VERTICAL DISTRIBUTION AND ABUNDANCE OF COPEPOD NAUPLII AND
ICHTHYOPLANKTON IN NORTHERN BAJA CALIFORNIA DURING STRONG INTERNAL
TIDAL FORCING.

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ABSTRACT

In this study, we explored the changes in the vertical distribution and abundance of copepod nauplii and ichthyoplankton every hour in three different strata during a period of strong internal tides, which have been shown to accumulate and transport plankters. In the deeper stratum, the abundance of copepod nauplii was significantly greater, significantly increased during the cold phase of the internal tide, and was significantly correlated with both total and baroclinic current flows in the direction of internal tide propagation. On the other hand, ichthyoplankton abundance was generally low, with no stratification in vertical distribution, no significant changes across the two phases of the internal tide, and no correlation at any depth with any current flows. The cold phases of the internal tide were characterized by a shallow thermocline, a cooler water column, and a significant increase in the abundance of copepod nauplii in the bottom stratum. On the other hand, the warm phases of the internal tide were characterized by abrupt warming in surface waters, a depression of the thermocline, and a significant decrease of copepod nauplii in the bottom stratum. The depth distribution and buoyancy of the different groups of larvae may be responsible for the differences found.

KEY WORDS: early stages, copepod nauplii, ichthyoplankton, internal tide, buoyancy control

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INTRODUCTION

The relationship between zooplankton and physical processes has been relatively well-studied at different spatiotemporal scales (Haury *et al.*, 1978), particularly for seasonal and mesoscale processes. Aggregations of planktonic organisms have been associated with mesoscale phenomena such as fronts (McCulloch and Shanks, 2003; Shanks and McCulloch, 2003) and upwelling (Morgan *et al.*, 2009; Morgan and Fisher, 2010), which can modify both the distribution and abundance of plankters. However, the effect of higher-frequency coastal processes, such as internal tidal waves, on the distribution and abundance of zooplankton has not been studied with the same detail, especially for early stages, and the literature to date has mainly focused on cyprid barnacle larvae (e.g. Pineda 1991,1999; Tapia and Pineda, 2007; Tapia *et al.*, 2010). Understanding how internal tidal waves modulate the distribution and abundance of other zooplankton groups has been largely neglected, in part due to the high frequency sampling effort required to detect changes in the distribution and abundance of organisms at shorter temporal and spatial scales.

Internal tides are known to cause significant changes in water column properties at short temporal scales (Ladah *et al.*, 2012). In a stratified water column, abrupt bathymetry promotes the generation of internal tides, often forced by the barotropic tide (e.g. Baines, 1982; Vlasenko *et al.*, 2005; Lamb, 2013). The internal tide manifests as an internal wave associated with current shear at the tidal frequency near the coast (Helfrich and Melville, 2006; Lamb, 2013). Propagation dynamics are characterized by two alternating phases and associated baroclinic flows (Pineda, 1994). The cold phase is characterized by the flow of cold water shoreward at depth, with offshore currents near the surface. When the cold bottom water nears the shore, it upwells, generating a hydrostatic instability that promotes vertical mixing near the coast (Sandstrom and Elliot, 1984; Pineda, 1994). During the warm phase, the colder water previously upwelled nearshore sinks and flows offshore at depth, while warmer waters are advected onshore at the surface (Pineda, 1994). This complex and dynamic system produces strong thermal fronts, identified by abrupt and rapid changes in temperature (Pineda, 1991). These are often accompanied by non-linear internal waves of higher-frequency (e.g. Helfrich and Melville, 2006) that can be observed as surface slicks.

Internal waves have been proposed as a mechanism for transport of particles and plankton (e.g. Shanks, 1983; Pineda, 1991; Lamb, 1997, 2002; Helfrich and Pineda, 2003), either through small displacements by high frequency solitary waves, which may cause substantial transport when they occur in packets (Lamb, 1997), through transport by trapped cores in solitons (Lamb, 2002), through advection if they are concentrated in front of, behind or offshore of the propagating feature (Franks 1997, Helfrich and Pineda 2003), especially for inefficient swimmers, or through accumulation by

avoiding downwelling at the front by more buoyant particles and better swimmers (Helfrich and Pineda 2003). Transport and accumulation, regardless of the mechanism, depends on the vertical and spatial distribution, specific behaviour, and buoyancy of the marine larvae in question and their ability to respond to flows by either swimming, sinking or floating (Helfrich and Pineda, 2003).

Most studies have focused on the effect of internal tides on benthic meroplankton (e.g. Pineda 1994, 1999; Ladah *et al.*, 2005; Tapia and Pineda, 2007), whose early life stages require transport to the coast to complete their life history and settle in the littoral zone (Pineda *et al.*, 2007). Early stages of barnacles can be accumulated above the thermocline (Liévana-MacTavish *et al.*, 2016) and can then be transported to the coast in surface water during the warm phase of the internal tide (Pineda *et al.*, 2007). Conversely, larval crabs have been observed in cold water below the thermocline (Leichter *et al.*, 1998), and increase their abundance during the cold phase of the internal tide at depth (Liévana-MacTavish *et al.*, 2016), potentially due to advection from offshore deeper waters. Both the depth distribution of these organisms (Tapia *et al.*, 2010; Liévana-MacTavish *et al.*, 2016, Liévana-MacTavish and Ladah, 2017), and their behaviour (Pineda, 2000; Pineda *et al.*, 2009; Pineda and Reynolds, 2018) can determine where, when and how their distribution and abundance changes during the internal tide. However, it is practically unknown how the internal tide affects other meroplanktonic groups such as ichthyoplankton, and holoplanktonic organisms (e.g. copepods), which form important links in the marine trophic chain (Stibor *et al.*, 2004).

The life stages of ichthyoplankton and holoplankton (e.g. copepods) have different displacement capabilities in the water column, depending on their ontogeny (Moser, 1996; Mauchline, 1998). In general, more mature life stages can control their buoyancy and swimming, while early life stages depend more on environmental conditions (Franks, 1992). For example, early copepod nauplii contain lipid droplets, which affect their buoyancy (Mauchline, 1998; Lee *et al.*, 2006). They can move in all directions using their appendages, although they are weak swimmers (Mauchline, 1998). For early stages of ichthyoplankton, fish eggs begin with a yolk mass and an oil globule (Moser, 1996). When fish eggs hatch, fish larvae develop a yolk sac (Moser, 1996). Both fish eggs and vitelline larvae have positive buoyancy but with null swimming capacity (Pittman and McAlpine, 2001).

The corresponding depth distribution of ichthyoplankton and holoplankton, and their ability to swim, sink or float can affect their transport during internal tides (Franks, 1992). Higher abundances of adult and juvenile calanoid copepods have been reported to occur below the thermocline during internal tides (Haury *et al.*, 1983; Leichter *et al.*, 1998). On the other hand, fish larvae have been observed in surface slicks during internal tide events (Shanks, 1983; Kingsford and Choat, 1986).

The objective of the present study was to understand how the abundance and vertical distribution of copepod nauplii and ichthyoplankton (fish eggs and larvae) change during the passage of strong internal tidal waves. We predicted that the abundances of organisms that show strong stratification in their vertical distribution would change significantly during the internal tide at the depth where they have the highest abundances. Based on the various forms of accumulation explained in Helfrich and Pineda (2003), we predicted an increase (decrease) in abundance during the cold phase of the internal tide for organisms with greater abundance below (above) the thermocline.

METHODS

The Bahia Todos Santos study site is a semi-enclosed bay located in the northern part of the Baja California peninsula in Mexico (Fig. 1). Its abrupt topography favours the generation and propagation of strong internal tides in summer when the water column is well stratified (Ladah *et al.*, 2012; Filonov *et al.*, 2014).

Physical and biological data were taken during the FLOO-2009 expedition at the N4 site (Fig. 1) on the 19-20 of August, 2009, during daylight hours (Liévana-MacTavish *et al.*, 2016; Ibáñez-Tejero *et al.*, 2018). Zooplankton sampling was carried out with a conical plankton net (150 μm mesh size with a mouth diameter of 0.5 m), with a closing mechanism designed to sample different water column strata, with a flowmeter at the mouth to determine the amount of water sampled. Zooplankton was sampled from three different strata (surface, 0-6 m; mid-water, 6-15 m; and bottom 15-28 m), with a sample taken every 20 min, resulting in an hourly cycle to cover the 3 strata. A thermistor chain (Onset HOBO TidbiT with ± 0.2 degrees C accuracy) was deployed at 30 m depth, with loggers placed every meter between 3 and 26 m depth, which recorded temperature every minute. An Acoustic Doppler Current Profiler (Sentinel Workhorse ADCP, 614 kHz, Teledyne RD Instruments) was deployed at 30 m depth and recorded currents and echo intensity every 30 s in 1 m bins.

The warm phase of the internal tide was identified by abrupt changes in temperature that exceeded 2°C at 5 m depth. The cold phase was identified by temperatures $\leq 15^{\circ}\text{C}$ at 9 m depth (see Liévana-MacTavish *et al.* (2016) for details).

The principal axis of variation of the current was calculated from the east and north components at each depth (Kundu and Allen, 1976) and the time series were rotated into the depth-averaged axis (u' , v'). A second-order polynomial equation was then used to separate the tidal and subtidal processes in the bay (Ibáñez-Tejero *et al.*, 2018). The subtidal flow was removed and internal tidal

currents (U' , V') were filtered through a Godin filter to remove the variability at periods < 60 min (Godin, 1991).

Zooplankton was separated, identified and quantified. Aliquots of 25 mL (1/6 of the sample) were used to quantify copepod nauplii. To explore if an aliquot of 25 mL provided an adequate representation of the sample, for a subset of samples, copepod nauplii were quantified in the whole sample and compared to results from 3 different aliquots of 25 mL. The estimated error of using aliquots to represent the entire sample was $< 5\%$. The entire sample was used to quantify fish eggs and larvae, independent of species. Subsequently, organism abundance was standardized using the volume of water filtered through the net and expressed in ind. m^{-3} . Fish larvae were identified to the highest taxonomic level possible (Moser, 1996).

Statistical analysis

A factorial ANOVA and a *post hoc* Fisher LSD test was used to analyse organism counts at an alpha of 0.05 (Zar, 2010) to explore the abundance of copepod nauplii and ichthyoplankton (fish eggs and larvae) in each internal tide phase (cold vs. warm) and in the surface and bottom collection strata, in order to examine if organism abundances increased in a particular phase of the internal tide and at what depth. We also explored if there was a significant relationship between organism abundance and the baroclinic (U' , V') and total currents (u' , v') in the stratum they were sampled from, averaged over a period of 30 min before and 30 min after (60 min in total) each biological sample collection time using a Pearson correlation (Zar, 2010), as in previous studies (Pineda, 1994; Liévana-MacTavish *et al.*, 2016).

Pearson correlations (Zar, 2010) were also used to explore the relationship between environmental variables (temperature, sea level and total kinetic energy) and the abundance of copepod nauplii and ichthyoplankton (fish eggs and larvae) in the different strata (surface, mid-water and bottom). All environmental variables were again averaged for each stratum over the collection period as explained above for currents.

RESULTS

Environmental conditions

Sea level showed a tidal range of ± 1 m at a semidiurnal frequency (Fig. 2a). The time series of temperature and currents showed a semidiurnal internal tide during both days of study (Fig. 2b, c, d).

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Temperature data showed a stratified water column with the 15 °C isotherm associated with the position of the thermocline. Semidiurnal internal tidal waves were evident, particularly at the thermocline (Fig. 2b). Two cold phases and two warm phases of the internal tide occurred each day at a semidiurnal frequency. The cold phases were characterized by the pumping of cold (≤ 15 °C) water upwards. The warm phases were characterized by as strong increases in temperature (> 2 °C) in a few minutes near the surface accompanied by a sinking of warm water in the mid-water stratum. High-frequency internal waves formed above the 15 °C isotherm.

The baroclinic tide showed current speeds near 0.15 m s^{-1} . The onshore current direction (U') was towards 34° clockwise with respect to east (Fig. 2c). The alongshore current direction (V'), and the principal direction of propagation of the internal tidal was towards 56° anticlockwise with respect to north (into the bay) (Fig. 2d).

Vertical distribution and changes in abundance during the internal tide

Although we found more fish larvae ($10.54 \text{ ind. m}^{-3}$) in the surface stratum on the first day of sampling (August 19) (Fig. 2c) and more fish eggs in the surface stratum (9.14 ind. m^{-3}) on the second day of sampling (August 20) during the warm phase of the internal tide (Fig. 2b), overall, fish egg and fish larvae abundances did not show any significant stratification (Fig. 2b, c, Fig. 3a,b, Table I), or changes between the cold and warm phases of the internal tide (Fig. 3a,b; Table I). The majority of ichthyoplankton consisted of fish eggs, and most (80 %) of the fish larvae identified had a yolk sac, showing the presence of early life stages in the area (see Table II). There was no significant relationship of fish egg or larvae abundances with any environmental variable (temperature, sea level, onshore currents, total kinetic energy, alongshore total or baroclinic currents) (Fig. 4, Table III).

On the other hand, copepod nauplii showed higher abundances at depth compared to the surface stratum (Fig. 3c; Table I), with the highest abundance on the first day of sampling in the deeper strata (2402 ind. m^{-3} for 19 August) (Fig. 2d). A significant increase in abundance of copepod nauplii was found during the cold phase of the internal tide in the deeper stratum ($p=0.001$), with a significant interaction between internal tidal phase and sampling strata ($p=0.013$, Fig. 3c, Table I). During the warm phase, the abundance of copepod nauplii was significantly lower at all depths. The Pearson correlations did not show any significant relationship of copepod nauplii abundance with temperature, sea level, onshore currents or total kinetic energy. However, a significant relationship between alongshore current flows and the abundance of copepod nauplii in the deep stratum was found, with increased abundances at depth associated with both the overall and baroclinic current flow into the bay, in the southeastward direction (Fig. 4, Table III).

DISCUSSION

In this study, early life stages of copepod nauplii showed significantly greater abundances in the deeper stratum during the cold phase of the internal tide, as was predicted for zooplankton with a stratified distribution with more larvae below the thermocline. Fish eggs and larvae, on the other hand, had low overall abundances, showed no clear stratification pattern in their distribution, and no significant changes in vertical distribution or abundance during any phase of the internal tide at any depth. Changes in organism abundance during the internal tide involves the interaction between vertical and spatial distribution, larval buoyancy, swimming ability, behaviour, preference for food and light, and predator avoidance (Franks, 1992; Pineda *et al.*, 2009; Pineda and Reynolds, 2018), which may all account for the differences found herein for the different groups of organisms. There is little lab work to explore the detailed response of these organisms to different flows, as there exists in the literature for barnacles (Helfrich and Pineda, 2003; Scotti and Pineda, 2007), making the interpretation of the mechanism behind the increase in abundance speculative. This study, however, does support the idea that not all stages and groups of zooplankton respond in the same way as described in the established literature for some merozooplankton during internal tidal forcing (Pineda, 1999; Liévana-MacTavish *et al.*, 2016). This study further demonstrates that changes in abundance during the internal tide is a complex process involving a suite of factors that must be taken into consideration when making predictions about how organisms are accumulated and/or transported during dynamic coastal phenomena such as internal tides.

The higher abundances of copepod nauplii found at depth may be related with the location of hatching copepod eggs, which are dense and sink in the column water, sometimes even as resting stages on the benthos (Mauchline, 1998). Copepod nauplii are often found in deeper chlorophyll-rich layers associated with phytoplankton in coastal waters (Fernández, 1979; Bautista *et al.*, 1994). Early copepod nauplii feed on their oil sacs and then often on phytoplankton (Sekiguchi, 1974; Green *et al.*, 1992). Because the swimming velocity of copepod nauplii is low, $0.5 - 2 \text{ mm s}^{-1}$ (Mauchline, 1998), their ability to move horizontally is unlikely, however as they exhaust their oil sac, their buoyancy may change and they may further sink, leading to some ontogenetic control of their depth, which could lead to retention of later stage nauplii in deeper offshore waters (Mauchline, 1998; Golçalves *et al.*, 2012).

The increase of copepod nauplii abundance during the cold phases of the internal tide in our study may have been due to advection when water from deeper offshore layers, abundant in nauplii, shoaled into the sampling site, and potentially further into the bay, related with the baroclinic southeastward current at depth, rather than due to accumulation, as they are not strong swimmers. The increase in

chlorophyll and phytoplankton associated with deeper water when it shoals during the cold phase of the internal tide (Witman *et al.*, 1993; Leichter *et al.*, 1996; Ladah *et al.*, 2012) could favour herbivorous copepod nauplii, advecting them close to their potential food source (Golçalves *et al.*, 2012). As internal tidal waves propagate into the Bay of Todos Santos, they become increasingly non-linear as they cross shallower isobaths, eventually breaking entirely and forming bores before reaching shore (Filonov *et al.*, 2014). Therefore, if organisms were advected during the cold phase of the internal tide, they could have been mixed into the water column, thereby avoiding being swept back offshore by the alternating flow. On the other hand, the pattern of increased abundance herein was similar to that found for crabs in a previous study in this region (Liévana-MacTavish *et al.*, 2016). Crab larvae are strong swimming meroplankters and have the behaviour for accumulation (Shanks, 1983; Liévana-MacTavish *et al.*, 2016). The increase in abundance measured herein for copepod nauplii in the cold phase could have been due to accumulation by the internal tidal front, by cumulative packets of high frequency internal waves, or by advection of water masses from depths where nauplii were more abundant.

Because early stages of ichthyoplankton such as fish eggs and vitelline larvae have positive buoyancy, we expected to find a strong stratified distribution in the water column, with higher abundances above the thermocline, and therefore predicted an increase in abundance in the surface stratum in the warm phase of the internal tide, similar to barnacle larvae (Helfrich and Pineda, 2003). However, our results showed no significant stratification (a requirement for some types of accumulation, see Helfrich and Pineda, 2003), low overall numbers, no significant temporal or depth changes in any internal tidal phase, and no relationship with currents. Some studies have found an accumulation of fish larvae in surface waters associated with high-frequency internal waves (Shanks, 1983; Kingsford and Choat, 1986). Very high frequency internal waves, seen in our physical data at the scale of minutes, were beyond the scope of this study due to the inability to sample the biology at that temporal scale, although if high-frequency internal waves were accumulating ichthyoplankton in the surface at this site, we might have expected some cumulative evidence of that (Lamb, 2002), as the warm phases we studied were replete with high frequency events. Overall, ichthyoplankton showed low abundances and high variability, most likely complicating the ability to detect a difference between depths and internal tidal phases, even if one did exist.

The ichthyoplankton samples we found were principally fish eggs, or fish larvae still in their yolk sac. This may indicate a spawning area nearby (Pittman and McAlpine, 2001). The fish larvae detected were species typical of this coastal area, e.g., *Paralichthyidae* spp., *Scomber japonicus* or *Engraulis mordax* (Moser, 1996; Valencia-Gasti *et al.*, 2015).

The high frequency of biological sampling required to study changes during the internal tide renders difficult this type of study. The data herein represent a significant observational effort at sea to produce relatively sparse coverage with high variability during limited periods. Plankton are generally patchy and the timing of the warm and cold phases of the internal tide cannot be predicted without some preliminary sampling, as these are highly non-linear events. Therefore, testing these predictions requires many hours of sampling to capture and resolve differences in abundances across both the cold and warm phases. For this reason, it is recommended that future studies sample for more days, over many tidal cycles, as frequently as possible, to guarantee that there will be enough samples and replicates during the period of strong internal tidal forcing, which in this site usually lasts only a few days. However, the issue of low numbers and patchiness in the plankton is often still unavoidable and not easily overcome, even with increased samples or replicates.

We predicted that the increase in abundance during the cold phase at depth found for nauplii could occur due to various forms of accumulation as explained in [Helfrich and Pineda \(2003\)](#). However, as discussed previously, advection of deeper water masses where copepod nauplii were more abundant, although less efficient, is another explanation of the patterns found. There could also have been a diel response that we were unable to detect, as we only sampled during the day. However, the likelihood that a diel migration would result in a confounded increase during the study period is low. The internal tide behaves differently each day, even on consecutive days, as it is a non-linear phenomenon and depends on stratification and barotropic tidal forcing, which also change from day to day and hour to hour. Finally, the idea that the patterns observed were due to sampling the same circulating patch of plankton on the consecutive days and that this resulted in the patterns observed is unlikely per the particle vector analysis on water parcel movement (see supplementary material), although we cannot completely rule this out as there is no way of knowing the extent of the patch being sampled. Regardless of the mechanism, we were able to support our predictions that even weak swimming, holoplanktonic organisms, with strongly stratified distributions above and below the thermocline, can show significant changes in abundance during the internal tide at the depth where they have their highest abundance, similar to many meroplanktonic organisms studied to date.

CONCLUSIONS

Using the two phase internal wave model and what has been previously established for meroplankton studies, we were able to predict an increase of copepod nauplii, but not groups of ichthyoplankton, during the internal tide. We conclude that they differed in their responses to internal tidal forcing

because of differences in their buoyancy and depth distribution (copepods sink and are abundant at depth, whereas fish eggs and larvae did not show any significant stratification in their depth distribution). Understanding how the internal tide impacts zooplankton groups beyond just intertidal meroplankton such as barnacles is important for modelling coastal productivity, particularly at small scales, and for ultimately understanding transport. A deeper understanding of the behaviour of different zooplankton organisms (ichthyoplankton and holoplankton) in coastal areas is required to increase our knowledge of productivity in the nearshore during dynamic internal tide events. This is important for teasing apart how the internal tide, mesoscale, and seasonal processes are all nested together.

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TABLE AND FIGURE LEGENDS

Table I. Factorial ANOVA, with internal tidal phase (cold vs. warm) vs. strata (surface and bottom) for fish eggs, fish larvae and copepod nauplii.

Table II. Principal fish larvae identified and their life stage. The majority had the yolk sac (79.52 %), with a small percentage in the pre-flexion (18.57 %) and flexion (1.91 %) stages. Fish larvae made up 31.66 % of the ichthyoplankton quantified, with 68.34 % being fish eggs.

Table III. Correlation results for the relationships between zooplankton abundance (fish eggs, fish larvae and copepod nauplii) and the movement of the water (the integral of the current [u' , v' , U' , V'], as in Liévana-MacTavish *et al.*, 2016), temperature, sea level and kinetic energy, for each stratum over a period of 30 min before and 30 min after (60 min in total) each biological sample collection time. Significant correlations are shown in red ($p < 0.05$).

Fig. 1. (a) Location, (b) Study area: N4 (30 m depth) indicates the sampling site for net hauls, and the thermistor line and ADCP deployment; arrows show alongshore v' and onshore u' flow direction.

Fig.2. For the period 19 - 20 August, 2009 at N4: (a) Sea level. (b) Temperature vs. depth; heavy black line shows 15 °C isotherm (thermocline); overlaid white circles represent the abundance of fish eggs with abundances ranging from 0.44 to 9.14 ind. m^{-3} (dots are zero abundance). (c) Onshore (positive towards 34°) current component U' vs. depth; overlaid white circles represent the abundance of fish larvae, with abundances ranging from 0.12 to 10.54 ind. m^{-3} (dots are zero abundance). (d) Alongshore (negative towards 56°) current component V' vs. depth; overlaid white circles represent copepod nauplii, with abundances ranging from 2.11 to 2402.2 ind. m^{-3} . In (b), (c) and (d), the black crosses correspond to times with no biological data. The vertical dotted blue line corresponds to the start of the cold phase and the vertical red line corresponds to the start of the warm phase. In (d), the blue rectangle represents sunrise and black rectangle represents sunset.

Fig. 3. Mean abundances of organisms in each internal tidal phase (cold and warm) and stratum (surface and bottom) for (a) fish eggs; (b) fish larvae; (c) copepod nauplii. Vertical bars denote standard error. Numbers above each line show P values comparing the two internal tidal phases for each strata when less than 0.05 from the post-hoc Fisher LSD. NS denotes not significant.

Fig. 4. Abundance vs. alongshore total current v' : (a) Fish eggs; (c) Fish larvae; (e) Copepod nauplii. Abundance vs. alongshore internal tide (baroclinic) current V' : (b) Fish eggs; (d) Fish larvae; (f) copepod nauplii. Red circles represent abundance in surface stratum; green circles represent abundance in mid-water stratum; blue circles represent abundance in bottom stratum.

Fig. 1. (a) Location, (b) Study area: N4 (30 m depth) indicates the sampling site for net hauls, and the thermistor line and ADCP deployment; arrows show alongshore v' and onshore u' flow direction.

632x500mm (96 x 96 DPI)

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1270x877mm (96 x 96 DPI)

Fig. 3. Mean abundances of organisms in each internal tidal phase (cold and warm) and stratum (surface and bottom) for (a) fish eggs; (b) fish larvae; (c) copepod nauplii. Vertical bars denote standard error. Numbers above each line show P values comparing the two internal tidal phases for each strata when less than 0.05 from the post-hoc Fisher LSD. NS denotes not significant.

223x80mm (144 x 144 DPI)

Fig. 4. Abundance vs. alongshore total current v' : (a) Fish eggs; (c) Fish larvae; (e) Copepod nauplii. Abundance vs. alongshore internal tide (baroclinic) current V' : (b) Fish eggs; (d) Fish larvae; (f) copepod nauplii. Red circles represent abundance in surface stratum; green circles represent abundance in mid-water stratum; blue circles represent abundance in bottom stratum.

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TABLES
Table I.

FISH EGGS	SS	DF	MS	F	p
Phase	4.434	1	4.434	1.781	0.199
Strata	1.881	1	1.881	0.755	0.396
Phase*Strata	0.398	1	0.398	0.16	0.694
Error	44.825	18	2.49		
FISH LARVAE	SS	DF	MS	F	p
Phase	<0.001	1	<0.001	<0.001	0.998
Strata	3.238	1	3.238	0.605	0.447
Phase*Strata	2.251	1	2.251	0.42	0.525
Error	96.389	18	5.355		
COPEPOD NAUPLII	SS	DF	MS	F	p
Phase	1180062	1	1180062	6.2	0.023
Strata	987033	1	987033	5.185	0.035
Phase*Strata	1455495	1	1455495	7.647	0.013
Error	3426228	18	190346		

Table II.

FAMILY	SPECIES	TOTAL LARVAE (ind)	
Paralichthyidae	<i>Citharichthys stigmaeus</i>	Yolk sac	64
		Pre-flexion	8
	<i>Paralichthys californicus</i>	Yolk sac	3
		Pre-flexion	1
	<i>Hippoglossina stomata</i>	Yolk sac	2
Labridae		Yolk sac	31
		Pre-flexion	4
Engraulidae	<i>Engraulis mordax</i>	Yolk sac	19
		Pre-flexion	11
Scombridae	<i>Scomber japonicus</i>	Yolk sac	25
Serranidae	<i>Paralabrax clathratus</i>	Yolk sac	8
		Pre-flexion	3
		Flexion	1
	Others	Yolk sac	6
		Pre-flexion	4
Clupeidae	<i>Sardinops sagax</i>	Yolk sac	5
		Pre-flexion	2
Others		Yolk sac	2
		Pre-flexion	6
		Flexion	3
Unidentified		Yolk sac	2
		Destroyed	6

Table III.

		u' (Total current)		U' (Baroclinic current)		v' (Total current)		V' (Baroclinic current)		Temperature		Sea level		Kinetic energy	
		r	p	r	p	r	p	r	p	r	p	r	p	r	p
FISH EGGS	Surface	0.207	0.52	0.195	0.544	0.074	0.82	0.022	0.95	0.102	0.753	-0.145	0.654	-0.354	0.259
	Mid-water	-0.171	0.596	-0.206	0.521	0.184	0.567	0.223	0.486	0.447	0.145	0.329	0.296	-0.475	0.118
	Bottom	0.314	0.32	0.39	0.21	0.294	0.354	0.222	0.488	0.344	0.274	0.012	0.971	-0.189	0.556
FISH LARVAE	Surface	-0.193	0.548	0.17	0.598	-0.259	0.416	-0.214	0.503	0.257	0.42	0.248	0.437	0.114	0.723
	Mid-water	-0.231	0.47	-0.3	0.35	-0.274	0.388	-0.28	0.379	-0.571	0.053	-0.355	0.257	0.116	0.72
	Bottom	0.55	0.064	0.546	0.066	-0.077	0.813	-0.05	0.878	0.214	0.503	0.138	0.669	0.204	0.525
COPEPOD NAUPLII	Surface	0.008	0.98	0.001	0.998	-0.125	0.7	-0.106	0.742	0.198	0.537	0.176	0.584	-0.205	0.523
	Mid-water	0.093	0.772	-0.068	0.833	0.029	0.93	0.098	0.763	-0.313	0.322	-0.476	0.118	-0.239	0.455
	Bottom	0.401	0.196	0.418	0.176	-0.673	0.017	-0.668	0.018	-0.537	0.072	-0.569	0.054	-0.274	0.389

SUPPLEMENTAL MATERIAL – PVD

Methods:

Pseudo-trajectories were calculated using progressive vector diagrams (equation 1) for each depth layer for the surface, mid-water and bottom strata. This analysis gives an idea of the displacement of the water parcel and its contents (e.g. zooplankton) from the sampling point over time (Thompson and Emery, 2014).

$$(x, y) = (x_0, y_0) + \sum (u_i v_i) \Delta t_i \quad (1)$$

where, x_0, y_0 is the origin of the parcel of water, u_i, v_i the components of current for the times Δt_i for observation $i = 1, 2, 3, \dots$

Results:

Movement of water parcels around the sampling point

The pseudo-trajectories (Fig. 1a- f) showed flow was generally out of the bay to the northwest in the surface stratum. Warm layer oscillations associated to ebb and flood current flows at the semidiurnal frequency can be seen (Fig. 1a). In the mid-water stratum, where the greatest internal wave displacement of isotherms occurs, the flow was towards the inside of the bay (Fig. 1b). In the deep stratum, the flow was to the southwest, with a direct flow in the offshore direction during the first 24 hours, after which time the flow showed oscillatory ebb and flood current flows (Fig. 1c).

However, when the subtidal flow was removed, the oscillation of the internal tide could be more clearly observed (Fig. 1d, e, f). In the surface layer, the flow oscillated north of the sampling site (N4 at 0h) during the first 24 hours and the flow oscillated south of the sampling site between 30 - 48 h. Although the flow would not have resulted in the return of specific water parcels to the sampling site during the second day, the internal tidal flow did oscillate near the site (Fig. 1d). The internal tidal flow tended to move to the southwest in the mid-water stratum (Fig. 1e). Finally, in the deep stratum, a clear oscillation of the flow occurs south of the sampling site during the first 24 hours and north of the sampling site during the second 24 hours on the second day. The internal tidal flow did not result in parcels returning to the sampling site in any stratum (Fig. 1f).

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Discussion:

Pseudo-trajectories suggested the same patch was not sampled on the different days of the study, however this is difficult to deduce based solely on the current flows of the water parcels because we have no information on patch size or extent. Patch size depends on many different processes at various spatiotemporal scales (Marquet *et al.*, 1993). The changes in the abundance of planktonic organisms shown in the present study might be associated with different planktonic concentrations above and below the thermocline, as has been modelled for internal waves (Lennert-Cody and Franks, 1999). The effect of the mesoscale upwelling event, the diurnal sea breeze, and the semidiurnal internal tide is evident in the trajectories for both days of study (Ibáñez-Tejero *et al.*, 2018), all of which could have affected plankton patchiness in some way. Until a better way to sample plankton at smaller spatiotemporal scales is developed, net tows will be unable to determine patchiness as necessary and it remains an important yet untractable unknown.

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Fig. 1:

Pseudo-trajectories of the total currents from 0 h 19 August to 0 h 21 August 2009: (a) Surface stratum centered at 6 m; (b) Mid-water stratum centered at 9 m; (c) Bottom stratum centered at 18 m. Pseudo-trajectories of currents after removal of subtidal component: (d) Surface stratum centered at 6 m; (e) Mid-water stratum centered at 9 m; and (f) Bottom stratum centered at 18 m. The numbers represent hours of day, 0 h to 48 h (with displacements marked every 3 hr as in Fig. 2 of the manuscript) for 19 and 20 August, 2009. The black circle corresponds to the start of the trajectories at N4.