High frequency (hourly) variation in vertical distribution and abundance of meroplanktonic larvae in nearshore waters during strong internal tidal forcing

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ABSTRACT

We related the vertical distribution and abundance of nearshore meroplankton at hourly time scales with internal tidal wave events. We proposed that significant changes in plankter abundance would occur across internal tidal fronts, and that surface and bottom strata would respond in opposite fashions. First-mode internal tidal bores propagating in the alongshore direction were detected in water-column currents and baroclinic temperature changes. Surface and bottom currents always flowed in opposite directions, and abrupt flow reversals coincided with large temperature changes during arrival of bores. Crab zoeae and barnacle cyprids were more abundant in the bottom strata, whereas barnacle nauplii showed the opposite pattern. Significant changes in vertical distribution and abundance of target meroplankters occurred across internal tidal fronts, especially for crabs at depth, with surface and bottom organisms responding in opposite fashions. Changes in plankter abundance were significantly correlated with current flows in the strata where they were most abundant. The manner in which plankters were affected (increasing or decreasing abundance) appeared to be modulated by their vertical position within the water column. The significant differences found at the high frequencies of this study, maintained across sampling days, suggest that nearshore meroplankton populations may have greater and more consistent temporal and vertical variability than previously considered.

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1. Introduction

The life history of many species of benthic marine invertebrates entails a series of ontogenetic larval stages, during which individuals reside at different depths within the water column and at varying distances offshore of their natal sites. Pelagic larvae of benthic invertebrates must eventually return to an appropriate intertidal or subtidal habitat to metamorphose into benthic juveniles and recruit to adult populations. The return of pelagic larvae to shore is dependent on oceanographic processes implicated in transport and on the horizontal and vertical distribution of larvae in the water column, which is, in part, controlled by larval behavior (e.g., Scheltema, 1986; Eckman, 1996; Shanks, 1995, 2006).

Both larval transport, defined as the translocation of larvae from one point in the ocean to another (Pineda et al., 2007), and larval dispersal, defined as the geographic range between spawning site and settlement site (Pineda et al., 2007), are restricted by the total amount of time that larvae may remain in the plankton, which is species dependent (e.g., McEdward, 1995; Shanks, 1995; Shanks et al., 2003). Biological limits to the time spent in the plankton suggest that larvae have evolved to regulate their horizontal distance from suitable settlement sites by modifying their vertical distribution in the water column (Shanks et al., 2003). As larval dispersal distances differ by at least six orders of magnitude between species (Gaines et al., 2007), it is likely that different meroplankton species will accumulate in offshore larval pools at different distances from the coast and with different vertical distributions.

As swimming behavior alone cannot account for the larval transport distances of the majority of meroplanktonic species, the horizontal translocation of planktonic larvae relies on physical mechanisms of alongshore and cross-shore transport (e.g., Shanks, 2006; Pineda, 1999; Lamb, 1997). Both ciliated and non-ciliated meroplankton may be able to exploit different flow regimes by...
changing their vertical position in the water column via swimming or buoyancy in order to take advantage of different horizontal flows (Shanks, 1995; Lamb, 1997). The suite of cross-shelf transport mechanisms available to meroplankton will therefore result in transport of different magnitudes and directions, depending on the vertical position larvae occupy within the water column, which varies between species and between ontogenetic stages (Pineda, 1991, 1994; Shanks, 1995).

Of the various transport mechanisms operating within the California Current system that have been hypothesized to account for the onshore transport of meroplankton, three have received significant attention in the literature. Ebert (1983) proposed transport by the relaxation of wind-forced upwelling, while Shanks (1983) proposed the onshore transport of neustonic larvae via surface slicks associated with propagating internal waves. A third mechanism, and the focus of this study, is transport by internal tidal bores (Pineda, 1991).

Cross-shelf transport by internal tidal bores, or breaking internal waves, is intriguing as this transport mechanism operates on shorter temporal scales than others (e.g., Cairns, 1967; Pineda, 1991, 1994, 1999; Leichter, 1996; Leichter et al., 2005). Internal waves and bores are important in linking the offshore and onshore environments (e.g., Shanks 1987; Shanks et al., 2003; Leichter et al., 2003) and the conditions needed for their generation are found in waters on every continental shelf (Shanks, 1995; Leichter et al., 2005). In coastal oceans, the degree of stratification is often highest along a primary pycnocline, which acts as a path upon which internal waves travel (Leichter et al., 2005). Internal tides, internal waves at a tidal frequency, are thought to play an important role in cross-shelf transport, not only because of their near ubiquitous presence in coastal oceans (Leichter et al., 2005), but also because they are very energetic in the cross-shore direction (Pineda, 1994). Internal tidal bores occur when energetic propagating internal waves shoal and break, causing internal surf and resulting in strong current surges with accompanying large changes in temperature (e.g., Pineda, 1994).

As internal bores propagate, they may be recognized in time series of water-column temperature data by large temperature changes on the order of 2–5°C that occur over times scales of minutes (Cairns, 1967; Pineda, 1991). The depth at which the most abrupt temperature change occurs can indicate the size of the bore event, with only large-event bores showing cold temperatures throughout the entire water column (Cairns, 1967; Pineda, 1991). As such, changes in surface water temperatures due to large-event bores are capable of producing upwelling events of short duration (hours) by bringing water from below the thermocline to the surface (Pineda 1991; Leichter, 1996). These water column changes can result in elevated concentrations of plankton and dissolved nutrients, sometimes orders of magnitude higher than background levels (Leichter et al., 1998, 2003; Ladah et al., 2012).

Pineda (1994) proposed a two-phase system to explain internal tidal bores. During the first phase, warmer, lighter waters are displaced offshore by the upwelling of cold, heavier water moving onshore, resulting in a front at the surface separating warmer surface water, offshore, from cooler surface water, onshore. This condition results in an imbalance in hydrostatic pressure and is unstable. Due to this instability, gravity currents result from the dense nearshore water sinking and moving offshore, which is followed by the subsequent onshore advection of warm surface waters (Pineda, 1994). This reversal of water flow at the surface and near the bottom marks the transition to the second phase of an internal tidal bore. Observations suggest that warm events follow large internal tidal bores (Pineda 1991, 1994). It has been proposed that the first phase of an internal tidal bore transports water-column taxa to shallower depths onshore (Pineda 1991; Leichter 1998), whereas the second phase is proposed to transport neustonic larvae onshore (Pineda, 1994). Given the nature of horizontal flows during an internal tidal bore event, the transport direction and any change in abundance of planktonic organisms should depend on the vertical distribution of the plankters in the water column.

Due to the importance of the vertical distribution of meroplanktonic larvae in their cross-shelf transport, settlement and eventual recruitment, this work aimed to evaluate high-frequency changes (sampling every 20 min at 3 depths, resulting in an hourly sample for each strata) in the vertical distribution of target meroplankters (crabs and barnacles) during a period of strong internal tidal forcing in summer, when many larvae settle and recruit to nearshore populations. We proposed that significant changes in plankter abundance would occur across internal wave fronts and that plankter abundance in the surface and the bottom strata of the nearshore water column would respond in an opposite fashion, correlated with opposite flows of the bore.

To our knowledge, this is one of the first attempts to study changes in meroplankton abundance that occur while internal waves are propagating in the alongshore direction. Internal wave systems that propagate alongshore may be of special importance for transporting meroplankton into semi-closed coastal areas, like bays, however little work has been undertaken to evaluate their importance. Understanding how the vertical distribution of these important taxa change during the internal tide can help elucidate specific transport mechanisms important in supply-side ecology and eventually lead to a better understanding of recruitment and population dynamics of nearshore benthic invertebrates.

2. Materials and methods

2.1. Study site

Playa San Miguel (Fig. 1) [31°55′N, 116°38′W], in the northern part of Todos Santos Bay, Baja California, Mexico, is a rocky shore exposed to wave action, especially during the winter months; during the spring, NW winds result in upwelling, while a strong semi-diurnal internal tide predominates during summer months when the water column is highly stratified (Ladah et al., 2005; 2012; Filonov et al., 2014). Amongst the marine invertebrates in the area, red urchins (*Mesocentrotus franciscanus*), purple urchins...
(Strongylcentrotus purpuratus), the barnacles Chthamalus spp. and Balanus glandula, crabs such as Loxohynchus spp., Pugettia spp. and Cancer spp., and the bryozoans Membraniopora membranacea are common.

2.2. Oceanographic data collection and processing

As part of the Fluxes Linking the Offshore with the Onshore (FLOO-09) project, two nearshore sampling points within 40 m of each other were sampled during daylight hours for at least four full cycles of the semidiurnal internal tide: N3 (31°53.525′N, 116°44.470′W) and N4 (31°53.38′N, 116°44.635′W), in 22 m and 30 m of water, respectively (Fig. 1). At both points, a vertical array of thermistors spaced vertically every 2 m along a line, and programmed to record temperature every minute. These thermistors have an accuracy of ± 0.21 °C, a response time of 5 min in water, and a stability (drift) of 0.1 °C per year according to the user manual. Internal tidal fronts were defined as temporal changes in temperature that exceeded 2 °C in less than 1 hour at 5 m depth and that persisted for at least 2 hours, during the internal tidal wave or bore. In addition, cold water pulses were defined as temperatures less than or equal to 15 °C at 9 m depth that persisted for more than two hours.

An Acoustic Doppler Current Profiler (ADCP) was installed at the N4 site. Current profiles of the water column at N4 were produced by averaging the ADCP data into one meter depth bins using data collected every minute, thus producing time series that coincided with the temperature measurements taken with the thermistors. Current velocity was measured via three components: \( u \) oriented east–west, \( v \) oriented north–south and \( w \) oriented vertically. From \( u \) and \( v \), the horizontal component of the current velocity with greatest variability was calculated with the following equation:

\[
u' = u \cos(a) + v \sin(a)
\]

The angle between the reference system of \( u \) and the reference system of \( u' \) is shown by \( a \). Positive \( u' \) current velocities indicate alongshore current propagation at San Miguel, to the southeast, towards the interior of the Todos Santos Bay, while negative \( u' \) velocities also indicate alongshore propagation at San Miguel, but to the northwest, or away from and out of Todos Santos Bay (Fig. 1). The time series of the integrals of \( w \) and \( u' \) were low-pass filtered (Butterworth filter, 10 cph) and then used to evaluate the relationship between the movement of the water and changes in the abundance of meroplankton.

Internal wave phases were defined as phase \( a \) or \( b \), based on the model of a two-phase internal tidal bore (Pineda, 1994) propagating in the cross-shore direction but adapted to the unique conditions observed at San Miguel. At this study site, the direction of propagation of internal waves is alongshore and the Pineda (1994) model for cross-shore internal tidal bores had been adapted as follows: the first phase of an internal tidal bore (\( a \)) at San Miguel is characterized by bottom currents propagating towards and into Todos Santos Bay while surface currents propagate out and away from the bay; during the second phase (\( b \)), currents at the surface and bottom invert and propagate in the directions opposite to those of first phase (\( a \)).

2.3. Zooplankton sampling and identification

Zooplankton was sampled at N3 and N4 via a conical sampling net (150 μm mesh, 1.5 m long, with a ring diameter of 0.5 m) equipped with a messenger system that permitted the net to be closed underwater, thus allowing different strata of the water column to be sampled independently. The water column was divided into three strata: surface (surface – 6 m), midwater (6–15 m), and bottom (15 m – bottom). The net was allowed to rest open at the base of the strata for 1 min, then pulled to the top of the desired strata, closed, and subsequently pulled to the surface. Samples were fixed immediately in 4% formaldehyde. The water volume sampled was estimated by a flowmeter attached to the center of the net. Zooplankton was sampled approximately every 20–30 min, which resulted in a sampling frequency of approximately one hour for each strata. This high-frequency sampling was essential for detecting changes in the vertical distribution of zooplankton that occurred across the fronts at short time scales.

Identification of zooplankton samples was carried out in the laboratory and organisms were identified to the lowest taxonomic level possible. However, only two larger taxonomic groups were utilized for data analysis: barnacles and crabs. Barnacle larvae were represented by late-stage nauplii and although some cyprids were present, cyprid abundance comprised a very small percentage of the total (< 0.05%), and were excluded from analysis. Crab zoeae included representatives from the families Brachyura and Porcellanidae.

Data were expressed as abundances which were normalized for amount of water filtered. In order to compare general patterns among different taxa, the number of larvae sampled at each time and depth was converted to a mean percent of abundance by dividing the number of larvae at each depth by the total number of larvae at all depths for that sampling period at that site, yielding percentage data independent from overall abundance, and therefore allowing for an improved comparison between different days and taxa (Pineda, 1999).

2.4. Data analysis

Cochran’s test of homogeneity of variance was implemented before statistical tests were carried out (Underwood, 1997). An ANOVA was used determine the effects of taxa, strata, and internal wave phase (\( a \) or \( b \), as previously defined) on the abundance and mean percent of meroplankton. Multiple post-hoc comparisons were carried out via Fisher’s LSD test. In addition, correlation analyses were carried out to evaluate the relationship between the time series of meroplankton abundance for each taxa and strata, and the time series of current velocities in each strata.

3. Results

3.1. Oceanographic conditions

The internal waves observed at San Miguel propagate along the shore, resulting in a system that may not follow the biological predictions of Pineda’s (1994) model for cross-shore internal tidal bores. In the San Miguel system, it would seem that the interior of the bay, which does eventually get shallower, may be analogous to the shore in the Pineda (1994) model, while the exterior of the bay would then be analogous to the offshore environment described by the model.

During morning zooplankton collections, a cold-water pulse was detected reducing water-column stratification at both the N3 and N4 stations. The cold water pulse observed at N4 on the 19th of August ended at 9:48 h, while at N3 on the 20th of August the cold water pulse observed ended at 10:52 h (Fig. 2). Following each cold-water pulse, the temperature of the water column abruptly increased, fronts were detected, and the water column became highly stratified. After the fronts were detected, the direction of currents at the surface changed from a northwestern
flow, out and away from Todos Santos Bay, to a southeastern flow, towards and into the bay; with opposite current inversions observed in the bottom portion of the water column at both sites (Fig. 2). The observed changes in current direction coupled with the change in water column temperature marked the transition from internal wave phase a to phase b. This sudden change in water column conditions, particularly in temperature and currents, is characteristic of internal tidal bore activity (Pineda, 1994).

3.2. Vertical and across front changes in meroplankton abundance

In general, there were more target meroplankters found in the deeper strata, driven mainly by crab zoeae, which presented significantly greater abundance in the bottom strata at all sampling times and stations, whereas barnacle nauplii showed the opposite pattern with greater abundance at the surface, and a lower overall abundance (Figs. 3 and 4, Table 1). Cyprids, although found in very low abundances throughout the study, were more abundant in the bottom strata (3.6 individuals per m³ in the deeper strata versus 0.33 and 0.29 per m³ in the midwater and surface strata).

Across internal wave fronts between phase a, which tended to be cold and stable, and phase b, which tended to be warm and variable, the abundance of crab zoeae in the bottom strata dropped significantly, with an overall pattern of double the abundance in phase b versus phase a of the internal tidal bore (Fig. 5). Barnacle nauplii showed no significant change in abundance across fronts (Fig. 5). However, when mean percent of abundance was analyzed, both crab zoeae in the bottom strata and barnacle nauplii in the surface strata, showed significant and opposite changes across fronts, with crabs decreasing and barnacle nauplii increasing from phase a (cold) to phase b (warm) of the internal bore (Fig. 5). Cyprids were not analyzed due to their very low abundances.

The magnitude of change across fronts in the mean percent abundances of barnacle nauplii and crab zoeae was greatest in the strata where each presented their highest abundances, and similar between taxa (about 20%), with barnacle nauplii increasing significantly at the surface and crab zoeae decreasing significantly in the bottom strata during phase b of the bore (Fig. 5). Using mean percent abundance, rather than abundance, allows for comparison between different study periods, normalizing differences in abundance between different sampling days and different taxa.

The increase in barnacle nauplii abundance was significantly correlated with southeastern current flow at the surface for all samples \( r = 0.94, p < 0.01 \), the strata where they had their highest abundances. The opposite pattern was found for crab zoeae in the bottom strata, where crabs were most abundant, with a significant decrease in abundance occurring after the appearance of the front.
and the subsequent current inversion, which was significantly correlated with northwestern current flow in the bottom strata for all samples (r = 0.90, p < 0.01).

4. Discussion

In this study, the abundance of meroplankton in the water column changed significantly at an hourly frequency, in particular across internal tidal fronts, as proposed. Changes in meroplankton abundance across internal tidal fronts has been previously suggested (Ewing, 1950; Zeldis and Jillet, 1982; Shanks, 1983; Pineda, 1991, 1994) and this process has been modeled as well (Franks, 1997; Helfrich and Pineda, 2003; Scotti and Pineda, 2007). Empirical data presented by various studies (Zeldis and Jillet, 1982; Kingsford and Choat, 1986; Pineda, 1999; Mattos and Mujica, 2012) also show that there can be large changes in zooplankton abundance across fronts in the nearshore ocean. Our results support these findings. Furthermore, our results show, as proposed, that changes in meroplankton occur in a unique fashion in different strata of the water column, and that the changes observed are correlated with horizontal flow in those strata. These results further emphasize that zooplankton experience vertical changes in their abundances at very short temporal scales dependent on their depth distribution, and are thus subject to changes in horizontal flows which likely result in their transport.

The results of this study are in agreement with the results obtained by Lennert-Cody and Franks (1999) who predicted that weakly swimming planktonic organisms would be subject to transient changes in abundance resulting from internal wave activity and with results obtained from Scotti and Pineda (2007) who suggested that plankton concentrations may not only vary before and after a front, but along the front as well. The implication from the work of Scotti and Pineda (2007) is that establishing clear-cut relationships between meroplanktonic abundance and internal wave fronts is inherently difficult given the nature of the variability of plankton concentrations along the front. However, given that in this study similar relationships between meroplanktonic abundance and internal tidal fronts occurred on the different days of the study, it may be possible to establish consistent relationships between meroplanktonic abundance in the water column and internal wave activity at a local site level. This result is an encouraging step toward the development of an overall model of how meroplanktonic taxa respond to internal wave activity in the coastal ocean.

Within the surface strata, Pineda (1999) showed that abundances of meroplankton were different before, inside, and after fronts associated with internal bores that propagated onshore in the first 4 m of the water column. Mattos and Mujica (2012) found a higher abundance of barnacle larvae in surface slicks than outside of slicks as did Pineda (1994). The results of this study obtained with barnacle taxa support these observations, as we also found significant differences in surface barnacle nauplii mean percent abundance before and after fronts associated with internal tidal bores. Furthermore, a new contribution of this study is the finding of significant differences in crab zoeae abundance and mean percent abundance in deeper strata, suggesting that internal bores are capable of modifying the abundance of meroplankton in the
levels (*** denotes when $p < 0.001$). Crabs showed significantly greater abundance overall, particularly in the bottom strata (Fisher LSD, $p < 0.001$). Crabs in the bottom strata as well as barnacle nauplii in the surface strata, showed significantly different mean% abundance with strata, with barnacle nauplii significantly greater at the surface (Fisher LSD, $p < 0.001$) and crab zoeae significantly greater at the bottom (Fisher LSD, $p < 0.001$). See Table 1 for ANOVA results.

The results of this study indicate that alongshore propagating internal waves are capable of modifying the vertical distribution of meroplankton taxa in predictable ways that are consistent between internal wave events on different days in the nearshore ocean. Alongshore propagating internal waves may be important mechanisms for the transport of meroplankters into semi-closed coastal areas, such as bays, where once inside, the direction of propagation eventually becomes cross-shore. In addition, if larvae are located within a front traveling along the shore, the direction of their transport may vary along the front, with organisms located nearer to shore more likely to be pushed into the surfzone due to refraction of the internal wave, also resulting in cross-shore transport. Pineda (1994) observed that all fronts, both cross-shore and alongshore, seemed to disappear at the surfzone. If an alongshore front reaches the surfzone, it is likely that any material traveling in the front would then be subject to flows characteristic of the surfzone and change from an alongshore direction of travel to a cross-shore direction of travel in shallow water due to refraction (see Filonov et al. (2014)). Therefore, internal waves moving in the alongshore direction may also be responsible for the cross-shore transport of meroplanktonic larvae, especially at their shallower edge nearest to shore.

Given that conditions for the generation of internal waves are present in coastal oceans worldwide (Cairns, 1967; Lamb, 1997; Cummings et al., 2003; Shanks and Brink, 2005), it is important to understand how they modify the vertical distribution and abundance of different taxa. While significant, the changes in abundance observed in this study appeared to not be of long duration. One conclusion may be that internal waves do not operate on a long enough temporal scale to contribute in an appreciable way to the overall distribution of meroplankton. However, results from Weidberg et al. (2004) showed that upwelling flow was related to the abundance of barnacle cyprids only when integrated over a period of weeks, suggesting that the changes in meroplanktonic distributions in the nearshore ocean may be cumulative in nature. Therefore, while the changes in meroplanktonic abundance did appear to be transient in this study and changed within a few hours, similar patterns occurred on consecutive sampling days, therefore the cumulative effects of such changes related to tidally induced flows may play a significant role in determining the horizontal and vertical distributions of meroplankton and therefore may play a substantial role in regulating their distribution and abundance when integrated over time.

If meroplankton have evolved in concert with tidally driven flows, then taxa should not be distributed uniformly throughout the water column and we would expect taxa to show greater abundance in particular strata of the water column during different ontogenetic stages. In addition, this ontogenetic preference for a particular strata should be linked with advantageous flows that are tied to a greater probability of survival and reproductive

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**Table 1**

Factorial ANOVA for abundance and mean percent of abundance data. Significant $p$ values in italics.

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If meroplankton and not only near the surface, as has been previously suggested (Pineda, 1994), but not demonstrated at this temporal scale in the literature at depth.

As the internal waves at this study site are mode one (Filonov et al., 2014), we would expect to see opposite changes in meroplanktonic abundance above and below the thermocline, as we did. As opposed to other studies that have evaluated the interaction between meroplankton and internal tidal bores that propagate in the cross-shore direction, to our knowledge, this is the first study to evaluate this relationship with internal waves that propagate along the shore. It is possible that alongshore internal waves may not be as effective in modifying the vertical distributions of meroplanktonic larvae as those internal waves that propagate in the cross-shore direction given that an internal wave propagating along the shore would not necessarily encounter a progressively shallower water column like it would in the cross-shore direction moving towards the coast (Cairns, 1967). However, in this case, the alongshore propagation actually does result in a progressively shallower water column, and greater non-linearity (see Filonov et al. (2014)), as the alongshore propagation moves the wave into a shallow (< 50 m) bay (Todos Santos Bay). This may explain why we were still able to detect significant changes across the fronts.
success. Barnacle nauplii presented higher abundance in surface waters and crab zoeae presented greater abundance in deeper waters. This result is in agreement with work by Tapia and Pineda (2007) and Tapia et al. (2010) who found barnacle nauplii near the surface in California waters and with work by Leichter et al. (1998) who reported the highest abundance of crab zoeae near the bottom in Florida. These results suggest that organisms in the nearshore ocean congregate at consistent depths globally, and that this relationship exists over a wide range of sites and seasons. Meroplanktonic larvae may, therefore, have evolved to take advantage of predictable flow regimes in the coastal ocean. In this study, the stratum in which each meroplanktonic taxa was most abundant was the stratum in which changes in meroplanktonic abundance of that taxa showed a significant relationship with internal bore phases. Meroplankton may therefore accumulate at depths where they will most likely be affected by current flows.

The large changes in meroplanktonic larval abundance (at times, a doubling) that occurred within a few hours were significantly correlated with current flows associated with internal tidal bore passing. This seems to indicate that the changes in abundance were due to the forcing of the internal tide, further implicating internal waves as important mechanisms capable of modifying the distribution of planktonic organisms in the ocean and supporting the work of many others (Shanks, 1983, 1987, 1988, 1995; Pineda, 1999; Pineda et al., 2007; Leichter, 1996; Mattos and Mujica, 2012), who have demonstrated that internal
waves can affect the distribution and abundance of meroplanktonic larvae in the water column. Given that internal tidal flow has a somewhat predictable periodicity (Arthur, 1954; Cairns, 1967; Pineda, 1991, 1995; Leichter et al., 2005), it follows that meroplankton may have been able to evolve to utilize these flows. Our results indicate that meroplankton taxa accumulate at specific depth ranges in the water column and that this accumulation is subject to modification via flows indicative of internal wave activity.

It is important to note that there exist important logistical limitations to this type of study, primarily due to the inevitable disparity between oceanographic and biological sampling frequencies. The high biological sampling frequency of this work allowed for the observation of changes in the abundance of meroplankton in the water column related to internal wave events at a temporal scale that few studies have evaluated. Furthermore, the nearshore sampling scheme undertaken in this study highlights the importance of internal tidal bores as a mechanism capable of transporting larvae very close to the shore where potential settlement sites exist. The results of the combined high-frequency sampling of this study and the nearshore collection of meroplanktonic larvae also indicate that future studies must tackle work at these scales to fully understand the interaction between meroplanktonic larvae, internal tidal bores and onshore settlement. In addition, future studies should sample in multiple nearshore locations simultaneously, with even higher biological sampling frequencies (2–3 samples per hour per stratum) for extended periods of time wherever possible.

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