations of *C. fissus* cyprids ranged from 36 to 4609 (± 91.7) no. larvae m^{-3} (Fig. 2.7E; Table 2.1). Although the maximum concentration was generally in the 2-3m depth bin, several times during larval sampling, cyprid concentrations evened out through the water column and accumulated near the surface (Fig. 2.7E). Cyprid concentrations fluctuated substantially and large increases in concentrations corresponded to alongshore current reversals, with higher concentrations when flows shifted from northward to southward (Fig. 2.7D, E).

2.1.1 *Diel larval distribution patterns*

Larval concentrations were higher overall in 2018, and cyprids were most abundant during Cruise 3 and 5 (Table 2.1, Appendix D). The vertical position and concentration of *C. fissus* cyprids differed between day and night (Fig 2.8A, B, Appendix B). Overall, *C. fissus* cyprid concentrations were 30% higher during the day (Fig. 2.8A) than at night (Fig. 2.8B). The center of mass of cyprid distribution was between 2-3m during both day and night, yet distribution changes were observed in the surface- (0-1m) and bottom-most (3-4m) sampling depth bins (Fig. 2.8A, B). Cyprid concentrations were relatively high at 3-4m and low at 0-1m depth bins during the day, while at night concentrations near the surface increased and became very low at 3-4m depths (Fig. 2.8A, B). To further elucidate the differences between day and night patterns, we examined how the average proportion of *C. fissus* cyprids changed for each hour of the day sampled. Cyprid proportions in the 2-3m depth bin remained mostly stable when comparing the average proportion during the day (34%) and at night (35%) (Fig. 2.8C). Similarly, cyprid proportions in the 1-2m bin had an average proportion of 20% during the day and 26% at night. Contrastingly, the 0-1m depth bin had an average proportion of 12% during the day and 24% at night, and the 3-4m depth bin an average proportion of 34% during the day and 15% at night (Fig 2.8C). Interestingly, cyprids displayed changes in vertical distribution in the hours corresponding to sunset and sunrise, ascending to shallow depths during sunset and going deeper around

sunrise (Fig. 2.8C). Diel changes in cyprid concentrations was not related to diel changes in thermal stratification, which were marginally insignificant between day and night (p=0.087).

MDD values were significantly different between day and night (p= 0.011, Table 2.2; Fig. 2.8A, B). The MDD was deeper during the day (Day MDD= 2.30m, Night MDD= 2.06m, Fig. 2.8A, B). The depth of the maximum concentration for *C. fissus* cyprids was also significantly different for day and night (p= 0.009, Table 2.2), and was deeper during daytime than at night (Day= 2.62m and Night = 2.14m).

2.4.3 Larval distribution and relationships between physical variables

To test whether distribution patterns were influenced by the water height, water levels were calculated by sorting daily tidal level data from Scripps Institution of Oceanography (gauge #9410230) collected by the National Oceanographic and Atmospheric Association (NOAA) into thirds to determine when sea level was considered low (<0.73m), medium (>=0.73m and <1.138m) and high (>=1.138m). The tidal station is located 10 km north of our field site. A one-way ANOVA between MDD and water levels showed no significant difference for MDD at different water levels (p= 0.563, Appendix B). In addition, we checked if tidal ebbing/flooding and time of day affected MDD. Ebbing conditions included all data points in which the tide was retreating, and flooding included those when the sea level was rising. We conducted a one-way ANOVA to test if the MDD was significantly different

during ebb/flood conditions (p=0.284; Appendix B). Additionally, there was no significant correlation between MDD and thermocline depth (p=0.278), or thermal stratification (p=0.805; Appendix E).

However, there was a positive correlation between the VDD and the depth of the thermocline (Pearson's R= 0.423, p=0.000 (Fig. 2.9A), as well as VDD and thermal stratification (Pearson's R= 0.333, p=0.001) (Appendix E). This indicates *C. fissus* cyprids were distributed more evenly throughout the water column when the thermocline was deeper and thermal stratification was highest (Fig. 2.9A, B). VDD did not vary significantly between day and night (p=0.269, Appendix B). Additionally, there was a positive correlation between the depth of the thermocline and thermal stratification (Pearson's R= 0.425, p=0.000) (Fig. 2.9B). No clear pattern was observed between larval distributions and current velocities. However, alongshore currents seem to have greater relevance on mean larval concentrations (Appendix F).

2.5 Discussion

Chthamalus fissus was the dominant larval barnacle species at Bird Rock, La Jolla, California, USA during both 2017 and 2018. The hydrographic and hydrodynamic conditions of the water column varied between all sampling cruises, still, cyprids displayed consistent vertical distribution patterns. Even though we sampled at a relatively shallow station, cyprids remained deeper in the water column during the day, specifically within the two bottom depth bins (2-3m and 3-4m). At night, cyprids migrated away from the bottom and were

rarely found deeper than 3m. Since cyprids are non-feeding, this migration is not to track prey but could be driven by other evolutionary responses such as avoidance of visual predators (Clark et al. 2003), which is a common response of meroplankton in deeper waters (Thorson 1964, Zaret and Suffern 1976, Forward and Rittschof 2000). Regardless of the time of day, ~40% of cyprids remained within the 2-3 meter depth. This depth-distribution is consistent with those found in other studies, where cyprids were observed around 15-25m depth at a station that was 30m deep (Tapia et al. 2010), and at mid-depth of the water column at stations extending 1km offshore and to 12m depth (Hagerty et al. 2018). It is possible that deep waters are preferable for the non-feeding cyprids because cooler waters extend the lifespan of their lipid reserves, providing them with more time to reach the intertidal and increase their chances of successful settlement (see Satuito et al. 1996).

This study showed a small (~0.2m) but apparent diel difference in the center of mass of the vertical distribution of cyprids, driven by concentration changes at the bottom and surface bins around sunrise and sunset. The loss in thermal stratification at night can weaken the density gradients of the water column and decrease internal motion propagation (Walter et al. 2012, Sinnett and Fedderson 2019), potentially eliminating the mechanism that keeps cyprids near the bottom.

During periods of greatest offshore (8m deep station) stratification, we observed the highest larval concentrations (Cruises 3 and 5), which further supports the finding that increased offshore stratification leads to more

nearshore (at 4m depth) larval accumulation (Hagerty et al. 2018). Increases in thermal stratification could lead to more energetic cross-shore currents that allow internal tides to propagate shoreward enhancing larval transport and retention (Pineda 1999, Shanks et al. 2014, Wiedberg et al. 2019), and for the internal wave-guide to penetrate into shallower waters. Previous literature suggests cyprids use cool, deep bores to transport closer to shore before reaching the intertidal (Pineda 1991, Shanks et al. 2014, MacTavish et al. 2016, Fernandez-Aldecoa et al. 2019). Increases in stratification limits vertical mixing and promotes sheared flows (Winant and Bratkovich 1981, Walter et al. 2014), including two-way horizontal flows (e.g., Hagerty et al. 2018). So, changes in larval vertical distribution (Lloyd et al. 2012, Hagerty et al. 2018) could allow larvae to better regulate their horizontal distribution and their distance from shore (Shanks and Shearman 2009, Domingues et al. 2012, Pineda and Reyns 2018). For some cruises, increases of larval abundance could potentially be explained by this dynamic. However, results at the 4m station show that offshore thermal stratification does not necessarily promote a sharp thermocline at 4m. It is possible that at 4m deep, thermal stratification can become weakened by small changes in forcing such as diurnal heating near the surface, sea breeze (Woodson et al. 2007), rapid changes in bathymetry (Holloway 1987), surface waves (Sinnett and Fedderson 2019), or a deeper offshore thermocline, which affects the sharpness and depth of the thermocline close to shore (Zimmerman and Robertson 1985). These changes in thermocline have implications for onshore larval transport as seen in the

diminished high frequency flows during warm El Niño periods (Pineda et al. 2018) and reduced settlement related to low stratification (Pineda and Lopez 2002, Pineda et al. 2018). Variability of cyprid concentrations in the water may be significantly impacted by hourly temperature changes and hydrodynamic activity in nearshore waters (Fernandez-Aldecoa et al. 2019), suggesting that larval abundances and onshore transport may be driven by temperature changes driven by tidal bores and winds, which can have greater impact within the nearshore when the water is more stratified.

Despite the different hydrographic conditions during each cruise, results showed that cyprid MDD did not vary with the depth of the thermocline. These results agree with those of Hagerty et al. (2018) who found no relationship between the depth of the thermocline and cyprid MDD. Further, hourly values of MDD did not vary clearly with changes in the hydrographic and hydrodynamic variables suggesting that larval vertical distribution patterns are very dynamic.

Clear patterns between larval concentrations and currents could not be deciphered. This might be due to the limitations of our instrument, which is inherently noisy, and cannot measure currents near the bottom or at the surface. Additionally, the rough bathymetry of our study site likely added noise to the ADCP data, further muddling patterns. However, in some cases (e.g., Cruises 1, 2, 5) increased larval concentrations appeared to be associated with alongshore current reversals. These reversals might be related to surface or internal tides. For instance, Wiedberg et al. (2019) found larvae to aggregate at

the same depth where baroclinic tidal forces caused shoreward flows. Still, more studies should be conducted to test whether reversals generate fronts that might accumulate larvae on hourly time scales. Additionally, northward currents might be important drivers of onshore transport for cyprid larvae at this site. These results agree with recent findings that found alongshore currents have implications for larval transport in the nearshore (MacTavish et al. 2016). It is possible that strong northward currents promote downwelling onshore flow, due to rotation effects (Winant 1980, Smith 1981), causing an increase in larval supply at this station. These findings support the inference that in open coastlines, alongshore currents tend to be more energetic and could potentially be as relevant to larval transport by impacting the cross-shore currents (Pineda 2000, Lentz and Fewings 2012).

Further, the number of cyprid larvae collected for this study supports previous findings that cyprid larvae aggregate close to shore before reaching the intertidal (Tapia and Pineda 2007, Shanks and Shearman 2009, Morgan et al. 2017, Hagerty et al. 2018). Cyprids were abundant during all cruises and had over 20 times greater concentrations for Cruises 3 and 5. Cruises 3 and 5 had the most stratified conditions both offshore and at 4m where plankton collection was conducted. In contrast, Cruise 4 had well-mixed, unstratified conditions at both the 5m and 4m deep stations for the duration of sampling and had the lowest concentration of cyprids. We hypothesize that during Cruises 3 and 5, the zone of larval accumulation (typically ~4m deep where stratification breaks down, Hagerty et al. 2018) penetrated further into shallow

waters (< 4m deep) due to the increased stratification we observed in shallow water., This high stratification potentially allowed for offshore internal motions to propagate inshore, transporting larvae even shallower. Contrastingly, the decrease in stratification at 4m for the remaining three cruises suggests that waters were better-mixed, and suggests that the zone of larval accumulation was more extended in the cross-shore dimension, and/or deeper, than where we sampled, leading to lower overall larval concentrations at 4m. Conditions during Cruise 4, with lowest overall stratification, and lowest larval concentrations further support this hypothesis.

Additionally, our results showed that the variance in mean depth distribution (VDD) better represented the vertical distribution of cyprids in the water column than MDD, and that these variations related to the thermocline depth and thermal stratification at 4m deep. During stratified conditions, both the depth of the thermocline at the 4m deep station and VDD increased, meaning that cyprids were distributed more evenly throughout the water column. Enhanced stratification in shallow water (4m deep) may be due to increased offshore (8m deep) stratification and diurnal surface heating and could have a positive impact on the extent to which internal motions penetrate our 4m deep station, thereby increasing larval onshore transport. Moreover, the higher stratification corresponded to the presence of a sharp and deep thermocline at the 4m deep station, which promoted a more homogenous vertical distribution of cyprids. We propose that during these conditions the thermocline reaches shallower depths, and that cyprids are able to be

transported closer to shore. We hypothesize that the deep thermocline and shallow bathymetry squeeze cyprids out into the mixed layer above the thermocline and that this potentially allows them to remain near shore, and not be transported offshore during internal motion reversals (Pineda 1994). While, this study is not able to elucidate if cyprid distribute more evenly in the water column as a response to decreases in density gradients or physical processes that enhance mixing above the thermocline, larvae that are more homogenously distributed in the water column might be guaranteeing that at least some individuals make it onshore if currents are vertically sheared and dynamic (changing frequently).

This study showed that cyprid larvae underwent diel changes in their vertical distribution where cyprids were generally distributed slightly shallower at night. Additionally, the hourly sampling indicated that larval distribution was dynamic, possibly as a response to physical conditions in the water column. We demonstrated that cyprid concentration was related to thermal stratification in shallow water, and that these conditions vary at the scale of hours and days. We conclude that thermal stratification is a key factor in larval transport and accumulation at this site, and that both behavior and physical factors play an important role in facilitating successful onshore transport and accumulation of barnacle cyprids in shallow waters, with positive implications for larval supply and recruitment to the intertidal.

2.6 Literature cited

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Table 2.1 Cruise summaries with date, hours sampled, thermal stratification ($\Delta°Cm^{-1}$) at 8m- and 5m-deep mooring stations (SBE 56 thermistor data) and 4m-deep plankton station (CTD data), and *Chthamalus fissus* cyprid concentrations (no. m^{-3}): Cruise 1 (N=52 samples), Cruise 2 (N=56 samples), Cruise 3 (N=92 samples), Cruise 4 (N=76 samples), Cruise 5 (N=96 samples).

Cruise	**Date**	**Hours of sampling (PST)**	**Mean** ± SE **8m** ($\Delta°Cm^{-1}$)	**Mean** ± SE **5m** ($\Delta°Cm^{-1}$)	**Mean** ± SE **4m** ($\Delta°Cm^{-1}$)	**Mean** ± SE **concentration (range)**
1	July 16-17, 2017	17:00-5:00	0.482 ± 0.059	0.296 ± 0.045	0.153 ± 0.030	93.5 ± 2.10 (4-536)
2	July 25-26, 2017	17:00-6:00	0.433 ± 0.029	0.383 ± 0.031	0.260 ± 0.037	80.7 ± 7.44 (8-288)
3	June 6-7, 2018	10:00-9:00	0.507 ± 0.021	0.207 ± 0.014	0.328 ± 0.030	739.1 ± 98.6 (0-6434)
4	June 21-22, 2018	16:00-13:00	0.254 ± 0.005	0.087 ± 0.012	0.064 ± 0.010	40.4 ± 5.88 (18-280)

5	July 16-17, 2018	11:00-11:00	0.549 ± 0.023	0.221 ± 0.017	0.304 ± 0.020	871.42 ± 91.7 (37-4609)

Table 2.2 Results of one-way ANOVAs testing for differences in MDD, VDD, and the depth of maximum concentration of *Chthamalus fissus* cyprids during day and night. Significant differences are indicated in bold.

Variable	F	p
MDD	6.766	**0.011**
VDD	1.239	0.269
Depth Max. Concentration	7.110	**0.009**

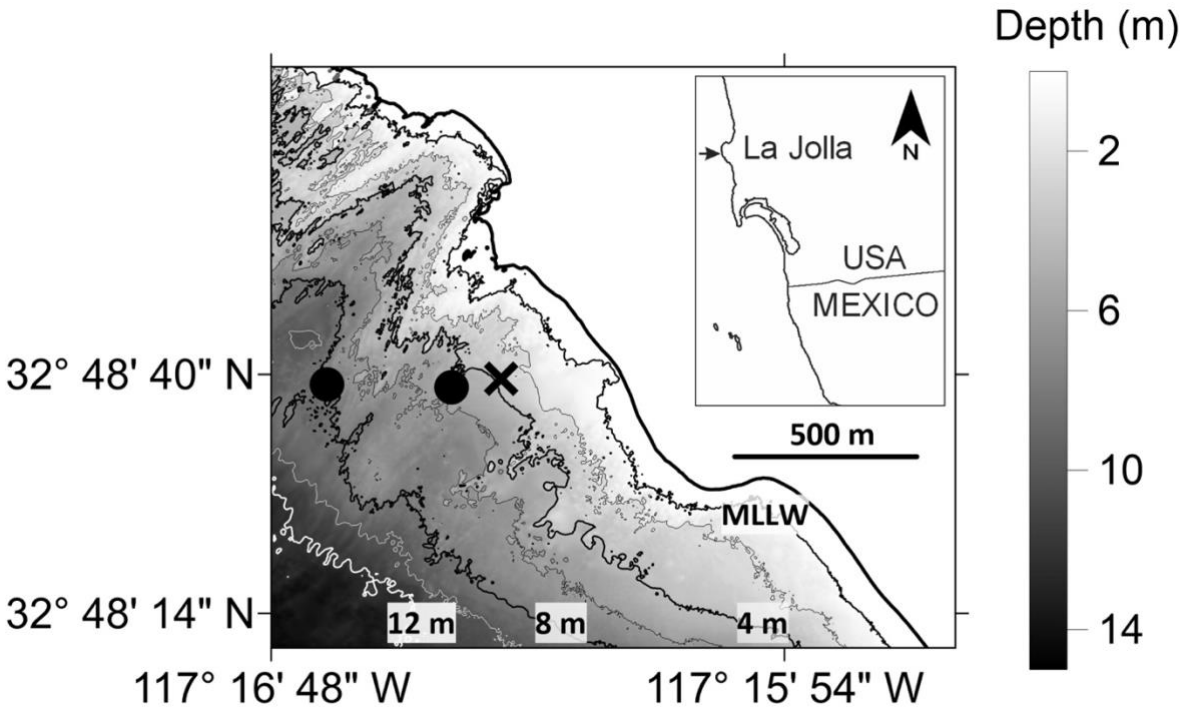

Figure 2.1 (A) Inset showing study region (indicated by arrow) off La Jolla, California, USA. **(B)** Study site at Bird Rock with nearshore bathymetry (lines = 2m isobaths). Black cross represents the 4m deep larval and CTD sampling station (280m from shore); the two black circles represent the 5m- and 8m-deep mooring stations; Nortek Aquadopp Profiler (ADCP) was also deployed near the 5m deep mooring (circles overlap).

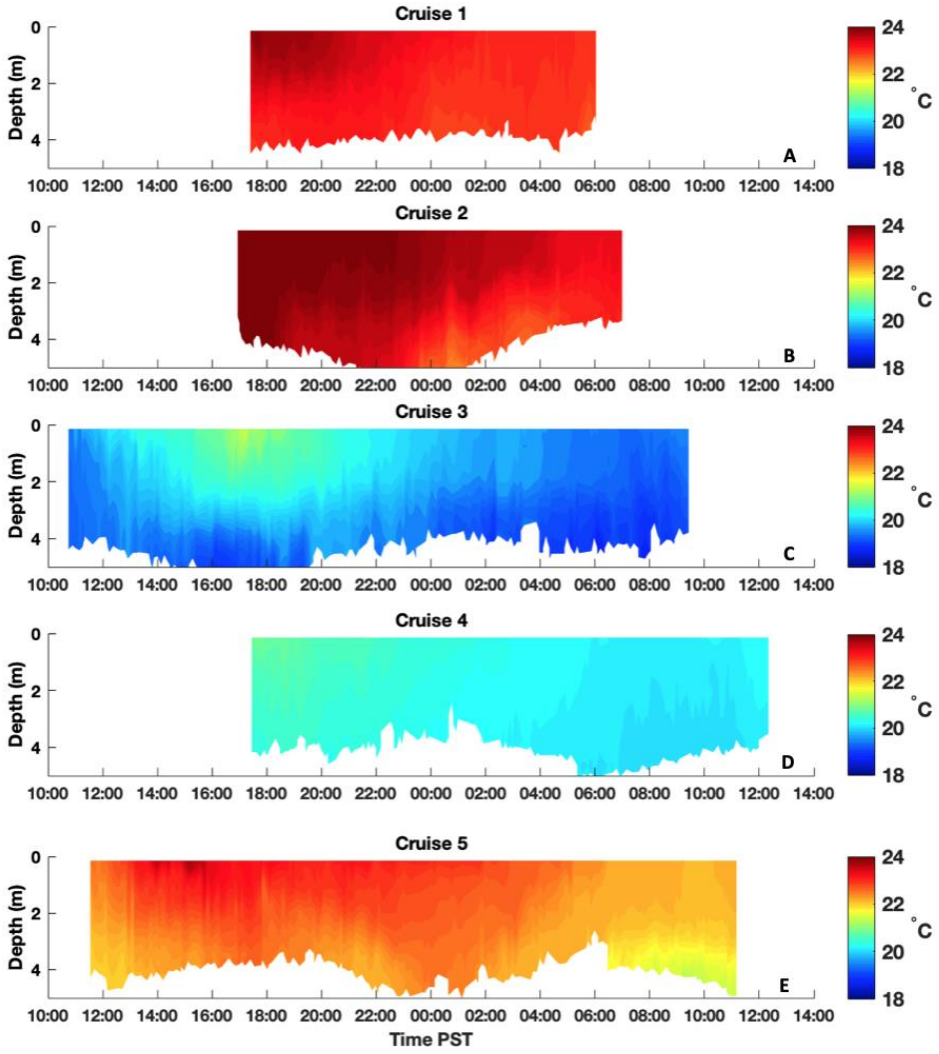

Figure 2.2 Temperature contours of CTD data collected at 4m deep station for all cruises in the summer 2017 and 2018. **(A)** Cruise 1: July 16-17, 2017 (13 hours), **(B)** Cruise 2: July 25-26, 2017 (14 hours), **(C)** Cruise 3: June 6-7, 2018 (23 hours), **(D)** Cruise 4: June 21-22, 2018 (19 hours), **(E)** Cruise 5: July 16-17, 2018 (24 hours). Note that each cruise had a varying number of sampling hours. Night-time for these sampling periods was from ~ 20:00-5:00 (PST).

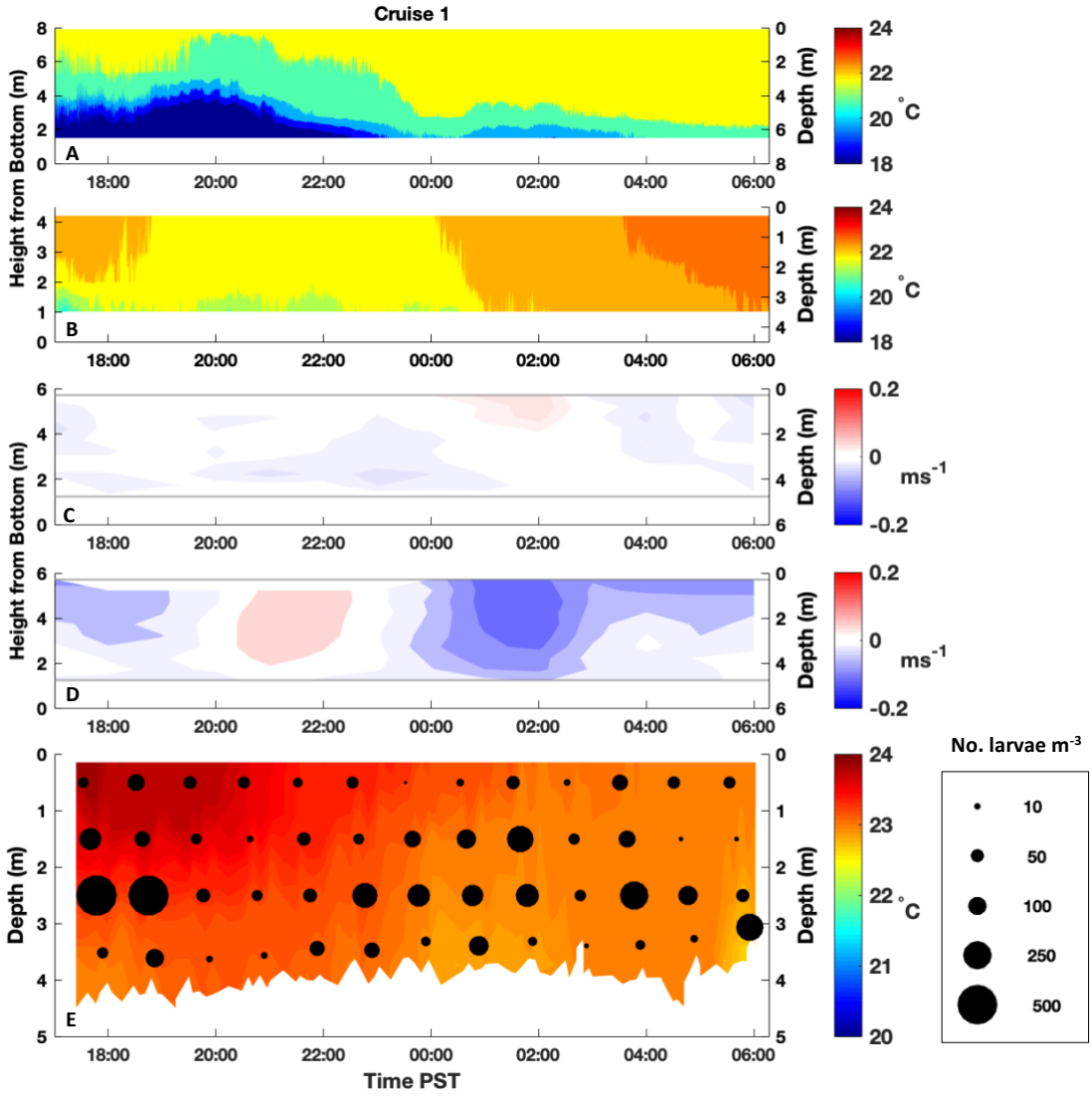

Figure 2.3 Cruise 1 (July 16-17, 2017) temperature contour plots using **(A)** SBE56 thermistors for 8m deep mooring site, and **(B)** 5m deep mooring site. Contour plots of currents (ms-1), with **(C)** cross-shore (*u*) component (positive values corresponding to onshore or eastward flow), and **(D)** alongshore (*v*) component (positive values corresponding to southward flow). The gray horizontal lines indicate the depths above and below which ADCP data are missing. **(E)** temperature contour plot using CTD data at 4m deep site with overlaid black circles representing *Chthamalus fissus* cyprid concentrations (no. m-3) in each sampling depth bin for each hour of sampling. The white area below the contour plot shows the changing water depth due to the tides. Temperature ranges vary for the 4m deep station.

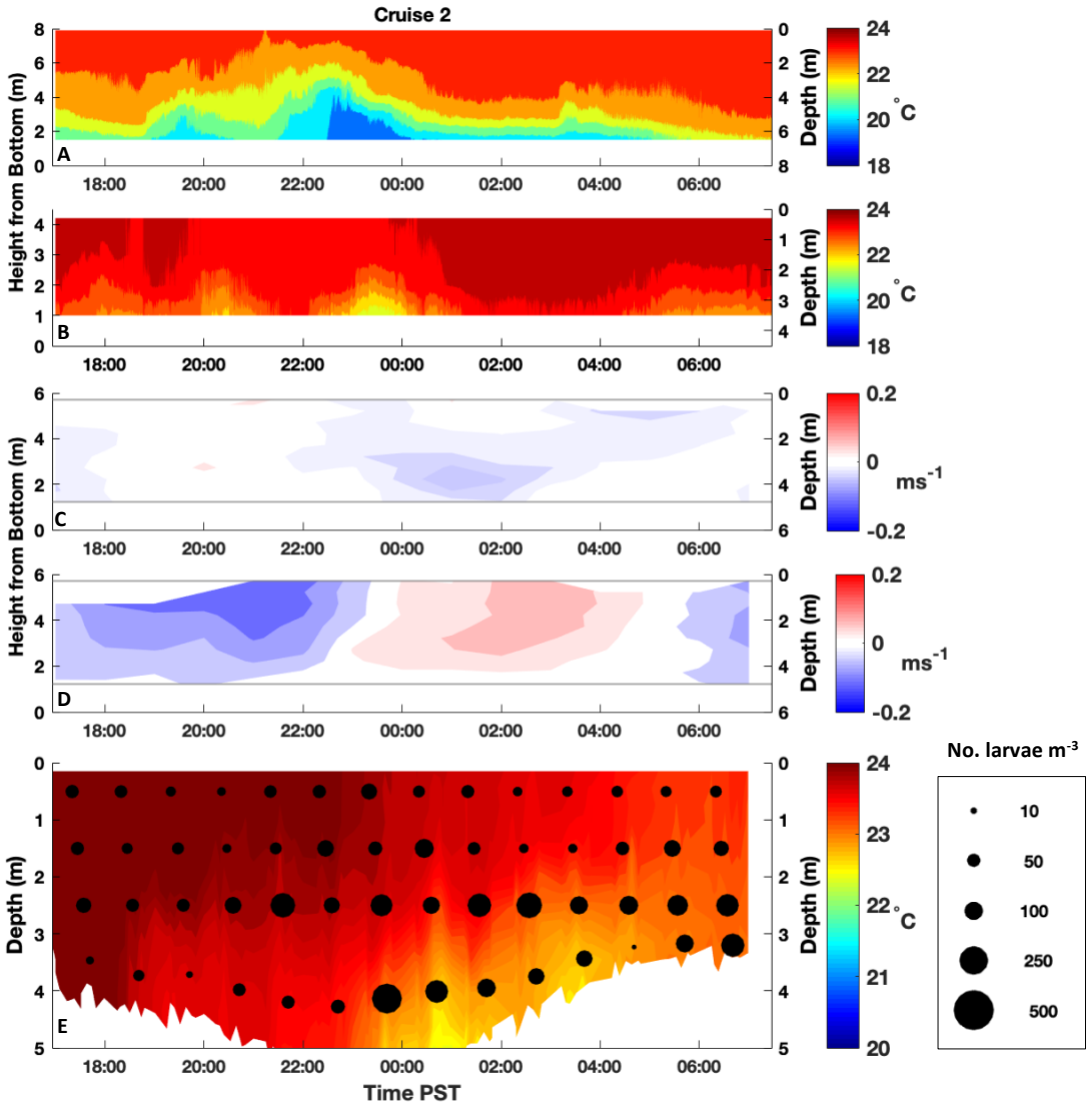

Figure 2.4 Cruise 2 (July 25-26, 2017) temperature contour plots using **(A)** SBE56 thermistors for 8m deep mooring site, and **(B)** 5m deep mooring site. Contour plots of currents (ms-1), with **(C)** cross-shore (*u*) component (positive values corresponding to onshore or eastward flow), and **(D)** alongshore (*v*) component (positive values corresponding to southward flow). The gray horizontal lines indicate the depths above and below which ADCP data are missing. **(E)** temperature contour plot using CTD data at 4m deep site with overlaid black circles representing *Chthamalus fissus* cyprid concentrations (no. m-3) in each sampling depth bin for each hour of sampling. The white area below the contour plot shows the changing water depth due to the tides. Temperature ranges vary for the 4m deep station.

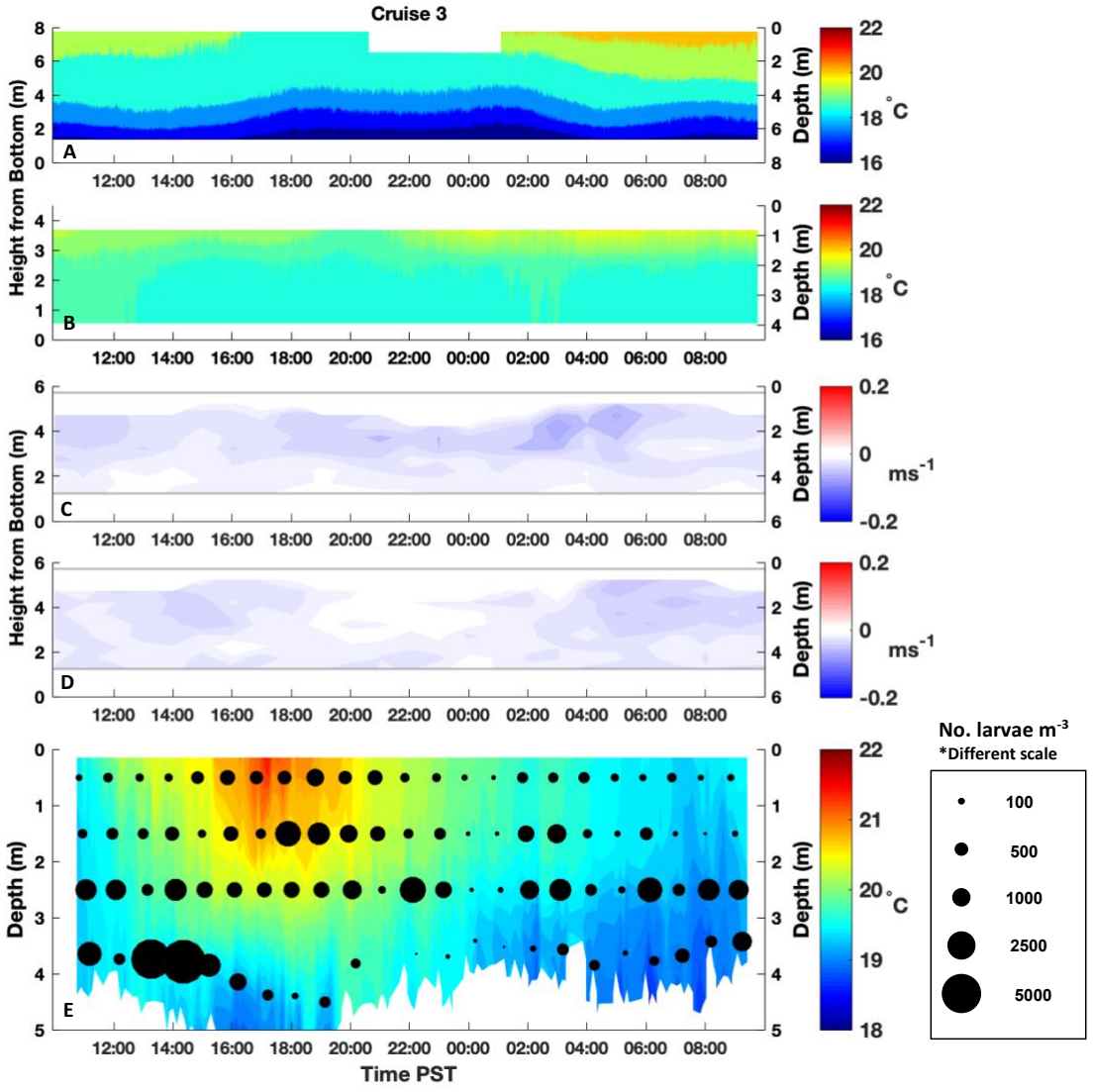
Cruise 3
Height from Bottom (m)
Depth (m)
A
B
C
D
E
°C
ms-1
12:00 14:00 16:00 18:00 20:00 22:00 00:00 02:00 04:00 06:00 08:00
Time PST
No. larvae m-3
*Different scale
100
500
1000
2500
5000

Figure 2.5 Cruise 3 (June 7-8, 2018) temperature contour plots using **(A)** SBE56 thermistors for 8m deep mooring site, and (B) 5m deep mooring site. White box at 8m site represents missing data from surface-most thermistor during low tide. Contour plots of currents (ms^{-1}), with **(C)** cross-shore (*u*) component (positive values corresponding to onshore or eastward flow), and **(D)** alongshore (*v*) component (positive values corresponding to southward flow). The gray horizontal lines indicate the depths above and below which ADCP data are missing. **(E)** temperature contour plot using CTD data at 4m deep site with overlaid black circles representing *Chthamalus fissus* cyprid concentrations (no. m^{-3}) in each sampling depth bin for each hour of sampling. The white area below the contour plot shows the changing water depth due to the tides. Note that circles denoting larval concentrations have been re-scaled relative to those depicted in Cruises 1, 2, and 4 to enhance visibility of temperature contours. Temperature ranges vary for the 4m deep station.

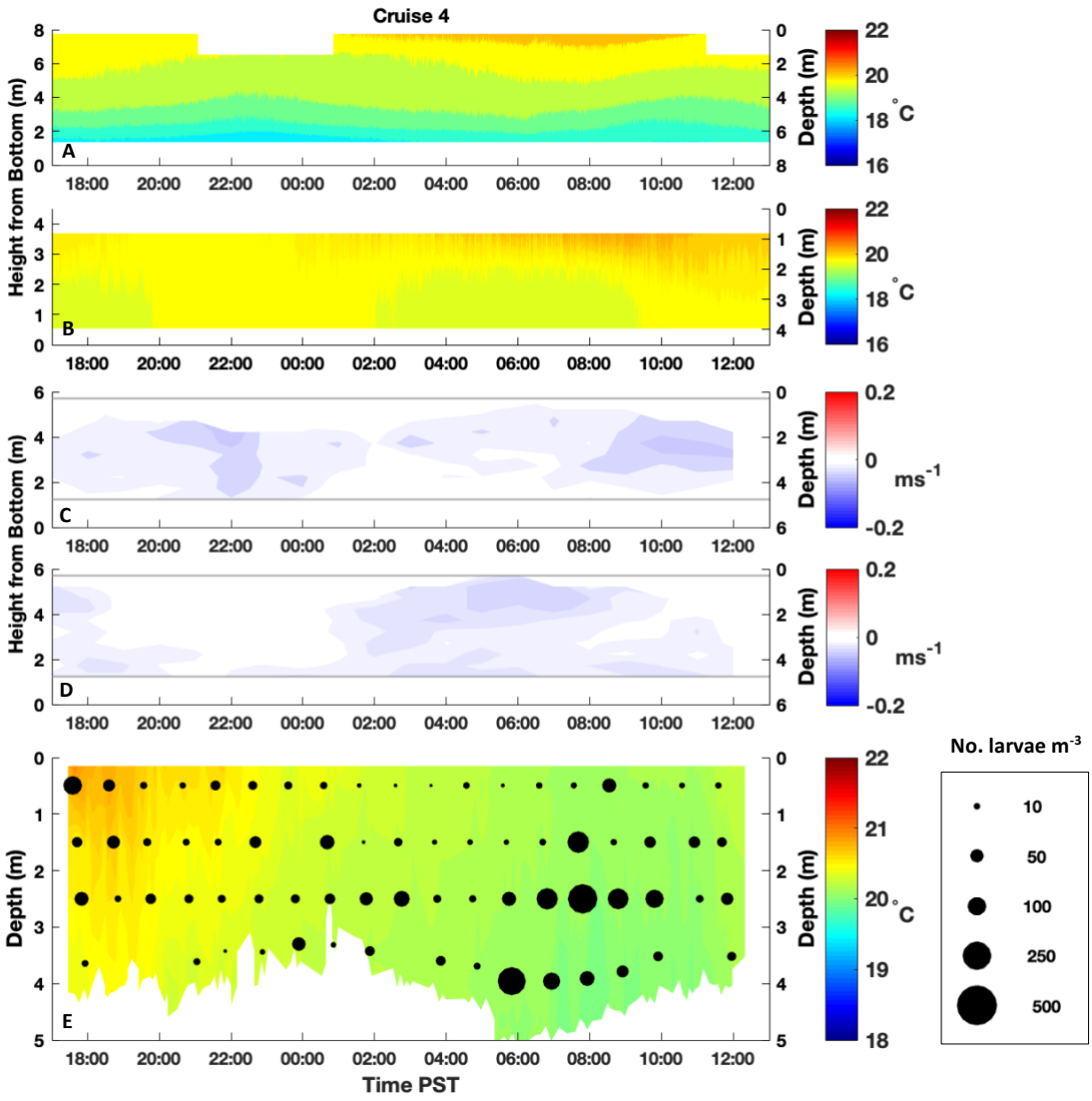

Figure 2.6 Cruise 4 (June 21-22, 2018) temperature contour plots using **(A)** SBE56 thermistors for 8m deep mooring site, and **(B)** 5m deep mooring site. White box at 8m site represents missing data from surface-most thermistor during low tide. Contour plots of currents (ms-1), with **(C)** cross-shore (*u*) component (positive values corresponding to onshore or eastward flow), and **(D)** alongshore (*v*) component (positive values corresponding to southward flow). The gray horizontal lines indicate the depths above and below which ADCP data are missing. **(E)** temperature contour plot using CTD data at 4m deep site with overlaid black circles representing *Chthamalus fissus* cyprid concentrations (no. m-3) in each sampling depth bin for each hour of sampling. The white area below the contour plot shows the changing water depth due to the tides. Temperature ranges vary for the 4m deep station.

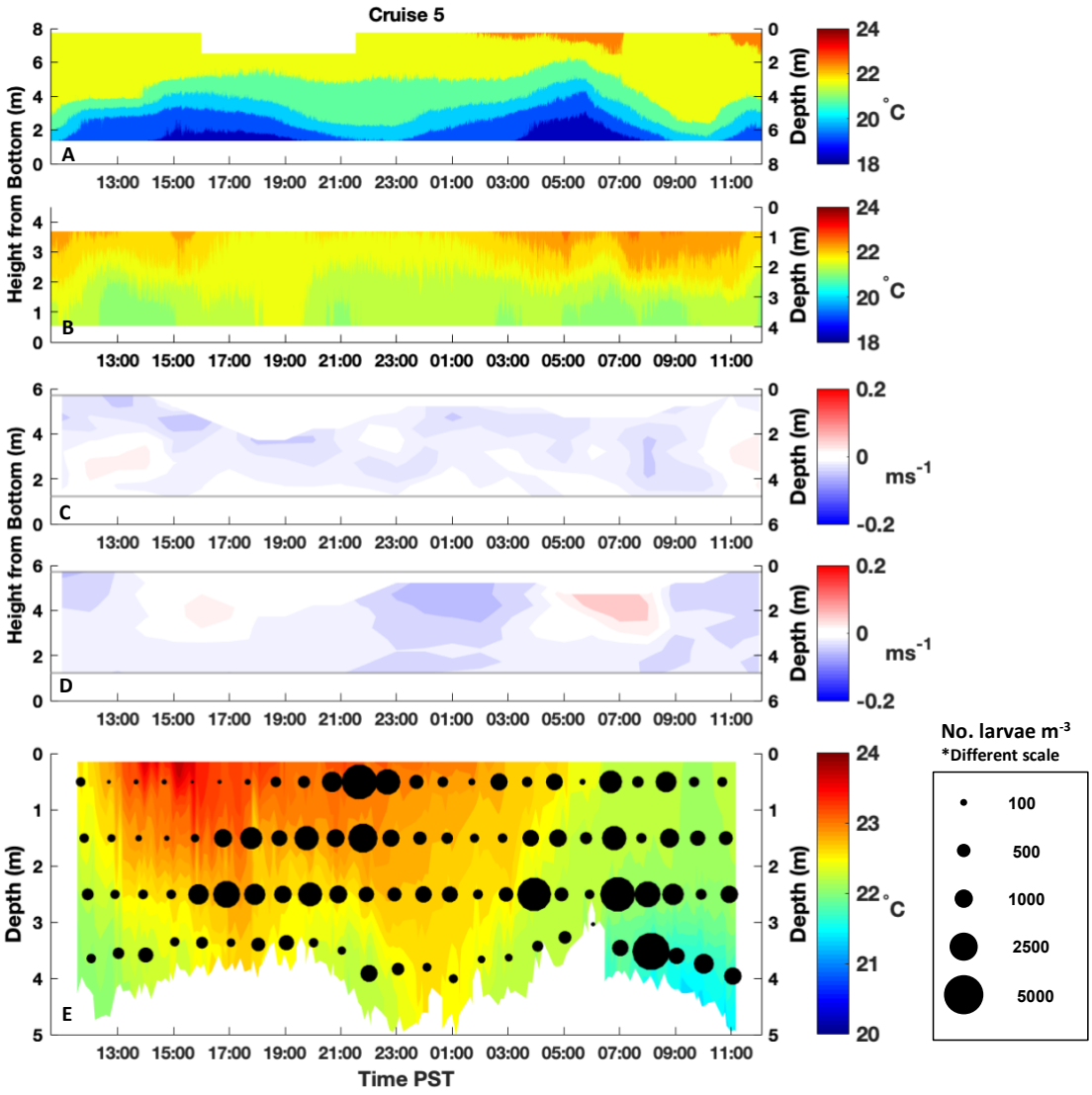
Cruise 5
Height from Bottom (m)
Depth (m)
A
B
C
D
E
°C
ms-1
Time PST
13:00 15:00 17:00 19:00 21:00 23:00 01:00 03:00 05:00 07:00 09:00 11:00
No. larvae m-3
*Different scale
100
500
1000
2500
5000

Figure 2.7 Cruise 5 (July 16-17, 2018) temperature contour plots using **(A)** SBE56 thermistors for 8m deep mooring site, and **(B)** 5m deep mooring site. White box at 8m site represents missing data from surface-most thermistor during low tide. Contour plots of currents (ms^{-1}), with **(C)** cross-shore (*u*) component (positive values corresponding to onshore or eastward flow), and **(D)** alongshore (*v*) component (positive values corresponding to southward flow). The gray horizontal lines indicate the depths above and below which ADCP data are missing. **(E)** temperature contour plot using CTD data at 4m deep site with overlaid black circles representing *Chthamalus fissus* cyprid concentrations (no. m^{-3}) in each sampling depth bin for each hour of sampling. The white area below the contour plot shows the changing water depth due to the tides. Note that circles denoting larval concentrations have been re-scaled relative to those depicted in Cruises 1, 2, and 4 to enhance visibility of temperature contours. Temperature ranges vary for the 4m deep station.

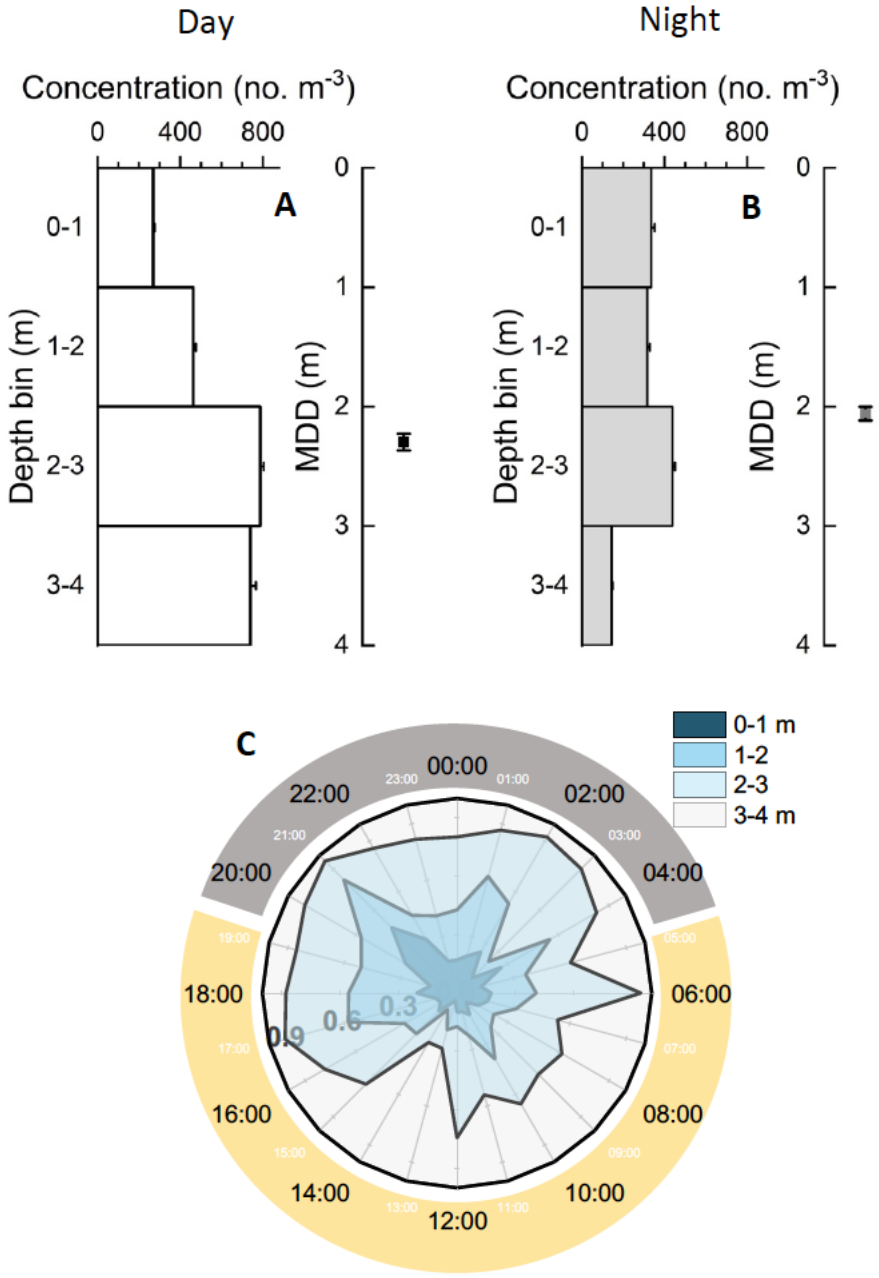

Figure 2.8 Diel distribution patterns of *Chthamalus fissus* cyprids. Mean concentration (no. larvae m-3) and MDD (± standard error) for all sampling hours conducted during the (**A**) day (N=48) and (**B**) night (N=45). (**C**) Proportion of cyprids found in each sampling depth bin (0-1m; 1-2m; 2-3m; 3-4m) for each hour of the sampling period. Yellow outline represents day hours and gray represents night hours.

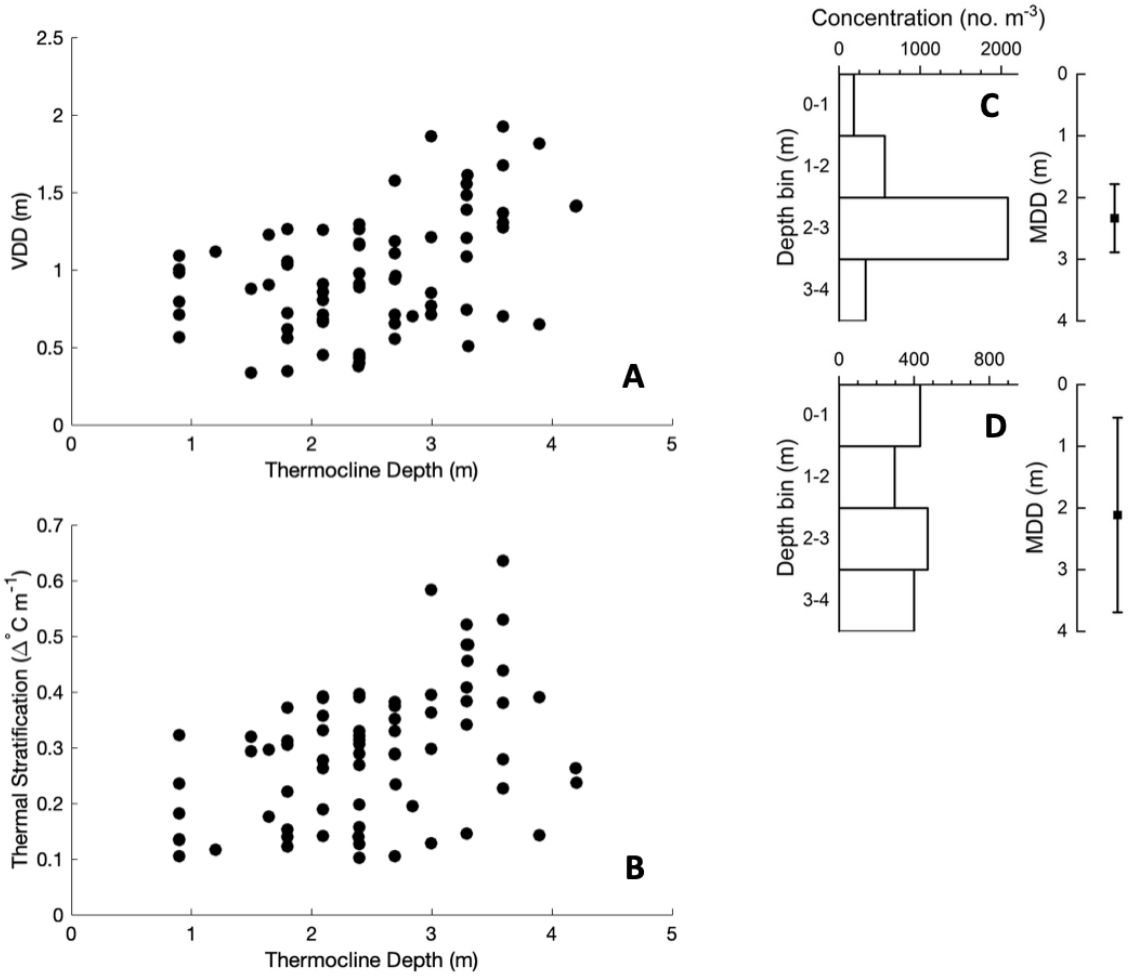

Figure 2.9 Scatter plot **(A)** Thermocline depth vs. VDD for all cruises. **(B)** Thermocline depth vs. thermal stratification for all cruises. **(C)** Representation of cyprid distribution for a small VDD for one single sample. Bars represent average concentration (no. larvae m^{-3}); black square represents MDD (2.33m) and error bars represent VDD (0.552). **(D)** Representation of cyprid distribution for a large VDD for one single sample. Bars represent average concentration (no. larvae m^{-3}); black square represents MDD (2.11m) and error bars represent VDD (1.58).

CHAPTER 3: Conclusions

In summary, this study aimed to answer three main research questions. First, we looked to answer how the vertical distribution of *C. fissus* cyprids changes during a diel cycle. We found that cyprid distribution varied slightly between day and night periods, as during the day, cyprids remained in the lower half of the water column (between 2-3 and 3-4m deep), and at night, they avoided the 3-4m depth bin. We also found that cyprids exhibit some vertical migration at night. However, our results also indicated that the vertical distribution of cyprids was highly dynamic during the day and changed for all cruises at the scale of hours.

This study also aimed to examine the relationship between the hydrographic and hydrodynamic conditions and the vertical distribution of cyprids. Our results showed that there was no significant correlation between MDD and thermocline depth, and MDD and thermal stratification. Interestingly, VDD, the variance in MDD, had a positive correlation with both the thermocline depth and stratification. These results suggest that VDD is a better descriptor than MDD at explaining how larvae vertically distribute themselves as a response to small-time scale variations in the physical properties of the water column. We also found that higher thermal stratification yielded higher larval concentrations at our 4m station. This agrees with the previous findings at this site in which larvae were found closer to shore when thermal stratification offshore increased. Our results show that not only is this the case when stratification offshore increases, but also when thermal

stratification at the 4m station persists. This stratification in shallow water might be influenced by diurnal heating and may allow offshore internal motions to penetrate shallower and increase onshore larval transport. Our findings also showed that alongshore reversals likely related to tidal forcings coincided with periods of higher larval concentrations at our 4m deep station.

Finally, we also aimed to answer how the depth of the thermocline influenced the vertical distribution of cyprids over a 24-hour period. Our results indicate that the thermocline depth at 4m tended to vary at the scale of hours, and that it was positively correlated to thermal stratification. Our findings show that when stratification increased at 4m, the thermocline depth was deeper, and cyprids were more evenly distributed throughout the water column. We speculate that the offshore thermocline is able to penetrate the 4m deep station when stratification is high, and that cyprids might get squeezed out due to the shallowing bathymetry. We hypothesize having a deeper thermocline created a more homogenous water column at the 4m deep station, allowing cyprids to regulate their vertical position and exploit the internal motions travelling towards shore in most of the water column.

Overall, these results suggest that cyprids are better able to use behavior to transport when thermal stratification is highest, and that alongshore reversals, specifically those associated with tides, can be associated with periods of nearshore cyprid accumulation. The resulting hypothesis is that as thermal stratification increases at the 4m deep station, the thermocline penetrates closer to shore, transporting more cyprids to the site. We

hypothesize that the homogenous spread of cyprids in the water column that arises from having a deep sharp thermocline near the bottom at the 4m site can increase settlement and recruitment to the intertidal.

As with most studies, these results provoke several questions that should be studied further. For instance, are these patterns of onshore transport and behavior applicable to other organisms and coastal systems? The homogenous distribution of cyprids at 4m when the thermocline was close to the bottom could be due to behavior or mixing of the water. Future research is needed to better understand the hydrodynamic patterns at 4m, and if cyprid settlement increases during periods of higher stratification and peak larval concentrations.

APPENDIX

Appendix A - Summary time series plot for each cruise

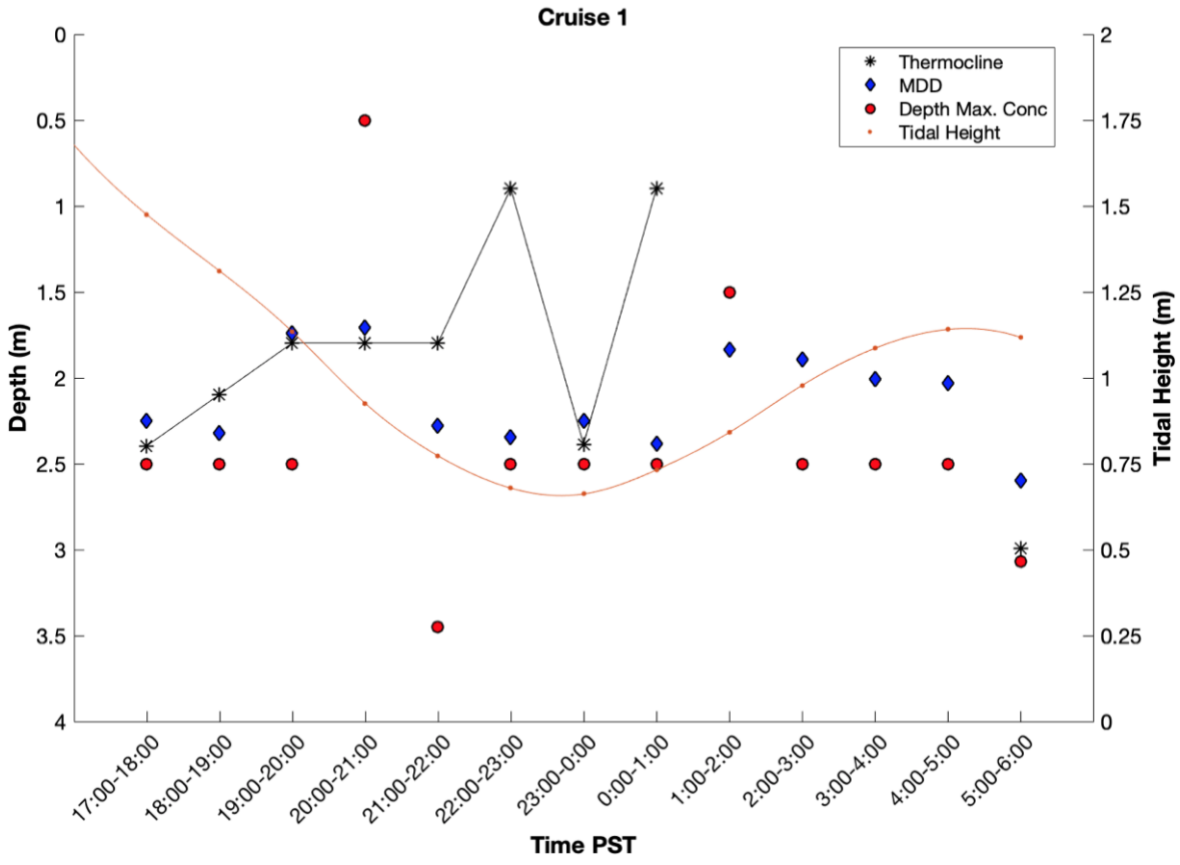

Figure A1 Cruise 1 (July 16-17, 2017) time series variation for the (black asterisk) thermocline depth (m), (blue diamond) MDD (m), (red circle) hourly depth with maximum concentration of *C. fissus* cyprids (m) and (orange dot) tidal height (m). Missing values for thermocline depth indicate hours of unstratified conditions ($\Delta°Cm^{-1} < 0.1$).

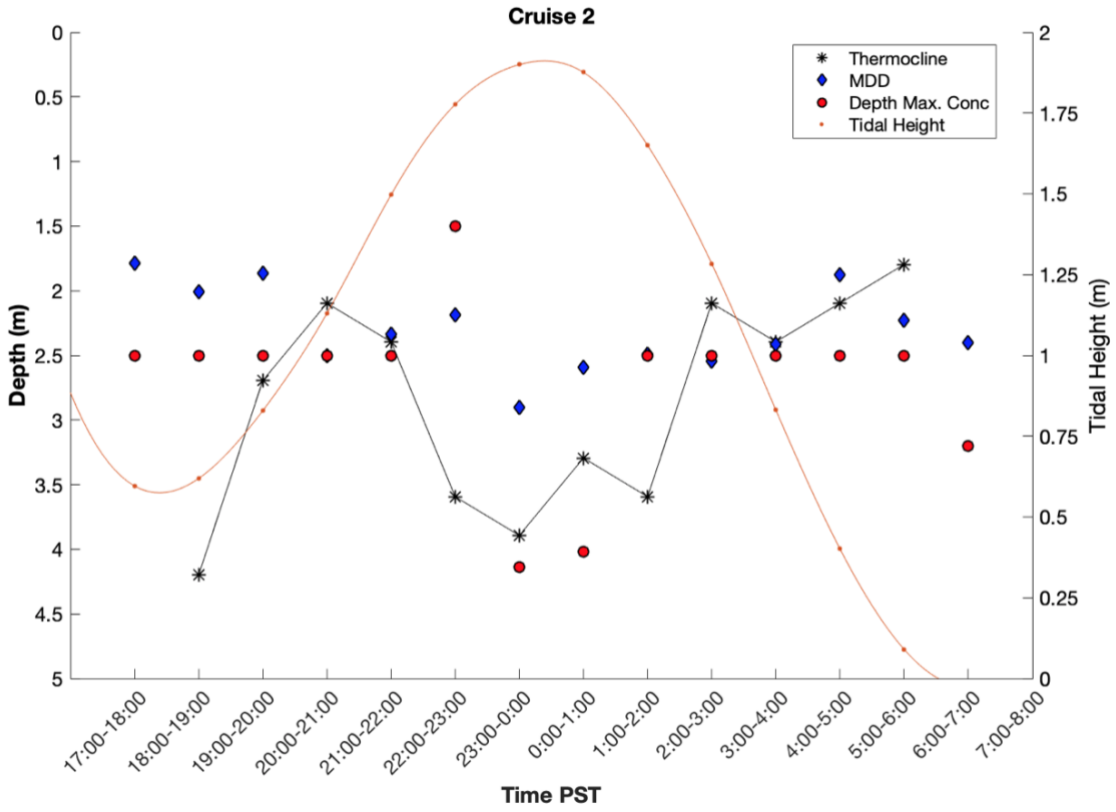

Figure A2 Cruise 2 (July 25-26, 2017) time series variation for the (black asterisk) thermocline depth (m), (blue diamond) MDD (m), (red circle) hourly depth with maximum concentration of *C. fissus* cyprids (m) and (orange dot) tidal height (m). Missing values for thermocline depth indicate hours of unstratified conditions ($\Delta°Cm^{-1} < 0.1$).

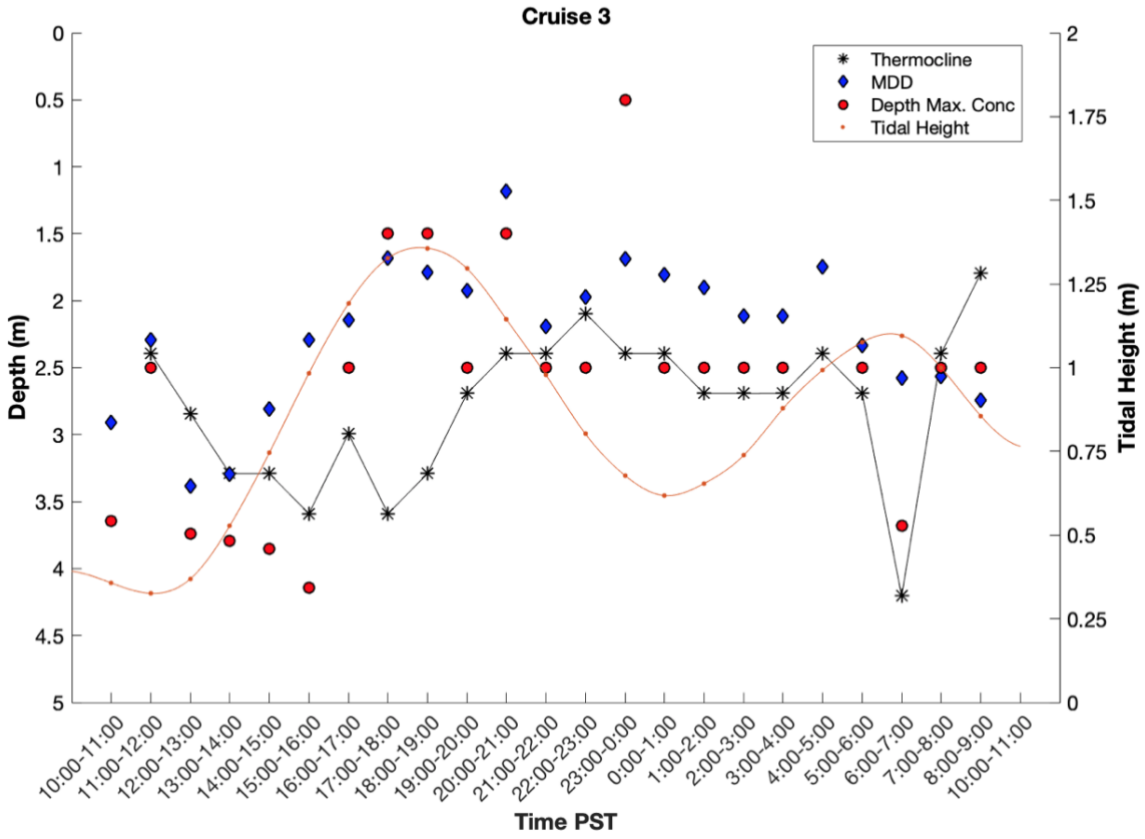

Figure A3 Cruise 3 (June 7-8, 2018) time series variation for the (black asterisk) thermocline depth (m), (blue diamond) MDD (m), (red circle) hourly depth with maximum concentration of *C. fissus* cyprids (m) and (orange dot) tidal height (m). Missing values for thermocline depth indicate hours of unstratified conditions ($\Delta°Cm^{-1} < 0.1$).

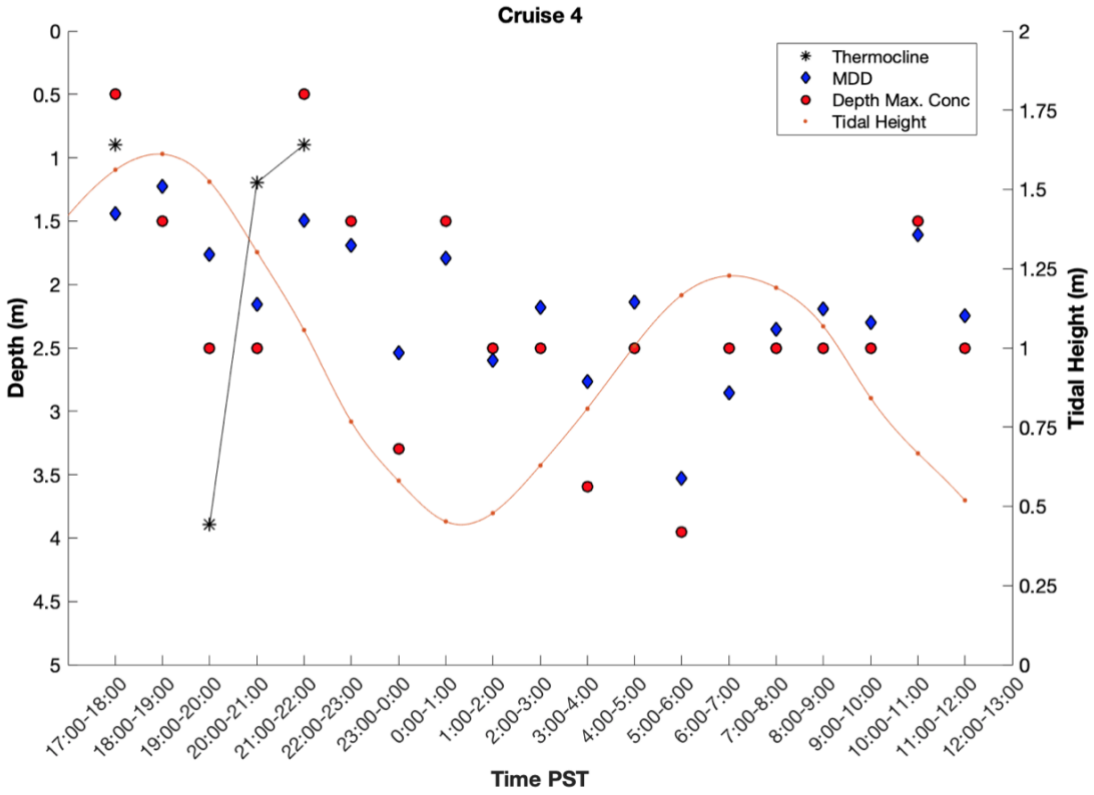

Figure A4 Cruise 4 (June 21-22, 2018) time series variation for the (black asterisk) thermocline depth (m), (blue diamond) MDD (m), (red circle) hourly depth with maximum concentration of *C. fissus* cyprids (m) and (orange dot) tidal height (m). Missing values for thermocline depth indicate hours of unstratified conditions ($\Delta°Cm^{-1} < 0.1$).

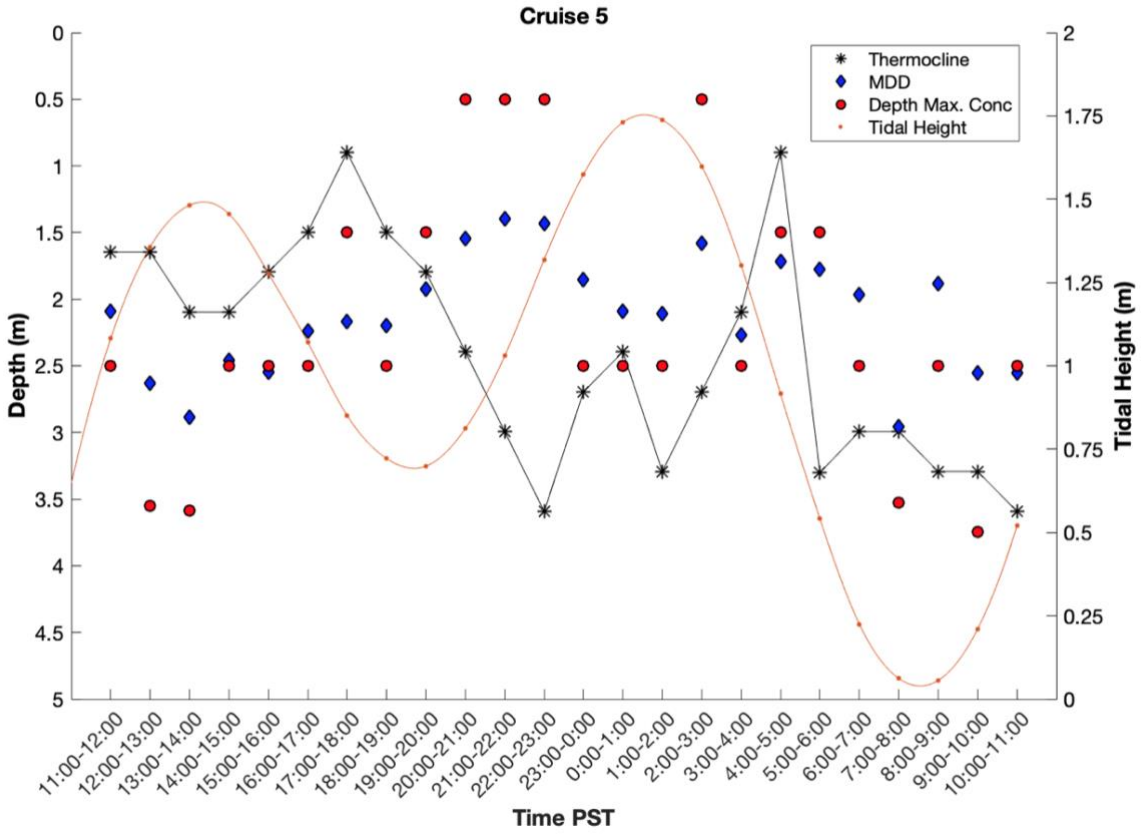

Figure A5 Cruise 5 (July 16-17, 2018) time series variation for the (black asterisk) thermocline depth (m), (blue diamond) MDD (m), (red circle) hourly depth with maximum concentration of *C. fissus* cyprids (m) and (orange dot) tidal height (m).

Appendix B – Summary tables for complementary ANOVA's

Table B1 - Results of one-way ANOVAs testing for differences in MDD (m) of *Chthamalus fissus* cyprids between tidal flow: flooding (N=46 samples) and ebbing (N=47 samples), and water levels (m): low level (N=29 samples) and high level (N=15 samples).

Variable	F	p
Tidal Ebbing/Flooding	1.160	0.284
Water Height	0.341	0.563

Table B2 - Results of one-way ANOVAs testing for differences in thermocline depth between day (N= 39 samples) and night (N= 34 samples), stratification ($\Delta°Cm^{-1}$) and VDD (m) between day (N= 48 samples) and night (N= 45 samples). Difference in sample values for thermocline depth represent the lack of thermocline during stratified conditions.

Variable	F	p
Thermocline depth (m)	1.330	0.253
Stratification	2.984	0.087
VDD (m)	1.239	0.269

Appendix C – Summary temperature time series for the 8m and 5m mooring thermistor data

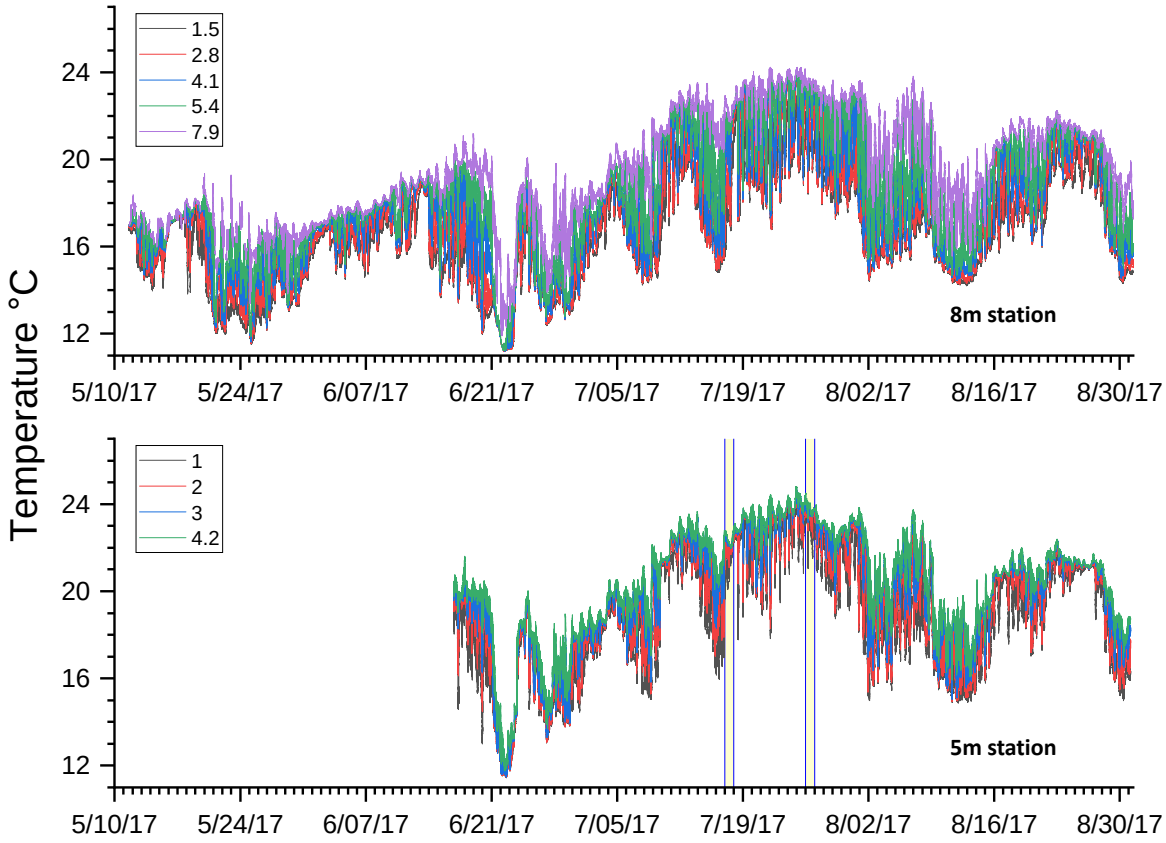

Figure C1 Temperature time series from the 8m-deep and 5m-deep stations for all of the summer of 2017. Blue guide marks represent days of sampling.

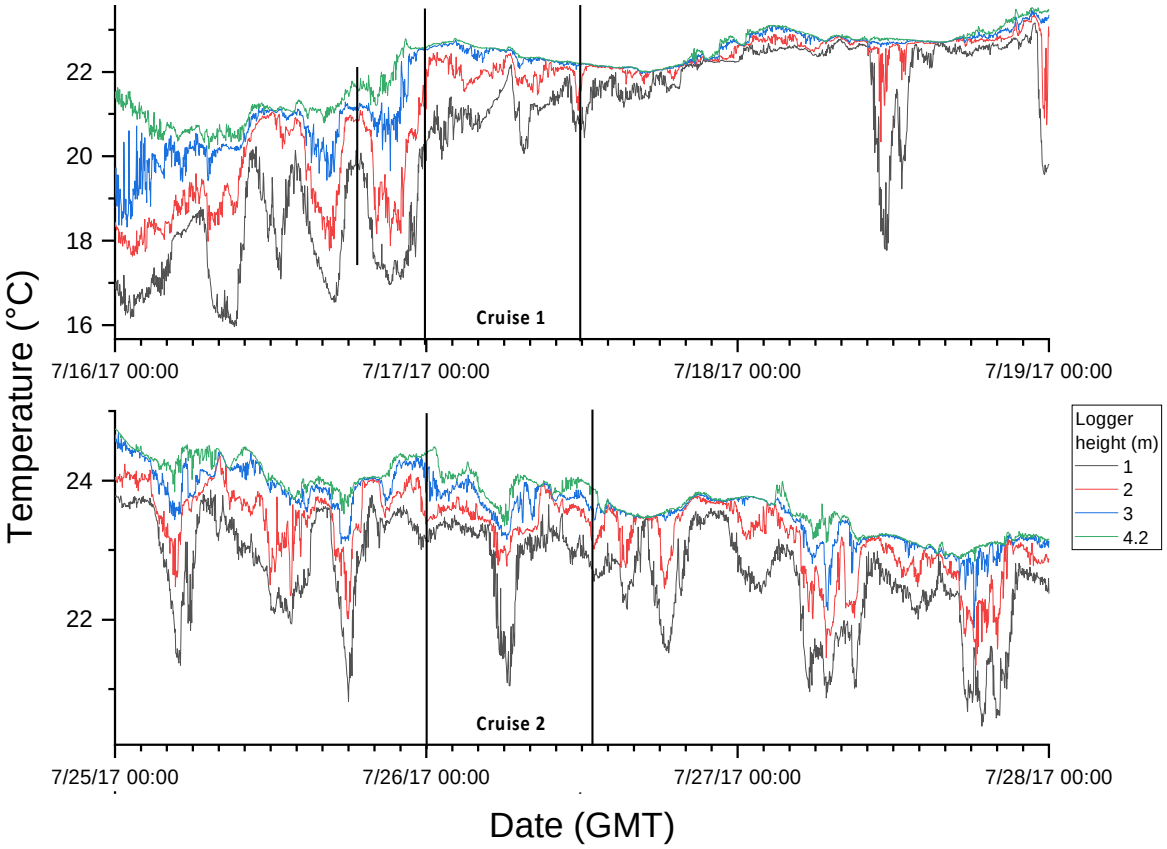

Figure C2 Temperature time series from the 5m-deep station for the sampling dates of the summer of 2017. Black lines enclose periods of plankton collection.

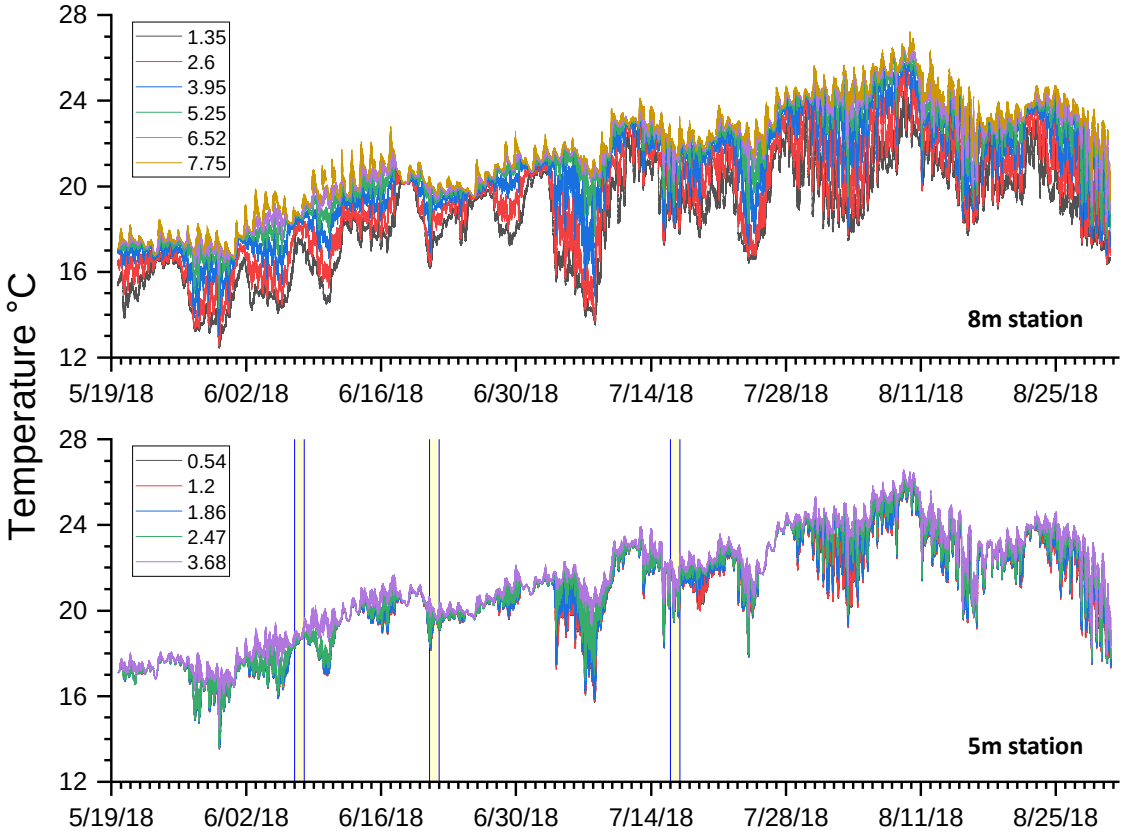

Figure C3 Temperature time series from the 8m-deep and 5m-deep stations for all of the summer of 2018. Blue guide marks represent days of sampling.

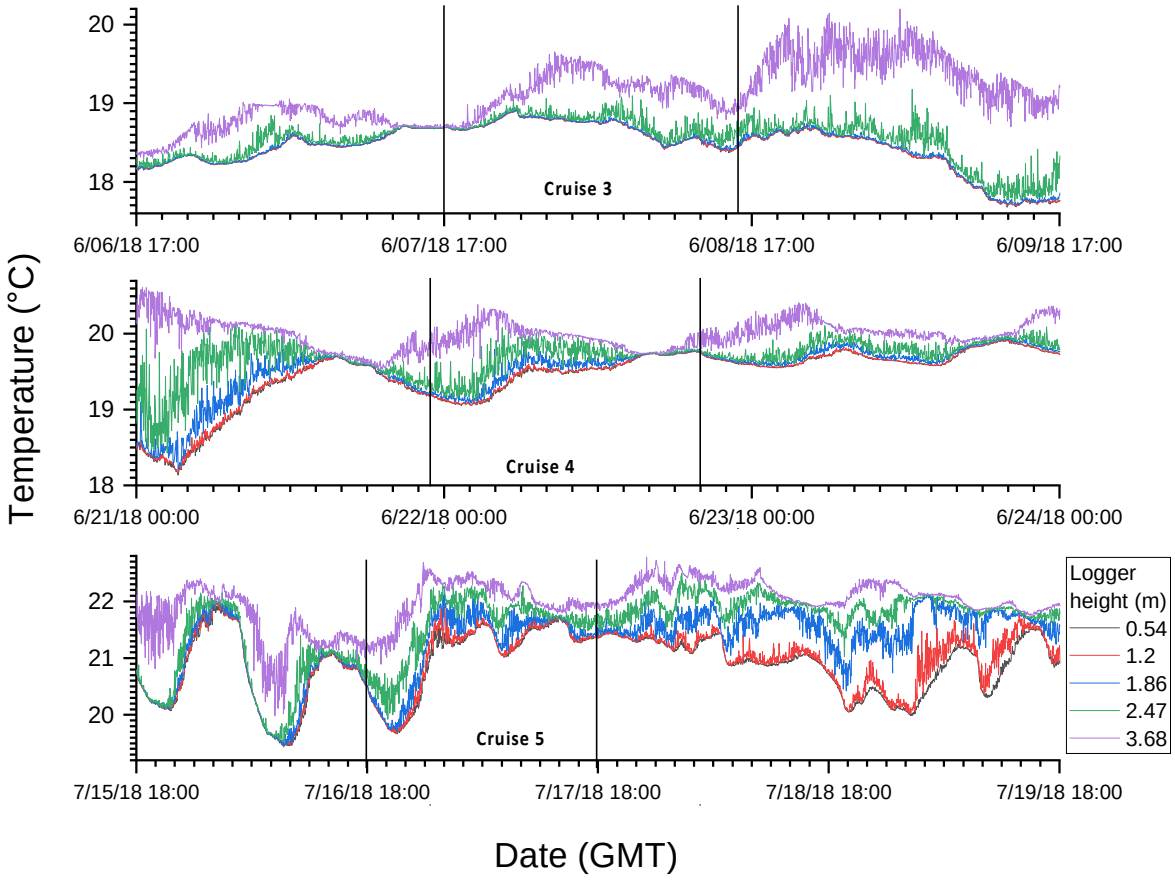

Figure C4 Temperature time series from the 5m-deep station for the sampling dates of the summer of 2018. Black lines enclose periods of plankton collection.

Appendix D – Hourly concentration summary for each cruises

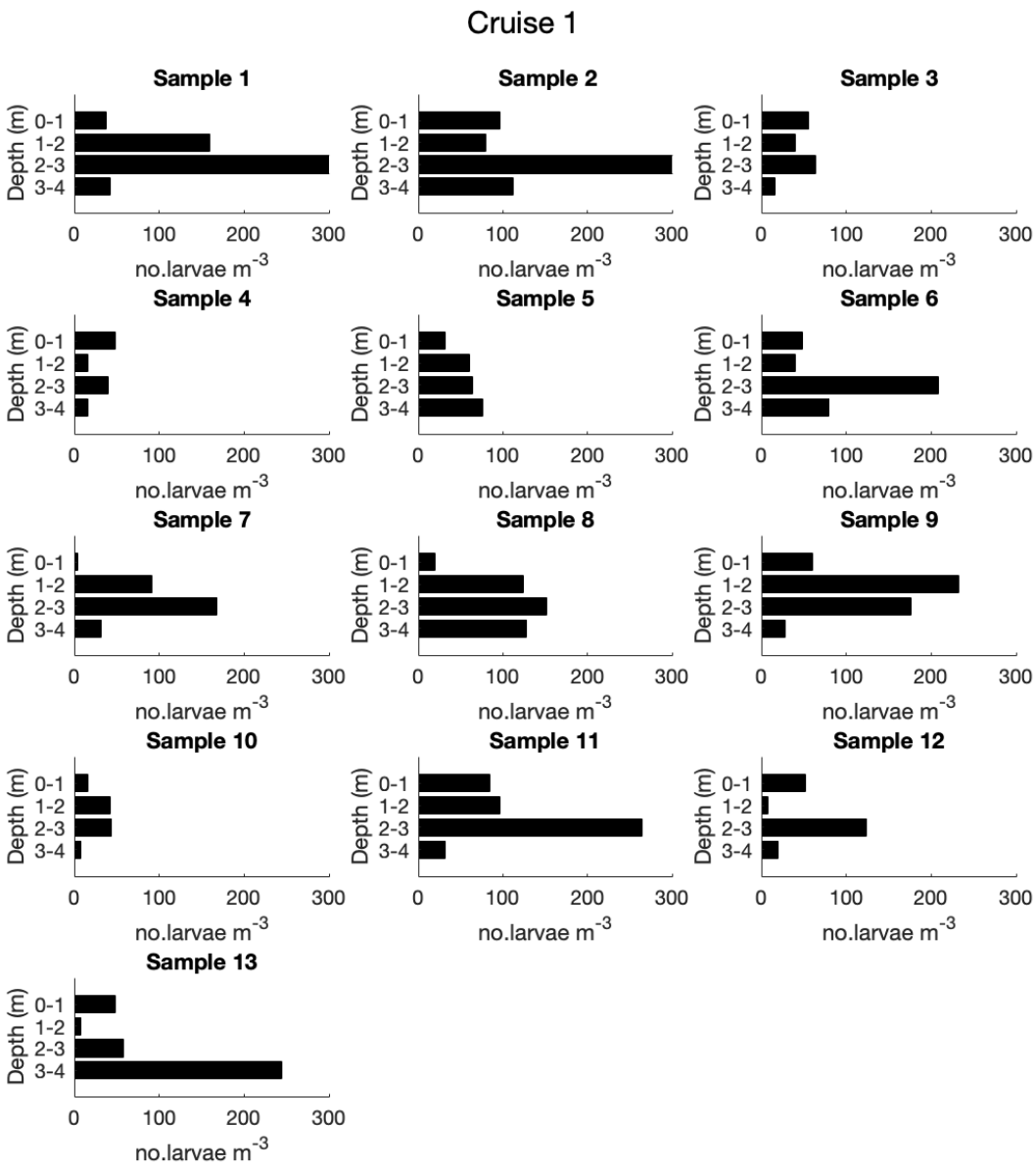

Figure D1 Cruise 1 (July 16-17, 2017) *Chthamalus fissus* concentration (no. larvae m-3) collected at each depth interval (m) for every hour of sampling. Samples were conducted at hourly intervals (Start time sample 1: 17:00 PST).

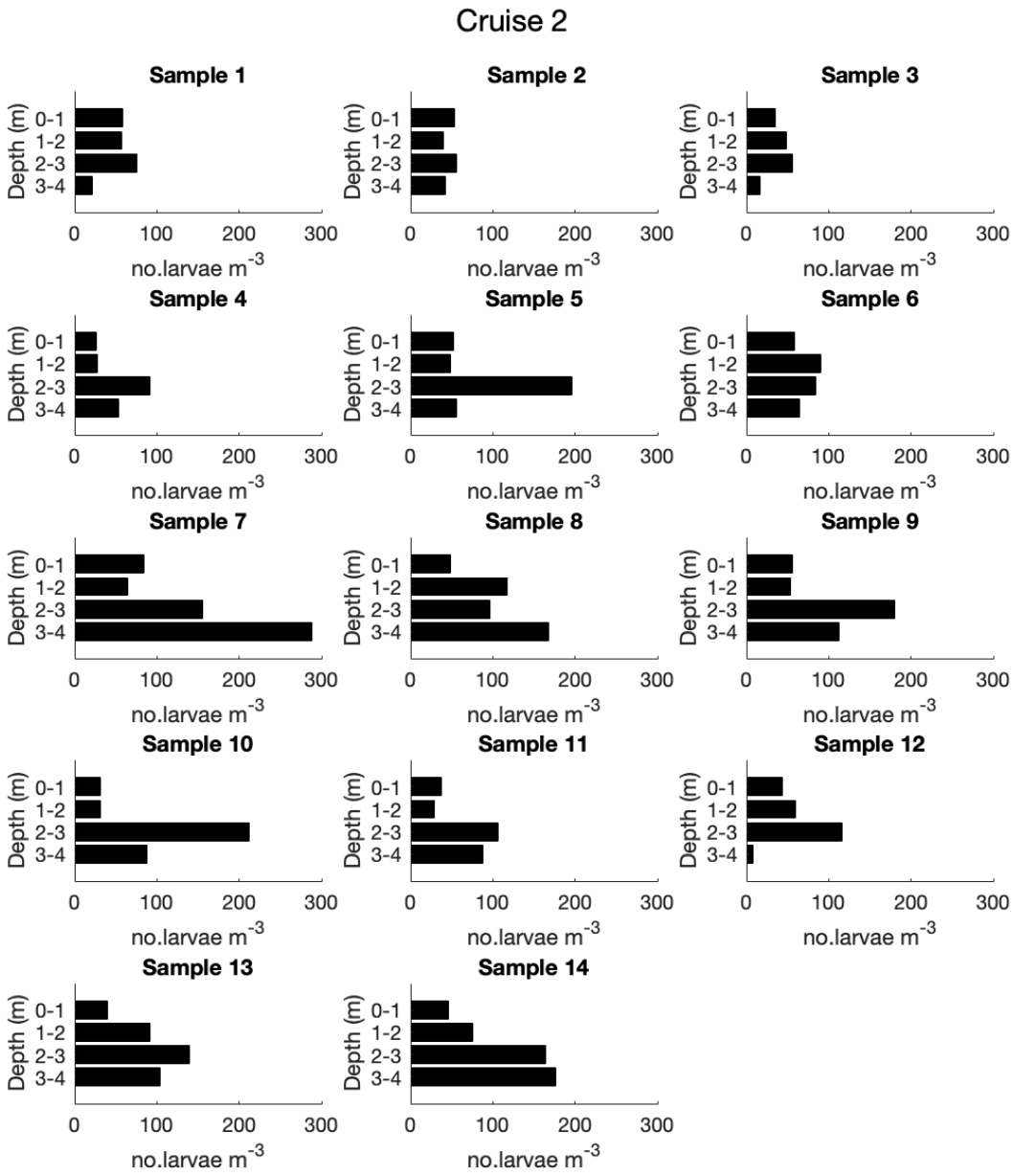

Figure D2 Cruise 2 (July 25-26, 2017) *Chthamalus fissus* concentration (no. larvae m-3) collected at each depth interval (m) for every hour of sampling. Samples were conducted at hourly intervals (Start time sample 1: 17:00 PST).

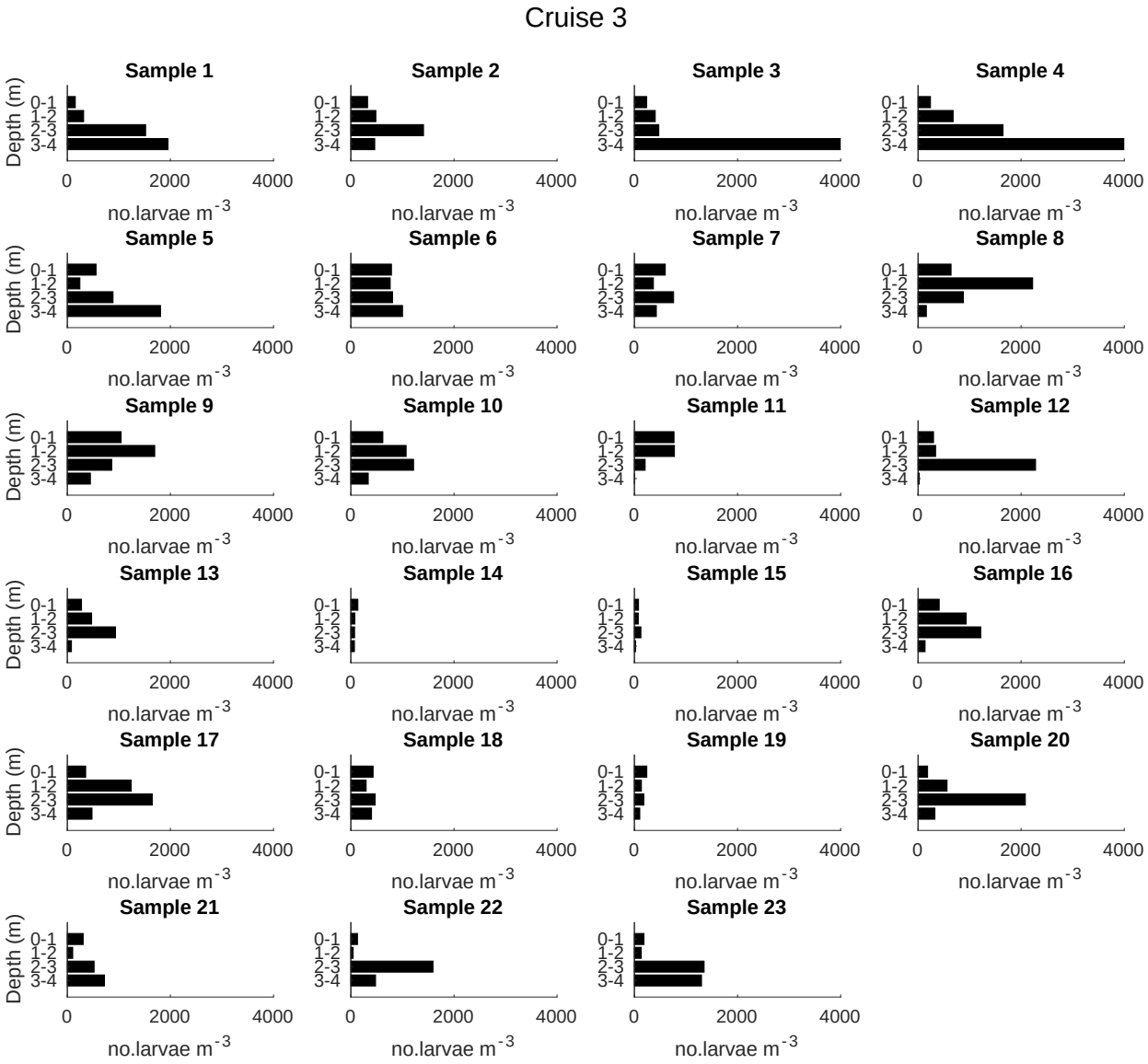

Figure D3 Cruise 3 (June 7-8, 2018) *Chthamalus fissus* concentration (no. larvae m-3) collected at each depth interval (m) for every hour of sampling. Note scale for concentration (no. larvae m-3) is different relative to cruise 1, 2 and 4. Samples were conducted at hourly intervals (Start time sample 1: 10:00 PST).

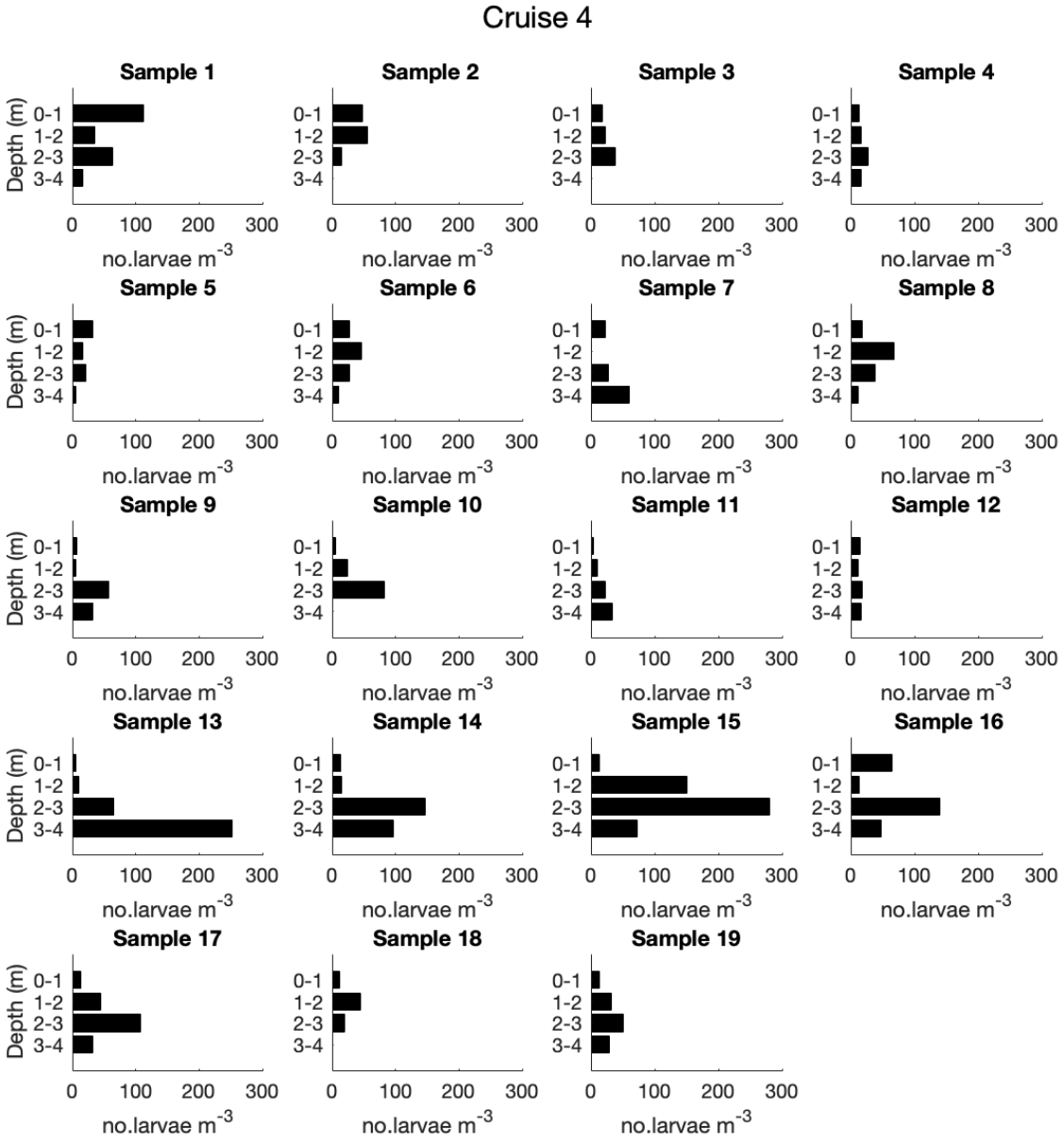

Figure D4 Cruise 4 (June 21-22, 2018) *Chthamalus fissus* concentration (no. larvae m-3) collected at each depth interval (m) for every hour of sampling. Samples were conducted at hourly intervals (Start time sample 1: 16:00 PST).

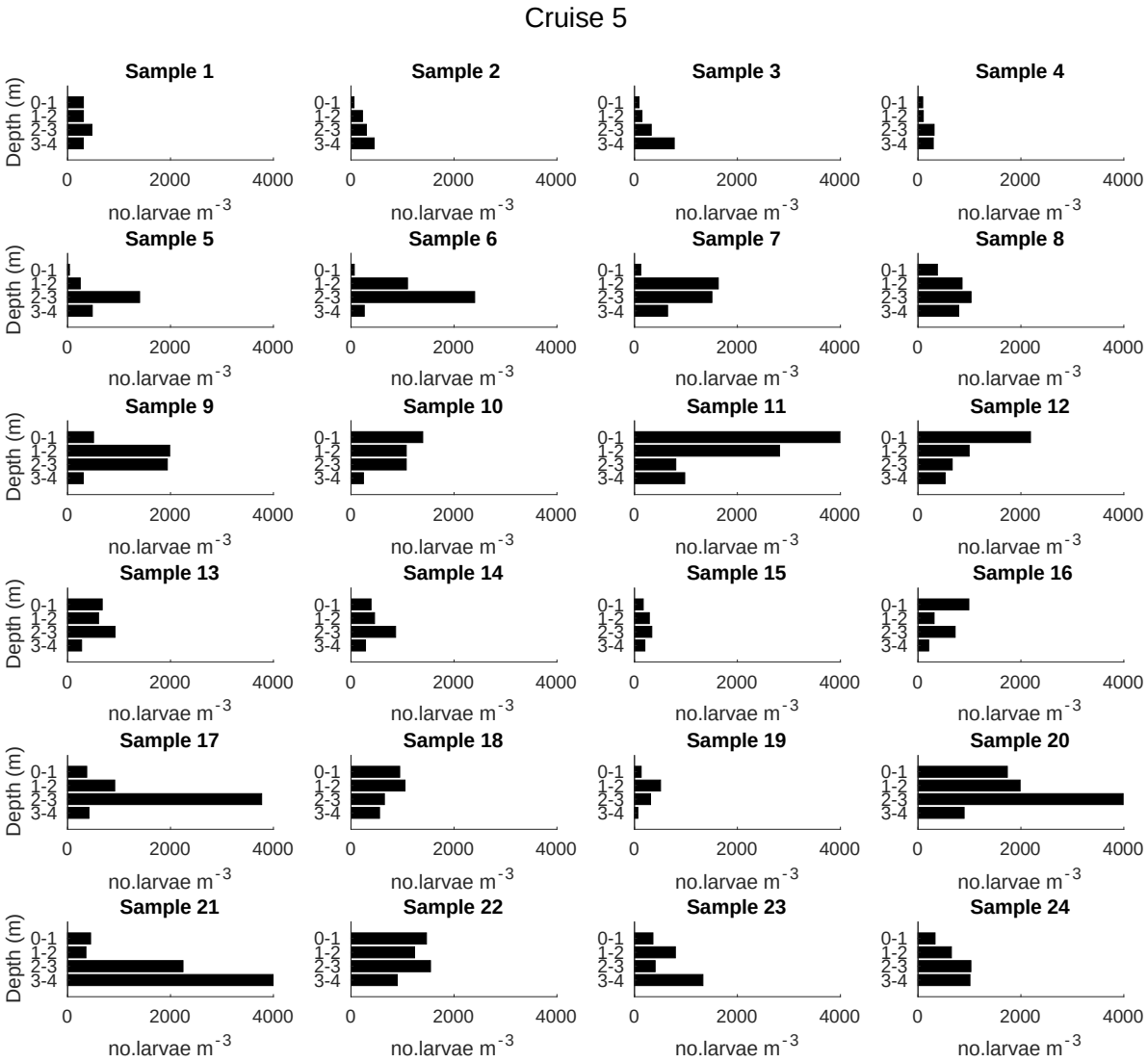

Figure D5 Cruise 5 (July 16-17, 2018) *Chthamalus fissus* concentration (no. larvae m-3) collected at each depth interval (m) for every hour of sampling. Note scale for concentration (no. larvae m-3) is different relative to cruise 1, 2 and 4. Samples were conducted at hourly intervals (Start time sample 1: 11:00 PST).

Appendix E – Correlation between larval distribution and physical variables

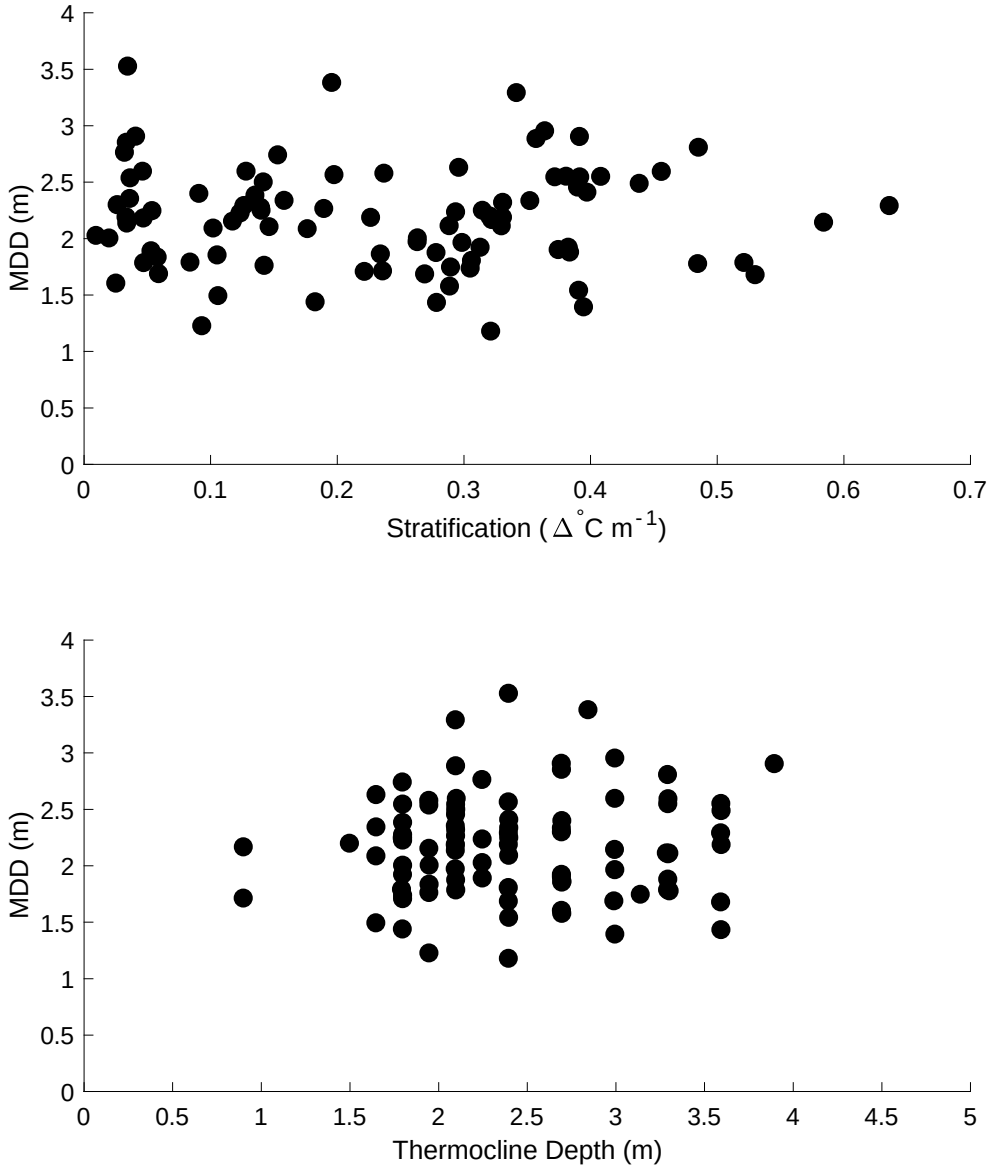

Figure E1 Relationship between MDD (m) and thermal stratification (Δ°Cm-1) and MDD and thermocline depth (m) for all hours of sampling.

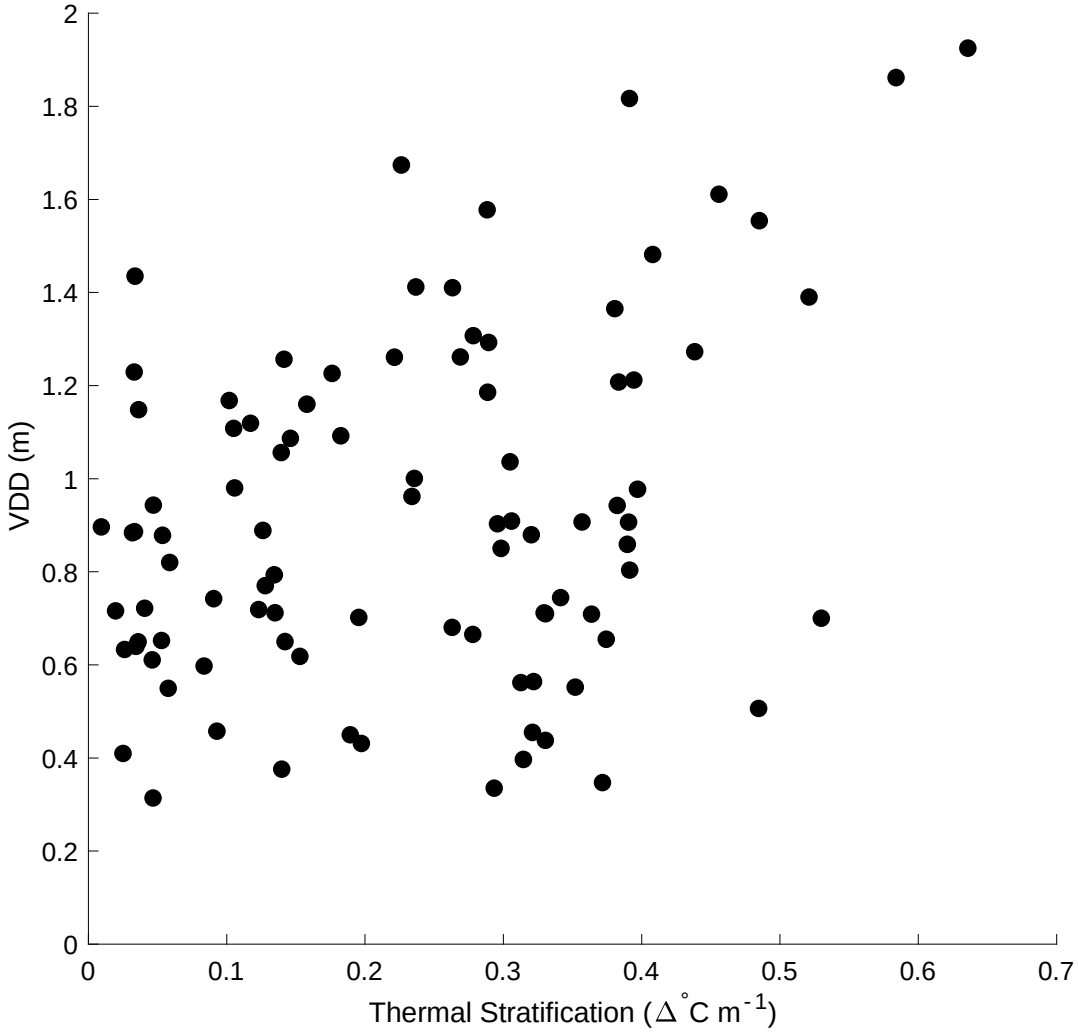

Figure E2 Relationship between VDD (m) and thermal stratification ($\Delta°Cm^{-1}$).

Appendix F – Relationship between mean current velocities and mean larval concentrations

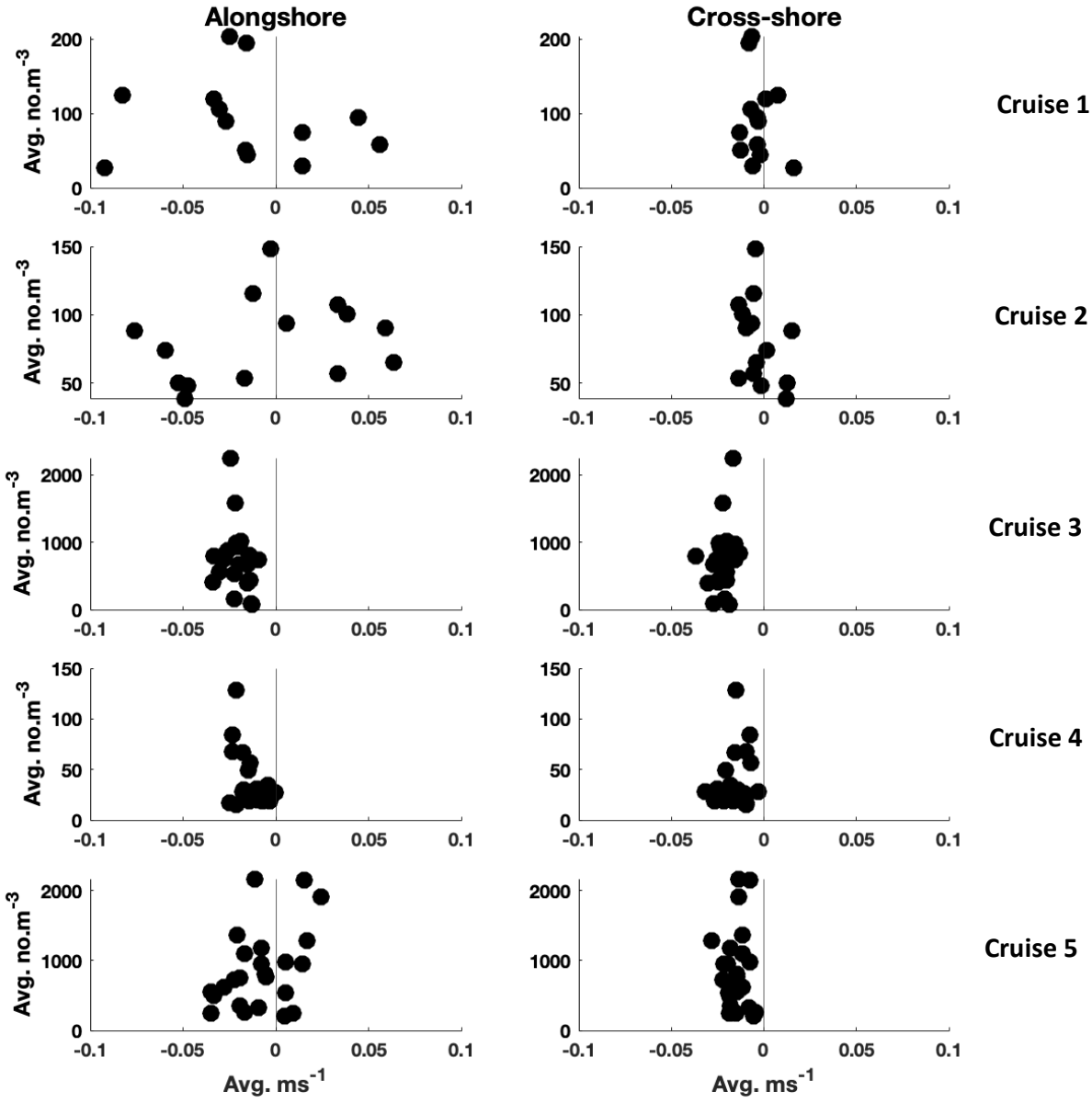

Figure F Relationship between the hourly mean concentration (no. larvae m^{-3}) and mean current velocity (ms^{-1}) for all cruises in both the alongshore and cross-shore direction.