


ARTICLE

Special Feature: Honoring Charles H. Peterson, Ecologist

Habitat partitioning by mobile intertidal invertebrates of sandy beaches shifts with the tides

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Abstract

Coexistence of similar species can be influenced by the intensity of interspecific interactions, which often depends on the availability of limiting resources. Habitat availability varies strongly with tidal phase in many intertidal ecosystems, potentially affecting interspecific interaction strength, particularly for mobile species. Four closely related species of highly mobile intertidal detritivores (talitrid amphipods *Megalorchestia californiana*, *M. corniculata*, *M. benedicti*, *M. minor*) inhabit sandy beaches in southern California, where they consume wave-cast macroalgal wrack originating on coastal reefs. Their coexistence suggests that mechanisms, such as niche separation, are operating to weaken competition among these species. To evaluate this possibility, we explored how tidal phase may mediate temporal and spatial patterns of habitat use among these closely related congeners. We hypothesized that neap tides that reduce intertidal habitat would strengthen temporal separation between species, whereas spatial separation would be greater during spring tides when more habitat is available. We investigated these questions during spring and neap tide phases using (1) comparisons of intertidal distributions of burrowed amphipods and (2) observations of surface activity of amphipods from pitfall traps and mesocosms. We found significant effects of tide phase and species identity on mean intertidal positions and separation of burrowed amphipods. Intertidal distributions of the four species overlapped during neap tide and were significantly separated during spring tide when more intertidal habitat was available. Surface activity patterns differed among species and were more widely separated in time during neap tide than during spring tide. Consequently, the cumulative activity time of all species on neap tides was twice that observed during spring tides. Our findings suggest that mobile intertidal species, like these sympatric talitrid amphipods, can avoid interspecific competition by shifting their activity patterns with tide phase and beach condition. As rising sea levels reduce beach habitat, interspecific competition among these

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important intertidal consumers may increasingly influence their behavior and coexistence.

KEYWORDS

interspecific competition, *Megalorchestia*, niche separation, sandy beach, Special Feature: Honoring Charles H. Peterson, Ecologist, talitrid amphipods, tide phase, zonation

INTRODUCTION

Species coexistence is central to the maintenance and promotion of biodiversity (Chesson, 2000). Niche differentiation and consequent reduction in interspecific competition for limiting resources have long been thought to be the most important general mechanism for coexistence (Hutchinson, 1961; Tilman & Pacala, 1993). The apparent coexistence of ecologically similar species, however, has challenged this idea (Leibold & McPeck, 2006; Levine & HilleRisLambers, 2009; Mayfield & Levine, 2010) and engendered many potential explanations and hypotheses (Palmer, 1994; Wilson, 1990a; Wright, 2002), particularly neutral processes (Hubbell, 2011). Nevertheless, specialization of many niche dimensions may not be readily apparent (Futuyma & Moreno, 1988); for example, ecologically similar species can avoid competitive exclusion by partitioning their habitat and food resources across time as well as space (Cloyd & Eason, 2017; Jensen et al., 2017; Lea et al., 2020; Sala & Ballesteros, 1997; Schoener, 1974) by developing activity patterns that differ from potential competitors (Albrecht & Gotelli, 2001; Gertsch & Riechert, 1976).

The mechanisms of stabilizing coexistence were summarized by Chesson (2000) and divided into two primary categories based on the role of heterogeneity. Variation-independent mechanisms of stabilizing species coexistence occur in the absence of spatial or temporal heterogeneity and include resource partitioning and frequency-dependent predation (Chesson, 2000; Levine & Hart, 2020). Variation-dependent mechanisms of stabilizing coexistence include temporal and spatial storage effects, temporal and spatial relative nonlinearity of competition, and fitness-density covariance (Chesson, 2000; Levine & Hart, 2020). Determining the role of heterogeneity is a scale-dependent question, as heterogeneity, and its importance for coexistence, is expected to decline with habitat area (Snyder & Chesson, 2003). The role of spatial scales with respect to species coexistence is complex, but a unifying feature is the function of tradeoffs across environmental conditions and spatial scales (Kneitel & Chase, 2004). Coexistence across patches depends on the degree of heterogeneity, dispersal among patches, and species similarity (Mouquet & Loreau, 2002), and can occur through habitat (Stewart et al., 2010; Streams, 1987) and

food selection (Oakley-Cogan et al., 2020; Pardo et al., 2015), or intraspecific aggregation (Ives, 1991; Presa Abos et al., 2006). Time is also a segregable niche dimension (Carothers & Jaksic, 1984; Castro-Arellano & Lacher, 2009). Separation of the timing of resource use (food or habitat), for example, can occur via avoidance or differential activity periods on diurnal or longer scales (Adams & Thibault, 2006; Albrecht & Gotelli, 2001; Stewart et al., 2002) and successional patterns of colonization (Edwards & Stachowicz, 2010; Young et al., 1996).

Such mechanisms of niche separation are profoundly affected by environmental variability, the magnitude of which strongly influences the strength and outcome of competitive interactions (Levins, 1979; Li & Chesson, 2016). For example, a harsh and fluctuating environment can slow the process of competitive exclusion (Chesson et al., 2004; Chesson & Huntly, 1997). In harsh environments, some argue that the intensity and importance of competitive interactions decrease in favor of positive interactions or facilitation (Barrio et al., 2013; Fugère et al., 2012; Kawai & Tokeshi, 2007, but see Hart & Marshall, 2013). However, such conditions may also make species less tolerant of competitive interactions and promote niche differentiation through environmental fluctuations (Chesson & Huntly, 1997). Gutt (2006) suggests that the ability of similar species to coexist, therefore, is dependent on minimizing competitive displacement by maximizing utilization of environmental variability.

Intertidal marine ecosystems provide ideal systems to explore how spatial and temporal heterogeneity affect species coexistence and community dynamics. Studies of competitive interactions in unvegetated soft-sediment ecosystems, such as mudflats and sandy beaches, are relatively limited (Peterson, 1991) compared to the rocky intertidal, where interactions among sessile or sedentary species can shape zonation and other aspects of community structure (Chesson, 1985; Connell, 1961a; Dayton, 1971; Paine, 1974). However, the potentially important role of competitive interactions in soft-sediment marine ecosystems was illuminated by the pioneering work of Peterson (1977, 1982) and Peterson and Andre (1980) on intertidal bivalves in lagoons along with studies of a variety of infaunal taxa (Drolet et al., 2013; Gallagher et al., 1983, 1990; Martinetto et al., 2007; Wilson, 1990b). On the open coast, the intertidal zone of

sandy beaches has traditionally been described as a harsh environment where ecological communities are structured primarily by strong physical factors (waves, tides, and grain size) rather than biotic interactions (Defeo et al., 2003; McLachlan, 1990). However, this long-standing paradigm has been challenged in recent years (Bruce & Soares, 1996; Dugan et al., 2004; McLachlan, 1998) and falls short in addressing the high biodiversity of intertidal communities on sandy beaches that receive large subsidies of marine macrophytes or wrack, such as kelp and seagrass, from nearshore reefs (Dugan et al., 2003; Schooler et al., 2017).

On beaches, numerous similar species of mobile invertebrates depend on wrack subsidies for food and habitat (Colombini et al., 2000; Dugan et al., 2003; Olabarria et al., 2007). One possible mechanism of coexistence for these animals is the spatial or temporal partitioning of intertidal habitat by species. Spatial zonation is common among rocky intertidal organisms, especially sessile biota (Harley & Helmuth, 2003), but is less distinct in the mobile biota of soft-sediment ecosystems (Peterson, 1991). On sandy beaches, where mobility of infauna is particularly high, zonation patterns are dynamic, and many species actively migrate on diurnal and tidal scales (Dugan et al., 2013; Jaramillo et al., 1993, 2000; Jaramillo & Fuentealba, 1993). These movements can be in response to water levels and the distribution of resources, for example, wrack deposits, as well as avoidance of potentially negative biotic interactions, such as competition and predation (Colombini et al., 2013). Tides, a zeitgeber of the shore, may benefit sandy beach macrofauna by aiding their orientation and locomotion or providing cues to signal the need to relocate (Fanini et al., 2016; Rossano et al., 2008; Scapini, 2006; Scapini et al., 2019). Because they include many components (diurnal, semilunar, lunar, and longer) which drive much of the inundation and desiccation patterns on intertidal beaches it is likely they mediate the behavior of sandy beach organisms.

Sandy beaches in southern California can support a species rich and functionally redundant community of upper beach macroinvertebrates (Schooler et al., 2017), providing an ideal system to evaluate how similar species can coexist in a dynamic and harsh ecosystem. We explored niche partitioning among four congeneric species of talitrid amphipods found on southern California beaches in (1) space, via occupation of different levels of the intertidal zone and (2) time, via different periods of activity. We hypothesized that neap tides that reduce the area of preferred intertidal habitat would strengthen temporal niche separation in these species, whereas spatial separation would be more evident during spring tides, when a wider habitat zone is available. We also hypothesized that body size may

affect surface activity patterns with the two large-bodied species having an advantage over the two small-bodied species and juveniles.

METHODS

Study sites and species

Our field surveys (spatial coring and pitfall sampling) were conducted on an unmanaged, unarmored beach with no vehicle access or beach grooming, located east of Goleta Beach County Park in Santa Barbara, California, USA (34°25'02.1"N, 119°48'56.7"W). The mesocosm experiments were conducted at nearby Campus Point Beach (34°24'22.6"N, 119°50'38.0"W) for access and safety reasons. All species of talitrid amphipods (*Megalorchestia californiana*, *M. corniculata*, *M. minor*, *M. benedicti*) used in the mesocosm study were collected by hand at local beaches (where they are highly abundant) on the morning of each experiment. *M. corniculata* was collected at Isla Vista Beach (34°24'33.6"N, 119°52'23.0"W), *M. minor* at R beach (34°24'58.1"N, 119°53'12.3"W), and *M. californiana* and *M. benedicti* at Goleta Beach. This guild of congeners is the dominant wrack-associated taxon in the study region in terms of abundance and biomass (Dugan et al., 2003). These highly mobile species are most active on the sand surface at night when they forage on kelp and other wrack. During the day, they occupy freshly dug intertidal burrows in damp sand that are typically aggregated into distinct, often species-specific, beds of characteristically bioturbated sand (Dugan et al., 2013).

Spatial distribution surveys

To compare zonation patterns and spatial separation across species, we quantified the distribution and abundance of wrack-associated macroinvertebrates on two dates with contrasting spring and neap tide phases (2 [spring] and 10 [neap] August 2016). All surveys were conducted during the day when the majority of animals were burrowed in the sand. For each survey, six shore-normal transects were set up to extend from the upper beach boundary (cliff base) to the water table outcrop during low tide. We measured the abundance of macrophyte wrack as cover on each transect using a line intercept method (Dugan et al., 2003). Along each transect, we also collected 30 evenly spaced cores (10 cm diameter, 20 cm depth) from the upper beach boundary to the lowest distribution limit of upper beach macroinvertebrates. Each core was placed in a 1.5-mm

mesh bag sieve, rinsed in seawater, and the contents were bagged and frozen. Each frozen sample was sorted in the laboratory and invertebrates were identified to species level, counted, and weighed. For the purpose of this study, we focused on the spatial distributions of the four congeneric species of talitrid amphipods (*M. californiana*, *M. corniculata*, *M. minor*, *M. benedicti*) that coexist on sandy beaches in our study region. Juvenile *Megalorchestia* (length <8 mm) were included as a separate group because they make up a large portion of total talitrid abundance on the beach and prior research has shown that juvenile activity differs from that of adults (Lastra et al., 2010).

Temporal distribution—Surface activity

Surface activity patterns of the four *Megalorchestia* species were assessed using observations in controlled mesocosm experiments and through pitfall trapping on the beach during spring and neap tide phases. The observational study used mesocosm containers placed on the upper beach at Campus Point Beach in Santa Barbara, California on contrasting neap and spring tide phases, 31 July and 7 August 2017, respectively. The mesocosms ($n = 4$ per species) consisted of 18.9 L buckets filled to a depth of 20 cm with sieved dry sand and wetted using filtered seawater. Eighty individuals of each species were collected the morning of each experiment from the local beaches described above, and single-species treatments were set up with 20 individuals per bucket (four replicates per species) with a fresh blade of giant kelp (*Macrocystis pyrifera*) as a food source and habitat element. The 16 mesocosms were set up in the laboratory and left to acclimate for approximately 6 h before observations commenced. After the acclimation period, buckets were buried to 20 cm depth on the upper beach (the same depth as the sand in the bucket) to help maintain ambient temperature and lighting conditions. Every hour for 24 h, the total number of individuals active on the surface was observed for 1 min and recorded.

Pitfall traps were used to assess *in situ* surface activity patterns of *Megalorchestia* spp. along the high tide line of Goleta Beach on contrasting neap and spring tide phases (16 [neap] July and 8 [spring] August 2017). Traps were placed at the high tide line where most of the fresh kelp wrack is deposited and where these organisms aggregate to feed. After high tide on each sampling date, twelve 470-ml cups with lids were buried flush with the sand surface 0.5 m apart along the high tide line, parallel to the water in randomized order (from 1 to 12). This was replicated in four groups with each group of 12 cups 10 m apart. Seawater mixed with a few drops of dish soap

was added to the bottom of each cup to prevent trapped organisms from escaping. One trap in each of the four groups was opened for 30 min every 2 h for 24 h. The organisms collected in the traps were transferred to labeled bags and frozen for later processing. The contents from each trap were sorted in the laboratory, identified to species level, and counted.

Data analysis

For the spatial distribution surveys, we calculated the mean position, P , for each species during each tide phase as:

$$P = \frac{\sum n_i \times D_i}{\sum n_i},$$

where n_i is the number of individuals at each sampling distance from the bluff D_i . Within-species mean positions were compared between the two tide ranges using Student's t test. One-way analysis of variance (ANOVA) was used to compare mean position by species on the neap tide and on the spring tide. Mean positions of the four species were also compared using a two-way ANOVA with mean positions as the response variable and species and tide as fixed factors. The percent increase in habitat area, H , was calculated as:

$$H = \frac{n - s}{n} \times 100\%,$$

where n is the mean position of the neap tide high tide strandline and s is the mean position of the spring high tide strandline.

Observational data from the mesocosm experiments were averaged for the four species across the four replicates and were analyzed using circular statistics. We calculated the mean time of activity (\pm standard deviation) for each species on each tide phase based on the number of individuals observed each hour. We also calculated Rayleigh's Z for each species on each tide phase, which serves as a measure of how clumped (high values) or dispersed (low values) observations were around the mean hour over the 24-h period. Lastly, we determined the total time range of activity by calculating the number of hours from when the first maximum number of individuals of one species was observed to when the last maximum number of individuals of some other species was observed for each tide phase. This time range, therefore, contained the peaks of activity for all four species and was used to estimate temporal separation among the species on the different tide phases.

Data presented for the pitfall traps include three *Megalorchestia* spp., as *M. corniculata* adults were not caught in pitfall traps. Numerous juvenile *Megalorchestia* were also caught and analyzed as an independent group because their activity may differ from that of adults (Lastra et al., 2010). As with the observational study, we calculated the total time range of activity across the three adult species by determining the number of hours between the first peak of activity for one species and the last peak of activity for the remaining species to estimate temporal separation among the species in the field on the different tide phases. The data from pitfall traps were analyzed using circular statistics to determine the mean time of activity (\pm standard deviation) for each species based on the mean number of individuals trapped every 2 h for each tide phase. We also calculated Rayleigh's Z for each species on each tide phase. Circular statistics analyses were done using Oriana v4 (Kovach, 2011); all other analyses were conducted with base R (R Core Team, 2019) and Tidverse (Wickham et al., 2019).

RESULTS

Spatial distribution

Our samples from quantitative field surveys included adult individuals of all four species of *Megalorchestia* as well as unidentified juveniles in both the spring and neap

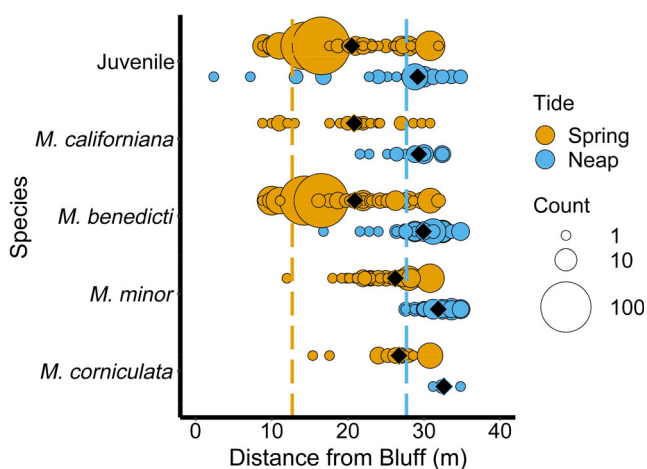


FIGURE 1 Location along the cross-shore beach profile (from bluff = 0 moving toward the ocean) where talitrid amphipods (*Megalorchestia* species including juveniles) were burrowed during a neap (blue) and spring (gold) tide. The size of each circle corresponds to the number of individuals in the core sample at that location. The black diamonds represent the mean position of the species relative to the bluff. Vertical dashed lines represent the location of the high tide strandline on the neap (blue) and spring (gold) tide

tide phase surveys (Figure 1). From the neap tide to the spring tide survey, the location of the high tide strandline shifted 15 m higher on the beach. The corresponding increase in habitat area, H , was 54.1%. The abundance of macrophyte wrack (cover) did not differ between our neap ($3.79 \text{ m}^2 \text{ m}^{-1}$) and spring ($3.31 \text{ m}^2 \text{ m}^{-1}$) tide surveys (one-way ANOVA, $F = 0.42$, $p = 0.53$). The mean positions of *Megalorchestia* in relation to the back-beach limit (bluff base) varied across species and tide phase. Among the four species, *M. californiana* adults were located farthest from the water and closest to the bluff at $29.3 \pm 1.4 \text{ m}$ (mean \pm standard deviation) on the neap tide and $20.8 \pm 3.5 \text{ m}$ on the spring tide. Moving down the beach toward the water, *M. benedicti* were next, with mean positions of $29.9 \pm 1.2 \text{ m}$ on the neap tide and $20.9 \pm 4.8 \text{ m}$ on the spring tide. *M. minor* were lower on the beach at $31.2 \pm 1.4 \text{ m}$ on the neap tide and $26.2 \pm 2.4 \text{ m}$ on the spring tide. Mean positions of *M. corniculata* were closest to the water at $32.6 \pm 0.4 \text{ m}$ on the neap tide and $26.7 \pm 1.7 \text{ m}$ on the spring tide. Juvenile *Megalorchestia* were closest to the bluff on average, at $29.2 \pm 3.6 \text{ m}$ on the neap tide and $20.5 \pm 5.0 \text{ m}$ on the spring tide. The order of mean positions was the same for spring and neap tide ranges with juveniles nearest to the bluff, then *M. californiana*, *M. benedicti*, *M. minor*, and finally *M. corniculata* closest to the water. However, the range of positions for adults of the four species was nearly double on the spring tide (5.9 m) than on the neap tide (3.3 m), and mean positions on the spring tides differed significantly from mean positions on the neap tide for all four adult species and juveniles (pairwise t tests, p values for all five groups ≤ 0.001). The spread of *Megalorchestia* (i.e., mean position standard deviations) across the beach face was also greater for all species and juveniles on the spring tide with the net increase in SD ranging from 1.0 to 3.6 m. On the neap tide, the mean positions of adults of the four talitrid amphipod species and juveniles were spatially compressed and did not differ significantly ($F = 2.7$, $p = 0.06$, $n = 27$). In contrast, during the spring tide, adults of the four species and juveniles were more widely separated and their mean positions differed significantly ($F = 4.2$, $p = 0.01$, $n = 29$). We found a significant effect of species (two-way ANOVA, $F = 4.8$, $p = 0.002$, $n = 56$) and tide phase ($F = 86.5$, $p < 0.001$, $n = 56$) on mean position, and no significant interaction between species and tide phase ($p = 0.5$).

Temporal distribution—Surface activity

Observations of adults of the four species of *Megalorchestia* in the mesocosms for 24 h revealed different temporal patterns in surface activity between the neap tide and the

spring tide phases. On the neap tide, the four species exhibited distinctly different peaks in surface activity, whereas on the spring tide there was large overlap in surface-active periods (Figure 2). During the neap tide, there was also a greater time range of surface activity (7.5 h, Appendix S1: Figure S1) compared to the spring tide (4 h, Appendix S1: Figure S1). The mean hour of surface activity, derived from the number of individuals active each hour, was earlier in the night for the two larger species (*M. californiana* and *M. corniculata*) than for the two smaller species (*M. minor* and *M. benedicti*) on both tide phases (Table 1). Rayleigh's *Z* values, a measure of clustering, that is, how concentrated the data are

around the mean for each species, varied across tide phases for all species, with only *M. minor* having notably higher values on both tides, indicating relatively narrow windows of peak activity (Table 1).

In the pitfall trap samples, we captured adults of three of the four species (no *M. corniculata*), and many juveniles (length <8 mm). As with the mesocosm experiments, the time peaks when individuals were active (caught in pitfall traps) were more distinct on the neap tide compared to the spring tide, where we observed much greater overlap in the surface-active periods of the species (Figure 2). During the neap tide, the overall duration of surface activity of the amphipods (adult species

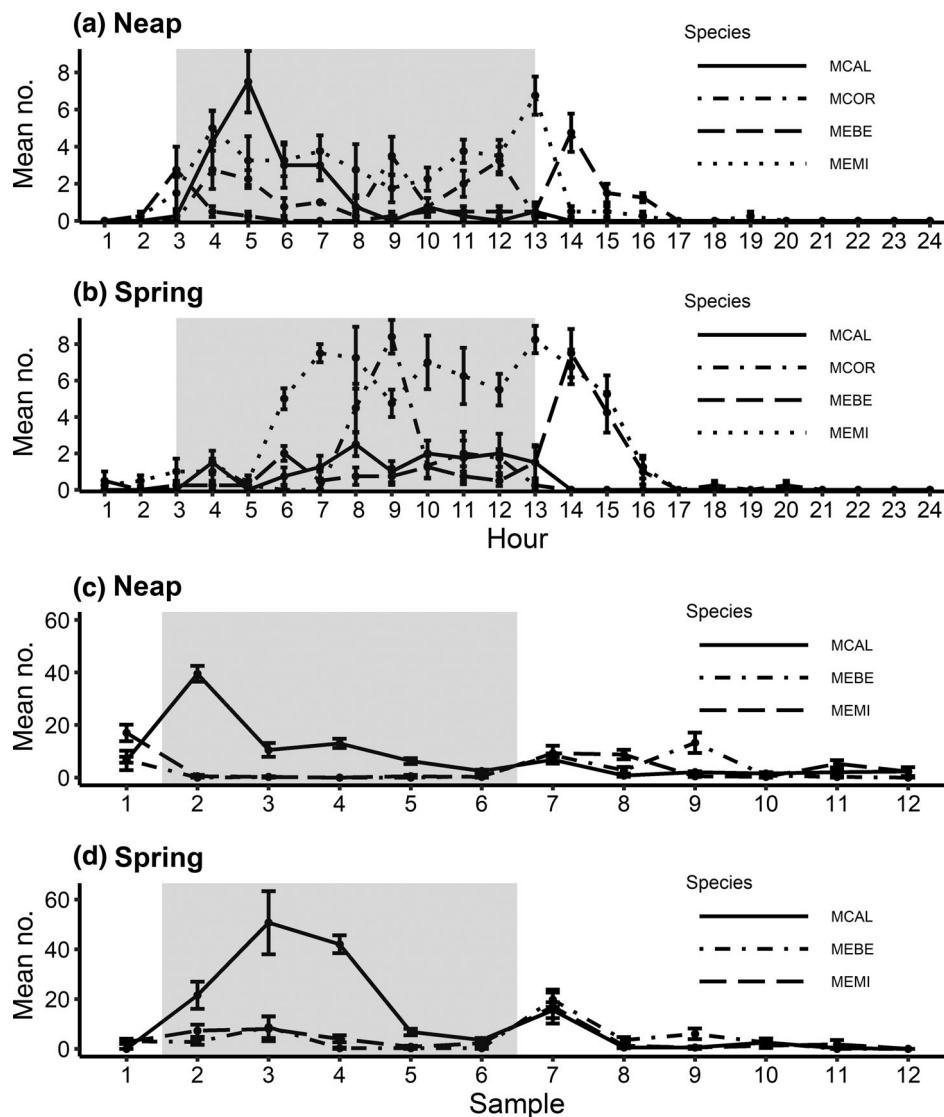


FIGURE 2 The mean number of surface-active individuals (\pm SE) of *Megalorchestia californiana* (MCAL), *Megalorchestia corniculata* (MCOR), *Megalorchestia benedicti* (MEBE), and *Megalorchestia minor* (MEMI) observed at each hour in mesocosms during the (a) neap and (b) spring tides on Campus Point Beach that began at 6:00 PM Pacific Daylight Time (PDT) and from pitfall trap samples every 2 h (12 samples for the 24-h period) during the (c) neap and (d) spring tide phase on Goleta Beach that began at 7:00 PM PDT. The gray shading represents nighttime hours from sunset to sunrise

TABLE 1 Mean time of activity (Pacific Daylight Time, UTC-07:00) with standard deviations (SD) and values of Rayleigh's Z (higher values relative to other groups indicate clumped activity distributions or relatively tight windows of peak activity observations) for *Megalorchestia californiana* (MCAL), *Megalorchestia corniculata* (MCOR), *Megalorchestia benedicti* (MEBE), and *Megalorchestia minor* (MEMI) and juvenile *Megalorchestia* spp. (J) during the neap and spring tide mesocosm experiments on Campus Point Beach and the neap and spring tide pitfall sampling on Goleta Beach

Statistic	MCAL	MCOR	MEBE	MEMI	J
Neap tide mesocosm					
Mean	22:35	1:14	7:11	1:33	N/A
SD	1:28	3:01	4:51	3:34	N/A
Rayleigh Z	17.2	9.1	2.2	16.2	N/A
Spring tide mesocosm					
Mean	2:20	2:02	5:56	3:22	N/A
SD	2:56	1:54	3:53	3:18	N/A
Rayleigh Z	8.3	17.2	8.2	32.1	N/A
Neap tide pitfall					
Mean	22:18	N/A	10:34	14:37	23:36
SD	4:00	N/A	4:16	6:17	4:43
Rayleigh Z	31	N/A	9.1	2.8	56.2
Spring tide pitfall					
Mean	0:12	N/A	6:58	2:39	0:26
SD	3:00	N/A	5:32	5:49	3:05
Rayleigh Z	77.2	N/A	5.7	4.5	384.2

Note: Values were calculated using the circular statistics program Oriana (v4).
Abbreviation: N/A, not applicable.

and juveniles) was double (14 h, Appendix S1: Figure S2) that observed for the spring tide (7 h, Appendix S1: Figure S2). Similar to the results of the mesocosm experiment, the larger species (*M. californiana*) was active earlier in the night compared to the two smaller species (*M. minor* and *M. benedicti*) during both tide phases (Table 1). Large Rayleigh's Z values indicated that *M. californiana* and juvenile *Megalorchestia* had aggregated activity distributions, or relatively tight windows of peak activity, during both tide phases, while the two small-bodied talitrid species were more dispersed across time in their activity (Table 1).

DISCUSSION

The interspecific spatial and temporal niche separation that we found suggests that negative biotic interactions, such as competition, are operating on dynamic open coast sandy beaches. In sheltered habitats, such as mudflats and marshes, soft-sediment infauna spatially partition habitat to reduce competition for space (Peterson & Andre, 1980; Wilson, 1990b; Woodin, 1974). Our results demonstrate that mobile intertidal species inhabiting apparently harsh sandy beach habitats also partition habitat in space

and time, and that this partitioning varies with tide phase. The degree of spatial and temporal separation of the four congeneric species of intertidal talitrid amphipods we observed varied strongly with tide phase and the resulting >50% change in habitat availability, with stronger temporal patterns in niche separation on a neap tide when habitat is most limiting, and greater spatial separation on a spring tide when more habitat is available.

Strong interspecific temporal variation in surface activity of the four amphipod species was observed *in situ* in the presence of congeners, with pitfall sampling, and in mesocosms in the absence of congeners, suggesting that these behavioral patterns were entrained responses to tide phase (Enright, 1965, 1972; Hastings, 1981; Naylor, 1985). Such temporal separation in activity may be a mechanism of avoiding competitive interactions over limiting resources like food and habitat, but may trade-off with other potential foraging costs, such as predation and desiccation risk (Beyst et al., 2002; Williams, 1980). During the neap tide phase, when biotic interactions are expected to be more intense due to habitat limitation, a longer overall period of active surface time was observed across the four species than during the spring tide, reflecting interspecific separation of activity peaks. On

the spring tide when more habitat was available and spatial separation possible, higher overlap in peak surface activity was observed, suggesting that ideal activity and foraging time might be the same for these similar species absent interspecific interaction. Tidal fluctuation on the sandy beach may therefore provide a means of niche expansion via a reduction in competitor densities (Bolnick et al., 2010; Crego et al., 2018; Petrozzi et al., 2021).

The role of fluctuating conditions, such as tides, in mediating biotic interactions is relatively unexplored, but our study results and others imply that the tide phase is an important factor to consider with respect to coexistence, particularly of mobile intertidal species (Berglund, 1982; Lea et al., 2020; Steibl & Laforsch, 2019). Zonation has been well studied for rocky intertidal shores providing valuable insights on the relative influence of physical factors and biotic interactions in setting patterns (Connell, 1972; Harley & Helmuth, 2003; Menge & Sutherland, 1976; Tomanek & Helmuth, 2002). However, the majority of those observational and experimental studies have focused on sessile or sedentary organisms whose zonation is relatively stable over time and mediated by physical stressors including temperature, inundation period, waves, wind, oxygen availability, and desiccation (Connell, 1961b; Lubchenco, 1980; Newell, 1976; Underwood & Denley, 1984; Wefhey, 1984). Although tolerance to physical factors sets up the broader intertidal zones that species can inhabit, within these zones the effects of biotic interactions can be strong including competitive interactions for food and space (Dayton, 1971; Paine, 1971; Peterson, 1982, 1991; Yamada & Boulding, 1996). For the diversity of mobile intertidal species of soft sediment and even of rocky shores, those classic tenets concerning zonation and the relative roles of physical factors and biotic interactions may not apply. The zonation of mobile intertidal species can be tightly coupled to their behavioral adaptations (Gravem & Morgan, 2017) with tidal migration of different frequencies a commonly observed response (Dugan et al., 2013). On the sandy beach, where all organisms are highly mobile and interact with water motion, including tidal fluctuations as well as other physical factors by moving (McLachlan, 1988), intertidal zonation patterns are far more dynamic. Understanding how mobile species partition the intertidal zone provides a fresh dimension for evaluating the role of biotic interactions in intertidal habitats.

Activity patterns of intertidal sandy beach invertebrates have been related to species-specific needs, such as burrowing to avoid predation and desiccation during the day or migrating to optimize feeding in the swash, on wrack, or on carrion on the sand surface at night when the temperature

and predation risks are lower (Brown & McLachlan, 1990; Cardoso, 2002; Gibson, 2003; Naylor & Rejeki, 1996; Scapini et al., 1992). We would expect wrack availability to significantly influence both community composition and behavior (Dugan et al., 2003; Fanini et al., 2016; Michaud et al., 2019; Poore & Gallagher, 2013). However, we found no differences in wrack abundance between the spatial distribution surveys conducted during neap and spring tides in our study. The relatively consistent environmental conditions other than tide during both our surveys strengthen the evidence pointing to the mediating effect of tide phase on species interactions and their mechanisms of avoidance of potentially negative biotic (interspecific and intraspecific) interactions. Biotic rather than environmental factors are likely driving the spatial separations and activity patterns observed for intertidal invertebrates with overlapping niche spaces on sandy beaches.

Different species tailor surface activity periods to time of day, tides, moon phase, predation risk, sea conditions, and more (Colombini et al., 1994, 1996, 1998, 2000; Fallaci et al., 1996; Lastra et al., 2010). At higher trophic levels, shorebirds spatially partition habitat use to reduce antagonistic interactions but also structure their foraging habits around tide level with species-specific foraging times in relation to low tide rather than time of day (Burger et al., 1977; Neuman et al., 2008). On southern California beaches, shorebirds feed using visual cues, tactile probing, and active foraging/gleaning for prey whose abundances fluctuate with the amount of wrack inputs and beach conditions (Dugan et al., 2003, 2008, 2013). Shorebirds opportunistically feed at all intertidal levels ranging from the dry upper beach, through the high tide strandline and into the swash zone (Hubbard & Dugan, 2003; Lafferty, 2001). While shorebirds feed across the intertidal zone, primarily along or below the high tide strandline where we found the greatest abundance of talitrid amphipods, it is unlikely that the talitrid spatial patterning we observed is a mechanism of avoidance of shorebird predation. Rather, the nighttime surface activity observed across species may reduce predation threats from visual predators in addition to lowering the desiccation risk associated with daytime surface activity.

Mobile species with larger body size likely have a competitive edge over smaller species, allowing them to occupy prime locations and time periods that maximize access to resources and limit risk factors, such as predation, cannibalism by adults on juveniles, and desiccation (Norkko et al., 2013; Wallace & Temple, 1987; Woodward et al., 2005). Interestingly, small juvenile *Megalorchestia* and the species with the smallest adult body size, *M. benedicti*, occupied the widest habitat distribution during both tide phases. While avoidance of negative biotic interactions may drive the observed spatial separation of all

of these species during spring tides when more suitable habitat is available, such interactions (i.e., competition, predation, cannibalism; see Duarte et al., 2010) may be acting on the smaller talitrid amphipod species as well as the juveniles of all species regardless of tide phase. This may push them into less suitable habitats and activity times to avoid competitive exclusion or predation by larger congeners across tide phases.

Our study results suggest that beach habitat loss and intertidal zone compression due to wave events, seasonal changes, El Niño, and sea level rise (Dugan et al., 2013; Vitousek et al., 2017), and coastal armoring (Dugan et al., 2008, 2017; Jaramillo et al., 2021; Myers et al., 2019) have implications for habitat partitioning to avoid biotic interactions (Gilman et al., 2010). Future reductions of intertidal habitat area due to climate change may increase competitive exclusion, causing a loss of similar species and functional redundancy with consequent effects on biodiversity and ecosystem functioning (Emery et al., 2021). Competitive interactions in highly mobile intertidal species can be more challenging to observe than in sedentary or sessile taxa, but niche separation and coexistence of such species may depend on their mobility and ability to respond to changing environmental conditions. Such behavioral plasticity may not only mitigate the effects of changing environmental conditions (Colombini et al., 2013), but also alters the strength of biotic interactions on both temporal and spatial scales. Activity modifications due to circalunar rhythms by the invertebrate community at large may in fact be a mechanism of stabilization for the community and therefore a mechanism of coexistence (i.e., diversity of biological rhythm) (Mougi, 2021). Our findings for talitrid amphipods are consistent with a strong role of biotic interactions in structuring the highly mobile intertidal communities of dynamic harsh ecosystems where physical factors have long been assumed to control community structure.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Santa Barbara Coastal LTER et al., 2021a, 2021b) are available from the Environmental Data Initiative: <https://doi.org/10.6073/pasta/6ebbf53d2d41abb90b3803b150d244c2> and <https://doi.org/10.6073/pasta/f8266e765d666ce35e2805978989c675>.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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