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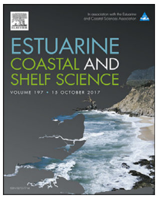

Effects of tidal cycles on shorebird distribution and foraging behaviour in a coastal tropical wetland: Insights for carrying capacity assessment

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ABSTRACT

Wetland loss has driven negative effects on biodiversity by a reduction in potential available habitats, directly impacting wetland-dependent species such as migratory shorebirds. At coastal areas where tidal cycles can restrict food access, the degree to which density of foraging birds is mediated by conspecific abundance or by the available areas is crucial to understanding patterns of bird distribution and wetland carrying capacity. We used the bathymetry of two sectors modeled with two numerical matrices to determine the availability of intertidal foraging areas in relation to tidal level (spring and neap tides), and this information was used to estimate shorebird density and foraging activity throughout the low-tide cycle in a tropical coastal lagoon in northwestern Mexico. Relative to spring tides, an 80% reduction in available foraging areas occurred during neap tides. Overall shorebird abundance was significantly reduced during neap tide periods, with differences between species. Densities of shorebirds increased during neap tides, particularly in one sector, and remained similar throughout the low-tide period (i.e. 4 h) either during spring or neap tides. Time spent foraging was consistently lower during neap-tides relative to spring-tides, especially for Long-billed curlew (44% reduction), Willet (37% reduction) and Black-necked stilt (29% reduction). These decreases in foraging activity when available habitats became reduced can hamper the opportunities of migratory shorebirds to reach their daily energy requirements to survive during the non-breeding season. This study shows that when intertidal habitats are severely reduced an important fraction of shorebird populations would probably be forced to find alternative areas to forage or increase foraging time during the night. Serving an essential function as top-predators, these results can have important implications on carrying capacity assessment for shorebirds at coastal wetlands.

1. Introduction

Wetlands provide essential habitat for a variety of aquatic and terrestrial species, as well as numerous ecosystem services (Constanza et al., 1989). However, during the last 150 years human activities have globally modified wetlands and today more than half have been altered, degraded or lost (Gardner et al., 2015), with even higher impact in tropical areas (Zedler and Kercher, 2005). Main sources of wetland loss and degradation include land-use changes from agriculture and aquaculture (Valiela et al., 2001; Newbold et al., 2015), as well as residential, commercial and industrial developments (Asselen et al., 2013; Sica et al., 2016). Along with climate effects derived from global change (Erwin, 2009), wetland loss has driven negative effects on biodiversity by a reduction in potential available habitats (Quesnelle et al., 2013), directly impacting ecologically dependent species (Zwarts et al., 2009; Ma et al., 2010; Murray et al., 2014). Hence, at coastal areas intertidal wetlands represent critical foraging habitats to migratory waterbird populations during the non-breeding season (van de Kam et al., 2004). Since migratory animals couple biodiversity and ecosystem functioning (Bauer and Hoye, 2014), and waterbirds provide crucial supporting and regulation ecosystem services at wetland areas (Green and Elmberg, 2014), reductions of intertidal

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foraging grounds are thus of crucial concern for biodiversity conservation.

At coastal wetlands tidal cycles determine the spatial and temporal availability of the foraging areas (Burger et al., 1977; Ribeiro et al., 2004), with foraging activity of many waterbirds mainly restricted to low tide periods (Burton et al., 2004; Piersma et al., 1995). Daily (low-high tide cycles) and biweekly (neap-spring tide cycles) fluctuations can further restrict the time and area available for foraging and critically influences the foraging behavior of several species (Clausen, 2000; Dias et al., 2006; Granadeiro et al., 2006). Changes in the availability of intertidal foraging grounds may also affect energy budgets and patterns of abundance and distribution of waterbirds (Calle et al., 2016), with potential consequences in species survival (Goss-Custard, 1980). Among waterbirds, many shorebirds (Charadrii) populations that are declining worldwide (Morrison et al., 2006; Bart et al., 2007; Andres et al., 2012) depend on intertidal mudflats to forage during the non-breeding season (Granadeiro et al., 2007). Hence, due to both temporally and spatially restricted foraging habitats, they present different morphoevolutive and behavioural adaptations that have evolved to increase foraging efficiency (see Barbosa and Moreno, 1999) and reduce interspecific competence by niche partitioning (Burger et al., 1977). Understanding how spatial and temporal changes in availability of intertidal areas affect distribution and foraging activity of different shorebird species (Durell et al., 2005) will help to assess effects of wetland loss on associated biodiversity.

Reductions in feeding opportunities can affect foraging shorebirds by increasing associated density-dependent processes (Santos et al., 2005). While some individual birds may eventually leave the intertidal areas to forage at alternative sites (Navedo et al., 2013; Dias et al., 2014), it is expected that their first reaction would be to redistribute themselves within the estuary with the consequent increase in densities of foraging birds at those areas that remain available (Goss-Custard and Durrell, 1990). Competition for prey may increase when density rises, resulting in more frequent agonistic (Duijns and Piersma, 2014) or cryptic interferences (Bijleveld et al., 2012), followed by an overall reduction in the intake rate (Caldow et al., 1999). However, the intensity of competition greatly varies both between species with different foraging strategies (Folmer et al., 2010) and functional responses (Goss-Custard et al., 2006), as well as between individuals because dominance relationships usually dictate the ease of access to resources (Vahl et al., 2005). In each case, available foraging area is a critical factor in the search for food requirements in a confined environment (Goss-Custard, 1980).

The combination of topographic variation and depth of water provide a range of intertidal foraging habitats for shorebirds (Ma et al., 2010). Models flooding coastal wetlands have recently been used to assess the abundance and distribution of waterbirds in relation to available foraging areas derived from differences in tidal amplitude (Calle et al., 2016). In addition, modeling intertidal habitats can provide additional insights to understand whether observed variation in bird densities at local scale (e.g. Granadeiro et al., 2007) is a consequence of redistribution of birds within remaining patches or of differences in overall bird abundance within the wetland. Whether density of foraging birds is mediated by conspecific abundance or available areas is crucial to understand patterns of bird distribution and wetland carrying capacity (Goss-Custard et al., 2002), especially at coastal areas where birds experienced spatial and temporal foraging restrictions associated to tidal cycles.

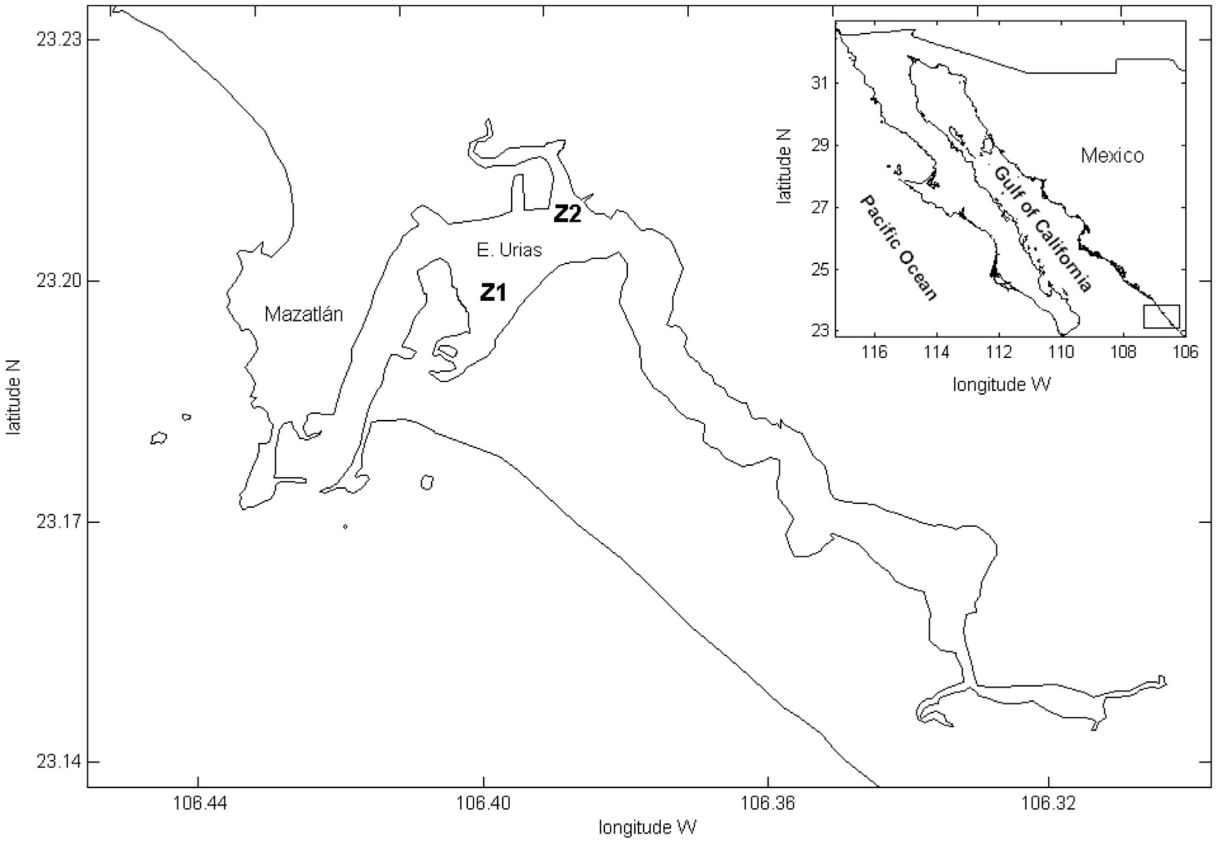

Fig. 1. Location of the study area in the Estero de Urías, Sinaloa, NW Mexico.

Here we applied bathymetry of two sectors modeled with two numerical matrices to determine the availability of intertidal foraging areas in relation to the level of the tides, and combined this information with shorebirds counts to estimate shorebird density throughout the low-tide cycle in a tropical coastal lagoon that regularly supports high numbers of shorebirds during the non-breeding season (Navedo et al., 2015). Our aim was to evaluate the effect of spatial and temporal restrictions associated to tidal cycles in distribution patterns and foraging activity of shorebirds on a tidal wetland. We expected differences among species related to their foraging performance and microhabitat requirements. We predict that territorial species will be most affected by reduced available foraging habitat than gregarious foraging species, which are more accustomed to forage aggregated in a fraction of available habitat. Finally, during periods of reduced foraging opportunities (i.e. neap tides) we expect an overall reduction in shorebird foraging activity compared to periods of spring tides, associated to an increase in agonistic interactions and consequent cessation of foraging activity by subordinate individuals. Our results will be useful to understand effects of foraging habitat loss to wetland carrying capacity for shorebirds.

2. Materials and methods

2.1. Study area

Estero de Urías is a wetland complex located on the southeast coast of the Gulf of California (23°11′ N, 106°22' W) (Fig. 1). It has an area of 11 km^2 with a maximum depth of 21 m (in the mouth) and average depth of 3.4 m (Montaño-Ley et al., 2008). This wetland presents diverse habitats such as intertidal mudflats, emergent brackish marshes and surrounding mangrove fringes (*Rizophora mangle*) and is classified as a coastal lagoon of low energy (Lankford, 1977). The tide is predominantly mixed semidiurnal, with a tidal range of 1.20 m (during this study) and form number (K1+ O1)/(M2 + S2) of 0.576. The estuary has limited freshwater discharges, with salinity range of 25.8–38.4 g kg^{-1} (Montaño-Ley et al., 2008). Intertidal foraging areas for shorebirds at Estero de Urías are mainly restricted to two sectors (Navedo et al., 2015), denominated as Z1 and Z2 throughout this study (Fig. 1).

2.2. Bathymetry

A detailed bathymetric survey was conducted during spring tides to quantify the intertidal surface available to foraging shorebirds depending on the tide, and hence determine the density of birds. Depth measurements were performed with a VIDEO SOUNDER GPS MAP-440S GARMIN installed on the gunwale of a boat that navigated in the sectors. The survey route in the Z1 was 24.2 km and 4.6 km in the Z2 based on previously determined transects. The records were made at an average distance between two points of ~40 m. At each point, the latitude, longitude and depth was recorded, and the later was subsequently corrected by the tide level. The amplitude of the tide was estimated from the tide tables for Mazatlán city provided by the CICESE (http://predmar.cicese.mx/calendarios/). Bathymetric records along with records of the shore (obtained from Google Earth) were interpolated using MATLAB functions. The interpolation generated two matrices, the first matrix modeled sector Z1, with size of 381 rows by 421 columns with 63588 wet nodes (points that have tidal influence) and total area of 158.9 ha. The second matrix modeled the sector Z2, with a size of 211 rows per 181 columns with 8992 wet nodes and a total area of 22.4 ha. The separation between nodes is 5 m. The wet nodes have the numerical value of the depth (bathymetry) with respect to the mean sea level; while nodes with zero value represent the mainland and serve as reference to outline the exposed foraging area. It should be emphasized that difference in the tidal wave elevation between Z1 and Z2, which are separated c. 2 km, is less than 2 cm and thus the delay of the tidal wave among them is negligible for the purpose of this study. This as a consequence of the tidal phase speed.

Table 1
Compared mean number of individuals (± SE) of most abundant and frequent shorebird species during periods of spring and neap tides in Estero de Urías. * < 0.05; ** < 0.01; *** < 0.001, ns = not significant.

Species	Abundance ± SE		*U*	*P*
	Spring tide	Neap tide		
Black-necked stilt	69.1 ± 7.54	49.6 ± 5.13	135	**
Dowitchers	229.3 ± 35.4	162.9 ± 21.9	165.5	*
Long-billed curlew	24.4 ± 3.4	27.5 ± 4.7	197.5	ns
Marbled godwit	222.6 ± 18.47	194.3 ± 13.6	190	ns
Western sandpiper	1144.6 ± 254.1	203.6 ± 51.7	38.5	***
Whimbrel	26.5 ± 2.7	27.2 ± 3.9	236	ns
Willet	718 ± 49.7	239.6 ± 26.4	16	***

2.3. Shorebird counts

We visited the study area during the winter season (n = 19 days, from October to December 2015) when shorebird populations are relatively constant at Estero de Urías (Navedo et al., 2015). Each sector (Z1 and Z2) was surveyed five days during spring and another five days during neap tides, except for Z1 during spring tides that were surveyed only four days due to logistic constraints. Preliminary observations in the study area showed the intertidal area available at Z2 for foraging shorebirds during the peak of the neap tide periods was negligible, and there were no shorebirds (J.Fonseca and J.G.Navedo pers. obs). Therefore, since we were interested in comparing shorebird density at both sectors during spring and neap tide periods, we decided to conduct surveys two days before or two days after the peak of the neap tide period, thus assuring that at least some area was available for shorebirds to forage at Z2. Spring tide surveys were made any of three days of maximum tidal amplitude. The counts of the shorebirds were made only during the day, that is, between the sunrise and sunset. It should be noted that during the three months of study the highest amplitudes of low tide were recorded during the day, according to the tide tables of CICESE.

We used a motorized boat to reach Z1 sector and a 4 × 4 vehicle to reach Z2 sector. We arrived 3 h before the low-tide peak and remained hidden there before starting to count in order to not disturb shorebirds. During each survey we counted shorebirds and estimated foraging activity (proportion of birds foraging), using direct observation techniques with a spotting scope (20–60×). If the activity of an individual could not be determined instantaneously (e.g., a bird with its back to the telescope), the individual was observed for 1–5 s to determine its foraging activity (Navedo and Masero, 2007).

All shorebirds were identified to species, except for the two dowitcher species, Short-billed dowitcher (*Limnodromus griseus*) and Long-billed dowitcher (*Limnodromus scolopaceus*), which could not be reliably distinguished in the field. Counts were made at intervals of 1 h throughout the low-tide cycle, starting 2 h before low tide and finished 2 h after low tide (−2, −1, 0, +1, +2). All counts (n = 95) were made by the same observer (JF). For this reason it was not possible to simultaneously count at both sectors, so that counts at Z1 and Z2 were always made on consecutive days.

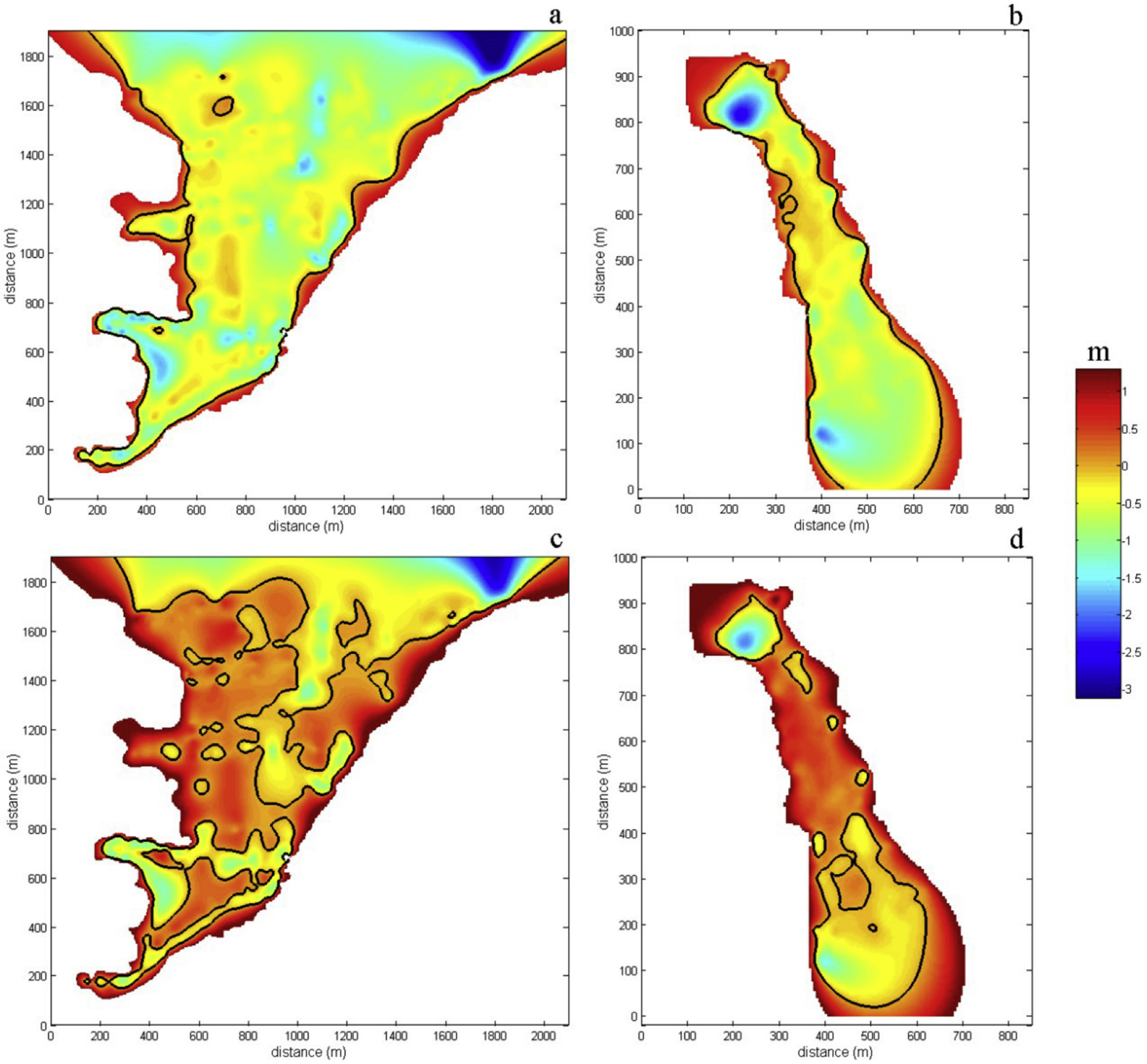

Fig. 2. Low water bathymetry of the study area, showing the reduction in area available for shorebird feeding during neap tides relative to spring tides. Neap tides are shown on top panels (a) Z1, (b) Z2, and spring tides (c) Z1, (d) Z2, on bottom panels. The black line separates the area with water (colors tend to blue) of the exposed area (colors tend to red). The vertical scale indicates the depth in meters, with reference to mean lower low water (MLLW). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.4. *Statistical analysis*

We calculated density as the number of birds counted in each area during each tidal period (spring vs neap) divided by the total area available as estimated by the bathymetric matrix. The foraging area was calculated by adding up the exposed nodes (dry nodes) of the bathymetric matrix, according to the tide condition during each shorebird count. It should be noted that the sectors (Z1 and Z2) are flooded at high tide during spring tides. Each dry node represented 25 m^2. We first used a Student *t*-test to assess whether the number of individuals of each species varied in each sector (Z1 and Z2) depending on availability of foraging areas (i.e. spring versus neap tide periods). A Mann-Whitney *U* test was applied for those species that did not met normality assumptions and homoscedasticity. A Pearson correlation was used to evaluate if overall shorebird abundance varied at the study area throughout the study period. The abundance of shorebirds was analyzed using generalized linear models (GLM) with sector (Z1 and Z2), tidal time (−2, −1, 0, +1, +2) and tidal amplitude (spring-neap tide) as fixed factors. Density ($ind \cdot ha^{-1}$) and foraging activity (proportion of individuals feeding) for each shorebird species was analyzed separately as a dependent variable. Since an exploratory analysis revealed overdispersion, we then used GLMs with a negative binomial distribution and log-link function to analyze whether the density and foraging activity of each shorebird species varied throughout the low-tide cycle depending on availability of foraging areas. The density of shorebirds was modeled with abundance as the response variable and the area in each count of each sector as an offset. Each model included sector (Z1 and Z2), tidal time (−2, −1, 0, +1, +2) and tidal amplitude (spring-neap tide) as fixed factors. Least significant difference (LSD) Fisher tests were used a posteriori to examine differences between factor levels. All analyses were performed using SPSS version 22. Results are presented as means ± SE.

3. Results

A total of 14 species of shorebirds were observed foraging at Estero de Urías during the study period. To help interpretation of

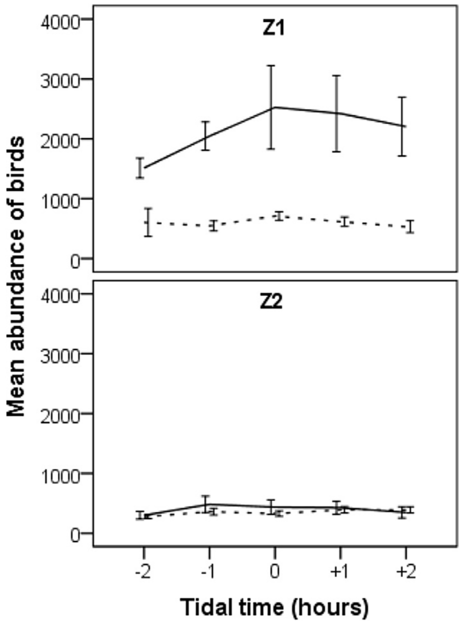

Fig. 3. Abundance (means ± SE) of shorebirds in each sector of the Estero de Urías (Z1 and Z2) during neap (dashed line) and spring (solid line) tides. The tidal time is measured in hours before (values -) and after (values +) low tide peak (= 0).

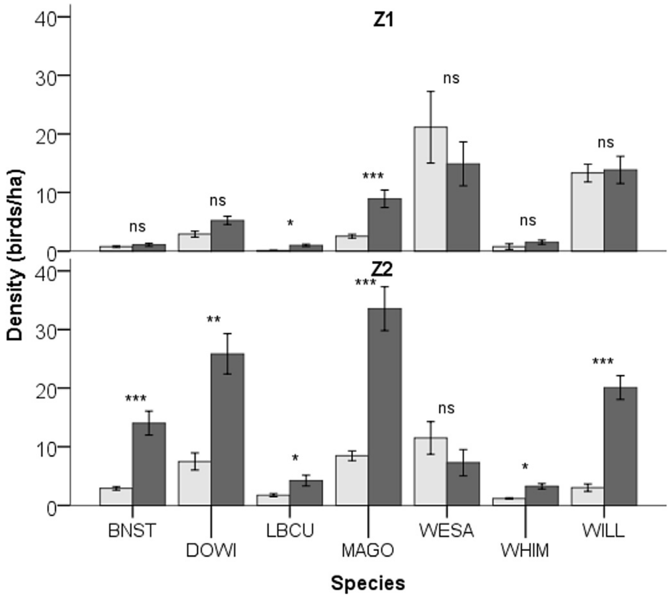

Fig. 4. Density (means ± SE) of each shorebird species within sectors Z1 and Z2 of the Estero de Urías during periods of spring (light grey) and neap (dark grey) tides. The names of the species are indicated with the first two letters of the common name. Significant differences are indicated by asterisk: * < 0.05; ** < 0.01; *** < 0.001, ns = not significant.

the data only species detected at least during 17 out of 19 surveys and whose mean abundance was higher than 10 individuals were further analyzed to examine their densities. These criteria restricted the analyses to the seven most frequent and abundant species; Western sandpiper (*Calidris mauri*), Willet (*Tringa semipalmata*), Marbled godwit (*Limosa fedoa*), Dowitchers (*Limnodromus* spp.), Black-necked stilt (*Himantopus mexicanus*), Whimbrel (*Numenius phaeopus*) and Long-billed curlew (*Numenius americanus*) (Table 1). Using mean lower low water as reference, during spring and neap tides the maximum values of the intertidal area for Z1 were 87.69 ha and 16.05 ha, respectively, whereas at Z2 there were 14.46 ha and 4.08 ha (Fig. 2). Therefore intertidal areas were overall reduced by 80% during neap tides.

In general, counts of shorebirds were lower during the neap tide periods than during spring tide periods, but do not significantly differ throughout the study (Pearson correlation: $r = 0.032$, $P = 0.757$). Overall abundance was 2530.5 ± 556.9 shorebirds during spring tide periods, significantly reduced up to 950.9 ± 190.5 individuals during neap tides *Wald* $X^2_1 = 11.178$, $P < 0.001$. Shorebird abundance was also significantly higher in Z1 respect to Z2 (*Wald* $X^2_1 = 29.090$, $P < 0.001$), but there was a significant interaction between tide period and sector (*Wald* $X^2_1 = 7.463$, $P < 0.01$), with abundance being higher in Z1 during spring tides but similar in Z2 (Fig. 3). Interestingly, shorebird abundance was rather similar within each sector throughout the low-tide period (*Wald* $X^2_1 = 1.071$, $P = 0.899$) (Fig. 3). Following the general pattern, abundance of all species was lower during neap tides relative to spring tides, except Long-billed curlew, Marbled godwit and Whimbrel that remained similar (Table 1). This pattern was derived from decreases in abundance in Z1 during neap tides ($P < 0.02$ in all cases), except for both *Numenius* spp. By contrast, in Z2 there was a significant increase in abundance during neap tides for Willet ($t_{48} = 4.729$, $P < 0.001$) and a significant reduction for Western sandpiper ($U = 115$, $P < 0.001$). Abundances of other species did not differ between tidal periods ($P > 0.23$ in all cases) in this sector.

Densities of different shorebird species overall increased during neap tides relative to spring tides, although this pattern differed between the two sectors (Fig. 4). During neap tides densities were significantly higher in Z2 for all species, except for Western sandpiper. In Z1, densities of Marbled godwit and Long-billed curlew were higher during neap tides relative to spring tides, but were similar between the two periods for the rest of the shorebird assemblage (Fig. 4). Additionally, there was a significant interaction between tidal period and sector for Willet (*Wald* $X^2_1 = 18.067$, $P < 0.001$), Black-necked stilt (*Wald* $X^2_1 = 8.628$, $P < 0.003$) and Long-billed curlew (Wald $X^2_1 = 7.282$, $P < 0.007$) showing higher densities in Z2 only during neap tides. Noticeably, densities during both spring and neap tides remained constant for each species within each sector throughout the low-tide period (i.e. 4 h).

Foraging activity, measured as the proportion of the flock actively feeding, was reduced during neap tides relative to spring tides in both sectors for all species, with differences between them (Fig. 5). However, it remained constant throughout the low-tide period (i.e. 4 h) within each sector (Fig. 5). Therefore, time devoted to forage throughout the low-tide period was significantly reduced during neap tides for Long-billed curlew (89%–45%), Willet (96%–59%), Black-necked stilt (81%–52%) and, though not statistically different, Marbled godwit (99%–71%) (Table 2). Finally, there was not a significant interaction between tidal period and sector, indicating a consistent pattern of foraging activity during spring and neap tide periods.

4. Discussion

This study shows how the tidal cycle affects both the spatial distribution and foraging activity of shorebirds during the non-breeding season at a coastal tropical wetland. Similar to other studies, shorebird abundance during low-tide was closely associated with the tidal amplitude (Nehls and Tiedemann, 1993; Granadeiro et al., 2006), with a higher abundance during spring tide periods. The bathymetric matrix showed that during neap tide periods the availability of intertidal foraging areas is reduced up to 80%, which was probably the main cause of the reduction in shorebird abundance observed at intertidal areas throughout the

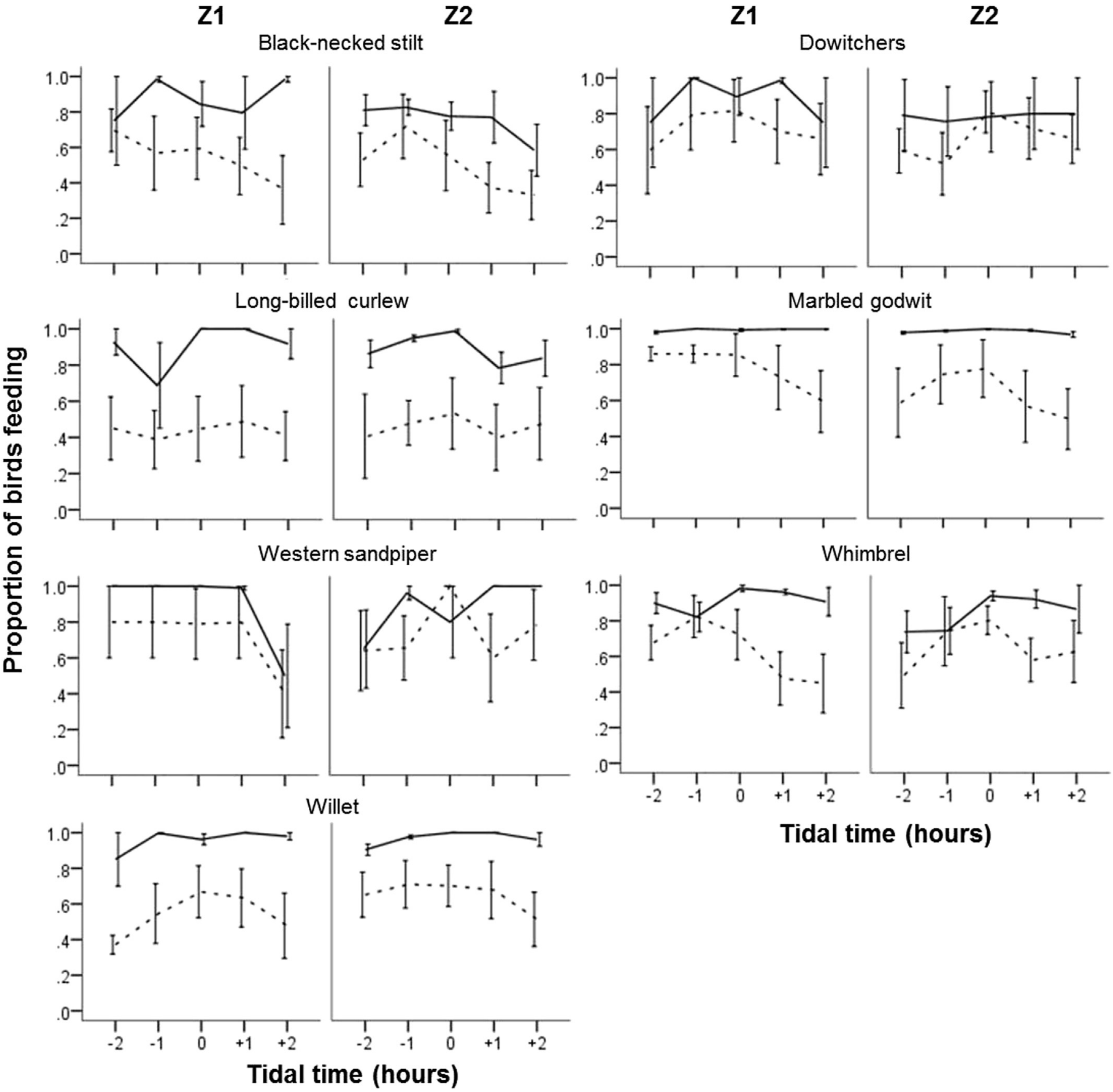

Fig. 5. Proportion (means ± SE) of shorebirds feeding in two sectors of the Estero de Urías (Z1 and Z2) during neap (dashed line) and spring (solid line) tides. The tide time is measured in hours before (values -) and after (values +) low tide (= 0). The bars represent the standard error.

Table 2
Proportion of birds feeding (mean ± SE) of common shorebirds in the Estero de Urías, in spring and neap tide periods, October to December 2015. * < 0.05; ** < 0.01; *** < 0.001, ns = not significant.

Species	Fraction feeding ±SE		Wald	gl	P
	Spring tide	Neap tide			
Black-necked stilt	0.8 ± 0.1	0.5 ± 0.1	4.5	1	*
Dowitchers	0.8 ± 0.1	0.7 ± 0.1	0.84	1	ns
Long-billed curlew	0.9 ± 0.1	0.4 ± 0.1	10.99	1	**
Marbled godwit	1.0 ± 0.1	0.7 ± 0.1	3.09	1	ns
Western sandpiper	0.9 ± 0.1	0.7 ± 0.1	0.95	1	ns
Whimbrel	0.9 ± 0.1	0.7 ± 0.1	2.32	1	ns
Willet	1.0 ± 0.1	0.6 ± 0.1	5.47	1	*

whole low-tide period. In addition, time devoted to forage during daylight was significantly reduced during neap tides for Long-billed curlew (44%), Willet (37%), Black necked stilt (29%) and a biologically meaningful reduction of 28% for Marbled godwit, with respect to spring tides. Individuals with a higher competitive ability could partly compensate by increasing their intake rate during these periods (Navedo et al., 2012), although this compensation should be possible within gregarious species eating soft macro-invertebrates such as godwits (e.g. Duijns et al., 2013) but not for territorial ones such as willets, stilts, curlews and whimbrels whose intake rate is largely affected by searching time (Goss-Custard et al., 2006). Since foraging time is an essential limiting factor for shorebirds to optimize intake rate (Evans, 1976), additional restrictions in foraging activity at intertidal areas can hamper the opportunities of shorebirds to reach their daily energy requirements to survive (Goss-Custard et al., 2002). Although nocturnal foraging is a common performance in shorebirds to meet their high daily energy requirements (Robert et al., 1989; McNeil and Rodríguez, 1996; Dodd and Colwell, 1998), availability of intertidal foraging habitats is even more restricted at night during the evaluated period (i.e. October–December) (data from www.cicese.mx), thus not allowing the birds to compensate for daytime losses by increasing nocturnal foraging activity at intertidal areas. Therefore our finding should be particularly relevant in estuaries and bays where tidal amplitude during the peak of the biweekly neap tide periods is negligible, such as small coastal wetlands within the Gulf of California (Carbajal and Backhaus, 1998).

We have also found several deviations from the general spatial distribution pattern between the two intertidal sectors within the wetland. During neap tide periods, shorebird density remained constant in the sector that showed a reduction in bird numbers, whereas density increased with respect to spring tide periods in the other sector that overall maintained shorebird abundance. Therefore, displaced shorebirds did not redistribute themselves within remaining available intertidal foraging areas during neap tides when exposed intertidal zones were restricted to both study sectors (Navedo et al., 2012), although some willets seem to do so in the sector with a small available foraging area. Although habitat heterogeneity and different food availability may explain the spatial distribution of foraging shorebirds (van Dusen et al., 2012; Ponsero et al., 2016), density dependence processes within the wetland seem to be triggered during periods of reduced foraging opportunities at intertidal areas (Goss-Custard, 1980; Santos et al., 2005), with different effects among species associated to foraging behavior, prey selection and microhabitat requirements (van de Kam et al., 2004; Colwell, 2010).

We predicted that territorial species should be more vulnerable to reduced foraging habitat availability since dominant individuals would tend to maintain their territories (Townshend, 1985). Willets and stilts maintained similar densities in the area with a bigger surface by reducing conspecific abundance there, and by reducing their time devoted to forage, with a significant decrease in total number of birds using intertidal areas within the wetland during neap tides. On the other hand, abundances of curlews and whimbrels at intertidal areas were not reduced, and therefore density increased, followed by an important loss in total time devoted to foraging throughout the low-tide period, especially for curlews, the biggest species. Territorial shorebirds are usually visual predators that disperse in intertidal foraging grounds (Nehls and Tiedemann, 1993; Navedo et al., 2012), especially those selecting epifaunal prey (such as fiddler crabs) that use to be present at high densities in the most exposed intertidal areas (Zwarts et al., 2011), a pattern indicating a high interference competition for visual foragers (Goss-Custard, 1970). When space is limited, dominant individuals may try to restrict access, forcing subordinates to wait or to use lower quality sites (Durell, 2000; Duijns and Piersma, 2014). This pattern could also be the case for western sandpipers, that showed a one magnitude order reduction in abundance within the wetland during neap tides, but densities remained similar at available foraging areas at both sectors. Although individuals of this species tend to be gregarious foragers at intertidal areas (Fernández and Lank, 2008) there could be a sex-specific variation when space is limited (Fernández and Lank, 2012), with territorial males defending remaining exposed areas and less-aggressive females using alternative foraging grounds during neap tides.

Conversely, godwits and dowitchers seem to be less affected by the reduced availability of exposed intertidal areas. Gregarious species that forage by probing tend to occupy a relatively small proportion of the available habitat (Folmer et al., 2010), which is consistent with their high densities observed during neap tides. Furthermore, the presence of conspecifics within a patch can be beneficial as it provides information on the availability of food and dilutes predation risk (Pulliam, 1973; Danchin et al., 2004). Godwits and dowitchers are tide-follower tactile predators (Granadeiro et al., 2006), and are probably less affected by a reduced exposed sediment area during neap tides, since both profitability for probing the substrate (Kuwae et al., 2010) and activity of their main prey (i.e. worms) (Dierschke et al., 1999) increase in shallower areas. Nonetheless, cryptic interference can reduce overall foraging activity even for gregarious tactile foragers (Bijleveld et al., 2012), and thus less-efficient individual godwits would need to compensate the important reduction registered in total time devoted to forage during low tide.

In summary, this study shows that when intertidal habitats are severely reduced during neap tides, an important fraction of shorebird populations, particularly individuals with lower competitive abilities (Caldow et al., 1999), experienced a reduction of more than 30% of total foraging time which can compromise to achieve their high energy demands. During these periods some individuals are probably forced to find alternative areas to forage during daylight (Elphick, 2000; Masero et al., 2000), such as surrounding shrimp-farms that are available as foraging grounds at the study area from October to December (Navedo et al., 2015), or increase foraging time during the night (Zwarts et al., 1990) at wetlands where intertidal areas are available. Otherwise a fraction of some shorebirds populations would leave a particular wetland altogether, thus reducing its overall carrying capacity in terms of bird-days (Goss-Custard et al., 2002). Moreover, additional spatial and/or temporal restrictions (e.g. associated to disturbances) in foraging activity (Navedo and Masero, 2007) can hardly be further compensated by shorebirds if no alternative foraging area is available. Since shorebirds serve an essential function as top-predators for wetland ecosystem service regulation (Green and Elmberg, 2014), our results can have important implications on carrying capacity assessment of coastal wetlands that had suffered an overall reduction of available intertidal foraging areas throughout the word.

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