Influence of thermo-haline fronts forced by tides on near-surface zooplankton aggregation and community structure in Bahía Magdalena, Mexico

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ABSTRACT: Zooplankton abundance and community structure were recorded across small thermo-haline fronts forced by tides in summer in the subtropical Bahía Magdalena, Mexico, during spring and neap tides. During spring tides, significantly greater plankton biomass occurred along the 300 m width of the tidal front as compared to locations over the continental shelf and the inner part of the bay. Hydrographic records indicate that the tidal front was more intense during spring tides than during neap tides, transporting zooplankton from the continental shelf to ~6 km inside the bay, based on a hydroacoustic survey. Dense surface aggregations, <15 m deep, of the temperate zone copepod *Calanus pacificus* occurred along the front during spring tides, which attracted zooplankton predators from throughout the water column, seabirds, and marine mammals. During neap tides, the front was weak. Contrary to expectations, zooplankton communities during neap tides along the front were similar to zooplankton in the lagoon and were composed mostly of *Paracalanus* spp. and *Clausocalanus* spp. Multivariate non-parametric analysis showed that variability of the zooplankton community was primarily related to a gradient across the mouth of the bay (continental shelf to tidal front to bay), followed by a secondary mode of variability of semi-diurnal and spring-neap tide time scales. We provide a conceptual model that integrates physical, chemical, and biological information to explain mechanisms of eutrophication coupled with zooplankton biodiversity and abundance that is promoted by tidal currents and supports higher trophic levels.

KEY WORDS: Zooplankton · Tidal currents · Tidal front · Surface aggregation · Copepods · Bahía Magdalena

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INTRODUCTION

Bahía Magdalena, a large lagoon of ~883 km², is a highly eutrophic coastal ecosystem that is part of the Bahía Magdalena–Bahía Almejas lagoon complex of ~1390 km² on the southwestern coast of the Baja California peninsula of Mexico. It is influenced by intense currents and mixing processes caused by tidal currents, where the adjacent continental shelf has semi-continuous coastal upwelling events forced by winds (Zaytsev et al. 2003). This lagoonal complex supports

the largest small pelagic fish, shrimp, blue crab, and clam fishery in the southern half of Baja California and has a considerable regional socio-economic impact (Mathews 1975, Sánchez-Ortiz & Gómez-Gutiérrez 1992, Félix-Uraga et al. 2004). Over the continental shelf, the strength of the California Current and northwest winds promote upwelling in late spring and summer (March to August), which in turn induces higher primary marine productivity, leading to highly eutrophic conditions. During fall and winter, intensification of northward advection of the North Equatorial

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Current gradually shifts to tropical mesotrophic environmental and biotic conditions (Gómez-Gutiérrez 1995, 1996, Gómez-Gutiérrez et al. 1995, 1996).

In spring and summer, a strong, horizontal thermo-haline and phytoplankton concentration gradient is common during spring tides at the mouth of this lagoon, which is 5.6 km wide. This tidal front is not evident in autumn and winter (Gómez-Gutiérrez & Robinson 2006). The intense gradient generates a temporary thermo-haline front that separates the water mass of the continental shelf from the shallow lagoon, forced by tidal currents (Robinson & Gómez-Aguirre 2004, Gómez-Gutiérrez & Robinson 2006). Reports have documented a significant increase in biomass concentration and eutrophication of phytoplankton and zooplankton along thermo-haline fronts (Pingree et al. 1975, 1977, Owen 1981, Yamamoto et al. 1981, Yamamoto & Nishizawa 1987, Franks 1992a,b, Gómez-Gutiérrez & Hernández-Trujillo 1994, Bakun 1996). The primary production associated with tidal fronts supports extensive vertical trophic-level interactions (Alldredge & Hamner 1980, Sims & Quayle 1998, Brodeur et al. 2000, Vlietstra et al. 2005). At least 3 mechanisms have been proposed to explain the increase in biomass of plankton along fronts: (1) passive accumulation of the planktonic organisms directed by ocean currents, (2) a large increase in population growth rates along the fronts (Uye et al. 1992, De Robertis et al. 2005, Morgan et al. 2005), and (3) active zooplankton accumulation promoted by the behavior of animals swimming against vertical currents to maintain a specific depth (Genin et al. 2005). The tidal fronts in Bahía Magdalena are transient structures that, with local tidal height variability, are expected to occur for <9 consecutive days in spring tides and <6 d in neap tides. They have a more dynamic ecological impact than the semi-permanent, oceanic thermo-haline front located perpendicular to the coast near Bahía Magdalena. This front, lasting more than 9 mo, separates the California Current from the North Equatorial Current and it is the most stable frontal system in the North Pacific, with a temperature gradient ranging between 0.01 and 0.10°C km⁻¹ (Etnoyer et al. 2004, 2006).

Zaytsev et al. (2003) proposed that wind-induced upwelling occurs over the narrowest continental shelf near the mouth of Bahía Magdalena, where the slope is 88 m in 11 km. The coastal upwelling events, coupled with forcing of the tidal currents and mixing processes are relevant mechanisms for introducing large amounts of nutrients and plankton into this subtropical bay. Using a 120 kHz, split-beam echo sounder, a submarine videocamera, and a 333 µm mesh plankton net, 1 m in diameter Gómez-Gutiérrez & Robinson (2006) discovered that high-density swarms of the neritic euphausiid *Nyctiphanes simplex* enter Bahía Magdalena

near the seafloor during spring and summer, but not in winter, even though flood current speeds in spring tides were statistically indistinguishable among seasons. Euphausiids apparently enter the bay by a selective stream transport, which involves active behavior, a component not taken into account by the hydrodynamic mechanisms proposed by Zaytsev et al. (2003).

In Bahía Magdalena, the role of the front, forced by tides, as a mechanism for concentrating zooplankton biomass has not been previously investigated. Several studies of circadian patterns of nutrients, zooplankton biomass, micronekton, and environmental conditions associated with tide height at a single station (Eulerian sampling strategy) have been conducted in the mouth of this bay (Acosta-Ruiz & Lara-Lara 1978, Guerrero-Caballero et al. 1988, Aceves-Medina et al. 1992, Palomares-García & Vera-Alejandre 1995, Rodríguez-Mata 2006). However, those studies took samples hourly throughout the circadian cycle and did not detect the tidal front per se.

For this study, we designed a sampling protocol based on (1) the visual signs of the tidal front during spring and neap tides, (2) continuous near-surface environmental sensors, (3) hydroacoustic recordings, and (4) plankton collections at discrete positions along the tidal front to characterize zooplankton composition typical of the shelf and lagoon water masses. Our goal was to describe the oceanographic dynamics of the tidal front near the mouth of Bahía Magdalena during 2 tidal periods of spring and neap tides to understand the mechanism of transport, accumulation of planktonic biomass, and variations in zooplankton community structure across the tidal front.

MATERIALS AND METHODS

Field sampling. From 30 June to 15 July 2004, a research vessel (RV 'El Puma') surveyed portions of the continental shelf, the mouth of Bahía Magdalena, and the inner lagoon. Data and samples were collected during spring (locally defined as daily tide range differences >1.5 m) and neap (<1.5 m range) tides (Figs. 1A, B & 2A). During the survey we focused on the speed and direction of the tidal current, measured with an acoustic Doppler current profiler (ADCP), and tidal status, categorized as flood versus ebb and spring versus neap tides, to avoid misclassification of the plankton communities associated with each side of the tidal front. We followed 3 sampling strategies to assess environmental and biological components of the thermo-haline front forced by tides:

(1) measuring vertical distribution of oxygen concentration, expressed as percentage of O₂ saturation; fluorescence, expressed as chl *a* concentration; and tem-

perature along an 18 km transect across the mouth of the lagoon during a circadian cycle (24 h) at spring tides and half circadian cycle (12 h) at neap tides (Figs. 1B, 2A–C, & 3A–R);

(2) recording surface features with continuous sensors, observing animals with a submarine and a video-camera, taking near-surface CTD recordings, and collecting oblique zooplankton samples to characterize

Fig. 1. Bahía Magdalena, Baja California Sur, Mexico. (A) Stations: over the continental shelf (●) and inner part of the bay (▲), collection during max. ebb tides. (B) Five stations (numbered) located along a hydrographic transect perpendicular to the lagoon inlet; (◇, △, □): data collection on various dates along specific sections of the tidal front and in 150 m bands on each side of the frontal zone at stations in the water column for dissolved oxygen, fluorescence expressed as chl *a* and temperature (18 km long, 48 h sampling period). B-TF: lagoon-tidal front side, TF: tidal front, CS-TF: continental shelf-tidal front side (<150 m)

Fig. 2. (A) Circadian tidal height (m) in Bahía Magdalena during the survey; rectangles show recording periods for vertical environmental variability; (B) spring tides (30 June to 1 July 2004), and (C) neap tides (8 to 9 July 2004). Bold lines with numbers: recording periods for dissolved oxygen, fluorescence, and temperature at the inlet to Bahía Magdalena. T₁ to T₄: periods when Bongo nets were used to collect samples in the tidal front and both sides of the front. Gray line: time of observations with an underwater video-camera near the tidal front. B₁ to B₃: periods of sampling at stations when fauna was typical of the central part of the bay. CS: sampling of stations over the continental shelf

Fig. 3. Vertical distribution of (A–F) oxygen saturation, (G–L) chl *a*, and (M–R) temperature for a complete circadian cycle during spring tides (30 June to 1 July 2004; A–D, G–J, M–P) and a half-circadian cycle during a neap tide (8 July 2004; E–F, K–L, Q–R). Arrows: relative intensity and direction of tidal currents deduced from the tidal amplitude (m) scaled to the arrow in panel E (1 m)

this ecotone; the tidal fronts were sampled from the continental shelf to the deeper basin in the bay (Figs. 1B & 2A) during 4 visually-distinct tidal fronts and for 150 m on both sides of the fronts;

(3) sampling zooplankton over the shelf and the inner part of the lagoon to characterize zooplankton communities in the 2 distinctly different marine habitats and compare them to the zooplankton communities along and adjacent to the tidal fronts (Figs. 1A, B & 2A).

Environmental variation induced by tidal currents across the inlet. The 18 km oceanographic transect across the inlet to Bahía Magdalena was monitored several times during each 24 h survey, during spring tides on 30 June at 18:30 h to 1 July at 21:43 h (Fig. 2B), and neap tides on 8 July at 05:23 h to 9 July at 05:10 h (Fig. 2C) to record flood and ebb tide circadian variations of oxygen saturation in the water column, chl *a*, and temperature at the 5 stations in the transect, which was repeated at least 4 times (Fig. 1B). Each survey

across the inlet was monitored for approximately 5 h, which permitted 4 sets of recordings during each circadian cycle. Some data were lost during 2 neap tide periods.

At each station, a CTD (General Oceanics Mark III) fixed in a rosette frame recorded temperature at the surface and 5, 10, 15, 20, 25, 30, 40, 50, and 75 m depths and collected water samples in 10 l Niskin bottles. A multi-sensor probe (YSI model 58) was inserted in each Niskin bottle immediately after sampling to measure dissolved oxygen ($\text{mg O}_2 \text{ l}^{-1}$). Percentage of oxygen saturation ($\%\text{O}_2$) was estimated from oxygen solubility calculated from *in situ* temperature, salinity, and dissolved oxygen concentration using the oxsat equation (Sea-Bird Electronics, www.seabird.com/application_notes/AN64.htm). A 1 l sample from each bottle was taken to the research vessel's laboratory within 5 min and maintained under red light at 22°C to immediately measure fluorescence with a fluorometer (Turner Designs model 10-AU-005-CE). Duplicate

measurements were compared to control samples containing distilled water. Fluorescence (F) recorded in the field was calibrated with laboratory measurements of standard chl *a* concentrations ($n = 10$; Turner Designs) using: $\mu\text{g chl } a \text{ l}^{-1} = 1.1303 \times \text{RF} - 0.0388$ ($r^2 = 0.987$, $p < 0.0001$). Percentage of O_2 saturation, concentration of chl *a*, and temperature were plotted as a function of depth at each station with the Kriging interpolation technique in Surfer v. 8.0 software. The environmental and biological variables were nonquantitatively compared to tidal status, specifically, the spring versus neap tide or flood versus ebb tide periods, and quantitatively compared to zooplankton composition and abundance, using nonparametric multivariate methods. The tide height for the sampling dates were obtained from the JTides v. 4.8 numerical model (www.arachnoid.com/JTides/) for Puerto San Carlos, Baja California Sur (BCS), northeast of the study area ($24^\circ 46' 99'' \text{ N}$, $112^\circ 07' 00'' \text{ W}$).

Characterization of a tidal front at short spatial and temporal scales. During spring tides during daylight, the research vessel followed a zig-zag path crossing the tidal front 6 times (each transect crossing the tidal front was ~ 300 m long) on 1, 3, and 4 July 2004; only data from 3 July are shown (Figs. 2A, 4, 5A). During a neap-spring transition on 14 July from a fixed anchorage, we sampled bay, tidal front, and shelf water masses during the inflowing current that moved the thermo-haline front forced by tides toward the research vessel's position (Figs. 2A, 4, 5A). In general, the tidal front was recognizable by an abrupt change in the color of the water, confirmed in real time by continuous records at 5 s intervals to measure dissolved oxygen and temperature with a multi-parametric sensor (Win-situ model 9000) that was calibrated twice during the cruise. The sensors were installed in the instrument compartment located in the ship's hull at 4 m below sea surface. Continuous data on fluorescence were collected continuously from water pumped from this depth from a clean-water intake located at the bow of the ship, while traveling at an average speed of 8 km h^{-1} . Fluorescence was measured with a 340 to 500 nm excitation signal and an emission signal > 665 nm and compared to distilled water samples as a control. The continuous records of oxygen concentration and fluorescence were converted into percentage of oxygen saturation and concentration of chl *a*, as explained previously.

Acoustic signal strength was recorded with a standard ADCP SonTek, with 3 transducers at a frequency of 250 kHz, to detect mesozooplankton and other small particles in the water column (SonTek 2001). The cell size for the ADCP acoustic analysis covered 2 m vertically with pulses at 5 s intervals. Simultaneous acoustic signals to detect vertical and horizontal distribution of macrozooplankton and micronekton across the tidal

front were transmitted with a split-beam echo sounder (SIMRAD model EY-60) at 120 kHz in a 7° beam angle with a pulse duration of 0.1 ms and a repetitive pulse of 3 pings s^{-1} (Gómez-Gutiérrez & Robinson 2006). For acoustics analysis and viewing the echograms, we used the Sonar 4 v. 5.9 software. The backscattering below an area (MacLennan et al. 2002) was calculated for 5 to 25 m depth along the zig-zag path across the thermo-haline front.

Zooplankton biomass and community structure associated with tidal fronts. The tidal front could not be seen at night; therefore, we collected zooplankton samples only from 10:00 to 19:00 h on 1, 3, 4, and 14 July 2004 ($n = 15$). The tidal front of 1 July was sampled twice to measure zooplankton biomass and identify species. Each of the Bongo nets had a 60 cm diameter, 500 and 300 μm mesh, and was equipped with a digital flowmeter (General Oceanics). The net was towed obliquely from ~ 40 m toward the surface at 6.5 km h^{-1} , following standard procedures (Smith & Richardson 1979). To compare the tidal front samples at a meso-scale ($> 2 \text{ km}$), we analyzed 3 zooplankton samples collected in the innermost part of Bahía Magdalena, $\sim 2 \text{ km}$ from the tidal front during ebb tides and 16 zooplankton samples collected over the shelf along 4 transects perpendicular to the coast during neap tides. We assumed that the effect of tide height over the shelf was negligible. Zooplankton samples were preserved with 96% denaturalized ethanol and changed at the end of the oceanographic survey. Immediately after the cruise, zooplankton biomass was measured by volume displacement (Beers 1976). Zooplankton samples were split into smaller assay samples using a Folsom plankton splitter into $< 1/16$ aliquots that were at least 5 ml in volume. Zooplankton was identified to the lowest possible taxonomic level for copepods (Palomares-García et al. 1998), euphausiids (Baker et al. 1990, Brinton et al. 2000), and other zooplankton (Todd et al. 1996, Young et al. 2002).

Data reduction and statistical methods. To define the main modes of multi-dimensional variability and assess which environmental variables had stronger influences on zooplanktonic distribution, abundance, and community structure during spring and neap tides in the 2 habitat zones, we conducted a multivariate analysis with a non-metric, multi-dimensional scaling (NMDS) technique using the Bray-Curtis (Sørensen) distance measure in PC-ORD v. 4.25 beta software (McCune & Mefford 1999, McCune et al. 2002). We used 2 matrices. The 'species' matrix had 35 stations as rows $\times$ 42 taxa identified to the lowest possible taxon as columns. The 'environmental' matrix had the same 35 stations as rows in the same sequential order $\times$ 12 environmental variables as columns that measured salinity, temperature, chl *a*, percentage of oxygen saturation,

average current speed, depth of the station, zooplankton biomass, tide height at phase of the tide, state of the tide flux, depth of the thermocline, vertical density gradient, and sampling region, which was not a numerical variable.

Once the main environmental variables affecting biomass, community structure, and distribution of zooplankton were identified with the NMDS technique, we used the multi-response permutation procedure (MRPP) to test several null hypotheses that abundance of species and zooplankton community structure differ significantly in the 3 marine environments (continental shelf, tidal front bay), during tidal phases, and in intensity of upwelling (McCune & Mefford 1999, McCune et al. 2002).

The indicator species analysis (ISA) was used to describe the typical species composition of each sampling group, defined according to the null hypotheses that were statistically rejected by the MRPP analysis. The ISA measures the faithfulness of the occurrence of taxa within a particular group of stations defined by a null hypothesis. It produces a value for each species in each environmental station group that ranges from 0 (no group indicator) to 100 % (perfect group indicator). The highest value for each species is tested for statistical significance with a Monte Carlo randomization technique (Dufrene & Legendre 1997, McCune et al. 2002). For the ISA, only plankton identified to the genus or species level was used.

RESULTS

Environmental conditions associated with tidal current time scales

Tide height

Tide height at Puerto San Carlos, BCS, during the spring tide of 30 June to 1 July 2004 and the neap tide of 8 to 9 July 2004 had a mixed, semi-diurnal pattern (Fig. 2A–C). During spring tides, the greater sea level range of –0.36 m to 2.16 m was associated with intense flood and ebb tidal currents, usually up to 150 cm s^{-1} , measured with the ADCP (Fig. 2B). During neap tides, the smaller sea level range of 0.25 m to 1.34 m was associated with tidal current speeds that never exceeded 70 cm s^{-1} (Fig. 2C).

Dissolved oxygen, fluorescence, and temperature in the water column

Tidal fronts in Bahía Magdalena are usually more intense and relatively easier to recognize during

spring than neap tides. During intense spring tides, currents at the lagoon inlet and adjacent shelf had an average oxygen saturation of 44 % in the top 20 m during flood currents that was associated with upwelling subsurface water (Fig. 3D), and was lower than the 55 % average during intense ebb tide currents (Fig. 3B).

Concentrations of chl *a*, which were always higher inside the lagoon, averaged $11.27 \mu\text{g l}^{-1}$ and declined at the inlet and over the shelf, averaging $6.87 \mu\text{g l}^{-1}$ (Fig. 3G–J). In the inlet, lower chl *a* ($8.06 \mu\text{g l}^{-1}$) occurred during flood tides (Fig. 3J) than during ebb tides ($13.89 \mu\text{g l}^{-1}$; Fig. 3H). This gradient demonstrates that lagoon phytoplankton populations were regularly transported seaward during ebb tides.

Temperature was strongly influenced by the combined effects of wind-induced upwelling over the continental shelf and tidal currents across the mouth of the lagoon. During the first ebb tide cycle, the top 15 m of surface water, at 14.6 to 18°C , flowed as much as 2 km from the coast. The tidal front was not well defined (Fig. 3M). During intense ebb tide currents, the water mass of the bay, at $<17^\circ\text{C}$, moved across the inlet (Fig. 3N). During flood tides, the cold water of the shelf, at 14.4 to 15.1°C , flowed across the inlet to the lagoon (Fig. 3P). In the central part of the lagoon, the tidal front is easily detected by the change in direction of the 16 and 17°C isotherms (almost vertically) that mark the tidal front water mass to a depth of ~10 m (Fig. 3M, O, P). The tidal front penetrated 5 to 8 km into the lagoon, reaching its innermost section when maximum flood tidal currents combined with intense upwelling events over the continental shelf. During the study, we had no quantifiable data to estimate the coverage and influence of the tidal front when it moved outside the lagoon during maximum ebb tides; however, observations from the peak of 1 of the highest points on Isla Magarita on 10 July 2004 showed that the sharp and distinct color associated with the tidal front had migrated ~3 km over the shelf during ebb and slack tides (C. Robinson & J. Gómez-Gutiérrez pers. obs.). Stratification of the water column was significantly more intense (mean $\Delta \sigma_t = 0.026$, $n = 5$) during the next ebb tide cycle than during flood tides (mean $\Delta \sigma_t = 0.012$, $n = 15$) when the water column was relatively more mixed (Student's *t*-test, $p = 0.041$, $df = 18$).

During the ebb cycle of neap tides, the top 10 m had high oxygen saturation of $<52\%$ over the shelf compared to the rest of the area (Fig. 3E). In the inlet and inner part of the lagoon, higher oxygen saturation occurred during flood tides than ebb tides (Fig. 3E, F). Average concentration of chl *a* was lower during neap tides ($4.5 \mu\text{g l}^{-1}$) than during spring tides ($6.3 \mu\text{g l}^{-1}$). During flood tides, a 10 m thick homogeneous layer

contained a relatively high chl *a* content ($9.5 \mu\text{g l}^{-1}$). During ebb tides, high chl *a* ($>10 \mu\text{g l}^{-1}$) occurred mostly over the shelf, and low concentrations ($<5 \mu\text{g l}^{-1}$) occurred inside the lagoon (Fig. 3K, L).

During neap tides, temperatures in the top 40 m were significantly warmer and more stratified (Fig. 3Q, R) than during spring tides (Fig. 3M–P). During neap tides, the surface layer, <15 m, was relatively homogeneous at 18°C inside the lagoon and over the shelf; thus, during neap and ebb tides, the tidal front was significantly less evident than at other times. The cold water mass over the shelf, $<15^\circ\text{C}$, never passed the inlet of the lagoon (Fig. 3Q, R). These 3 environmental variables showed significantly greater time and area variability during spring than neap tides.

Temperature, oxygen saturation, and concentration of chl *a* across the tidal front

We estimated that the tidal front influence was ~ 300 m wide, based on continuous measurements of temperature, O_2 saturation, and chl *a* recorded at a depth of 4 m across the front at T_2 , which was crossed 6 times. The water mass over the shelf side was significantly colder (Student's *t*-test, $t = -12.93$, $p < 0.0001$), contained less oxygen (Student's *t*-test, $t = -15.52$, $p < 0.001$), and contained significantly less chl *a* (Student's *t*-test, $t = -7.11$, $p < 0.001$) than the water mass inside the lagoon (Fig. 4). The average temperature gradient across the tidal front ($n = 6$) was 0.71°C ($0.0024^\circ\text{C m}^{-1}$, $s_x = 0.0001^\circ\text{C m}^{-1}$); the average oxygen saturation gradient was 16.7% (0.0556% , $s_x = 0.0034\% \text{ m}^{-1}$), and the average chl *a* gradient was $2.46 \mu\text{g l}^{-1}$ ($0.0082 \mu\text{g l}^{-1} \text{ m}^{-1}$, $s_x = 0.0007 \mu\text{g l}^{-1} \text{ m}^{-1}$; Fig. 4). The steepest gradients of these variables did not always coincide with the position of the most abrupt change in color (Fig. 4).

Zooplankton biomass and community structure across the tidal front

Location of the tidal front and its biological characteristics

Abrupt color changes of the surface water, typically green in the lagoon and deep blue offshore, were the main features that distinguished the tidal front (Fig. 5A). Seagrass, mangrove leaves, zooplankton, pelagic red crabs, and many feeding seabirds (pelicans and allies) overhead were additional features connected with the tidal front. The signal strength recorded by the ADCP increased as the research vessel crossed the tidal front (Fig. 5B), suggesting that dense aggregations of mesozooplankton were concen-

Fig. 4. Measurements at 4 m below the surface of (A) temperature, (B) oxygen saturation, and (C) fluorescence expressed as chl *a* measured every 5 s on 3 July 2004 in a zig-zag path across the tidal front (crossed 6 times) starting on the continental shelf side and moving toward the lagoon. (□): time when RV 'El Puma' crossed the tidal front indicated by abrupt change of seawater color

trated in the top 15 m (Fig. 5B). During spring tides, high zooplankton biomass was attributed to near-surface aggregations of the temperate copepod *Calanus pacificus* (Fig. 5C). The split beam echosounder detected the scattering layer caused by aggregations of macrozooplankton and micronekton throughout the water column (Fig. 5D). The continuous acoustic analysis showed that scattering area (sa) values ($\text{m}^2 \text{ m}^{-2}$) increased abruptly at the tidal front (Fig. 5E). Both acoustic systems indicated that concentrations of plankton and nekton declined horizontally within bands that were no more than 150 m wide on each side of the tidal front (Fig. 5B, D, E). Simultaneous observations with a submarine videocamera (DeepSea Power and Light) showed that the acoustic scattering-layer consisted of dense aggregations of red crab *Pleuroncodes planipes* and schools of Pacific sardine *Sardinops sagax caeruleus*, mackerel *Scomber japonicus*, fish of the family Carangidae, and lower numbers of juvenile giant squid *Dosidicus gigas* (Fig. 5E). Seabirds overhead included the magnificent frigate-

Fig. 5. (A) Abrupt change in surface water color (deep blue = offshore water mass, green = lagoon water mass) indicates tidal front. (B) ADCP (250 kHz) echogram showing backscattering of zooplankton aggregations at the tidal front (TF), central part of the lagoon (B) and continental shelf (CS). (C) Zooplankton aggregations (<15 m deep) along the tidal front at spring tide mostly included temperate copepod *Calanus pacificus*. (D) Echogram recorded with split beam Simrad EY-60 (120 kHz). (E) Area backscattering coefficient (s_a) recorded from 5 to 25 m depth along a zig-zag path. (F) Simultaneous observations with submarine videocamera showed that the scattering layer included red crab *Pleuroncodes planipes*, Pacific sardine *Sardinops sagax caeruleus*, and Pacific mackerel *Scomber japonicus*

bird *Fregata magnificens*, western gull *Larus occidentalis*, brown pelican *Pelecanus occidentalis*, and double-crested cormorant *Phalacrocorax auritus*. Large predatory sea mammals, including sea lions *Zalophus californiensis* and common dolphins *Stenella* spp., actively preyed on schools of fish and red crab along the tidal front.

Zooplankton biomass and species richness

Pooling all stations, median quantities of zooplankton biomass (in ml 1000 m⁻³) were significantly higher during spring tides (1134, SE = 370, n = 9) than during neap tides (177, SE = 31, n = 4; Mann-Whitney test, $W = 32$, $p = 0.018$). Zooplankton biomass was significantly higher and more variable (expressed in terms of SE, $s_x = 387$) along the tidal front than on either side of the tidal front ($s_x < 167$). Mean zooplankton biomass gradually in-

creased from the continental shelf (491) toward the offshore band of the tidal front (847), peaked at the tidal front (1488), decreased in the shoreside band of the front (180), and declined to a low biomass (average of 45) in the center of the lagoon (Fig. 6A). Average species richness inside the lagoon was relatively higher than in offshore areas. However, given the high variability in species richness among the sections of the study area, expressed as S_x , average species richness of zooplankton was statistically indistinguishable among regions (Student's t -test, $t < 0.9988$, $p > 0.169$, Fig. 6B).

Abundance and community structure across the tidal front

Among the 42 zooplankton taxa identified, there were 15 copepod genera or species, 2 euphausiid species, chaetognaths (*Sagitta* spp.), and larvae and adults

Fig. 6. Mean and standard error S_x of (A) zooplankton biomass and (B) species richness collected over the continental shelf (CS), in the continental shelf side of the tidal front (CS-TF), at the tidal front (TF), in the lagoon side of the tidal front (B-TF), and in the central part of Bahía Magdalena (B) during ebb tides

of other taxa identified above genus level. Of these, 3 copepods, *Calanus pacificus*, *Paracalanus* spp., and *Acartia clausi*, and 1 euphausiid, *Nyctiphanes simplex*, contributed >90% of zooplankton biomass (Fig. 7). Post-analysis of the zooplankton samples indicated that ~86% of *Paracalanus* specimens at the tidal front in July 2004 were *P. parvus*. *C. pacificus* and *N. simplex* were significantly more abundant at the tidal front than on either side (Fig. 7A, D). On average, *P. parvus* was more abundant in the center of the lagoon, but occasionally stations with high abundance were observed in the inlet and over the shelf (Fig. 7B). *A. clausi* was occasionally more abundant over the shelf than in the other 2 areas (Fig. 7C).

Data reduction and statistical analyses

Non-metric multi-dimensional scaling (NMDS)

The coefficient of determination of correlations between ordination distances and distances in the original n-dimensional space was 0.270 for the first axis and 0.432 for the second axis. The 2 axes explained ~70% of the total variability of the zooplankton community structure (Table 1). The first axis, maximized for stations across the inlet of Bahía Magdalena, showed that the zooplankton community was closely related to depth and concentration of dissolved oxygen ($r > 0.3$, $p < 0.05$, Fig. 8, Table 1). Two clusters of

Fig. 7. Abundance (ind. 1000 m⁻³; median, q_1 , q_3) of 4 numerically dominant zooplankton species collected within the ~150 m band on both sides of the front. (A) *Calanus pacificus*, (B) *Paracalanus* spp. (*P. parvus* ~86% and *P. acuelatus* ~14%), (C) *Acartia clausi*, and (D) *Nyctiphanes simplex*

oceanographic stations were found; stations sampled in the lagoon and near the tidal front were clustered mostly to the right side of horizontal axis 1 in the NMDS plot (white), while stations sampled over the shelf were clustered mostly to the left side of this axis (gray). Stations on the shelf near the tidal front and at the tidal front were clustered near the central part of the NMDS axis 1 gradient.

The second axis explained the variability of the zooplankton community structure mainly as a function of zooplankton biomass and tide height; the order of

Table 1. Results of non-metric multidimensional scaling (NMDS) analysis showing the coefficient of determination (r^2) and the Pearson-Kendall (r) correlation for the association between ordination distances and distances of the original n-dimensional environmental space. Randomization of the Monte Carlo test gave the probability ($p = 0.0196$) that the final stress level 9.87 could have been obtained by chance

Environmental variables	Axis 1 ($r^2 = 0.270$)	Axis 2 ($r^2 = 0.432$)	Axis 3 ($r^2 = 0.206$)
	r	r	r
Sea surface salinity	0.055	-0.011	0.087
Sea surface temperature	-0.003	-0.123	-0.435
Chl <i>a</i>	-0.147	0.266	-0.503
O ₂ saturation (%)	0.317	-0.001	-0.203
Speed of current	-0.090	0.225	0.023
Station depth	-0.395	-0.041	-0.522
Zooplankton biomass	-0.202	0.415	0.087
Flow vs. ebb tides	0.267	-0.391	0.021
Spring vs. neap tides	-0.152	-0.326	-0.364

Fig. 8. NMDS showing the stations in the species space. Stations coded by location during ebb tides: continental shelf (CS), continental shelf side of the tidal front (CS-TF), tidal front (TF), lagoon side of the tidal front (B-TF), and center of the lagoon (B). The positions of the zooplankton species were calculated as weighted averages of their abundances in the ordination space. Arrow direction: direction of the correlation with the stations and the percent of variance (%) in the zooplankton data explained by each environmental variable. Names of numerically dominant species are shown; other species are abbreviated: *Cl*: *Caligus* spp., *Lb*: *Labidocera* spp., *Em*: *Euchaeta media*, *Cos*: *Cosmocalanus* spp., *Op*: *Oithona plumifera*, *Ps*: *Phaena spinifera*, *Rn*: *Rhincalanus nasutus*, *Oc*: *Oncaea* spp., *Ac*: *Acrocalanus* spp., *Cc*: *Corycaeus* spp., *Cg*: *Centropages gracilis*, *Nd*: *Nematoscelis difficilis*, *ZCb*: zoea of *Callinectes bellicosus*, *Ok*: *Oikopleura* spp. Gray shading includes most continental shelf stations, and white shading includes most lagoon stations

influence was flood and ebb tides followed by spring and neap tides. Oceanographic stations sampled during spring tides were mostly located in the upper part of axis 2 of the ordination, and neap tides in the lower part of the second axis, indicating a temporal difference between spring and neap tides. Stations within the tidal front were located along the entire range of axis 2, demonstrating that the zooplankton community structure at this region changed as a function of semi-diurnal (flood–ebb tides) and weekly (spring vs. neap tides) time scales (Table 1, Fig. 8). During spring tides in flood phase, the tidal front region was dominated by the copepod *Calanus pacificus* and other species typical of the continental shelf, particularly *Nyctiphanes simplex* and *Nematoscelis difficilis*, which were positively associated with axis 2. During neap tides, the tidal front region was dominated by *C. pacificus* and

Paracalanus parvus. This second species is usually more abundant in the lagoon.

Multi-response permutation procedure (MRPP)

Using only the variables that explained most of the differences in zooplankton distribution, abundance, and composition of species in the NMDS analysis, we tested 10 null hypotheses (Table 2). The purpose of this non-parametric statistical analysis was to compare the zooplankton assemblage in the tidal front to the remaining areas (Table 2). The MRPP indicated significant differences in zooplankton community structure between spring and neap tides, mainly associated with the magnitude of the concentration of zooplankton ($p = 0.0052$; Table 2). Contrary to results expected from NMDS

Table 2. Multi-Response Permutation Procedure (MRPP) analysis for comparison of the zooplankton community structure as a function of significant coefficients of determination calculated in the NMDS analysis. We defined 5 regions among the sampling stations: Continental Shelf (CS), Continental Shelf near the Tidal Front (CS-TF, <150 m), Tidal Front (TF), Bahía Magdalena near the Tidal Front (B-TF), and the central part of Bahía Magdalena (B). A is a descriptor of within-group homogeneity compared to random expectation ($A = 1 - [\text{observed delta}/\text{expected delta}]$). $A_{\max} = 1$ when all items are identical within groups (delta = 0); if heterogeneity equals chance expectation, then $A = 0$, and if there is less agreement within station groups than expected by chance, then A has a negative value. This test generates a p-value to evaluate the likelihood that an observed difference occurred by chance

Group of sampling stations tested for the following null hypotheses (H_0)	t -statistic	A	p-value
Spring tides vs. neap tides (all regions)	-4.08	0.046	0.0052
Flood vs. ebb tides (all regions)	0.37	0.004	0.5411
Upwelling intensification (<16°C, <6 mg O ₂ l ⁻¹) vs. upwelling relaxation	-1.05	0.013	0.1384
CS, CS-TF vs. TF vs. B-TF, B	-1.58	0.026	0.0752
CS vs. CS-TF, TF, B-TF vs. B	-2.91	0.050	0.0117
CS, CS-TF, TF vs. B-TF, B	-0.75	0.009	0.1812
CS, CS-TF vs. TF, B-TF, B	-1.90	0.021	0.0543
CS vs. CS-TF vs. TF vs. B-TF vs. B	-1.63	0.040	0.0658

analysis, MRPP indicated that differences between flood and ebb tides were not statistically different ($p = 0.54$), suggesting that differences in zooplankton community structure at a scale <6 h were relatively stable within spring or neap tides (Table 2). We also found no statistical difference in the zooplankton community structure during intense upwelling versus relaxation of upwelling conditions ($p = 0.14$, Table 2). Geographical comparisons, using the MRPP technique, indicated that samples collected along and adjacent to the tidal front, a band of ~300 m, were statistically distinguishable from zooplankton composition and biomass from stations typical of the shelf and central part of the lagoon ($p = 0.01$, Table 2). Again, contrary to expectations, in terms of zooplankton composition the tidal front area was marginally more similar to the zooplankton off the central area of Bahía Magdalena ($p = 0.054$) than off the shelf ($p = 0.18$; Table 2). Apparently, zooplankton composition at the tidal front alone, where surface water color abruptly changed, was not statistically distinguishable from the rest of the areas sampled ($p = 0.075$), supporting the impression that the distinctive community structure

typical of the tidal front system was evident in a band of at least 300 m width ($p = 0.012$) (Table 2).

Indicator Species Analysis (ISA)

We show only the MRPP null hypothesis that was statistically significant to identify which species were significantly associated with specific environmental or area characteristics. The copepods *Calanus pacificus*, *Corycaeus* spp., *Caligus* spp. (a genus of fish parasite), adult red crab *Pleuroncodes planipes*, and neritic euphausiid *Nyctiphanes simplex* larvae were more common during spring tides than neap tides, except *Caligus* sp., a relatively rare species (Table 3). Only 5 taxa showed statistical differences between flood and ebb tides; all were characteristic of ebb tides, with no species indi-

Table 3. Indicator Species Analysis (ISA) for the genera and species in the study area, showing only species with significant fidelity ($p < 0.05$) to a specific event: spring tides (ST) vs. neap tides (NT); flood tides (FT) vs. ebb tides (ET) or a specific area: continental shelf (CS), areas near the tidal front (CS-TF, TF, B-TF), and the central part of Bahía Magdalena (B). The percent of fidelity and probability of the Monte Carlo test for each species is shown. The remaining 20 genera and species did not show significant differences in statistical comparisons

Indicator Species	Indicator group	(%) indicator value of null hypothesis tested		Monte Carlo p-value	
		Spring tides	Neap tides		
<i>Calanus pacificus</i>	ST	61.8	38.8	0.047	
<i>Corycaeus</i> spp.	ST	60.8	39.2	0.025	
<i>Nyctiphanes simplex</i> (larvae)	ST	67.6	32.4	0.016	
<i>Caligus</i> spp.	ST	76.3	23.7	0.018	
<i>Pleuroncodes planipes</i> (adults)	ST	60.2	39.8	0.035	
		Flow tides	Ebb tides		
<i>Paracalanus</i> spp.	ET	60.6	39.4	0.0010	
<i>Corycaeus</i> spp.	ET	63.6	36.4	0.0010	
<i>Oithona plumifera</i>	ET	72.8	27.2	0.0090	
<i>Zoea C. bellicosus</i>	ET	67.7	32.3	0.0400	
<i>Oikopleura</i> spp.	ET	62.5	37.5	0.0460	
Regions		CS	CS-TF-B-TF	B	
<i>Euchaeta media</i>	CS	63	18	18	0.0160
<i>Paracalanus</i> spp.	CS-TF, TF, B-TF	33	40	27	0.0790
<i>Subeucalanus</i> spp.	CS-TF, TF, B-TF	9	82	9	0.0280
<i>Labidocera</i> spp.	CS-TF, TF, B-TF	9	82	8	0.0030
<i>Cosmocalanus darwini</i>	B	27	7	66	0.0300
<i>Acrocalanus</i> spp.	B	17	16	66	0.0210

cators of flood tides (Table 3). Of the taxa in each area, only the oceanic copepod *Euchaeta media* was a significant indicator of the shelf area; *Paracalanus parvus*, *Subeucalanus* spp., and *Labidocera* spp. were indicators of the 300 m tidal front band; and *Cosmocalanus darwini* and *Acrocalanus* spp. were indicators of the center of Bahía Magdalena (Table 3).

DISCUSSION

Previous reports assessing the variability of nutrients and zooplankton biomass in this lagoon used Lagrangian sampling techniques, which did not provide enough resolution to detect the tidal front when it moved across fixed sampling stations (Acosta-Ruiz & Lara-Lara 1978, Guerrero-Caballero et al. 1988, Aceves-Medina et al. 1992, Palomares-García & Vera-Alejandro 1995, Rodríguez-Mata 2006). This sampling strategy made detection of aggregations of phyto- and zooplankton along the tidal front almost impossible. In our study, the use of continuous temperature, oxygen concentration, and fluorescent measurements through the mouth of the bay provided the data necessary to describe the tidal front and monitor its evolution during spring and neap tidal cycles with unprecedented detail and sampling effort. The thermo-haline front forced by tidal currents in Bahía Magdalena is a very conspicuous feature that is not only visible in the color of the water, but also in environmental gradients; for example, the average temperature gradient across this tidal front at 4 m was 24 to 240 times more pronounced, at $0.0024^{\circ}\text{C m}^{-1}$, than the latitudinal oceanic front off Bahía Magdalena, at 0.00001 to $0.0001^{\circ}\text{C m}^{-1}$ (Etnoyer et al. 2004, 2006). This pronounced thermo-haline gradient in spring and summer along the tidal front during spring and neap tides suggest that this is a temporary condition that significantly concentrates zooplankton on a semi-diurnal scale. Aggregations of surface zooplankton, mostly copepods, that occur with tidal fronts are likely to be repeated mostly during the flood phase for several consecutive days when spring tides occur for ~9 d in spring and summer and biomass productivity is usually high (Gómez-Gutiérrez & Robinson 2006). This process is absent in autumn and early winter because primary and secondary productivity over the shelf and in the center of the lagoon decline significantly (Gómez-Gutiérrez et al. 1995, 1996, Gómez-Gutiérrez 1996). Also, it is autumn to early winter when tropical water enters the lagoon, which is usually warm and attenuates contrasting thermal conditions between the offshore area and the lagoon (Gómez-Gutiérrez et al. 2001, Gómez-Gutiérrez & Robinson 2006). Hence, we tested the unique summer conditions when intense upwelling activity occurs offshore and

the temperature in the relatively shallow lagoon, less than 40 m deep, increases from high insolation. Under this set of conditions, formation of a more evident and intense tidal front during spring tides than during neap tides occurs. This causes conspicuous aggregations of plankton and a predator response from a large assemblage of marine animals on this temporary, aggregated resource.

Uye et al. (1992) proposed that phytoplankton biomass greatly increases along tidal fronts, which are areas favorable for grazing and population increases of zooplankton, mostly copepods. Although copepods had anomalously high concentrations with relatively elevated egg production along tidal fronts in response to the increased concentration of chl *a*, very high mortality of copepod larvae, nauplii, and copepodites is caused by zooplankton predators. Because tidal fronts forced by tides in Bahía Magdalena are formed with the local semi-diurnal tidal pattern of <6 h and accumulation of zooplankton occurs in this short time frame, it is unlikely that secondary production of dominant zooplankton crustacean species compensates for or even balances local populations lost by nekton and plankton predation. Monthly average female copepod weight-specific growth rates for the 5 most abundant copepod species (*Paracalanus parvus*, *Acartia lilljeborgi*, *A. clausi*, *Centropages furcatus*, *Labidocera trispinosa*) in Bahía Magdalena vary seasonally and interspecifically between 0.31 and $12.22 \mu\text{g C female}^{-1} \text{d}^{-1}$ (Gómez-Gutiérrez et al. 1999, Palomares-García & De Silva-Dávila, in press).

Numerical simulations using current measurements made with an ADCP indicate increased tidal current speed near the lagoon inlet. This is caused by funneling the water mass across the opening, which was estimated, by instantaneous ADCP measurements, at $172\,000 \text{ m}^3 \text{ s}^{-1}$ during a flood tide and $162\,000 \text{ m}^3 \text{ s}^{-1}$ during an ebb tide. Speed of the current was progressively reduced with penetration into the lagoon (Obeso-Nieblas et al. 1999, Robinson & Gómez-Aguirre 2004, Sanchez-Montante 2004).

A Lagrangian 3-dimensional model for baroclinic circulation suggests that non-vertical migratory particles seeded homogeneously in Bahía Magdalena tend to remain inside the bay and after 8 d concentrate along the inner side of Isla Magdalena and Isla Margarita (Morales-Zarate et al. 2006). Three other predictions of this numerical model include (1) only under rare western wind conditions could particles seeded on the northwestern Bahía Magdalena continental shelf enter the lagoon system, (2) under more typical northwest winds, no particles enter the bay, and (3) particles seeded in the main mouth of the bay always penetrate inside to the shallower part of the bay (Morales-Zarate et al. 2006). Our observational study demonstrates that

introduction of species typical of the adjacent shelf into the bay is more frequent and intense than in the Fundy 6.5.1 numerical model prediction (Morales-Zarate et al. 2006), and that a large fraction of plankton from the continental shelf located in the mouth of the bay usually does not penetrate (<6 h) into shallower parts of the bay as the numerical model suggests.

However, the tidal front as such is apparently not an effective wall separating zooplankton fauna of either water mass, because *Calanus pacificus* is frequently collected in low concentrations within the lagoon and *Paracalanus parvus* is found offshore. This is a simple explanation for why these species were relatively ineffective indicators of a water mass, despite their dominance (ISA results). Gómez-Gutiérrez & Robinson (2006) proposed that the tidal front roughly delimits the distribution of juveniles and adults of the numerically-dominant neritic euphausiid *Nyctiphanes simplex* inside the lagoon, although we found calyptopis and furcilia larvae in low concentrations within the central deeper part of the lagoon. In Bahía Magdalena, there are so far no reports or observations of beach-stranding of euphausiids, as observed in the Gulf of California (Montemayor-López & Cisneros-Mata 1999, De Silva-Dávila et al. 2004, López-Cortés et al. 2006). Aurióles-Gamboa et al. (1994) reported year-to-year massive micronektonic red crab *Pleuroncodes planipes* beach stranding on the inner beaches of Isla Magdalena and Isla Margarita. We frequently observed large numbers of red crab on both sides of the tidal front. It is likely that the fraction of the population that crosses the tidal front and spreads into the lagoon becomes stranded from internal circulation patterns, as suggested by the retention pattern of particles seeded inside the hydrodynamic Fundy 6.5.1 numerical model (Morales-Zarate et al. 2006). Therefore, in the strict sense, tidal fronts do not delimit plankton species distribution in the lagoon, but enhance their abundance through concentration mechanisms.

To integrate and summarize our observations and review the oceanographic and biological information published in the last 15 yr on Bahía Magdalena (not including the inlet channels and Bahía Almejas), we devised a conceptual model of the behavior of some of the dominant biotic and abiotic variables during summer to compare spring versus neap tides and flood versus ebb tides along the 18 km transect across the inlet to Bahía Magdalena (Fig. 9).

We propose that significantly different aggregates of zooplankton and community structure occur along the tidal front during spring–neap tides (3 to 9 d) than during flood–ebb tide time scales (<6 h). Our explanation is that intensification of tidal currents during spring tides causes a short shelf water residence time (~5 to 6 tidal cycles) inside the lagoon that promotes greater

environmental variability, which greatly modifies the composition of zooplankton species. This contrasts with a longer residence time usually observed during neap tides (21 to 30 tidal cycles) in the lagoon (Sánchez-Montante 2004). This change in community structure is regulated by 2 processes: (1) during neap tides, zooplankton community structure is stable and relatively more diverse, probably associated with longer residence time of the water mass and less heterogeneous environmental conditions than during spring tides; (2) the variability of the structure of the zooplankton community is less at semi-diurnal time scales than at weekly time scales and is strongly controlled by advective water processes, that is, species behavior of diel vertical migration and speed and direction of the tidal currents.

This study was performed in summer, when the most intense stratification of the water column and maximum concentrations of the nutrients NO_3^- , NO_2^- , and NH_4^+ and chl *a* occur, particularly in deeper waters of the lagoon (Rosales-Villa 2004, Rodríguez-Mata 2006). Nitrates were commonly more concentrated at the inlet of the lagoon than inside Bahía Magdalena, and the highest concentrations of chl *a* near the surface occurred during ebb tides. This suggests that out-bound currents periodically transport phytoplankton biomass onto the shelf water mass (Álvarez-Borrego et al. 1975, Acosta-Ruiz & Lara-Lara 1978, Guerrero-Caballero et al. 1988, Rosales-Villa 2004, Rodríguez-Mata 2006). These studies concluded that this lagoon is primarily a limited-nitrogen rather than limited-phosphate system and depends on transport of benthic nutrients from the continental shelf when upwelling intensifies and intense flood currents enter the lagoon (Fig. 9A–D). As in Bahía Magdalena, high levels of fluorescence have been observed in the stratified and warmer side of tidal fronts in the Gulf of Alaska (Vlietstra et al. 2005). According to the authors, mixed water at the front delivers nutrients, either by diffusion or vertical mixing, across the pycnocline and into the euphotic and stratified water layer, most likely on the side containing the higher phytoplankton concentration.

During spring tides, the copepod *Calanus pacificus* was the dominant zooplankton species at the tidal front and offshore, followed by *Paracalanus parvus* and *Acartia clausi* (Fig. 9). *C. pacificus*, a temperate species typical of the southern part of the California Current, is the only species of this genus found in Bahía Magdalena and is usually present in relatively low numbers (Palomares-García & Gómez-Gutiérrez 1996, Palomares et al. 1998, Hernández-Trujillo et al. 2004). Its overwhelming dominance along the tidal front indicates that, during spring tides, accumulation of plankton along the tidal front comes primarily from offshore

Fig. 9. Conceptual model of tidal front dynamics and plankton and nekton transport across the inlet to Bahía Magdalena during summer, 18 km in length: spring (A, B) and neap (C, D) tides and flood (A, C) and ebb (B, D) tides. TF: tidal front; CS: continental shelf; B: central lagoon. Gray: relative position of the scattering layer (SL) recorded with a split-beam echosounder during diurnal vertical migration (DVM). The bird in (A) indicates flocks actively feeding on plankton and micronekton. Schools of small pelagic fish (fish graphic) avoid regions with elevated current speeds, aggregate during spring tides and disperse during neap tides. Pie graphs: mean relative abundance (%) of numerically dominant zooplankton calculated from standardized abundance (ind.1000 m⁻³) at Shelf, Mouth and Bay during spring and neap tides. (E) Vertical current speed profile measured with an ADCP in the inlet to Bahía Magdalena during spring and neap tides (Robinson & Gómez-Aguirre 2004)

water. This evidence is supported by the presence of *Nyctiphanes simplex*, a neritic species typical of shelf water. Inside the lagoon, *P. parvus* is a typical resident species. During neap tides, it was dominant. This indicates high variability in the transport and concentration of plankton along the tidal front. It is notable that only copepod species were significant indicators of the habitats: *Euchaeta media* in offshore water; *P. parvus*, *Subeucalanus* spp., and *Labidocera* spp. in the frontal

zone; and *Cosmocalanus darwini* and *Acrocalanus* spp. in the lagoon. It is unlikely that this pattern occurs during other seasons because these species are usually replaced by tropical species during autumn and winter; for example, *P. acuelatus* replaces *P. parvus* and *Acartia tonsa* replaces *A. clausi* and *A. lillgeborgi* (Palomares-García & Gómez-Gutiérrez 1996).

We suggest a mechanism for how zooplankton accumulates along the tidal front that differs from previous

proposals (De Robertis et al. 2005, Genin et al. 2005, Morgan et al. 2005, Vliestra et al. 2005). During spring tides, the fastest current during the flood phase occurs at depths between 10 and 20 m (Robinson & Gómez-Aguirre 2004). By comparison, slower, near-surface water accumulates zooplankton as the tidal front moves toward the lagoon. During ebb tides, the fastest current is closer to the surface (<10 m) and probably disperses aggregations of surface zooplankton (Fig. 9E). In our study, zooplankton community structure, abundance, biomass distribution, and the scattering layer recorded with the ADCP demonstrated that along the front, plankton are concentrated exclusively near the surface (<15 m), a layer that contains relatively high chl *a* and very little vertical transport. This favors surface aggregation of zooplankton. Echograms from the ADCP and Simrad EY-60 echosounders indicated that within the 300 m wide frontal band, concentrations of plankton and nekton decreased abruptly at the lateral edge of the zig-zag transects. Vliestra et al. (2005) described how small zooplankton that are poor swimmers, such as euphausiid larvae, which have a shorter vertical migration range than adult euphausiids, are entrained by local currents (<4 m s⁻¹) and are concentrated in surface waters and temporarily become attractive to top marine predators that ordinarily feed on large juvenile and adult euphausiids. For the west coast of the Baja California peninsula, using this scenario, tidal fronts, such as that which occurs at Bahía Magdalena, may enhance the food value of small-sized prey to seabirds, prey that may not be routinely consumed.

Schools of fish are strongly attracted by concentrations of food. Most of the nektonic animals detected with the Simrad EY-60 echosounder were distributed throughout the water column, indicating a distribution independent of local currents. Under typical conditions and concentrations, fish schools avoid seabird predation. However, when highly-concentrated, planktonic prey becomes attractive quarry. Our observations and sampling with a submarine videocamera, plankton tows, and Isaacs-Kidd net midwater trawls along the tidal front showed that scattering layers comprised mostly red crab *Pleuroncodes planipes*, sardine *Sardinops sagax caeruleus*, and Pacific mackerel *Scomber japonicus* that were actively feeding on zooplankton. Sardines in Bahía Magdalena actively feed on phytoplankton and copepods (Romero-Ibarra & Esquivel-Herrera 1989), as well as swarms of decapod larvae, stomatopods, and euphausiid larvae (J. Gómez-Gutiérrez unpubl data). Shoals of small pelagic fish tend to avoid regions with tidal currents >100 cm s⁻¹, a condition usually found at the inlets of the lagoon complex, presumably to avoid consuming energy to maintain their position against flood tidal currents (Robin-

son et al. 2007). They concentrate near the tidal front (at the side of the bay), where the current speed is usually reduced (Fig. 9A). Carnivores aggregate along the tidal front to prey on zooplankton, red crab, and sardine. Of 80 seabird species inhabiting the lagoon complex, 10 of the most abundant seabirds in the lagoon, pelicans and their allies, actively prey on schools of fish. Isla Margarita harbors a colony of ~3000 pairs of brown pelicans (Zarate-Ovando et al. 2006). Thus, these surface aggregations of plankton and nekton are always preyed on by large numbers of seabirds. Predictable food supplies at tidal fronts, where a high density of easily accessible prey is promoted by currents, allow micronektonic animals, seabirds, and marine mammals to spend time and energy here, which they would otherwise spend on other activities, such as reproduction (Vlietstra et al. 2005).

Our conceptual model indicates that accumulation of plankton along tidal fronts in the subtropical Bahía Magdalena is a seasonal event, when spring tides are prominent during spring and summer. This is an influential oceanographic process that modifies multi-trophic level ecology of subtropical lagoons. To reach an even better understanding of this process and the area of influence of the tidal front, vertical plankton sampling, along with a more sophisticated measurement of horizontal gradients, will be necessary.

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