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Doctorado en Ciencias en Ecología Marina

Internal waves in the Mexican Pacific: Meroplankton accumulation in surface slicks and the evaluation of supply-side control in the rocky intertidal

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Andrea Liévana MacTavish

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Tesis defendida por

Andrea Liévana MacTavish

y aprobada por el siguiente Comité

Dra. Lydia Betty Ladah
Director de tesis

Dr. Luis Eduardo Calderón Aguilar

Dr. José Luis Ochoa de la Torre

Dr. James Leichter

Dr. María Lucila del Carmen Lares Reyes
Coordinador del Posgrado en Ecología Marina

Dra. Rufina Hernández Martínez
Directora de Estudios de Posgrado

Resumen de la tesis que presenta **Andrea Liévana MacTavish** como requisito parcial para la obtención del grado de Doctor en Ciencias en Ecología Marina

Internal waves in the Mexican Pacific: meroplankton accumulation in surface slicks and the evaluation of supply-side control in the intertidal

Resumen aprobado por:

Dra. Lydia Betty Ladah
Director de tesis

El suministro de larvas a zonas costeras es importante para la persistencia de poblaciones de invertebrados marinos y depende de las condiciones oceanográficas que puedan influir sobre procesos físicos de transporte. Las ondas internas son capaces de acumular material en huellas superficiales y se han asociado con cambios en la abundancia de meroplancton a lo largo de la columna de agua. La acumulación de meroplancton en huellas superficiales asociadas a la actividad de ondas internas fue evaluado en tres sitios: Barra de Navidad, JA; La Paz, BCS; y San Juanico, BCS. La hipótesis de que habrá una mayor abundancia de meroplankton en la superficie fue evaluada en cada sitio. Muestras que fueron tomadas adentro de las huellas superficiales contenían significativamente una mayor cantidad de meroplancton que muestras tomadas afuera de las huellas. Este resultado indica que las huellas superficiales asociadas a ondas internas son importantes en los tres sitios para la acumulación de meroplancton en el mar costero y para el transporte potencial subsecuente de meroplancton hacia la costa donde existen sitios de asentamiento intermareales o submareales. La persistencia de poblaciones de invertebrados en el intermareal depende de entrada de reclutas nuevos, pero también depende de controles posteriores al reclutamiento, como la competencia o la depredación. La supervivencia de reclutas nuevos de *Chthamalus* en Playa San Miguel, BC, fue evaluada por más de un año para determinar si la población se encontraba bajo control posterior al reclutamiento o control de lado del suministro de reclutas nuevos. Para esto, fue necesario evaluar si el suministro de reclutas nuevos resultaba ser de mayor importancia que factores posterior al reclutamiento, como la competencia o depredación, en la determinación de la densidad de adultos. Se hipotetizó que la densidad de reclutas *Chthamalus* durante el estudio será una predictor robusto de la densidad de adultos al final del estudio y se esperó encontrar una relación recluta-adulto positiva en la cual los factores de competencia o depredación no jugarían un rol significativo en determinar la densidad de adultos. Durante este estudio, se encontró que la densidad de reclutas era una predictor robusto de la densidad de adultos, a pesar de la presencia débil de mortalidad denso-dependiente. Ni la depredación ni la competencia afectaron de manera significativa la supervivencia de reclutas y no lograron disociar la relación entre las densidades de reclutas y adultos, sugiriendo que es improbable que los controles posteriores al reclutamiento juegan un rol importante sobre el tamaño de la población de *Chthamalus* en Playa San Miguel. Los resultados de este estudio indican que la población de *Chthamalus* están bajo control del lado del suministro en Playa San Miguel.

Palabras clave: Ondas internas, meroplankton, ecología de la oferta, *Chthamalus*, intermareal rocoso

Abstract of the thesis presented by **Andrea Liévana MacTavish** as a partial requirement to obtain the Doctor of Science degree in Marine Ecology

Internal waves in the Mexican Pacific: meroplankton accumulation in surface slicks and the evaluation of supply-side control in the intertidal

Abstract approved by:

Dr. Lydia Betty Ladah
Thesis Director

The supply of larval subsidies to coastal habitats is important for the persistence of invertebrate populations and can vary depending on oceanic conditions that may affect physical transport processes. Internal waves are capable of accumulating material in slicks that form at the surface and are associated with changes in meroplanktonic abundance throughout the water column. The accumulation of meroplankton in surface slicks associated with internal wave activity was evaluated in three sites: Barra de Navidad, JA; La Paz, BCS, and San Juanico, BCS. The hypothesis that there would be a greater abundance of meroplankton within surface slicks was evaluated in each site. Samples taken from within surface slicks contained a significantly greater abundance of meroplankton than samples taken outside of slicks. This result indicates that internal wave slicks in all three sites are important for meroplankton accumulation in the coastal ocean and for the subsequent potential onshore transport of meroplankton to intertidal and subtidal settlement sites. The persistence of invertebrate populations in the intertidal depends on the input of new settlers, but may also depend on postrecruitment controls, such as competition and predation. The survivorship of *Chthamalus* recruits in Playa San Miguel, Baja California, was evaluated for over a year to determine if the population was under supply-side or postrecruitment control. To do this, it was necessary to determine if the supply of new recruits was of greater importance than the postrecruitment factors of competition and predation in determining adult density. It was hypothesized that *Chthamalus* recruit density during the study would be a robust predictor the adult density at the end of the study and it was expected that a positive recruit-adult relationship would be observed in which neither predation nor competition would play significant roles in determining adult density. During this study, recruit density was found to be a robust predictor of adult density despite the presence of weak density-dependent mortality. Neither predation nor competition significantly affected the survivorship of recruits and did not decouple the relationship between recruit and adult densities, suggesting that these postrecruitment controls are unlikely to play important roles in determining the population size of *Chthamalus* barnacles at Playa San Miguel. The results of the study indicate that the *Chthamalus* population at Playa San Miguel is under supply-side control.

Keywords: Internal waves, meroplankton, supply-side ecology, *Chthamalus*, rocky intertidal

Dedication

For Maya and Mateo:

Remember to be true to yourselves,

be kind,

and watch the tide come in when you can.

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Chapter 1. Introduction

1.1. Supply-side ecology

In 1986, Lewin published a paper in Science titled “Supply-Side Ecology”, in which he chronicled the development of supply-side ecological theory by highlighting the studies of leaders in the field such as Underwood, Roughgarden and Connell. These studies came to the conclusion that factors operating within communities, such as predation, competition and disturbance, were insufficiently able to explain patterns of species abundance, diversity and richness. Essentially, the patterns observed in an intertidal community indicated that there were additional factors, most likely related to the nearshore ocean, that influenced the structure and organization of the community under study. Thus, it could no longer be ignored that the nearshore ocean was a source of ecological subsidies to intertidal populations and that these ecological subsidies should be important determining factors to the structure of the community. Some of the most important ecological subsidies to an intertidal community are the larvae of marine invertebrate species that arrive to settle and continue their lives as benthic organisms. Therefore, at the center of supply-side ecology lies the importance placed on both the arrival of subsidies to a particular intertidal community and the influence of those subsidies on the structure of that community after arrival.

After the publication of Lewin (1986), supply-side ecology took on an increasingly important role in intertidal marine research. A particular area of interest in supply-side ecology deals with how subsidies arrive to intertidal sites via physical transport processes. Ecological subsidies refer to inputs to a community such as nutrients, organic matter, or individuals (Palumbi, 2003). Given that physical transport processes vary in scale, time, and space, the manner in which ecological subsidies arrive to the coast may have profound implications on the dynamics of intertidal populations (Pineda, 1991, 1994a; Shanks & Brink, 2005; Shanks, et al., 2000; Witman et al., 1993). To date, a variety of studies have been carried out to better understand how subsidies are transported to the coast by evaluating potential physical transport processes in the coastal ocean with simultaneous measurements of larval settlement rates in the intertidal zone (Krenz et al., 2011; Ladah, et al., 2005; Leichter et al., 1998; Menge et al., 2003; Navarrete et al., 2005; Pineda & López, 2002; Shanks et al., 2000). From these studies, a clear link between potential physical transport processes and larval settlement rates has been established. For example, in Playa San Miguel, BC, Ladah et al. (2005) found that *Chthamalus* settlement was significantly associated with internal wave activity in the coastal ocean. As physical transport processes are likely to be differentially affected by changing ocean conditions, it is important to evaluate their potential to transport larvae to coastal sites to better understand how these areas may be affected in the future, as well as to evaluate the importance of invertebrate recruits on the structure of intertidal communities.

1.2. Internal waves as a physical transport process

Internal waves and bores are capable of causing high-frequency variations in temperature, salinity, current speeds, concentrations of planktonic organisms, and sediments in the nearshore zone making them a key component linking offshore and onshore environments (Cairns, 1967; Leichter et al., 2005; Leichter et al., 1996; Pineda, 1991, 1994, 1999; Shanks, 1987). Internal waves have been shown to be of importance in the cross-shelf transport of invertebrate larvae, in part due to their ability to propagate into shallow water and to break near the shore (Leichter et al., 1996; Pineda & López, 2002; Pineda, 1994; Winant, 1974). In addition, non-linear internal waves propagating in the alongshore direction are equally capable of modifying the vertical distribution of meroplankton and thus may also be of particular importance in the transport of larvae into bays and other semi-enclosed coastal areas (Liévana MacTavish et al., 2016).

An internal wave oscillates at the interface between two layers of differing density (Roberts, 1975; Haury et al., 1979; Gill, 1982). Internal waves can be observed in the atmosphere and inside the ocean or in any other medium that contains at least two layers of differing densities (Roberts, 1975; Gill, 1982). Inside the ocean, an internal wave is generated via the vertical displacement of a water parcel (Roberts, 1975; Gill, 1982). If the displacement is upward, the restorative force of gravity acts to return the water parcel to its initial position; however, the water parcel will continue to travel downwards until its own buoyancy acts to return the water parcel to its initial position given that the water parcel does not stop instantaneously (Roberts, 1975; Gill, 1982). The upward movement of the water parcel continues and eventually surpasses its initial position until gravity acts once more to change the direction of movement downward (Roberts, 1975; Gill, 1982). The result of this movement is an oscillation between two layers of differing density, called an internal wave.

Internal waves may oscillate with different periods that vary from minutes (solitons in the coastal zone), to hours, to multiple days (Rossby waves) (Roberts, 1975). The differences in the periods observed pertaining to internal waves in the ocean depend, in part, on the forcing mechanisms that act to provoke the initial vertical displacement (Roberts, 1975). Internal waves in the ocean are commonly forced by winds or by tides. Internal waves forced by the tide are generated by a periodic force (the tide) and have periods associated with tidal components; therefore, the internal tide is an internal wave of tidal period (Steward 2004). The tide has various components, the most notable being: M2 (principal lunar semidiurnal; 12.4206 h period), S2 (principal solar semidiurnal; 12 h period), K1 (lunar diurnal; 23.9344 h period), O1 (principal lunar diurnal; 25.8194 h period) and P1 (principal solar diurnal; 24.0659 h period) (Godin, 1988). In front of Playa San Miguel, BC, the tide is characterized as mixed, with a dominant semidiurnal signal (Filonov et al., 2014; Godin, 1988).

Internal waves forced by the tide in a stratified water column are the product of the interaction between the bottom topography, the degree of stratification in the water column, and the strength of tidal forcing present (Farmer & Smith, 1980; Haury et al., 1979). As the tide ebbs offshore and passes over steep bottom reliefs, such as banks, canyons or the continental shelf, a lee wave is formed (Farmer & Smith, 1980; Haury et al., 1979). When the tide turns to flood, the lee wave produced may propagate forward, steepen and develop undulations and nonlinear characteristics (Farmer & Smith, 1980; Haury et al., 1979). As the amplitude of an internal wave in shallow water increases, its asymmetry also increases and may result in the wave breaking internally while continuing to travel forward as internal surf or a bore (Pineda, 1991). As internal waves or bores propagate, they may be recognized in time series of water-column temperature data by large changes on the order of 2 to 5 degrees Celsius that occur in time scales of minutes (Cairns, 1967; Pineda, 1991), by spectral analyses that determine the relative energy associated with a particular period (Filonov et al., 2014), and by the surface manifestation of slicks due to the formation of conversion zones capable of accumulating inorganic and organic materials (Ewing, 1950; Shanks 1983, 1987; Thorpe, 1995).

An internal wave results in convergent and divergent areas that form at the surface, the result of circulation cells that form perpendicular to the direction of internal wave propagation (Thorpe 1995). In Figure 1, modified from Thorpe (1995), the direction of propagation of an internal wave is indicated by two large arrows. An internal wave, represented by a dashed line, propagates from right to left. The circulation cells are drawn indicating the direction of water movement within each cell. At the surface, particles are represented by circles and are distributed between numbered locations (1-3). Locations 1 and 3 indicate maximum surface current speeds when the propagation direction of the surface current is in line with the internal wave, while location 2 indicates maximum surface velocity in opposition to the direction of internal wave propagation. At location 1.5, a divergence area forms between cells, resulting in the movement of nearby particles to the right of location 1.5 towards location 2, where they increase in speed and are moved further towards location 2.5. Location 2.5 represents the center of surface convergence area over the internal wave around which the surface slick forms and the accumulation of particles is most likely to occur.

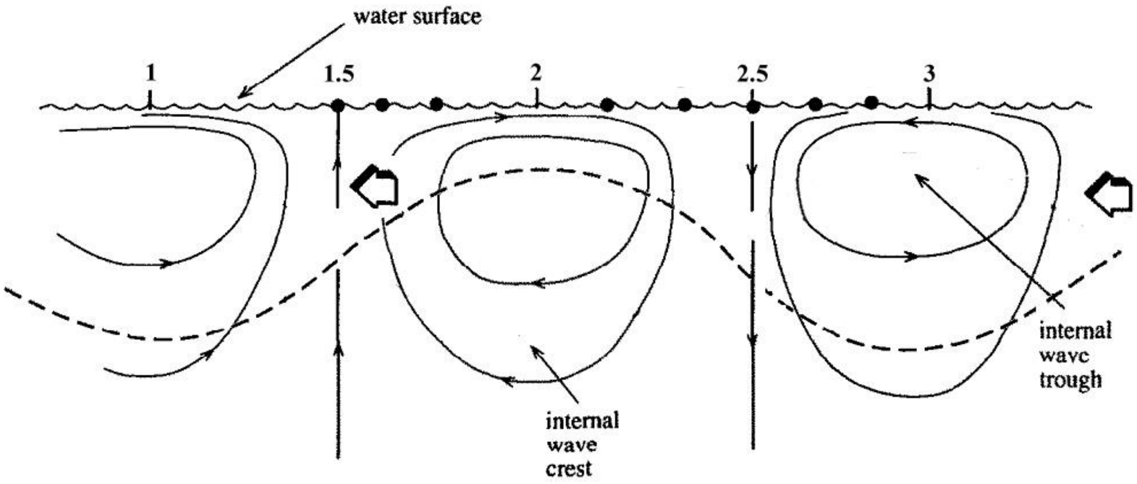

Figure 1. Diagram modified from Thorpe (1995) of an internal wave, represented by the dashed line that propagates from right to left. The direction of propagation of the wave is shown by the two large arrows. Circulation cells are drawn indicating the direction of water movement within each cell. At the surface, particles are represented by circles and are distributed between numbered locations (1-3). Locations 1 and 3 indicate maximum surface current speeds when the direction of propagation of the surface current is in line with that of the internal wave. Location 2 indicates the maximum surface current velocity in opposition to the direction of internal wave propagation. At location 1.5, a divergent area forms between cells, resulting in the movement of nearby particles towards location 2, where they increase in speed and are moved further towards location 2.5. Location 2.5 represent the center of surface convergent area over the internal wave, resulting in the manifestation of a surface slick over the internal wave in which the accumulation of particles is most likely to occur.

The strength of tidal forcing influences the amplitude of internal waves with stronger ebb tides producing more energetic internal waves. The amplitude of tidally-forced internal waves varies with the spring to neap tidal cycle (Cairns, 1967). In addition, increased stratification has been shown to influence the formation and characteristics of internal waves, with increased stratification resulting in more energetic internal waves (Cairns, 1967; Farmer & Smith, 1980). At San Miguel, the most asymmetric and energetic internal waves should coincide with spring tides during summer and fall, when the water column is most stratified.

While internal waves can be highly energetic, the temporal and spatial scales in which they operate are relatively small compared to other physical transport mechanisms such as upwelling that have been shown to be of great importance in the supply of larval subsidies to coastal settlement sites and in the structuring of intertidal and subtidal communities (Krenz et al., 2011; Menge et al., 2003; Navarrete et al., 2005; Wing et al., 1995). Internal waves have been shown to be important purveyors of invertebrate larvae and nutrients to rocky shores (e.g., Pineda,1991, 1994b; Pineda and Lopez, 2002; Ladah et al., 2005; Valencia-Gasti & Ladah, 2016); yet, the question remains as to whether or not the scale of internal waves in coastal oceans is sufficient to result in a meaningful influence on intertidal communities. While upwelling-related events have been shown to influence community structure at the local level, non-linear internal waves have not yet been evaluated in depth for their potential to modify and shape the structure of rocky shore intertidal communities. It is possible that physical transport mechanisms that operate on smaller scales are of either insufficient duration or strength to provoke changes in onshore populations. One must bear in mind that net transports caused by incoming internal waves are not predicted by simple linear theory; without braking or highly non-linear terms, waves in general produce minimal net transports. On the other hand, incoming internal waves evolve into bore- and soliton-like behavior as they propagate inshore, thus provoking sets of net transport pulses.

1.3. Meroplankton

Benthic intertidal invertebrates release either gametes, fertilized eggs, or hatched larvae into the water column, where multiple physical transport mechanisms act to facilitate their dispersal to onshore communities (e.g., Krenz et al., 2011; Pineda et al., 2007; Pineda, 1991; Shanks, 1986; Thorson, 1950; Wing et al., 1995). Intertidal invertebrate communities are composed of open populations of organisms whose life cycles include various nearshore or pelagic phases or both (Thorson, 1950). Invertebrate larvae in the plankton belong to a sub-group referred to as meroplankton and begin their development into competent larvae in an environment that is presumably freer from stressors that might hinder their growth, such as predation or environmental variation. Intertidal communities are therefore connected, to varying degrees, through oceanic meroplankton pools (Gaines et al., 2007; Pineda et al., 2007).

Stage-specific horizontal and vertical patterns in the ocean have been observed for both barnacle and mussel larvae. Barnacle larvae pass through multiple ontogenetic stages that can be divided into two general body forms, the early naupliar stages and the later cyprid stage, while mussel larvae first present the trochophore body form before developing into veligers (Young et al., 2002). Tapia & Pineda (2007) found that early naupliar stages of *Balanus glandula* and *Chthamalus* spp. were more abundant near the coast while nauplii in later stages were more abundant offshore. In addition, cyprids (the last barnacle larval stage before settlement) were always more abundant close to shore. Furthermore, barnacle cyprid larvae tend to maintain themselves in the lower layers of the water column near the bottom, while higher abundances of barnacle nauplii larvae have been found near the surface, indicating a possible additional ontogenetic preference for water column depth (Tapia & Pineda, 2007; Tapia et al., 2010). In contrast, mussel veligers have been shown to present a relatively homogenous vertical distribution throughout the water column, but significantly higher abundances near the coast (Porri et al., 2014; Weidberg et al., 2015). These results support the conceptual model of an oceanic larval pool capable of uniting coastal habitats.

The preference of larvae to remain at a particular depth may be due to certain species-specific or stage-specific needs or behavior. If the ability of a physical transport mechanism to advect larvae varies with depth, then larvae may be transported in various directions and over various distances depending on their vertical distribution in the ocean. By taking advantage of different flow regimes in the water column, larvae may maintain or modify their horizontal location in the ocean by means of the modification of their vertical position. The dispersal distances of marine benthic larvae may vary by orders of magnitude and the time required to arrive to potential settlement sites can range from days to months (Thorson, 1950; Gaines et al., 2007). This variation is due to the interaction between planktonic larval duration and physical transport mechanisms that act to move meroplankton throughout the ocean.

The amount of time that meroplanktonic species may remain the in the water column is a function of the time necessary for competent larvae to form, environmental conditions, and larval feeding strategies (Roughgarden et al.,1988; Scheltema, 1986). Provided that conditions are ideal, barnacle and mussel larvae may remain in the plankton for two to four weeks (Lohse & Raimondi, 2007, Lopez-Duarte et al., 2012). During their time in the water column, meroplankton of different species and of different ontogenetic stages maintain certain control over their vertical and horizontal distributions through swimming behavior and buoyancy control (Pineda 1991, 1994a; Metaxas 2001; Tapia & Pineda, 2007; Tapia et al., 2010). Barnacle and mussel larvae swimming speeds and strategies vary greatly. Barnacle nauplii use their antennae and mandible to swim while cyprids use six pairs of thoracic appendages (Chia et al., 1984). In contrast, mussel veligers use cilia to swim, alternating between an upward swim and a downwards sinking motion (Chia et al., 1984). The swimming speeds of the *Balanus improvisus* nauplii range between 1.5 $cm \cdot s^{-1}$ to 1.8 $cm \cdot s^{-1}$, cyprids of *Balanus crenatus* show rates between 0.17 $cm \cdot s^{-1}$ to 0.55 $cm \cdot s^{-1}$, and veligers of *Mytilus edulis* show speeds of 0.11 $cm \cdot s^{-1}$ (Chia et al., 1984). Given these speeds, mussel veligers are capable of swimming nearly 4 meters in one hour, while nauplii may swim upwards of 20 meters in the same time showing that changes in their vertical position within the water column may be achieved through swimming behavior.

The complex interaction between physical transport mechanisms and biological variables (e.g., ontogeny, the time required to produce a competent larvae, horizontal and vertical distributions in the water column) results in transport over the continental platform and influences eventual meroplanktonic settlement in costal sites. Of the various potential physical transport processes that exist, such as upwelling or wind-driven currents, internal waves may be of particular importance as they have been shown to change the abundance of meroplankton throughout the water column and surface slicks associated with their activity have been shown to accumulate meroplankton (Liévana MacTavish et al., 2016; Shanks, 1983).

1.4. Intertidal community controls

Invertebrate population regulation in the intertidal requires the presence of density dependence at some demographic stage and at some spatio-temporal scale in order for the population in question to persist (Hassell, 1986; Hixon et al., 2002). Each invertebrate population within the intertidal may have differing degrees of demographic density dependence, in addition to unique supply rates of new individuals, due to the different life histories and ecological functions of the species within the community (Jenkins et al., 2008; Menge, 2000a; Minchinton & Scheibling, 1991; Navarrete et al., 2008). An assessment of the dynamics of a particular community begins with an evaluation of how the populations within the community are regulated by quantifying the recruitment of new individuals, their subsequent mortality, and the presence of regulatory mechanisms such as competition, which is density-dependent, or predation, which may be either density-dependent or density-independent (Caley et al., 1996; Hixon et al., 2002). This approach stresses field work done at a local level. Such research is the first step in the generation of models that may predict of how forces acting on populations present within a community might produce changes in its structure (Harley et al., 2006; Hixon et al., 2002).

Postrecruitment controls may be of great importance in determining the structure of an intertidal community if they are capable of modifying the distribution and abundance of individuals in the intertidal such as competition and predation have been shown to do by increasing the mortality of recruit, juvenile and adult cohorts (Connell, 1961, 1983; Dayton, 1971; Menge & Sutherland, 1987;

Menge, 1972, 1979, 2000; Navarrete et al., 2000; Paine, 1974, 1995; Paine & Levin, 1981; Underwood, 1978).

1.5. Recruitment limitation and the recruit-adult hypothesis

In 1981, Doherty proposed the Recruitment Limitation Hypothesis which states that the supply of new individuals to a given population may limit the future size of the population, the implication being that supply may be insufficient for density-dependent processes, such as competition, to affect future population size. Stemming from this hypothesis are three predictions that should be evident in populations under recruitment limitation: the first being that postrecruitment mortality will be density-independent, the second being that the size differences of consecutive cohorts will be clearly apparent in the age-structure of populations, and the third being that variations in recruitment will be highly correlated with local population size (Caley et al., 1996; Doherty & Williams, 1988). However, Caley et al. (1996) argue that postrecruitment density-dependent mortality may be low to moderate and result in only a “slight dampening” of the recruitment signal in future population size, effectively rendering the first two predictions unnecessary for a population to be under recruitment limitation. In addition, the case may be made for the presence of variable density-independent mortality which is likely to result in recruitment being uncorrelated with population size, indicating that the last prediction need not be observed for recruitment limitation to be present (Caley et al., 1996). The evaluation of recruitment limitation within a population should therefore be based on the evaluation of the relationship present between a cohort’s recruit and adult densities.

The degree to which a population may be under recruitment limitation may be evaluated using the “recruit-adult hypothesis” proposed by Menge (2000a), based on work by Gaines & Roughgarden (1985) and Roughgarden et al. (1988), which can be broken down into two alternate scenarios. The recruit-adult hypothesis states that when recruitment is high, recruit density poorly explains the variation in adult density (scenario 1) and conversely, when recruitment is low, recruit density explains a high proportion of the variance in adult density (scenario 2). Under the first scenario of the recruit-adult hypothesis, processes that result in postrecruitment mortality, such as competition and predation, are responsible for explaining the decoupling of cohort’s recruit density from its adult density. If a population is found to conform to this scenario, it may be said that future population size is under postrecruitment control. A population that conforms to the second scenario of the recruit-adult hypothesis may be said to be under recruitment limitation or supply-side control given that postrecruitment processes do not obscure the relationship between a cohort's recruit and adult densities.

The determination of whether a population is under postrecruitment or supply-side control is an important component in the evaluation of how the population is regulated. If a population is found to be under postrecruitment control, identifying the postrecruitment mechanisms present that are exerting control over the size of the population is of utmost importance (Hixon et al., 2002). Competition and predation are two key postrecruitment regulatory mechanisms in the intertidal and have been shown to limit the distributions of benthic invertebrates thereby influencing intertidal zonation (Connell, 1961, 1983, Menge, 1991, 2000a; Menge & Sutherland, 1987; Navarrete et al., 2000; Paine, 1974; Shinen & Navarrete, 2010). On the other hand, if a population is under supply-side control, and postrecruitment processes are not largely determinant of population size, then evaluating the distribution and abundance of the larvae in the water column, the physical mechanisms that bring the larvae onshore to settlement sites, the timing of settlement and density of recruits become primary concerns in evaluating how the population is regulated.

1.6. Barnacle populations in the intertidal

Barnacles are one of the most widely studied intertidal invertebrates. Interspecific and intraspecific competition, mainly for substrate space, between newly settled barnacle recruits, algae and other intertidal invertebrates may be a significant source of postrecruitment mortality and is likely to increase as newly settled barnacle recruits grow in size (Berlow, 1997; Bertness, 1998; Carroll, 1996; Connell, 1961; Dayton, 1971; Denley & Underwood, 1979; Farrell, 1991; Menge, 1991). Acorn barnacle cyprids prefer to settle near conspecifics as a means to enhance their future reproductive success, to avoid predation, to protect from thermal and desiccation stress, and to increase structural support (Beermann et al., 2013; Bertness et al., 1998; Hooper & Eichhorn, 2016; Knight-Jones, 1953; Raimondi, 1991; Wethey, 1986). However, the need for acorn barnacles to aggregate during settlement comes at a cost, as this preference may lead to increased intraspecific competition in the form of crowding or crushing between individuals resulting in increased mortality (Connell, 1961; Hooper & Eichhorn, 2016). The balance between the need for closeness between neighbors and the freedom from increased competitive pressure may depend on density. Zabin (2015) found that competition did not play a role in determining the adult abundance of *Chthamalus proteus* (Dando & Southward, 1980) when recruit densities were low. Hills & Thomason (1996) demonstrated that the settlement preference of the barnacle *Semibalanus balanoides* (Linnaeus, 1767) near conspecifics only held at low densities while there appeared to be an avoidance of the same at high densities. Jenkins et al. (2008) evaluated the recruitment and postrecruitment mortality of *Semibalanus balanoides* and found that despite the presence of strong density-dependent mortality, recruit density was a good predictor of adult population size through a positive recruit-adult relationship present under low recruitment (scenario 2) and via a negative recruit-adult relationship under conditions of high recruitment (scenario 1). In other words, postrecruitment mechanisms resulted in significant recruit mortality under conditions of high recruitment and were responsible for the resultant negative recruit-adult relationship. While the authors suggest competition as the possible postrecruitment mechanism responsible for the observed mortality of recruits, the study did not include treatments that may have been able to test this hypothesis. In addition, Shinen & Navarrete (2010) found evidence of weak competition between two species of chthamaloid barnacles, *Jehlius cirratus* (Darwin, 1854) and *Notochthamalus scabrosus* (Darwin, 1854), that did not interfere with recruit growth patterns, presumably due to the equal competitive abilities of the two species, even at higher recruit densities. Therefore, the presence of potential competitors is not enough to assume competition may be acting to increase the mortality of barnacle recruits, especially when recruitment is relatively low.

Predation, perhaps more so than competition, is an important source of postrecruitment mortality in intertidal barnacles. Many examples of predatory control over barnacle abundance can be found in the literature and highlight the key role this postrecruitment process can play in the structure of an intertidal community. In an experimental study by Fairweather (1988), an entire newly recruited barnacle cohort of *Tesseropora rosea* (Krauss, 1848) was almost eliminated when exposed to the predatory marine gastropod *Morula marginalba* (Blainville, 1832). In the northern Gulf of California, Lively et al. (1993) demonstrated that the local abundance of *Chthamalus* barnacles was controlled by the predatory snail *Acanthina angelica* (Oldroyd, 1918). Similarly, Berlow (1997) demonstrated that the presence of the predatory gastropods, *Nucella emarginata* (Deshayes, 1839) and *Nucella canaliculata* (Duclos, 1832), in experimental treatments resulted in a scarcity or absence of *Balanus glandula* (Darwin, 1854) barnacle recruits, which facilitated colonization by the barnacle *Chthamalus dalli* (Pilsbry, 1916). The facilitation of *Chthamalus* due to the removal of *Balanus* via predation by *Nucella* is well documented and highlights the importance of predation in determining the population sizes of intertidal invertebrates by acting as an important source of postrecruitment mortality (Connell, 1961; Dayton, 1971). While *Nucella* prefers *Balanus* to *Chthamalus*, young *Nucella* prefer smaller prey and are more likely to consume prey located near their potential refuges, suggesting that *Chthamalus*, which contains the same energy content as

Mytilus mussels, which is the preferred prey item of *Nucella*, is likely to be consumed by newly recruited *Nucella* predators (Gosselin & Chia, 1996; Lively et al., 1993). *Chthamalus* barnacles are the preferred prey item of *Mexacanthina lugubris* (Sowerby, 1821) (Fenberg et al., 2014) while *Nucella emarginata* prefers to consume mussels rather than barnacles although barnacles are an important component of the diet of *N. emarginata* (Gosselin & Chia, 1996; Palmer, 1984). *Pisaster ochreceus* (Brandt, 1835) also prefers to consume *Mytilus* mussels rather than *Chthamalus* barnacles, yet approximately 10% of its diet is composed of these two prey items (Newman & Abbott, 1980). In intertidal communities in Baja California, both *M. lugubris* and *N. emarginata* along with *P. ochreceus* may play key roles in determining intertidal barnacle abundance.

Initial barnacle recruit densities can determine the potential for predation to act as a limiting factor of subsequent adult barnacle population size. Menge (1991) reviewed data collected in two locations, Panama, in which recruitment limitation was likely present and New England, in which recruitment rates were an order of magnitude larger and therefore unlikely to be limiting. In New England, predation accounted for approximately 50% of the variation in the adult population size of sessile invertebrates, including chthamaloid barnacles, demonstrating its importance as a postrecruitment control of population size when recruit densities are high, while in Panama, predation only accounted for approximately 8% indicating that initial barnacle recruit densities may determine the potential for predation to act as a regulatory mechanism of subsequent adult barnacle population size. Results such as these suggest that variable initial barnacle recruit densities may result in different predatory responses, although it is not always the case that a greater predatory response should be expected with a greater number of barnacle recruits, as Carroll (1996) found that predation by *Nucella* was greater when recruitment of the barnacles *Semibalanus* and *Balanus* was relatively low.

1.7. Study questions

Two questions are proposed to evaluate the importance of internal waves to sites along the Mexican Pacific coast:

1. Are meroplankters accumulating in slicks associated with internal wave activity in various sites along the Mexican Pacific coast (San Juanico, BCS; La Paz, BCS, and Barra de Navidad, JAL)?

2. In a site where barnacle (*Chthamalus* spp.) settlement is associated with internal wave activity (San Miguel, BC), is the barnacle population under supply-side or postrecruitment control?

1.8. Justification

An evaluation of how larval subsidies arrive to a particular intertidal community and the influence of those subsidies on the structure of that community after arrival is necessary for understanding how the intertidal community might respond to change. Potential meroplanktonic transport in internal wave fronts or surface slicks has been shown to be variable due to the complex interactions between internal waves and meroplankton (Shanks, 1983; Pineda 1994a; Lamb, 1997; Pineda et al., 2007; Scotti & Pineda, 2007; Shanks & Shearman, 2009; Filonov et al., 2014). To evaluate the potential of internal waves to transport meroplankton in a given site, an evaluation of the accumulation of meroplankton in surface slicks in the nearshore is important. In addition, in the intertidal, both recruitment and postrecruitment mortality will contribute to observed adult population sizes; however, the degree to which either postrecruitment control or supply-side control acts to shape populations within a community may vary greatly between sites (Caley et al., 1996; Connell, 1985; Hixon et al., 2002; Jenkins et al., 2008; Menge, 1991, 2000a; Minchinton & Scheibling, 1991; Navarrete et al., 2005). Evaluating the input of settlers to a particular site and their subsequent survivorship to determine if the population is under supply-side or postrecruitment control is necessary for classifying the regulatory mechanisms shaping the community.

1.9. Objectives

1.9.1. General objective

To evaluate the potential importance of internal waves to intertidal sites along the Mexican Pacific by quantifying the accumulation of meroplankton in surface slicks associated with internal waves in three sites (San Juanico, BCS; La Paz, BCS; and Barra de Navidad, JAL) and by determining if supply-side or postrecruitment control is present over the population of *Chthamalus* spp. barnacles in a site where *Chthamalus* settlement is known to be associated with internal wave activity (Playa San Miguel, BC).

1.9.2. Specific objectives

1. To quantify the abundance of barnacle and mussel larvae at the surface within surface slicks associated with internal wave activity and outside of surface slicks in three sites: San Juanico, BCS; La Paz, BCS; and Barra de Navidad, JAL.

2. To evaluate the recruitment and survivorship of *Chthamalus* spp. barnacles in in a site where barnacle settlement is known to be associated with internal wave activity (Playa San Miguel, BC) and to determine if predation or competition act to decouple the relationship between recruit and adult densities in that site.

Chapter 2. Interaction between internal waves and meroplankton

2.1. Hypothesis

Zooplankton samples taken from within surface slicks associated with internal wave activity will contain a greater abundance of barnacle and mussel larvae than samples taken outside of surface slicks.

2.2. Objective

To quantify barnacle and mussel larvae within and outside of surface slicks associated with internal wave activity in three sites: San Juanico, BCS; La Paz, BCS; and Barra de Navidad, JAL.

2.3. Materials and Methods

2.3.1. Study sites

Barra de Navidad, JAL (19° 13’ N, 104° 42’ W) is located along the western coast of Mexico, approximately 30 km west of Manzanillo, and is set within a small bay with a deeply sloping continental shelf that quickly drops off to 200 m depth within 15 km from the coast (Filonov et al., 2005). Within the bay, a strong semidiurnal internal tide is present resulting in nonlinear internal waves of 10 m amplitudes that propagate in the cross-shore direction (Filonov et al., 2005). San Juanico, BCS (26° 14’ N, 112° 27’ W) is also located along the western coast of Mexico, approximately 110 km south of Punta Abreojos. The San Juanico bay is relatively small and hosts an important lobster fishery. Within the bay, diurnally forced internal waves are present (Ladah, pers. comm., 2015). The bay of La Paz, BCS is the largest bay within the Gulf of California. During the summer and fall, it presents strong stratification that dissipates during winter and spring, and in the upper mixed layer, diurnal tidal motions account for a third of the total energy in currents (Zaytsev et al., 2010).

2.3.2. Oceanographic data collection and processing

A vertical array composed of ten of Onset® HOBO® Temperature TidbiT data loggers with ±0.2°C precision (Onset computer corp., Massachusetts, U.S.A) were used to obtain temperature profiles of the water column in each site. Each vertical thermistor array consisted of a polypropylene line attached to a dead weight and was vertically suspended in the water column by mid-water and surface buoys. Thermistors were evenly spaced either every meter or every two meters along each line and were programmed to record either every minute or every five minutes (Table 1).

Table 1. Thermistor line installation depths and thermistor spacing and recording intervals

Site	Installation depth	Spacing interval	Recording interval
Barra de Navidad	11 m	1 m	1 min
San Juanico	12 m	1 m	1 min
La Paz	15 m	1 m	1 min

In addition, an RDI Broadband Workhorse Acoustic Doppler Current Profiler of 614.4 KHz (Teledyne RD Instruments, California, USA) was installed next to the thermistor lines in Barra de Navidad and San Juancio but was unavailable during the La Paz sampling expedition, as such no current data exists for the La Paz data set. The ADCP was programmed to record current velocities every minute in one meter bins and was used to capture three current components within the water column, *u* orientated east–west, *v* orientated north–south and *w* orientated vertically. From *u* and *v*, the horizontal component of the current velocity with greatest variability (*v′*) was calculated utilizing the following equation:

$$v' = u\sin(\theta) + v\cos(\theta)$$

where θ is the angle between the reference system of *u* and *v* and the reference system of *u′* and *v′* (Protter & Morley 1977). The angle θ of greatest variability was calculated using a principal component analysis of the current at 10 meters above bottom (MAB) for both sites, corresponding to a depth of 1 and 2 meters below the surface for Barra de Navidad and San Juanico, respectively. For an explanation of the vector rotation used and a description of the principal component analysis, please see appendices. The orientation of *v′* with respect to the coastlines of San Juanico and Barra de Navidad is shown in

Figure 2. Positive *v′* velocities indicate onshore current propagation in the direction of internal wave propagation, while negative *v′* velocities indicate offshore current propagation in San Juanico. In Barra de Navidad, both positive and negative *v′* velocities indicate onshore current propagation; however, positive *v′* velocities indicate southwestern current propagation towards the nearest coast. In this site, internal waves enter this small bay from the southeast and reflect off the northern coast, continuing on in a southwest direction (A. Filonov, pers. comm., 2017).

Figure 2. Diagram of *v′* orientation with respect to the coastlines of Barra de Navidad (left) and San Juanico (right). Positive *v′* velocities indicate onshore current propagation in the direction of internal wave propagation, while negative *v′* velocities indicate offshore current propagation in San Juanico. In Barra de Navidad, both positive and negative *v′* velocities indicate onshore current propagation; however, positive *v′* velocities indicate current propagation towards the nearest coast.

2.3.3. Meroplankton collection

Zooplankton samples were collected via a conical net with a mesh size of 150 µm in Barra de Navidad, JAL (BN) from May 25 to 28, 2010. Sampling was carried out every 10-20 minutes, alternating between both depths, from a floating platform, 1 km from shore, beginning at approximately 08:00 h and ending at 18:00 h each day.

Zooplankton samples were collected via two pumps installed at 1 and 3 m depth from May 27 to 30, 2011, in San Juanico, BCS (SJ). Sampling was carried out every 20 minutes, alternating between both depths, beginning at approximately 08:00 h and ending at 13:00 h each day.

Zooplankton samples were collected simultaneously via three pumps installed at 2 m depth in La Paz, BCS (LP) from June 6 to 10, 2013. Sampling was carried out every hour, day and night, for five consecutive days beginning at 21:00 h on the first night and ending at 05:00 h on the last day.

In all three sites, zooplankton sampling was carried out next to an installed thermistor line and samples were immediately fixed in 70% alcohol. The meroplanktonic taxa of interest were barnacle nauplii and cyprids, as well as mussel veligers. In addition, the visual detection of surface slicks was recorded during sampling. In total, 571 zooplankton samples were collected between the three sites: 144 from BN, 169 from SJ, and 258 from LP.

2.3.4. Data analysis

From the vertical thermistor array installed at each site, a time series of vertical temperature profiles of the water column during the course of zooplankton sampling was generated. The time series of vertical temperature profiles was used to obtain the thermocline depth time series for each site. To determine the depth of the thermocline, the derivative with respect to depth was taken of each vertical temperature profile and depth at which the maximum absolute value of the derivative occurred was deemed to be the depth of the thermocline. During times in which the stratification of the water column was less than 1°C, the depth of the thermocline was set to the surface if the average temperature of the water column for that profile was less than the overall average for the site, indicating that cold water from below the thermocline had been pulsed upward to the surface; conversely, if the average temperature of the water column was greater than the overall average, the depth of the thermocline was set to the bottom indicating that warm water from above the thermocline had been pulsed downward to the bottom. From these depths, a thermocline depth time series was generated which was subsequently low-pass filtered to remove high-frequency variability (greater than or equal to 3 cph).

A proxy for internal wave activity was used to compare internal wave activity between sites. The internal wave proxy was calculated by taking the absolute value of the derivative with respect to time of the thermocline depth time series. The internal wave proxy represents the vertical velocity of the thermocline (VVT) in $m \cdot min^{-1}$.

After obtaining *v′*, current data were low-pass filtered to eliminate high-frequency variability (greater than or equal to 3 cph). Filtered *v′* velocities near the surface were used to determine periods of time during which surface slicks may have been present. Given that surface slicks are likely to occur in surface convergence zones that form over internal waves, a criteria was established to determine periods of time when surface slicks would theoretically be present during zooplankton sampling. This criteria was used to determine the percentage of observed slicks that were recorded during times in which the conditions at the surface were likely present for slick formation. After removing the mean current from *v′*, a change in the direction of the current (from negative to positive) that occurred prior to maximum values of onshore flow was used to identify these periods of time when slicks could potentially form. Please see appendices for an explanation of the criteria implemented.

ANOVA analyses were used to test for differences in the abundance of meroplankton inside and outside of slicks that were visually detected and Pearson correlations were used to evaluate the relationship between the number of slicks observed and meroplankton abundance. Prior to carrying out the analyses, data normality and homogeneity of variances were checked using the Shapiro-Wilks normality test and Bartlett's test of homogeneity of variances. When appropriate, a log transformation was applied to the data.

2.4. Results

2.4.1. Barra de Navidad, JAL

Water column temperatures during zooplankton sampling were characteristic of Filonov's 2011 description of internal wave activity in BN. Figure 3 shows the time series of water column temperatures during zooplankton sampling with the thermocline superimposed (black line). Colder water from below the thermocline was pulsed upward towards the surface, creating nearshore small-scale upwelling events, while warm water from above the thermocline was alternately pulsed downward, suggesting non-linear internal wave activity (Filonov, 2011; Pineda, 1994a). Warm-water pulses and mixing were substantially strong given that the water column was not only oftentimes homogeneously warm, but reverted to being homogenously warm following cold-water pulses in less than 20 minutes (Fig. 3).

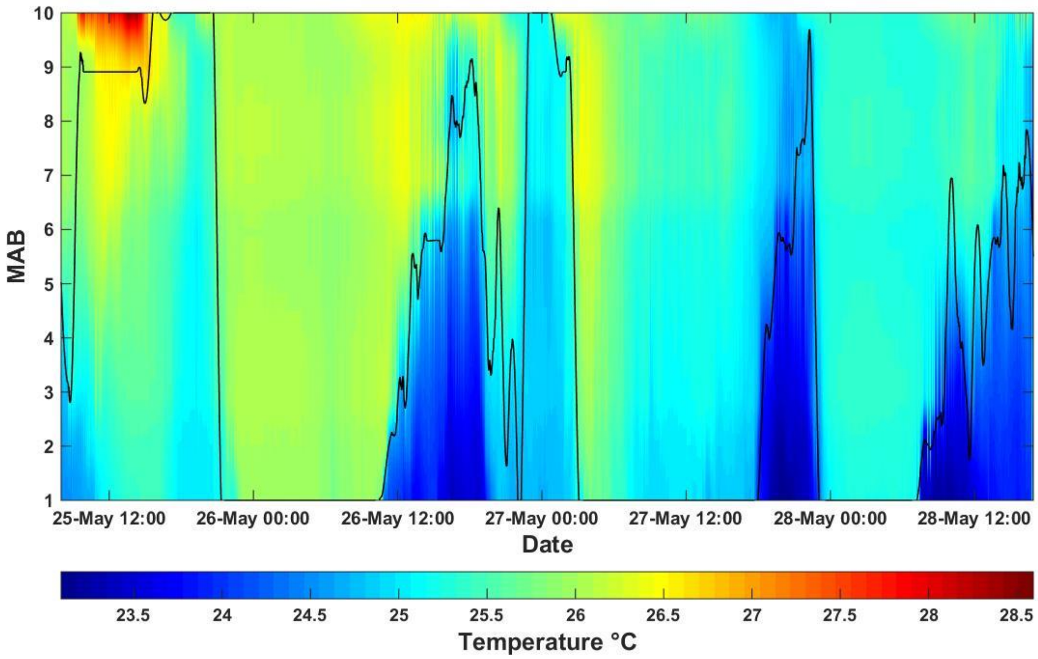

Figure 3. Time series of water column temperature in Barra de Navidad during zooplankton sampling (May 25th to May 28th, 2010). The vertical axis shows the depth of the water column in meters above the bottom. The horizontal axis shows date and time. The color axis shows temperature in degrees Celsius. The black line superimposed onto the temperature data is the calculated depth of the thermocline (see methods).

The values of the VVT indicated strong internal wave activity in BN. Vertical changes in the depth of the thermocline of 25 cm that occurred in under a minute were observed multiple times on most days (Fig. 4). In addition, a change in thermocline depth of more than 30 cm·min^{-1} was observed on the 28th of May. Periods of time when the value of VVT was equal to 0 m·min^{-1} were reflective of a homogenous water column with no stratification present, the result of strong upward cold-water pulses or downward warm-water pulses. The presence of periods of time where VVT was equal to 0 m·min^{-1} that persisted for hours, coupled with the large values of VVT observed in between these periods, indicated strong internal wave activity present in BN.

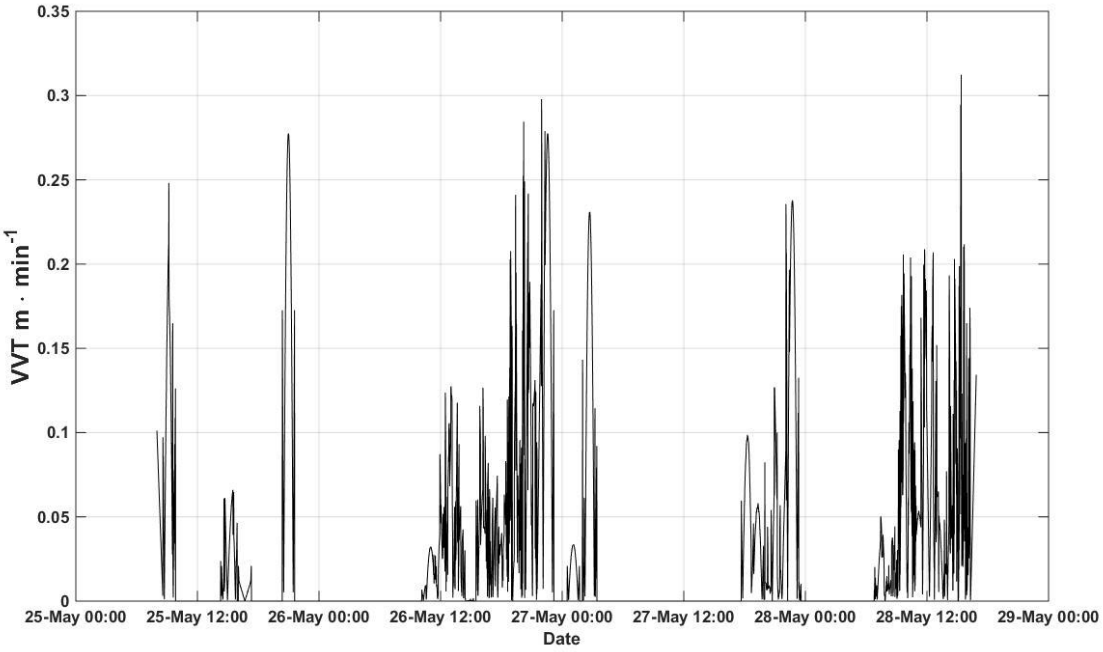

Figure 4. Time series of the vertical velocity of the thermocline (VVT) in Barra de Navidad during zooplankton sampling (May 25th to May 28th, 2010). The vertical axis shows the values of VVT in $m \cdot min^{-1}$. The horizontal axis shows date and time.

Bottom currents from 2 to 7 MAB showed little variability and reduced strength with onshore (+*v′*) and offshore (-*v′*) velocities ranging between ±100 $mm \cdot min^{-1}$ and rarely exceeding ±75 $mm \cdot min^{-1}$ (Fig. 5). Above 7 MAB, current propagation was predominately in the onshore direction and current strength was much stronger, with maximum velocities of almost 600 $mm \cdot min^{-1}$. According to Pineda's 1994 two-phase model of internal bore behavior in the nearshore, surface currents are expected to flow offshore while bottom currents are expected to flow onshore during phase one, before inverting during phase two. While periods of opposing flow in the surface and the bottom can be seen on most days, the water column current data from BN does not adhere closely to Pineda's 1994 two-phase bore model. Oftentimes, surface and bottom currents can be seen flowing in the same direction and clear distinctions between phase one and phase two of Pineda's model are largely absent. This may be due to internal waves being reflected off of the northern coast before reaching the sampling site (A.Filonov, pers. comm., 2017).

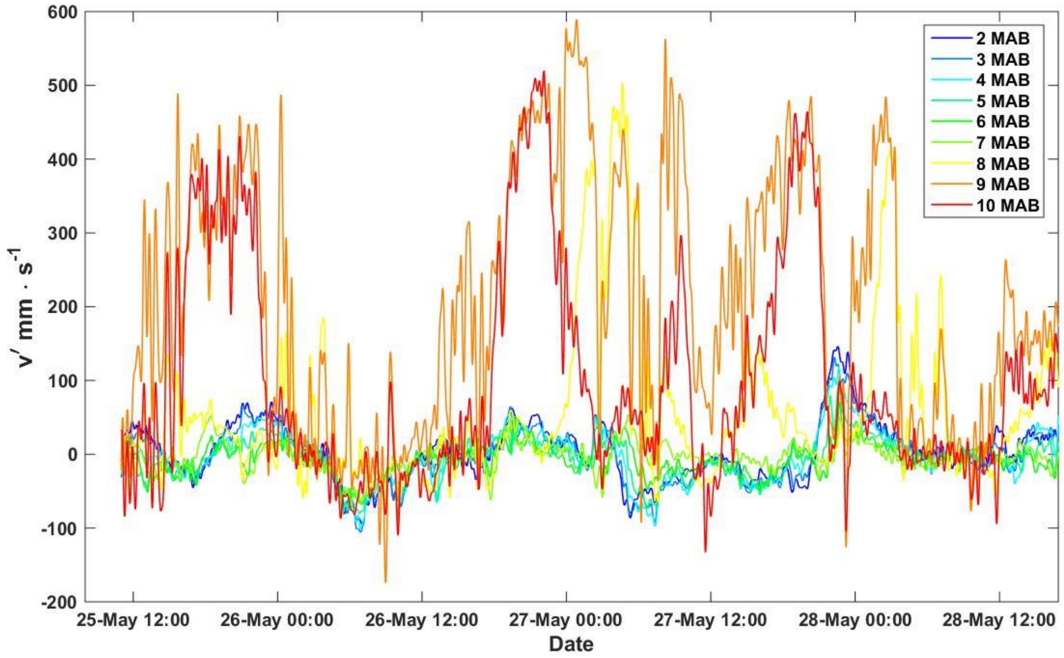

Figure 5. Time series of *v′* current velocities for Barra de Navidad during zooplankton sampling (May 25th to May 28th, 2010). The horizontal axis shows date and time and the vertical axis shows the values of *v′* in mm·s^{-1}.

The slick criteria implemented to evaluate the percentage of observed slicks that occurred is shown in Figure 6. Times in which slicks were visually observed and recorded are graphed as dashed vertical black lines, while *v′* at 10 MAB is graphed as a black line. The superimposed blue series represents the times in which surface slicks may theoretically have been present. On average, 9.25 slicks were observed each day (SE = ± 1.11) and 72 % of visually-detected slicks occurred during times in which slicks may have theoretically been present.

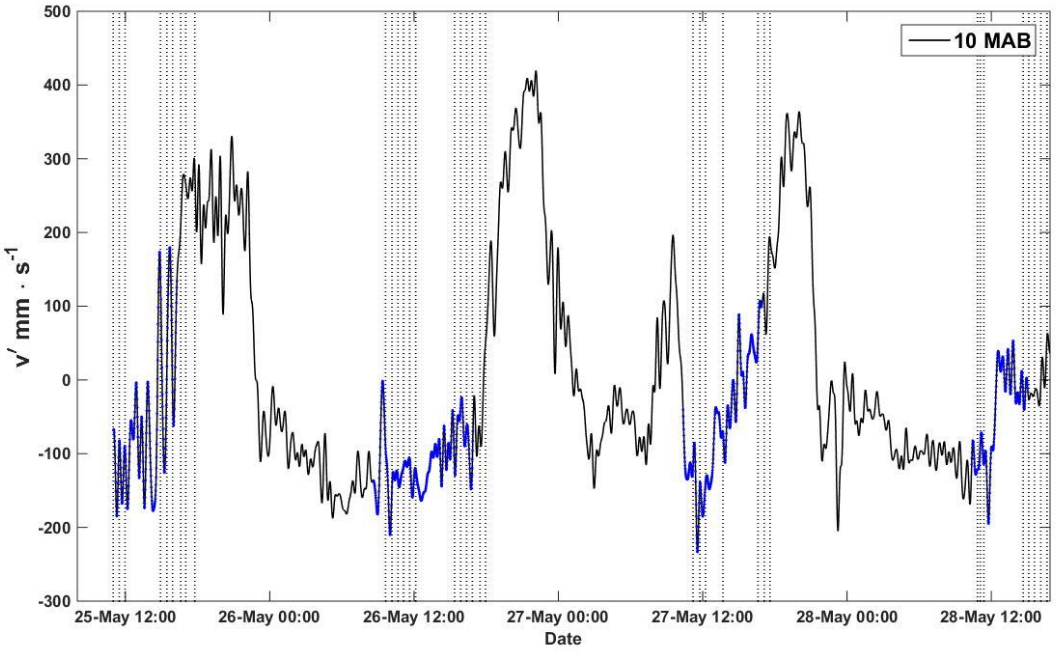

Figure 6. Time series of *v′* in at 10 MAB showing when potential slicks theoretically should have been observed during zooplankton sampling (May 25th to May 28th, 2010). The vertical axis shows values of *v′* in mm·s^{-1}. The horizontal axis shows date and time. Vertical black dashed lines indicate times in which slicks were visually observed and recorded during sampling. The superimposed blue series represents the times in which surface slicks theoretically should have been present in surface convergence areas.

A greater abundance of *Chthamalus* nauplii was observed at 1m depth during the first two days of zooplankton sampling, with 35% of the samples containing more than 1000 nauplii m^{-3} on May 25th and 26% of the samples containing more than 500 nauplii m^{-3} on May 26th (Fig. 7, top panel). *Chthamalus* cyprid abundance was highest on the first and last day of sampling when 30% of the samples contained more than 1000 cyprids·m^{-3} (Fig. 7, middle panel). Mussel veliger abundance was high on the first, second and fourth day of sampling with more than 25% of the samples containing more than 1000 veligers·m^{-3} (Fig. 7, bottom panel). On May 27th, the abundance of all three taxa was low and no sample contained more than 100 individuals·m^{-3}.

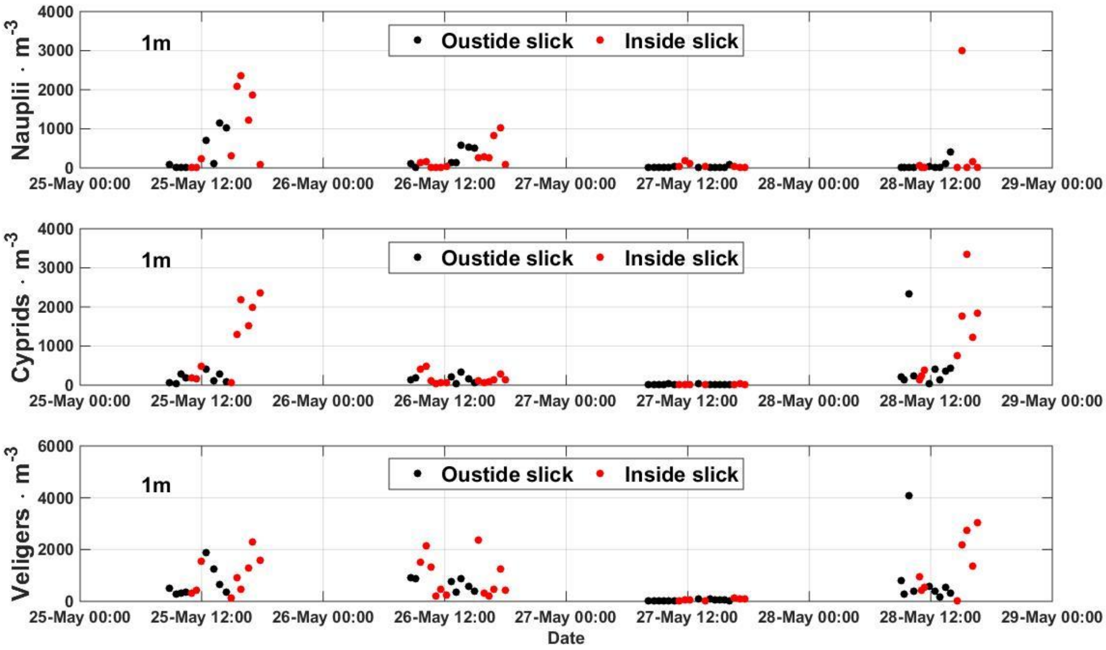

Figure 7. Abundance of *Chthamalus* nauplii and cyprids and mussel veligers at 1m depth during zooplankton sampling (May 25th to May 28th, 2010). Top panel: *Chthamalus* nauplii abundance in nauplii·m^{-3}. Middle panel: *Chthamalus* cyprid abundance in cyprids·m^{-3}. Bottom panel: Mussel veliger abundance in veligers·m^{-3}. The horizontal axis for each panel shows the date and time. The horizontal axis for each panel shows the abundance of each respective taxa. Each point represents one sample. Red points indicate samples taken within slicks that were visually detected during sampling.

At 5 m depth, abundance of *Chthamalus* nauplii and cyprids and mussel veligers was high on the first, second and fourth day of sampling (Fig. 8). As observed at 1 m depth, a low abundance of all three taxa was recorded on May 27th with all but three samples containing less than 100 individuals·m^{-3}. Only 7% of the samples contained more than 50 nauplii·m^{-3}, while only 8% of the samples contained more than 1000 cyprids·m^{-3}, and 5% of the samples contained more than 1000 veligers·m^{-3}.

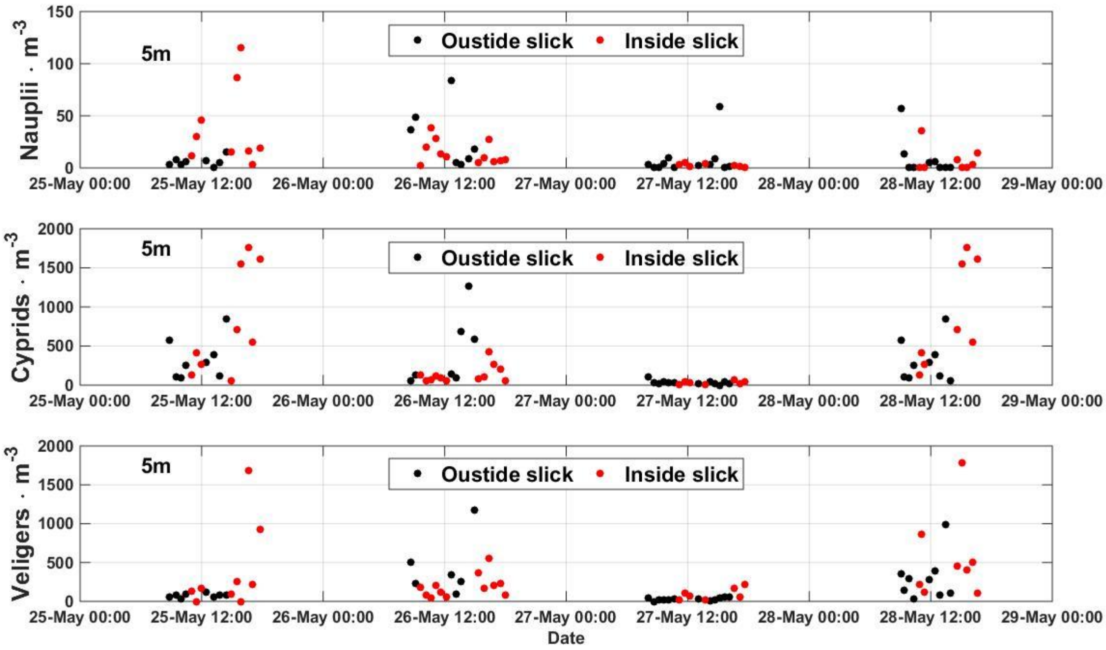

Figure 8. Abundance of *Chthamalus* nauplii and cyprids and mussel veligers at 5m depth (May 25th to May 28th, 2010). Top panel: *Chthamalus* nauplii abundance in nauplii·m^{-3}. Middle panel: *Chthamalus* cyprid abundance in cyprids·m^{-3}. Bottom panel: Mussel veliger abundance in veligers·m^{-3}. The horizontal axis for each panel shows the date and time. The horizontal axis for each panel show the abundance of each respective taxa. Each point represents one sample. Red points indicate samples taken within slicks that were visually detected during sampling.

Abundances of *Chthamalus* nauplii and cyprids and mussel veligers were log transformed prior to carrying out the two-way analysis of variance utilizing the factors of *slick presence* and *depth*. The ANOVA results indicate a significant effect of *slick presence* on meroplankton abundance for all three taxa, while *depth* was only significant for *Chthamalus* nauplii and mussel veligers (Table 2). The interaction between slick presence and depth was not significant for any taxa ($p>0.05$). *Chthamalus* nauplii and mussel veliger abundance was lower at 5 m than at 1 m; however, there was no significant difference in cyprid abundance between 1 m and 5 m depth. There was a significantly greater abundance of meroplankton in samples taken within surface slicks than in samples taken outside of surface slicks.

Table 2. ANOVA results for *Chthamalus* nauplii, *Chthamalus* cyprids, and mussel veligers

Chthamalus nauplii

Source of variation	**Sum of squares**	**Degrees of freedom**	**Mean square**	**F**	**p**
Slick presence	3.46	1	3.47	4.91	**0.028**
Depth	19.97	1	19.67	28.32	**0.001**
Slick presence-Depth	0.40	1	0.41	0.57	0.45
Residuals	98.69	140	0.71		

Chthamalus cyprids

Source of variation	**Sum of squares**	**Degrees of freedom**	**Source of variation**	**Sum of squares**	**Degrees of freedom**
Slick presence	3.05	1	3.06	6.04	**0.015**
Depth	0.03	1	0.027	0.054	0.83
Slick presence-Depth	0.04	1	0.45	0.09	0.77
Residuals	70.78	140	0.51		

Mussel veligers

Source of variation	**Sum of squares**	**Degrees of freedom**	**Source of variation**	**Sum of squares**	**Degrees of freedom**
Slick presence	2.06	1	2.06	4.25	**0.041**
Depth	3.18	1	3.18	6.56	**0.012**
Slick presence-Depth	0.19	1	0.19	6.40	0.53
Residuals	59.65	123	0.49		

To evaluate a potential relationship between the number of visual detected slicks per day and meroplankton abundance, Pearson correlation analyses were carried out after abundances of *Chthamalus* nauplii and cyprids and mussel veligers were log transformed (Table 3). No significant correlations between slick abundance and meroplankton abundance were found for any taxa or depth.

Table 3. Correlation results for *Chthamalus* nauplii, *Chthamalus* cyprids, and mussel veligers

***Chthamalus* nauplii**

Depth	r	p
1 m	0.78	> 0.05
5 m	0.49	> 0.05

***Chthamalus* cyprids**

Depth	r	p
1 m	0.37	> 0.05
5 m	0.38	> 0.05

Mussel veligers

Depth	r	p
1 m	0.65	> 0.05
5 m	0.49	> 0.05

2.4.2. San Juanico, BCS

Water column temperatures during zooplankton sampling in SJ reflected strong stratification and little mixing, contrary to what was observed in BN (Fig. 9). The behavior of the thermocline (black line in Fig. 9) reflects non-linear internal wave activity and Pineda's 1994 two-phase internal bore model can be observed in water-column temperatures as colder water from below the thermocline is pulsed upward towards the surface, while warm water from above the thermocline is alternately pulsed downward. As can be observed, cold-water pulses increased in strength during the course of zooplankton sampling (Fig. 9). By the 29th of September, the water column was mostly cold as the cold-water pulses reached the surface and resulted in a homogenously cold water column, while warm-water pulses were only able to penetrate midway into the water column.

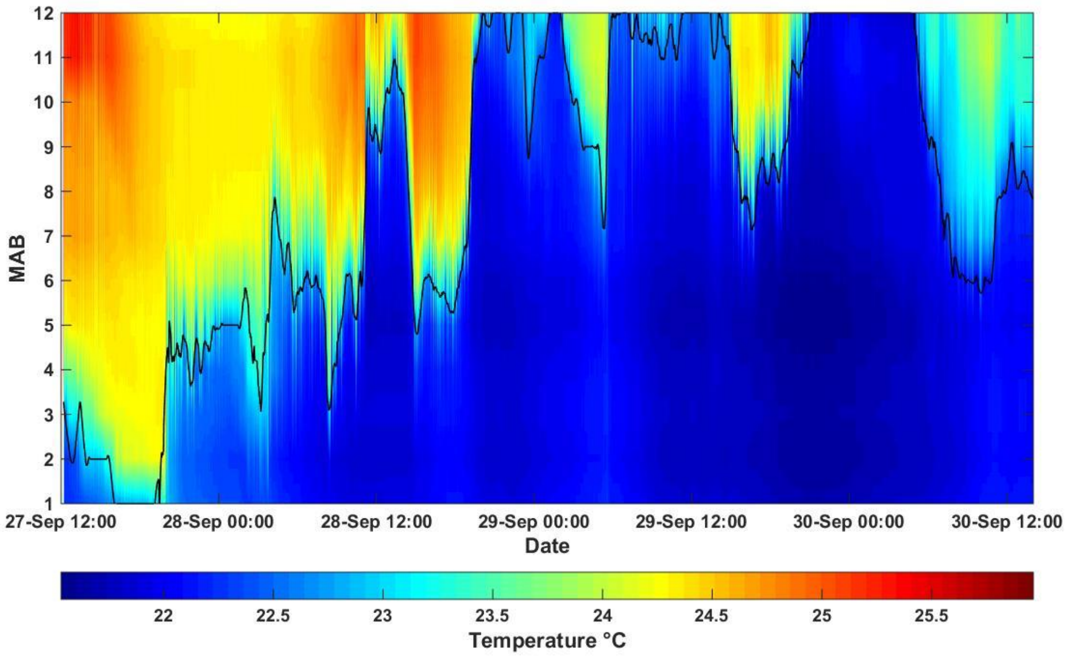

Figure 9. Time series of water column temperature in San Juanico during zooplankton sampling (September 27th to September 30th, 2011). The vertical axis shows the depth of the water column in meters above the bottom. The horizontal axis shows date and time. The color axis shows temperature in degrees Celsius. The black line superimposed onto the temperature data is the calculated depth of the thermocline (see methods).

The values of VVT indicate internal wave activity in SJ was not as strong as what was observed in BN, given that vertical changes in the depth of the thermocline rarely exceeded 20 $cm\cdot min^{-1}$ (Fig. 10). While a maximum value of VVT that exceeded 50 $cm\cdot min^{-1}$ was observed on the 27th of September, during the majority of time, VVT values were below 50 $cm\cdot min^{-1}$. As with BN, periods of time when the value of VVT was equal to 0 $m\cdot min^{-1}$ were present. However, the duration of these periods of time when VVT was equal to 0 $m\cdot min^{-1}$ were much shorter and were only observed twice, indicating that internal wave activity resulted in weaker pulses of cold or warm water. The lower values of VVT observed in SJ and the limited presence of periods of time were VVT was equal to 0 $m\cdot min^{-1}$, suggest that internal wave activity in SJ was not as strong as that observed in BN.

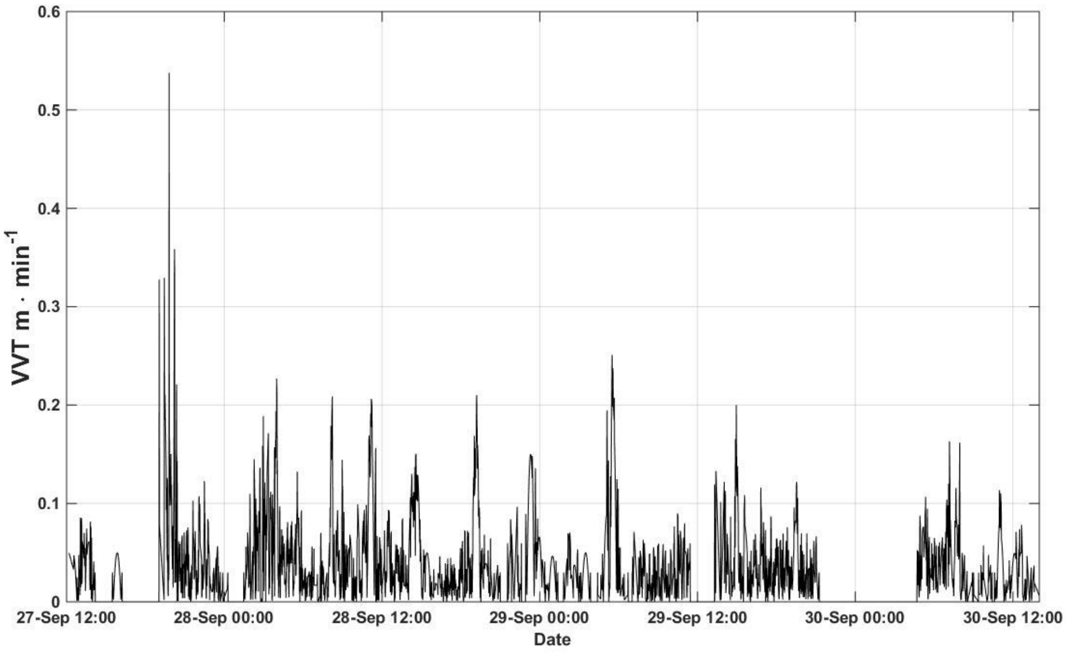

Figure 10. Time series of the vertical velocity of the thermocline (VVT) in San Juanico during zooplankton sampling (September 27th to September 30th, 2011). The vertical axis shows the values of VVT in m·min-1. The horizontal axis shows date and time.

As opposed to what was observed in BN, Pineda's 1994 two-phase model of internal bore behavior in the nearshore was well represented in SJ (Fig. 11). Shortly after 12:00 h and ending approximately 6-7 hours later on Sept. 27th, 28th and 29th, the water column can be seen to be in phase two of the Pineda model, with surface currents propagating onshore and bottom currents propagating offshore. During phase one, an inversion in the direction of bottom surface current propagation can be observed, with both surface and bottom currents showing lower velocities that rarely exceeded ±75 mm·min^{-1}. The strongest onshore flows can be observed at the surface during phase one with maximum velocities exceeding 300 mm·min^{-1}. As with BN, current flow in the bottom half of the water column was always reduced; however, the maximum velocities observed in SJ were much lower than those observed in BN.

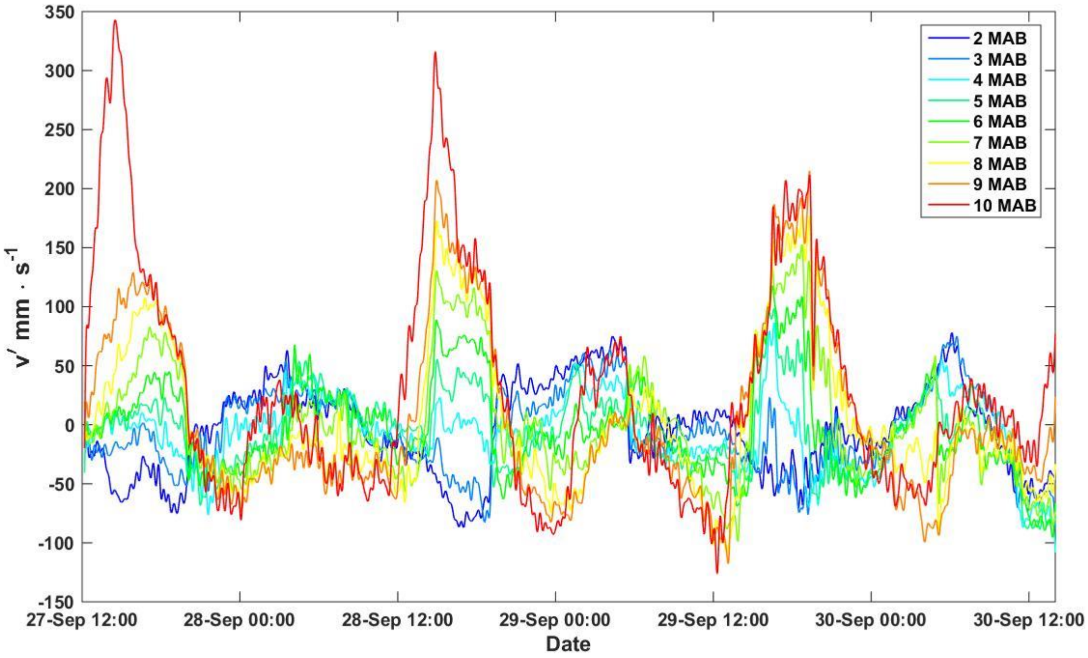

Figure 11. Time series of *v′* current velocities in for San Juanico during zooplankton sampling (September 27th to September 30th, 2011). The horizontal axis shows date and time and the vertical axis shows the values of *v′* in mm·s^{-1}.

The slick criteria implemented to evaluate the percentage of observed slicks that occurred during times that slicks could have theoretically occurred is shown in Fig. 12. Times when slicks were visually observed are graphed as dashed vertical black lines and, *v′* at 10 MAB is graphed as a black line. The superimposed blue series represents the times in which surface slicks may have been present. On average, 3.25 slicks were observed each day (SE = ± 1.11) and 79% of visually-detected slicks occurred during times in which slicks should theoretically have been present according to the current data.

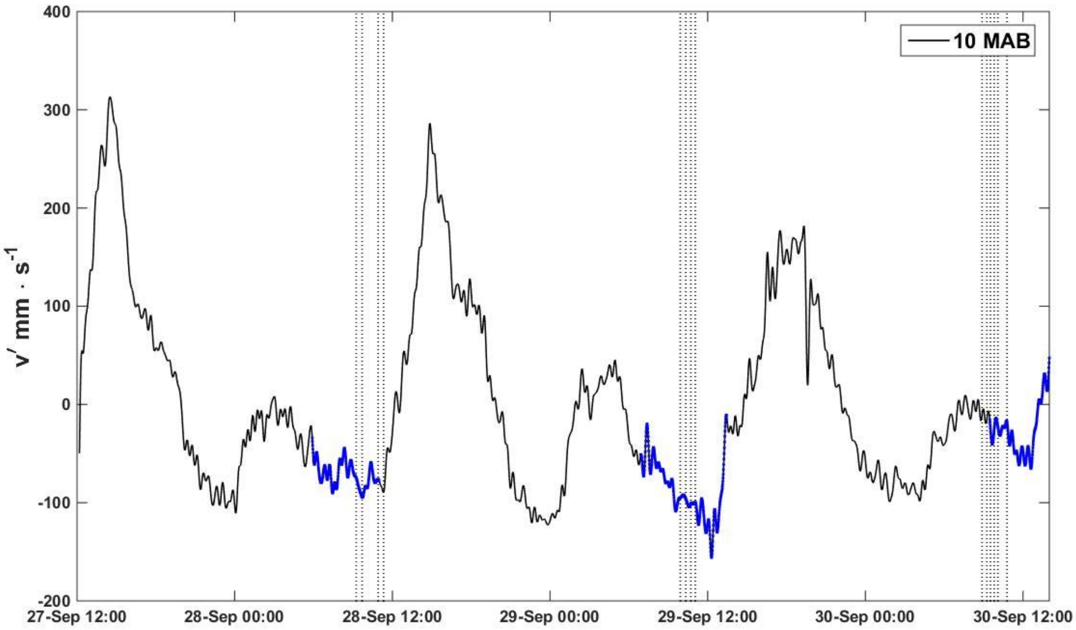

Figure 12. Time series of *v′* in at 10 MAB showing when potential slicks theoretically should have been present during zooplankton sampling (September 27th to September 30th, 2011). The vertical axis shows values of *v′* in mm·s^{-1}. The horizontal axis shows date and time. Vertical black dashed lines indicate times in which slicks were visually observed and recorded during sampling. The superimposed blue series represents the times in which surface slicks theoretically should have been present in surface convergence areas.

There was no appreciable abundance of *Chthamalus* nauplii or cyprids in samples from SJ; however, mussel veligers were present (Fig. 13). During the first three days of sampling, mussel abundance was low with only three samples containing more than 10 veligers·m^{-3}. During the last day of sampling on Sept. 30th, 45% of the samples at 1m depth contained more than 10 individuals·m^{-3} while at 3m depth, 90% of the samples contained more than 50 individuals·m^{-3}.

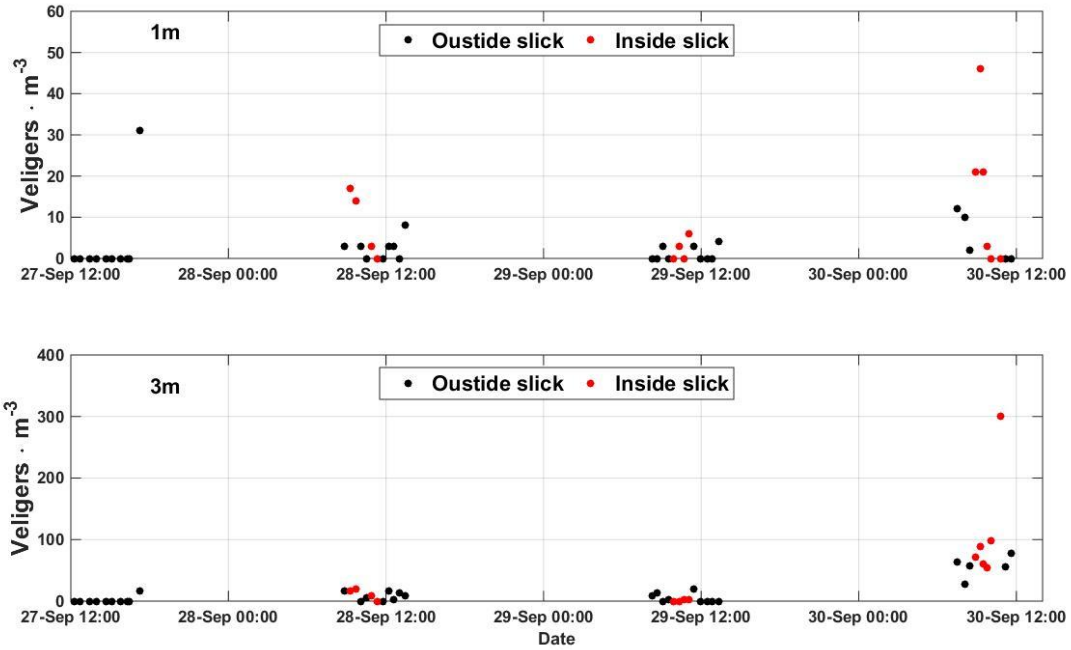

Figure 13. Abundance of mussel veligers at 1 and 3m depth. Top panel: Mussel veliger abundance at 1m depth. Bottom panel: Mussel veliger abundance at 3m depth. The horizontal axis for each panel shows the date and time. The vertical axis for each panel show the abundance of each respective taxa in veligers·m^{-3}. Each point represents one sample. Red points indicate samples taken within slicks that were visually detected during sampling.

Abundances of mussel veligers were log transformed prior to carrying out the two-way analysis of variance utilizing the factors of *slick presence* and *depth*. The ANOVA results indicate a significant effect of *slick presence* and *depth* on veliger abundance, while the interaction was not significant (Table 4). A greater abundance of mussel veligers was found at 3 m depth and within slicks.

Table 4. ANOVA results for mussel veligers

Mussel veligers

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	p
Slick presence	3.92	1	3.92	10.15	**0.002**
Depth	3.37	1	3.37	8.74	**0.004**
Slick presence-Depth	0.94	1	0.94	2.44	0.12
Residuals	33.96	88	0.38		

As with BN, the potential relationship between the number of visual detected slicks per day and meroplankton abundance was evaluated using Pearson correlation analyses. Abundances of mussel veligers were log transformed prior to carrying out the correlations (Table 5). No significant correlations between slick abundance and meroplankton abundance were found for any taxa or depth.

Table 5. Correlation results for mussel veligers

Mussel veligers

Depth	**r**	**p**
1 m	0.43	> 0.05
3 m	0.51	> 0.05

2.4.3. La Paz, BCS

Water column temperatures during zooplankton sampling in LP reflected strong stratification, although some mixing was observed during the 9th and 10th of June (Fig. 14). Pineda's 1994 two-phase internal bore model can be observed in water-column temperatures as colder water from below the thermocline is pulsed upward towards the surface, while warm water from above the thermocline is alternately pulsed downward. However, cold-water pulses were insufficiently strong to reach the surface and small-scale upwelling was not observed during the course of zooplankton sampling, as was observed in SJ and BN. However, warm-water pulses were able to reach the bottom for short periods of time, contrary to what was observed in SJ.

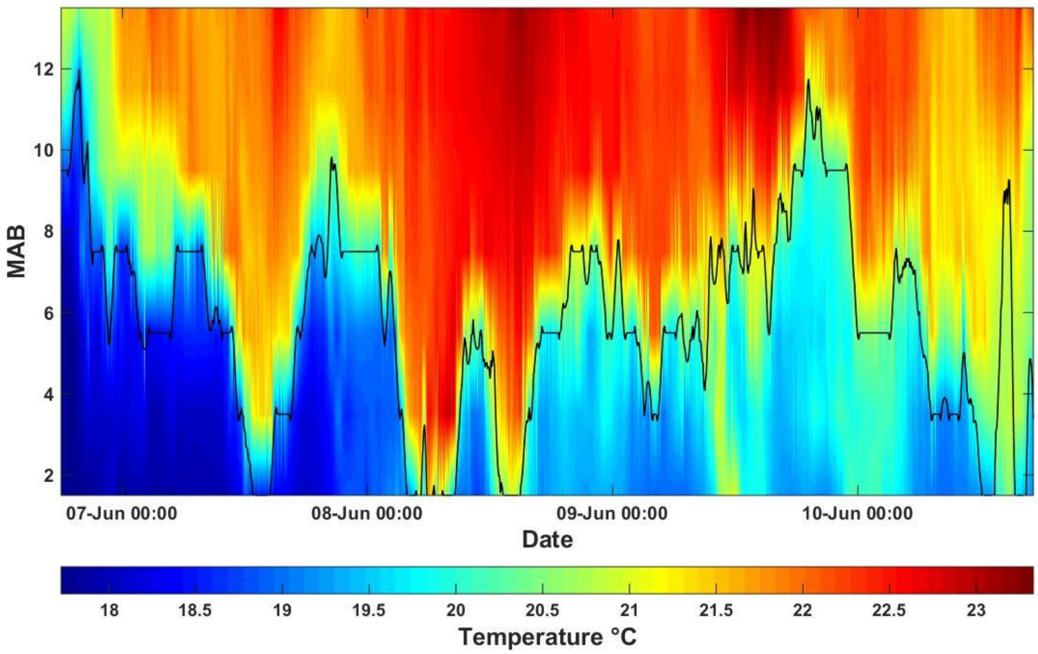

Figure 14. Time series of water column temperature in La Paz during zooplankton sampling (June 6th to June 10th, 2013). The vertical axis shows the depth of the water column in meters above the bottom. The horizontal axis shows date and time. The color axis shows temperature in degrees Celsius. The black line superimposed onto the temperature data is the depth of the thermocline.

In contrast to BN and SJ, vertical changes in the depth of the thermocline rarely exceeded 15 cm·min^{-1} and for the majority of time, VVT values were below 10 cm·min^{-1} (Fig. 15). Periods of time when the value of VVT was equal to 0 m·min^{-1} were present but of shorter duration than those observed in both BN and SJ, indicating that internal wave activity resulted in weaker pulses of cold or warm water. However, on the 10th of June, the maximum values of VVT observed exceeded 30 cm·min^{-1}. The lower values of VVT observed in LP compared to BN and SJ, coupled with the limited presence of periods of time where VVT was equal to 0 m·min^{-1}, suggest that internal wave activity in LP was weaker than that observed in BN and slightly weaker than that observed in SJ. Few slicks were observed in LP, in contrast to what was observed in SJ and BN. On average, only 1.4 slicks were observed each day (SE = ± 0.97).

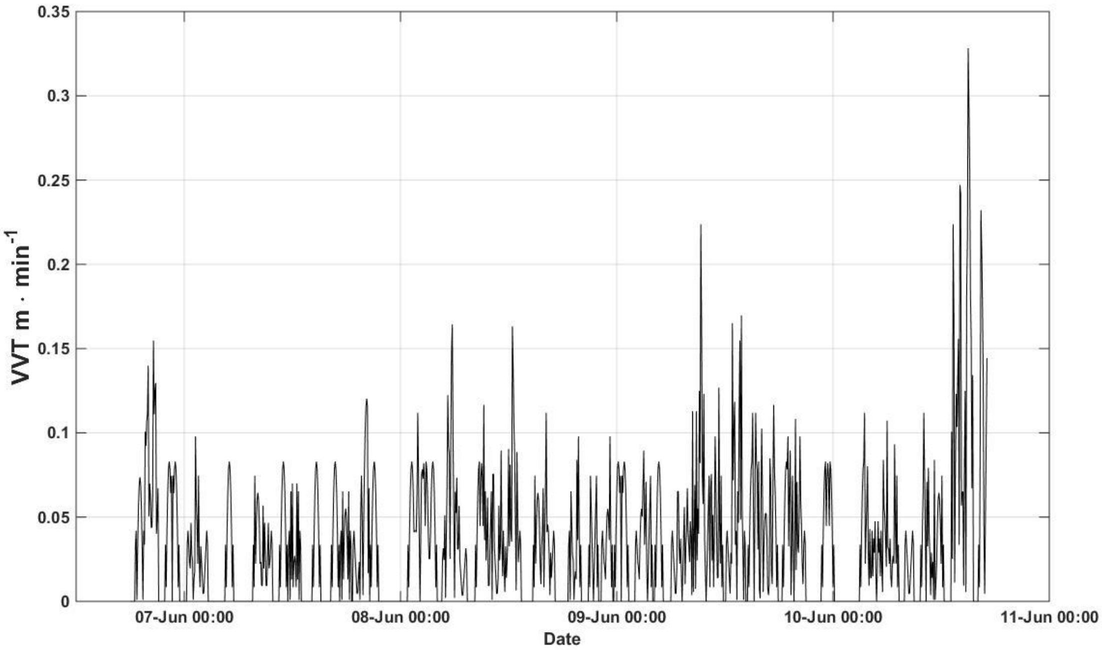

Figure 15. Time series of the vertical velocity of the thermocline (VVT) in La Paz during zooplankton sampling (June 6th to June 10th, 2013). The vertical axis shows the values of VVT in m·min^{-1}. The horizontal axis shows date and time.

Chthamalus nauplii were largely absent from samples collected in LP; however, *Chthamalus* cyprids and mussel veligers were present. Veliger abundance averaged 463 veligers·m^{-3} during the course of zooplankton sampling, while average cyprid abundance was 30 cyprids·m^{-3} (Fig. 16). Both cyprids and veligers presented maximum abundances on the June 8th, with more than 2000 veligers·m^{-3} and more than 200 cyprids·m^{-3}.

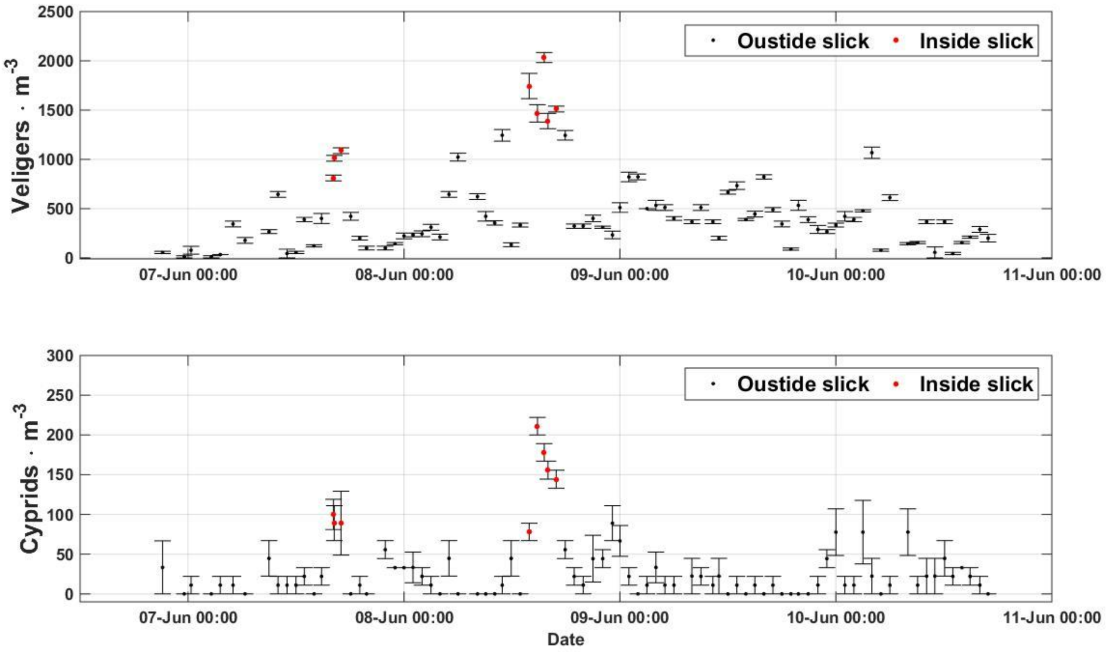

Figure 16. Abundance of *Chthamalus* cyprids and mussel veligers at 2m depth during zooplankton sampling (June 6th to June 10th, 2013). Top panel: Mussel veliger abundance in veligers·m^{-3}. Bottom panel: *Chthamalus* cyprid abundance in cyprids·m^{-3}. The horizontal axis for each panel shows the date and time. The vertical axis for each panel show the abundance of each respective taxa. Each point represents the average of the three replicate samples taken simultaneously with the associated standard error. Red points indicate samples taken within slicks that were visually detected during sampling.

Abundances of mussel veligers and *Chthamalus* cyprids were log transformed prior to carrying out the two-way analysis of variance utilizing the factors of *slick presence* and *night or day*. The ANOVA results indicate a significant effect of *slick presence* but not of *night or day* (Table 6). *Chthamalus* cyprid and mussel veliger abundance was always greater within slicks that outside of slicks.

Table 6. ANOVA results for *Chthamalus* cyprids and mussel veligers

***Chthamalus* cyprids**

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	p
Slick presence	9.02	1	9.02	22.70	**<0.0001**
Night or day	0.90	1	0.91	2.26	0.14
Residuals	32.99	83	0.40		

Mussel veligers

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	p
Slick presence	3.54	1	3.54	22.63	**<0.0001**
Night or day	0.204	1	0.20	1.31	0.26
Residuals	12.98	83	0.16		

As with BN, the potential relationship between the number of visual detected slicks per day and Pearson correlation analyses were carried out to evaluate the potential relationship between slick abundance and meroplankton abundance. Abundances of mussel veligers were log transformed prior to carrying out the correlations (Table 7). No significant correlations between slick abundance and meroplankton abundance were found for any taxa or depth.

Table 7. Correlation results for *Chthamalus* cyprids and mussel veligers

***Chthamalus* cyprids**

Depth	r	p
2 m	0.28	> 0.05

Mussel veligers

Depth	r	p
2 m	0.46	> 0.05

2.5. Discussion

According to the internal wave proxy utilized, the strongest internal wave activity was observed in Barra de Navidad. The largest values of VVT recorded, coupled with extended periods of time when the water column was relatively homogenous, reflected strong upward and downward pulses of water in this site. Downward warm-water pulses were particularly strong compared to those observed in either La Paz or San Juanico. In contrast, the weakest internal wave activity was observed in La Paz. In this site, the lowest values of VVT were recorded and cold-water pulses were never able to reach the surface. In San Juanico, both cold-water and warm-water pulses resulted in a loss of stratification; however, for shorter periods of time than those observed in Barra de Navidad. Therefore, the ranking of sites according to the strength of internal wave activity during zooplankton sampling is as follows: 1) Barra de Navidad, 2) San Juanico, and 3) La Paz.

The strength of internal wave activity in each site was also reflected in the number of slicks observed during zooplankton sampling. Barra de Navidad, in addition to presenting the strongest internal wave activity, presented the greatest average number of visually-detected slicks per day, followed by San Juanico and La Paz. In this study, no significant correlations between slick and meroplankton abundance were found for any taxa, depth or site. This result differs from what Shanks (2006) determined after analyzing samples collected off the Scripps Oceanographic Institute pier from 1982-1984, in which crab megalopae abundance was positively correlated with slick abundance. Despite the ability of slicks to concentrate plankton, a greater abundance of slicks is not necessarily associated with an increase in meroplankton abundance due to the high degree of patchiness present in the plankton (Franks & Chen, 1996; Lennert-Cody & Franks 1999, 2002; Tapia & Pineda, 2007; Tapia et al., 2010; Anderson & Taylor, 2011) and due to the behavior of the larvae within the internal wave (Franks, 1992; Kushnir et al., 1997; Largier, 2003; Pineda, 2000; Pineda et al., 2007; Shanks, 2009).

The visual detection of slicks was validated by the current data for both Barra de Navidad and San Juanico. In both sites, over 70% of the surface slicks that were visually detected occurred during times in which slicks could theoretically been present based on Thorpe’s 1995 model of internal wave behavior. Studies that have only utilized the visual detection of slicks without water column data have been criticized in the literature (Lamb 1997). However, after comparing visually detected slicks with current meter data, the visual detection of slicks was a valid indicator of internal wave activity.

When comparing the abundance of meroplankton between sties, large differences are present. While barnacle larvae were only found in La Paz and Barra de Navidad samples, mussel veligers were present in all three sites. The greatest abundance of mussel veligers was found in Barra de Navidad, followed closely by La Paz. San Juanico presented the lowest abundance of mussel veligers, one order of magnitude lower than either Barra de Navidad or La Paz. Of the three sites, San Juanico presented the lowest abundance of meroplankton and yet is ranked second in terms of internal wave activity. While the site is apt for the onshore transport of meroplankton via internal waves and associated surface slicks, during the study, meroplankton pools may have been highly patchy or the overall abundance of meroplankton may have been low and thus, limited potential onshore transport of surface meroplankters in slicks was observed.

For every site, a greater abundance of meroplankton was found in samples taken from within surface slicks. This result coincides with studies carried out by Shanks (1983), Kingsford & Choat (1986) and Mattos & Mujica (2012). In Southern California, Shanks (1983) determined that concentrations of meroplankton were 6-40 times greater within surface slicks associated with tidally-forced internal waves. Similarly, Kingsford & Choat (1986) in New Zealand reported greater zooplankton concentrations within surface slicks associated with internal waves, with maximum concentrations within slicks that were 40 times more abundant than concentrations outside of slicks. Similarly, in Chile, Mattos & Mujica (2012) found that surface slicks contained 6 times more barnacle cyprids. In our study, surface slicks in Barra de Navidad contained on average twice the amount of meroplankton as samples taken outside of slicks, while slicks in San Juanico and La Paz contained four times the amount of meroplankton. These results highlight the importance of internal waves as a potential physical mechanism for the surface transport of meroplankton in slicks.

Chapter 3. *Chthamalus* recruitment and supply-side control in Playa San Miguel, BC

3.1. Hypothesis

Chthamalus spp. recruit density will be a robust predictor of adult density and a positive recruit-adult relationship in which neither predation nor competition played a significant role in the resultant adult densities will be observed.

3.2. Objective

To evaluate the recruitment and survivorship of *Chthamalus* spp. barnacles in in a site where barnacle settlement is known to be associated with internal wave activity (Playa San Miguel, BC) and to determine if predation or competition act to decouple the relationship between recruit and adult densities.

3.3. Materials and Methods

3.3.1. Study Area

Playa San Miguel (31° 55′ N, 116° 38′ W), Baja California, located within the northern portion of Bahía Todos Santos (BTS), served as our study site. The BTS is located approximately 100 km south of the USA-Mexico border and presents a narrow continental shelf and an average depth between 25-30 m (Filonov et al. 2014). Playa San Miguel (SM) is a rocky shore composed of volcanic boulders which is exposed to wave action year round, although intense wave action is present mostly during the winter months. During the spring, strong upwelling occurs, while during summer, the nearshore water column is highly stratified with the predominance of a strong semidiurnal internal tide in the northern portion (Filonov et al. 2014; Ladah et al. 2005, 2012; Liévana MacTavish et al. 2016).

The location of BTS places SM in a region where the distributions of the only two *Chthamalus* barnacle species reported for the region potentially overlap: *Chthamalus fissus* (Darwin, 1854) and *Chthamalus dalli* (Pilsbry, 1916) (Miller et al., 1989). *C. fissus* and *C. dalli* barnacles are notoriously difficult to distinguish in the field given their similar morphologies; as such, identification was carried out to the genus level. *Chthamalus* barnacles dominate the upper rocky intertidal of SM. In the mid intertidal, *Chthamalus* spp. are prevalent along with the barnacle species *Tetraclita rubescens* (Darwin, 1854) and *Balanus glandula* (Darwin, 1854), both of which can also be found in the lower intertidal. In addition, other invertebrate species such hermit crabs (*Pargurus,* spp.), shore crabs (*Pachygrapsus* spp.), limpets (*Lottia* spp.), chitons (*Nuttallina fluxa* (Carpenter, 1864)), the red urchin *Mesocentrotus franciscanus* (A Agassiz, 1863), the purple urchin *Strongylocentrotus purpuratus* (Stimpson, 1857), the sea hare *Aplysia californica* (JG Cooper, 1864), the predatory sea snails *Nucella* spp. and *Mexacanthina lugubris* (Sowerby, 1821), and the sea star *Pisaster ochraceus* (Brandt, 1853) are present at SM, though in recent years, *Pisaster* abundance has declined considerably.

3.3.2. *Chthamalus* recruitment

Chthamalus barnacles have multiple recruitment events from spring to fall in southern California and in northern Baja California (Broitman et al., 2008; Ladah et al., 2005; Pineda, 1994; Pineda & López, 2002; Valencia-Gasti & Ladah, 2016). At SM, Valencia-Gasti & Ladah (2016) reported settlement peaks for *Chthamalus* during the late summer and early fall of 2009, with the highest peaks observed during September, while Ladah et al. (2005) reported settlement peaks for *Chthamalus* during spring, summer and fall in SM, with the highest settlement peaks observed in June. It is worth mentioning that Valencia-Gasti & Ladah (2016) sampled from July to September and thus data for potential settlement peaks during spring or early summer of 2009 are not available. Given the available settlement data for the site from previous years, four periods of strong *Chthamalus* settlement and subsequent recruitment were expected during the course of this study: September of 2013, April 2014, June 2014, and September of 2014.

The recruitment and subsequent survivorship of *Chthamalus* was quantified beginning in Septermber 2013 and ending in December 2014. Intertidal sampling was performed monthly during winter 2013 and every two weeks beginning in spring 2014. *Chthamalus* settlers were deemed to be recruits if they survived the period between sampling periods. Fifty boulders measuring approximately 50-70 cm in diameter and free of any visible organisms were collected from above the high intertidal and moved to the upper-mid intertidal, placed in between existing boulders parallel to the shore and tagged. Playa San Miguel is composed of tightly packed boulders. By removing an existing boulder and replacing it with a tagged boulder in the space created, each relocated boulder was tightly secured and able to withstand wave action. One plot measuring 20 cm^2 was delineated on each tagged boulder. The recruitment and subsequent mortality of *Chthamalus* individuals on each plot was captured via photograph and quantified using the program ImageJ with the Cell Counter plugin which allowed for individual barnacles to be tracked in the successive photos of each plot (Schneider et al., 2012).

3.3.3. Evaluation of supply-side control vs. post-recruitment control over the survivorship of *Chthamalus* spp. recruits

Prior to beginning field work in August of 2013, quadrat sampling was carried out utilizing 30 $0.5m^2$ quadrats along a 30 m transect, one per meter, placed parallel to the shore in the mid-intertidal, where the plots would be placed in the following month. From the quadrat survey, the natural densities of potential predators: *Nucella emarginata* and *Mexacanthina lugubris*, and *Pisaster ochreceus,* and potential competitors: *Stenoplax conspicua* (Pilsbry, 1982) and *Lottia* spp. were determined. In addition, the percent cover of *Chthamalus* barnacles and that of potential competitors: *Balanus glandula*, *Tetraclita rubenscens* (Nilsson-Cantell, 1931), red turf algal assemblages, and *Endocladia muricata* (Agardh, 1841) were estimated.

Both intraspecific and interspecific competition and predation were evaluated in the study. Intraspecific competition was evaluated via the calculation of density-dependent mortality, and interspecific competitors were considered to be organisms not of the *Chthamalus* genera found within the plots that could potentially compete for substrate space. Other potential interspecific competitors included small limpets (*Lottia* spp.), red turf algal assemblages, the turfweed *E. muricata*, and small chitons *S. conspicua*. To evaluate the percentage of available substrate, the percent cover of free space within plots was estimated using the point-intercept technique with a 121 point grid.

In order to determine the type of control (supply-side or postrecruitment) acting over the survivorship of barnacle recruits during the course of the study, the relationship between a cohort’s recruit and adult densities was evaluated. In the case that *Chthamalus* was found to be under postrecruitment control, an experiment was designed to distinguish between the two primary postrecruitment mechanisms that could be responsible for decoupling a cohort's recruit and adult densities, namely predation and competition. The experiment consisted of five treatments in which the presence of potential competitors or predators was either allowed or denied. The treatments were defined as follows: (1) both predators and competitors allowed access to plots (+P+C), (2) predators denied while competitors allowed access to plots (-P+C), (3) predators allowed while competitors denied access to plots (+P-C), (4) both predators and competitors denied access to plots (-P-C), and (5) predator-exclusion cage control in which both predators and competitors were allowed access to the plots (CC). Potential competitors were physically removed from the plots in the competitor exclusion treatments (+P-C, -P-C) utilizing a small scalpel to dislodge the organisms. Potential predators were denied access to plots by the use of a cage that surrounded each plot pertaining to a predator exclusion treatment. The cages were constructed of a metal frame which was covered with a fine mesh that allowed for the movement of water and particles over the plot when the cages were submerged. The CC treatment was used to account for any potential cage effects, such as shading or sedimentation, on the mortality of barnacle recruits. Plots belonging to this treatment did not include the wire mesh but were fitted with the metal frame of the cages used in the other treatments. Ten replicas were used per treatment for a total of 50 plots when the experiment began. Due to storm activity during the winter months and to periods of intense wave action, some plots were lost; as a result, at the end of the experiment, each treatment contained at least seven replicas.

An ANOVA was used to test for differences in the survivorship of adult barnacles between treatments. Prior to carrying out the ANOVA analysis, data normality and homogeneity of variances were checked using the Shapiro-Wilks normality test and Bartlett's test of homogeneity of variances. A significant difference ($\alpha < 0.05$), resulting from Tukey's HSD post hoc test, between treatments -P-C and -P+C, would indicate that competition was acting as an important controlling factor over the survivorship of *Chthamalus* spp. recruits. If predation was also acting as a controlling factor, then we would expect a significant difference between treatments -P-C and +P-C. Perhaps most importantly, if no significant difference was found between treatments +P+C and -P-C, then neither the postrecruitment factors of predation nor competition would play important roles in the structuring of *Chthamalus* spp. populations in SM.

Recruit density at the end of the initial recruitment period (RD), maximum recruit density (MRD), and postrecruitment mortality (PRM) were calculated as described by Minchinton & Scheibling (1991). RD is the number of surviving recruits observed during week 47 of the study, which corresponds to the conclusion of the only recruitment period observed. AD is the number of surviving recruits observed at the conclusion of the experiment during week 62. MRD is the recruit density observed during week 41. MRD is reflective of the first and by far the largest influx of new recruits to the intertidal zone at SM during 2014. PRM is the difference between MRD and AD, expressed as a percentage of MRD. To evaluate the relationships between PRM, RD, MRD and AD, linear regression analyses were carried out (AD vs RD and PRM vs MRD). A significant relationship between MRD and PRM would indicate that density-dependent mortality was present at SM. Furthermore, if postrecruitment control was present over the survivorship of *Chthamalus* spp. recruits in SM, we would not expect RD to be a good predictor of AD.

3.4. Results

From preliminary sampling in August 2013, the mean percent cover of barnacles and seaweeds indicated the presence of free space within the mid-intertidal (Table 8). *Chthamalus* showed a greater percent cover than either *Balanus glandula* or *Tetraclita rubenscens*. Red turf algal assemblages, a potential competitor, were more prevalent than *Endocladia muricata*, while potential competitors *Lottia* spp. and *Stenoplex conspicua* were present in similar densities. In addition, the predator *Mexacanthina lugubris* was present in greater densities than either predator *Nucella emarginata* or *Pisaster ochreceus*.

Table 8. Mean densities (MD, individuals·m^{-2}) and percent cover (PC) and associated standard errors (SE) of potential predators and competitors present in San Miguel in August 2013 prior to the start of field work.

Potential Competitors

Lottia spp		*S. conspicua*		*Chthamalus* spp.		*B. glandula.*		*T. rubenscens*		*Red turf algal assemblages*		*E. muricata*	
MD	SE	MD	SE	PC	SE	PC	SE	PC	SE	PC	SE	PC	SE
11.33	1.05	11.73	1.29	45.63	1.64	4.46	0.52	2.9	0.32	16.33	1.63	7.3	0.78

Potential Predators

M. lugubris		*N. emarginata*		*P. ochrceus*	
MD	SE	MD	SE	MD	SE
18.46	2.05	11.13	1.16	1.2	0.18

Once field work commenced, the amount of available free space per plot was tracked throughout the experiment (Fig. 17). Prior to the start of the IRP (weeks 41-45), the mean available free space per plot was greater than 80%. Following the end of the IRP, beginning in week 47, the available free space per plot dropped to 30% and remained consistent through week 62.

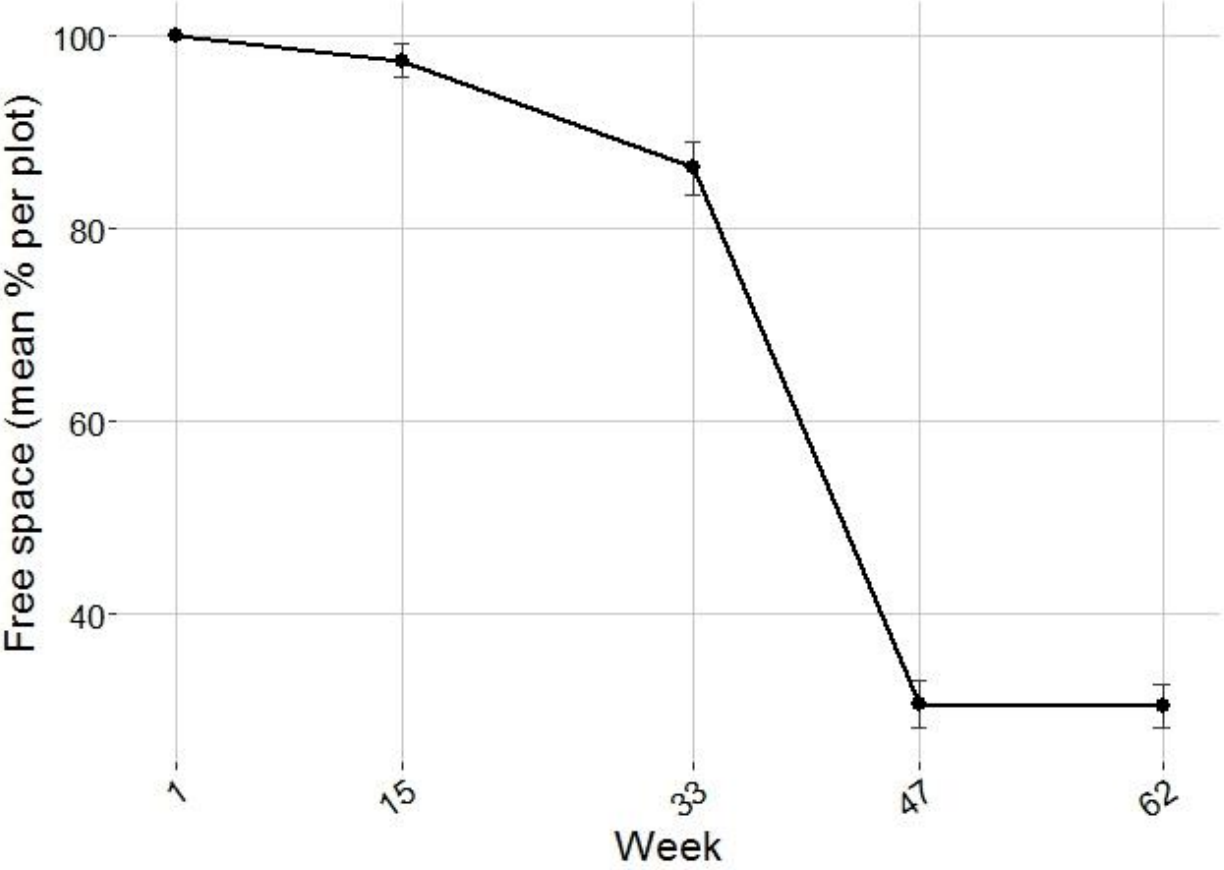

Figure 17. Mean % free space +/- standard error per plot for weeks 1, 15, 33, 47, and 62 (n=30). Prior to the start of the IRP (weeks 41-45), the mean available free space per plot was greater than 80%. Week 47 corresponds to the first sampling date (August 2014) following the end of the IRP where the available free space per plot dropped to less than 31% for the remainder of the experiment.

While other barnacle species such as *Tetraclita rubescens* and *Balanus glandula* are present at the site, only *Chthamalus* barnacles settled within the plots. *Chthamalus* recruitment was almost absent from plots from September 2013 (week 1) until July 2014 (week 41), when an average of 439 new ind·20cm^{-2} (SD=233) were recorded per plot (Fig. 18). Two smaller peaks in recruitment were observed in July 2014 (week 43) and August 2014 (week 45) with an average per plot of 119 new individuals·20 cm^{-2} (SD=79) and 108 new individuals·20 cm^{-2} (SD=89), respectively. These three notable peaks in the *Chthamalus* recruitment constitute the initial recruitment period (IRP) of the study. The expected recruitment events of September 2013, April 2014, and September of 2014 were not observed during our study, while the expected June 2014 recruitment event appears to have been delayed by one month. Nearly all new *Chthamalus* barnacles present in SM during 2014 were recruited during the IRP and constitute the only *Chthamalus* cohort present at SM during 2014.

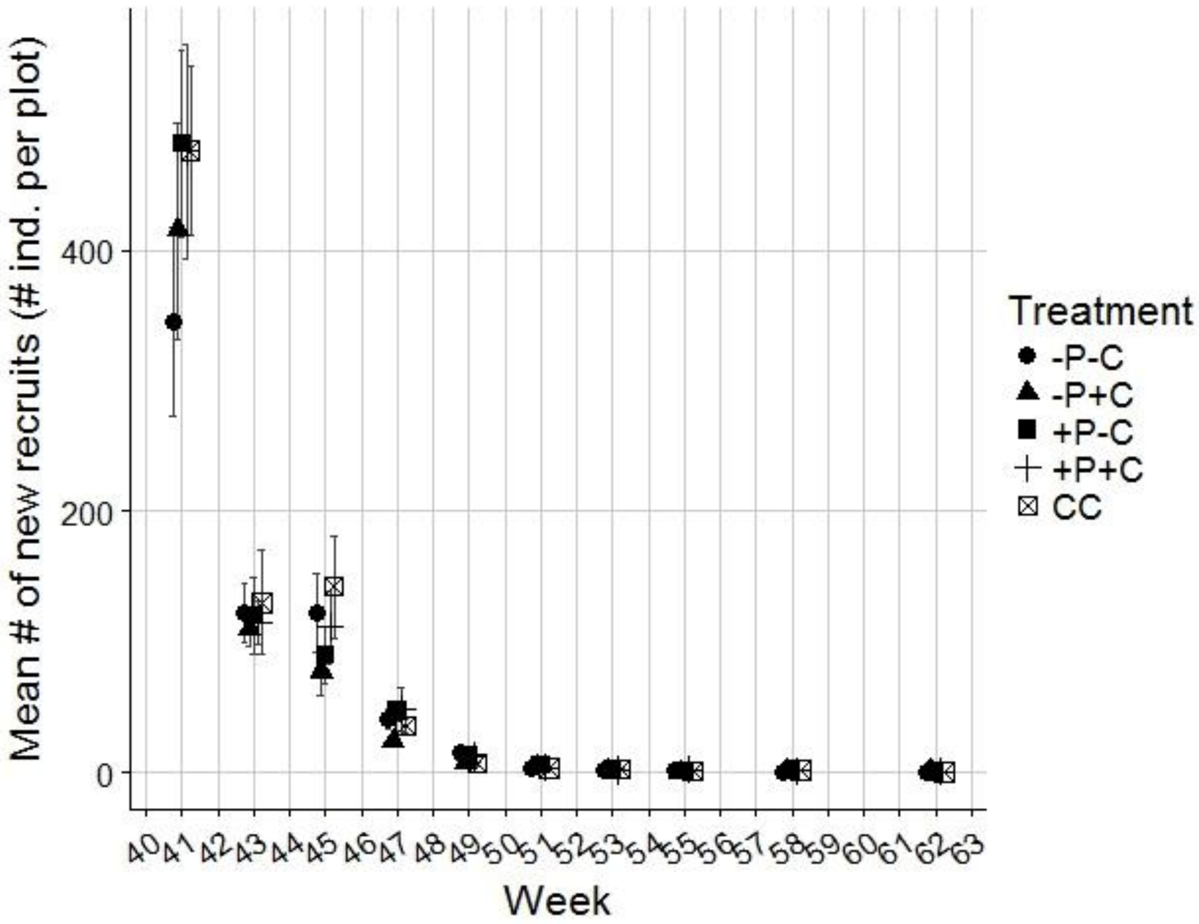

Figure 18. Mean number +/- standard error of new recruits from September 2013 (week 41) through December 2014 (week 62) for each experimental treatment (n=7). Treatments were defined as follows: both predators and competitors allowed access to plots (+P +C), predators denied while competitors allowed access to plots (-P +C), predators allowed while competitors denied access to plots (+P -C), both predators and competitors denied access to plots (-P -C), and predator-exclusion cage control in which both predators and competitors were allowed access to the plots (CC).

During the IRP, the average survivorship of the *Chthamalus* recruits per plot recorded during week 41 was 67% (SD=14), followed by an average survivorship of 82% (SD=5) and 65% (SD=17) for recruits recorded in week 43 and week 45, respectively. After the IRP, when the lowest recruit survivorship was recorded, recruit survivorship increased and remained between 89% and 92% for the duration of the experiment (i.e, after an initial period of high mortality shortly after settlement, cohort survivorship was quite high thereafter). Between treatments, CC, +P+C, and +P-C showed the highest recruitment and subsequent survivorship after the IRP, in contrast to -P+C and -P-C were consistently lower (Fig 19). Of all the individuals recruited during the IRP, 41% survived until the end of the study.

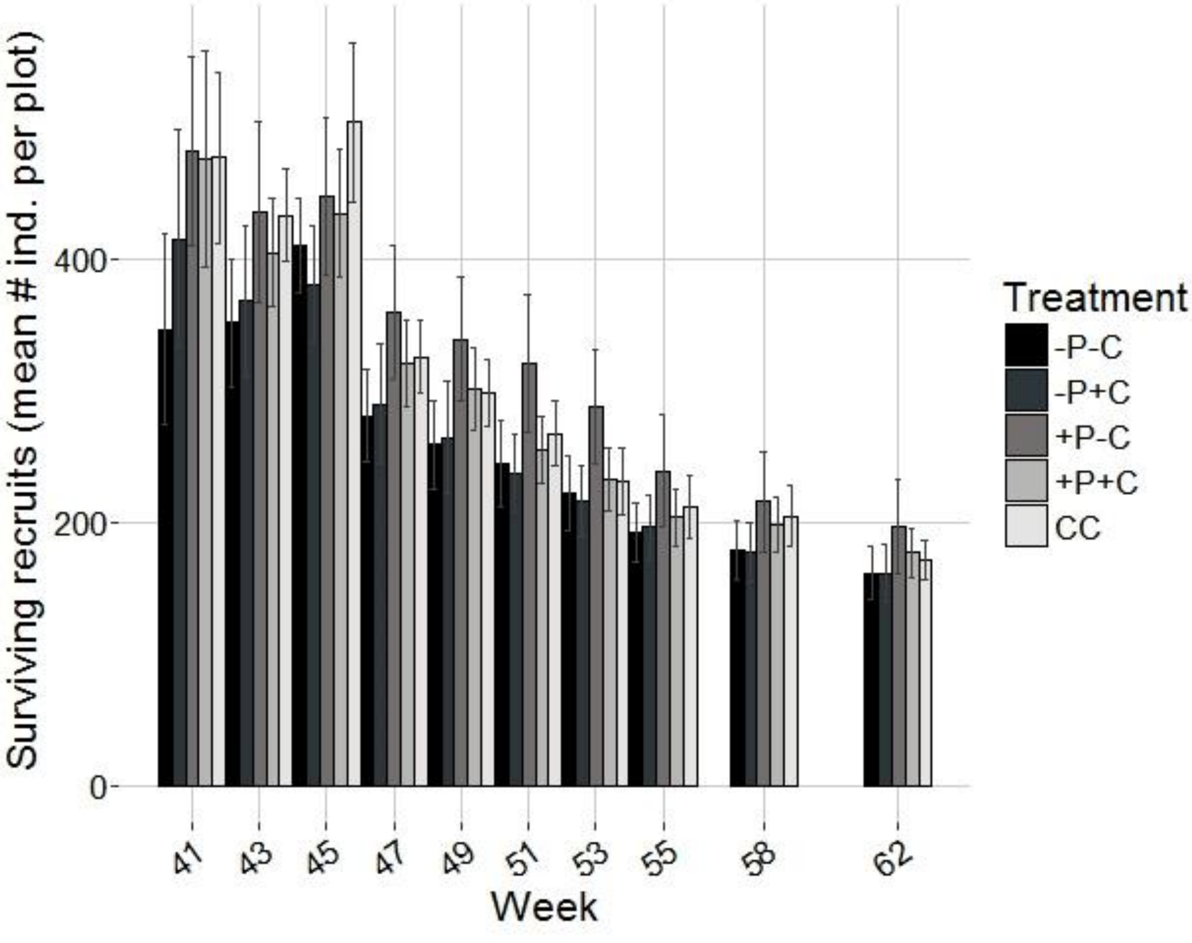

Figure 19. Mean number +/- standard error of surviving *Chthamalus* spp. recruits from July 2013 (week 41) through December 2014 (week 62) for each experimental treatment (n=7). Treatments were defined as follows: both predators and competitors allowed access to plots (+P +C), predators denied while competitors allowed access to plots (-P +C), predators allowed while competitors denied access to plots (+P -C), both predators and competitors denied access to plots (-P -C), and predator-exclusion cage control in which both predators and competitors were allowed access to the plots (CC). After the initial recruitment period (IRP weeks 41-45), when the lowest recruit survivorship was recorded, survivorship increased and remained high (between 89% and 92%) for the duration of the experiment. Of the *Chthamalus* individuals recruited during the IRP, 41% survived until the end of the year.

The relationship between the 2014 *Chthamalus* cohort's recruit (RD) and adult densities (AD) as well as the relationship between postrecruitment mortality (PRM) and maximum recruit density (MRD) were evaluated via regression analysis (Fig. 20). Linear regression results showed RD to be a very strong predictor of AD, ($R^2 = 0.88$, $F_{(1,33)} = 240.2$, $p < 0.001$), indicating that a decoupling between the cohort's recruit and adult densities was not observed (Fig. 20a). The evaluation of density-dependent mortality was carried out by a nonlinear regression utilizing a logarithmic model ($R^2 = 0.61$, $F(1,32) = 50.21$, $p < 0.001$) (Fig. 20b). At SM, there appears to be weak density-dependent PRM operating when MRD is below 400 individuals per plot, after which, PRM appears to be density-independent. Although weak density-dependent PRM was present, it did not interfere with the relationship between successive life history stages of *Chthamalus* recruits at SM. Furthermore, there were no significant differences in *Chthamalus* recruit survival between any treatments (-P-C, -P+C, +P-C, +P+C, or CC) (ANOVA, $F(4,30) = 0.4$, $p = 0.81$), indicating that the postrecruitment mechanisms of competition and predation did not significantly affect the survivorship of barnacle recruits. These result indicate supply-side control over the *Chthamalus* population present at SM.

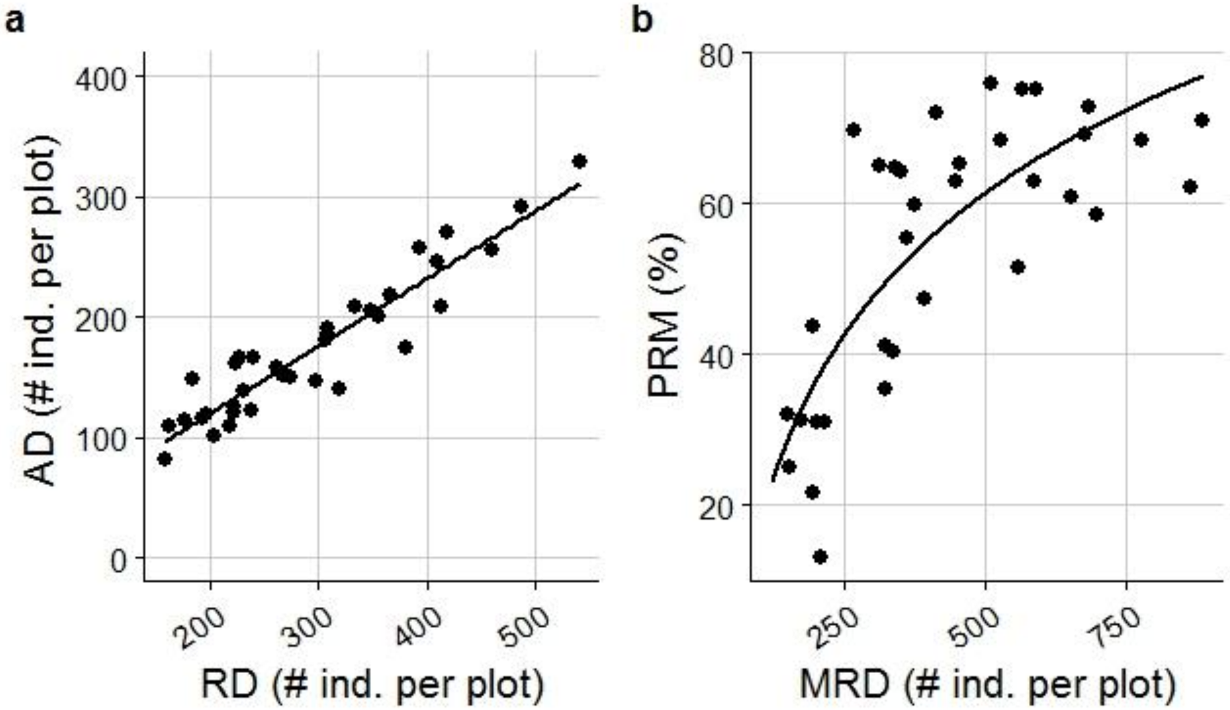

Figure 20. Relationships between (a) adult density (AD) and recruit density at the end of the initial recruitment period of the study (RD) ($y = 0.559x + 8.175$, $R^2 = 0.61$, $p < 0.001$) and (b) between postrecruitment mortality (PRM) and maximum recruit density (MRD) observed during week 41 of the study ($y = 27.062\ln(x) - 106.884$, $R^2 = 0.88$, $p < 0.001$). RD is a strong predictor of AD indicating that a decoupling between the cohort's recruit and adult densities was not observed. At SM, there appears to be weak density-dependent PRM operating when MRD is below 400 individuals per plot, after which, PRM appears to be density-independent.

3.5. Discussion

During this study, as hypothesized, recruit density was a robust predictor of adult density, despite the presence of weak density-dependent mortality when recruit densities were below 400 individuals per plot (20 cm^2). The presence of density-dependent mortality indicates some postrecruitment control over the survivorship of *Chthamalus* spp. recruits; yet, this control was insufficient to interfere with the relationship between successive life history stages of *Chthamalus* barnacles. Our results are similar to those found by Minchinton & Scheibling (1991) for the survivorship of *Semibalanus balanoides* settlers in Nova Scotia, Canada, where the presence of density-dependent mortality also did not impede a direct relationship between recruit and adult densities. These results support the idea that density-dependent mortality may operate within a community at a level below the threshold where it would begin to interfere with the relationship between a cohort's recruit and adult densities and suggests that its presence alone in a site is insufficient to discard supply-side control as the predominant force acting to shape communities.

Predation did not act as a postrecruitment control over the survivorship of *Chthamalus* spp. recruits as evidenced by the lack of significant differences in adult densities between treatments at the end of the experiment. The *Chthamalus* predators, *Nucella emarginata* and *Mexacanthina lugubris*, were visibly present during most sampling visits and were often seen in the study area on rocks covered with *Chthamalus* barnacles, including in open plots belonging to the treatments +P-C,+P+C and CC. The predator densities recorded during preliminary sampling indicated that predation could possibly act as a postrecruitment control over the population of *Chthamalus*; however, we expected to see a greater abundance of *Mexacanthina lugubris* at SM given that Fenberg et al. (2014) reported that the highest abundances of this predatory gastropod in the region are found a few kilometers to the south of Playa San Miguel (35 $ind{\cdot}m^2$). Nevertheless, predation did not significantly affect the survivorship of *Chthamalus* recruits.

Arguably the most important potential limiting resource for invertebrates in the intertidal is space (Dayton 1971). The amount of free space available to *Chthamalus* barnacles observed during preliminary sampling in August 2013 did not appear to be limiting, suggesting that competition at SM was unlikely to be observed. After sampling commenced in September 2013, the percentage of available free space never dropped below 30%. Given that the presence of competitors did not significantly influence the mortality of *Chthamalus* recruits, competition for space or other potential resources in Playa San Miguel did not act as a postrecruitment control over the survivorship of *Chthamalus* barnacles. This result may be in part due to the initial density of *Chthamalus* recruits. Zabin (2015) found that competition did not play a role in determining the adult abundance of *Chthamalus proteus* (Dando & Southward, 1980) when recruit densities were low. In our study, *Chthamalus* recruitment was much lower than that reported in the study by Raimondi et al. (1990) for *Chthamalus anisopoma* (Pilsbry, 1916) in the Gulf of California in which intraspecific competition did not influence the growth or survivorship of *C. anisopoma* recruits. In our study, as *Chthamalus* barnacles were only identified to the genus level, intraspecific competition between *C. dalii* and *C. fissus* was only indirectly assessed via the evaluation of density-dependent mortality; however, given that these two species are so similar, competition between them might not be strong enough to negatively affect their development. For example, Shinen & Navarrete (2010) found evidence of weak competition between two species of chthamaloid barnacles, *Jehlius cirratus* (Darwin, 1854) and *Notochthamalus scabrosus* (Darwin, 1854), that did not interfere with recruit growth patterns, presumably due to the equal competitive abilities of the two species, even at higher recruit densities.

Under the recruit-adult hypothesis (scenario 2), the density of recruits is a robust predictor of adult density indicating the presence of supply-side control. In Playa San Miguel, scenario 2 of recruit-adult hypothesis was supported for the *Chthamalus* population. *Chthamalus* has also been shown to be under supply-side control by Menge (2000b) who reported that the density of *Chthamalus* adults was more dependent on recruit density than on postrecruitment factors in Oregon. However, postrecruitment factors appeared to be more important for *Balanus* populations in the same site, possibly due to *Chthamalus* being more tolerant of biotic and abiotic forces present while *Balanus* is less so. In addition, Navarrete et al. (2005) found that along the northern portion of the coastline of central Chile (between 29°S and 32°S), chthamaloid barnacle recruit density determined adult cover, suggesting that supply-side control was the dominant force in the northern region while to the south (between 33°S and 35°S), populations of chthamaloid barnacles were under postrecruitment control. However, when an evaluation of the recruit-adult hypothesis was carried out at the local site level, supply-side and postrecruitment control varied between sites throughout the entire study region. Given these results, different species within the same site may be under opposite controls and overall regional patterns of control are likely to breakdown at the local level.

Valencia-Gasti & Ladah (2016) suggest that physical transport mechanisms operating within the bay are likely to interact at a local level with water-column larvae resulting in temporally and spatially variable chthamaloid barnacle settlement that is site-specific. Ladah et al. (2005) reported that large barnacle settlement events were associated with strong internal tidal forcing while Valencia-Gasti & Ladah (2016) reported the same for sites less than a kilometer to the south. Valencia-Gasti & Ladah (2016) suggest that while internal waves are likely the primary mechanism bringing *Chthamalus* larvae close to the surf zone in SM, other processes may at times be responsible for transporting meroplankton into the intertidal. From these results of previous studies in the site, it appears that internal wave activity is an important physical transport mechanism at SM, capable of closing the gap between meroplankton in the water column and intertidal settlement sites.

Internal wave activity varies from the northern portion of the Bahía de Todos Santos, where tidally-forced semidiurnal internal waves predominate, to the southern portion, where wind-forced diurnal waves prevail (Filonov et al. 2014). If *Chthamalus* settlement is related to internal wave forcing as the above studies that have taken place during years when *Chthamalus* settlement has not been reduced and punctuated suggest, *Chthamalus* settlement within Bahía Todos Santos should vary along this gradient of internal tidal forcing, with barnacle population dynamics also varying between adjacent sites. This potential variability could also in part be due to a decoupling between larval supply and settlement, which might arise due to multiple factors, such as the vertical distribution of larvae in the water column and the surf-zone processes (Rilov et al. 2008) or perhaps the most important factor, larval behavior (Pineda et al., 2010). Within the Bahía de Todos Santos, meroplankton presents a highly patchy structure throughout the water column which, given the aforementioned studies, is likely lead to highly variable settlement within the bay (Ladah et al. 2005; Liévana MacTavish et al. 2016).

In southern California, *Chthamalus* has been reported to settle during April, May and June as well as during August and September (Pineda & López 2002; Pineda 1994). In our study, *Chthamalus* spp. settlement was only observed during the latter half of July and to a lesser extent, during the beginning of August 2014. At this same site, Ladah et al. (2005) reported *Chthamalus* spp. settlement peaks in April, June and September with no appreciable settlement during June or August, while Valencia-Gasti & Ladah (2016) reported settlement peaks in September. In comparison to these studies, no spring or autumn recruitment events were recorded for 2013 or 2014 while recruitment was only observed during late July and early August

2014. The lack of settlement observed during spring and autumn of 2014 and the delay observed in summer 2014 may have been related to the developing 2015-2016 El Niño and the anomalously warm temperature anomalies reported by Bond et al. (2015) that developed in the NE Pacific Ocean during the winter of 2013-2014. The warm water anomalies reached the coasts of California in spring and summer 2014 (Bond et al., 2015) and resulted in decreased nutrient concentrations and phytoplankton production in Baja California (Gómez-Ocampo et al., 2017) which may have potentially affected the timing of *Chthamalus* reproduction or meroplanktonic survival. The difference might also be due to interannual variation affecting the number of larvae in the water column, reproduction at the coast or larval survivorship in the water column. It is however highly irregular for chthamaloid barnacle recruitment to be so concentrated and punctuated at SM (Ladah et al. 2005, Valencia-Gasti & Ladah 2016).

Menge et al. (2009) evaluated changes in climate associated with the ENSO, NPGO, and PDO on phytoplankton and mussel recruitment at rocky intertidal sites along the California current and concluded that basin scale oceanographic and atmospheric fluctuations were likely to affect supply-side ecological processes in coastal ecosystems while local ecological interactions were likely to buffer large scale change. The results of our study suggest that this conclusion may only apply in sites where postrecruitment controls exert influence over recruit densities and may not be present in sites like Playa San Miguel, where postrecruitment controls appear to be unimportant. In Playa San Miguel, local community interactions are not likely to be sufficiently strong enough to dampen the relationship between a cohort's recruit and adult densities indicating that variations in the supply of new chthamaloid barnacles to the site will be reflected in the age-structure of the *Chthamalus* barnacle population.

In conclusion, supply-side control as the primary factor structuring the intertidal *Chthamalus* population as neither the weak density-dependent mortality observed in Playa San Miguel, nor the effects of competition or predation, were sufficient to decouple the relationship between recruit and adult densities. It is important to evaluate populations within intertidal communities individually in order to determine the type of control present regulating future population size. Knowing which type of control is acting over each population will facilitate an assessment of their potential for persistence in the future as well as their vulnerability to changing ocean conditions given the complex suite of interactions responsible for regulating the dynamics of intertidal populations.

Chapter 4. Conclusions

4.1. Summary

Previous research in the area of supply-side intertidal ecology has mostly focused on the potential impact invertebrate settlers associated with upwelling events have had on intertidal communities (e.g., Krenz et al., 2011; Menge et al., 2003; Schoch et al., 2006; Wieters, 2005). However, this research focus has broadened to include processes that operate on smaller scales and at higher frequency, in particular, internal waves (Pineda & López 2002, Ladah et al. 2005, Pfaff et al. 2015, Valencia-Gasti & Ladah 2016). To evaluate the potential importance of internal waves to intertidal sites along the Mexican Pacific, two specific questions were proposed. First, are meroplankters accumulating in surface slicks associated with internal wave activity in various sites along the Mexican Pacific coast (San Juanico, BCS; La Paz, BCS, and Barra de Navidad, JA) and second, in a site where barnacle (*Chthamalus* spp.) settlement is associated with internal wave activity (San Miguel, BC), is the barnacle population under supply-side or postrecruitment control?

For internal waves to transport meroplankton, they must modify the distribution of meroplankton in the water column; this modification should be observed via differences in meroplankton abundance between different parts of the internal wave; i.e., between fronts or within slicks (Liévana MacTavish et al., 2016; Macías et al., 2010; Pineda, 1991, 1999; Scotti & Pineda, 2007; Shanks, 1983). The importance of internal waves in three representative sites of the Mexican Pacific was evaluated by determining if internal waves could accumulate meroplankton in each site and therefore potentially transport them onshore. The results from chapter two showed that nonlinear internal wave activity existed in all three sampling sites during zooplankton collection, and that in the slicks associated with these internal waves, the concentration of meroplankton was significantly greater than in the surrounding waters, supporting the hypothesis that internal waves can accumulate meroplankton in surface slicks. Therefore, for San Juanico, BCS; La Paz, BCS; and Barra de Navidad, JAL, internal wave slicks are important for meroplankton accumulation and potentially for their subsequent onshore transport. Internal waves have also been implicated in the onshore transport of meroplankton to Playa San Miguel, where Ladah et al. (2005) suggested that internal tidal bores are likely the key mechanism responsible for the onshore transport of *Chthamalus* cyprids.

In chapter three, following up on the results from chapter two and work by Ladah et al., (2005) and Valencia-Gasti & Ladah (2016) that definitively support the idea that internal waves accumulate and potentially transport meroplankton larvae in various sites in Mexico, a particularly well-studied site (Playa San Miguel, BC) was used to explore the fate of *Chthamalus* spp. recruits. Although the one large settlement peak recorded occurred during a period of time when internal wave activity was present, due to the lack of recurrent settlement peaks (a rarity for this site), it was not possible to link settlement with internal wave activity. However, the one cohort that recruited during the study provided the opportunity for straightforward analyses to explore whether or not recruitment potentially induced by internal waves was important for barnacle population under study, and by extension, to the structure of the San Miguel intertidal community. In Playa San Miguel, neither competition nor predation significantly affected the survivorship of *Chthamalus* recruits and did not decouple the relationship between recruit and adult densities, despite the presence of weak density-dependent mortality when recruit densities were low. The presence of density-dependent mortality indicates some postrecruitment control over the survivorship of *Chthamalus* spp. recruits; nevertheless, the *Chthamalus* population at Playa San Miguel appears to be under supply-side control.

In conclusion, in San Juanico, BCS; La Paz, BCS, and Barra de Navidad, JA, internal waves were found to accumulate larvae in surface slicks, and as such, may be important for the transport and eventual settlement of barnacle and mussel larvae along the Mexican Pacific coast. In addition, in San Miguel, BC, a well-studied nearshore intertidal site where barnacle settlement has been shown to be associated with internal wave activity, the *Chthamalus* spp. population was found to be under recruitment limitation or supply-side control, indicating that the future persistence of the population depends heavily upon the manner in which competent cyprids arrive to the site. As such, internal waves may play important roles in the structuring of intertidal communities along the Mexican Pacific coast.

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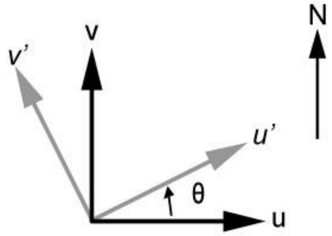
Appendices

Rotation of u and v

In the diagram to the right, the original vectors u (orientated east-west) and v (orientated north-south) and the rotated vectors *u’* ad *v’* are shown.



The matrix (R) that rotates a vector (u or v) counterclockwise through angle θ is the following:

$$R = \begin{bmatrix} \cos(\theta) & -\sin(\theta) \\ \sin(\theta) & \cos(\theta) \end{bmatrix}$$

Multiplying vectors u and v by R, we obtain *u’* and *v’*:

$$\begin{bmatrix} \cos(\theta) & -\sin(\theta) \\ \sin(\theta) & \cos(\theta) \end{bmatrix} \begin{bmatrix} u \\ v \end{bmatrix} = \begin{matrix} \mathrm{u}\cos(\theta) - v\sin(\theta) \\ \mathrm{u}\sin(\theta) + vcos(\theta) \end{matrix}$$

$$u' = \mathrm{u}\cos(\theta) - v\sin(\theta)$$

$$v' = \mathrm{u}\sin(\theta) + vcos(\theta)$$

Principal component analysis

This procedure is based on methods described by Presiendorfer (1988).

Step 1: Generate a matrix based on time series observations. In the case of this study, the matrix generated was based on the horizontal components of the current velocity u and v.

Given a time series $x'(w)$ where the average $\bar{x}$ is given by

$$\bar{x} = \sum_{w=1}^{n} x'(w)$$

$\bar{x}$ is subtracted from $x'(w)$. This step is repeated for both time series $x'(w)$ and $y'(w)$ and a matrix is created with the two resulting vectors.

Step 2: Find the variance $s^2(\theta)$ of both time series contained in the matrix.

Variance of the first time series:

$$sxx = (n-1)^{-1} \sum_{w-1}^{n} x^2(w)$$

Variance of the second time series:

$$syy = (n-1)^{-1} \sum_{w-1}^{n} y^2(w)$$

When $\theta = 0$, $s^2(\theta) = sxx$. When $\theta = \frac{\pi}{2}$, $s^2\left(\frac{\pi}{2}\right) = syy$.

Therefore, when θ varies between 0 and 2π, $s^2(\theta)$ takes on all values of sxx and syy.

Step 3: Find the covariance of the matrix.

$$syx = (n-1)^{-1} \sum_{w-1}^{n} x(w)y(w)$$

Step 4: Find the principal angles θ that occur at the maximum and minimum values of $s^2(\theta)$ via the following equation:

$$\theta' = \frac{1}{2} arctan \left\lfloor \frac{2sxy}{sxx - sxy} \right\rfloor$$

There are two values of θ' that are 90° from one another where the extreme values of $s^2(\theta)$ occur. The angle where $s^2(\theta)$ is maximum is the first principal angle.