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Daytime, tidal amplitude and protected areas influence movements and habitat use on mudflats of wintering black-tailed godwits

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ABSTRACT

Understanding environmental factors underlying animal foraging distribution is of major importance in defining priority conservation actions. During their wintering stage, most shorebirds depend on intertidal areas, as foraging grounds, and on supratidal areas, as high tide roosts. The accessibility of foraging areas and food resources is thus limited, and most wintering shorebirds have to forage whenever mudflats are available, both day and night, to fulfil their daily energetic demands. However, current knowledge of shorebirds' spatio-temporal use of foraging habitats is often restricted to the daylight period. In that context, we investigated the spatial distribution and habitat selection of wintering black-tailed godwits *Limosa limosa islandica*, during both the day and night, and in relation to the environmental characteristics. We equipped wintering black-tailed godwits at two different sites on the Pertuis Charentais (Atlantic French coast) with miniaturised GPS loggers. We then tested the hypothesis that godwits feed both during day and night, and show contrasting foraging behaviours and distribution in response to different visual capacities, prey [availability](#), predation risks and human activities. The selection of feeding areas was highly variable according to nycthemeral periodicities, [with little change in the habitat types selected](#). The estimated nocturnal [surface of](#) feeding areas were two times smaller than daytime ones, and located closer to the coastline. Moreover, birds largely foraged inside protected areas during the daytime, while most of them foraged outside at night. Finally, godwits with the smallest feeding home ranges stayed inside the Nature Reserves, during both day and night, while the others prospected outside the protected areas more often, preferentially at night.

Keywords: Coastal ecology, Protected areas, GPS tracking, Intertidal habitats, Nycthemeral movements, *Limosa limosa*,

1. Introduction

Understanding feeding habitat selection by animals and variations in their movements in space and time is crucial for their conservation, especially in rapidly changing environments and under increasing anthropogenic pressures (Fuller, 2012; Davidson et al., 2020). The choice of where and which resource to forage is critical for individuals, and relies primarily on a trade-off between starvation and predation risk (Lima, 1986; McNamara and Houston, 1990; Quinn et al., 2012). Furthermore, integrating the specific requirements that might explain the animals' foraging distribution and habitat use is of major importance in order to define conservation actions and priorities aiming to maintain habitat quality and protect birds over the long term. Shorebird populations are facing important modifications of their habitats, as well as various threats from human activities, on their breeding, migratory or wintering sites (Gill et al., 2007; Loss et al., 2012; Pearce-Higgins et al., 2017). As a consequence, most of large shorebird species have an unfavourable conservation status (Pearce-Higgins et al., 2017). During the wintering stage, most shorebirds depend on intertidal areas, accessible at low tide only, as foraging grounds, and on supratidal areas, accessible at high tide, as roosts (van de Kam et al., 2004). The accessibility of foraging grounds and food resources is thus limited throughout the day, and most wintering shorebirds have to forage whenever mudflats are available, both during the day and at night, to fulfil their daily energetic demands (McNeil et al., 1992; Dodd and Colwell, 1998; Lourenço et al., 2008). However, the current knowledge of these birds' spatio-temporal use of foraging habitats is often restricted to the daylight period, during which they can be visually observed. Some rare studies have shown significant variations in shorebirds' behavior between day and night, constrained by temporal differences in food availability, predation pressure or human disturbance (Robert and McNeil, 1989;

Mouritsen, 1994; Lourenço et al., 2008), while others studies showed no big differences between day- and night-time foraging activities as for the red knots wintering in Wadden Sea (van Gils et al., 2006). This demonstrates that determining possible day and night differences in habitat use and selection in such dynamic and human-influenced environments is essential to defining adapted protected areas and management measures.

In this context, we investigated the winter distribution and habitat use of the black-tailed godwit *Limosa limosa islandica* (hereafter ‘godwit’) during both the day and night and in relation to the characteristics of its environment. To this end, we focused on one of the main mudflat areas of the European Atlantic coast: the Pertuis Charentais. This region is a set of large intertidal mudflats on the French coast of international importance for migrating and wintering shorebirds (Delany et al., 2009), and is considered the first wintering area for shorebirds in France (Mahéo et al., 2020). The coastline of the Pertuis Charentais is subject to strong urban pressure linked to tourism and the settlement of retired people (Zaninetti, 2006). Leisure activities are mainly carried out on the beaches during school holidays, but there is still pressure during the rest of the year due to nautical activities, shellfish fishing or the hunting of waterbirds.

Godwits can reach a maximum of c. 14,000 individuals in mid-winter in the Pertuis Charentais (Mahéo et al., 2020), representing 28% of the population and 65% of the national counts (Bocher et al., 2013a). The increase in *L. l. islandica* numbers in France since 1990-1991, after a decrease from 1977 to 1990, is mainly due to the arrival of more juveniles each year since the sustained increase of the population in Iceland (Gunnarsson et al., 2005; Bocher et al., 2013b; Alves et al., 2019). Moreover, the design and implementation of Nature Reserves during the 1990s, with the protection of suitable habitats for wintering shorebirds, could facilitate the arrival of these individuals and explain the recent population dynamics and distribution of wintering black-tailed godwits in France. Indeed, Nature Reserves ensure the

protection of these key habitats and associated resources for godwits, and reduce local human activities known to disturb birds. However, these protected areas generally cover a small portion of the functional areas only, with limited support capacity, and sometimes only roosts or foraging areas.

The species was previously described locally as molluscivorous when feeding on bare mudflats, and as herbivorous when feeding on seagrass belts (Robin et al., 2013). Nevertheless, diets were either described through indirect approaches as isotope analysis of blood, making impossible to discriminate between day and night (Bocher et al., 2014) or through direct evaluations which only focused on daytime as feces analysis (Robin et al., 2013), ignoring possible prey shift during night. Previous studies exploring night foraging in wintering shorebirds on intertidal mudflats estimated a more important diurnal foraging in black-tailed godwits, which most likely fed at night when low temperatures increased their energy requirements (Dugan, 1981; Kersten and Piersma, 1987; Lourenço et al., 2008). However, all other species needed to forage during low tides both day and night (Pienkowski, 1982; Pienkowski, 1983; Lourenço et al., 2008). In this study, we equipped wintering black-tailed godwits at two different sites on the Pertuis Charentais with miniaturised GPS loggers. Concurrently, we sampled benthic macrofauna communities in order to map the distribution of habitats in mudflats. We then tested the hypothesis that black-tailed godwits feed both day and night, and show contrasting foraging behaviour and distribution in response to different visual capacities, prey availabilities, predation risks and human activities such as hunting. We predicted smaller feeding home ranges at night due to difficulties for birds to visually detect prey (Turpie and Hockey, 1993), suggesting more probing of sediment and therefore less movement (Pienkowski, 1983; Lourenço et al., 2008). We also predicted a stronger use of habitats distributed within the Nature Reserves during the day than at night when human activities and predation risks are reduced.

2. Methods

2.1 Study site

Black-tailed godwits were surveyed and captured in September and October 2017, at two main wintering sites on the Pertuis Charentais: Yves Bay (Fig. 1a; 46°02'N, 01°03'W) and Marennes-Oléron Bay (Fig. 1b; 45°55'N, 01°10'W). The Yves Bay includes an intertidal area of 2,300 ha with a marked north-south particle-size gradient (sandflat in the north and mudflat in the south) (Philippe et al., 2016). The Marennes-Oléron Bay extends from the continental coast to Oléron Island and covers 3,800 ha of intertidal areas, mainly characterised by bare mudflats on the mainland side and seagrass beds on the Oléron side. On these sites, godwits are known to roost in coastal marshes inside the National Nature Reserves of Marais d'Yves (192 ha, only marshes) and of Moëze-Oléron (6320 ha of sea and 320 ha of land surfaces). Hereafter, we distinguish the two study sites according to the main high tide roost locations: the 'Yves' site, including the Yves bay and the Charente Estuary (the largest estuary in the Pertuis Charentais, located between both bays and mainly edged by 1,200 ha of bare mudflat); and the 'Moëze' site, including the mainland intertidal area of Marennes-Oléron Bay.

2.2 Godwit capture and tracking

A total of 12 black-tailed godwits were captured on Yves (n=4) and Moëze (n=8), during two sessions on non-moonlit nights. Mist nets were used to catch birds arriving at their high tide roosts inside the Nature Reserves. The biometry of each bird (wing length, tarsus length and bill length) was measured using standard methods (Demongin, 2016). Birds were sexed according to the allometric equation calculated by Gunnarsson et al. (2006). No individuals with measurements located in the range of biometric overlap between males and females were found among the 12 birds. Age was determined according to the plumage pattern (Demongin, 2016). Godwits were then marked with a metal ring and a unique color ring combination, and

equipped with a GPS-UHF logger (STERNA UHF-SRD with solar charger, Ecotone, Gdansk, Poland; 35 x 16 x 10 mm, 7.5g). The weight of the tag did not exceed 3% of the bird body mass. GPS loggers (tested mean accuracy of ± 10 m) were attached according to the ‘leg-loop’ method (Mallory and Gilbert, 2008), with a 2 mm Teflon thigh harness (on the lower back), and recorded bird positions every 30 minutes. Among the 12 equipped godwits, two birds from Moëze were excluded from the analyses because their GPS provided data for one to two weeks only, after which the batteries failed. The 10 other birds were divided into a first batch consisting of four individuals monitored simultaneously at Yves for one month (from 22nd September to 22nd October 2017), and a second batch of seven individuals (including one bird previously equipped at Yves) simultaneously tracked at Moëze for one month (from 22nd October to 22nd November 2017; Table 1). Data were stored and processed in a PostgreSQL/PostGIS database.

2.3 Habitat mapping

Habitat description at the two study sites was carried out by determination of the benthic macrofauna and granulometry of the sediment, as well as by manual digitisation of satellite images of clearly identifiable habitats (e.g. seagrass beds, oyster parks, littoral biogenic reefs, coastal saltmarshes, etc.) during the study period. Previous studies by Philippe et al. (2016) and Robin et al. (2015) provided a first description of the benthic macrofauna distribution on Yves and Moëze. Following the same sampling method described in Bocher et al. (2007), 34 additional sediment core samples were obtained from the centroid of each foraging core area of the monitored godwits during the present study, based on GPS locations. This additional core sampling consisted of a squared grid of nine replicates of sediment cores spaced 10 meters apart and arranged around the central reference point of the station – that is, the centroid of the corresponding foraging area. Samples were collected on foot (during low tide) or by boat, depending on the accessibility of the area. Both methods provided identical

estimates (Bijleveld et al., 2012). Two specific sediment cores were collected for each replicate. For samples collected by foot, a first 15 cm diameter sediment core (0.018 m²), to a depth of 15 cm (the maximum depth reached by foraging birds according to the mean bill length of females), was sieved over a 1 mm mesh size to identify all living invertebrates, excluding *Hydrobia ulvae*. A second sediment core of 70 mm diameter (0.0037 m²), to a depth of 5 cm, was sieved in the laboratory over a 0.5 mm mesh to exclusively sample the potentially small and abundant mudsnail *H. ulvae*. For inaccessible points, covered by the tide or located on very soft sediments, the samples were collected from a boat (inflatable zodiac or small vessel) with two sediment cores of 10 cm diameter, covering 0.018 m² in total, to a depth of 15 cm. Only one core was processed to identify *H. ulvae*, and both were considered for all others species. Annelids were taken apart on site and stored in 70° ethanol, and living molluscs were stored at -20°C until sorted in the laboratory. In the laboratory treatment, identification of organisms was done at the species level when possible, and the length of molluscs was measured with an accuracy of 0.1 mm.

At each sampling station, an additional sediment core (depth of 5 cm) was collected to characterise the particle size of the substrate by measuring the mean grain size (mm) and the percentage of silt (fraction < 63 µm) and using a Malvern Mastersizer 2000 diffraction laser (particle sizes analysed from 0.04 to 2000 µm).

The combination of benthic macrofauna data, particle size characteristics of the sediment, and digitisation of hard substrate habitats from satellite images and field knowledge allowed for the production of a fine-scale habitat typology on intertidal areas of study sites. Habitat determination was based on the European Nature Information System (EUNIS) classification of coastal habitats (Bajjouk et al., 2015).

2.4 Home ranges and habitat selection

To determine the spatial distribution of godwits, the utilization distribution (UD) was determined through kernel density estimates (KDE) (van Winkle, 1975; Worton, 1989; Laver and Kelly, 2008), using the function 'kernelUD' (package 'adehabitatHR') (Calenge, 2020). The KDE method describes the UD through estimation of a home range (95% isopleth kernel) and a core area (50% isopleth kernel) for each animal, from individual locations and time spent in the corresponding area (Worton, 1989). Two main bandwidth methods exist for the estimation of kernel home ranges: the Least-Square Cross Validation (LSCV) and the reference bandwidth (ad-hoc), generally recognised as giving an under-smoothing factor (h_{LSCV}) and an over-smoothing factor (h_{ad-hoc}), respectively (Kie, 2010; Schuler et al., 2014). We retained an intermediate approach and used smoothing factor value h such as $h_{LSCV} < h < h_{ad-hoc}$, with h_{LSCV} and h_{ad-hoc} the minimum values computed by 'LSCV' and 'ad-hoc' methods over all individuals monitored. This resulted in an 95% kernel home-range polygon that was as contiguous as possible without including proximal areas known to not be used by birds (e.g. proximal supratidal resting areas during feeding distribution). Hence, we applied an identical smoothing factor $h = 120$ for all our monitored birds, in order to compare UD between individuals. The grid resolution was set to 20 m, in accordance with the accuracy of locations provided by GPS loggers (± 10 m).

First, we estimated the global UD of each bird, from all locations collected during the monitoring period. Then, we considered the foraging distribution (when GPS positions were on intertidal areas at low tide) and the roosting distribution (when GPS positions were on supratidal lagoons and marshes at high tide) independently. We also differentiating daytime and nighttime locations (sunrise and sunset data from the R package 'GeoLight'). [In this study, we only presented the home ranges of godwits on intertidal area corresponding to foraging periods \(Feeding Home Range, FHR\). Given the movements of the birds on the mudflat during low tide from the GPS positions and occasional visual observations, it is noted](#)

that they remain mobile and are certainly foraging for food most of the time. If a bird visited exceptionally inland marshes outside the roosting area, these areas could also be considered as foraging area, but were not considered for calculation of feeding home range if it was limited to very few GPS positions. Considering that roosting home ranges were not presented in this study, the values for home range did not correspond to the total home ranges of birds during the study periods. Foraging distributions of godwits were then used to investigate the importance of foraging habitats through a habitat selection analysis using Manly's selection ratios (Manly et al., 2002) with the R package 'adehabitatHS' (Calenge, 2011). We analysed the habitat selection as design II (second order) – that is, at the individual scale and considering the same availability of habitats for all birds (Johnson, 1980). The delineation of habitats considered as 'available' for birds was determined from the Minimum Convex Polygon (MCP) of foraging points from all monitored birds. Finally, we explored the interindividual variations in the habitat selection through an Eigen analysis of selection ratios (Calenge and Dufour, 2006). This multifactorial analysis projects birds in a factorial plan described by the habitat types and best explains the heterogeneity of the selection. The result should be able to highlight if groups of godwits using habitats in the same way exist. All statistical analyses were performed with the software R (3.6.1) (R Core Team, 2020).

2.5 Daily activity rhythm

To analyse the daily activity rhythm of godwits, which alternates between intertidal mudflats for feeding at low tide and coastal marshes for roosting at high tide, we measured the shortest distance from the coast of each bird over time and throughout the monitored period. We distinguished daytime and nighttime GPS locations in order to explore differences in the shortest distance from the coast between diurnal and nocturnal foraging activities. We also considered the water height variation over time, along with changes in luminosity through moon phases (new, crescent, quarter, gibbous and full moon), to investigate their effect on the

daily pattern of distance to the coast by foraging godwits (analysis of variance, ANOVA). After quickly finding there was no effect of moon-phase brightness on the bird distance to the shoreline, we did not explore this hypothesis further, and will not detail the results in this study. The low number of high tides during which godwits remained on the intertidal areas to rest, and the difficulty in distinguishing roosting fixes from foraging ones, led us to consider all GPS locations over mudflats for each bird to estimate its foraging distribution.

2.6 Availability of main prey in used habitats

On the basis of dropping analyses collected during daylight in a previous study, godwits in the Yves and Marennes-Oléron bays fed predominantly on bivalves (mainly *Macoma balthica*), whereas the godwits on Ile de Ré had a diet mainly of rhizomes of *Zostera noltei* (Robin et al., 2013). In this study, large worms (*Nereidae*) and small worms (*Capitellidae* and *Maldanidae*) accounted for less than 0.5% of the diet. The molluscivorous diet of godwits at these sites was confirmed by isotopic analyses of blood in a study on trophic resource partitioning within the local shorebird community (Bocher et al., 2014). Thus, we looked at the availability of bivalves *Macoma balthica* and *Scrobicularia plana* inside the most-used habitats – that is, the most common habitats in the feeding core areas (FCA) of godwits. As the surfaces of the different habitats were not equal, the number of sediment core samples per habitat type was not similar. We therefore expressed the availability of preferential prey in terms of density per surface. In order to identify the availability of profitable prey for godwits, prey density by size class was also detailed.

3. Results

3.1 Day and night feeding areas

During the study periods, all monitored individuals fed exclusively on the intertidal mudflats of Yves and Moëze, except BLTG08, which foraged for six consecutive days in inland

marshes east of the Moëze roosts (Fig. 2). The main roosts were located inside both Nature Reserves, but godwits also occasionally used the intertidal mudflats to rest during high neap tide, when the upper foreshore remained submerged. Individual FCAs were different in size between day and night at both sites (Table 1). Diurnal FCAs, with a mean of 343 ± 131 ha (min-max: 148 – 428 ha, $n = 4$) at Yves and of 273 ± 118 ha (92 – 439 ha, $n = 7$) at Moëze, were more than two times larger than nocturnal ones at Yves: 161 ± 44 ha (108 – 207 ha; $t = 3.54$, $df = 3$, $p = 0.04$) and at Moëze: 124 ± 48 ha (50 – 209 ha; $t = 4.60$, $df = 6$, $p < 0.01$). The same magnitude of differences in size was observed for feeding home ranges (FHR) between day and night at both sites. Diurnal and nocturnal FHR were $1,341 \pm 359$ ha (803 – 1,537 ha) and 768 ± 250 ha (416 – 954 ha), respectively, for birds monitored at Yves ($t = 7.45$, $df = 3$, $p < 0.01$), and $1,271 \pm 446$ ha (539–1,722 ha) and 694 ± 237 ha (295–1,043 ha) for those at Moëze ($t = 4.98$, $df = 6$, $p < 0.01$).

Thus, at both sites, monitored godwits always used smaller feeding areas at night, and were also located closer to the coast than in the daytime (see below, Fig. 2). The day-night differences in the location of feeding areas were confirmed by the calculation of overlapping rates (Table 1), with a mean individual day-night FCA overlapping rate of $16 \pm 16\%$ (2-39%) at Yves and $12 \pm 10\%$ (2-25%) at Moëze. Day-night FHR also overlapped at low rates, with $22 \pm 10\%$ (13-35%) at Yves and $26 \pm 11\%$ (13-42%) at Moëze. In addition, day and night feeding areas stood out on a north-south axis on Moëze mudflats, according to the border of the Nature Reserve. By day, tracked godwits were mainly restricted to the southern part of the mudflat, with a mean FCA of $83 \pm 20\%$ (43-100%) inside the Nature Reserve. By night, birds were located further north, with only $51 \pm 35\%$ (5-92%) of FCA still located inside the Nature Reserve.

3.2 Habitat diversity and structure

In total, 15 intertidal habitat types were described at the two study sites (Fig. 3). Differences in habitat typology and distribution were described between Yves and Moëze, and partially within each site, according to a north-south gradient. At both sites, along the coastline, upper intertidal areas were bordered by habitats of strandline (A2.21), coastal saltmarshes (A2.5) or rocky facies, alternately. These micro-habitats were not considered in the habitat selection analysis. At Yves, the dominance of sandy habitats in the north of the bay (A2.241 and A2.244) and of muddy habitats in the south (A2.311, A2.313 and A2.321) illustrated the strong north-south particle size gradient (Fig. 3b). In the northern part, the main habitat A2.241 was characterised by the bivalve *Macoma balthica* and the polychaete *Arenicola marina*. The other, more restricted habitat, A2.244, was dominated by crustaceans *Bathyporeia pilosa* and *Corophium arenarium*. Artificial oyster grow-out tables (oyster parks) and associated littoral biogenic oyster reefs (A2.7X) were dominant on the eastern and northern parts of the bay, with rocky substrates sheltering littoral rock pool communities (A1.4). In the south, the habitat A2.313, dominated by the polychaete *Hediste diversicolor* and the bivalves *M. balthica* and *Scrobicularia plana*, and the habitat A2.311, characterised by polychaete *Nephtys hombergii* and *M. balthica*, were predominant. The muddy habitat A2.321 in the southeastern part of the bay was mainly described by the dominance of the polychaetes *N. hombergii* and *Streblospio shrubsolii*. Finally, seagrass beds of the phanerogam *Zostera noltei* (A2.6111) were present in patches on the upper tidal area of the bay. The lower part of tidal areas was covered by mussel culture (mussel parks). The main habitats on the Charente Estuary were again habitats A2.311 and A2.313. Mussel and oyster parks or biogenic reefs were present in the lower part of the intertidal area.

At Moëze, the particle size features of the sediment were more homogeneous over the site, with a dominance of muddy substrates (Fig. 3c). Habitats A2.311 and A2.313 were dominant in the upper tidal area. Habitats A2.32 and A5.43, not observed at Yves, extended

over large surfaces in the medium and lower intertidal areas. Habitat A2.32 was composed of a low diversity and abundances of polychaetes and oligochaetes, and habitat A5.34 by a fine mud with a low abundance of invertebrates. Littoral biogenic reefs on abandoned oyster parks (A2.7X) were widespread in lower intertidal areas, as were the still-active oyster and mussel parks, but to a lesser extent.

3.3 Foraging habitat use and selection

The monitored godwits foraged in several habitats at Yves (from 4 to 10) at Moëze (from 3 to 8) among all available ones (Fig. 4). Nevertheless, the proportion of habitats identified within FCA emphasised the predominant use of a few habitat types.

At Yves, the habitats A2.311, dominated by *N. hombergii* and *M. balthica*, and A2.313, dominated by *H. diversicolor*, *M. balthica* and *S. plana*, were mainly used, during both day and night (Fig. 4). Seagrass beds (A2.6111) were the third habitat identified in FCA in terms of surface used. Habitat A2.241, with dominant *M. balthica* and *A. marina*, and habitat A2.321, characterised by polychaetes *N. hombergii* and *S. shrubsolii*, were secondarily used by birds. This selection of some specific habitats for foraging illustrated the diurnal and nocturnal non-random habitat selection, both when pooling the four monitored birds (Daytime: $\chi^2 = 919.9$, $df = 44.0$, $p < 0.001$; Nighttime: $\chi^2 = 2113.2$, $df = 44.0$, $p < 0.001$) and at the individual scale (Daytime: $\chi^2 = 810.2$, $df = 11.0$, $p < 0.001$; Nighttime: $\chi^2 = 2028.7$, $df = 11.0$, $p < 0.001$). All main habitats were selected (all global selection ratios > 1), except A2.241 (Supplementary Material Fig. S1). Habitats A2.6111 (*Z. noltei*) and A2.313 (*H. diversicolor*, *M. balthica* and *S. plana*) had the highest selectivity indexes. Although it was selected during the day, the non-use of the habitat A2.321 (*N. hombergii* and *S. shrubsolii*) at night, in favour of a greater use of habitats A2.313 and A2.6111, constituted the main

differences between diurnal and nocturnal habitat selection in godwits at Yves (Fig. 4 and Supplementary Material Fig. S1).

Diurnal and nocturnal FCA at Moëze were predominantly located in habitat A2.313, followed to a lesser extent by habitathome range

Home range Godwits also foraged secondarily in habitat A5.34 during the daytime, but not at night. At night, all monitored godwits reduced their prospection in habitat A2.311 and increased their presence in habitat A2.313. These results highlighted the significant selection of habitats by godwits, non-randomly used both day and night, when considering individuals independently (Day: $\chi^2 = 853.8$, $df = 7.0$, $p < 0.001$; Night: $\chi^2 = 2091.9$, $df = 7.0$, $p < 0.001$) as well as when combining all the seven birds monitored (Day $\chi^2 = 993.1$, $df = 49.0$, $p < 0.001$; Night: $\chi^2 = 2520.2$, $df = 49.0$, $p < 0.001$). The results of Manly selectivity measures confirmed a clear selection of habitat A2.313 (global selection ratio = 1.1) over habitat A2.311 (GSR = 1.9) by day (Supplementary Material Fig. S2). At night, A2.313 (GSR = 2.1) was selected more than A2.311 (GSR = 1.5), illustrating a shift in habitat preferences during the night, previously observed with FCA locations (Fig. 4 and Supplementary Material Fig. S2).

Within sites, despite the use of the same habitats for foraging, godwits showed inter-individual differences in the proportion of each habitat used for feeding (FCA) during daytime and nighttime, both at Yves (Day: $\chi^2 = 109.7$, $df = 33.0$, $p < 0.001$; Night: $\chi^2 = 84.5$; $df = 33.0$; $p < 0.001$) and Moëze (Day: $\chi^2 = 139.3$, $df = 42.0$, $p < 0.001$; Night: $\chi^2 = 428.3$, $df = 42.0$, $p < 0.001$).

3.4 Foraging distance to the coast

Analysis of monitored godwit positions over time and in relation to the coastline revealed a cyclical movement pattern not only dependent on the tidal cycle. Schematically, godwits

moved away from the coast during ebbing tide and were approaching the coast during rising tide to return to their roosts during high tide. Nevertheless, movements from the coast to intertidal feeding areas during low tide underlined marked differences between diurnal and nocturnal movements. At both sites, the mean distances of feeding godwits to coastline were higher during daytime than nighttime. At Yves, the mean distance to the coast of 429 ± 11 m during the day was significantly higher than during the night, when there was a mean distance of 303 ± 6 m (KW $\chi^2 = 10.84$, $df = 1$, $p\text{-value} < 0.001$). The difference in distances was more substantial at Moëze, with a mean distance to the coastline during the day of 611 ± 12 m and only of 380 ± 7 m at night (KW $\chi^2 = 121.45$, $df = 1$, $p\text{-value} < 0.001$). These differences in nycthemeral distributions on mudflats depended on tidal amplitude, but were obviously particularly discernable during spring tides, when more mudflat areas were available (Supplementary Material Fig. S3 and Fig. S4). In addition, day and night differences in foraging distances to the coastline varied according to the tide amplitude tendency. There were significant differences in mean distances to coastline during decreasing water heights from one tide to the other at Yves (day: 436 ± 547 m; night: 256 ± 255 m; KW $\chi^2 = 15.62$, $df = 1$, $p\text{-value} < 0.001$) and Moëze (day: 655 ± 769 m, night: 287 ± 367 m; KW $\chi^2 = 191.5$, $df = 1$, $p\text{-value} < 0.001$). Conversely, no significant differences were observed in the distance to coast during increasing water heights at Yves (day: 422 ± 524 m; night: 350 ± 381 m; KW $\chi^2 = 0.32$, $df = 1$, $p\text{-value} = 0.6$; Fig. 5) and Moëze (day: 565 ± 675 m; night: 475 ± 528 m; KW $\chi^2 = 2.78$, $df = 1$, $p\text{-value} = 0.09$; Fig. 6). This general pattern, observed at each site when all equipped birds were pooled, was also observed at the individual level for most godwits (Supplementary Material Fig. S5 and Fig. S6).

3.5 Availability of bivalves as prey in the main used habitats

At both sites, the two main foraging habitats used by godwits were A2.311 and A2.313. In these habitats, *M. balthica* and *S. plana*, considered the main prey, differed in density and size

distribution (Fig. 7). At Yves, the size-class density distribution of *M. balthica* in the range of optimal prey sizes (5-16 mm) (Robin, 2011) did not differ significantly between A2.311 and A2.313 ($t = 0.12$, $df = 18.14$, $p\text{-value} = 0.906$), but the density of *S. plana* underlined more individuals per square metre in habitat A2.313 for optimal size classes (4-15 mm (Robin, 2011); $t = 4.43$, $df = 11$, $p\text{-value} = 0.001$). At Moëze, the densities of *M. balthica* and *S. plana*, in the range of optimal prey sizes for godwits, were largely higher in habitat A2.313 (*M. balthica*: $t = 2.66$, $df = 10.92$, $p\text{-value} = 0.022$; *S. plana*: $t = 4.30$, $df = 11.42$, $p\text{-value} = 0.001$).

4. Discussion

The analysis of habitat use and selection in wintering Icelandic black-tailed godwits highlighted, for the first time and at a very fine scale, the influence of the time of day on their spatial distribution. The monitored godwits showed a high variability in the selection of feeding areas according to nycthemeral periodicities, with little change in the habitat types selected. Indeed, the size of feeding areas and their distance to the coast differed significantly between day and night, with nocturnal feeding areas being two times smaller than daytime ones, and located closer to the coastline. These day and night differences in the distance of foraging areas to the coastline also depended on the tidal cycle (neap tides vs spring tides) and tidal range tendency, with the most marked differences occurring during a decreasing tidal amplitude of spring tides. Moreover, the protected status of mudflat areas also showed an influence on the diurnal and nocturnal distribution of godwits. Hence, at Moëze, where both ‘protected’ and ‘not protected’ areas were adjacent on mudflats, birds largely foraged inside the protected areas during the daytime, while most of them foraged outside those areas at night. Finally, at both sites, a significant inter-individual variability in the size and the location of diurnal and nocturnal foraging areas was observed, although the same habitat

types were used and in close proportions. At Moëze, godwits with the smallest feeding home ranges stayed inside the Nature Reserve, during both the day and night, while the others prospected outside the protected areas more often, preferentially at night.

Lourenço et al. (2008) investigated the energetic importance of night foraging for shorebirds in intertidal mudflats, and concluded that wintering Icelandic godwits were able to fulfil their daily energy requirements on a single tide, while all other studied species needed to forage during both day and night low tides. Hence, in the Tagus Estuary in Portugal, godwits achieved much a higher energy consumption during the day, and the species was seldom seen foraging at night, except during the nights with **lower temperatures**. The authors explained this unusual activity at night by higher energy needs during cold spells (Dugan, 1981; Kersten and Piersma, 1987). Conversely, at our study sites, godwits also had to feed at night, and we hypothesise that they could not meet their daily energetic requirements by feeding during daylight low tides only. It is thus possible that individuals wintering at higher latitudes, with lower temperatures, may face higher thermoregulatory costs and energy requirements (Wiersma and Piersma, 1994).

Consequently, godwits were dependent on the availability of emerged mudflat according to tidal rhythm for feeding, whatever the time of the day, as previously observed for many species of coastal shorebirds (McNeil et al., 1992; McNeil and Rodriguez, 1996; Dodd and Colwell, 1998; Lourenço et al., 2008; Jourdan et al., 2021). Nevertheless, the nycthemeral patterns of monitored godwits highlighted differences in space use between diurnal and nocturnal feeding activities. Piersma et al. (2006) already observed contrasting areas used between day and night in some foraging non-breeding shorebirds, but without exploring the characteristics of these feeding areas. Burton and Armitage (2005) and Dwyer et al. (2013) also observed the use of contrasting foraging areas between day and night among wintering redshanks *Tringa totanus*, with larger foraging home ranges and core areas

observed at night. Hence, our observations of distinct distributions between day and night in black-tailed godwits are consistent with those of previous studies, although the smaller-size pattern of nocturnal feeding home range (nFHR) and core areas (nFCA) differ from redshanks (Burton and Armitage, 2005) but not from bar-tailed godwits (Jourdan et al., 2021). Such differences between diurnal and nocturnal foraging home ranges could be related to birds' feeding method. Lourenço et al. (2008) showed a more frequent pecking behaviour among black-tailed godwits in the Tagus estuary during the day, and the dominance of stitching and sweeping movements at night. These changes in foraging behaviour, also observed in dunlins (*Calidris alpina*) (Mouritsen, 1994), are assumed to be an adjustment to visual conditions, birds preferring visual foraging methods (pecks) during daylight, but needing tactile capacities (stitches, swipes) to forage at night (Mouritsen, 1994; Lourenço et al., 2008; Cunningham et al., 2013). Larger prospecting areas could then result from the higher step rate associated to direct visual searches by day, while the reduced step rate associated to tactile methods could limit the size of night foraging range (Lourenço et al., 2008). Nevertheless, the predominant use of pecking at day is not consistent with birds' diet, made of bivalves at both our study sites (Robin et al., 2013). These preys being detected tactilely by probing, godwits need to walk longer to increase the probability of detecting them.

The size of foraging home ranges could consequently depend on the prey density at diurnal and nocturnal grounds. Results of habitat selection underlined that godwits selected the intertidal sandy mud habitat A2.313 both during day and night, but in greater proportions during nocturnal feeding. Compared to the second most used habitat, A2.311, the density of the preferred prey *M. balthica* (Robin et al., 2013) in the optimal range size (5-16 mm) was significantly higher in habitat A2.313. In case of higher prey density on nocturnal foraging grounds, the intake and spatial turning rates are assumed to increase (Zharikov and Skilleter, 2003, Dias et al. 2009), resulting in sinuous low-speed searches (Nolet and Mooij, 2002) and

smaller prospecting areas. In addition, the higher surface activity of intertidal invertebrates by night, including bivalves such as *M. balthica*, could constitute better prey-catching opportunities for godwits than in the daytime (Esser et al., 2008), and could amplify the prey availability dependent behaviour of birds (Evans, 1987).

Further, although the preferred prey *M. balthica* was abundant in habitat A2.311, godwits selected habitat A2.313, which combined a higher harvestable prey density of *M. balthica* and *S. plana*. The presence of *S. plana* in habitat A2.313 could constitute additional feeding opportunities (Moreira, 1994; Robin et al., 2013), with an optimal prey size (4-15 mm) well represented. Moreover, during night, godwits could feed on siphons of larger *S. plana* than initial optimal range size. Indeed, the increased surface activity of bivalves at night (Esser et al., 2008) would make *S. plana* siphons more abundant and available to birds in the nearshore habitat A2.313, allowing them to feed closer to the shoreline.

In contrast to previous observations, which highlighted an avoidance of the nearshore by non-breeding shorebirds during nocturnal foraging due to an increased predation risk (Sitters et al., 2001; Piersma et al., 2006;), godwits in the Pertuis-Charentais fed at a higher distance from the coast by day. In addition to the aforementioned prey availability, this pattern could arise from an increased human disturbance during daytime, such as recreational activities, which already showed an effect on feeding opportunities, flight movements and use/avoidance of some feeding areas in some shorebird species (Thomas et al., 2003; Navedo and Masero, 2007; Burger and Niles, 2013). During the day, black-tailed godwits at Yves and Moëze seemed to move away from the coast, the likely source of disturbance, to enter the less interesting but still suitable habitat A2.311. At night, with the decrease in human disturbance on the coastline, godwits could get closer to the coast to reach the most profitable habitat, A2.313, which provided a higher density of *M. balthica* and *S. plana*. In addition, the presence of public lighting around inhabited areas could allow for good feeding efficiency at

night, as shown for the redshanks on the Forth Estuary in Scotland (Dwyer et al., 2013). Indeed, although our two study sites were not directly under the influence of artificial lighting, significant light pollution appears in the study area ("<https://lighttrends.lightpollutionmap.info>"), and would be worth measuring in future research. However, the benefit of artificial lighting is unlikely to solely explain the nocturnal feeding observed near the coast.

This distance of foraging birds from the coast was different between tidal cycles (i.e. neap tides or spring tides), but also between tidal trends (i.e. decreasing or increasing tidal amplitude). During neap tides, intertidal areas available at low tide were obviously limited and the selection of habitats further away from the coast could not be prospected, reducing differences between day and night. Moreover, the upper foreshore remained available at high neap tides, and birds did not necessarily reach marshes for roosting. In spring tides, during which the low tides expose almost all the intertidal areas and the high tide completely covers them, the bird distance from the shoreline highlights an alternation between intertidal feeding period and supratidal roosting time. Thus, day and night differences in the foraging habitat selection, according to the aforementioned anthropogenic disturbance and prey availability, can easily appear. However, in our study this behaviour pattern depended on the tidal tendency, so that the significant distinct distribution of godwits between day and night during neap and spring tides was mainly observed during decreasing tidal ranges but not during increasing ones.

The presence of birds of prey could also influence bird activity and their presence near the coast during the day with possible perching sites such as the cliffs at Yves. The recent increase in peregrine falcon populations and the presence of some individuals on the coast in winter could also explain the avoidance of the coast during the day, at least for the Yves site, the only site with cliffs of more than several meters in height. The influence of anthropogenic

disturbances on the distribution of black-tailed godwits was also highlighted by the alternation of ‘protected’ and ‘unprotected’ foraging areas. Most of the diurnal foraging areas were located inside the National Nature Reserve of Moëze-Oléron. Hunting is largely prohibited in the Nature Reserve, but authorised from August to January from the sunrise to 10 a.m. in its north and south sectors (Delaporte and Guéguen, 2017; Delaporte, *Pers. Com.*). Although hunting pressure was not surveyed in the area during the study period, the presence of hunters all along the beach north to the nature reserve produced disturbances in the area. In addition, morning and recreational walks (with dogs) later during the day produced also disturbances that could explain the limited number of tracked godwits outside the Nature Reserve during daylight. Additional studies must be undertaken to measure human activity and its disturbance impact on feeding areas, which would constrain the birds’ ability to meet their energy needs in the long term.

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Figure captions

Figure 1 Map of the Pertuis Charentais (Central French Atlantic coast) and location of the study sites. (a) Yves site includes the Yves Bay and Charente Estuary and (b) Moëze site corresponds to east side of Marennes-Oléron Bay. Dark grey represents the mainland and light grey the intertidal area.

Figure 2 Diurnal and nocturnal foraging home ranges of black-tailed godwits on (a) the Yves site from mid-Sep to mid-Oct and (b) the Moëze site from mid-Oct to mid-Nov. Feeding home ranges were calculated as 50% (core areas) and 95% (home ranges) kernel density contours.

Figure 3 Habitat typology in (a) all areas, (b) Yves Bay and Charente Estuary; and (c) Eastern area of Marennes-Oléron Bay.

Figure 4 Day and night proportion of habitat types on feeding core areas (50% kernel density contour) of each black-tailed godwit at Yves and Moëze.

Figure 5 Distance of godwits from the coast according to tendency of the tides (increasing or decreasing) and period (day 'D' or night 'N') at the Yves site.

Figure 6 Distance of godwits from the coast according to tendency of the tides (increasing or decreasing) and period (day 'D' or night 'N') at the Moëze site.

Figure 7 Distribution of prey sizes for *Macoma balthica* (MAC) and *Scrobicularia plana* (SCR) in the two most represented habitats in the feeding core areas of godwits, i.e. A2.311 and A2.313. Dashed lines represent the range of optimal prey sizes of MAC (5-16 mm) and SCR (4-15 mm) for godwits.

Table 1 Sex, age and biomass of tagged black-tailed godwit. Size of diurnal and nocturnal feeding areas (Convex Polygon, FCA feeding core areas 50%, FHR feeding home ranges 95%) and their overlap rate.

Site	Logger_ID	Sex	Age	Mass (g)	Day			Night			Overlap dFCA/ nFCA (%)	Overlap dFHR/ nFHR (%)
					GPS fixes	dFCA (ha)	dFHR (ha)	GPS fixes	dFCA (ha)	dFHR (ha)		
Yves	BLTG01	M	Ad.	292	465	428	1537	503	186	954	11	23
	BLTG02	M	Ad.	292	408	148	803	471	108	416	39	35
	BLTG03	F	Ad.	365	375	383	1495	391	207	936	13	18
	BLTG04	F	Ad.	345	369	412	1530	448	143	767	2	13
Moëze	BLTG04	-	-	-	354	346	1461	373	132	657	2	16
	BLTG05	M	Ad.	376	397	439	1722	446	209	864	2	19
	BLTG06	M	Ad.	290	370	311	1488	426	131	1043	19	42
	BLTG07	M	Ad.	298	273	283	1334	241	92	572	4	13
	BLTG08	M	Juv.	305	246	92	539	393	50	295	20	34
	BLTG09	F	Ad.	345	219	145	760	269	131	646	15	37
	BLTG10	M	Ad.	281	396	292	1596	286	123	781	25	18

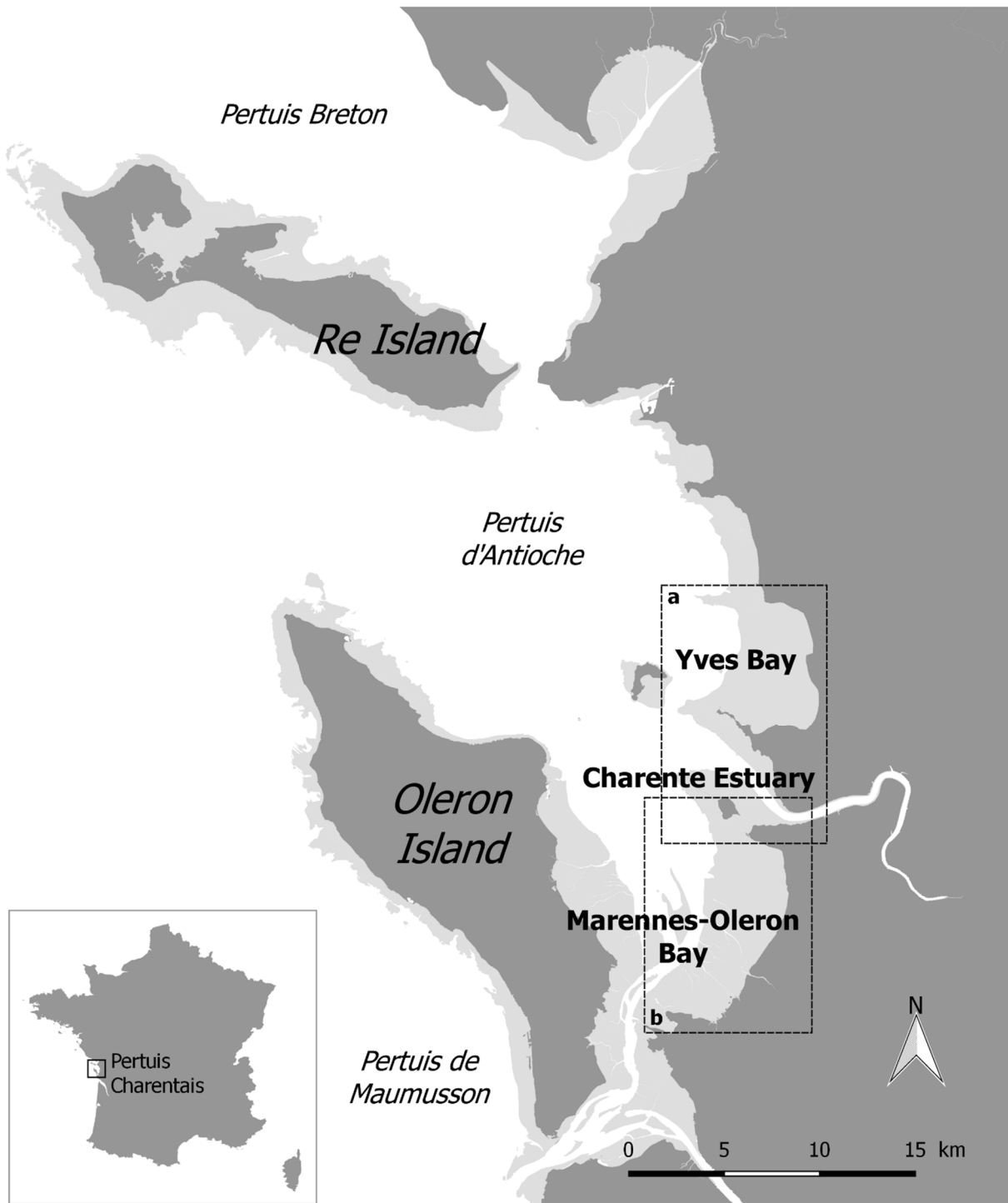


Figure 1

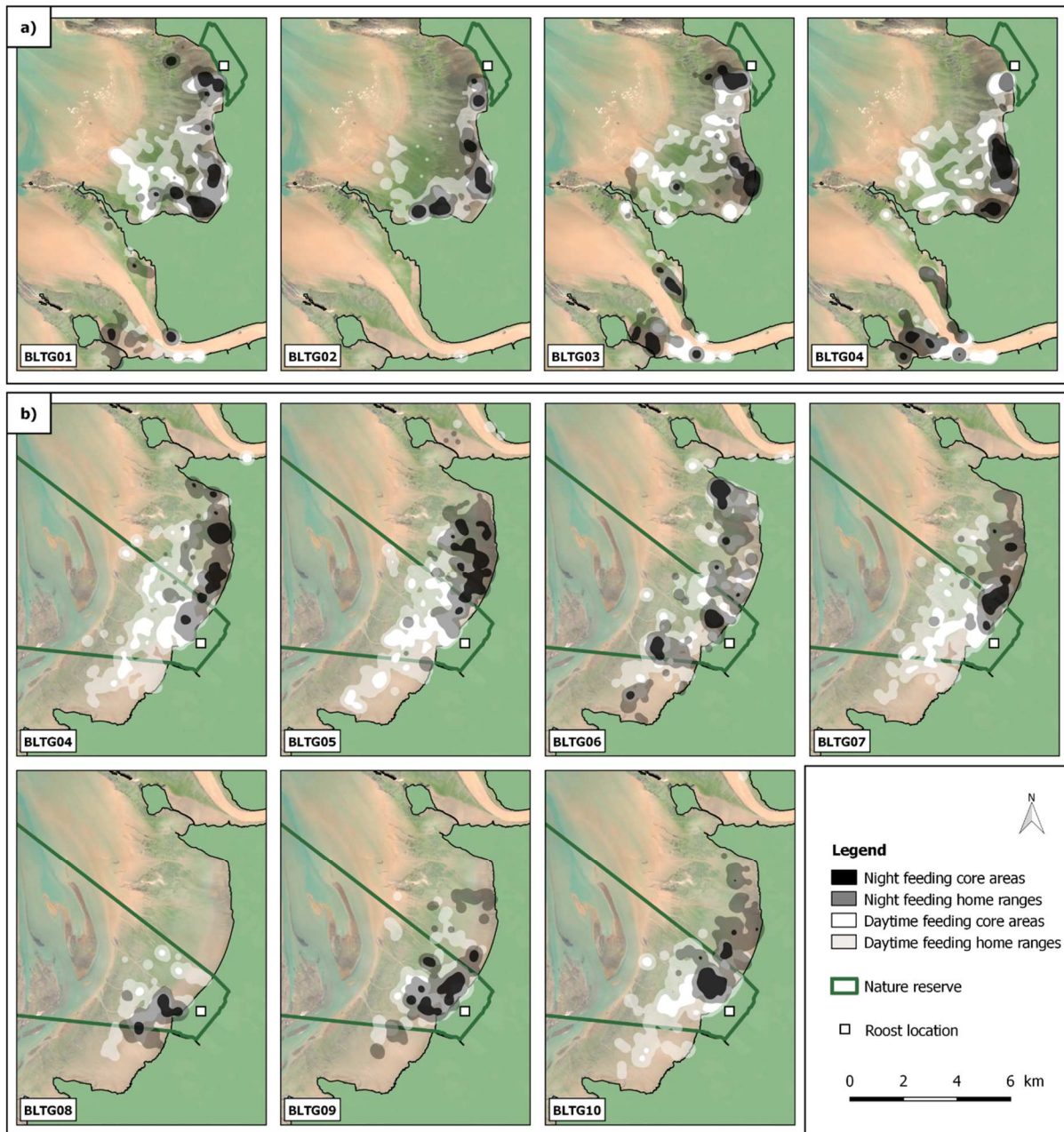


Figure 2

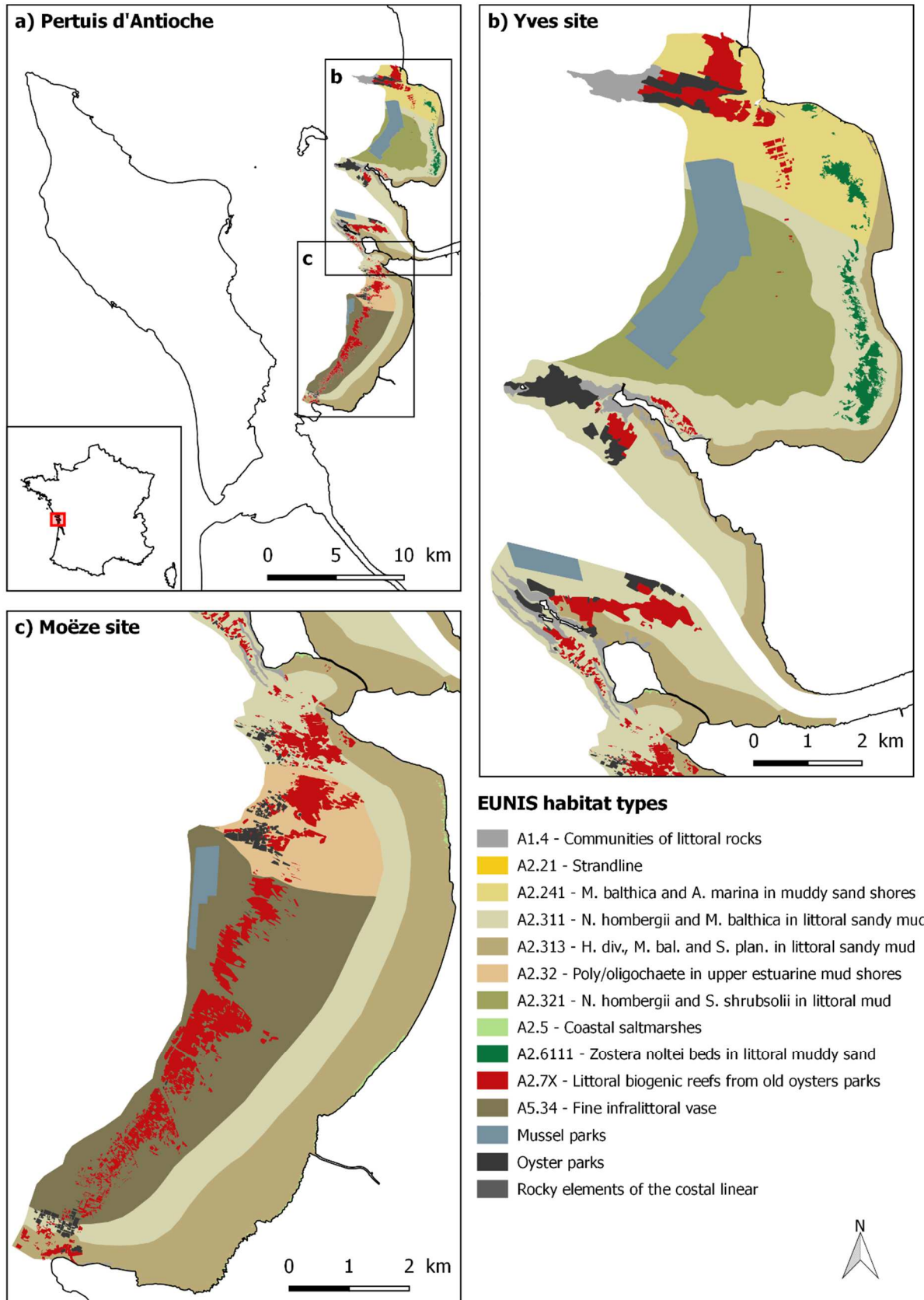


Figure 3

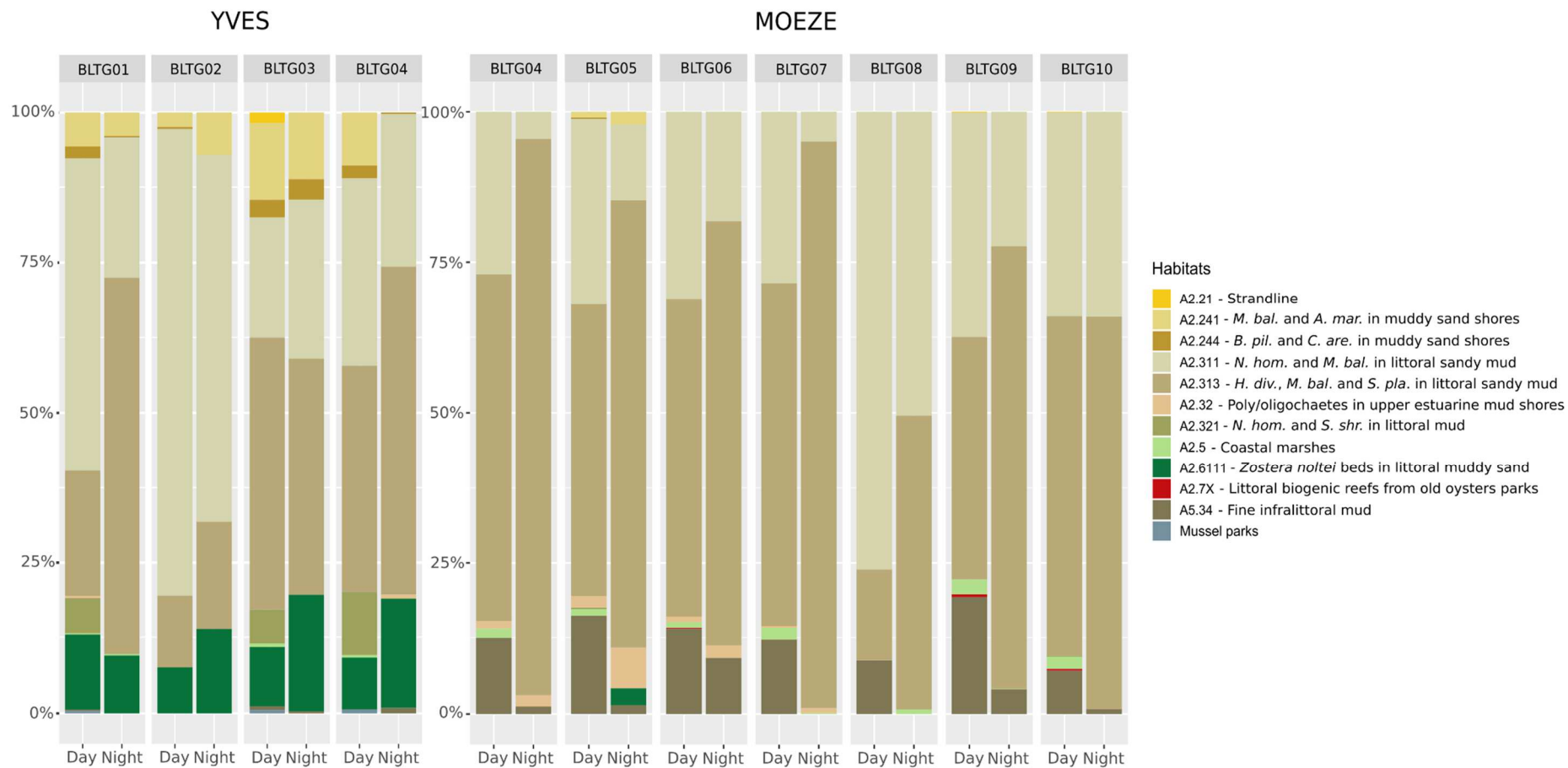


Figure 4

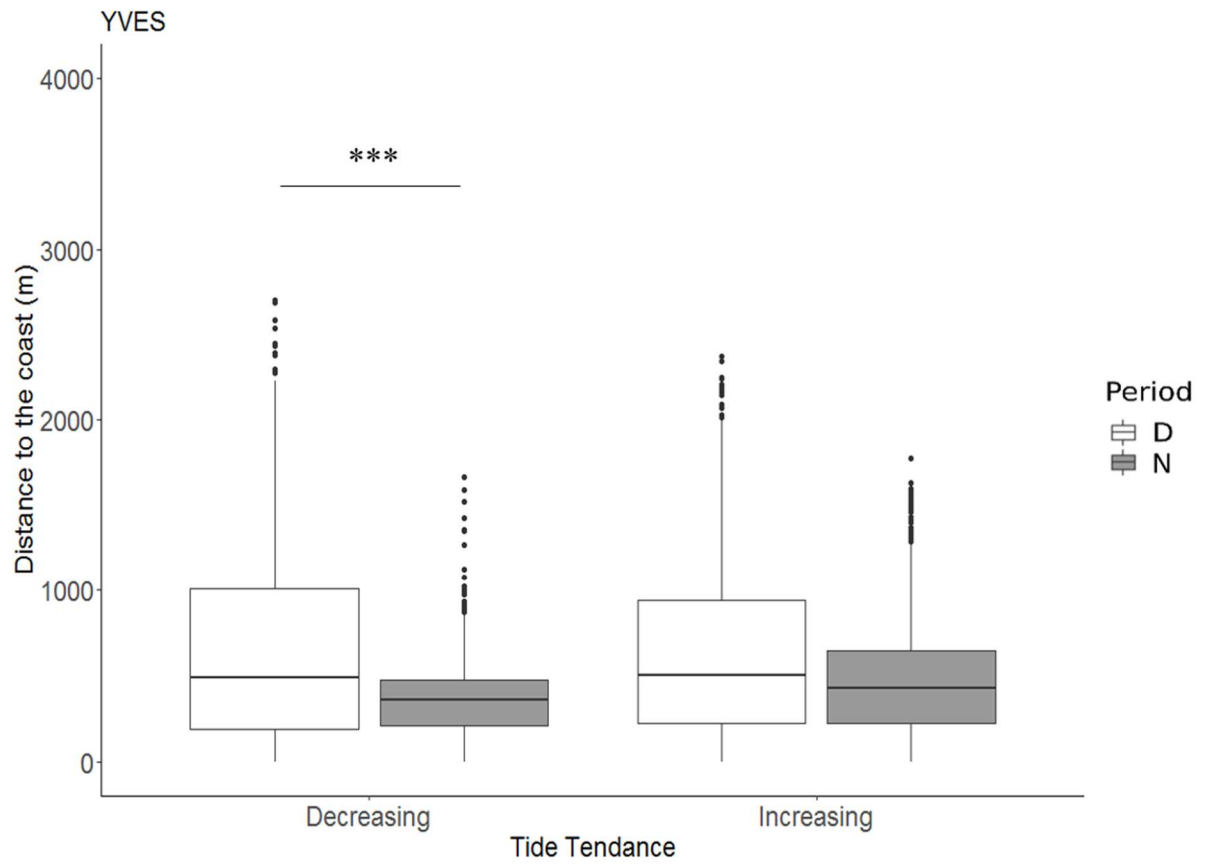


Figure 5

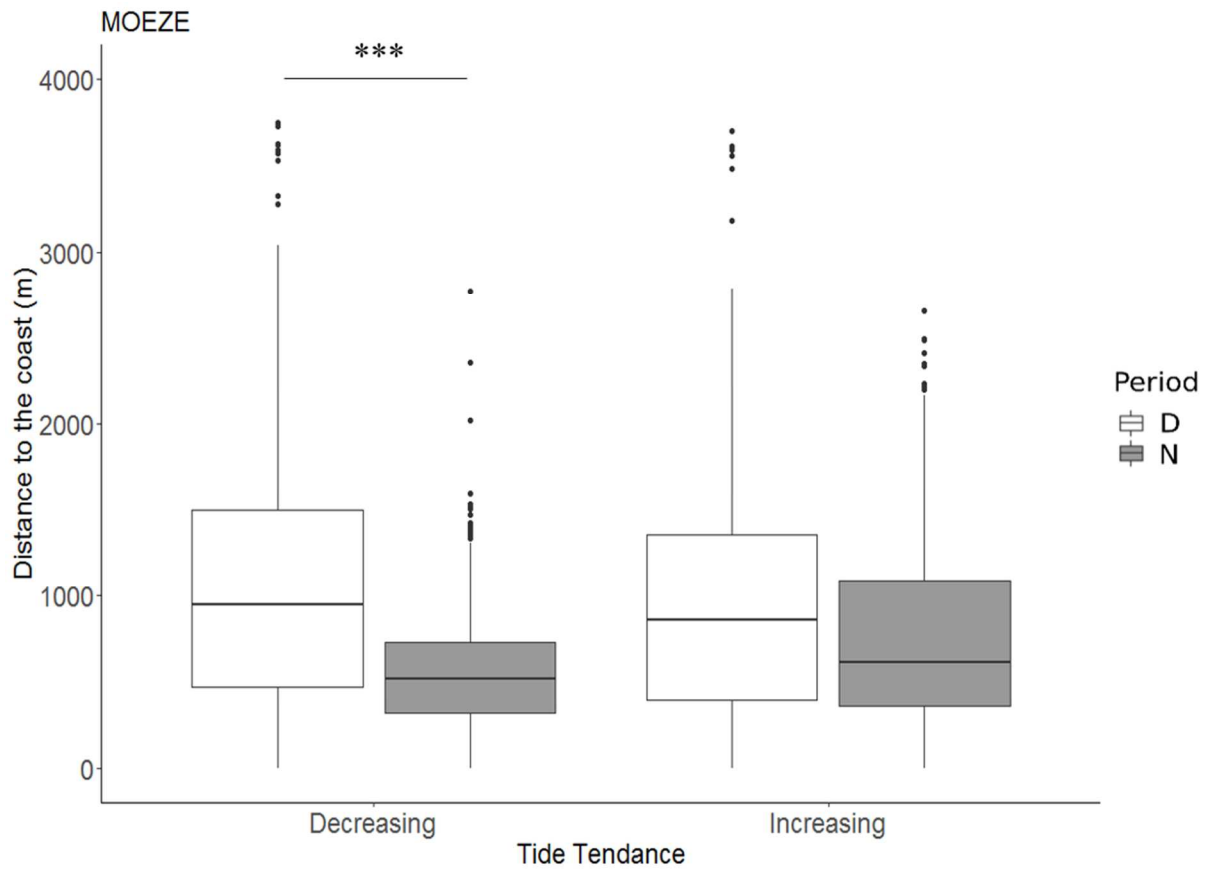


Figure 6

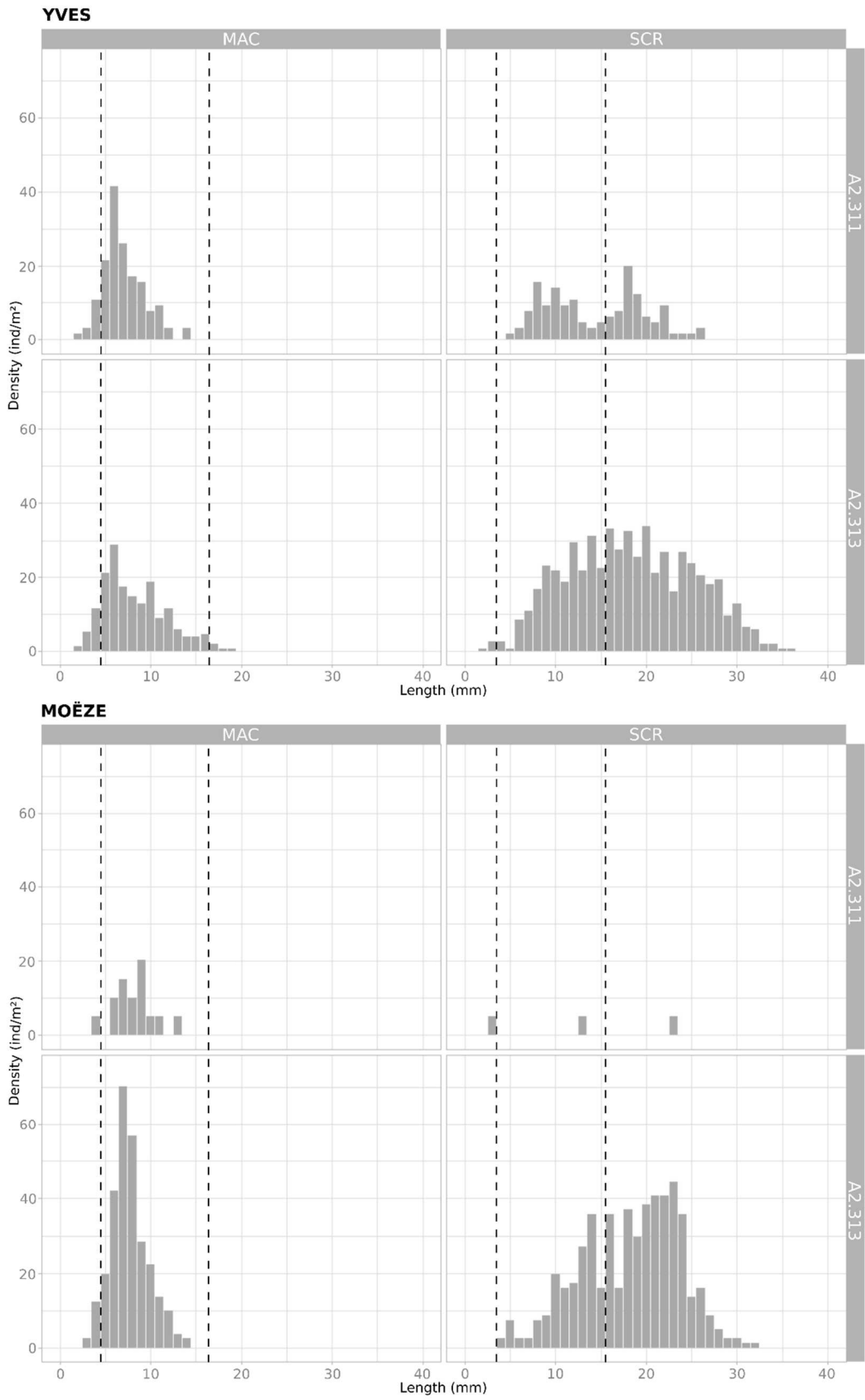


Figure 7