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en Ecología Marina**

**Distribution and delivery of meroplanktonic larvae in the Bay
of Todos Santos: the role of internal tidal waves**

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Román Gerardo Fernández Aldecoa

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Tesis defendida por
Román Gerardo Fernández Aldecoa

y aprobada por el siguiente Comité

Dra. Lydia Betty Ladah
Director de tesis

Dra. Ma. Elena Solana Arellano

Dr. José Luis Ochoa de la Torre

Dr. Steven G. Morgan

Dr. Enric Pallas Sanz



Dr. Jorge Adrián Rosales Casián
Coordinador del Posgrado en Ecología Marina

Dra. Rufina Hernández Martínez
Directora de Estudios de Posgrado

Resumen de la tesis que presenta **Román Gerardo Fernández Aldecoa** como requisito parcial para la obtención del grado de Doctor en Ciencias en Ecología Marina

Distribución y aporte de larvas meroplantónicas en la Bahía de Todos Santos: el rol de las ondas internas de marea

Resumen aprobado por:

Dra. Lydia Betty Ladah
Director de tesis

Las larvas de invertebrados marinos se acumulan a diferentes distancias de la costa debido a su comportamiento, su ontogenia, hábitat y a la variabilidad de los mecanismos físicos que actúan sobre la plataforma continental. Este estudio es uno de los primeros esfuerzos para comprender el papel que tienen las ondas internas de marea en el viaje de los últimos estadios larvarios a sus sitios de asentamiento, enfocado en los últimos 2 km antes de llegar a la costa. El objetivo fue evaluar los cambios de alta frecuencia (cada hora) en la abundancia y la variabilidad vertical del meroplancton (gasterópodos, ostiones, balanos y briozoarios) en un arreglo de tres estaciones perpendiculares a costa (2 km, 1.3 km y 10 m de la costa). El estudio se realizó durante un periodo de fuerte forzamiento de ondas internas de marea en verano, cuando larvas de muchas especies meroplanctónicas, algunas de valor comercial, se asientan y reclutan en esta área. Se midieron variables físicas como la temperatura, corrientes y vientos de manera simultánea con las mediciones de meroplancton. Se encontró que las ondas internas de marea de frecuencia semidiurna dominaron los campos de corrientes y temperatura, especialmente desde media agua hasta el fondo, y fueron los mecanismos responsables de agregar meroplancton en diferentes sitios dependiendo de sus preferencias de hábitat. Los cifonautas se concentraron en profundidad durante la fase cálida de la marea interna únicamente en la estación a 2 km de la costa, donde fueron más abundantes. A 1.3 km de la costa, los gasterópodos se concentraron en profundidad durante la fase fría de la onda de marea interna, donde fueron más abundantes. El aporte de gasterópodos al sitio más costero fue explicado por una interacción entre los cambios de temperatura relacionados con las ondas internas de marea y la brisa marina, siendo la primera vez que se ha encontrado una interacción entre ambos factores como un mecanismo de aporte larval a un sitio tan cerca de la costa. Las cypri de balanos se encontraron solo en el sitio más costero y los picos en abundancia se relacionaron con el quiebre de las ondas internas de marea en la costa. Los resultados de esta tesis enfatizan aún más el complicado impacto que las ondas internas podrían tener en la modulación de las comunidades intermareales.

Palabras clave: zooplancton, aporte larval, macareo interno de marea, vientos hacia costa, costa rocosa

Abstract of the thesis presented by **Román Gerardo Fernández Aldecoa** as a partial requirement to obtain the Doctor of Science degree in Marine Ecology

Distribution and delivery of meroplanktonic larvae in the Bay of Todos Santos: the role of internal tidal waves

Abstract approved by:

Dra. Lydia Betty Ladah
Thesis Director

Marine invertebrate larvae accumulate at different distances from the coast due to their behavior, ontogenic stage, habitat and the variability of physical mechanisms on the shelf. This study represents one of the first efforts to understand the role of internal tidal waves along the last part of the journey that larvae must undergo to arrive at their settlement site, focusing on the 2 km just before reaching the shore. We evaluated high-frequency changes (hourly) in the abundance and vertical variability of target meroplankters (gastropods, oysters, barnacles, and bryozoans) using a cross-shore array of three stations in the coastal ocean (2 km, 1.3 km and 10 m from shore) during a period of strong internal tidal forcing in summer, when many larvae settle and recruit in this area. Concurrent measurements of temperature, currents, and winds helped to identify the mechanisms occurring while meroplankton abundance was measured. Semidiurnal internal waves dominated the temperature and current fields, especially from the midwater to the bottom, and were most likely responsible for aggregating organisms at different sites depending on their habitat preferences. Cyphonautes were concentrated at depth during the warm phase of the internal tide only at 2 km from shore, where they were most abundant. At 1.3 km from shore, gastropods were more concentrated at depth during the cold phase of the internal tidal bore, where they were most abundant. Gastropods appeared to be delivered to coast by an interaction between changes in temperature related to breaking internal tidal waves and onshore winds, showing for the first time an interaction between both forcing factors as a mechanism of delivery. Barnacle cyprids were found only at the subtidal site and peaks in abundance were related to breaking internal tidal waves at the shore. The results of this thesis further emphasize the complicated impact that internal waves might have on structuring intertidal communities.

Keywords: zooplankton, larval supply, internal tidal bore, onshore winds, rocky shore

Dedication

*Para Ana Luisa:
Así como las larvas buscan la corriente que las lleve a su destino final,
así encuentra tu camino y llega a tu meta, sin olvidar jamás lo más
importante: ¡disfrutar el viaje!*

“The sea, once it casts its spell, holds one in its net of wonder forever”.

**Jacques-Yves Cousteau
(1910-1997)**

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Chapter 1. Introduction

1.1 Background

The life history of many invertebrates that inhabit coastal environments is intriguing and complex, characterized by a larval phase in the plankton and an adult phase adapted to the benthos (Thorson, 1950). Organisms with this biphasic life cycle are known as meroplankton. The larval phase develops in waters on the continental shelf for periods that range from a couple days to several months depending on the species (Shanks, 2009). When reaching the last larval stage, the organisms are ready for the journey to shore in order to settle and recruit to the adult population (Gaines et al., 2007; Pineda et al., 2007).

Understanding the complexity of larval return to shore has been a challenge for marine scientists since the last century, principally because this journey depends on two highly variable factors: the horizontal and vertical distributions of larvae in the water column and oceanographic transport mechanisms (Scheltema, 1986; Shanks, 1995, 2006). Rapidly changing conditions of the coastal ocean and larval patchiness increase the difficulty to link both parameters. Nonetheless, many studies have started to address this issue using high frequency sampling to evaluate transport mechanisms with simultaneous measurements of larval abundance in the nearshore (Ladah et al., 2005; Liévana MacTavish et al., 2016). Studying changes in the vertical and horizontal distributions of meroplankton when transport mechanisms are operating is a first step towards understanding the complex dynamics of larval dispersion, and the consequences for coastal populations.

1.2 Meroplankton

The pelagic phase of coastal meroplanktonic organisms starts when the adults release their gametes or fertilized eggs into the water column (Thorson, 1950; Shanks, 1986; Pineda 1991). Afterwards, larvae hatch and are advected far from their natal sites, ideally in an environment far from stressors or predators that may inhibit their development. The initial distance of advection of early larval stages depends on various factors (Metaxas, 2001; Shanks, 2009; Weidberg et al., 2015), such as the swimming capacity of larvae and the timing of release related to coastal oceanographic features (e.g. spring or

neap tides). Meroplankters progress through a number of stages until they are competent to settle, and can last from a couple of days to several months in the water column, depending on the species and feeding habits, where planktotrophic species tend to live for shorter periods of time in the plankton than lecithotrophic species (Scheltema, 1986; Roughgarden et al., 1988). After reaching the last ontogenic stage, meroplankters need to return to an intertidal or subtidal habitat to complete their development and recruit to an adult population (Yoshioka, 1982; Gaines et al., 2007; Pineda et al., 2007).

Meroplanktonic larvae must complete a journey across the continental shelf to reach the coastal habitat, and this journey depends on physical transport mechanisms, as well as the horizontal and vertical distributions of the larvae in the ocean (Shanks, 1986; Pineda, 1994; Shanks & Brink, 2005; Scotti & Pineda, 2007). Because transport mechanisms vary with depth, larvae may be transported in different directions with different magnitudes over the continental shelf depending on their vertical distribution. Therefore, the preference of larvae to remain at a particular depth is intrinsically related to the stage of development or the species (Tapia & Pineda, 2007; Tapia et al., 2010). For example, Tapia & Pineda (2007) found that the nauplii of the barnacles *Balanus glandula* and *Chthamalus* spp. showed different horizontal distributions related with the ontogenetic stage of the larvae. The early naupliar stages were more abundant at surface near the coast, while later stages were more abundant in the open sea. Additionally, cyprid larvae (a barnacle's last larval stage) were always more abundant near the coast and close to the bottom. We would expect to observe freshly spawned larvae and/or competent larvae near the coast, whereas larvae at various intermediate stages of development would be expected far from the coast in larval collections.

Many species of meroplanktonic organisms live in the intertidal and subtidal environments of the West coast of North America. Understanding their life histories, adaptations and vertical distributions throughout their larval development will help us understand the mechanisms involved in their return to shore. Some of the most important organisms in coastal waters which are the focus of this thesis are discussed below.

1.2.1 Bryozoans



Figure 1. Larval form of bryozoans, called cyphonautes. Recovered from: <https://wikivividly.com/wiki/Cyphonautes>

The most conspicuous species of bryozoan in the coastal waters of California is *Membranipora membranacea*, which creates colonies that are fixed to the blades of the giant kelp *Macrocystis pyrifera* (Yoshioka, 1982). The larval form called cyphonautes hatches from eggs (Fig.1). Cyphonautes larvae can remain in the water column for one to two months as it is planktotrophic (Yoshioka, 1982). Populations of *M. membranacea* are seasonally abundant from May to September (Harvell, 1990).

The vertical positioning of these larvae in the water column is a function of their stage of development. During their first weeks in the plankton, cyphonautes present positive phototaxis and negative geotaxis, which results in a swimming behavior directed towards the surface. However, for their final period in the plankton, the opposite occurs, resulting in a tendency to swim towards the bottom (Wendt & Woollacott, 1999). The swimming speed of cyphonautes reaches $0.19 \text{ cm}\cdot\text{s}^{-1}$, comparable to that of barnacle nauplii. This is generally considered low speed for larvae, and horizontal advection is minimum by this mean (Konstantinova, 1966), therefore, to achieve horizontal transport, buoyancy control is necessary to take advantage of stratified currents.

1.2.2 Barnacles



Figure 2. Cyprid, the last larval stage of barnacles prior to settlement. Recovered from: <https://scripps.ucsd.edu/zooplanktonguide/species/barnacle-larvae>.

Barnacles are filter feeders fixed to a hard substrate, like rocks or other organisms in the intertidal zone (Young et al. 2002). The most common species along the Pacific coast of Northern Baja California include *Balanus glandula* and *Chthamalus* spp. (Ricketts & Calvin, 1968). Barnacles are hermaphroditic and spawn throughout the year, with a peak in summer (Hines, 1978). Barnacles have two larval forms: the feeding nauplii and the non-feeding cyprid (Fig. 2) (Strathmann, 1987; Young et al., 2002), transitioning through 6 naupliar stages and a last cyprid stage, during 2–5 weeks in the pelagic environment (Walley, 1969). As mentioned previously, they are generally considered poor swimmers (0.17 to $0.55 \text{ cm}\cdot\text{s}^{-1}$) (Chia et al., 1984), in comparison with megalopas of brachyuran crabs that reach speeds of $10 \text{ cm}\cdot\text{s}^{-1}$ (Rasmuson & Shanks, 2014).

Cyprid vertical distribution may vary depending on oceanographic conditions or behavior. Cyprids have been found at near-bottom depths (Barnett & Jahn, 1987; Pineda, 1991; Bonicelli et al., 2016), perhaps because they seek bottom currents propagating onshore, preparing to settle at the intertidal zone (Grosberg, 1992). Nevertheless, cyprid larvae have also been observed in surface waters (Le Fèvre & Bourget, 1992), sometimes associated with transient internal bore warm fronts (Pineda, 1999).

1.2.3 Gastropods



Figure 3. 5 days old veliger of *Tegula funebralis* (Moran, 1997).

Gastropods are one of the most abundant and diverse class of organisms that inhabit coastal zones around the world, displaying an impressive diversity of developmental and life history characteristics. Some intertidal species have separate sexes and undergo copulation and internal fertilization, depositing encapsulated eggs onto rocky substrate that later releases free-swimming veliger (Fig. 3) or trochophore larvae (Brusca & Brusca, 2003). However, a few species lack a planktonic larval stage in their life cycles and hatch as crawling juveniles (e.g., species of *Nucella*).

Nerita and *Tegula* spp. are some of the most common gastropod groups with a planktonic phase on the rocky shores of Baja California. For both *Tegula funebralis* and *Nerita* spp., the spawning season lasts all year, with a peak in the summer months, with larval periods that reach approximately 14 days (Hewatt, 1934). There is limited information about the vertical distribution of this species in the water column, however, due to its restricted swimming capabilities and shell weight, it is expected that in the latter stages of larval development they tend to concentrate near the bottom.

1.2.4 Bivalves (mussels and oysters)



Figure 4. Veliger larvae of the mussel *Mytilus californianus*. Recovered from: <https://www.researchgate.net/publication/307878463> Validation of trophic and anthropic underwater noise as settlement trigger in blue mussels/figures?lo=1

Both mussels and oysters form large aggregations on rocks in the upper intertidal zone on the open coast, where they are exposed to wave action. *Mytilus californianus* is native from the West Coast of North America and the most conspicuous mussel in Baja California, while *Crassostrea gigas* is an oyster with worldwide distribution. Adults release their eggs into the seawater where they are fertilized externally. After 4-5 hours, cilia first appear and the embryo begins to swim. Larvae go through several larval forms: trochophore, various prodissoconch, veliconcha and finally the pediveliger, the last being the settling and metamorphic stage (Young et al., 2002). If conditions are ideal, mussel and oyster larvae may remain in the plankton for two to four weeks (Shatkin et al., 1997; López-Duarte et al., 2012), and settlement season takes place during summer months for oysters and from late autumn to early winter for mussels.

Veligers move using cilia and can reach speeds of $0.1 \text{ cm}\cdot\text{s}^{-1}$ (Chia et al., 1984), being capable to swim nearly 4 meters in one hour. Therefore, significant changes in the vertical positioning within the water column may be achieved through swimming behavior, although horizontal advection due may be not significant. Veliger larvae are negatively phototactic and positively geotactic, displaying a preference to concentrate near the bottom as they begin to select a site for settlement and a benthic mode of life (Baker, 1997).

1.3 Physical transport processes over the shelf

Larvae are transported across the shelf by one or more mechanisms, including wind-driven surface currents, upwelling and relaxation circulation, and breaking internal tidal waves, often termed bores (Ladah et al., 2005; Jacinto & Cruz, 2008; Shanks et al., 2014; Morgan et al., 2018). These mechanisms may be of particular importance as they have been shown to change the abundance and accumulate meroplankton throughout the water column (Shanks, 1983; Liévana MacTavish et al., 2016).

Plankton can be transported onshore by winds, which can result from various mechanisms. The sea breeze, which occurs due to a temperature gradient that is generated between the land and the ocean, can result in onshore surface currents of up to 10 cm s^{-1} over an area of influence of about 3 km from shore (Tapia et al., 2004; Woodson et al., 2007), and can transport surface zooplankton shoreward (Shanks, 1995). Wind forced upwelling-downwelling circulation occurs when equatorward winds, generally associated with large-scale geostrophic pressure systems, displace coastal surface waters offshore due to Ekman transport, which are replaced with colder, denser, upwelled waters that can transport zooplankton from deeper layers shoreward. When these winds relax or change direction, the colder and denser waters sink, and the warmer surface waters that were initially pushed offshore return to shore, transporting surface zooplankton shoreward (Wing et al., 1995; Shanks et al., 2000; Almeida & Queiroga, 2003).

Internal tidal waves are another mechanism that can transport particles to shore. 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). The barotropic tide is the main periodic force that generates internal tidal waves, having similar periods than tidal components, like M2 (12.42 h period) (Godin, 1988). Onshore transport of larvae by internal tidal bores consists in two phases (see Fig.5) (Pineda, 1995, 1999). As the internal tide enters shallow waters, it becomes unstable and breaks, causing waters from below the thermocline to shoal and move shoreward, known as the cold phase or bore (Pineda, 1991). Afterwards, as the cold, dense water sinks and is advected offshore, warmer surface waters move back onshore, called the warm phase or bore. These two alternating phases occur once each tidal cycle and are characteristic of a mode-1 internal wave, with currents flowing in opposite directions above and below the thermocline (Shanks, 1983; Pineda et al., 2007).

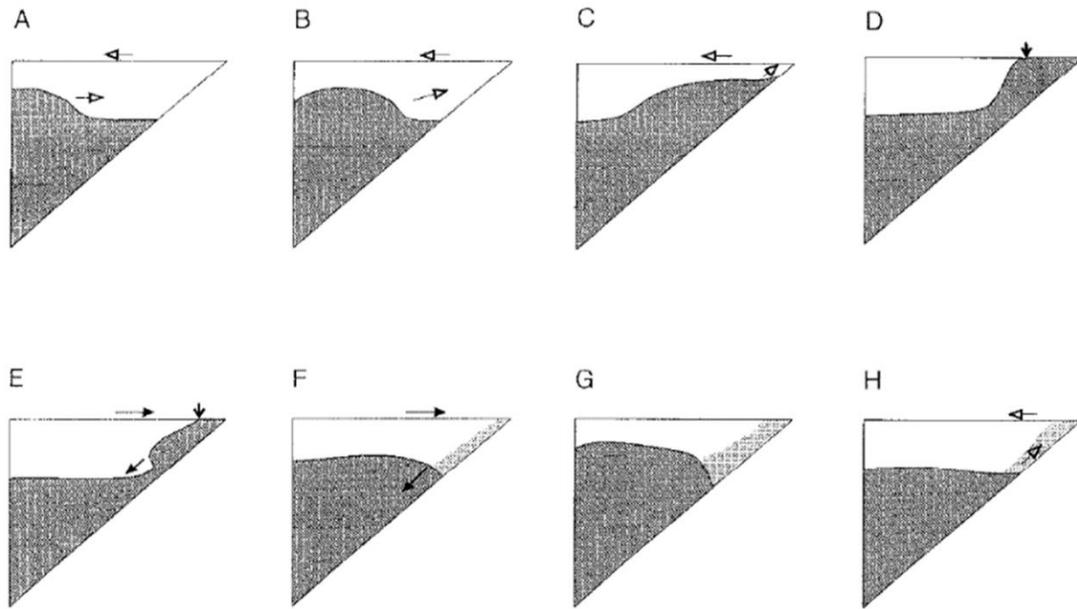


Figure 5. Phases of an internal tidal bore. During the cold phase (A, B, C and D), colder and deeper waters move towards the coast, while surface warmer waters move away from coast, creating a cold front (Shanks, 1995). During the warm phase (E, F, G and H), surface waters move towards the coast, while cold waters sink and are advected away from shore. The front, an interface separating warm (cold) onshore and cold (warm) offshore waters during the cold (warm) phase, has the capacity to accumulate and transport larvae to shore. Depending on the depth larvae are located, they will be transported to shore by either the cold or the warm phase (Pineda, 1994, 1999) (modified from Pineda et al., 2007, p. 25).

Therefore, for a semidiurnal internal tide, two cold and two warm bores are expected each day. Warm bores have been shown to transport organisms that are near the surface in the direction of the propagating wave (Pineda, 1991; Leichter et al., 1998), while cold bores can transport organisms from deeper strata in the direction of the propagating wave (Pineda, 1994). 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 (Cairns, 1967; Farmer & Smith, 1980).

1.4 Larval transport by internal tidal waves in the Bay of Todos Santos

Internal tidal waves have been well characterized in the Northern part of the Bay of Todos Santos, Baja California, Mexico (Ladah et al., 2005; Ladah et al., 2012; Filonov et al., 2014). In front of San Miguel, the tide is characterized as mixed, with a dominant semidiurnal signal (Godin, 1988; Filonov et al., 2014). The internal tide can produce changes in temperature larger than 10 °C in a span of 24 h. The energetic uplifting of the pycnocline produced by internal tidal waves often causes strong alternating currents with depth which can result in physical transport of tracers and organisms, linking the nearshore ocean with offshore waters through cross-shelf fluxes. These fluxes have been studied in this area for the past 15 years through the FLOO projects (Fluxes Linking the Offshore and the Onshore) in the Interdisciplinary Coastal Ecology Lab at the Centro de Investigación y Educación Superior de Ensenada (CICESE).

Internal tidal bores modulate changes in the vertical distribution, abundance, and settlement of meroplankton in the Northern part of the bay. Liévana MacTavish et al. (2016) showed significant changes in the vertical distribution and abundance of barnacles and crabs in the water column across internal tidal fronts, and internal tidal bores have been associated with settlement of the barnacle *Chthamalus* spp. in the intertidal zone (Ladah et al., 2005; Valencia-Gasti & Ladah, 2016). The most asymmetric and energetic internal waves tend to coincide with spring tides during summer and fall, when the water column is most stratified. And although our knowledge about internal tidal waves in the Bay of Todos Santos has improved, further exploration of their ability to deliver larvae to nearshore waters is necessary for understanding the dynamics of coastal populations, especially during peaks in larval abundance of target coastal organisms such as in summer months in this bay (Franks, 1997; Helfrich & Pineda, 2003).

1.4.1 Problem statement

Many questions remain regarding the evolution of the internal tide as a mechanism of transport across the shelf and the connection of offshore waters with the shallow subtidal and intertidal environments. Nearshore waters are truly dynamic, with high spatial and temporal variability in oceanographic and meteorological conditions, such as in temperature, and in wind and tidal forcing (Pineda & Lopez, 2002; Lamb, 2014), further complicating matters. Although Liévana MacTavish et al. (2016) addressed the variability in larval distribution on the shelf, where internal tidal waves showed an alongshore

propagation into the bay (Filonov et al., 2014) in the area offshore of San Miguel, the study could only speculate on the link between the changes in larvae in offshore waters. In this thesis, the study sites were chosen to be nearer to the coast, using a cross-shore array of instruments and sampling, where the propagation of internal waves was more directly cross-shore due to refraction, to explore how internal waves affect larval concentrations and transportation at nearshore and onshore sites. Past research closer to shore at this site by Valencia-Gasti & Ladah (2016) shows that the settlement of barnacles in the intertidal zone is linked with internal waves, however there has been a gap in data between the offshore waters on the shelf and the very inshore and intertidal sites. This thesis arises as a vehicle to begin to fill in this gap and to complement our understanding of the physics of the internal wave field with biological data. Through a biological-physical coupling approach, we can further our understanding of how offshore waters are linked with inshore productivity through cross-shore fluxes.

1.5 Study question

- How is the nearshore distribution and abundance of meroplankton affected by internal tidal bores across the shelf?

1.6 Justification

Larvae of different species will most likely accumulate at different distances from the coast due to their behavior, their ontogenetic stage, and the variability of physical mechanisms over the shelf. Therefore, an evaluation of how larval subsidies arrive to the intertidal community is necessary for understanding how nearshore populations of meroplankton, some with important fisheries implications, might respond to change. Potential meroplanktonic transport by internal tidal wave bores has been shown to be variable due to the complex interactions between internal waves and meroplankton (Shanks, 1983; Pineda et al., 2007; Shanks & Shearman, 2009; Filonov et al., 2014). This study aims to fill the gap between shelf waters and the intertidal zone, and will provide insight that can be applied to everything from understanding when and how larvae settle to inform fisheries and extraction quotas to the understanding of connectivity of populations to inform the design of marine reserves.

1.7 Objective

1.7.1 General objective

We aimed to evaluate high-frequency changes (hourly) in the abundance and vertical variability of target meroplankters (gastropods, mussels, oysters, barnacles, and bryozoans) and holoplankton (foraminifera and ostracods) in the coastal ocean during a period of strong internal tidal forcing in summer, when many larvae settle and recruit in this area. Concurrent measurements of temperature, currents, and winds helped to identify the mechanisms occurring while zooplankton abundance was measured.

1.7.2 Specific objectives

1. Evaluate how the abundance and vertical distribution of meroplankton change across shore sites, strata and phases of the internal tidal bore.
2. Explore the temporal relationship between larval supply to the nearshore with various physical factors (internal tidal fronts, winds and tidal height).

Chapter 2. Nearshore cross-shelf distribution of meroplankton during internal tidal forcing

2.1 Hypothesis

- Changes in abundance of meroplankton across the shelf will be synchronous
- Meroplankton abundance will be vertically stratified at all sites across the shelf (habitat preference)
- Abundance of meroplankton will change between phases of the internal tidal bore

2.2 Objective

- Measure the cross-shore thermal structure of the water column using an array of thermistors
- Identify cold and warm bores using in-situ temperature and current data
- Determine the abundance and vertical distribution of meroplankton at across shore sites
- Evaluate how the abundance of meroplankton changes between sites, strata, and phases of the internal tidal bore

2.3 Materials and Methods

2.3.1 Study area

The study was conducted in front of Playa San Miguel, in the Northern part of the Bay of Todos Santos, Baja California, Mexico ($31^{\circ} 55' N$, $116^{\circ} 38' W$), near Ensenada (Fig. 6). Summertime conditions at this site are characterized by a highly stratified water column, with strong semidiurnal

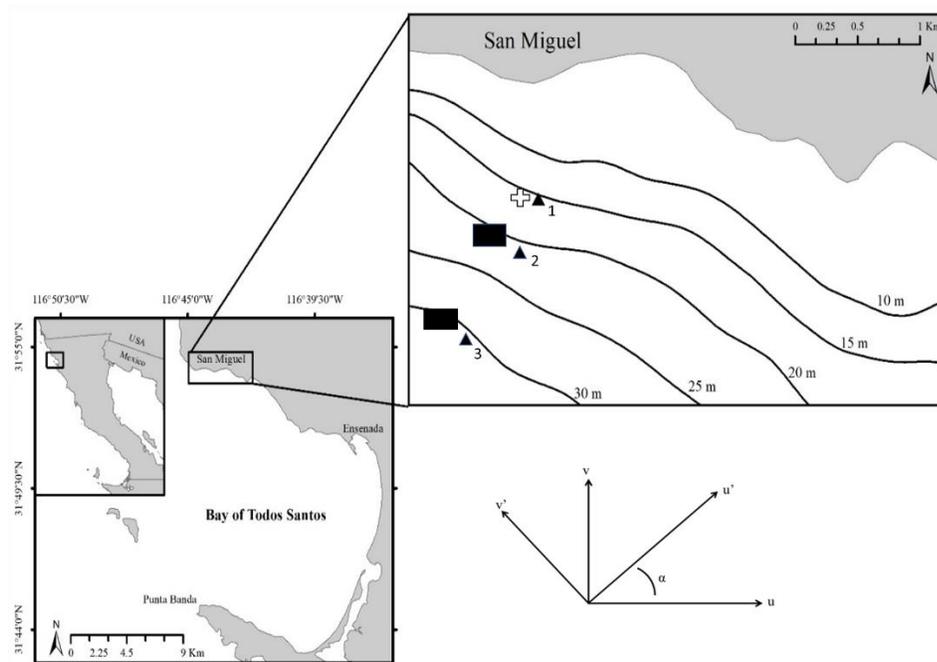


Figure 6. Location of study site in the northern part of the Bay of Todos Santos, in front of Playa San Miguel. Offshore mooring stations 1, 2, and 3 were located on the 15, 22, and 30 m isobath respectively. A thermistor line (\blacktriangle) was deployed next to each station, a boat (\blacksquare) next to station 2 and 3 and an Acoustic Doppler Current Profiler (ADCP) (+) was deployed next to station 1. The north–south current velocity component (v), was graphed against the east–west current velocity component (u), and the major axis u' (rotated $\alpha=42.03^{\circ}$), indicated principal current direction either onshore (positive u' values) or offshore (negative u' values). Bathymetry was provided by Dr. Ruiz de Alegria-Arzaburu's laboratory.

2.3.2 Data collection

Sample collection was performed every hour in triplicate for three continuous days from August 31 to September 2, 2015. Zooplankton samples were taken from two stations: the offshore boat, located at 30

m depth (2 km offshore), and the inshore boat, at 22 m depth (1.3 km offshore). To collect zooplankton, pumps were connected to wide-mouthed hoses (5.08 cm in diameter), with one end of the hose weighted to sample at two depths (4 and 14 m). The other end of the hose fed into a nytex (150 μm) mesh bag to collect filtrate (Fig. 7). Pump rates were adjusted and standardized to collect 100 L of water. The contents were filtered and fixed in 92% ethanol immediately after collection. The high-frequency sampling was essential for detecting changes that occur at hourly scales in response to breaking internal tidal waves at the coast. Identification to the lowest taxonomic level was performed using a stereomicroscope (32x objective). All meroplankton taxa and the most abundant holoplankton taxa were enumerated.



Figure 7. Zooplankton sampling. A hose was placed to pump water at 4 and 14 m depth (left). The other end of the hose poured water into a nytex mesh to filter zooplankton bigger than 150 μm (right).

A set of instruments recorded physical variables near the study area. Temperature of the water column was measured using a vertical array of thermistors (HOBO® Tidbit v2, Onset Computer Corp., USA) deployed every meter at three mooring stations located 850 m, 1.3 km, and 2 km offshore of the coast, in 15 m, 22 m, and 30 m depth, respectively (Fig.6). Instruments recorded temperature every minute. This type of array has been used previously to identify anomalies in temperature characteristic of internal waves with periods greater than 10 min at this site (see Ladah et al. 2012, Filonov et al. 2014). An Acoustic Doppler Current Profiler (ADCP, RDI workhorse 600 Khz;

<http://www.teledynmarine.com/rdi/>) was deployed at 15 m depth set to record every minute in 1-m bins.

2.3.3 Data processing

We defined the different phases of the internal tidal bore (cold or warm) separated by a front where temperature changes exceeded 2 °C in less than 1 hour at the mid-water depth, and which persisted for at least 2 hours, during the internal tidal wave (Liévana MacTavish et al., 2016). Current velocities and direction were decomposed into their Cartesian components u (East-West) and v (North-South). To calculate the horizontal component with the greatest variability, we used the following equation:

$$u' = u \cos(\alpha) + v \sin(\alpha) \quad (2)$$

The angle between the reference system of u and the reference system of u' for current velocity was α (Fig.6). Positive u' current velocities indicate current propagation towards the northern part of the bay (onshore), while negative u' velocities indicate current propagation away from the northern part of the bay (offshore).

2.3.4 Data analysis

A log transformation was used to obtain normality and homogenize variances to meet the assumptions for all statistical analyses. Pearson correlations between abundances from the offshore and inshore boats were calculated. A factorial ANOVA with $\alpha = 0.05$ was performed to determine the effect of strata and internal tidal bore phase (cold or warm) on the abundance of meroplankton for each taxon for each boat. *A posteriori* comparisons were performed using a Fisher LSD test (StatSoft, Inc. 1984-2005).

2.4 Results

2.4.1 Meroplankton

Late-stage larvae represented nearly 40% of enumerated zooplankters at both boats. Cyphonautes, gastropod late larvae, *Mytilus* spp., and *Crassostrea* spp. were the main meroplanktonic taxa found at this site. At the offshore site (Table 1), cyphonautes were the most abundant meroplankters with 28.5% of the total abundance. At the inshore boat (Table 2), gastropod late larvae were the most abundant meroplankters making up nearly 17% of the total abundance.

Table 1. Mean concentration (# zooplankters . 100 L⁻¹), standard error (+SE), and percentage of zooplankton collected from 31 August to 2 September, 2015 at the offshore boat.

Taxon	Mean	SE	%
Cyphonautes	131.98	23.67	28.5
Larvaceans	121.65	23.46	26.27
Euphasiid zoea	56.23	10.82	12.14
Foraminifera	37.54	11.37	8.11
Gastropod late larvae	37.35	4.52	8.06
<i>Mytilus</i> spp.	18.50	18.30	3.52
Hydromedusae	10.58	2.44	2.28
<i>Crassostrea</i> spp.	5.33	2.50	1.44

Table 2. Mean concentration (# zooplankters . 100 L⁻¹), standard error (+SE), and percentage of zooplankton collected from 31 August to 2 September, 2015 at the inshore boat.

Taxon	Mean	SE	%
Protozoa euphasiid	143.09	39.42	33.22
Euphasiid zoea	73.02	25.72	16.95
Gastropod late larvae	72.94	15.21	16.93
Cyphonautes	69.70	17.77	16.18
<i>Mytilus</i> spp.	30.30	5.20	8.06
Foraminifera	22.13	5.22	5.14
Larvaceans	15.91	5.91	3.70
Hydromedusae	4.60	1.51	1.07
<i>Crassostrea</i> spp.	4.20	2.10	1.44

2.4.2 Changes in meroplanktonic abundance across the shelf

Most changes in abundance between boats were not coherent. The Pearson analysis showed no significant correlation in changes in abundance between boats for the main meroplanktonic taxa at either depth (Table 3). Only for *Crassostrea* spp. were changes in abundance significantly correlated between boats and only at the 4 m depth (Fig. 8).

Table 3. Pearson correlation coefficient (r and r^2) between meroplanktonic abundances at offshore and inshore boats. Significant r -values are shown in red ($p < 0.05$).

Taxa	r	r^2	p
Gastropods			
4m	0.38	0.14	0.22
14m	0.12	0.01	0.71
<i>Mytilus</i> spp.			
4m	0.01	0.01	0.98
14m	0.13	0.01	0.69
Cyphonautes			
4m	0.18	0.03	0.57
14m	0.16	0.02	0.62
<i>Crassostrea</i> spp.			
4m	0.60	0.36	0.03
14m	0.13	0.01	0.68

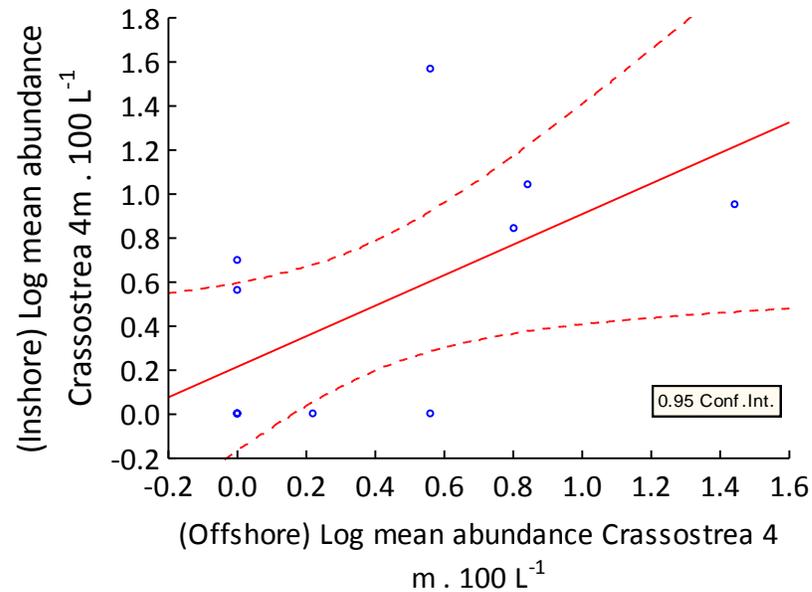


Figure 8. Scatterplot between offshore and inshore boat mean abundances of *Crassostrea* spp. at 4 m depth.

However, some taxa did show differences in abundance as a function of distance from shore (Fig. 9). Gastropods were significantly more abundant at the inshore boat, showing an accumulation closer to shore, in a nearshore habitat, while in the case of cyphonautes, the opposite pattern was found, with greater abundance at the offshore site, suggesting a preference for a habitat further from shore. However, for *Crassostrea* spp., there were no significant differences in abundance between boats, showing no cross-shore habitat preference.

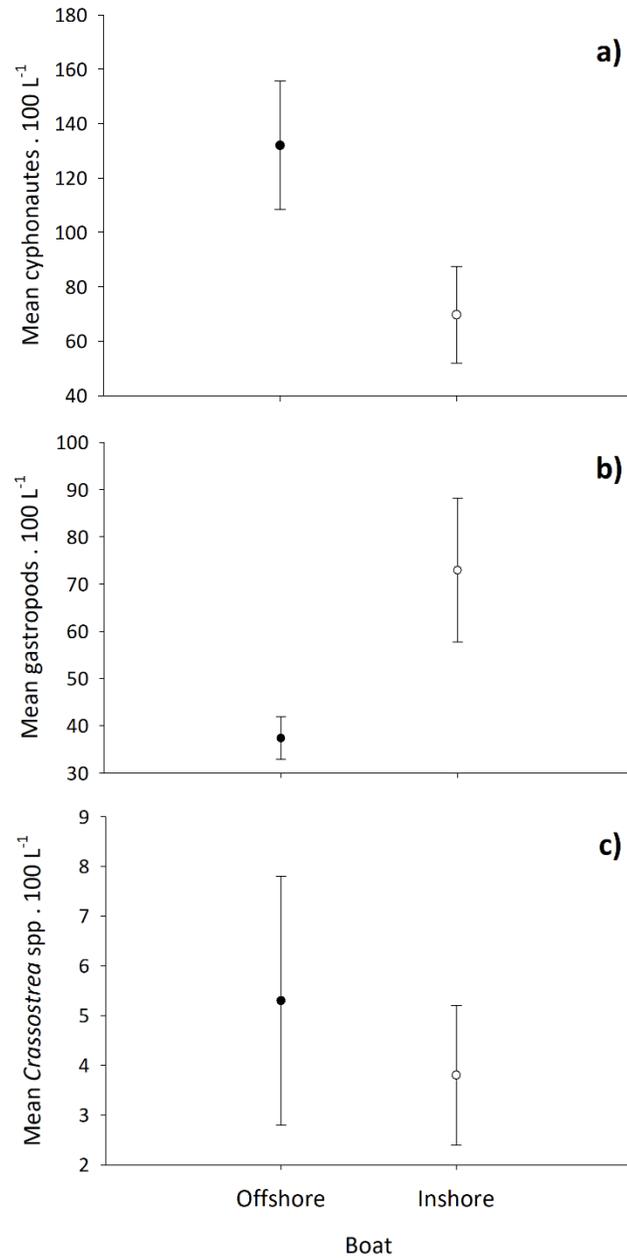


Figure 9. Mean abundances of meroplankton between offshore and inshore boat: a) cyphonautes; b) gastropod late-larvae; and c) *Crassostrea* spp. Error bars: \pm SE.

2.4.3 Internal tidal bores nearshore

Temperature differences between the surface and bottom thermistors reached over 7 °C during periods of high stratification (Fig. 10 a, b, c). Cold and warm water fronts alternated approximately every 6 h and coincided with fluctuations of the thermocline and movement of water in opposite directions depending

on the depth (Fig. 10d). For example, a cold front was detected on September 1, starting at around 0200 h and ending at 0700 h, with currents flowing in the southwestern direction (offshore flow) near the surface, while bottom currents showed a northeastern direction (onshore flow). Following the cold front, the temperature of the water column abruptly increased, as a warm front began around 0800 h and ended at noon, with currents switching direction, above and below the thermocline.

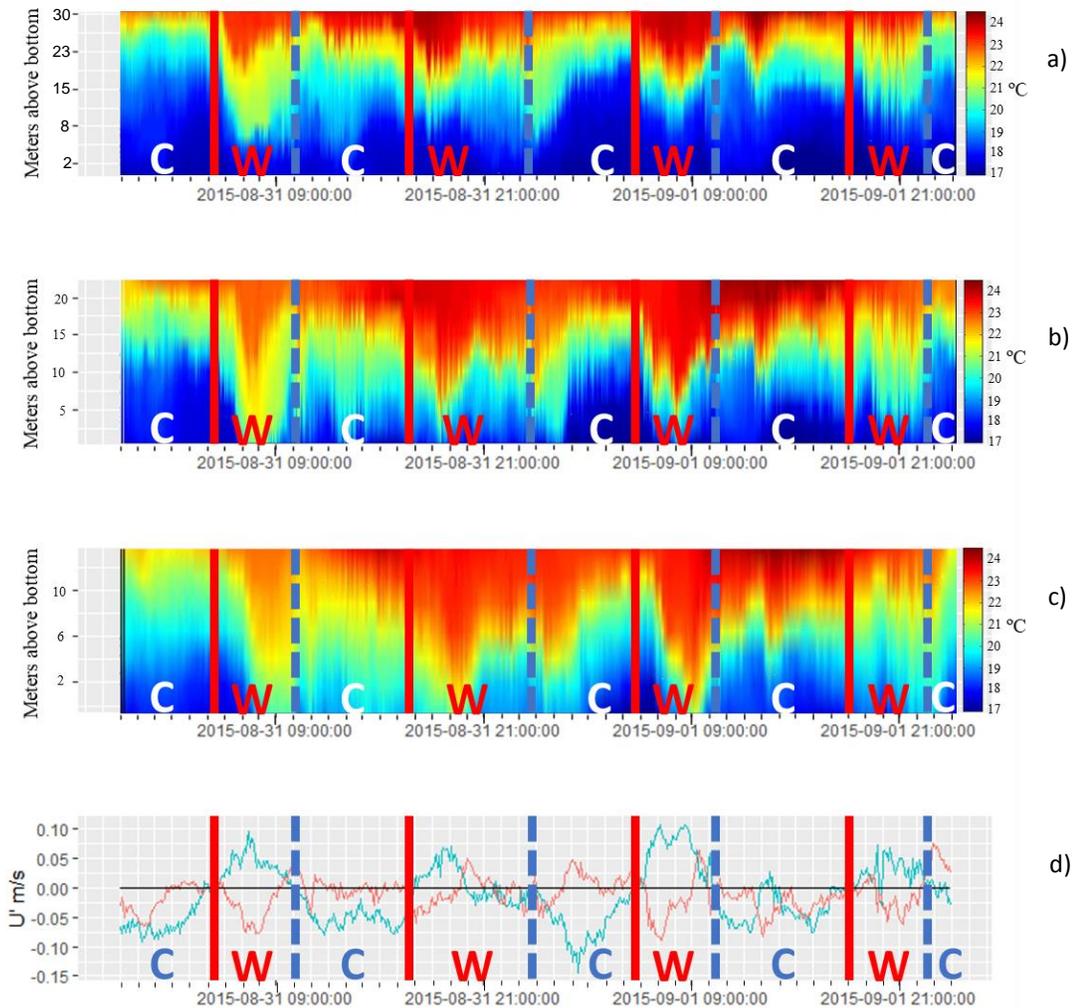


Figure 10. Time series of a) temperature of the water column at the 30 m mooring station; b) temperature of the water column at the 22 m mooring station; c) temperature of the water column at the 15 m mooring station; and d) cross-shore current velocity, u' at 3 m (red line) and 11 m (blue line) above bottom, positive values are onshore flow and negative values are offshore flow.

The progression of internal tidal bores shoreward and upslope was observed across the moorings. The temperature drops at the 30, 22 and 15 m moorings at the mid water depth of 8, 10 and 15 m, respectively, were not in phase, indicating propagation. Time lag was approximately 25 minutes

between stations. For example, at midnight of September 1, the temperature dropped at the 30 m mooring, followed by a similar temperature drop at the 22 m mooring 25 minutes later (Fig. 11). This leads to a bore speed of about 0.46m/s.

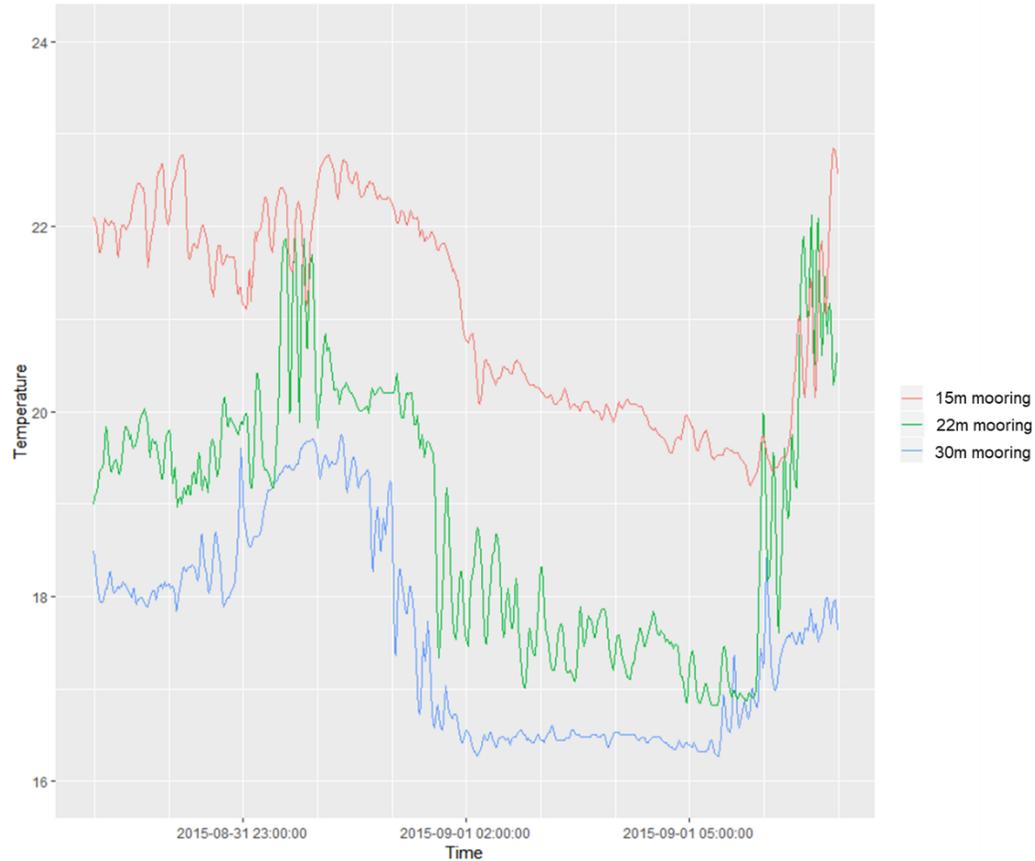


Figure 11. Time evolution of temperature at mid water across mooring stations, at midnight of September 1, 2015. Depths graphed from the 15, 22 and 30 m mooring at 8, 10, and 15 m depth, respectively.

2.4.4 Changes in meroplankton across phases of the internal tidal bore

Changes between strata and phase of internal tidal bores were found for some taxa of meroplankton (Table 4). For cyphonautes, an effect of the strata-phase interaction was seen for the offshore boat, where they were more abundant (Fig. 12). For gastropods and *Crassostrea* spp., there was no effect of strata, but there was an effect of phase, yet only at the inshore boat, where they were more abundant. There was also a tendency for gastropods and *Crassostrea* spp. to be more abundant during the cold phase of the internal tide, with a significant increase only at depth.

Table 4. Factorial analysis of variance (ANOVA) to determine the effect of strata and internal tidal bore phase (cold or warm) on the abundance of meroplankton for each taxon. Sum of squares (SS), degrees of freedom (DF), mean square (MS), F ratio and p values (p) are shown. Significant r-values are shown in red ($p < 0.05$).

Taxa	SS	DF	MS	F	p
Cyphonautes					
Strata	2.56	1	2.56	13.04	<0.01
Phase	0.03	1	0.03	0.15	0.69
Strata*Phase	0.76	1	0.76	3.89	0.04
Error	15.54	79	0.19		
Gastropods					
Strata	0.58	1	0.58	1.88	0.17
Phase	1.26	1	1.26	4.09	0.04
Strata*Phase	0.33	1	0.33	1.08	0.30
Error	18.59	60	0.30		
Crassostrea spp.					
Strata	0.07	1	0.07	0.28	0.59
Phase	1.24	1	1.24	5.01	0.02
Strata*Phase	0.11	1	0.11	0.44	0.50
Error	14.96	60	0.24		

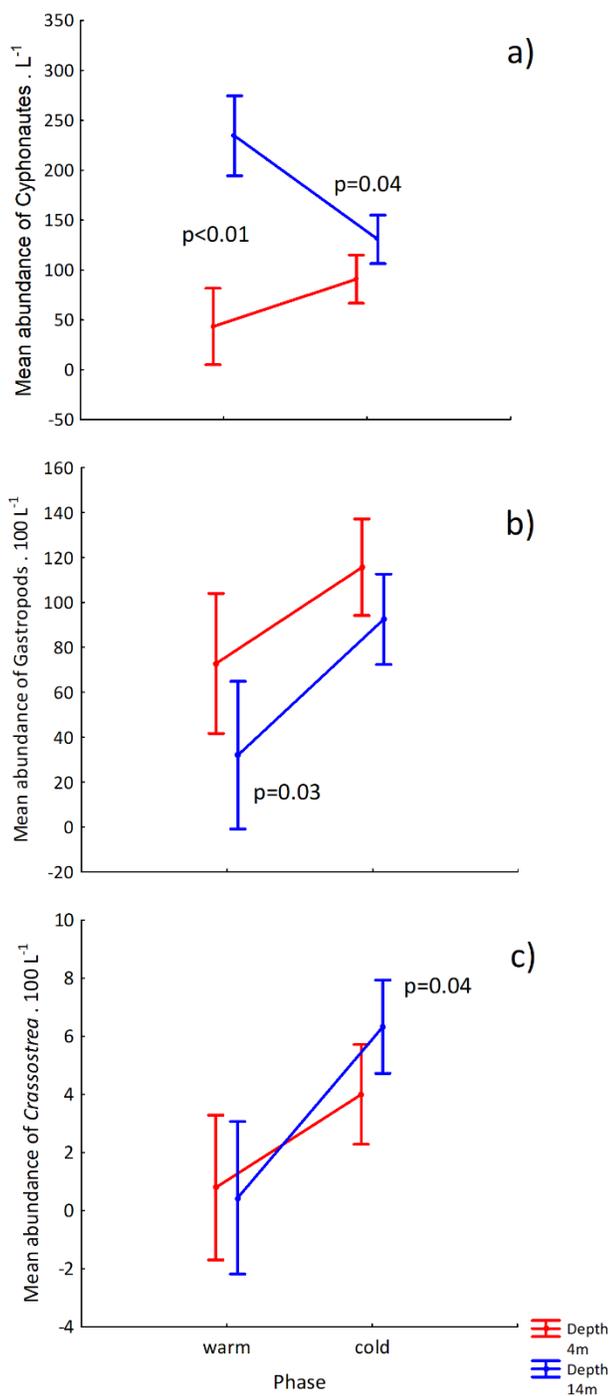


Figure 12. Mean abundance of meroplankters at 4m (red line) and 14 m (blue line) depth at different boats: a) cyphonautes at the offshore boat; b) gastropod late-larvae at the inshore boat; and c) *Crassostrea* spp. at the inshore boat. Error bars: ± Standard Error (SE).

2.5 Discussion

Habitat preference was demonstrated by cyphonautes and gastropod abundances in a cross-shore array of sampling stations (offshore vs inshore), with a lack of synchrony between boats. The sampling stations were separated by 700 m and displayed a different composition of dominant meroplankton species, where cyphonautes were more abundant offshore, with gastropods more abundant inshore. Variability in meroplankton abundance at a certain distance from shore may be related to the location of the adult recruitment habitat.

In this study, for gastropods, the main species found belonged to the coastal organisms that settle in the rocky intertidal and shallow subtidal zones (Byers & Mitton, 1981; Bovbjerg 1984), such as *Nerita* and *Tegula* spp., coinciding with the nearshore distribution of their larvae. For cyphonautes, such as *Membranipora membranacea*, which settle on the blades of the giant kelp *Macrocystis pyrifera*, usually found in deeper waters, their larvae were found at a greater distance from shore. Our results are in agreement with those of Morris et al. (1980), who found that the cyprid larvae of barnacle species that settle in the intertidal zone were found nearer to coast, whereas the larvae of species whose adult habitat was in deeper waters were found further offshore. Also, Hagerty et al. (2018) found that during stratified conditions, like the ones herein, barnacle cyprids tended to concentrate closer to shore, and the horizontal resolution of these changes occurred across a couple hundred meters. Therefore, using our cross-shore array, we can begin to see habitat preferences over very short distances in nearshore waters for some of the species studied, such as for cyphonautes and for gastropods, but not for others. For example, *Crassostrea* spp. showed no habitat preference and its low abundance (least abundant meroplankton) did not change between the sampling stations. Rilov et al. (2008) found for other species of bivalves (e.g., mussels) that the location of the larval pool in the coastal sea was constant with a uniform horizontal distribution, and suggested that it was the vertical distribution of these meroplanktonic organisms that would influence their transport to the coast.

Seasonally, the larval abundance of the two principal meroplanktonic taxa found (cyphonautes and gastropods) occurs in summer (Harvell, 1990). The present study was performed in late August and early September, close to the end of the spawning season, so it was expected that later stages of these larvae would dominate our samples. Almost 95% of the meroplankton in the samples were late-stage larvae corresponding with previous literature that found that larvae in their later stages of development are generally found close to their adult habitat (Tapia & Pineda, 2007; Morgan et al., 2009; Hagerty et al.,

2018). No early or intermediate larval stages were found in the present study, however, it is important to note that in some cases when spawning occurs all year long, such as in the case of some gastropod or barnacle species (Hewatt, 1934), early larval stages (recently advected offshore) and late larvae (concentrated nearshore due to behavior) would be expected closest to the adult habitat. Yet it is important to consider that some larvae might be able to control their horizontal advection on the shelf, thereby staying close to shore during the entire larval phase, even for the mid stages that theoretically should be found further from shore (Hagerty et al., 2018).

During the plankton collections, semidiurnal internal waves were detected propagating across the shore at the 30, 22 and 15-m mooring stations. An alternating pattern of colder and warmer waters occurred approximately every 6 h, with circulation above and below the thermocline flowing in opposite directions, as expected for a semidiurnal mode-1 internal tide. Mode-1 internal waves have been previously observed at this site in the nearshore water column during stratified conditions and strong atmospheric tides (Filonov et al., 2014). This circulation pattern follows the model proposed by Pineda (2000), showing how different phases of an internal bore can theoretically transport larvae to the coast as a function of depth. Bore speed was explored, reaching $0.40 \text{ m} \cdot \text{s}^{-1}$, which is in agreement Connor et al. (in prep), who found bore propagation speeds in the range of $0.20 - 0.50 \text{ m} \cdot \text{s}^{-1}$.

Meroplankton abundance and vertical distribution changed across phases of the internal tidal wave for cyphonautes, gastropods and *Crassostrea* spp., as proposed in the hypothesis. Gastropods and *Crassostrea* spp. aggregated at depth in the cold phase of the internal tidal bore at the inshore site. Both taxa develop geotaxis in the later stages of their larval phase, generally concentrating in deeper strata (Baker, 1997). This ontogenetic preference for a particular stratum is potentially linked with flows that will eventually transport them to a settlement site, helping larvae to achieve survival and reproductive success. Our results are also in agreement with previous studies, which suggest that weakly swimming meroplankton inhabiting mid-bottom waters, such as most of those found in our study, should be subject to changes derived from the activity of internal tidal waves (Pineda, 1991; Leichter et al., 1998; Franks, 1997; Liévana MacTavish et al., 2016). The further understanding of how meroplanktonic taxa respond to internal wave activity in the nearshore ocean is increasingly important as many of these organisms entail important fisheries and a true understanding of their population connectivity is not tractable without understanding how larvae are transported.

Cyphonautes showed vertical stratification during the warm phase, accumulating near the bottom. Pineda (1991, 1999) and Yoshioka (1982) report that *Membranipora* spp. in general tend to be more

abundant near the bottom than at the surface. Also, Pineda (1999) showed that the horizontal distribution of barnacle and *Membranipora* larvae were affected by the passage of internal tidal bores. In the present study, vertical stratification of cyphonautes during the warm phase of the internal tide would be expected as the thermocline is compressed to the bottom during the warm phase. Therefore, cyphonautes being concentrated in the deeper strata, would be expected to increase their stratified distribution. On the other hand, during the cold phase, when bottom waters reach up into the water column, stratification of these organisms might be reduced and they would be more evenly distributed throughout the water column, reducing vertical stratification in their abundances.

Internal tidal bore modulation of organism abundance appears to depend on habitat. Gastropods and *Crassostrea* spp. were affected by the phases of the internal tidal bore at the inshore boat, where they were more abundant, and for cyphonautes the same occurred in the offshore boat. Our results coincide with Liévana MacTavish et al. (2016), who found that the stratum where organisms were more abundant was the stratum where they showed a significant relationship with internal bore phases. Meroplankton may therefore accumulate at depths where they will most likely be affected by current flows. It has been found that when zonal stratification increases, cross-shore currents become more variable and energetic throughout the water column and larvae such as cyprids tend to be found closer to shore (Hagerty et al., 2018), suggesting that stratification can mediate cross-shore currents, and thus larval distributions. Given that conditions for the generation of internal waves are present in coastal oceans worldwide (Cairns, 1967; Lamb, 1997; Shanks & Brink, 2005), the way in which meroplanktonic organisms modify their vertical and horizontal distributions and abundance at the rapid time scales of internal waves may have a much more important role on coastal populations and productivity than previously thought.

Chapter 3. Delivery of meroplankton to the coast during internal tidal forcing and cross-shore winds

3.1 Hypothesis

- The abundance of the zooplankters increases when internal tidal bores reach the surf zone, particularly for taxa in mid-bottom waters.

3.2 Objective

- Identify internal tidal fronts in the nearshore water column using temperature and current data
- Explore the temporal relationship between larval supply to the nearshore with various physical factors (internal tidal fronts, winds and the tide)

3.3 Materials and Methods

3.3.1 Study area

The study was conducted in Playa San Miguel, a rocky wave-exposed beach, located in the northern part of the Bay of Todos Santos, Baja California, Mexico (31° 55' N, 116° 38' W), near Ensenada. The coastline orientation is 47° from geographic true north (facing the southeast) at this shore, and it is classified as a reflective beach due to its steep shore, narrow and energetic surf zone, and narrow beach with large boulders. Summertime conditions are characterized by a highly stratified

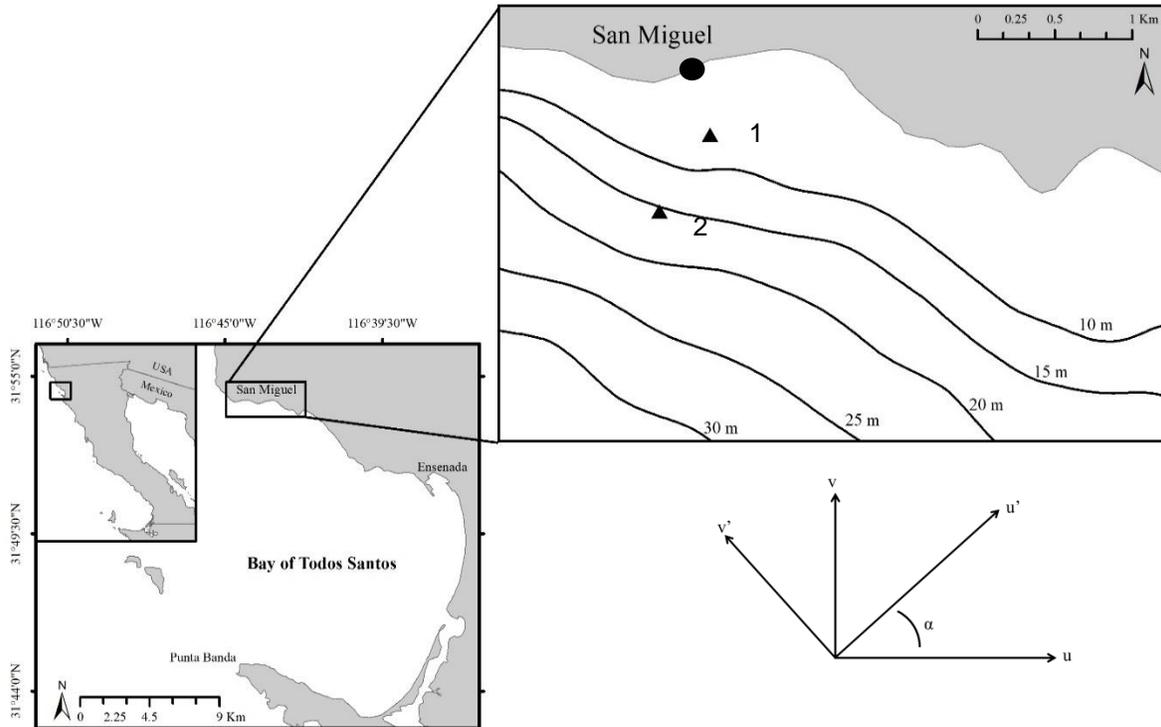


Figure 13. Location of study site in the Bay of Todos Santos. Playa San Miguel (●) is located in the northern part of the bay. Offshore mooring stations 1 and 2 (▲) were located on the 5 and 15 m isobath respectively. A thermistor line was deployed next to each station and an acoustic Doppler current profiler (ADCP) was deployed next to station 2. The north–south current velocity component (v), was graphed against the east–west current velocity component (u), and the major axis u' (rotated $\alpha=42.03^\circ$) indicates the principal current direction either onshore (positive u' values) or offshore (negative u' values).

3.3.2 Data collection

Zooplankton samples were collected every hour in triplicate for three continuous days from August 31 to September 3, 2015, from the low intertidal/shallow subtidal using pumps connected to wide-mouthed hoses (5.08 cm in diameter). One end of the hose was weighted and anchored to sample at 20 cm from bottom. The other end of the hose fed into a nytex (150 μm) mesh bag to collect filtrate (Fig. 14). Pump rates were adjusted and standardized to collect 100 L of water. The contents were filtered and fixed in 92% ethanol immediately after collection. The high-frequency sampling was essential for detecting changes that occur at hourly scales in response to breaking internal tidal waves at the coast.

Identification to the lowest taxonomic level was performed using a stereomicroscope (32x objective). All meroplankton taxa and the most abundant holoplankton taxa were enumerated.

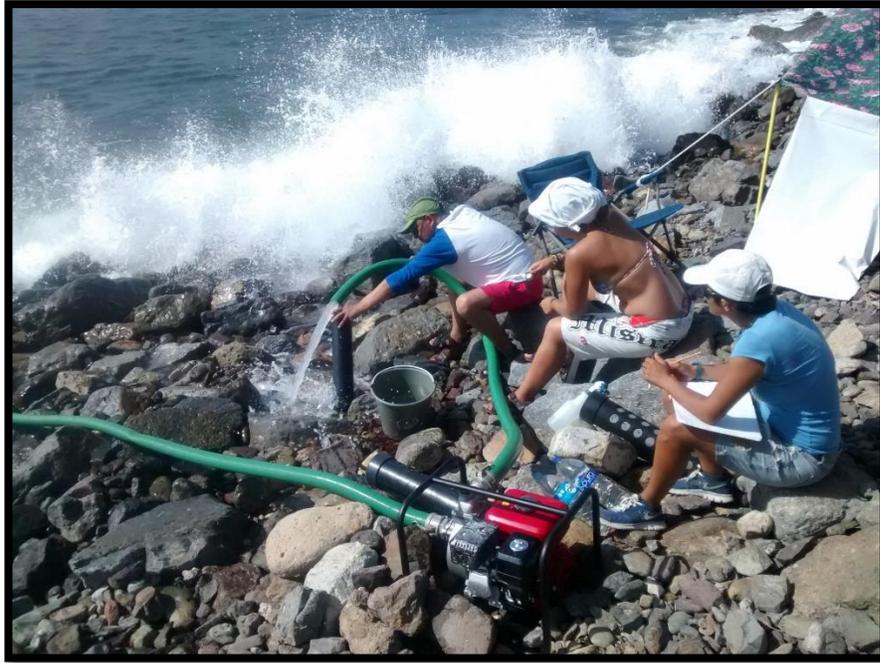


Figure 14. Subtidal zooplankton sampling. A hose was placed to pump water from the subtidal. The other end of the hose poured water into a nytex mesh to filter zooplankton bigger than 150 μm .

A set of instruments and a weather station recorded physical variables near the study area. Temperature of the water column was measured using a vertical array of thermistors (HOBO® Tidbit v2, Onset Computer Corp., USA) deployed every meter at two mooring stations located 450 m and 850 m offshore of the intertidal site, in 5 m and 15 m depth, respectively (Fig. 13). Instruments recorded temperature every minute. This type of array has been used to identify internal waves with periods greater than 10 min at this site (see Ladah et al., 2012; Filonov et al., 2014). Winds were measured every 5 min from the CICESE Observatory at El Sauzal (http://observatorio.cicese.mx/cicese/Current_cicese.htm), located 2 km from the study area. Tidal heights, specific for this bay were provided by the MAR program V 1.0 2011 (<http://predmar.cicese.mx/>) specific for this bay. A 600 kHz acoustic Doppler current profiler (ADCP; RDI workhorse <http://www.teledynemarine.com/workhorse-sentinel-adcp?BrandID=16>) was deployed at 15 m depth set to record every minute in 1-m bins.

3.3.3 Data processing

Rapid temperature changes characteristic of internal waves were explored using the absolute value of the difference of temperature at the 5-m depth mooring every hour to correspond with hourly plankton samples (equation 1), where T_t is the temperature at a time t and T_{t+1hr} is the temperature at one hour later. Temperature data were taken from the 3 m depth thermistor, creating a new time series used in further analyses explained below.

$$\Delta T = |T_{t+1hr} - T_t| \quad (^\circ\text{C}) \quad (3)$$

Wind speeds and directions were decomposed into their Cartesian components u (East-West) and v (North-South). Similarly, current velocity components were decomposed. To calculate the horizontal component with the greatest variability (i.e., principal axis), we used the following equation:

$$u' = u \cos(\alpha) + v \sin(\alpha) \quad (4)$$

The angle between the reference system of u and the reference system of u' for current velocity was α (Fig. 13). Positive (negative) u' current velocities indicate current propagation towards onshore (offshore). For wind speed, the angle between the reference system of u and u' was $\alpha = -21.6^\circ$. Shoreline orientation of the study site is facing the southeast. Thus, the west - northwesterly sea breeze corresponds roughly to cross-shore winds, with positive (negative) velocities indicating onshore (offshore) winds. The v' component of the wind has a north-south principal direction at the study site. Cold and warm phases of the internal tidal bore were detected as rapid changes in temperature that exceeded at least 2°C that lasted longer than 2 hours. In addition, changes in the direction of stratified currents must have been detected.

3.3.4 Data analysis

Because high-resolution measurements were taken over time, autocorrelation in the zooplankton dataset was expected, potentially resulting in non-independence of data. To remove the autocorrelation, we fit an ARIMA model (autoregressive integrated moving average) to the zooplankton data. The

residuals from the ARIMA model were then used in the analysis of variance (ANOVA) and generalized linear models (GLM), to avoid the problem of non-independence. A one-way ANOVA with a $\alpha = 0.05$ was performed to determine differences in the abundance of larvae with *a posteriori* comparisons using a Fisher's least significant difference (LSD) test (StatSoft, Inc. 1984-2005). GLM (with identity link function) were performed, where rapid temperature change (see eq. 1 above), wind speed u' and v' (see eq. 2 above), tidal height and their interactions were used as predictors for zooplankton abundance for every taxon. The Akaike information criteria (AIC), the proportion of the explained Deviance (D_2), and the independence of the residuals from the model (Durbin Watson test), were used as criteria to identify which physical mechanism best explains the variability of zooplankton abundance in the surf zone. Spectral analyses were used to determine patterns in the vertical and temporal variability in the temperature time series at both moorings, and coherence analyses were used to explore the relationship of temperature variability with the tide and the sea breeze. Periodograms of temperature were smoothed to just three frequencies due to the short sampling period (7 d, August 27 – September 2, 2015).

3.4 Results

3.4.1 Internal tidal bores nearshore

Water-column temperature at the 15-m mooring station showed diurnal fluctuations in temperature near the surface, with a stronger semidiurnal signal (12.4 h) below the thermocline and near the bottom (Fig. 15a). Temperature differences between the surface and bottom were over 5 °C during periods of high stratification (Fig. 16d). Cold and warm water fronts alternated approximately every 6 h and coincided with fluctuations of the thermocline and movement of water in opposite directions above and below the thermocline.

Nearer to shore, at the 5-m mooring station, mixing due to breaking internal tidal bores were apparent in the temperature time series, resulting in periods of little to no stratification, that lasted at times longer than the expected 6 h periods (Fig. 16e). For example, on August 31, around 0900 h, the water column temperature was below 21 °C. Following this event, the entire water column warmed, and 4 h later reached above 23 °C. The spectral analysis of the averaged water column temperature at the 5-m

mooring generally showed a weaker peak in the semidiurnal band than the temperature at most depths of the 15-m mooring (Fig. 15b).

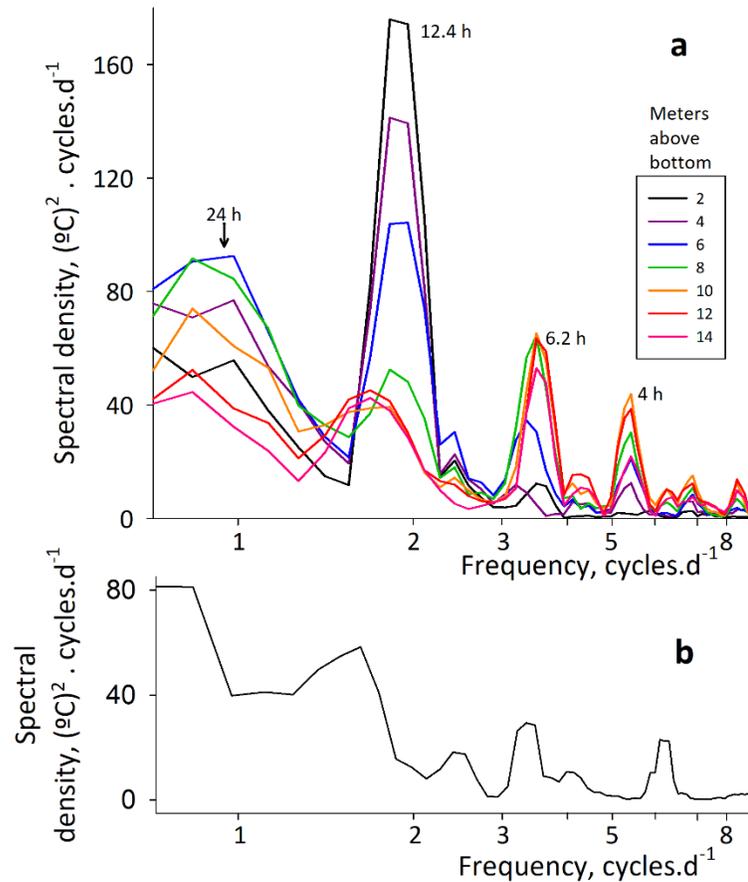


Figure 15. Spectra (periodogram, $\text{cycles} \cdot \text{d}^{-1}$) of temperature at the 15-m mooring (a) and 5-m mooring (b). All depths were averaged for the 5-m mooring.

During the three days of sampling, 12 cold or warm fronts reached the nearshore site (Fig. 16d). The bores were highly non-linear, most of them breaking before reaching the subtidal, resulting in strong water column temperature changes for at least a few hours in most cases. However, on August 31, the strongest change in temperature of the study period occurred and temperature was maintained around 24 $^{\circ}\text{C}$ for a full 16 hours (Fig 16e).

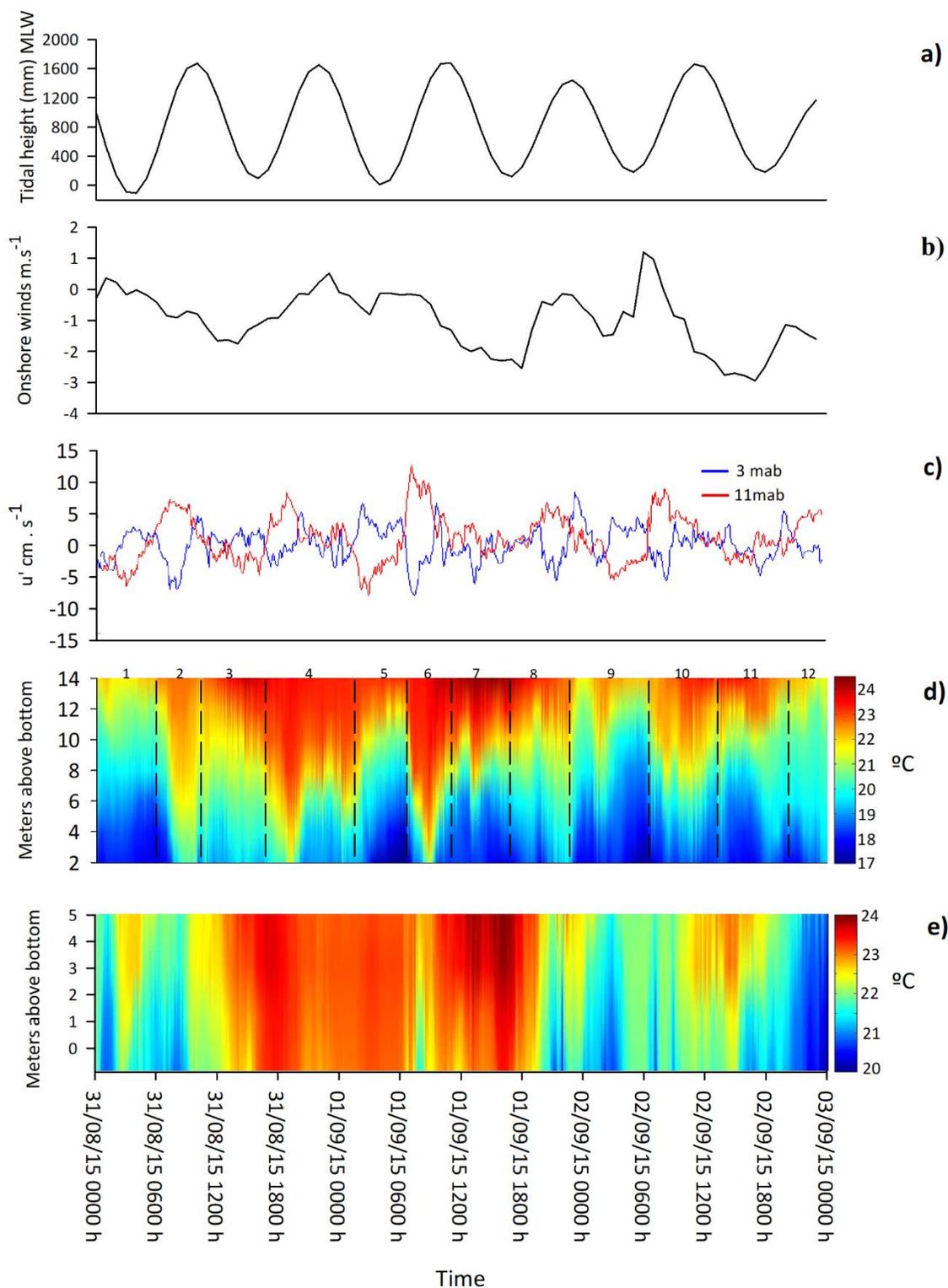


Figure 16. Time series of a) tidal height at San Miguel beach at MLW reference; b) cross-shore wind velocity, positive values are onshore winds and negative values are offshore winds; c) cross-shore current velocity, u' at 3 m (blue line) and 11 m (red line) above bottom, positive values are onshore flow and negative values are offshore flow; d) temperature of the water column at the 15 m mooring station; and e) temperature of the water column at

the 5 m mooring station, warm and cold fronts advecting to the intertidal are numbered and shown by dashed lines (d).

3.4.2 Sea breeze

Cross-shore winds were dominant during our study. Higher wind speeds occurred in the afternoons (Fig. 16b). The offshore component reached a maximum of nearly 3 m s^{-1} while onshore winds only reached 1 m s^{-1} . Water column temperature at the 15-m mooring and the sea breeze were coherent in the diurnal band and in phase near the surface layer (Fig. 17).

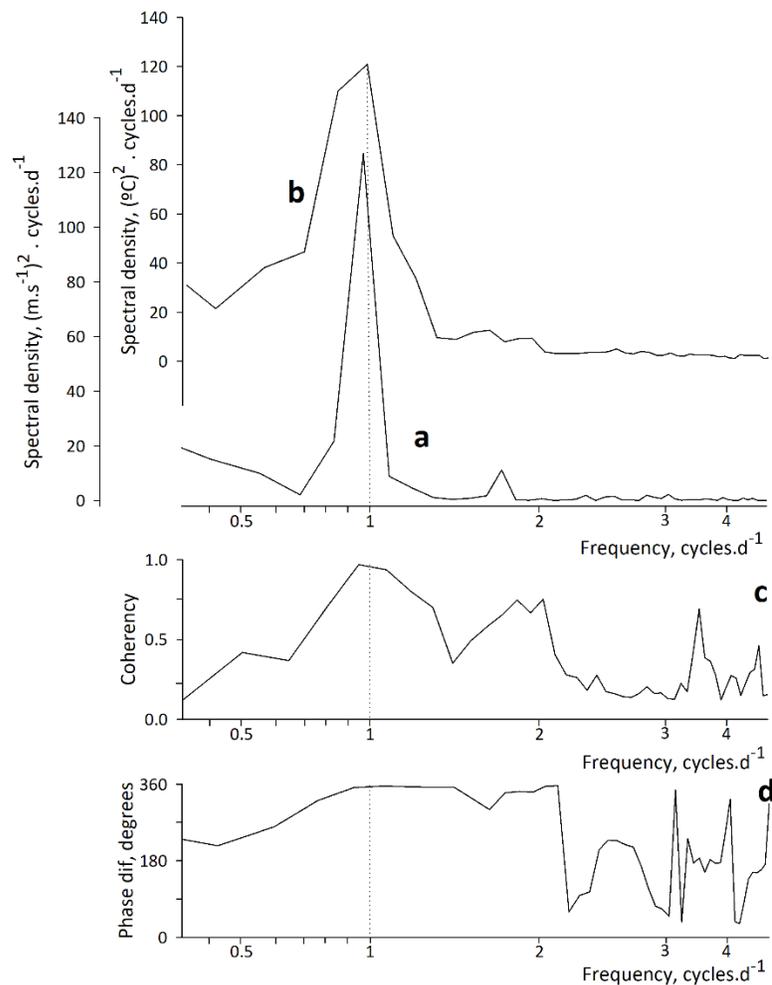


Figure 17. Spectral density (cycles.d⁻¹) of the (a) wind component u' and (b) temperature at 14 m above the bottom (near the surface); (c) coherence and (d) phase difference between the sea breeze (u') and temperature of the surface layer is shown. Vertical dashed lines represent the diurnal band.

3.4.3 Delivery of zooplankton to intertidal

The vast majority (85%) of the enumerated zooplankters were late-stage larvae (Table 5). Gastropods (late larvae) and foraminifera were the most abundant of meroplankton and holoplankton taxa, respectively. Zooplankton arrived to shore in pulses (Fig. 18), with nearly 60% of organisms arriving in a span of 6 hours (1200 h – 1800 h of August 31).

Table 5. Mean concentration (# zooplankters . 100 L⁻¹), standard error (+SE), and percentage of zooplankton collected from 31 August to 3 September, 2015 at San Miguel Beach.

Taxon	Mean	SE	%
Gastropod late larvae	131.96	16.34	76.25
Foraminifera	14.63	3.22	8.46
Ostracods	10.54	1.70	6.09
<i>Mytilus</i> spp. late larvae	7.56	1.71	4.37
<i>Crassostrea</i> spp. late larvae	3.24	0.86	1.87
Cyphonautes	2.98	0.54	1.72
Barnacle cyprids	1.66	0.89	0.96
Larvaceans	0.30	0.17	0.17
Crab zoea	0.11	0.09	0.06
Barnacle nauplii	0.07	0.05	0.04

The General Linear Models (GLM) explained the abundance patterns of gastropods, foraminifera, cyphonautes (bryozoan larvae) and barnacle cyprids (Table 6). For both gastropods and foraminifera, the models that incorporated all of the factors (changes in temperature, cross-shore winds, north-south winds, and tidal height) and their interactions best explained the abundance patterns. However, for cyphonautes and barnacle cyprids, the models that incorporated temperature change, tidal height and only the north-south winds showed the best fit.

The GLM analysis showed that rapid temperature changes, most likely related to tidal bores advecting to the nearshore explained nearly 25% of barnacle cyprid variability (Table 7). Also, the interaction between rapid temperature changes and cross-shore winds played an important role, explaining more than 30% and 25% of gastropod larvae and foraminifera variability respectively. For example, during a warm bore

arrival between 1300 – 1800 h on August 31, over 25% of all zooplanktonic organisms collected during the entire study were found. The tide also explained 10% of the variability of cyphonautes.

Table 6. Summary of the best models representing hypotheses of onshore larval transport at San Miguel beach. Model selection was based on lowest Akaike's information criteria (AIC) criteria and independence of residuals (Durbin Watson [D-W] statistic). Factors used in the candidate models included changes in temperature ($\Delta^{\circ}\text{C}$), cross-shore winds (Wcs), north-south winds (Wns) and tidal height (T). K is the number of parameters included in the model. AIC and results from the Durbin-Watson test are shown.

Taxon	Candidate model	K	AIC	Lag	Autocorrelation	D-W statistic	p value
Gastropod	$\Delta^{\circ}\text{C} + \text{Wns} + \text{Wcs} + \text{T} + \Delta^{\circ}\text{C} \times (\text{Wns} + \text{Wcs} + \text{T}) + \text{Wns} \times (\text{Wcs} + \text{T}) + (\text{Wcs} \times \text{T}) + (\Delta^{\circ}\text{C} \times \text{Wns} \times \text{T}) + (\Delta^{\circ}\text{C} \times \text{Wcs} \times \text{T}) + (\text{Wns} \times \text{Wcs} \times \text{T})$	15	786.94	1	0.04	1.91	0.37
Foraminifera	$\Delta^{\circ}\text{C} + \text{Wns} + \text{Wcs} + \text{T} + \Delta^{\circ}\text{C} \times (\text{Wns} + \text{Wcs} + \text{T}) + \text{Wns} \times (\text{Wcs} + \text{T}) + (\text{Wcs} \times \text{T}) + (\Delta^{\circ}\text{C} \times \text{Wns} \times \text{T}) + (\Delta^{\circ}\text{C} \times \text{Wcs} \times \text{T}) + (\text{Wns} \times \text{Wcs} \times \text{T})$	15	573.12	1	-0.26	2.53	0.09
Cyphonautes	$\Delta^{\circ}\text{C} + \text{T} + (\Delta^{\circ}\text{C} \times \text{T})$	3	332.1	1	-0.02	2.05	0.98
Barnacle cyprids	$\Delta^{\circ}\text{C} + \text{Wns} + \text{T} + \Delta^{\circ}\text{C} \times (\text{Wns} + \text{T}) + (\text{Wns} \times \text{T}) + (\Delta^{\circ}\text{C} \times \text{Wns} \times \text{T})$	7	410.12	1	0.07	1.85	0.33

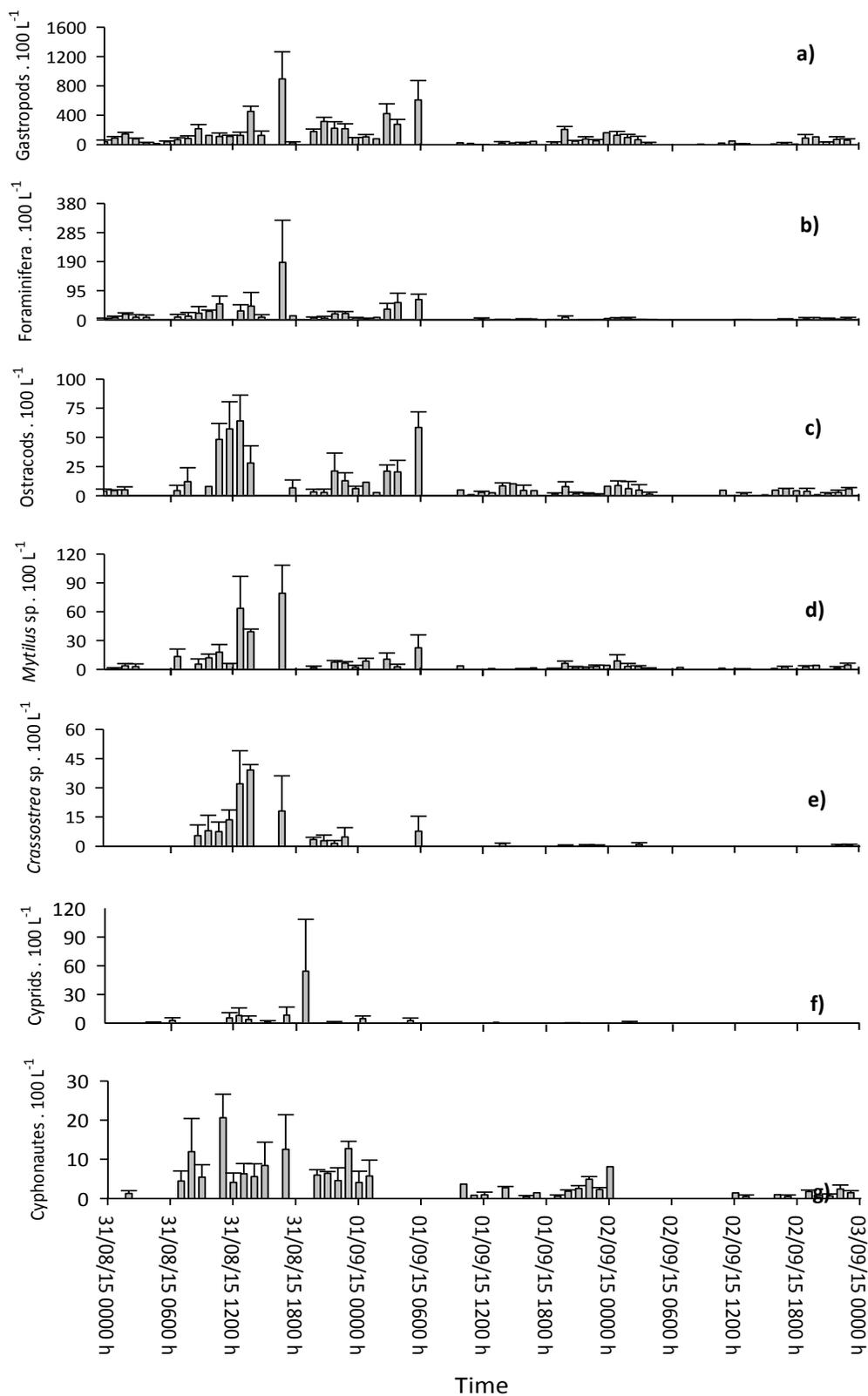


Figure 18. Time series of the most abundant zooplankton taxa, a) gastropods (late-stage larvae), b) Foraminifera, c) ostracods, d) *Mytilus* spp. (late-stage larvae), e) *Crassostrea* spp. (late-stage larvae); f) barnacle cypris; and e) cyphonautes. Error bars: $\pm \text{SE}$.

Table 7. Results from GLM analysis of the effect of physical factors on zooplankton concentrations (gastropods, foraminifera, cyphonautes, and barnacle cyprids). Significant correlations for changes in temperature ($\Delta^{\circ}\text{C}$), cross-shore wind (Wcs), north-south winds (Wns), tidal height (T), and interaction between factors on the concentration of zooplankton at the shore are shown in bold, $p < 0.05$. Percentage of variability (%) explained by the model is shown.

	Estimate	Std. Error	t value	Pr(> t)	%
Gastropods					
$\Delta^{\circ}\text{C}$	64.93	119.94	0.54	0.59	33
Wns	140.58	716.59	0.19	0.84	
Wos	45.24	40.23	1.12	0.26	
T	-0.01	0.04	-0.35	0.72	
$\Delta^{\circ}\text{C} \times \text{Wns}$	-271.84	762.59	-0.35	0.72	
$\Delta^{\circ}\text{C} \times \text{Wcs}$	-169.02	95.75	-1.76	0.08	
$\Delta^{\circ}\text{C} \times \text{T}$	-0.08	0.14	-0.61	0.54	
Wns \times Wcs	495.64	556.99	0.89	0.37	
Wns \times T	-0.13	0.56	-0.24	0.80	
Wcs \times T	-0.02	0.04	-0.44	0.65	
$\Delta^{\circ}\text{C} \times \text{Wns} \times \text{Wcs}$	-1909.91	781.43	-2.44	0.01	
$\Delta^{\circ}\text{C} \times \text{Wns} \times \text{T}$	1.02	0.88	1.15	0.25	
$\Delta^{\circ}\text{C} \times \text{Wcs} \times \text{T}$	0.04	0.12	0.32	0.74	
Wcs \times Wcs \times T	-0.48	0.45	-1.05	0.29	
$\Delta^{\circ}\text{C} \times \text{Wns} \times \text{Wcs} \times \text{T}$	2.35	0.93	2.52	0.01	
Foraminifera					
$\Delta^{\circ}\text{C}$	5.85	20.78	0.28	0.77	25
Wns	77.72	124.19	0.62	0.53	
Wos	11.05	6.97	1.58	0.11	
T	-0.01	0.01	-0.31	0.75	
$\Delta^{\circ}\text{C} \times \text{Wns}$	-93.36	132.16	-0.70	0.48	
$\Delta^{\circ}\text{C} \times \text{Wcs}$	-26.73	16.59	-1.61	0.11	
$\Delta^{\circ}\text{C} \times \text{T}$	-0.02	0.02	-0.83	0.40	
Wns \times Wcs	110.04	96.53	1.14	0.26	
Wns \times T	-0.05	0.09	-0.51	0.60	
Wcs \times T	-0.01	0.01	-0.53	0.59	
$\Delta^{\circ}\text{C} \times \text{Wns} \times \text{Wcs}$	-322.22	135.43	-2.37	0.02	
$\Delta^{\circ}\text{C} \times \text{Wns} \times \text{T}$	0.17	0.15	1.15	0.25	
$\Delta^{\circ}\text{C} \times \text{Wcs} \times \text{T}$	-0.01	0.02	-0.30	0.75	
Wcs \times Wcs \times T	-0.08	0.07	-1.09	0.27	
$\Delta^{\circ}\text{C} \times \text{Wns} \times \text{Wcs} \times \text{T}$	0.35	0.16	2.16	0.03	
Cyphonautes					
(Intercept)	-2.59	1.20	-2.07	0.04	10
$\Delta^{\circ}\text{C}$	2.77	2.25	1.23	0.22	
T	0.01	0.01	2.41	0.01	
$\Delta^{\circ}\text{C} \times \text{T}$	-0.01	0.01	-1.34	0.18	
Barnacle cyprids					
$\Delta^{\circ}\text{C}$	6.54	3.12	2.09	0.04	25
Wns	9.52	10.29	0.92	0.35	
T	-0.01	0.01	-0.35	0.72	
$\Delta^{\circ}\text{C} \times \text{Wns}$	18.99	15.59	1.21	0.22	
$\Delta^{\circ}\text{C} \times \text{T}$	-0.01	0.01	-1.00	0.31	
Wns \times T	-0.01	0.01	-1.00	0.31	
$\Delta^{\circ}\text{C} \times \text{Wns} \times \text{T}$	-0.01	0.01	-0.37	0.71	

3.5 Discussion

Rapid changes in temperature associated with internal tidal bores reaching the coast significantly explained the abundance patterns of late-stage larvae at an hourly scale at this rocky shore. For some organisms, there was also a significant interaction between internal tidal bores and onshore winds. Although these factors have independently been found in other studies to have a significant relationship with larval concentrations or larval settlement (Pineda, 1994; Tapia et al., 2004; Ladah et al., 2005; Shanks et al., 2014), our results support the proposal that for some taxa, both factors might act in concert to deliver larvae to shore.

At the 15-m mooring station, semidiurnal internal waves were detected propagating across the shore. An alternating pattern of colder and warmer waters occurred approximately every 6 h, with circulation above and below the thermocline flowing in opposite directions, as expected for a semidiurnal mode-1 internal tide. Mode-1 internal waves have been previously observed at this site in the nearshore water column during stratified conditions and strong atmospheric tides (Filonov et al., 2014). This circulation pattern follows the model proposed by Pineda (2000), showing how different phases of an internal bore can theoretically transport larvae to the coast as a function of depth.

In contrast, at the 5-m mooring station located 400 m from shore, just offshore of the surf zone, the shallow water column was completely flooded by either colder or warmer waters at a time. Water column temperatures showed little stratification, internal waves did not show the expected mode-1 signature, and there was no clear pattern of alternating warm and cold bores. The semidiurnal frequency typical of internal waves that was found at the 15-m mooring and that has been found previously at this site (Ladah et al., 2005; Ladah et al., 2012; Filonov et al., 2014) was not present in the 5-m mooring data, suggesting that as the internal waves propagated across the shore into shallower water, they broke up and overturned the water column. Warm bores were often strong enough to persist over more than the semidiurnal cycle, as subsequent bores did not replace the warm water that had been mixed onto the shelf. Circulation and retention times of bores in such shallow water have not been well studied and could be important in the delivery and retention of larvae (Mateos et al., 2009; Filonov et al., 2014).

For bryozoans (cyphonautes), the tidal height was the factor that best explained their abundance patterns. Saunders & Metaxas (2010) suggested that onshore transport of cyphonautes occurs during wind-driven downwelling events, however in our study we did not have any such events. Differences found in the delivery mechanism between studies may be related to regional variability in the vertical

distribution of larvae. For example, Saunders & Metaxas (2010) found higher abundances of cyphonautes closer to the surface in Nova Scotia, whereas in California, near our study site, other authors (Bernstein & Jung, 1979; Yoshioka, 1982; Pineda, 1999) found that they occurred below the thermocline in strongly stratified conditions, similar to those shown in the present study (Fig. 16d). The relationship detected between tidal height and abundance of bryozoans suggests that the incursion of water onto the shore by the tide, or some other factor related to the tide, may play a role in their delivery to shore. The different results found for different sites also underscore the importance of vertical position of zooplankters in determining to which transport mechanisms they are exposed (Paris & Cowen, 2004; Hare et al., 2005; Lloyd et al., 2012a).

Internal tidal bores, along with their interaction with onshore winds in some cases, explained the variability of barnacle cyprids, Foraminifera, and late-stage gastropod larvae. Other studies have found that internal motions are capable of delivering zooplankton to reflective shores (Shanks et al., 2014; Pfaff et al., 2015). In the case of barnacle cyprids, internal tides reaching the shore explained 25% of the variability in abundance at the study site, where previous studies found that daily settlement of intertidal barnacles *Chthamalus* spp. has been correlated to either the internal tide (Ladah et al., 2005) or onshore winds (Valencia-Gasti & Ladah, 2016) on different occasions. However, an interaction of both mechanisms has not been documented previously. In the present study, an interaction between onshore winds and internal waves was found for gastropods and Foraminifera for the first time in this area. Previous studies collected meroplankton in the water column far from the coast or entailed intertidal settlement surveys at a daily frequency (Ladah et al., 2005; Liévana MacTavish et al., 2016; Valencia-Gasti & Ladah, 2016), which may be the reason the combination of mechanisms had not been detected. In the present study, we may have been able to identify both mechanisms as important due to the high frequency of sampling and the proximity to the shore, as this was the first time the abundance of zooplankton at the coast was determined at an hourly scale at the Bay of Todos Santos. Also, because the vertical distribution of gastropods and foraminifera species occurs throughout the whole water column when in the nearshore, exposure to both mechanisms of transport to the coast might have occurred (Kuroyanagi & Kawahata, 2004; Lloyd et al., 2012b).

The vast majority of larvae collected at the coast in the present study were in the later stages of development. Larval behavior, related to developmental stage, plays an important role in the horizontal and vertical distribution of these organisms. Larvae can move into different depths to take advantage of stratified currents, thus controlling their cross-shore distribution (Tapia et al., 2010). Larvae may also respond to different environmental cues to change their behavior. For example, cyprids (last larval stage

of barnacles) respond to downwelling in the laboratory by swimming up in the water column (DiBacco et al., 2011). This behavior can help them concentrate in internal bore warm fronts that may transport them to shore, as other authors have found, where strong thermal stratification has been related to a greater abundance of barnacle cyprids closer to shore (Hagerty et al., 2018). It has also been suggested that earlier stages of larvae located throughout most of the water column avoid the coast by detecting turbulence and shear from breaking waves near the coast (Fuchs & Gerbi, 2016; Morgan et al., 2017, 2018), explaining their low numbers in our samples. On the other hand, late stage larvae of many species, including barnacles, crabs, and mussels, are more abundant at the shore (Morgan et al., 2017; Hagerty et al., 2018) as was found herein.

Changes in abundance and vertical distribution of plankton across the shelf have been well documented (Ladah et al., 2005; Shanks, 2006; Shanks et al., 2014; Valencia-Gasti & Ladah, 2016; Mactavish et al., 2016); however, there is limited information on the delivery of larvae to the coast, especially at reflective rocky shores. In situ sampling and numerical simulations of larval transport have been performed to better understand the process (Fujimura et al., 2014; Morgan et al., 2016), yet much still unknown. The present study represents a valuable step in comprehending how internal tidal waves and onshore winds may assist in transporting different species of larvae to shore at an hourly scale.

In the present study, delivery processes were consistent with the vertical distributions of zooplankton in the water column. These patterns may vary seasonally with wind variability and stratification of the water column, which is necessary for internal tidal motions during the year. It should be noted that the dataset is only 3 days long, hence the results, although statistically significant, are an early approach in understanding the delivery of larvae in the Bay of Todos Santos shores. The present study supports the hypothesis that internal tidal bores reaching the coast in summer, when the water column is strongly stratified, in concert with onshore winds, can accumulate zooplankton nearshore, suggesting that in many cases and for many organisms, these transport mechanisms do not act alone.

Chapter 4. Conclusions

4.1 Summary

This thesis represents one of the firsts efforts to understand the role of internal tidal bores in the journey that larvae must undergo over the last 2 km before reaching the shore. The study was conducted in an area where internal tidal wave propagation changes from alongshore to across shore as the coast is approached. Previous studies in the Bay of Todos Santos have looked at larval distribution further offshore or settlement in the intertidal zone (Ladah et al., 2005; Liévana MacTavish et al., 2016; Valencia-Gasti & Ladah, 2016). Therefore, studying the physical processes and larval distributions between the offshore environment and the coast, which was the purpose of this thesis, was a logical next step to better understand the intricate link between planktonic larvae and benthic adult populations.

Habitat selection of meroplanktonic species as they approach to coast was explored. The cross-shore array of stations helped differentiate the habitats of gastropods, cyphonautes (Chapter 2) and barnacle cyprids (Chapter 3). Gastropods and cyphonautes were the most abundant meroplanktonic taxa at the 3 stations (offshore, inshore, and coastal). Their dominance in the larval samples might be because the sampling period coincided with the reproductive season during summer. However, they were not evenly distributed. Gastropod abundances increased as they approached the coast and cyphonautes were more abundant at the offshore stations, decreasing shoreward. In the case of barnacle larvae, early phases were not found in any of the boat samples, however, cyprids (the later stages) were present at the coastal site, very close to the adult habitat in the intertidal zone, which would be expected as they prepared for settlement. In general, a clear differentiation of habitat can be seen for most of the larvae studied in this thesis (Fig. 19).

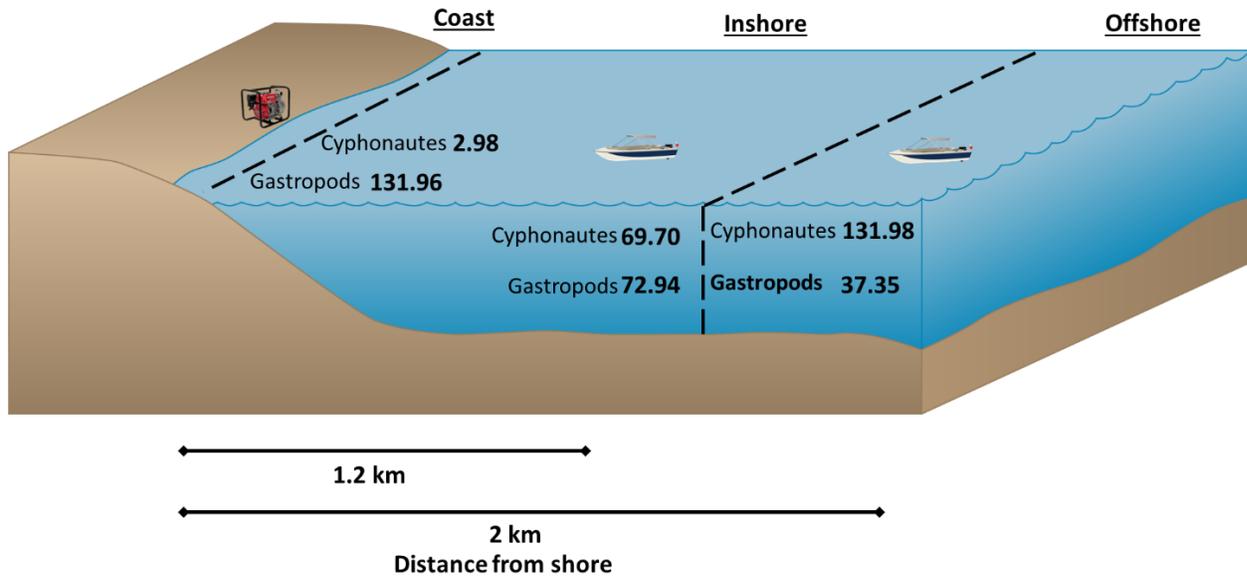


Figure 19. Mean abundances of cyphonautes and gastropods from the offshore boat to the coast. Image modified from: Tracey Saxby, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

From the physical data, we can see that propagation shoreward of semidiurnal internal tidal bores dominated the temperature and current fields, especially from the midwater to the bottom, in the coastal array of sampling stations, and were most likely responsible for aggregating organisms at different sites depending on their habitat preferences (Fig. 20). Cold/warm phases of the internal tidal wave propagated across both boats (sampling sites) to finally shoal and mix the water column between the 15 m station and the 5 m station (Fig. 21), producing changes in temperature that were out of phase with the bores further offshore. Near the boat sites, different phases of the bore appeared to play an important role in aggregating and transporting larvae. Cyphonautes were concentrated at depth during the warm phase only at the offshore boat site, where they were most abundant. On the other hand, at the inshore boat site, Gastropods were more concentrated at depth during the cold phase of the internal tidal bore. Gastropods also appeared to be delivered to the coast by an interaction between changes in temperature related to breaking internal tidal bores and onshore winds. This is the first time that an interaction between both forcing factors has been found as a mechanism of delivery at a coastal site. Barnacle cyprids were found only at the coastal site and peaks in abundance were related to breaking internal tidal waves at the shore.

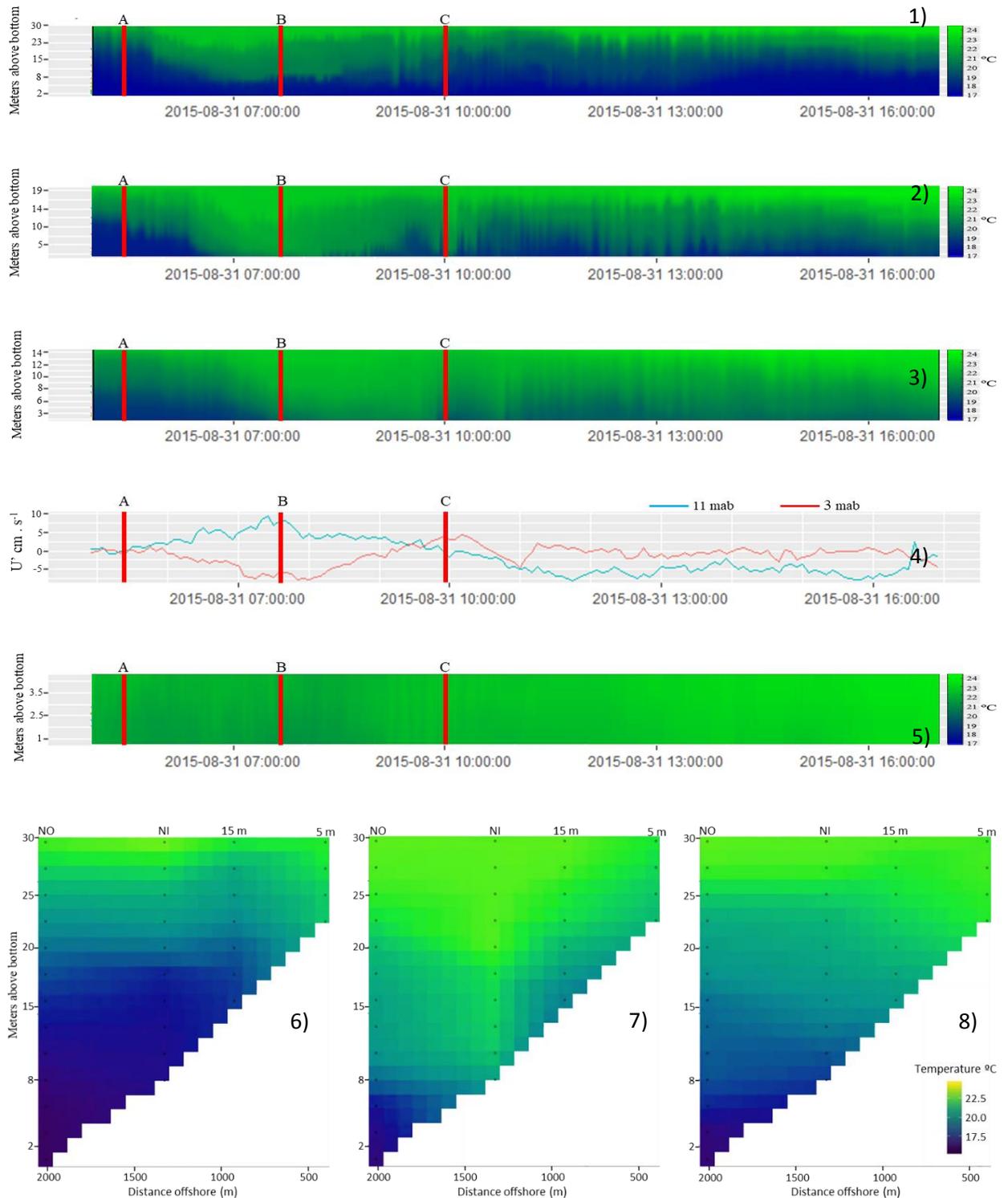


Figure 20. Propagation of the different phases of the internal tidal bore across the shelf. Time series of temperature of 1) 30 m, 2) 22 m, and 3) 15 m mooring stations; 4) cross-shore current velocity of the 15 m mooring station, u' at 3 m (red line) and 11 m (blue line) above bottom, positive values are onshore flow and negative values are offshore flow; 5) temperature of the water column at the 5 m mooring station. In panels 1), 2), 3), and 5), different moments of the phases of the internal tidal bore are shown in vertical lines: before the arrival of the warm phase (A), during the warm phase (B), and during the start of the cold phase (C). Panels 6), 7), and 8) represent the cross-shore spatial representation of the temperature for A, B and C moments respectively.

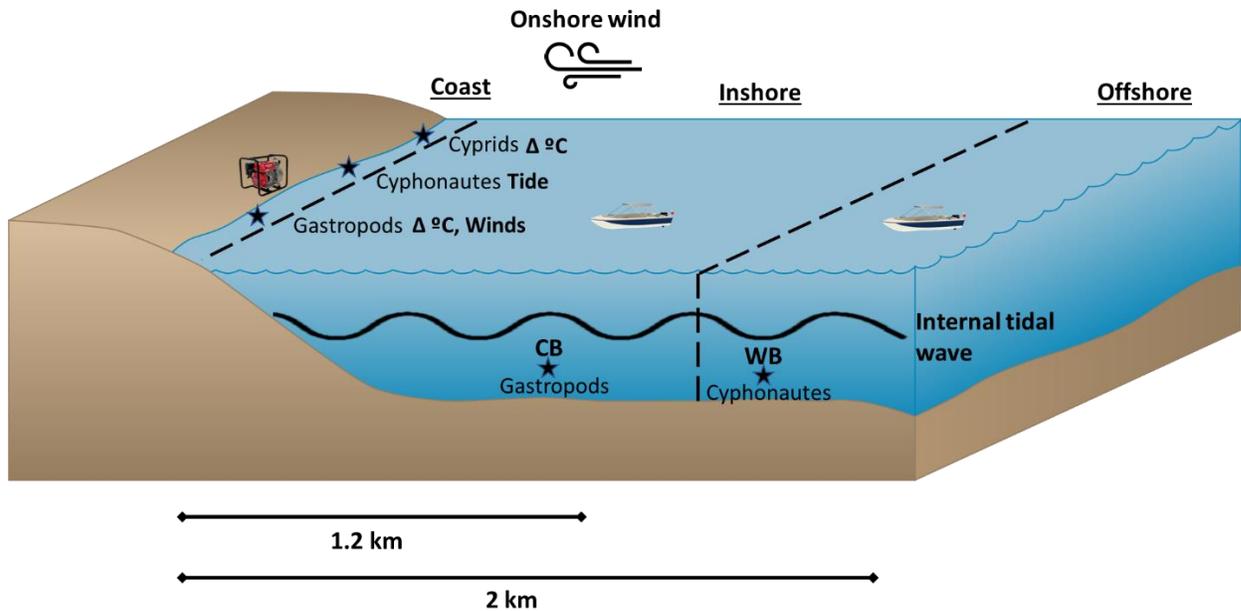


Figure 21. Mechanisms of accumulation of meroplankton through the shelf. Warm bores (WB), Cold bores (CB), Winds, Tide, or Changes in temperature (Δ °C). Image modified from: Tracey Saxby, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

In conclusion, during summer conditions in the Bay of Todos Santos, internal tidal bores played an important role in aggregating and delivering different taxa of meroplankton in the very nearshore ocean depending on their depth and cross shore distribution. As internal tidal bores start to dissipate during their coastal approach, interaction with other physical mechanisms may become important to assist larvae to reach their final destination at a coastal adult habitat.

The results of this thesis further emphasize the complicated impact that internal waves might have on structuring intertidal communities. Internal waves are strongly linked to temperature and ocean stratification, and because many of the fished and commercial species begin their life as meroplanktonic larvae, it is crucial to explore these interactions further under different climate change scenarios.

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