Constrained nearshore larval distributions and thermal stratification

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ABSTRACT: Vertical and cross-shore distributions and abundances of shallow-water barnacle larvae were characterized in La Jolla, southern California (USA), during a 2 yr period. Five stations located within 1 km of shore and ranging from 4–12 m water depths were sampled intensively in 2 m depth intervals during 27 cruises throughout spring–summer (April–July) and fall–winter (October–December) of 2014 and 2015. Larval abundances significantly decreased from 2014 to 2015, which could be related to the arrival of a warm-water anomaly (the so-called 'Blob') in 2014 and El Niño conditions in 2015. Despite the presence of these large-scale regional disturbances, vertical and cross-shore larval distributions were consistent throughout the 2 yr study period. Early-stage nauplii and *Chthamalus fissus* cyprids tracked bottom depth, and cyprids were on average deeper than nauplii. Vertical distributions were not related to the mid-depth of the thermocline or thermal stratification. Early-stage nauplii had a broader cross-shore distribution than cyprids, which were concentrated at inshore stations. Nearshore cyprid concentration had a positive relationship with thermal stratification, and the center of distribution of cyprids was farther offshore during fall–winter when stratification decreased. These results suggest that thermal stratification elicits enhanced behavioral control of cyprids to remain close to shore and reach the adult habitat.

KEY WORDS: Barnacle larvae · *Chthamalus fissus* · Early-stage nauplii · Cyprids · Hydrographic and hydrodynamic conditions

INTRODUCTION

Larval transport, defined as the mean horizontal translocation of larvae between one point and another along a specified spatial dimension (Pineda & Reyns 2018), is crucial to understanding population connectivity in marine environments, with implications for conservation, genetic diversity, and fisheries management (reviewed by Cowen et al. 2007). The biological and physical mechanisms of larval transport in the ocean are multifaceted and complex; they involve physical processes that have the potential to transport larvae, as well as behavioral responses to environmental cues that remain poorly understood (reviewed by Metaxas 2001, Epifanio & Cohen 2016, Pineda &

Reyns 2018), particularly in nearshore environments where sampling is challenged by the complexities of shallow bathymetric features (Davies 1977). A greater understanding of larval transport processes in nearshore systems has become increasingly essential, as studies reveal that larvae exhibit more constrained distributions than originally assumed (Tapia & Pineda 2007, Morgan et al. 2009, Shanks & Shearman 2009, Weidberg et al. 2015, reviewed by Pineda & Reyns 2018). Larval transport and dispersal mechanisms can inform the designation of marine reserves and marine protected areas (Shanks et al. 2003), and we cannot effectively manage these regions without a more complete grasp on dominant transport mechanisms and larval behavior in waters adjacent to the coast.

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The dispersal of intertidal organisms, such as barnacles, is carried out in the nearshore environment where physical processes are highly variable (Morgan & Fisher 2010, Bonicelli et al. 2016). Barnacles transition through 6 naupliar stages and 1 cyprid stage, typically during a 2–5 wk pelagic larval duration (Walley & Rees 1969). Cyprids are especially interesting because to complete their life cycle they must return to the intertidal zone to find suitable habitats and settle before metamorphosis into juveniles. Larvae can alter their behavior to move into different depths, thus controlling their cross-shore movements through exposure to varying currents (Metaxas 2001, Tapia et al. 2010, Pineda & Reyns 2018). Cues that might be used to make vertical changes in distribution include temperature. For example, gastropods, bivalves, and polychaetes in St. George's Bay, Nova Scotia, Canada, remained below the thermocline and pycnocline, and variations in their abundances were associated with temperature (Lloyd et al. 2012). Strong thermoclines can also restrict vertical distributions. Larval sea scallops were limited to bottom depths during a laboratory study when the water column was stratified (Daigle & Metaxas 2011), and were more aggregated when thermal stratification was higher at Georges Bank, Massachusetts, USA (Tremblay & Sinclair 1990). Changes in settlement of *Chthamalus fissus* barnacles were positively correlated with changes in stratification in La Jolla, California, USA, and there were significantly more settlers at this site than at a lesser-stratified location in northern Baja California (Pineda & López 2002). Stratification is correlated with shear and internal motions, and flows that reverse with depth are more likely to occur during highly stratified conditions (Winant & Bratkovich 1981). Stronger stratification may increase local retention of larvae that exploit more vertically sheared flows (Pineda & Reyns 2018).

Larvae also undergo ontogenetic vertical migrations (Paris & Cowen 2004, Butler et al. 2011). Older damselfish larvae off the west coast of Barbados migrated vertically to remain within deeper, onshore flowing currents and were consequently retained near their natal source (Paris & Cowen 2004). Early-stage larval spiny lobsters are positively phototactic, but this behavior diminished with age during laboratory tests (Butler et al. 2011). Dispersal simulations based on observed depth distributions revealed that twice as many larvae would successfully recruit to nurseries if they displayed ontogenetic vertical migration when compared with passive dispersers (Butler et al. 2011).

Additionally, larvae can respond to and accumulate in horizontal convergent flow (Pineda 1999, Shanks & Shearman 2009, Ryan et al. 2014). Barnacle cyprids respond to downwelling by swimming up in laboratory experiments (DiBacco et al. 2011), and this may be the mechanism that enhanced their concentration in internal bore warm fronts off the coast of southern California (Pineda 1999). An autonomous underwater vehicle (AUV) in Monterey Bay, California, sampled increased larval concentrations when frontal gradients were strongest and upwelling anomalies persisted (Ryan et al. 2014). This AUV study also found high abundances of larvae near the seafloor, assumed to result from accumulation in a frontal convergence zone due to swimming behavior and downwelling.

Larval supply to the intertidal can also be related to wave height; a study in southeastern Australia reported more barnacle cyprids arriving to shore when wave height was high (Jeffery & Underwood 2000), and a study in California and Oregon observed barnacle settlement when waves increased (Shanks et al. 2010). However, Pfaff et al. (2015) reported that swell height off the west coast of southern Africa facilitated delivery of mussel larvae, but not barnacle larvae. Onshore transport of barnacles occurred during downwelling, and settlement coincided with low swell, upwelling, and spring tides, suggesting that internal tides are associated with transport of larval barnacles to shore (Pfaff et al. 2015). Thus, varying hydrographic and hydrodynamic conditions can impact larvae, and understanding the vertical distribution of larvae in relation to such conditions is critical to determining larval transport and dispersal processes (discussed by Pineda & Reyns 2018). Given the recent findings on larval distributions constrained close to shore, studies need to resolve these distributions in the very nearshore.

In this study, we conducted fine-scale, high-repetition plankton collections to resolve barnacle larval distributions. Vertical sampling in stratified, 2 m depth intervals throughout the water column was coupled with high spatial resolution sampling at 5 cross-shore locations within 1 km from the intertidal, commensurate with physical measurements in the nearshore. We hypothesized that larval barnacle abundance and distributions would vary with ontogenetic stage, temperature and thermal stratification, currents, and wave height. Specifically, we addressed the following questions: What are the fine-scale patterns of vertical and cross-shore barnacle larval distributions in the nearshore? Do nauplii and cyprids display different distribution patterns? Are

patterns in larval distribution related to hydrographic and hydrodynamic conditions?

MATERIALS AND METHODS

Study site and system

This study was conducted offshore of Bird Rock, La Jolla, California, and included 5 sampling stations located at distances of 280, 460, 640, 820, and 1000 m from shore at water depths of 4, 6, 8, 10, and 12 m, respectively (Fig. 1). We selected this study area as the shoreline provides extensive adult barnacle habitat, particularly for the abundant *Chthamalus fissus,* and larvae of the predominant barnacle species in the region have been observed in surrounding nearshore waters (*C. fissus, Balanus glandula*, *Megabalanus californicus*, and *Pollicipes polymerus*; Hoffman 1989, Pineda 1991, 1999, Pineda & López 2002, Tapia & Pineda 2007, Tapia et al. 2010). Further, the shelf bathymetry is simple. Sampling occurred during April–July (hereafter spring–summer) and October–December (hereafter fall–winter) in 2014 and 2015, and consisted of plankton sampling cruises as well as hydrographic and hydrodynamic measurements obtained from instrument deployments (see below). Sampling periods were chosen to encompass times of barnacle settlement (Hines 1976, 1978, Pineda 1994), and during expected seasonal contrasts in hydrographic conditions: thermal stratification is greater in spring–summer than in fall–winter when the onset of cooling and increased storm activity enhances water column mixing (Winant & Bratkovich 1981, Palacios et al. 2004).

Plankton sampling

Plankton sampling was conducted using a 7.6 m boat with a davit, and included 27 cruises in total: 9 in spring–summer (May–July) and 6 in fall–winter (October–December) of 2014, 8 in spring–summer (April–July) and 4 in fall–winter (October–December) of 2015. During each cruise, plankton samples were collected using an Ebara 50DWXU6.4S Dominator submersible semivortex pump to filter 2 m^3 of seawater in discrete 2 m depth bins, while continuously oscillating the pump within the 2 m sampling interval. Sampling extended from the surface to the bottom at each of the 5 stations (20 samples cruise^{-1} with a few exceptions where sea state conditions or equipment failure interrupted sampling). Seawater was filtered through a 118 µm mesh net to capture barnacle larval stages (*C. fissus* larvae range in size from ~124 µm long × 206 µm wide as stage I nauplii through ~493 µm long × 246 µm wide at the cyprid stage; Miller et al. 1989), and samples were immediately preserved in 100% ethanol.

Plankton samples were sorted using a dissecting microscope, and barnacle larvae were enumerated. Nauplii were staged as early (II–III) or late (IV–VI) stage, and cyprids were classified to species based on published morphological descriptions (e.g. Lewis 1975, Branscomb & Vedder 1982, Brown & Roughgarden 1985, Miller et al. 1989, Miller & Roughgarden 1994, Shanks 2001). Species identifications were confirmed using molecular tools (M. Hagerty et al. unpubl. data). Early-stage nauplii could not be identified to species due to morphological degradation, but late-stage nauplii were classified as *C. fissus* or 'other' due to their distinct size and shape. *C. fissus* is the most abundant barnacle in the region,
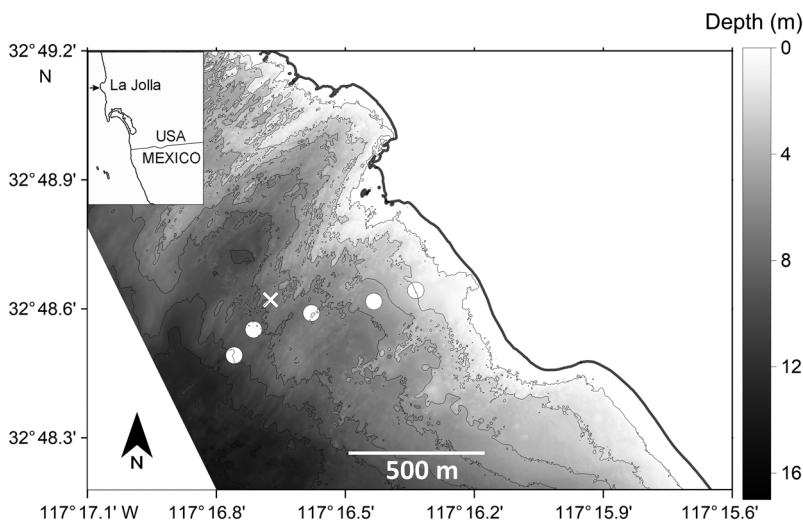

Fig. 1. Study site offshore of Bird Rock, La Jolla, southern California, USA. Circles indicate plankton sampling stations at 280, 460, 640, 820, and 1000 m from shore at a bottom depth of 4, 6, 8, 10, and 12 m, respectively, moving offshore from right to left. X indicates the location of the acoustic Doppler current profiler (ADCP) to measure currents, and pressure sensor to measure waves. Subsurface temperature mooring was deployed ~10 m from the ADCP. Bottom depth contours every 2 m relative to Mean Lower Low Water (MLLW), with the shallowest contour at MLLW. Lidar data from the 2013 NOAA Coastal California TopoBathy Merge Project, https://coast.noaa.gov/dataviewer/#/lidar/search/where:ID=2612

and most early-stage nauplii collected likely belong to this species. Stage I nauplii were not present in our samples, presumably due to the rapid transition to stage II after hatching (Brown & Roughgarden 1985, Miller et al. 1989).

Larval distributions

We described the vertical and horizontal larval distribution patterns of the most abundant barnacle species in our samples; thus, detailed analyses were conducted for early-stage barnacle nauplii (>98% of the total nauplii collected; Table 1) and *C. fissus* cyprids, which comprised >60% of the barnacle cyprids (Table 2). To characterize vertical distribution of larval stages, mean depth distributions (MDDs; Tapia et al. 2010) were calculated for each station according to the following equation:

$$\text{MDD} = \Sigma \text{ (no. m}^{-3} \text{ in sample interval} \times \text{mean depth of sample interval)} / \Sigma \text{ (no. m}^{-3} \text{ at station)} \quad (1)$$

Table 1. Nauplii concentration summaries for all sampling periods: 2014 spring–summer (N = 149 samples), 2014 fall–winter (N = 108), 2015 spring–summer (N = 136), 2015 fall–winter (N = 78)

Nauplii	2014 spring–summer	2014 fall–winter	2015 spring–summer	2015 fall–winter
Maximum concentration (no. larvae m^{-3})				
Early stage	2104.15	165.90	135.92	651.63
Late-stage *Chthamalus fissus*	0	5.99	11.99	3.99
Late-stage other	4.04	0	1.99	5.99
Mean concentration (no. larvae m^{-3}) ± SE				
Early stage	91.23 ± 21.66	16.41 ± 3.04	9.81 ± 1.73	50.49 ± 13.45
Late-stage *Chthamalus fissus*	0	0.09 ± 0.06	0.15 ± 0.09	0.36 ± 0.11
Late-stage other	0.10 ± 0.04	0	0.02 ± 0.02	0.17 ± 0.09
Percent of total nauplii (%)				
Early stage	99.90	99.44	98.34	98.97
Late-stage *Chthamalus fissus*	0	0.56	1.47	0.70
Late-stage other	0.10	0	0.18	0.33

Table 2. Cyprid concentration summaries for all sampling periods; sample sizes are given in Table 1 legend

Cyprids	2014 spring–summer	2014 fall–winter	2015 spring–summer	2015 fall–winter
Maximum concentration (no. larvae m^{-3})				
Chthamalus fissus	427.76	116.93	21.98	85.95
Balanus glandula	9.99	1.09	3.99	3.99
Pollicipes polymerus	11.99	17.98	13.14	7.99
Tetraclita rubescens	19.98	1.99	3.99	0
Megabalanus rosa	9.99	1.99	14.99	3.99
Balanus trigonus	11.99	0	0.49	3.99
Unknown	5.99	0	3.99	0
Mean concentration (no. larvae m^{-3}) ± SE				
Chthamalus fissus	20.48 ± 4.34	4.12 ± 1.25	1.86 ± 0.32	4.76 ± 1.48
Balanus glandula	0.58 ± 0.13	0.01 ± 0.01	0.08 ± 0.04	0.16 ± 0.08
Pollicipes polymerus	0.37 ± 0.11	0.24 ± 0.17	0.52 ± 0.15	0.36 ± 0.14
Tetraclita rubescens	0.75 ± 0.21	0.04 ± 0.03	0.06 ± 0.04	0
Megabalanus rosa	0.67 ± 0.14	0.04 ± 0.03	0.49 ± 0.17	0.08 ± 0.06
Balanus trigonus	0.11 ± 0.08	0	0.01 ± 0.01	0.16 ± 0.08
Unknown	0.26 ± 0.07	0	0.06 ± 0.04	0
Percent of total cyprids (%)				
Chthamalus fissus	88.11	92.56	60.51	86.29
Balanus glandula	2.51	0.23	2.63	2.90
Pollicipes polymerus	1.61	5.46	16.77	6.51
Tetraclita rubescens	3.21	0.82	1.91	0
Megabalanus rosa	2.87	0.94	16.02	1.39
Balanus trigonus	0.46	0	0.24	2.90
Unknown	1.12	0	1.91	0

We used a 1-factor analysis of variance (ANOVA) to test for differences in MDD of nauplii and cyprids between sampling periods (spring–summer 2014, fall–winter 2014, spring–summer 2015, fall–winter 2015). ANOVA assumptions of normality, homoscedasticity, and absence of collinearity were met. A paired *t*-test was also used to compare MDDs of early-stage nauplii to *C. fissus* cyprids.

To account for the vertical dilution of larvae when comparing larval concentrations at stations of varying depths, total larval concentration (no. m^{-3}) at each station was multiplied by station depth to standardize samples to larval density (no. m^{-2}). To determine if larval abundances varied across stations, we calculated the proportion of total early-stage nauplii and *C. fissus* cyprids at each station on a given cruise date, and used a 2-factor ANOVA to test for differences in larval proportions between stations and sampling periods (spring–summer vs. fall–winter). Additionally, we calculated the mean distance from shore (MDS; referred to as 'average distance offshore' in Shanks & Shearman 2009) of the larval stages for each cruise:

MDS = Σ (no. m^{-2} at a given station × distance from shore of station) / Σ (no. m^{-2} at all stations) (2)

A Student's *t*-test was used to compare MDS measurements of early-stage nauplii and *C. fissus* cyprids. Data were log-transformed to meet the assumption of equal variances. Finally, we developed a constrained-distribution index (CDI) that considered both the influence of larval proportion and distance from shore to further investigate cyprid distribution patterns. The CDI was only calculated for cruise dates where all 5 stations were sampled. First, larval proportion anomalies were calculated for *C. fissus* cyprids at each station as (the proportion of *C. fissus* cyprids at each station on a given cruise date) – (the average proportion of *C. fissus* cyprids at each station for all cruises). Then, for each cruise date, the CDI was calculated as:

CDI = Σ (larval proportion anomalies at stations 280 and 460 m from shore) – Σ (larval proportion anomalies at stations 640, 820, and 1000 m from shore) (3)

Thus, the resulting index value is positive when cyprid densities are higher than average at the 2 inshore stations, and negative if cyprid densities are lower than average at the 2 inshore stations. The CDI is simply an anomaly from a canonical distribution that can be used to test for hydrographic or hydrodynamic conditions under which cross-shore larval distribution patterns change. We chose the 2 inshore

stations as the basis for the index, because cyprid MDS (overall mean = 531.19 m, median = 521.34 m) was located between the stations 460 (6 m depth) and 640 (8 m depth) m from shore.

Temperature, currents, and pressure

A CastAway-CTD (SonTek) was used to obtain temperature and depth measurements before and after plankton pumping at each station. Salinity was not considered in this study because stratification at our study site is due to vertical differences in temperature rather than salinity (Hagerty 2017). Depth-averaged temperature, mid-depth of the thermocline, and thermal stratification were calculated for each station. The mid-depth of the thermocline was determined as the depth at which the greatest change in temperature occurred for a given CTD cast. Thermal stratification was defined as change in temperature m^{-1} (ΔT°C m^{-1}):

Thermal stratification = (temperature at surface – temperature at bottom) / (depth of bottom temperature – depth of surface temperature) (4)

Additionally, thermal stratification within our study site was calculated by averaging thermal stratification at the 3 offshore stations (640, 820, and 1000 m from shore with bottom depths of 8, 10, and 12 m, respectively) for each cruise, hereafter referred to as zonal stratification. These stations were selected to represent zonal thermal stratification as they most frequently exhibited the highest stratification at our site.

A 1200 kHz RDI acoustic Doppler current profiler (ADCP) was deployed between the plankton sampling stations 640 (8 m depth) and 820 (10 m depth) m offshore (Fig. 1) during the entire duration of each sampling period to record current velocities every 2 s throughout the water column in 0.4 m depth bins. Error velocities, percent good, beam correlation, signal strength anomaly, and bin-to-bin velocity differences were all examined as part of current profile quality control. All of these, but particularly signal strength, were useful in removing times when kelp contaminated the velocity measurements. Currents were rotated to align the predominant alongshore flow with the coastline, decomposed into alongshore (positive southward) and cross-shore (positive onshore) components, and depth-averaged. Currents associated with each cruise were calculated as the average of the 24 h previous to the cruise end time.

The relationship between zonal stratification and depth variability of the cross-shore currents was obtained for dates when all 5 stations were sampled. For each of these dates, current variability with depth was estimated by computing the standard deviation across depth of the hourly cross-shore currents. Twelve-hourly estimates of the standard deviation were then averaged and plotted against zonal stratification. These 12-hourly data corresponded in time to the measurements of zonal stratification during the cruise (ca. 4 h) and the time preceding the cruise (ca. 8 h).

Temperature was also concurrently measured at a subsurface mooring deployed ~10 m from the ADCP (Fig. 1). Temperature was measured every 5 s with 5 SBE 56 loggers spaced ~1.2 m apart, from 1.2 to ~6.5 m above bottom. To illustrate patterns of variability, zonal stratification and cross-shore currents were plotted for the corresponding cruise dates with the highest and lowest stratification. Temperature and cross-shore currents were averaged for the duration of each plankton cruise (ca. 4 h) by depth bin.

A Sea-Bird Electronics Seagauge was deployed on the ADCP frame, and configured to record pressure every 3 h. Significant wave height (SWH) was calculated as 4× the square root of the sea surface spectrum between periods of 4 and 30 s. We calculated the 24 h SWH average in the same way as previously described for currents.

Relationships between physical variables and larvae

Relationships between relevant physical variables (mid-depth of the thermocline, thermal stratification, zonal stratification, 24 h currents, and 24 h SWH) and larvae (larval density, MDD, MDS, and CDI) were analyzed using individual regression analyses for each physical predictor. Values are presented as mean (±1 SE) where applicable.

RESULTS

Physical conditions

Depth-averaged hourly alongshore currents were generally stronger in spring–summer (ranging from ~ −0.16 to 0.19 m s^{-1}, Fig. 2A) than fall–winter (ranging from ~ −0.20 to 0.10 m s^{-1}, Fig. 2B) in 2014, but stronger in fall–winter (ranging from ~ −0.20 to 0.43 m s^{-1}, Fig. 3B) than spring–summer (ranging from ~ −0.20 to 0.18 m s^{-1}, Fig. 3A) of 2015. Depth-averaged 24 h alongshore currents were southward (positive) on all but 7 cruise dates, ranging from −0.12 to 0.05 m s^{-1} with a mean value of 0.006 (±0.007) m s^{-1}. Depth-averaged hourly cross-shore currents were slower than alongshore currents and comparable across the 4 sampling periods, ranging from ~ −0.07 to 0.02 m s^{-1} (Figs. 2C,D & 3C,D). Depth-averaged 24 h cross-shore currents were offshore (negative) during 15 cruises and onshore (positive) during 12 cruises, ranging from −0.02 to 0.007 m s^{-1} with a mean of −0.003 (±0.001) m s^{-1}.

SWH ranged from ~0.25 to 3 m, and there were more peaks in SWH during fall–winter than spring–summer of both years (Figs. 2E,F & 3E,F). The largest waves during 2014 and 2015 were usually associated with southward and offshore current flows (Figs. 2A–F & 3A–F). The overall mean SWH for 2014 and 2015 was 0.54 (±0.03) m. The minimum 24 h SWH was 0.33 m (in 2014 spring–summer), while the maximum was 1.03 m (in 2015 spring–summer).

Hourly temperature varied with depth during spring–summer sampling periods, at times decreasing ~4 to 5°C from surface to bottom (Figs. 2G & 3G). Temperature differences with depth decreased during fall–winter of both years (Figs. 2H & 3H). Temperatures ranged from ~11 to 23°C in spring–summer sampling periods, and from ~16 to 23°C in fall–winter, with the highest temperatures occurring at the end of spring–summer and beginning of fall–winter during 2014 and 2015. Fall–winter of 2015 was the warmest sampling period, with water temperatures rarely falling below 19°C (Fig. 3H).

Depth-averaged temperature across stations was similar between sampling periods in 2014 (Fig. 4A), ranging from 18.2 to 19.7°C. However, fall–winter was considerably warmer than spring–summer in 2015 (Figs. 4B & 3G,H), with average station temperatures ranging from 16.9 to 20.8°C. Temperature decreased with distance from shore in spring–summer during both years, but this was not as obvious in 2014. In 2015, the inshore stations were noticeably warmer than the offshore stations. Cross-shelf temperature variation was minimal in fall–winter of both years. Thermal stratification increased with distance from shore during spring–summer cruises and was similar across stations during fall–winter cruises, but offshore stations were still slightly more stratified (Fig. 4C,D). Stratification was markedly stronger in spring–summer than fall–winter in both 2014 and 2015, averaging 0.23 (±0.03)°C m^{-1} in spring–summer and 0.06 (±0.005)°C m^{-1} in fall–winter.
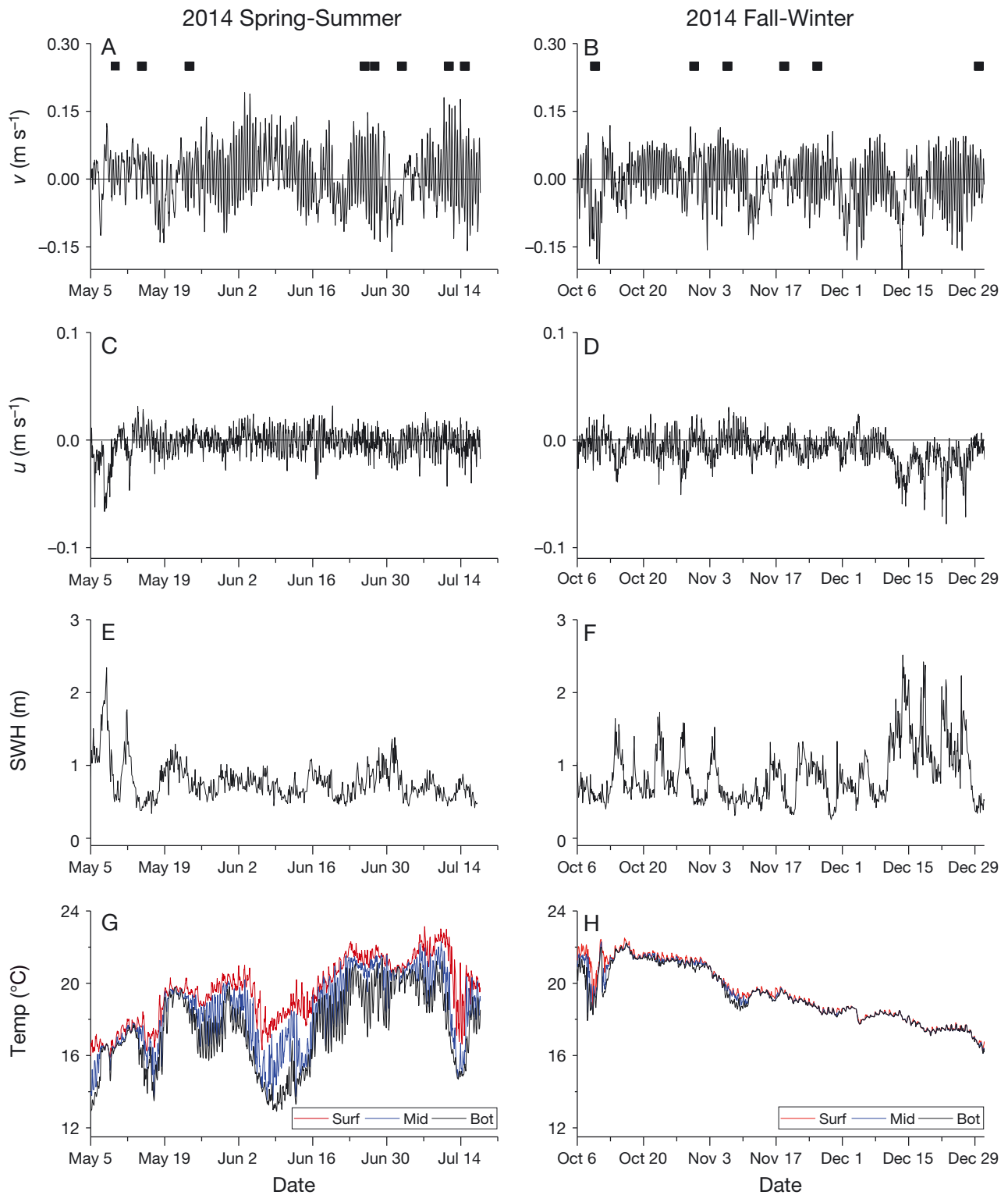
Fig. 2. Summary of hydrographic and hydrodynamic conditions in 2014. ADCP and temperature mooring deployments from spring–summer are shown in the left panels, and fall–winter in the right panels. (A,B) Depth-averaged alongshore currents (*v*), where positive is southward flow; (C,D) depth-averaged cross-shore currents (*u*), where positive in onshore (eastward) flow; (E,F) significant wave height (SWH); and (G,H) temperature. Surf: surface temperature at 6.5 m above bottom; mid: mid-depth temperature at 3.6 m above the bottom; bot: bottom temperature at 0.3 m above bottom. Black rectangles in panels A and B correspond with times of plankton sampling
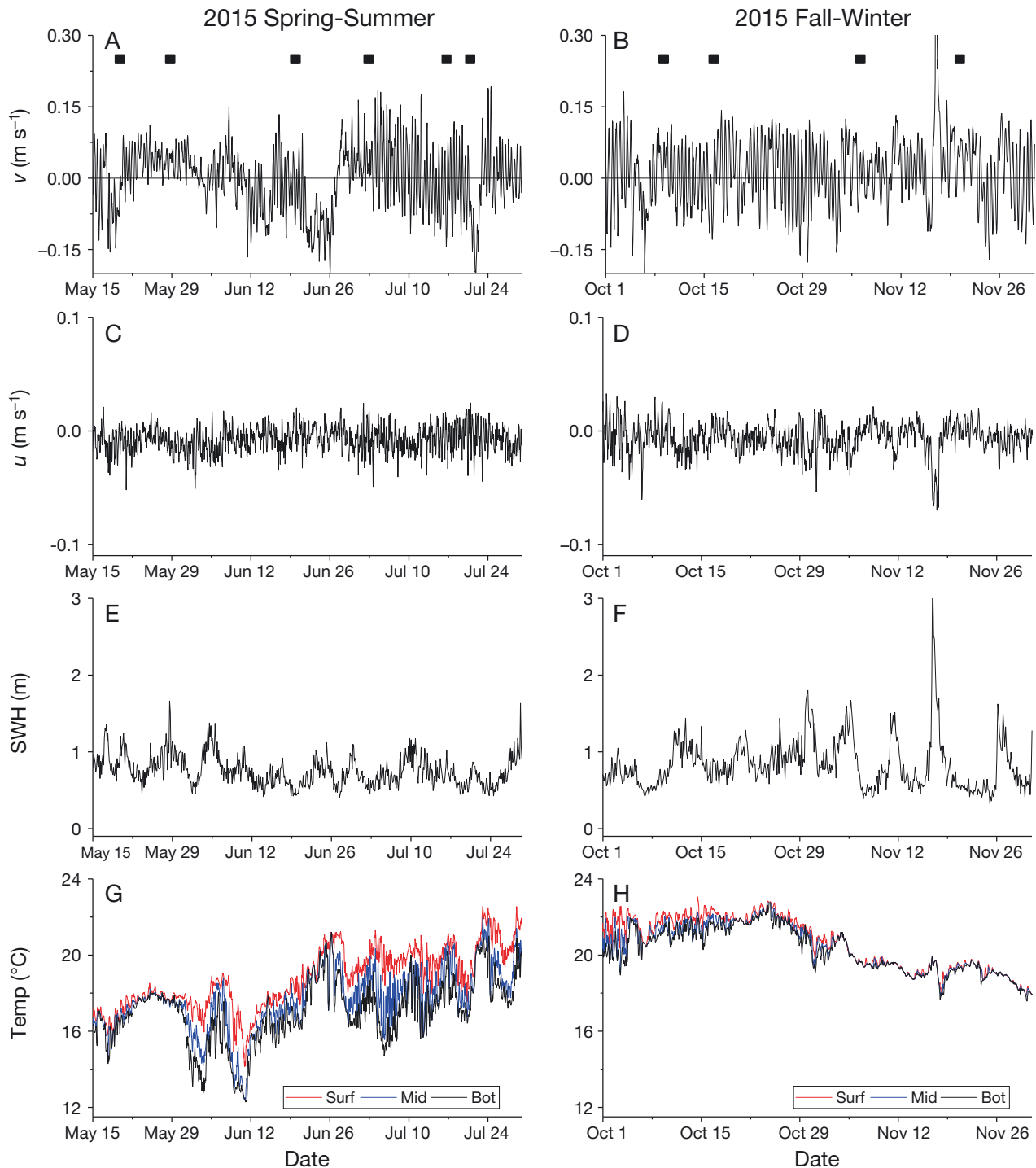
Fig. 3. Summary of hydrographic and hydrodynamic conditions in 2015. Details as in Fig. 2

Stratification and vertical variability in the cross-shore currents

The standard deviation across depth of the cross-shore currents tended to be high when stratification was elevated (Fig. 5A, R^2 = 0.55576, p = 0.0006). For example, the date with the highest zonal stratification (2 July 2015) had large variability in the surface and bottom currents, with currents that reversed with depth (Fig. 5B,C), whereas the date with the lowest stratification (6 November 2015) had smaller vertical variability in the cross-shore currents (Fig. 5D,E).
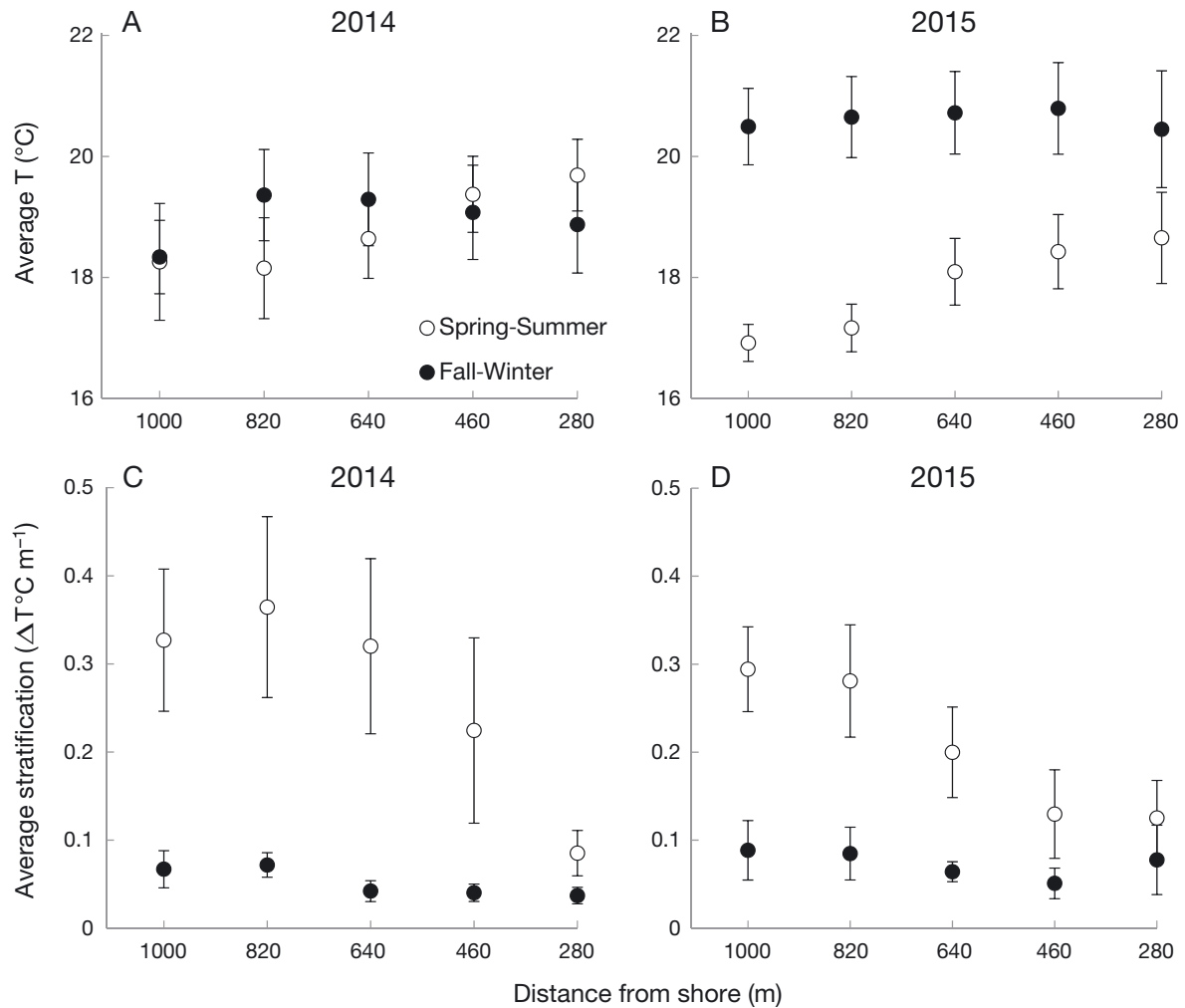
Fig. 4. Mean ± SE (A,B) depth-averaged temperature and (C,D) average thermal stratification at each station during 2014 and 2015 spring–summer and fall–winter sampling periods. Note that distance from shore increases from right to left (westward) to reflect the orientation of our study site

Temporal patterns of larval concentrations

Larval concentrations were higher for nauplii than cyprids, and varied by sampling period (Tables 1 & 2). Concentrations were higher overall in 2014 than 2015 (Table 3), and larvae were more abundant in spring–summer than fall–winter of 2014 (Tables 1 & 2). However, larvae were more abundant in fall–winter than spring–summer of 2015 (Tables 1 & 2). Most barnacle nauplii collected were early stage; of the late-stage nauplii, most were identified as *Chthamalus fissus* (Table 1). Six species of barnacle cyprids were identified at our study site, including *C. fissus*, *Balanus glandula*, *Pollicipes polymerus*, *Tetraclita rubescens*, *Megabalanus rosa*, and *Balanus trigonus* (Table 2). *C. fissus* comprised more than 86% of the cyprids in 2014 and fall–winter 2015, while in spring–summer 2015 *C. fissus* comprised only ~60% of the cyprids (Table 2). Overall, average cyprid concentrations were lowest during spring–summer 2015, but species were more equally represented in concentration (Table 2). Given the low concentrations of late-stage nauplii and cyprid species other than *C. fissus*, we did not examine the distribution patterns of scarce taxa. Hence, we analyzed the vertical and cross-shore distribution patterns of only the early-stage nauplii and *C. fissus* cyprids. The abundances of early-stage nauplii and *C. fissus* cyprids were not significantly correlated with SWH ($p > 0.46$), alongshore currents ($p > 0.67$), cross-shore currents ($p > 0.33$), or thermal stratification ($p > 0.27$) (see Hagerty 2017 for plots of these relationships).
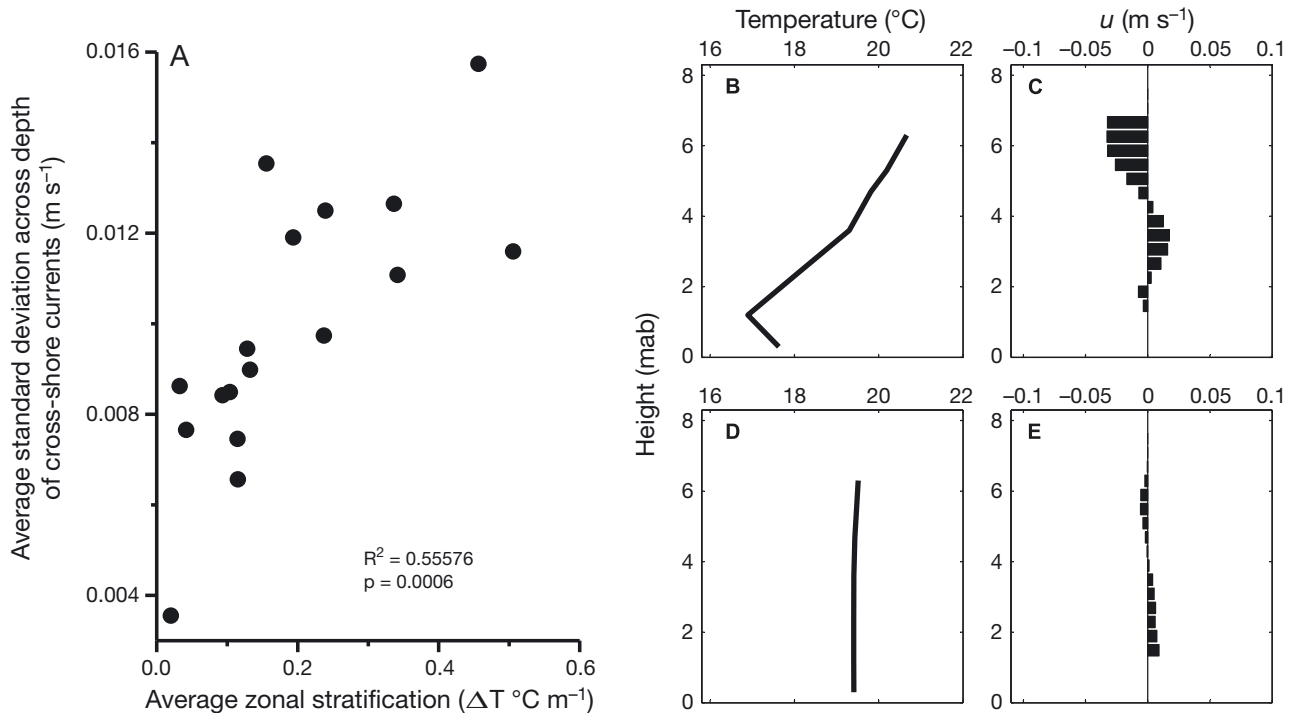
Fig. 5. (A) Average zonal stratification (average thermal stratification at stations 640, 820, and 1000 m from shore with bottom depths of 8, 10, and 12 m, respectively) and variability of the cross-shore (*u*-component) currents with depth, for the dates when all 5 stations were sampled. Examples of depth (mab: meters above bottom) variability of stratification and cross-shore currents during the cruises with the (B,C) highest (2 July 2015) and (D,E) lowest (6 November 2015) stratification

Table 3. Mean ± SE larval concentration (no. larvae m^{-3}) of nauplii and cyprids in 2014 (N = 257 samples) and 2015 (N = 214)

	2014	2015
Nauplii		
Early stage	59.79 ± 12.81	24.64 ± 5.18
Late-stage *Chthamalus fissus*	0.04 ± 0.03	0.22 ± 0.07
Late-stage other	0.06 ± 0.02	0.07 ± 0.03
Cyprids		
Chthamalus fissus	13.61 ± 2.62	2.92 ± 0.58
Balanus glandula	0.34 ± 0.08	0.11 ± 0.04
Pollicipes polymerus	0.32 ± 0.10	0.46 ± 0.11
Tetraclita rubescens	0.45 ± 0.12	0.04 ± 0.02
Megabalanus rosa	0.40 ± 0.08	0.34 ± 0.11
Balanus trigonus	0.06 ± 0.05	0.06 ± 0.03
Unknown	0.15 ± 0.04	0.04 ± 0.02

Vertical distributions of larvae

The MDDs of early-stage nauplii and *C. fissus* cyprids were deeper with increasing bottom depth and distance from shore, and cyprid MDDs were generally deeper than those of early-stage nauplii during all 4 sampling periods (Fig. 6). There was a significant difference between MDDs of early-stage nauplii and cyprids ($t = -5.547$, p < 0.0001), but there

were no significant differences between sampling periods for nauplii ($F_{1,110} = 0.458$, p = 0.499) or cyprids ($F_{1,97} = 0.221$, p = 0.639). The MDDs of early-stage nauplii and *C. fissus* cyprids were not correlated with the mid-depth of the thermocline (p > 0.14) or thermal stratification (p > 0.16) at any station (e.g. Fig. 6A–D), or 24 h alongshore (p > 0.12) or cross-shore (p > 0.22) currents at the station 640 m from shore (8 m depth), but early-stage nauplii MDD had a significant negative correlation with SWH (Pearson's r = −0.39, p = 0.047) (see Hagerty 2017 for plots of these relationships).

Cross-shore distributions of larvae

In general, the proportion of total early-stage nauplii increased with distance from shore (Fig. 7A–D), while *C. fissus* cyprid proportions decreased with distance from shore (Fig. 7E–H). These patterns were more distinct during spring–summer periods than fall–winter periods. There were differences among stations for early-stage nauplii and *C. fissus* cyprids, with significantly more nauplii at the offshore stations and significantly more cyprids at the inshore stations (Table 4). There was also a significant differ-
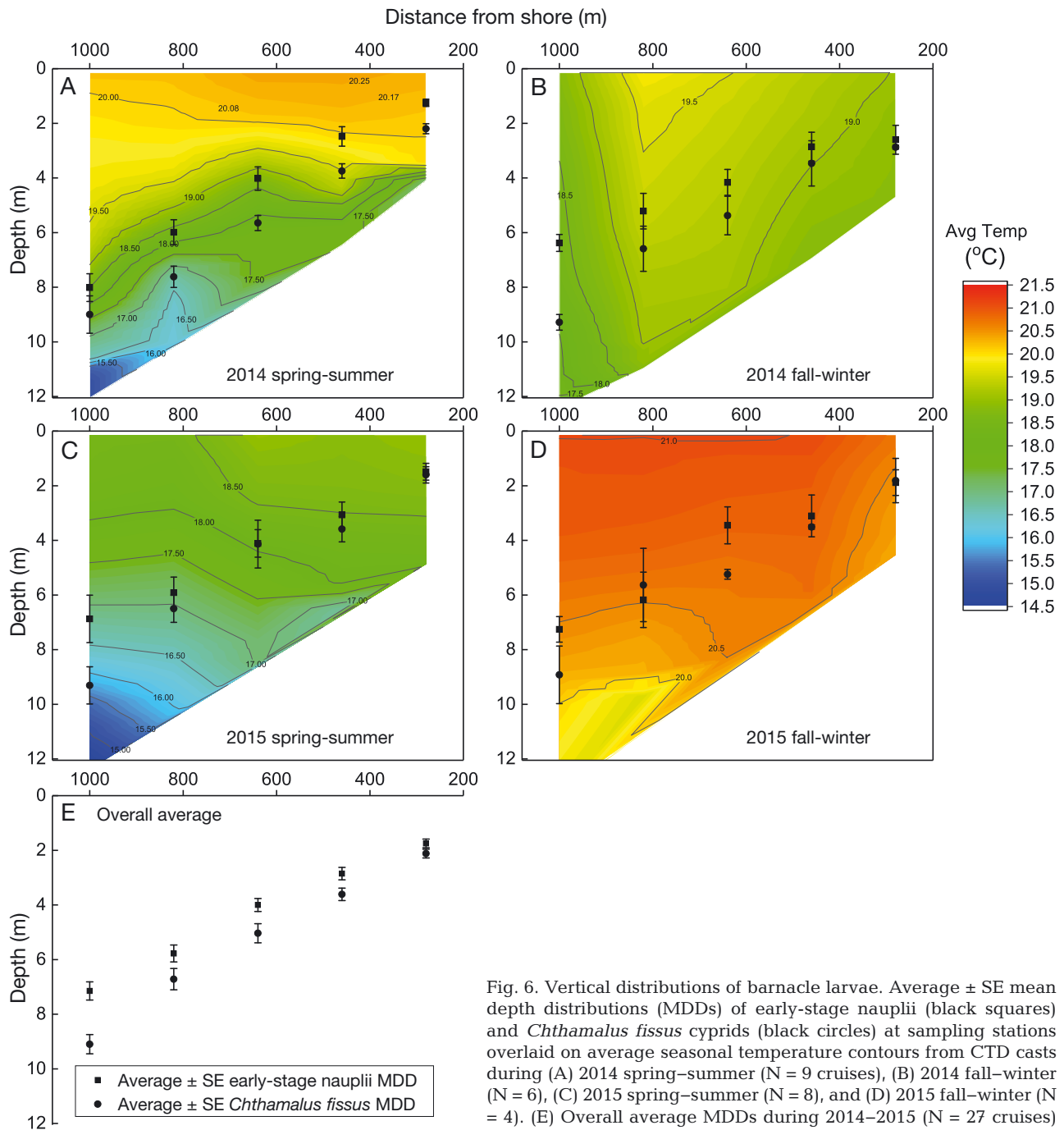
Fig. 6. Vertical distributions of barnacle larvae. Average ± SE mean depth distributions (MDDs) of early-stage nauplii (black squares) and *Chthamalus fissus* cyprids (black circles) at sampling stations overlaid on average seasonal temperature contours from CTD casts during (A) 2014 spring–summer (N = 9 cruises), (B) 2014 fall–winter (N = 6), (C) 2015 spring–summer (N = 8), and (D) 2015 fall–winter (N = 4). (E) Overall average MDDs during 2014–2015 (N = 27 cruises)

ence between sampling periods for cyprids, with more cyprids at the middle station (640 m offshore, 8 m depth) in fall–winter than spring–summer throughout the study duration (Table 4).

Early-stage nauplii were distributed farther offshore than *C. fissus* cyprids (MDS was significantly greater: $t = 5.350$, $p < 0.0001$; Fig. 8). Additionally, cyprids were closer to shore in spring–summer than fall–winter (comparing minimum and median MDS

values); however, their distributions were variable. The CDI revealed that cyprid densities were higher than average (i.e. CDI > 0) at the 2 inshore stations during 5 of the 17 cruises when all 5 stations were sampled (Fig. 9B). Four of these 5 cruises were in spring–summer (2 in 2014, 2 in 2015), and 1 was in 2015 fall–winter. The highest CDI measurement (0.536), representing the date when cyprids were most constrained nearshore, coincided with the high-
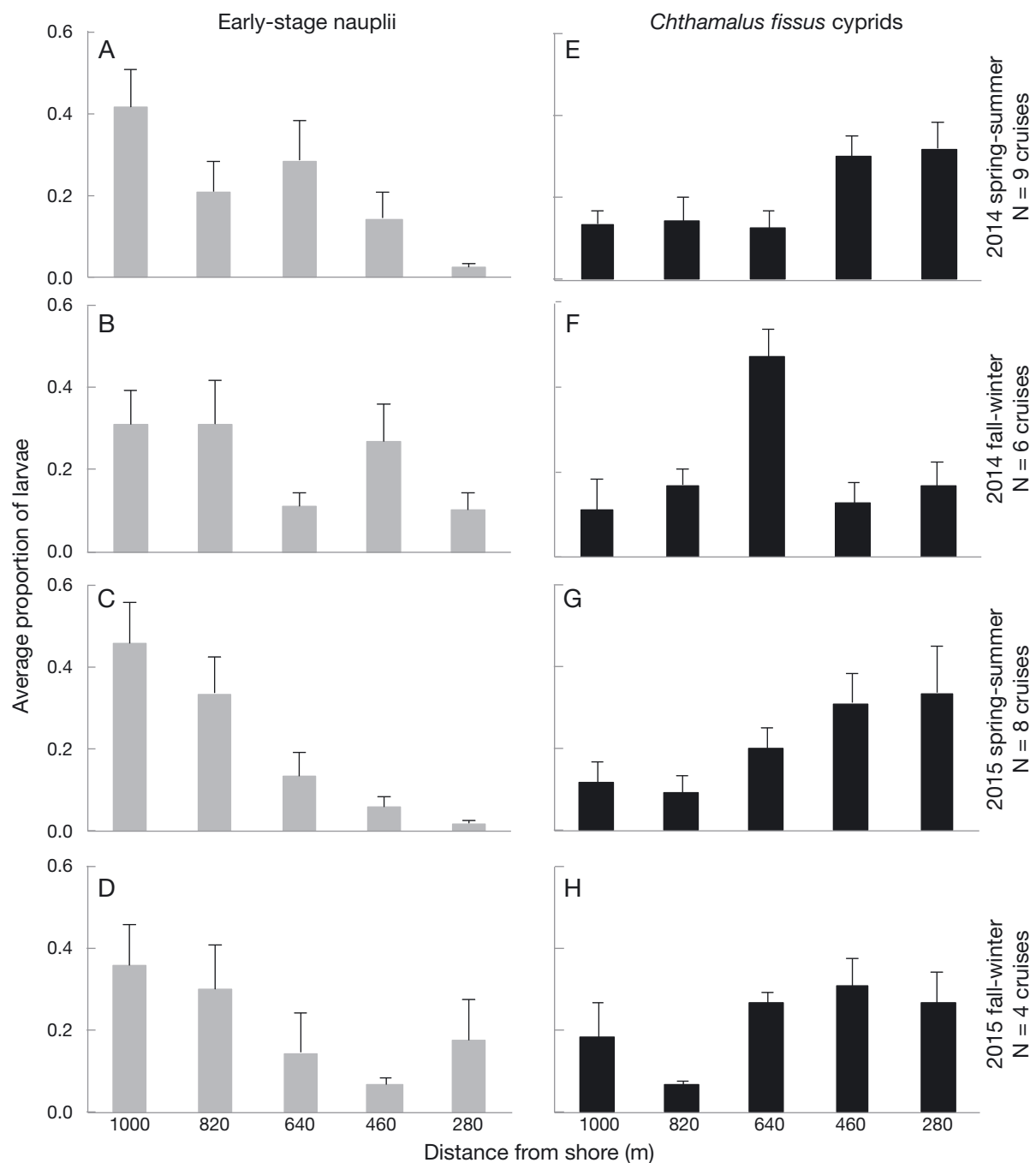
Fig. 7. Cross-shelf distributions of barnacle larvae. Average proportion of (A–D) total early-stage nauplii and (E–H) *Chthamalus fissus* cyprids present at each of the 5 stations during sampling periods (spring–summer versus fall–winter) by year (2014 versus 2015)

est zonal stratification (0.505°C m^{-1}). Average zonal stratification had a significant negative relationship with MDS and a significant positive relationship with the CDI for *C. fissus* cyprids (Fig. 9), but was not a significant predictor of early-stage nauplii MDS (R^2 = 0.024, p = 0.521).

Summary of larval distribution patterns

To summarize the 2014–2015 average barnacle larval distribution patterns, MDDs of *C. fissus* cyprids were deeper than those of early-stage nauplii, and MDD values increased with water depth and dis-

Table 4. Results of 2-factor ANOVAs testing for differences in proportions of early-stage nauplii and *Chthamalus fissus* cyprids among stations and between sampling periods. Significant differences ($\alpha = 0.05$) are indicated in **bold** and post hoc test results are shown (stations represented by their distances from shore) for group pairs with significant differences

Factor	F	p	Post hoc test results
Early-stage nauplii (df = 1, 115)			
Station	26.210	**<0.00001**	1000 m > 280 m, 1000 m > 460 m, 820 m > 280 m, 640 m > 280 m
Period	0.775	0.380	
Station × Period	1.534	0.218	
***Chthamalus fissus* cyprids (df = 1, 105)**			
Station	20.907	**<0.0001**	280 m > 1000 m, 280 m > 820 m, 460 m > 1000 m, 460 m > 820 m
Period	0.102	0.749	
Station × Period	5.704	**0.018**	640 m fall–winter > 640 m spring–summer ($F_{1,22} = 18.247$, **p < 0.001**)

tance from shore for both larval stages (Fig. 6E). Densities of nauplii increased with distance from shore (Fig. 10A) while densities of cyprids were higher nearshore (Fig. 10B), and nauplii were much more abundant than cyprids (Fig. 10A,B). The majority of nauplii were found in plankton samples from offshore stations at a mid- to near-bottom depth (Fig. 10C,E), while the majority of cyprids were in samples from inshore stations at near-bottom depths (Fig. 10D,F).
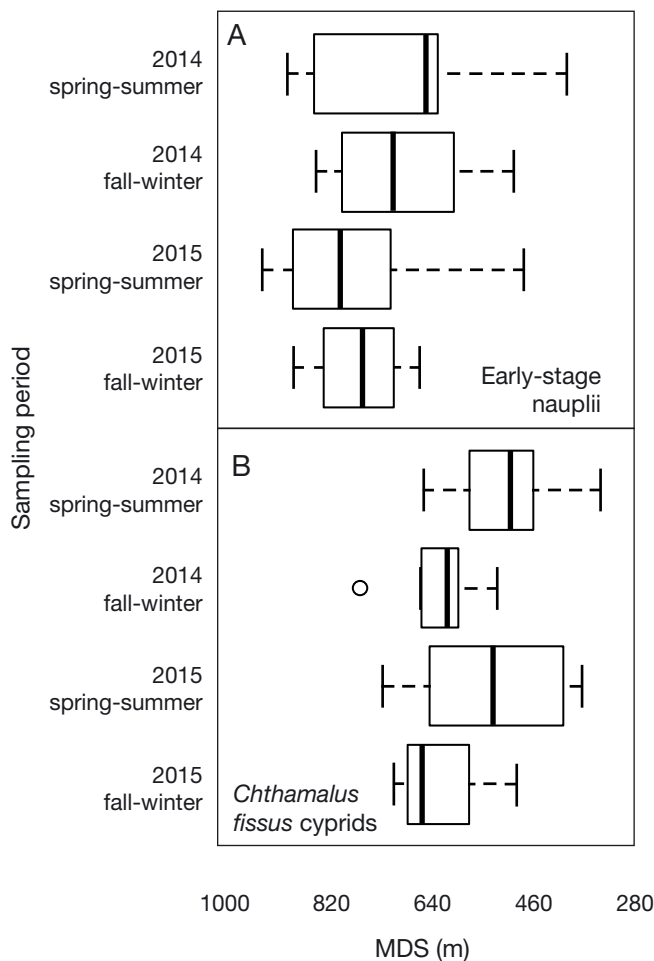

Fig. 8. Mean distance from shore (MDS) patterns of (A) early-stage nauplii and (B) *Chthamalus fissus* cyprids by sampling period and year. Lower and upper box limits are the first and third quartile, respectively, and box midline is median. Whiskers extend up to 1.5× the interquartile range to the farthest data point within that distance. Any data beyond that are shown individually as outlying points
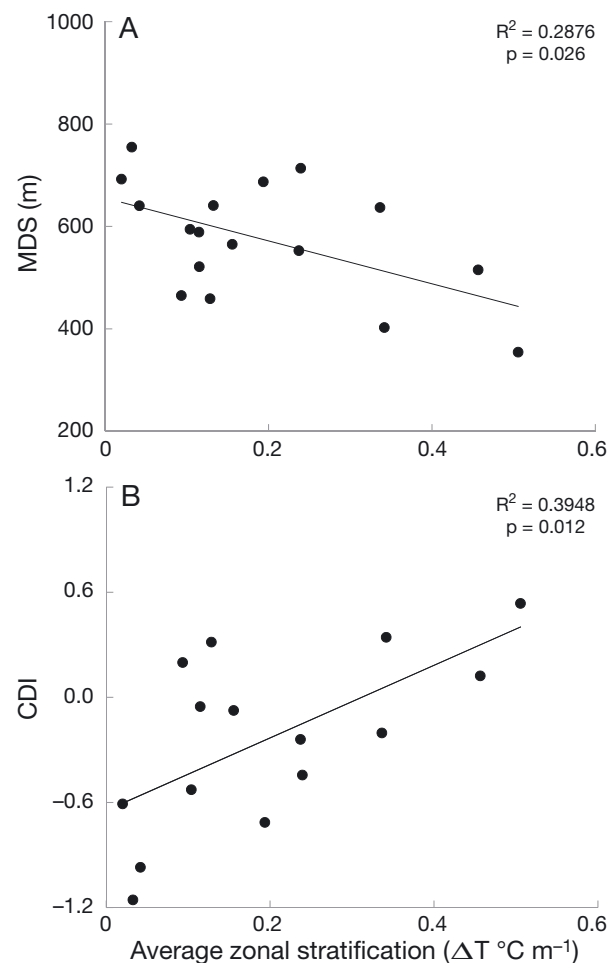

Fig. 9. Effect of zonal thermal stratification (average thermal stratification at stations 640, 820, and 1000 m from shore with bottom depths of 8, 10, and 12 m, respectively) on *Chthamalus fissus* cyprid (A) mean distance from shore (MDS) and (B) constrained-distribution index (CDI). CDI was calculated for cruise dates when all 5 stations were sampled. Only 15 data points are shown because no *C. fissus* cyprids were collected on 2 of the 17 cruise dates
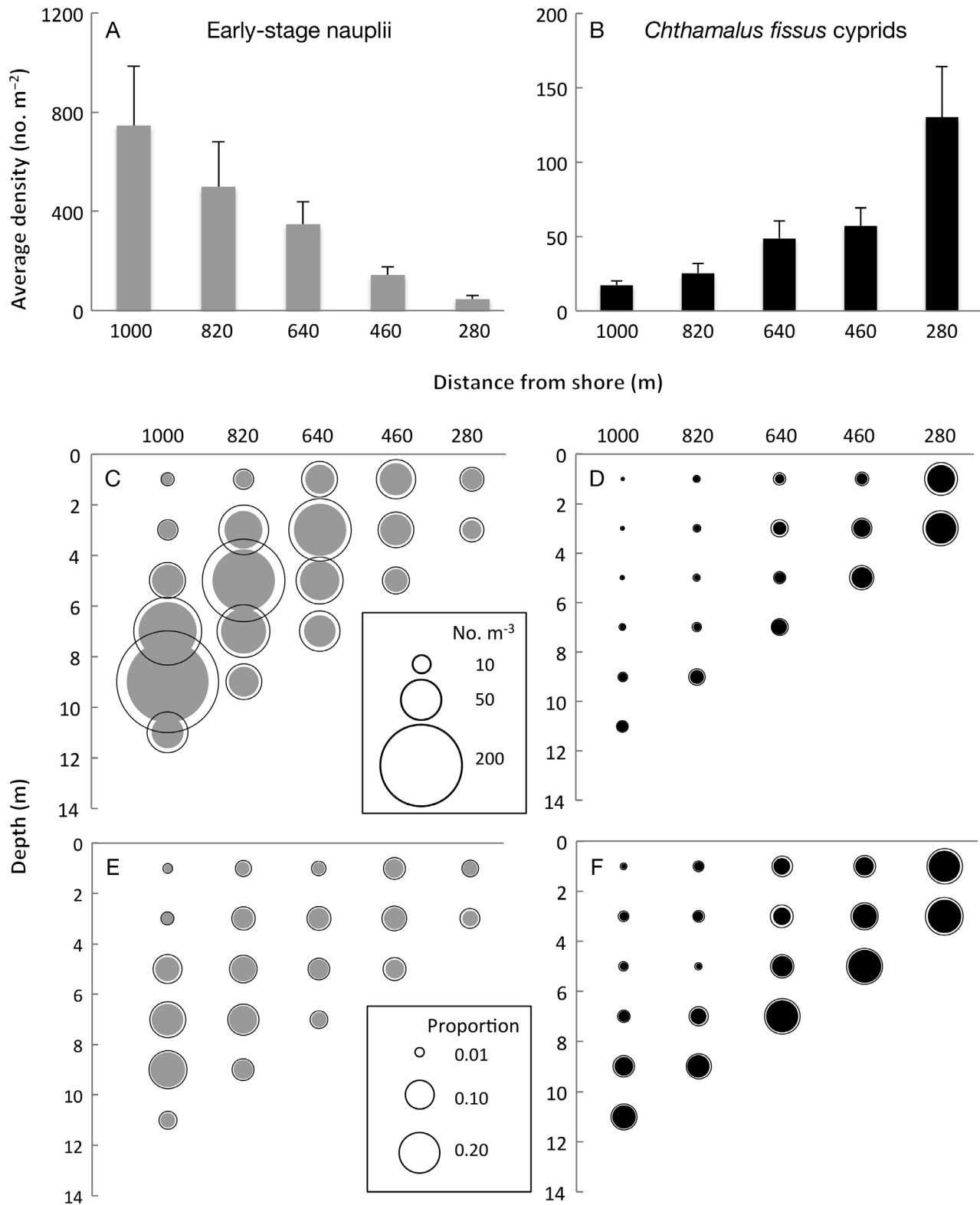
Fig. 10. Mean distributions for 2014 and 2015 (N = 27 cruises): overall cross-shore distribution patterns, showing average densities of (A) early-stage nauplii and (B) *Chthamalus fissus* cyprids at each station; average concentrations of (C) early-stage nauplii and (D) *C. fissus* cyprids in each plankton sample; and average proportions of (E) early-stage nauplii and (F) *C. fissus* cyprids in each plankton sample. Open circles surrounding the shaded averages represent SE

DISCUSSION

Although larval concentrations varied from being high in 2014 spring–summer, decreased in 2014 fall–winter, and remained low through 2015 spring–summer until increasing in 2015 fall–winter, vertical and cross-shelf distribution patterns of early-stage nauplii and *Chthamalus fissus* cyprids remained consistent despite significant seasonal and interannual variability. Mean larval concentrations decreased 2-fold for early-stage nauplii and 5-fold for *C. fissus* cyprids from 2014 to 2015, likely due to large-scale disturbances associated with a warm water anomaly commonly referred to as 'the Blob,' as well as El Niño conditions. Coastal sea surface temperatures in southern California began to warm as a result of 'the Blob' in mid-2014, after the start of our sampling regime, and remained anomalously warm until spring in 2015 (Leising et al. 2015). El Niño impacted southern California starting in spring 2015 and intensified in fall–winter of 2015, corresponding to the highest temperatures recorded at our site, lowest larval abundances, and the peak of the southern California coastal warm anomaly (Leising et al. 2015, Gentemann et al. 2017). Decreased larval abundances in 2015 could be associated with environmental conditions that may have increased larval mortality or offshore advection, diminished onshore larval transport, decreased adult reproduction, or a combination of these factors.

Early-stage nauplii abundances were considerably larger than those of cyprids, likely reflecting loss due to larval mortality or advection (Rumrill 1990, Tapia & Pineda 2007), and the potential species diversity of early-stage nauplii. In contrast, concentrations of cyprids were higher than those of late-stage nauplii during all sampling periods throughout the 2 yr study, suggesting that late-stage nauplii are advected farther offshore (>1 km) than our station located 1000 m from shore (12 m depth) before transitioning to the cyprid stage and returning to the intertidal. It is important to note that when sampling began in spring–summer of 2014, an additional station farther offshore at a 14 m depth was sampled during the first 3 cruises. This station was abandoned for the remainder of cruises due to plankton pump issues, but the mean density of late-stage nauplii (*C. fissus* and other species) at that station was 18.06 ($\pm$10.04) m^{-2}, while the mean density of late-stage nauplii in samples from all other stations was 1.22 ($\pm$0.73) m^{-2}, supporting previously observed patterns of early-stage nauplii closer to shore and later stages farther offshore (Tapia & Pineda 2007, Morgan et al. 2009).

Vertical distributions of early-stage nauplii and *C. fissus* cyprids moved deeper with increasing depth and distance from shore, suggesting that the larvae were tracking bottom depth. Cyprids were deeper than nauplii (as in Shanks & Shearman 2009, Tapia et al. 2010, Bonicelli et al. 2016), which could be due to the negative buoyancy of cyprids. Cyprids have been found at near-bottom depths (Barnett & Jahn 1987, Pineda 1991, Bonicelli et al. 2016); non-feeding cyprids may seek deeper, cooler waters to lower their metabolic rate, thus maintaining storage reserves and remaining competent longer before finding a suitable place to settle. Cyprid larvae, however, have also been observed in surface waters (Le Fèvre & Bourget 1991), sometimes associated with transient internal bore warm fronts (Pineda 1999). The pattern of cyprids deeper than nauplii was not as clear in 2015 as in 2014, and may be due to low larval abundance in 2015. Nauplii have been observed near the surface (Tapia et al. 2010), as well as in upper to middle depths of the water column (Bonicelli et al. 2016) and middle to bottom depths (Shanks & Shearman 2009, Morgan & Fisher 2010). However, early-stage nauplii (stages II and III, ~300 µm maximum dimension for most species sampled) passed through the net used by Morgan & Fisher (2010) (mesh aperture 335 µm) and the surface net used by Shanks & Shearman (2009) (mesh aperture 330 µm). Further, all of these previous studies were conducted in deeper water using coarser sampling intervals (ranging from 5 to 30 m, in contrast to our 2 m depth intervals). The majority of early-stage nauplii from our study were located at middle depths, but it cannot be discounted that later-stage nauplii assume a more surface-oriented distribution as they move farther offshore than our research area. Additionally, vertical distribution is likely to be species-specific (Le Fèvre & Bourget 1991, Morgan & Fisher 2010, Bonicelli et al. 2016), but this cannot be discerned here.

Larval depth distributions were not related to the mid-depth of the thermocline or station-specific thermal stratification, suggesting that there is no temperature effect on vertical distribution. The MDD of early-stage nauplii was shallower when SWH was higher, which could be a result of specific naupliar behaviors including an upward shift in swimming direction and increased swimming rate (Yule 1984) in response to increasing pressure.

Cross-shore distribution patterns varied with larval stage: early-stage nauplii densities increased and *C. fissus* cyprid densities decreased with distance from shore. These distribution patterns were generally more distinct in spring–summer, when thermal strati-

fication was strongest, than in fall–winter. As zonal stratification increased, the CDI increased, indicating that there were higher abundances of cyprids near-shore when zonal stratification was stronger. This relationship is further exemplified by the effect of decreasing cyprid MDS values with increasing zonal stratification. These results provide evidence that cyprids are constrained closer to shore when zonal stratification is higher, and are farther offshore when the water column is more well mixed. Higher stratification may enhance the behavioral control of horizontal distribution by allowing cyprids to exploit vertically sheared flows. Our results also indicate larger variability across depth of the cross-shore currents with increasing zonal stratification; such variability is expected to increase when currents are going in opposite directions, or when currents go in one direction, but magnitude changes with depth. Additionally, these findings could be related to shoreward transport of cyprids by the internal tide, motions that require water column stratification (Pineda 1999, Pfaff et al. 2015). When the water column is stratified and the internal tide occurs, cyprids could be transported from offshore waters to near our station 280 m from shore (4 m depth) where stratification weakens. Our findings explain the results of Pineda & López (2002) that changes in thermal stratification are positively correlated with changes in barnacle settlement.

Our results indicate that larval densities and distributions were not directly related to alongshore or cross-shore current velocities. However, when zonal stratification increased, cross-shore currents were more variable and energetic throughout the water column and cyprids were closer to shore, suggesting that stratification can mediate cross-shore currents, and thus larval distributions. Given that current measurements from an ADCP located between the 8 and 10 m stations may not accurately reflect currents throughout our site due to small-scale variability at the nearshore (reviewed by Lentz & Fewings 2012), physical measures that better resolve such small-scale variability are needed in the nearshore to resolve possible larval transport mechanisms.

In summary, distribution patterns of barnacle larvae within 1 km of the coast of La Jolla, southern California, were upheld across 27 sampling cruises over a 2 yr period despite varying environmental conditions from 2 large-scale disturbances: the warm 'Blob' and El Niño. For cyprids, cross-shore patterns varied seasonally. Our results support the inference that behavior plays a substantial role in facilitating transport during pelagic larval stages. Cross-shore distributions of cyprids were related to zonal stratifi-cation, which correlated with greater variability in the cross-shore vertical currents, but SWH did not significantly affect spatial patterns. These results support the hypothesis that the more thermal stratification there is, the more behavioral control can be exerted by cyprids to accumulate closer to shore, and that stratification is an important determinant of the successful larval transport of cyprid larvae. Near-shore accumulation of cyprid larvae has been previously observed (dos Santos et al. 2007, Tapia & Pineda 2007, Shanks & Shearman 2009). We hypothesize that thermal stratification mediates constrained larval distributions in nearshore waters. Vertically, larvae might maintain their positioning in more stratified waters. We propose that zonal stratification allows the internal tide to propagate shoreward. Where stratification breaks down, likely due to surface wave mixing, larvae will accumulate. In our case, accumulation of cyprids occurred at our most inshore station (280 m from the coast and 4 m deep), where stratification was weak during both spring–summer and fall–winter sampling periods. We hypothesize that higher stratification will allow larvae to better maintain more constrained distributions, both in the nearshore, and we expect settlement to be higher during these conditions (Pineda & López 2002).

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