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Diel variability in the vertical distribution of coastal barnacle larvae in the Bay of Cartagena, Chile

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Abstract

Background Vertical distribution of zooplankton is an important biological factor that can modulate zooplankton transport, dispersal, and survival in the ocean. Seawater temperature and the associated formation of a thermocline can affect the spatial distribution of organisms in the water column and possibly modulate larval vertical distribution in coastal waters. In this study, we examined larval vertical distribution over small spatial scales where environmental conditions could exhibit strong and fairly predictable variability.

Methods Diel variation in vertical distributions of barnacle larvae across the thermocline was characterized within the Bay of Cartagena of central Chile. Two intensive 21- and 24-h surveys were conducted in the northern (ECIM) and southern (CTGN) extremes of the bay in summer 2016 and spring 2017. In each survey, vertical tows were conducted at both sites every 3 h above and below the thermocline.

Results During summer 2016, larval vertical distribution differed between taxa (balanids and verrucids), barnacle stages (nauplii, cyprids), and sites within the bay. Of all taxa analyzed Balanid nauplii at ECIM were more abundant in the bottom layer during the day and at the surface during the night, suggesting they can control their vertical distribution and follow a diel pattern. According to the results all barnacle larvae were found in different positions in the water column between day and night during periods of high stratification in this survey. In spring 2017 all barnacle larvae were confined to the upper layer, despite the strength of stratification, potentially as a result of the intrusion of hypoxic water ($< 2 \text{ mL L}^{-1}$) at the bottom, which reached up to around 5 m deep.

Conclusions We conclude that diel vertical distribution is not uniform across different barnacle larvae taxa and stages within the Bay of Cartagena and is not affected by stratification. Of all the taxa analyzed, only balanid nauplii showed a pattern of diel vertical migration across the thermocline under certain hydrographic conditions.

Keywords Barnacle larvae, Chile, Vertical distribution

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Background

The vertical distribution of zooplankton species in the water column is probably one of the most important biological factors that can modulate and determine the transport, dispersal, and survival of these organisms in the ocean [15, 38, 41, 48]. Because the magnitude and direction of marine currents frequently vary with depth like most physico-chemical and biological variables (e.g., the distribution of predators and food), the transport and fate of zooplankton are expected to depend to a great extent on their depth in the water column. This is particularly crucial for the larvae of coastal benthic species, since vertical positioning can affect their effective dispersal as well as the possibility of returning to the coast to settle, metamorphose, and eventually contribute to the next generation [11, 29, 38, 39, 46, 50].

Unlike horizontal swimming, which is usually considered to have a minor impact on effective dispersal, vertical displacement can be significant for transport, escaping predators, and locating food. It also strongly depends on the organism's swimming behavior and buoyancy capabilities [17, 24, 54]. Vertical migration with well-defined temporal patterns occurs in most groups of zooplankton invertebrates [7, 16, 19, 54]. Species that perform the canonical diurnal vertical migration (DVM) move towards the surface at night and into deeper waters during the day [18, 21, 36, 54, 62]. There are many hypotheses offered to explain vertical migration patterns [7, 17, 22, 36, 78], however, whatever the determinants of vertical migration cycles, larval behavior that leads to different positions in the water column can have important consequences for transport whenever baroclinic ocean currents are encountered, thus potentially influencing cross-shore transport to the coast [1, 2, 38].

If the vertical distribution of meroplankton plays a role in increasing transport to settlement sites, one must expect their ability to position themselves in the water column to be highly plastic in order to be coupled to extremely variable oceanographic and biological conditions encountered in the coastal ocean, especially within the coastal boundary layer. Empirical studies in different oceans and model species have shown that changes in physical, chemical, and biological conditions of the water column can alter the vertical distribution of zooplankton over timescales of days to months [3, 5, 19, 41, 42, 54, 56, 75]. Seawater temperature and the associated formation of a sharp seasonal thermocline are among the most relevant physical factors that directly or indirectly affect the spatial distribution of organisms in the water column, and it is therefore usually involved in their vertical distribution and movement. Mean temperature affects larval metabolic and development rates [47] as well as feeding and swimming behavior [10, 14, 63]. Thus, in marine

environments where the influence of river plumes is mainly negligible, temperature is the main factor driving water density, and thermal gradients imply sharp density changes in the water column that can be critical for the distribution of particles, food, and predators, therefore affecting vertical migration behavior of larvae. Moreover, stratified water columns tend to have productive oxygen-rich waters above the thermocline and oxygen-poor conditions in deeper waters, which could be a lethal condition for meroplanktonic larvae, as was described by Vaquer-Sunyer & Duarte [71]. These authors have shown that oxygen values equal to or lower than 2 mg L^{-1} are lethal for species of gastropods, bivalves, fish, and crustaceans. Also, lower values of oxygen could modulate the distribution of larvae, since Lagos et al. [35] demonstrated through laboratory experiments that several marine invertebrate larvae avoid hypoxic water.

Here, we examine variation in larval vertical distribution over small spatial scales where environmental conditions could exhibit strong and fairly predictable variability. The Bay of Cartagena in central Chile is an open, wave-exposed bay that measures approximately 8–10 km across and exhibits strong spatial variability in water column structure between the southern and northern ends, scarcely 6 km apart [4]. Bonicelli et al. [4] showed that thermal diurnal fluctuations (i.e., during a 24-h period) and intensity of thermal stratification differ substantially between the ends of the bay, driven by variability in meridional winds. The southern end of the bay presents a more stratified water column despite the afternoon sea breeze and a strong influence of semidiurnal processes (tides), while the northern end displays surface temperature variability primarily associated with the diurnal wind cycle [4]. Through time-intensive surveys at each extreme of the bay, we assessed whether the vertical distribution of barnacle larvae was persistent over time and consistent with patterns of vertical migration.

Methods

Study area

The Bay of Cartagena is located in central Chile ($33^{\circ}31.2'S$, $71^{\circ}37.1'W$), leeward of the Matanzas-Punta Toro upwelling center and, as defined by Graham & Largier [28], this bay is considered a region of “upwelling shadow” [43, 65, 76]. As in other bays of similar features in northeastern Pacific regions of coastal upwelling [26–28, 58], the Bay of Cartagena is characterized by higher temperatures and lower concentrations of surface macronutrients as well as a highly stratified water column (17°C near surface and 12°C near bottom) during spring and summer months [4, 33, 43, 45].

Regarding its fauna the Bay of Cartagena is also quite similar to other coastal environments along the Chilean

coast. Its rocky intertidal community has been extensively documented [44, 61]. In this bay, there are three species of barnacles that dominate the intertidal rocky shores: the chthamalids *Jehlius cirratus* and *Notochthalmalus scabrosus* and the balanid *Notobalanus flosculus* in the lower intertidal zone [35]. Other barnacle species, *Balanus laevis* and *Austromegabalanus psittacus*, are common in the intertidal zone, but more abundant in subtidal habitats. There was little ecological information about the small *Verruca laevigata* species, although it is commonly found on rock surfaces and shells of other invertebrates in the Bay of Cartagena [9] as well as on the coasts of Iquique [67] and Concepción [40]. Therefore, this study also provides new information about the meroplanktonic larval composition within the Bay of Cartagena.

Near-shore surveys

Two intensive hydrographic and biological surveys were conducted in the Bay of Cartagena (Fig. 1) in summer 2016 (21-h survey, February 29 to March 1) and spring 2017 (24-h survey, October 23 to 24) onboard the research boat *Ilán* of the *Estación Costera de Investigaciones Marinas* in Las Cruces, Chile. Two oceanographic stations, one located at the bay’s northern extreme

(ECIM) and the other at the southern (CTGN), were sampled every 3 h during each survey period at bottom depths of less than 30 m (Fig. 1B). At each station, two vertical zooplankton tows were conducted within two layers: above (surface layer) and below (bottom layer) the thermocline, using a 0.5 m diameter closing net with 150 μm mesh. Zooplankton samples were preserved in 95% alcohol and analyzed in the laboratory under a dissecting microscope using published references [57, 73]. Thermocline position was defined aboard the watercraft as the approximate depth at which the sharpest vertical temperature change was observed. In order to calculate this, a CTD-OF (Conductivity, Temperature, Depth-Oxygen-Fluorescence, Sea-Bird 19) cast spanning the entire water column was conducted at each station to register temperature, dissolved oxygen, and fluorescence (which was used as a proxy of chlorophyll-*a*). Then, the program Sea-Save was used to visualize the CTD-OF temperature profile shortly after the cast and determine the position of the thermocline prior to each net tow. In general, the thermocline was located between 5 and 10 m depth. When the thermocline was well-defined, the surface layer tow was performed from the thermocline’s bottom depth to the water’s surface. For safety issues regarding the net

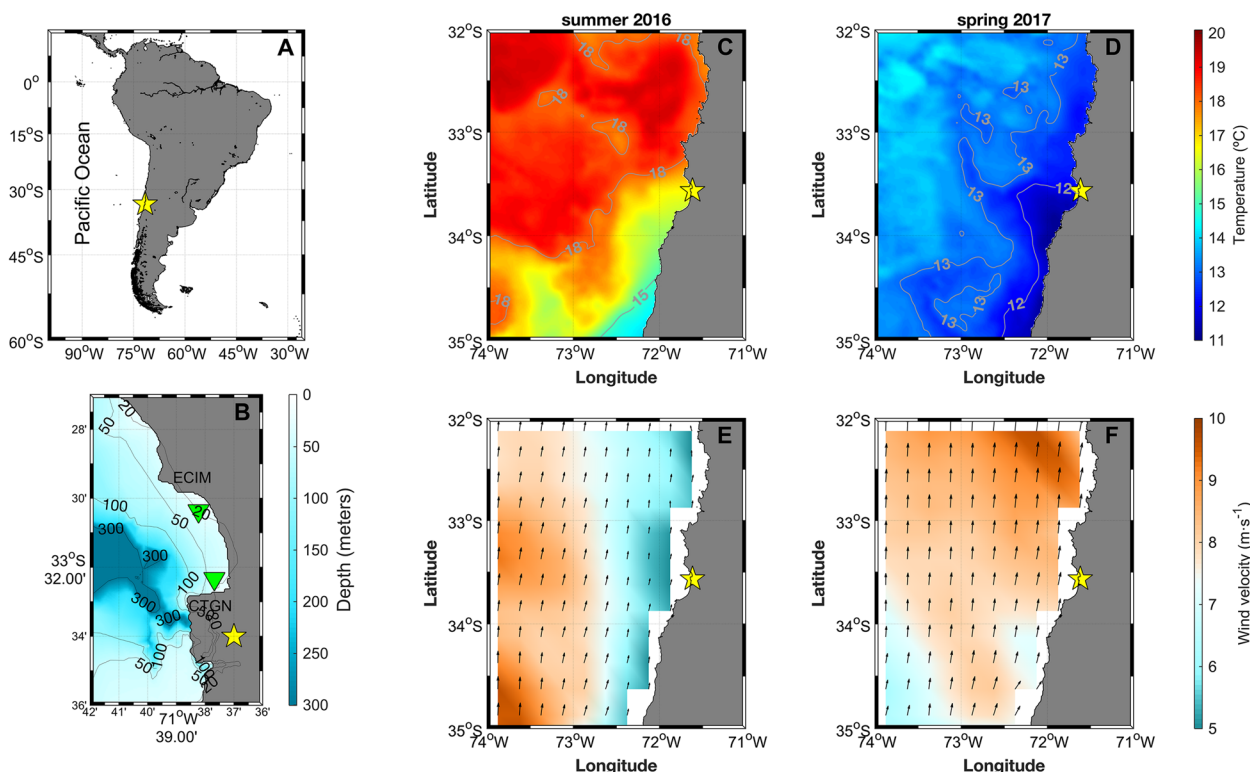


Fig. 1 Study area in central Chile (A) and locations of stations sampled (B). The yellow star marks the location of the Bay of Cartagena, and the green triangles denote the location of the station samples (B). Satellite images of regional sea surface temperature (C, D), and wind (E, F), during the summer 2016 survey (C, E) and the spring 2017 survey (D, F)

integrity, bottom tows were performed from 2 m above the seafloor to the bottom limit of the thermocline, considering that the depth of each station was 25 m approximately. The latter was defined as the depth at which the vertical thermal gradient decreased and coincided with the presence of a well-defined sub-thermocline fluorescence maximum as described and modeled by Varela et al. [72]. When there was no obvious thermocline, the surface layer tow was performed from 5 m depth to the surface.

Satellite images, sea level, and wind

The regional oceanographic and meteorological context for the plankton surveys was examined using available satellite imagery for sea surface temperature and wind. More specifically, we used the Multi-scale Ultra-high Resolution Sea Surface Temperature (MUR SST) data from NOAA's service alongside satellite wind data obtained from ASCAT scatterometer from IFREMER to produce images of 1-km and ~28-km resolution, respectively. Sea level data were obtained from the Sea Level Station Monitoring Facility (<http://www.ioc-sealevelmonitoring.org/station.php?code=valp>).

Data analysis

Barnacle larval vertical distribution were expressed as individuals per cubic meter since sample volume inevitably changed somewhat among surveys. Two samples were collected from each tow and depth, and then averaged to estimate larvae per cubic meter. Since this averaging and standardization made counts a quasi-continuous variable and since at large numbers of events (as was the case with larvae) the Poisson distribution that governs count processes can be approximated by and is indistinguishable from the Normal distribution (Laplace continuity theorem), we analyzed data under the approximate normality assumption and used ANOVA for significance tests. This ANOVA approach was preferred over modeling direct count observations with Generalized Linear Models with Poisson distribution using offset (volume sampled as covariate, e.g., 8) because we have nested structures of subsamples. We used two-way ANOVAs for each survey and site (ECIM and CTGN), considering day/night and depth as fixed factors. The samples collected 1 h before and after sunrise and 1 h before and after sunset were excluded from the analyses in order to more clearly define the samples within each level of the factor “day/night” and to avoid temporal dependency between day and night. The assumption of approximate normality was visually inspected on residuals and while some deviations occurred, they should not affect conclusions as ANOVA is robust to normality [55, 70]. To stabilize variances (assumption of homoscedasticity) for

Verruca sp. Nauplii, we transformed data using fourth root transformation, which was not necessary for other taxa”.

To explore the effect of stratification on diel vertical distribution the log response ratio (LRR) effect size metric was calculated. The LRR determines the effect size as the log-proportional change between the mean density of surface and bottom larval relative abundance $\ln(X_s/X_b)$, where X represents the surface (s) and bottom (b) abundance divided by the total abundance of the water column, including the bias-corrected estimator proposed by Pustejovsky [52] for small samples. This was calculated separately for each taxa, survey, day and night and during periods of high and low magnitude of thermal stratification. The magnitude of thermal stratification was estimated as the difference in temperature between the surface and 1.5 m below the thermocline. High (low) stratification values were considered as the ones greater (lower) than the 50th percentile of the distribution for each survey separately. The end points of the confidence intervals (CI) were estimated as was proposed by Pustejovsky [53]. Positive values indicate that larvae are positioned above the thermocline (i.e., 95% CI's above and do not overlap 0), while a negative value indicates that larvae are located below the thermocline (i.e., 95% CI's below and do not overlap 0). Thus, if stratification of the water column were to limit diurnal variability in the vertical distribution of larvae, we would expect positive or negative values of LRR during day and night at high stratification. On the other hand, under a scenario of weak stratification, the LRR would become positive during the night and negative during the day if barnacle larvae are exhibiting DVM behavior.. The relationship between dissolved oxygen and larval abundance was evaluated for each survey and taxon by a Pearson correlation analysis between the oxygen registered at 3 m depth and larval abundance in the surface layer, as well as the oxygen registered at 12 m depth and larval abundance in the bottom layer.

Results

Physical conditions

Oceanographic conditions between the two surveys varied substantially, as shown by available satellite data (Fig. 1) and the temperature time series from the CTD-OF casts (Figs. 2, 3). Conditions during the summer 2016 survey were indicative of generally warm waters throughout the region (Fig. 1C), most likely associated with the 2015–2016 El Niño event [60, 64]. During this survey, winds were weak (Fig. 1E) and the water column was more stratified (Fig. 2) throughout the entire Bay of Cartagena. However, there were slight differences in the temperature variability over the 21-h cycle between extremes

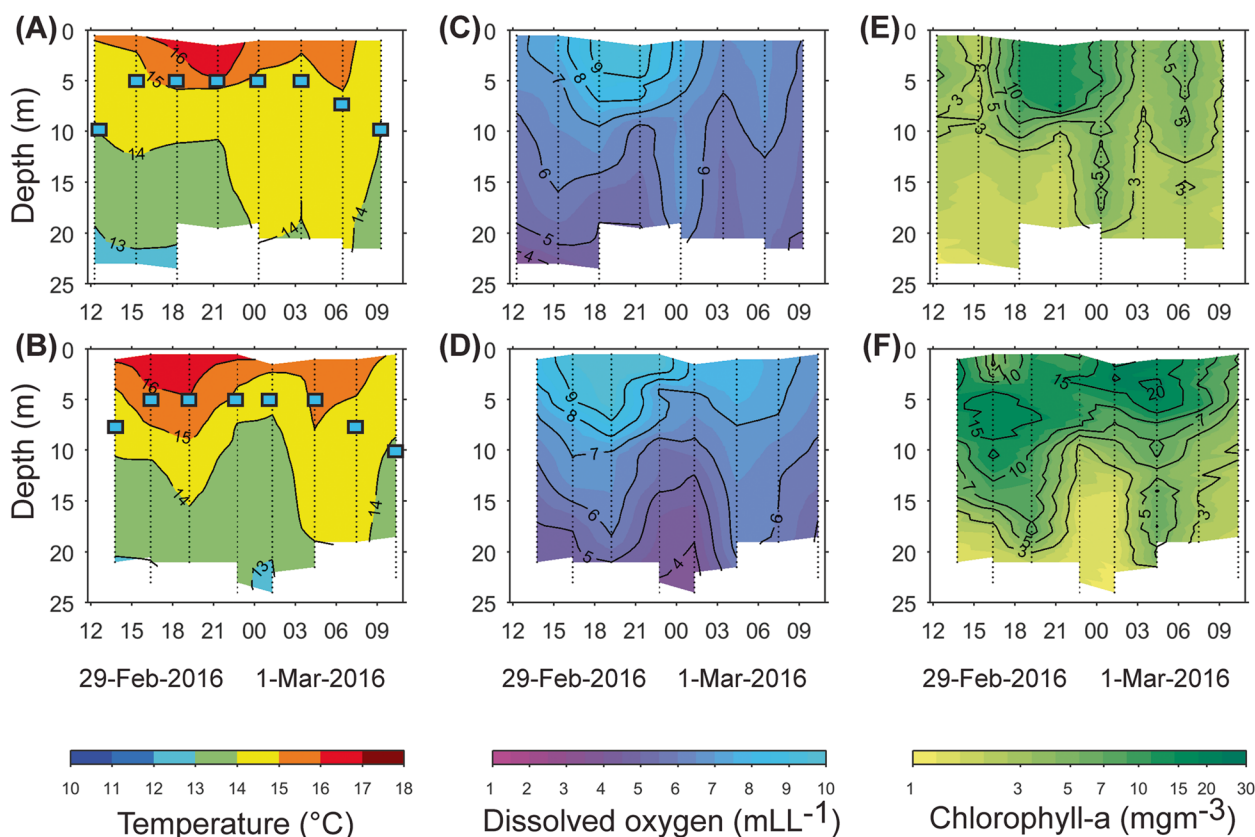


Fig. 2 Temperature (A, B), dissolved oxygen (C, D), and chlorophyll-a (E, F) profiles from the summer 2016 survey at ECIM (top panels) and CTGN (bottom panels). The blue rectangles mark the location of the thermocline defined aboard (see methods)

of the bay. Temperature at ECIM showed a clear diurnal signal; the isotherm of 14 °C remained at approximately 10 m depth from 12:00 to 21:00 h during the first day of the survey, while the next day, it dropped down to a depth of 20 m between midnight and early morning (Fig. 2A). Contrary to ECIM, CTGN showed a clear semi-diurnal signal. The 14 °C isotherm deepened twice during the entire survey, during the afternoon the first day and between 04:00 and 09:00 h the next day (Fig. 2B). Dissolved oxygen (DO) values were above 3 mL L⁻¹ throughout the water column at both sites (Fig. 2C, 2D). At ECIM, the highest values of DO (> 8 mL L⁻¹) and fluorescence (> 10 mg m⁻³) (Fig. 2E, 2F) were observed above 10 m depth during the first day of the survey, which coincides with the highest vertical gradient of temperature. At CTGN, however, fluorescence showed a clear semi-diurnal pattern, as the other variables, and minimum values were observed between 21:00 and 03:00 h below 10 m depth, which coincides with cold (< 14 °C) and low oxygen (< 6 mL L⁻¹) waters.

The spring 2017 survey presented conditions indicative of strong upwelling: strong equatorial winds (Fig. 1F), a characteristic band of cold surface waters nearshore

(Fig. 1D), and low temperatures throughout the water column (Fig. 3). Seawater temperatures were much lower—between 10.8 °C and 14.4 °C at both sites—and the water column was less stratified than during the first survey (Fig. 3A, 3B). Important differences in the thermal structure were again observed between the two sites. At ECIM, there was a clear diurnal signal, with the 11 °C isotherm located close to the bottom between 12:00 and 21:00 h and then ascending to the surface between 03:00 h and approximately 09:00 h (Fig. 3A). At CTGN, the diurnal or semi-diurnal signals were not clear, and the 11 °C isotherm was located between 15 and 10 m depth throughout the 24-h survey (Fig. 3B). Overall DO levels were much lower in the 2017 survey than in 2016 (compare Fig. 2 and Fig. 3). At ECIM, we observed a clear diurnal signal of DO and fluorescence (Fig. 3C, 3E), while at CTGN, the diurnal signal was less pronounced, with lower values of DO and fluorescence remaining below 5 m depth (Fig. 3D, 3F).

Larval vertical distribution

Differences in the abundance of balanid and *Verruca* sp. nauplii and balanid cyprids with depth were observed

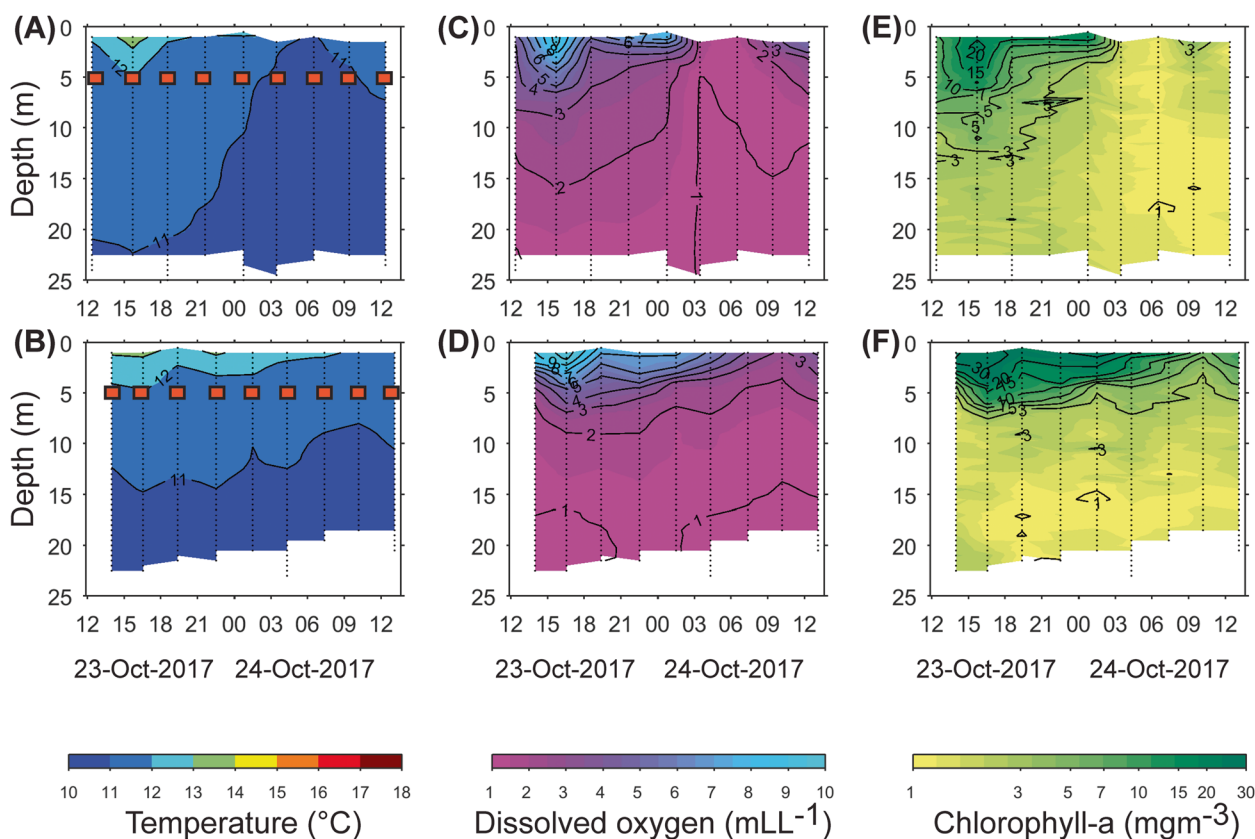


Fig. 3 Temperature (A, B), dissolved oxygen (C, D), and chlorophyll-*a* (E, F) profiles from the spring 2017 survey at ECIM (top panels) and CTGN (bottom panels). The orange rectangles mark the location of the thermocline defined aboard (see methods)

through time during both surveys. During the summer 2016 survey, at ECIM, balanid nauplii showed a switch in abundance between the surface and bottom layers over time (Fig. 4A). During the first day of the survey, larval abundance was greater within the bottom layer in the afternoon, and during the beginning of the night abundance began increasing at the surface and decreasing at the bottom (Fig. 4A). Between midnight and early morning, abundance was at a minimum in both layers, then increased again later that morning (Fig. 4A). For *Verruca* sp., nauplii abundance fluctuation exhibited a similar pattern between the surface and bottom layers (Fig. 4B). In both layers, larval abundance followed a semidiurnal fluctuation with peaks of abundance at noon, midnight, and early morning (Fig. 4B). Balanid cyprids also exhibited a similar fluctuation between layers; however, unlike *Verruca* sp., balanid cyprids showed a positive trend throughout the study period in the bottom layer and peaks of abundances after 21:00 h at the surface (Fig. 4C). At CTGN, balanid nauplii (Fig. 4D) and cyprids (Fig. 4F) showed minimum values during the day in both layers and increased to maximum values at night, but only at the surface. Meanwhile, *Verruca* sp. nauplii abundance

showed a positive trend through time in the bottom layer and peaks of abundances in the surface layer after 21:00 h (Fig. 4E).

During the spring 2017 survey, both the fluctuation and the vertical distribution during the 24-h cycle differed from the summer 2016 survey. At ECIM, balanid nauplii appeared in greater abundance at the surface during the first 12 h of the survey (Fig. 5A). Then, between 01:00 and 10:00 h, it decreased in both layers to minimum values (Fig. 5A) and increased again at noon. *Verruca* sp. nauplii (Fig. 5B) presented the same pattern as the balanid nauplii, though they declined to minimum values 6 h earlier. The contrary occurred for balanid cyprids, which showed minimum values during the first 9 h of the survey and then increased at midnight, especially in the surface layer (Fig. 5C). At CTGN, all three barnacles' abundances (Fig. 5D, 5E, 5F) were higher at the surface during the majority of the survey and showed the highest values around midnight.

Comparing the vertical distribution between daytime and nighttime during the summer 2016 survey at ECIM, we observed that only balanid nauplii showed a significant interaction between the factors day/night and depth

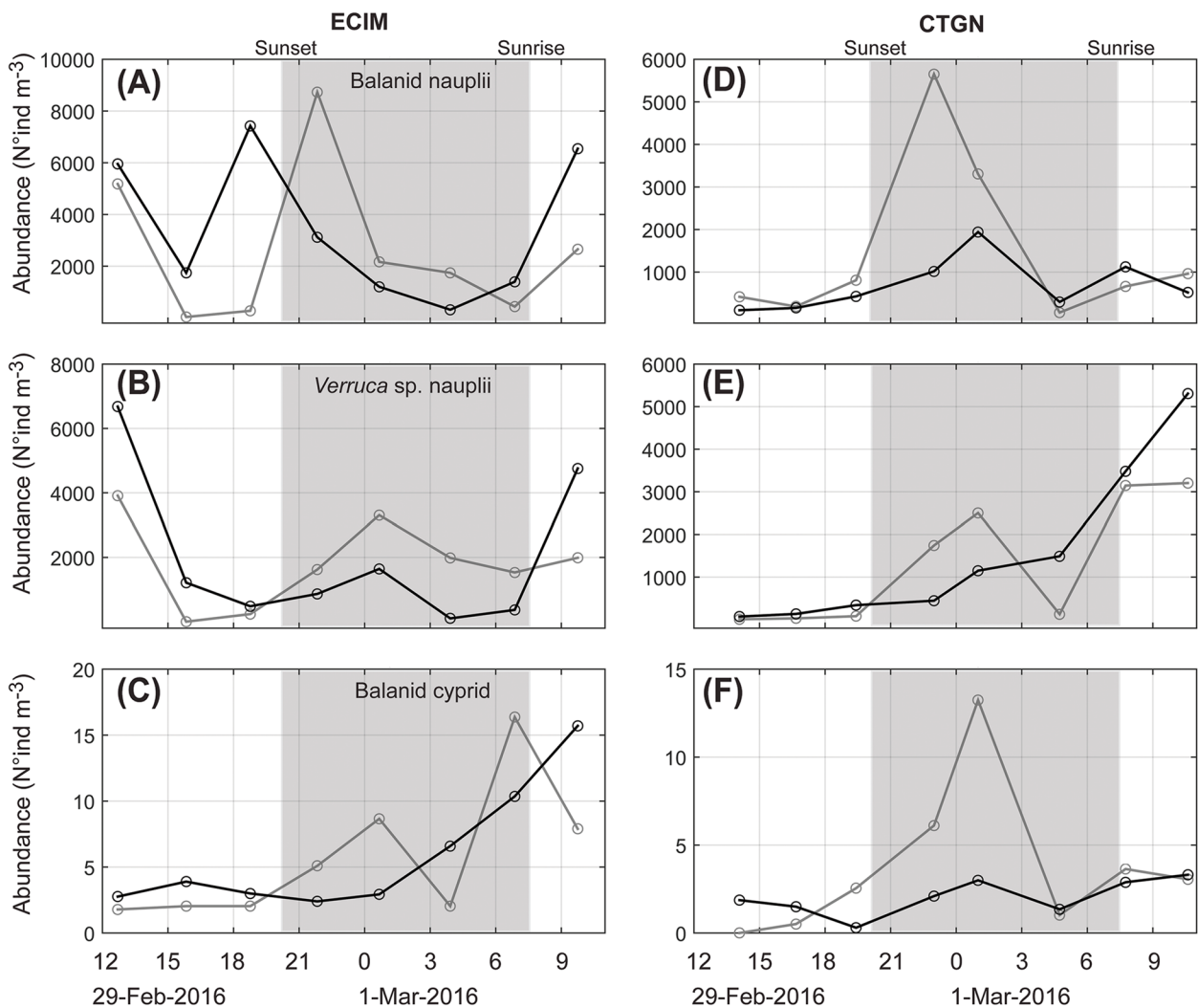


Fig. 4 Time series abundance for balanid nauplii (A, D), *Verruca* sp. nauplii (B, E), and balanid cyprids (C, F) above (gray line) and below (black line) the thermocline during the summer 2016 survey at ECIM (left panels) and CTGN (right panels)

(Table 1), which indicates vertical migration. The abundance was significantly greater during daytime in the bottom layer and in the surface layer at night (Fig. 6A), a pattern that was generally consistent with a posteriori classification of group combinations. At CTGN, however, balanid nauplii showed higher abundances at night than during the day in both layers, rendering significant the effect of depth and a non-significant interaction with day/night condition (Fig. 6B, Table 1). During the spring 2017 survey (Fig. 7), all larval taxa and stages presented significantly higher abundance in the surface layer than the bottom layer at both sites, independent of day/night condition (Table 1). In addition, regardless of the layer depth, *Verruca* sp. nauplii showed significantly greater abundance during the daytime than nighttime at ECIM, while balanid cyprids were more abundant during the nighttime (Fig. 7C, 7E, Table 1). However, at CTGN, the

vertical distribution of *Verruca* sp. nauplii (Fig. 7D) and balanid cyprids (Fig. 7F) varied significantly with time of the day only in the surface layer, thus a significant interaction between factors was observed (Table 1). However, the pattern of variability was not consistent with diel migration (Fig. 7C-F).

During the summer 2016 survey the vertical distribution of the three taxa across the thermocline was not affected by stratification since during high stratification LRR presented different values between day and night (Fig. 8A, 8B, 8C). For *Verruca* sp. nauplii (Fig. 8B) and Balanid cyprid (Fig. 8C) LRR showed positive values during night and negative values during day, meanwhile LRR for Balanid nauplii was positive during night and not different from zero during the day (Fig. 8A). During low stratification LRR for balanid nauplii was negative during day and not different from zero during night

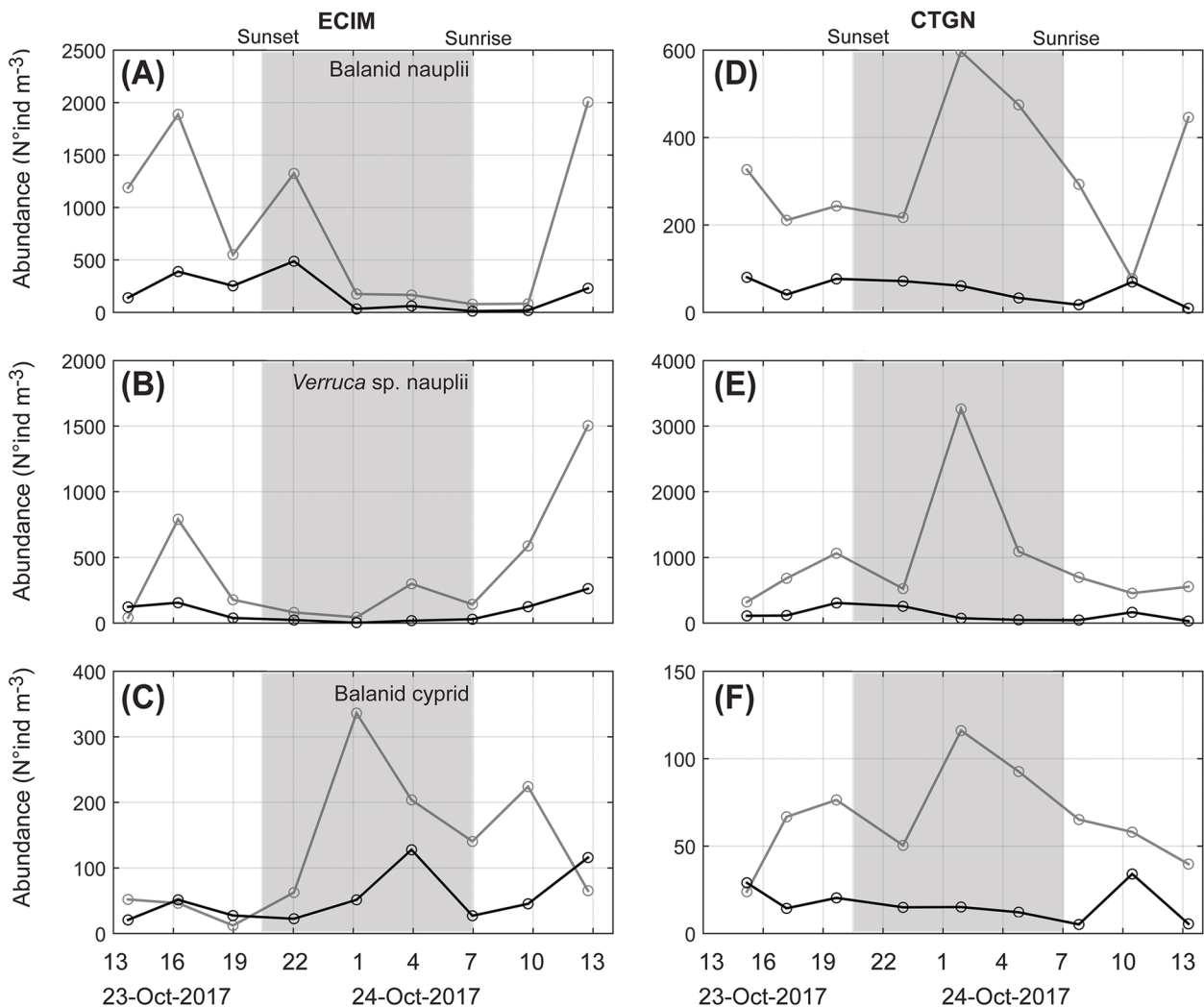


Fig. 5 Time series abundance for balanid nauplii (A, D), *Verruca* sp. nauplii (B, E), and balanid cyprids (C, F) above (gray line) and below (black line) the thermocline during the spring 2017 survey at ECIM (left panels) and CTGN (right panels)

(Fig. 8A), for balanid cyprid (Fig. 8C) was positive during day and not different from zero during night and for *Verruca* sp. nauplii was positive during night and negative during the day, as was also observed during high stratification (Fig. 8B). During the spring 2017 survey, the vertical distribution across the thermocline of all barnacles was not affected by strength of the thermocline, since LRR was positive during day and night and not associated with the magnitude of stratification (Fig. 8D, 8E, 8F). Finally, the relationship between DO and larval abundance was positive for the three taxa during the spring 2017 survey (Fig. 9D, 9E, 9F); however, only balanid ($r=0.72$, $P<0.001$) and *Verruca* sp. ($r=0.54$, $P<0.001$) nauplii showed significant correlations between variables. Contrarily, during the summer 2016 survey, the correlations were negative for the three taxa. However, only *Verruca* sp. nauplii ($r=-0.35$,

$P=0.04$) showed a significant correlation between variables (Fig. 9B).

Discussion

Our results indicate that diel vertical distribution of barnacle larvae in coastal waters changed between species, stages and sites within Cartagena Bay and is not affected by stratification. Instead, we show that barnacle larvae vertical distribution is highly influenced by the intrusion of hypoxic water into the near-shore, which may be a particularly important and usually overlooked factor in coastal environments.

During the summer 2016 survey balanid nauplii at the northern site (ECIM) were mainly distributed within the bottom layer during the day, but at night, they were slightly more abundant within the surface layer. This implies that balanid nauplii may have swum across

Table 1 Two-way ANOVAs to evaluate differences in barnacle larvae vertical distribution between daytime and nighttime as a proxy of DVM, using for each survey and for each site (ECIM and CTGN), with day/night and depth considered fixed factors. Bold numbers indicate $p < 0.05$

Summer 2016									
	Balanid nauplii			Balanid cyprids			Verruca sp. nauplii		
	d.f	F	P	d.f	F	P	d.f	F	P
ECIM									
depth	1	0.0403	0.8426	1	0.3911	0.5379	1	0.2715	0.6073
day/night	1	0.4359	0.5157	1	0.0931	0.7630	1	0.3272	0.5729
depth*day/night	1	7.3230	0.0126	1	1.9568	0.1752	1	4.2039	0.0519
CTGN									
depth	1	2.6847	0.1178	1	1.5702	0.2254	1	0.1218	0.7309
day/night	1	5.9757	0.0244	1	2.9690	0.1011	1	1.1659	0.2938
depth*day/night	1	1.4779	0.2390	1	3.1473	0.0921	1	0.1815	0.6749
Spring 2017									
ECIM									
depth	1	7.9226	0.0088	1	7.7850	0.0094	1	11.905	0.0018
day/night	1	1.6895	0.2043	1	5.5275	0.0260	1	15.3629	0.0005
depth*day/night	1	1.5577	0.2223	1	3.3459	0.0780	1	0.0031	0.9559
CTGN									
depth	1	24.9543	<0.0001	1	29.8676	<0.0001	1	49.7367	<0.0001
day/night	1	2.0647	0.1637	1	3.2714	0.0830	1	3.0444	0.0938
depth*day/night	1	1.8221	0.1897	1	6.4777	0.0178	1	5.1033	0.0332

the thermocline toward the surface during the night and toward the bottom during the day in the northern extreme of the bay. Another study performed at the Bay of El Quisco (20 km north of the Bay of Cartagena) also demonstrated a day/night variation in balanid nauplii vertical distribution, which was considered a proxy of DVM [5]. It is important to mention that the larval distribution sampling methodology in the present study, unlike the one used in El Quisco, allows us to identify the moment when larvae change their vertical position and cross the thermocline. Here, we observed that, at sunset, balanid nauplii abundance suddenly increases at the surface and decreases at the bottom, coinciding with low tide (Fig. 4, Fig. 10). This increase in abundance at the evening low tide suggests that both light and tidal oscillation may be important factors in determining vertical distribution throughout the water column. Several studies have demonstrated that diurnal vertical distribution for larval decapods is synchronized with tidal cycle, a potential mechanism to mediate dispersal [15, 23, 54]. Also, the sudden increase of larvae at the bottom during the day and at the surface at night (i.e., between 18:00 and 0:00 h) coincided with the highest concentration of chlorophyll-*a* found at the surface ($> 10 \text{ mg m}^{-3}$) during the survey, suggesting that this feeding stage could have swum

towards the surface to feed during the night. This was not the case for the balanid cyprid, in which the maximum surface abundance did not coincide with the chlorophyll-*a* peaks, thus suggesting some degree of ontogenetic variation in diel vertical distribution for these taxa. Ontogenetic differences in diel vertical distribution for balanids larvae have also been observed by Bonicelli et al. [5] at El Quisco; the authors attributed this to the physiological differences between cyprids and nauplii. While the nauplii stage must feed, the cyprid is a non-feeding stage and may prioritize remaining in lower temperatures to conserve energy and extend the critical competence period. This was not the case for *Verruca* sp. nauplii. The results for this taxon indicated that individuals did not change vertical position throughout the day at ECIM.. It is important to mention that the sampling resolution (i.e., one layer above and one below the thermocline) did not allow us to detect slight changes in their vertical distribution. It is possible that the larvae could be located within or slightly above the thermocline at night and slightly below it during the day, which would be impossible to detect with the methodology used in this study. Also, because of their small size, vertical movements may have not been captured with this methodology, since *Verruca* sp. nauplii are considerably smaller than balanid nauplii, and usually smaller larvae are slower swimmers [12].

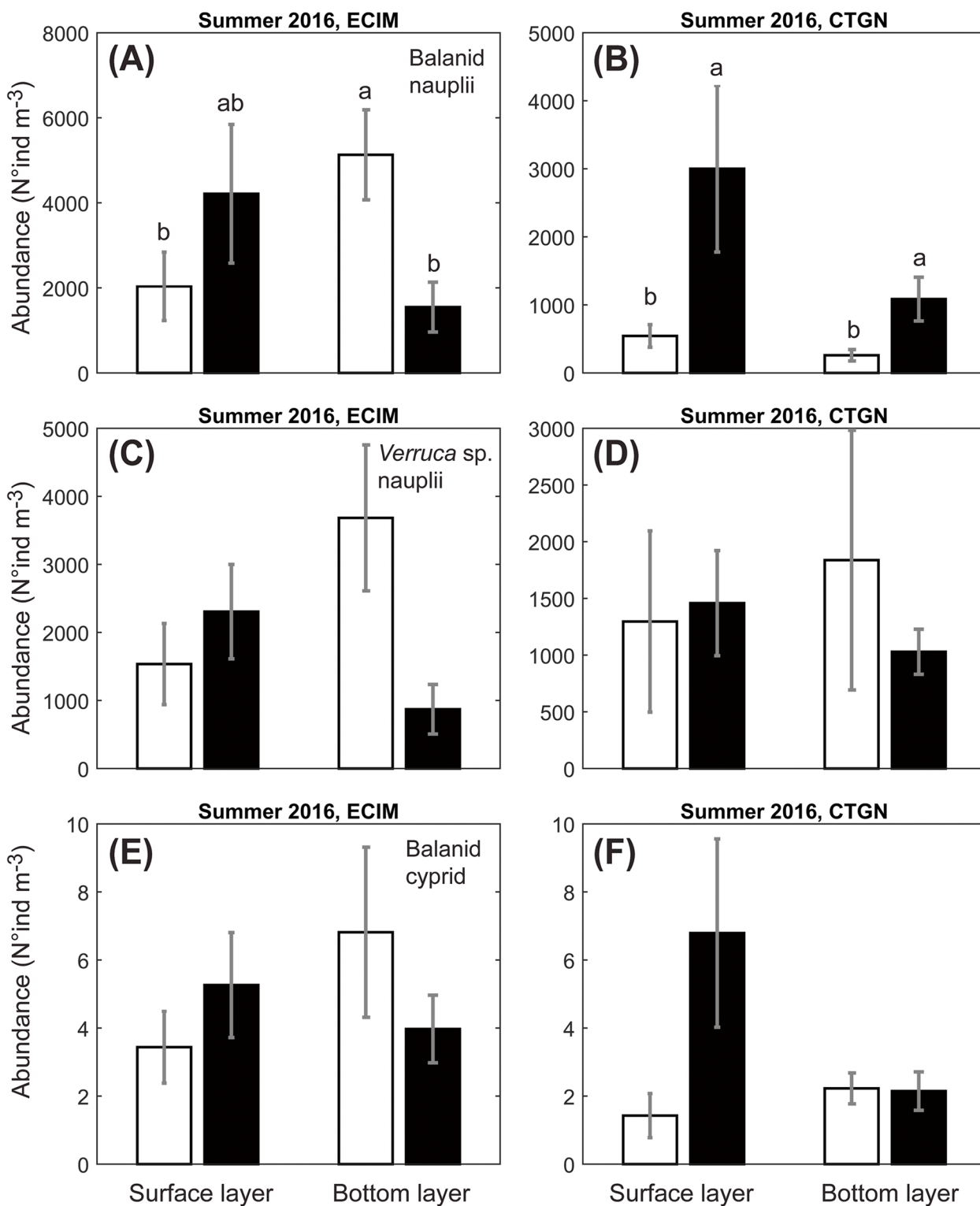


Fig. 6 Mean vertical distribution of barnacles: balanid nauplii (A, B), *Verruca* sp. nauplii (C, D), and balanid cyprids (E, F) during daytime (white bars) and nighttime (black bars) at ECIM (left panels) and CTGN (right panels) during summer 2016 survey. Error bars indicate standard error

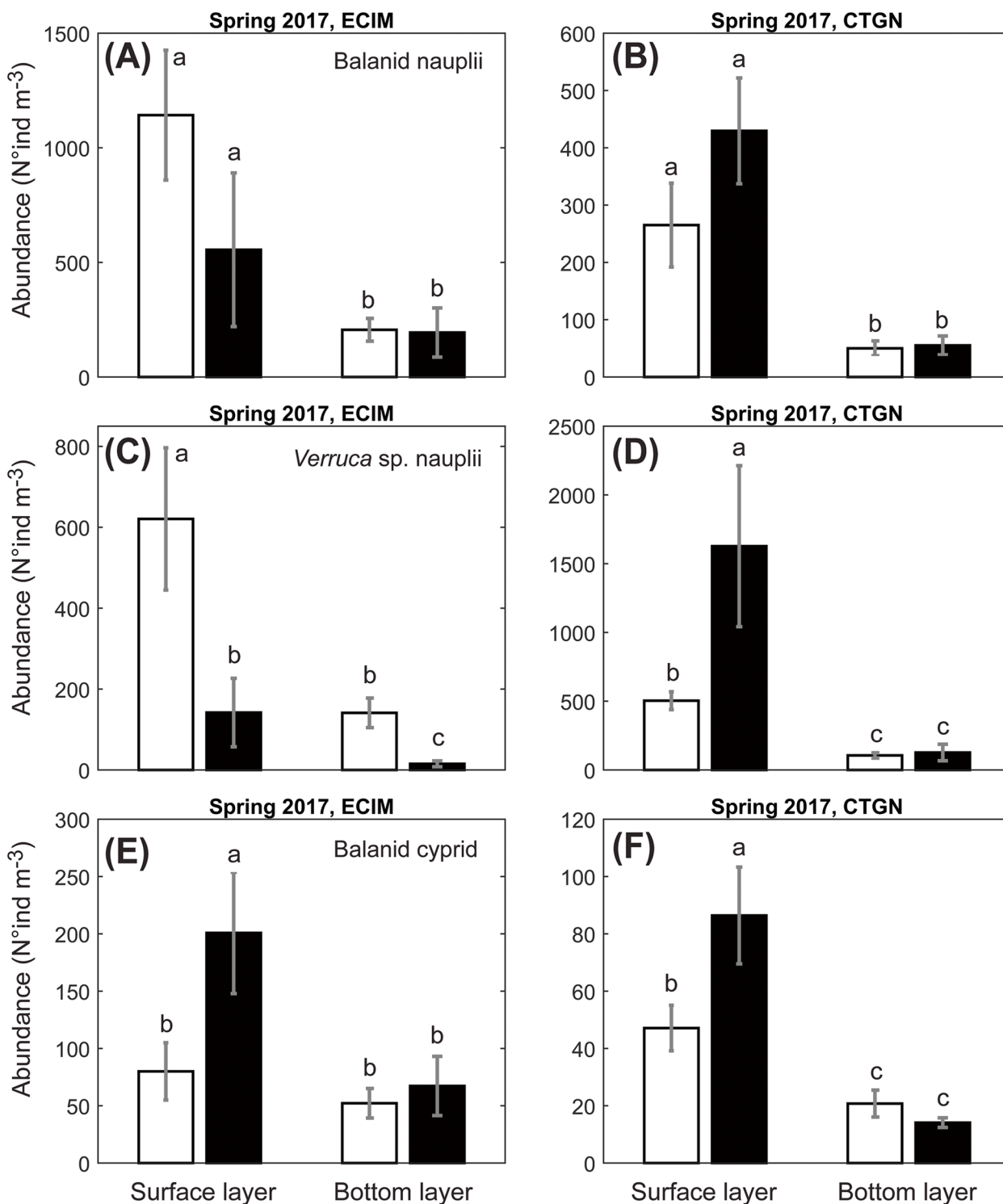


Fig. 7 Mean vertical distribution of barnacles: balanid nauplii (A, B), *Verruca* sp. nauplii (C, D), and balanid cyprids (E, F) during daytime (white bars) and nighttime (black bars) at ECIM (left panels) and CTGN (right panels) during spring 2017 survey. Error bars indicate standard error

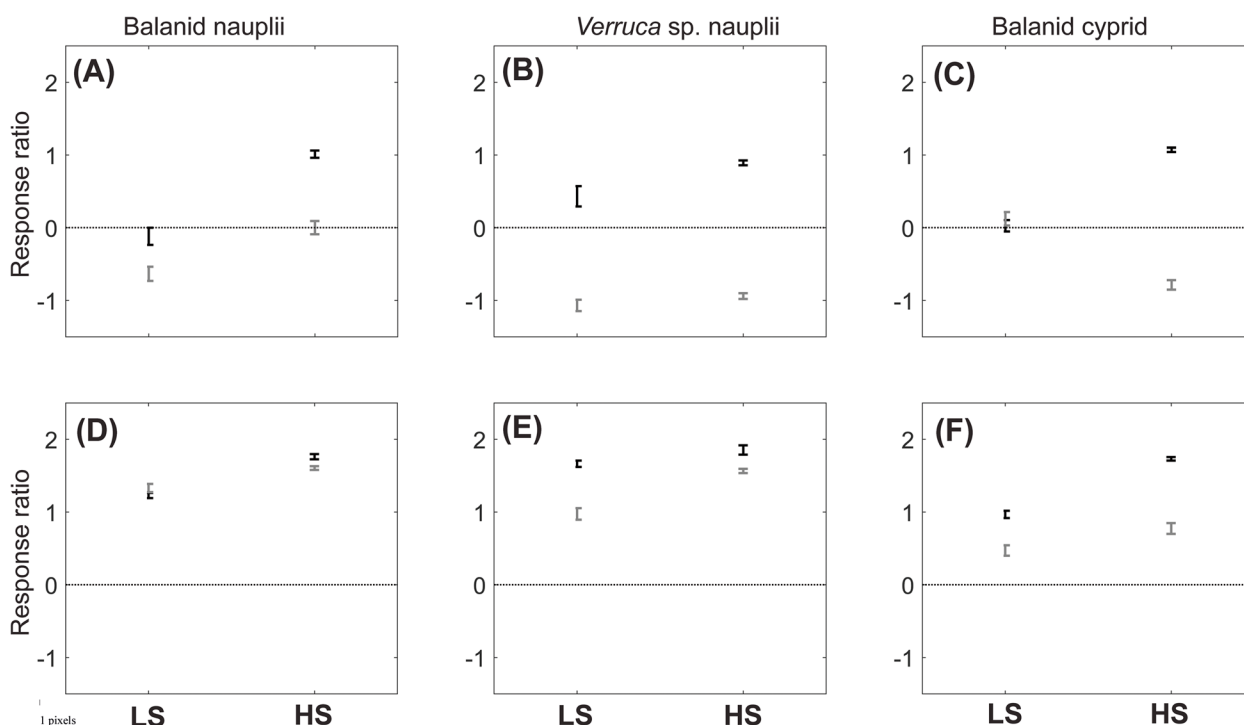


Fig. 8 Log response ratio of change in abundance between surface and bottom layer during day (grey) and night (black), and during low (LS) and high stratification (HS) of balanid nauplii (A, D), *Verruca* sp. nauplii (B, E), and balanid cyprids (C, F) during the summer 2016 (A, B, C) and spring 2017 (D, E, F) surveys. Positive numbers in the y-axes indicate that larval abundance was greater at the surface and negative numbers indicate the inverse

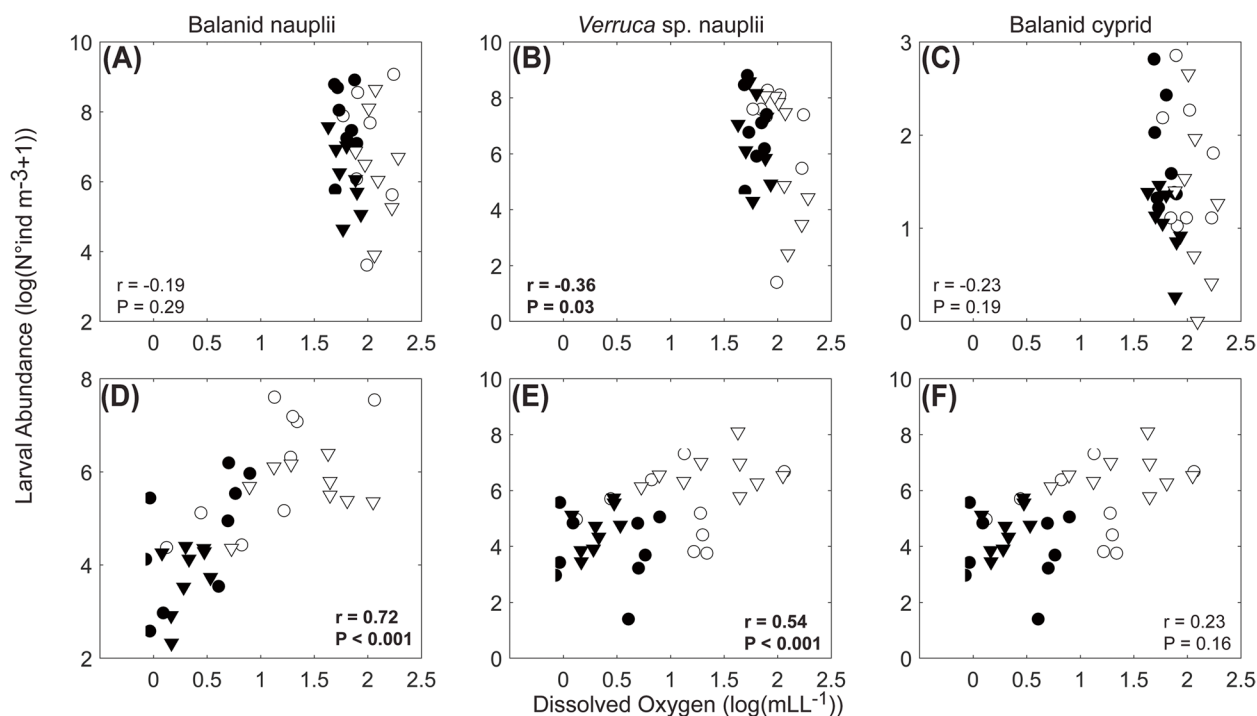


Fig. 9 Scatterplots and Pearson correlation between dissolved oxygen and larval abundance of balanid nauplii (A, D), *Verruca* sp. nauplii (B, E), and balanid cyprids (C, F) at the surface (white) and bottom (black) layers at ECIM (circles) and CTGN (triangles) during the summer 2016 (A, B, C) and spring 2017 (D, E, F) surveys

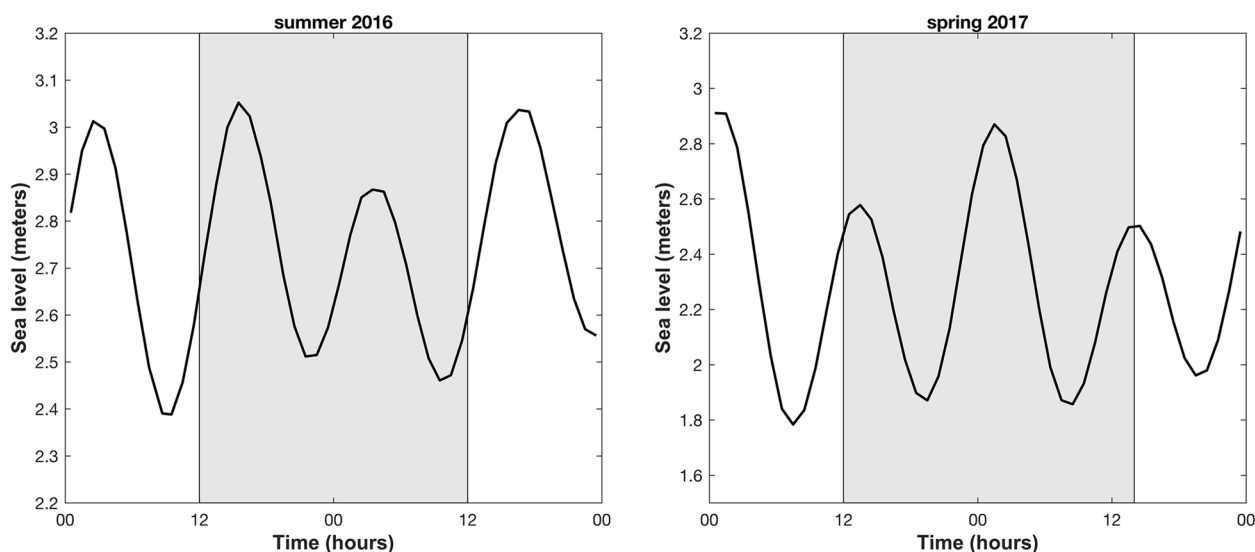


Fig. 10 Sea level obtained from the Sea Level Valparaiso Station Monitoring Facility during the summer 2016 survey (left panel) and the spring 2017 survey (right panel)

In contrast to the northern site of the bay, none of the three taxa presented diel variation in their vertical position in the southern site during the summer 2016 survey. This lack of consistency in vertical distribution across the bay may be associated with the spatial variability in the hydrographic condition of the water column between extremes of the bay [4] and a possible plastic behavior of barnacle larvae in response to different environmental conditions. Bonicelli et al. [4] observed that temperature oscillations at the less sheltered northern extreme of the bay were mainly diurnal and basically modulated by the sea breeze. In contrast, at the more sheltered southern site, there was a more stratified water column and the temperature variability was semidiurnal and in phase with the semidiurnal tide throughout the water column [4]. The results of the present study coincided with those of Bonicelli et al. [4], since the bay's southern extreme showed a stronger and more persistent stratification of the water column and a more pronounced semidiurnal signal on the temperature variability. Despite the fact that it is not possible to detect the physical mechanism that drives the semidiurnal temperature variability throughout the water column, the synchrony of larval variability between the surface and bottom layers at this end of the bay suggests that this could be a response to local barotropic tidal flow that transports larvae back and forth in the bay. Also, the sudden increase of balanid nauplii and cyprids as well as *Verruca* sp. nauplii in both layers between 21:00 and 3:00 h—which coincided with the rise of the 14 °C isotherm to shallower waters and flood tide (Fig. 10)—might suggest that cold, sub-thermocline water entered the bay, therefore assisting with larval

transport and increasing their abundance within the bay. Since in the present study there was only one station at each extreme, the results may not accurately reflect larval transport. That being said, this sudden increase in larvae of all three taxa at night and the low abundance they showed at the beginning of the survey both suggest horizontal larval advection rather than vertical movement. Furthermore, CTGN presented a stronger stratification than the northern end, a condition that favors cross-shore current intensity and variability across the water column [30] and increases the nearshore larval supply [74]. In addition, the presence of shoreward internal waves travelling within the thermocline is consistent with the observed isotherm rising, and these waves are known to affect larval vertical distributions and drive their onshore transport [49]. Therefore, the stratification we found at this end of the bay could favor cross-shore current and transport larvae into the bay, as seen in other systems [51, 74].

Our results show that thermal stratification did not affect diel vertical position in any of the larvae during the summer 2016 survey within the bay of Cartagena, since during high stratification we saw differences in the LRR between day and night, suggesting that they can cross a strong thermocline on a daily basis. Similar results have also been reported at El Quisco, where the majority of balanid nauplii were found below the pycnocline during the day and above the pycnocline at night despite thermal stratification, suggesting that these barnacles could cross the thermocline [5].

During the spring 2017 survey, when the water column was less stratified compared to the summer 2016 survey,

barnacle larvae mostly remained at the surface despite the strength of the thermocline. One reason for this may be the low oxygen concentrations ($<2 \text{ mL L}^{-1}$) that were registered below 5 m depth. It has been demonstrated that meroplanktonic larvae avoid swimming in hypoxic conditions [35] and that low oxygen concentration can increase mortality rates of invertebrate larvae [71]. Therefore, the low oxygen found in the bottom layer could have limited the distribution of the nauplii to the surface layer. Unlike balanid and *Verruca* sp. nauplii, balanid cyprids did not show a clear relationship with oxygen, suggesting that this larval stage may be more tolerant to low oxygen concentrations than nauplii. During the spring 2017 survey at ECIM, an increase in cyprid abundance was observed between 01:00 and 10:00 h, which coincides with the intrusion of dense, oxygen-poor water at the bay's surface. This could be the result of an intrusion of upwelled water into the bay that could favor the upward transport of cyprids, which are normally distributed close to the bottom of the water column [5, 30, 66]. This was not the case for the cyprids found at CTGN, which were mainly concentrated at the surface throughout the entire survey. This could be related to the greater stability of the water column we observed at this site. Meanwhile, in the summer 2016 survey, the oxygen concentrations presented values above 3 mL L^{-1} , and oxygen did not limit the vertical distribution of barnacle larvae, suggesting that the barnacle's tolerance threshold could be close to 3 mL L^{-1} and that values below this concentration, such as those observed in the 2017 survey, could affect barnacle vertical distribution and swimming capabilities. This is a hypothesis that should be tested in future investigations in upwelling systems like the coast of central Chile, where hypoxia is quite common, and waters with low oxygen concentrations can often be transported to the continental shelf by physical mechanisms [6, 20, 59].

The lack of consistency in diel vertical distribution between surveys could be due to interannual variability or seasonal changes (i.e., spring versus summer) in oceanographic conditions. The survey of summer 2016 was during El Niño 2015–2016, which was a relatively important El Niño events in the last decade [60, 64]. El Niño events are known to oxygenate the water column, which could expand the habitat for species that usually remain in the well-oxygenated layers [19] and avoid low oxygen waters [71]. This may facilitate vertical distribution of larvae throughout the water column, and may explain why we observed a further expansion of the larval vertical distribution during the summer 2016 compared to the spring 2017. Unfortunately, we could not discard seasonal variation, higher frequency variation in hydrographic conditions, or inter-annual variability associated with El Niño events. Clearly, more frequent studies

and on multiple years have to be made in order to better define the effects of seasonal and interannual variation in diel vertical distribution of barnacle larvae.

It is important to note that lack of spatial replication within each site of the bay (we had a unique location at each end of the bay) limited our statistical comparisons and precluded us from testing diel vertical distribution between sites. In this study, we prioritized temporal resolution over spatial replication within the Bay of Cartagena, which might have been compromised by high spatial autocorrelation within sections of the bay. Despite this limitation, this study provides evidence that barnacle larvae exhibit substantial variability in their diel vertical distribution within nearshore systems and across small spatial scales and suggests that coastal environmental conditions could overwhelm larval behaviors in these benthic species. Thus, the ability of barnacle larvae to control their vertical position is apparently influenced by hydrographic conditions that could vary within a 24-h period. This is especially important for coastal barnacle larvae, since their vertical position within nearshore environments modifies transport toward adequate settlement areas as was already documented [75].

Conclusions

- The vertical distribution changed between species, stages and sites within Cartagena Bay.
- Of all the taxa analyzed, only balanid nauplii showed a pattern of diel vertical migration across the thermocline during summer 2016 survey.
- Diel vertical distribution of barnacle larvae is not affected by stratification in a consistent manner in coastal waters.
- During spring 2017 survey barnacle larvae mostly remained at the surface layer possibly in response to the intrusion of water poor in dissolved oxygen.

Abbreviations

ECIM	Northern extreme of the Bay of Cartagena
CTGN	Southern extreme of the Bay of Cartagena
DVM	Diurnal Vertical Migration
CTD-OF	Conductivity, Temperature, Depth-Oxygen-Fluorescence
MUR SST	Multi-scale Ultra-high Resolution Sea Surface Temperature
DO	Dissolved oxygen
NOAA	National Oceanic and Atmospheric Administration
ASCAT	Advanced Scatterometer
IFREMER	Institut Français de Recherche pour l'Exploitation de la Mer
ANOVA	Analysis of Variance

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Authors' contributions

JB: Was in charge of the fieldwork and experimental design. Analyzed the data, interpreted the results and wrote the manuscript. MJJ: Analyzed the zooplankton samples in the laboratory. Was a major contributor in analyzing the data, interpreting the results and writing the manuscript. BB: Collaborated in the fieldwork. Was a major contributor in analyzing the data, interpreting the results and writing the manuscript. Also collaborated in the English translation revision. NW: Collaborated in the experimental design and in the fieldwork. Was a major contributor in analyzing the data, interpreting the results and writing the manuscript. KAP: Collaborated in the fieldwork and in the analysis of the samples. She also was in charge of the English translation revision. RC: Collaborated in the fieldwork and in the interpretation of the results. UC: Collaborated in the analysis of the data and interpretation of the results. DA: Collaborated in the analysis of the data and interpretation of the results. SAN: Collaborated in the experimental design. Was a major contributor in interpreting the results and writing the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable. author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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References

- Aiken CM, Navarrete SA, Pelegrí JL. Potential changes in larval dispersal and along shore connectivity on the central Chilean coast due to an altered wind climate. *J Geophys Res*. 2011. <https://doi.org/10.1029/2011JG001731>.
- Batchelder HP, Edwards CA, Powell TM. Individual-based models of copepod populations in coastal upwelling regions: implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention. *Prog Oceanogr*. 2002;53:307–33.
- Benneth WA, Kimmerer WJ, Burau JR. Plasticity in vertical migration by native and exotic estuarine fishes in a dynamic low-salinity zone. *Limnol Oceanogr*. 2002;47:1496–507.
- Bonicelli J, Mofatt C, Navarrete SA, Largier JL, Tapia FJ. Spatial differences in thermal structure and variability within a small bay: interplay of diurnal winds and tides. *Cont Shelf Res*. 2014;88:72–80.
- Bonicelli J, Tyburczy J, Tapia FJ, Finke GR, Parragón M, Dudas S, et al. Diel vertical migration and cross-shore distribution of barnacle and bivalve larvae in the central Chile inner-shelf. *J Exp Mar Biol Ecol*. 2016;485:35–46.
- Booth JAT, McPhee-Shaw EE, Chua P, Kingsley E, Denny M, Phillips R, et al. Natural intrusions of hypoxic, low pH water into nearshore marine environments on the California coast. *Cont Shelf Res*. 2012;45:108–15.
- Brinton E. Vertical migration and avoidance capability of euphausiids in the California current. *Limnol Oceanogr*. 1967;12:451–83.
- Campoy AN, Pérez-Matus A, Wieters EA, Alarcón-Ireland R, Garmedia V, Beldade R, Navarrete SA, Fernández M. The hidden diversity of temperate mesophotic ecosystems from central Chile (Southern Pacific Ocean) assessed through towed underwater video. *Diversity*. 2023;15: <https://doi.org/10.3390/d15030360>.
- Castilla JC. Perspectivas de investigación en estructura y dinámica de comunidades intermareales rocosas de Chile central. II Depredadores de alto nivel trófico. *Medio Ambiente*. 1981;5:190–215.
- Civelek CV, Daigle RM, Metaxas A. Effects of temperature on larval swimming patterns regulate vertical distribution relative to thermoclines in *Asterias rubens*. *J Exp Mar Biol Ecol*. 2013;445:1–12.
- Cowen RK, Paris CB, Srinivasan A. Scaling of connectivity in marine populations. *Science*. 2006;311:522–7.
- Chia FS, Buckland-Nicks J, Young CM. Locomotion of marine invertebrate larvae: a review. *Can J Zool*. 1984;62:1205–22.
- Criales-Hernández MI, Schwaborn R, Graco M, Ayón P, Hirche HJ, Wolff M. Zooplankton vertical distribution and migration off Central Peru in relation to the oxygen minimum layer. *Helgol Mar Res*. 2007. <https://doi.org/10.1007/s10152-007-0094-3>.
- Daigle RM, Metaxas A. Vertical distribution of marine invertebrate larvae in response to thermal stratification in the laboratory. *J Exp Mar Biol Ecol*. 2011;409:89–98.
- Dibacco C, Sutton D, Mcconnico L. Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay-ocean exchange. *Mar Ecol Prog Ser*. 2001;217:191–206.
- Dos Santos A, Santos AMP, Conway DVP. Horizontal and vertical distribution of cirripede cyprid larvae in an upwelling system off the Portuguese coast. *Mar Ecol Prog Ser*. 2007;329:145–55.
- Enright JT. Diurnal vertical migration: adaptive significance and timing. Part 1. selective advantage: a metabolic model. *Limnology and Oceanography*. 1977;22: 856–72.
- Enright J, Hamner W. Vertical diurnal migration and endogenous rhythmicity. *Science*. 1967;157:937–41.
- Escribano R, Hidalgo P, Krautz C. Zooplankton associated with the oxygen minimum zone system in the northern upwelling region of Chile during March 2000. *Deep-Sea Res*. 2009;56:1083–94.
- Fajardo M, Andrade D, Bonicelli J, Bon M, Gómez G, Riascos JM, et al. Macrobenthic communities in a shallow normoxia to hypoxia gradient in the Humboldt upwelling ecosystem. *PLoS ONE*. 2018. <https://doi.org/10.1371/journal.pone.0200349>.
- Fortier L, Leggett WC. Vertical Migrations and Transport of Larval Fish in a Partially Mixed Estuary. *Canadian Journal Fisheries and Aquatic Sciences*. 1983;40:1543–55.
- Forward RB Jr, Rittschof D. Alteration of photoresponses involved in diel vertical migration of a crab larva by fish mucus and degradation products of mucopolysaccharides. *J Exp Mar Biol Ecol*. 2000;245:277–92.
- Garrison LP. Vertical migration behavior and larval transport in brachyuran crabs. *Mar Ecol Prog Ser*. 1999;176:103–13.
- Genin A, Jaffe SJ, Reef R, Richter C, Franks PJS. Swimming against the flow: A mechanism of zooplankton aggregation. *Science*. 2005. <https://doi.org/10.1126/science.1107834>.
- Gerritsen J. Behavioral response of *Daphnia* to rate of temperature change: Possible enhancement of vertical migration. *Limnol Oceanogr*. 1982;27:254–61.

26. Graham WM. Spatio-Temporal Scale Assessment of an "Upwelling Shadow" in Northern Monterey Bay. *California Estuaries*. 1993;16:83–91.
27. Graham WM, Field JG, Potts DC. Persistent "upwelling shadows" and their influence on zooplankton distributions. *Mar Biol*. 1992;114:561–70.
28. Graham WM, Largier JL. Upwelling shadows as near-shore retention sites: the example of northern Monterey Bay. *Cont Shelf Res*. 1997;17:509–32.
29. Guizien K, Brochier T, Duchene JC, Koh BS, Marsaleix P. Dispersal of *Owenia fusiformis* larvae by wind-driven currents: turbulence, swimming behaviour and mortality in a three-dimensional stochastic model. *Mar Ecol Prog Ser*. 2006;311:47–66.
30. Hagerly ML, Reynolds N, Pineda J. Constrained nearshore larval distributions and thermal stratification. *Mar Ecol Prog Ser*. 2018;595:105–22.
31. Hentschel BT, Emlet RB. Metamorphosis of barnacle nauplii: effects of food variability and a comparison with amphibian models. *Ecology*. 2000;81:3495–508.
32. Huntley M, Brooks ER. Effects of Age and Food Availability on Diel Vertical Migration of *Calanus pacificus*. *Mar Biol*. 1982;71:23–31.
33. Kaplan DM, Largier JL, Navarrete SA, Guíñez R, Castilla JC. Large diurnal temperature fluctuations in the nearshore water column. *Estuarine, Coastal Shelf Science*. 2003;57:385–98.
34. Lagos NA, Navarrete SA, Véliz F, Masuero A, Castilla JC. Meso-scale spatial variation in settlement and recruitment of intertidal barnacles along the coast of central Chile. *Mar Ecol Prog Ser*. 2005;290:165–78.
35. Lagos ME, White CR, Marshall DJ. Avoiding low-oxygen environments: oxytaxis as a mechanism of habitat selection in a marine invertebrate. *Marine Experimental Progress Series*. 2015;540:99–107.
36. Lampert W. The adaptive significance of diel vertical migration of zooplankton. *Funct Ecol*. 1989;3:21–7.
37. Loose CJ, Dawidowicz P. Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. *Ecology*. 1994;75:2255–63.
38. Marta-Almeida M, Dubert J, Peliz Á, Queiroga H. Influence of vertical migration pattern on retention of crab larvae in a seasonal upwelling system. *Mar Ecol Prog Ser*. 2006;307:1–19.
39. Metaxas A, Saunders M. Quantifying the "bio-" components in biophysical models of larval transport in marine benthic invertebrates: advances and pitfalls. *The Biology Bulletin*. 2009;216(3):257–72.
40. Miranda L, Moreno RA. Epibiontes de *Lepidochelys olivacea* (Eschscholtz, 1829) (Reptilia: Testudinata: Cheloniidae) en la región centro sur de Chile. *Rev Biol Mar Oceanogr*. 2002;37(2):145–6.
41. Morgan SG, Fisher JL, Mcafee ST, Largier JL, Halle CM. Limited recruitment during relaxation events: larval advection and behavior in an upwelling system. *Limnol Oceanogr*. 2012;57:457–70.
42. Morgan SG, Fisher JL, Mcafee ST, Largier JL, Miller SH, Sheridan MM, et al. Transport of Crustacean Larvae Between a Low-Inflow Estuary and Coastal Waters. *Estuaries Coasts*. 2014;37:1269–83.
43. Narváez DA, Poulin E, Leiva G, Hernández E, Castilla JC, Navarrete SA. Seasonal and spatial variation of nearshore hydrographic conditions in central Chile. *Cont Shelf Res*. 2004;24:279–92.
44. Navarrete SA, Castilla JC. Resource partitioning between intertidal predatory crabs: interference and refuge utilization. *J Exp Mar Biol Ecol*. 1990;143:101–29.
45. Nielsen KJ, Navarrete SA. Mesoscale regulation comes from the bottom-up: Intertidal interactions between consumers and upwelling. *Ecology Letter*. 2004;7:31–41.
46. North EW, Schlag Z, Hood RR, Li M, Zhong L, Gross T, et al. Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. *Mar Ecol Prog Ser*. 2008;359:99–115.
47. O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, et al. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proc Natl Acad Sci*. 2007;104:1266–71.
48. Ospina-Alvarez A, Weidberg N, Aiken CM, Navarrete SA. Larval transport in the upwelling ecosystem of central Chile: The effects of vertical migration, developmental time and coastal topography on recruitment. *Prog Oceanogr*. 2018;168:82–99.
49. Pineda J. Internal tidal bores in the nearshore: Warm-water fronts, seaward gravity currents and the onshore transport of neustonic larvae. *J Mar Res*. 1994;52:427–58.
50. Pineda J. Linking larval settlement to larval transport: assumptions, potentials, and pitfalls. *Oceanography of the Eastern Pacific*. 2000;1:84–105.
51. Pineda J, Reynolds N, Lentz SJ. Reduced barnacle larval abundance and settlement in response to large-scale oceanic disturbances: Temporal patterns, nearshore thermal stratification, and potential mechanisms. *Limnol Oceanogr*. 2018;00:1–12.
52. Pustejovsky JE. Measurement-comparable effect sizes for single-case studies of free-operant behavior. *Psychol Methods*. 2015;20(3):342–59.
53. Pustejovsky JE. Using response ratios for meta-analyzing single-case designs with behavioral outcomes. *J Sch Psychol*. 2018;68:99–112.
54. Queiroga H, Blanton J. Interactions between Behaviour and Physical Forcing in the Control of Horizontal Transport of Decapod Crustacean Larvae. *Advance in Marine Biology*. 2004;47:107–214.
55. Quinn GP, Keough M. *Experimental design and data analysis for biologist*. Cambridge University, 2002. p. 537.
56. Rawlinson KA, Davenport J, Barnes DKA. Vertical migration strategies with respect to advection and stratification in a semi-enclosed lough: a comparison of mero- and holozooplankton. *Mar Biol*. 2004;144:935–46.
57. Ross PM, Burrows MT, Hawkins SJ, Southward AJ, Ryan KP. A key for the identification of the nauplii of common barnacles of the British Isles, with emphasis on *Chthamalus*. *J Crustac Biol*. 2003;23:328–40.
58. Roughan M, Mace AJ, Largier JL, Morgan SG, Fisher JL, Carter ML. Sub-surface recirculation and larval retention in the lee of a small headland: A variation on the upwelling shadow theme. *J Geophys Res*. 2005;110:1–18.
59. Sobarzo M, Bravo L, Donoso D, Garcés-Vargas J, Schneider W. Coastal upwelling and seasonal cycles that influence the water column over the continental shelf off central Chile. *Prog Oceanogr*. 2007;75:363–82.
60. Santoso A, McPhaden MJ, Cai W. The defining characteristics of ENSO extremes and the strong 2015/106 El Niño. *Rev Geophys*. 2017;55:1079–129.
61. Shinen JL, Navarrete SA. Coexistence and intertidal zonation of chthamalid barnacles along central Chile: Interference competition or a lottery for space? *J Exp Mar Biol Ecol*. 2010;392:176–87.
62. Stenevik EK, Sundby S, Cloete R. Diel vertical migration of anchovy *Engraulis encrasicolus* larvae in the northern Benguela. *Afr J Mar Sci*. 2007;29:127–36.
63. Storch D, Fernández M, Navarrete SA, Pörtner HO. Thermal tolerance of larval stages of the Chilean kelp crab *Talipes dentatus*. *Mar Ecol Prog Ser*. 2011;429:157–67.
64. Stramma L, Fischer T, Grundle DS, Krahnemann G, Bangel HW, Marandino CA. Observed El Niño conditions in the eastern tropical Pacific in October 2015. *Ocean Sci*. 2016;12:861–73.
65. Tapia FJ, Navarrete SA, Castillo M, Menge BA, Castilla JC, Largier J, et al. Thermal indices of upwelling effects on inner shelf habitats. *Prog Oceanogr*. 2009;83:278–87.
66. Tapia FJ, Dibacco C, Jarrett J, Pineda J. Vertical distribution of barnacle larvae at a fixed nearshore station in southern California: Stage-specific and diel patterns. *Estuar Coast Shelf Sci*. 2010;86:265–70.
67. Thiel M, Ullrich N. Hard rock versus soft bottom: the fauna associated with intertidal mussel beds on hard bottoms along the coast of Chile, and considerations on the functional role of mussel beds. *Helgol Mar Res*. 2002;56:21–30.
68. Thiyagarajan V, Harder T, Qiu JW, Qian PY. Energy content at metamorphosis and growth rate of the early juvenile barnacle *Balanus amphitrite*. *Mar Biol*. 2003;143:543–54.
69. Thiyagarajan V, Hung OS, Chiu JMY, Wu RSS, Qian PY. Growth and survival of juvenile barnacle *Balanus amphitrite*: interactive effects of cyprid energy reserve and habitat. *Mar Ecol Prog Ser*. 2005;299:229–37.
70. Underwood AJ. *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge University Press, 1997. p. 194–195.
71. Vaquer-Sunyer R, Duarte CM. Thresholds of hypoxia for marine biodiversity. *Proc Natl Acad Sci*. 2008;105:15452–7.
72. Varela RA, Cruzado A, Tintore J, García-Ladona E. Modelling the deep-chlorophyll maximum. A Coupled physical-biological approach. *Journal of Marine Research*. 1992;50:441–63.
73. Venegas RM, Ortiz V, Olguín A, Navarrete SA. Larval development of the intertidal barnacles *Jehlius cirratus* and *Notochthamalus scabrosus* (Cirripedia: Chthamalidae) under laboratory conditions. *J Crustac Biol*. 2000;20:495–504.

74. Yamhure GM, Reyns N, Pineda J. High larval concentrations and onshore transport of Barnacle Cyprids associated with thermal stratification. *Frontier in Marine Science*. 2021. <https://doi.org/10.3389/fmars.2021.748389>.
75. Weidberg N, Goschen W, Jackson JM, Patrick P, Mcquaid CD, Porri F. Fine scale depth regulation of invertebrate larvae around coastal fronts. *Limnol Oceanogr*. 2019;64(2):785–802.
76. Wieters EA, Kaplan DM, Navarrete SA, Sotomayor A, Largier J, Nielsen KJ, et al. Alongshore and temporal variability in chlorophyll a concentration in Chilean nearshore waters. *Mar Ecol Prog Ser*. 2003;249:93–105.
77. Williamson CE, Fischer JM, Bollens SM, Overholt EP, Breckenridge JK. Toward a more comprehensive theory of zooplankton diel vertical migration: Integrating ultraviolet radiation and water transparency into the biotic paradigm. *Limnol Oceanogr*. 2011;56:1603–23.
78. Zaret TM, Suffern S. Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol Oceanogr*. 1976;21:804–13.

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