

Habitat features and human presence as predictors of the abundance of shorebirds and wading birds wintering in the Gulf of Gabès, Tunisia

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ABSTRACT: Understanding ecological factors and processes affecting waterbird abundance is a major question in ecology and important for conservation purposes. In the Mediterranean, studies dealing with the determinants of waterbird abundance and distribution have mainly been concerned with European coastal habitats, whereas less attention has been paid to coastal areas in North Africa. In this work, we used count data to investigate the relevance of habitat features and human presence as predictors of the abundance of shorebirds and wading birds wintering in the Gulf of Gabès, a particularly important wintering quarter for many Palearctic waterbirds in Tunisia. We found that the strength and direction of the relationships between bird abundance and both habitat and human parameters varied among species, depending on their ecological requirements. Most species occurred more abundantly in large mudflats compared to narrow sandy beaches, while one species showed an opposite trend. We also found that the studied sites were frequently visited by local people, mainly for clam harvesting, thus sharing the intertidal habitats with birds. However, the abundance of most species did not decrease with increasing human presence, suggesting that traditional clam-harvesting activity did not seem to disturb birds. Nonetheless, we believe that further investigations of the interactions between birds and clam-harvesters are needed to better understand the role of traditional clam-harvesting activity in shaping the abundance and diversity of waterbirds wintering in the Gulf of Gabès.

KEY WORDS: Clam harvesting · Environmental factors · Intertidal area · Tunisia · Waterbirds

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INTRODUCTION

Intertidal habitats are among the most important areas for waterbirds during the wintering period (Zwarts 1988, Goss-Custard & Yates 1992, Lourenço et al. 2013). Many waterbirds depend on these habitats for feeding during low tide, and at high tide they move to roosting sites in supratidal areas (Burger et al. 1977). However, the quality of intertidal habitats in many regions of the world has deteriorated in recent years due to increasing human pressures and activities along coastal areas (Lotze et al. 2006, Kirwan & Megonigal 2013), which constitutes a serious threat against many waterbirds species (Lotze et al. 2006). For conservation purposes,

there is an urgent need to identify and understand the factors affecting waterbird abundance and distribution in these particularly threatened habitats.

It has been argued that the distribution and abundance of waterbirds in intertidal areas are determined by the availability and distribution of their prey (Hicklin & Smith 1984, Kalejta & Hockey 1994, Lunardi et al. 2012). Many habitat features, such as sediment composition, surface of the intertidal area and distribution of tidal channels, are known to strongly affect waterbird abundance through their effects on invertebrate diversity and biomass (Granadeiro et al. 2004, Lourenço et al. 2005, Miller & de Rivera 2014). This relationship has been demonstrated at a broad geographic scale (e.g. Bryant 1979,

Goss-Custard & Yates 1992, Yates et al. 1993, Spruzen et al. 2008), as well as at a small spatial scale of a few meters (e.g. Wilson 1990, Colwell & Landrum 1993). Human presence in intertidal areas can also affect the distribution and abundance of waterbirds by displacing them from preferred feeding areas to areas of poorer quality (Cayford 1993, Goss-Custard & Verboven 1993), which may increase their energy expenditure (Pfister et al. 1992, Navedo & Herrera 2012) and reduce their rate of food intake (Goss-Custard & Verboven 1993).

In the Mediterranean, studies dealing with the determinants of waterbird abundance and distribution have mainly been concerned with European coastal habitats (e.g. Rendón et al. 2008, Liordos 2010). Less attention has been paid to coastal areas in North Africa, despite some particular sites within this geographic region, such as the Gulf of Gabès in southern Tunisia, being particularly important wintering quarters for many Palearctic waterbirds (van Dijk et al. 1986, Spiekman et al. 1993, van der Have et al. 1997, Bos et al. 2001, Isenmann et al. 2005, Hamdi et al. 2008). The coastal area of the Gulf of Gabès supports regionally and internationally significant populations of a wide range of wintering waterbird species with different ecological requirements (van Dijk et al. 1986, Spiekman et al. 1993, van der Have et al. 1997, Bos et al. 2001, Hamdi et al. 2008). Seven sites within this gulf have been recognized as Important Bird Areas (BirdLife International 2015). The most abundant waterbirds typically wintering in the intertidal areas of this gulf are shorebirds and wading birds (van Dijk et al. 1986, Hamdi et al. 2008). These areas are also used by humans, mainly for traditional clam-harvesting and to a less extent for traditional fishing. Artisanal clam-harvesting represents an important economic activity for local people during the winter season. It is usually carried out in the intertidal areas during low tide, which coincides with the period of foraging activity of many waterbirds. However, little is known about the roles of habitat features and human presence in shaping the abundance of waterbirds wintering in the coastal area of the Gulf of Gabès.

In this work, we used count data collected at a large number of sites in the central part of the Gulf of Gabès to investigate the relevance of habitat features and human presence as predictors of the abundance of wintering shorebirds and wading birds. Because the studied species have different ecological requirements, the strength and direction of the relationships between abundance and both habitat and human parameters were expected to vary among species.

MATERIALS AND METHODS

Study area

The study sites were localized in the central part of the Gulf of Gabès, between Kneis Islands (34° 22' N, 10° 15' E) to the north and Boughrara Lagoon (33° 41' N, 10° 40' E) to the south (Fig. 1). This coastal area (~125 km) encompasses a range of intertidal habitats, including notably narrow sandy beaches and large mudflats crossed by tidal channels and wadi estuaries. Fifty sites, distant from each other by 2.5 km, were sampled for waterbird survey and habitat assessment. Site limits were defined using easily recognizable landmarks, such as tidal channels, sandbanks, saltmarsh patches and roads, which allowed us to determine its area.

Data collection

Bird count

Data used in this work were collected between December 10, 2012, and January 31, 2013. All coastal study sites were visited 5 times at different dates. During each visit, the observer (F. Hamza) recorded all birds detected using binoculars and a spotting scope (20 to 60×). Bird counts were repeated many times during 30 min, and the highest recorded number of birds of each detected species was retained. Bird counts usually took place in the morning during low tide and only under suitable meteorological conditions.

For each species, the collected count data (5 count replicates per site) were used to calculate the average number of recorded individuals at each site. This average number was divided by the area of the corresponding site to obtain a density value (expressed as birds km⁻²). The obtained density data were then used in the statistical analyses, but species that were recorded in a low number of sites were excluded from these analyses.

Ecological predictors

Five habitat variables were measured in each sampled site: intertidal flat width (km), tide channel number, seagrass cover (%), mud fraction of the sediment (%) and organic content of the sediment (mg g⁻¹). Most of these parameters have been previously recognized to influence waterbird abundance

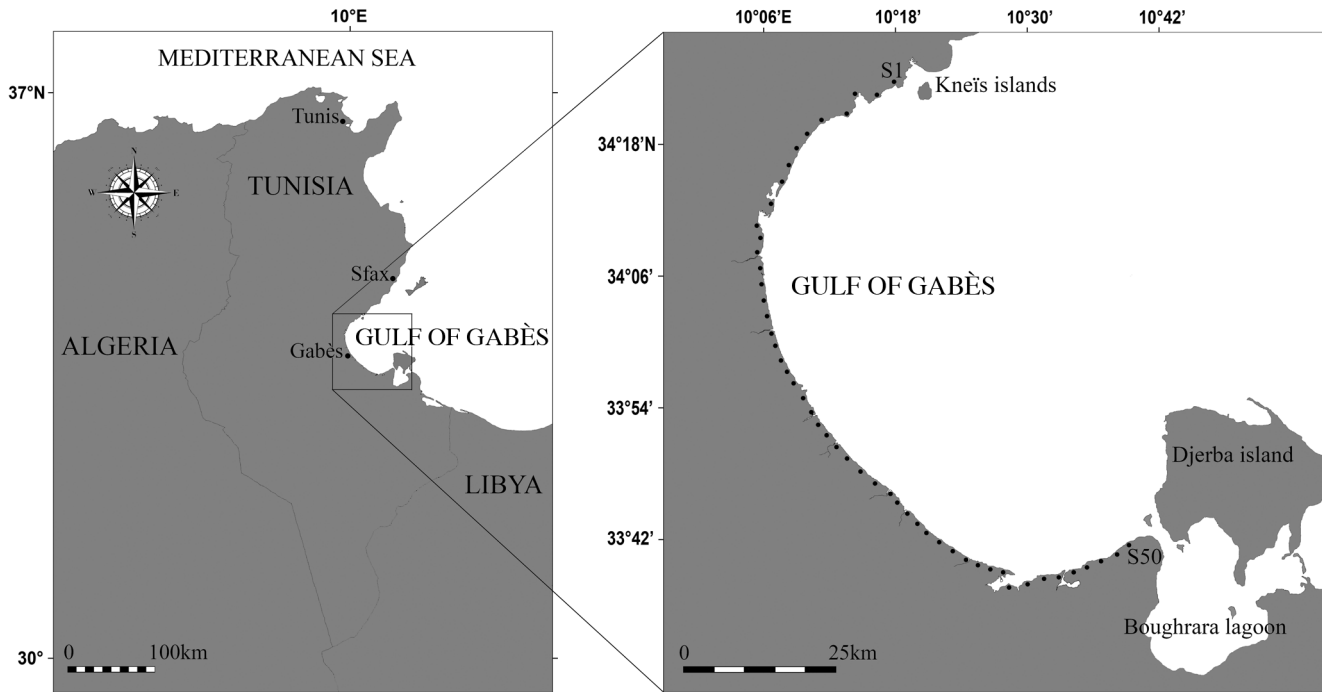


Fig. 1. Gulf of Gabès and location of the study sites (S1 to S50). (•) Sampling site

(Yates et al. 1993, Rosa et al. 2003, Granadeiro et al. 2004, 2007, Lourenço et al. 2005). Intertidal flat width, i.e. the distance between low water and high water, was directly measured in the field during low tide. Three measurement replicates were conducted on 3 transects orientated perpendicular to the shoreline, from high water to low water. Distance between transects was fixed to 400 m. The mean value was then retained. The number of tidal channels was also directly counted on the field and then verified using aerial images. In some sites, tidal channels were highly branched. In this case, major branches (i.e. exceeding approximately 50 m of length) were considered as separate channels. Seagrass cover, i.e. the percentage of intertidal area covered by seagrass, was estimated visually on the field, usually by the same observer (F. Hamza). At each site, we repeated the estimation 5 times, by considering 4 classes: <25%, 25–50%, 50–75% and >75%. The average value of the centers of the 5 obtained classes was then calculated and used as a measure of seagrass cover in the corresponding site.

With regard to sediment, 12 core samples (diameter: 5 cm, depth: 8 cm) were taken from each site: 4 samples were taken on each of the above-described transects. Distance between sampling points along the same transect varied depending on

flat width: 5 m on small beaches, 10 to 100 m in medium-sized flats and 500 m in the largest mudflats. Each collected sediment sample was divided vertically into 2 subsamples. In the laboratory, 1 subsample was used for determining the mud fraction of the sediment, while the second one was used for measuring the organic material. Mud fraction was determined by sieving 20 g of sediment, previously dried at 80°C, through a series of 2, 1, 0.5, 0.25, 0.125 and 0.063 mm meshes. The percent mass of particles whose diameter was less than 63 µm corresponded to the mud fraction of the sediment. To measure the organic content, sediment subsamples were first passed through a 0.5 mm mesh to remove the debris and then dried to constant weight at 90°C, weighed, burnt in a muffle furnace to constant weight at 550°C and reweighed. The difference in weight of the burnt sample from the dried one, expressed as a percentage of the dry weight, was then retained as a measure of the organic sediment content.

During the 5 survey visits, we also recorded the number of people present at each site, which allowed us to determine for each site: (1) the average number of recorded humans, and (2) the percentage of visits during which at least 1 human was recorded as an indicator of the regularity of site use by humans.

Data analyses

Because variables describing habitat features and human presence were highly inter-correlated ($p < 0.05$ in all pairwise correlations), a principal components analysis (PCA) was carried out to reduce them into a few independent factors, using the FACTOR procedure in SAS software (SAS Statistical Institute 1998). Only factors whose eigenvalues were greater than 1 were retained and investigated as possible predictors of the abundances of shorebirds and wading birds by means of multiple regressions. Given that the study units were spatial locations and that a possible problem of spatial auto-correlation may have occurred in the data, the regressions were performed using simultaneous autoregressive models (SAR) that assume that model residuals are correlated and their covariance is a function of the distance between pairs of sites (Kissling & Carl 2008). These spatial analyses were carried out using SAM software 4.0 (Rangel et al. 2006). In these analyses, species' densities were $\log(x+1)$ transformed to ensure normality.

RESULTS

There were important variations in the measured habitat and human parameters among the 50 sampled sites (Table 1). A PCA summarized these variables into 2 independent factors (PC1 and PC2) that accounted together for 70% of the variance in the original data (Fig. 2). PC1 (47% of the original variance) was positively correlated with intertidal flat width, number of tidal channels, seagrass cover, mud content of the sediment and organic matter of the sediment (Table 2, Fig. 2). However, PC2 (23% of the original variance) represents an axis of increasing human presence (Table 2, Fig. 2).

A total of 6 wading bird species and 21 shorebird species were recorded in the entire study area (Table 3). The most abundant species were dunlin (8739 ind.), greater flamingo (6815), Kentish plover (2094), common redshank (2211) and Eurasian cur-

Table 1. Habitat and human variables for the 50 sampled sites

Variable	Range	Mean \pm SE	CV (%)
Habitat variables			
Intertidal area width (km)	0–3.46	0.83 \pm 0.14	123
Sediment mud content (%)	0.04–24.75	4.57 \pm 0.76	118
Sediment organic matter (mg g ⁻¹)	1.18–5.27	2.56 \pm 0.13	36
Number of channels	0–16	3.46 \pm 0.64	132
Seagrass cover (%)	12.50–87.50	35 \pm 4.59	93
Human variables			
Rate of site occupancy by humans (%)	0–100	64.40 \pm 3.3	36
Avg no. of recorded humans per visit	0–39.80	11.82 \pm 1.5	89

Table 2. Pearson correlations and associated p-values of original habitat and human variables with the 2 factors extracted from the principal components analysis. Sample size: 50 sites

Variable	PC1		PC2	
	r	p	r	p
Intertidal area width	0.904	<0.0001	-0.138	0.3409
Sediment mud content	0.819	<0.0001	0.089	0.5410
Sediment organic matter	0.476	0.0006	-0.464	0.0007
Number of channels	0.860	<0.0001	-0.166	0.2509
Seagrass cover	0.839	<0.0001	0.003	0.9820
Rate of site occupancy by humans	0.226	0.1139	0.801	<0.0001
Avg no. of humans per visit	0.269	0.0586	0.842	<0.0001

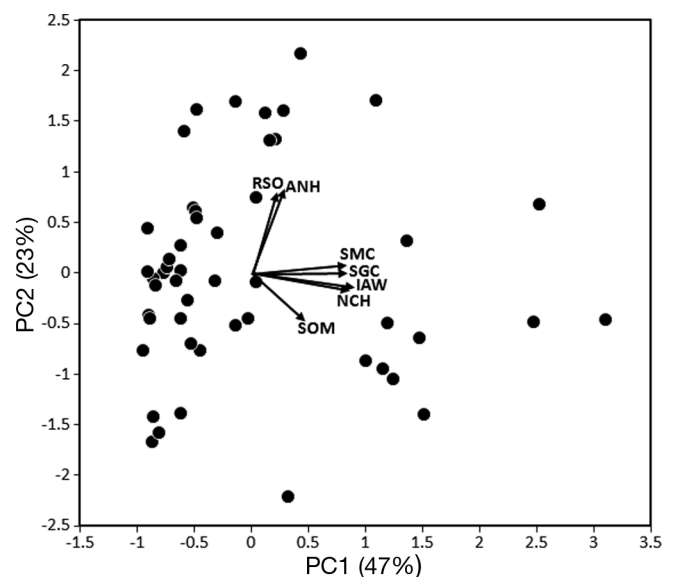


Fig. 2. Principal components analysis showing the relationship of the measured habitat and human variables. Black dots indicate observations. Directions of the arrows indicate positive or negative correlations with each principal component. IAW = intertidal area width; SMC = sediment mud content; SOM = sediment organic material; NCH = number of channels; SGC = seagrass cover; RSO = rate of site occupancy by humans; ANH = average number of humans per visit

Table 3. Recorded species and observed occupancy rates (number of sites where they were observed at least once in 5 visits divided by total number of monitored sites)

Common name	Scientific name	Occupancy rate (%)
Wading birds		
Great egret	<i>Casmerodius albus</i>	34
Little egret	<i>Egretta garzetta</i>	46
Grey heron	<i>Ardea cinerea</i>	72
Eurasian spoonbill	<i>Platalea leucorodia</i>	58
Black stork	<i>Ciconia nigra</i>	2
Greater flamingo	<i>Phoenicopterus roseus</i>	56
Shorebirds		
Water rail	<i>Rallus aquaticus</i>	2
Common moorhen	<i>Gallinula chloropus</i>	4
Eurasian oystercatcher	<i>Haematopus ostralegus</i>	48
Black-winged stilt	<i>Himantopus himantopus</i>	4
Pied avocet	<i>Recurvirostra avosetta</i>	2
Common ringed plover	<i>Charadrius hiaticula</i>	42
Kentish plover	<i>Charadrius alexandrinus</i>	88
Grey plover	<i>Pluvialis squatarola</i>	68
Northern lapwing	<i>Vanellus vanellus</i>	2
Dunlin	<i>Calidris alpina</i>	66
Sanderling	<i>Calidris alba</i>	44
Little stint	<i>Calidris minuta</i>	50
Common snipe	<i>Gallinago gallinago</i>	4
Bar-tailed godwit	<i>Limosa lapponica</i>	2
Eurasian curlew	<i>Numenius arquata</i>	68
Spotted redshank	<i>Tringa erythropus</i>	30
Common redshank	<i>Tringa totanus</i>	30
Marsh sandpiper	<i>Tringa stagnatilis</i>	58
Common greenshank	<i>Tringa nebularia</i>	58
Terek sandpiper	<i>Xenus cinereus</i>	2
Ruddy turnstone	<i>Arenaria interpres</i>	18

low (1054). Among the 27 species, 9 were recorded at few sites (1 to 2 sites) and were excluded from the analyses (Table 3, 'occupancy rate less than 5%').

For 7 species, namely the little egret, grey heron, oystercatcher, Kentish plover, little stint, marsh sandpiper and common greenshank, neither PC1 nor PC2 provided a significant predictor of local density (Table 4). However, the densities of 10 species were significantly correlated with PC1 (Table 4). For 9 species, namely the great egret, Eurasian spoonbill, greater flamingo, grey plover, dunlin, Eurasian curlew, spotted redshank, common redshank and ruddy turnstone, local density was positively correlated with PC1 (Table 4), suggesting that these species occurred more abundantly in large mudflats (high PC1 scores) compared to narrow sandy beaches (low PC1 scores). However, the sanderling showed an opposite trend (Table 4).

Our results also showed that the density of the common ringed plover was positively correlated with PC2, which suggests that this species was attracted to sites frequently used by humans. However, no species showed a significant interaction between the effects of PC1 and PC2.

Table 4. Regression analyses of species density as a function of the 2 factors (PC1 and PC2) derived from the principal components analysis of the original habitat and human variables, using a simultaneous autoregressive model that accounts for spatial autocorrelation in the data. Species abundance was $\log(x + 1)$ transformed. Significant effects indicated in **bold**

Species	R ² (%)	PC1			PC2			PC1 × PC2		
		$\beta \pm SE$	<i>t</i>	<i>p</i>	$\beta \pm SE$	<i>t</i>	<i>p</i>	$\beta \pm SE$	<i>t</i>	<i>p</i>
Great egret	50	0.21 ± 0.31	2.219	0.032	-0.02 ± 0.07	-0.184	0.855	0.01 ± 0.08	0.130	0.897
Little egret	17	0.15 ± 0.20	0.731	0.468	0.12 ± 0.15	0.791	0.433	-0.17 ± 0.18	-0.977	0.334
Grey heron	20	0.02 ± 0.23	0.078	0.939	-0.06 ± 0.17	-0.354	0.725	-0.06 ± 0.20	-0.294	0.770
Eurasian spoonbill	32	0.58 ± 0.19	3.123	0.003	0.14 ± 0.14	1.003	0.321	-0.03 ± 0.16	-0.195	0.846
Greater flamingo	48	1.03 ± 0.30	3.485	0.001	0.39 ± 0.22	1.773	0.083	0.20 ± 0.26	0.800	0.428
Eurasian oystercatcher	34	-0.02 ± 0.23	-0.088	0.930	0.02 ± 0.17	0.107	0.915	0.32 ± 0.20	1.602	0.116
Common ringed plover	32	0.01 ± 0.15	0.066	0.947	0.33 ± 0.11	3.085	0.003	-0.01 ± 0.13	-0.079	0.937
Kentish plover	20	0.01 ± 1.49	0.979	0.333	0.23 ± 0.14	1.626	0.111	-0.06 ± 0.17	-0.337	0.738
Grey plover	47	0.43 ± 0.19	2.232	0.031	0.22 ± 0.14	1.510	0.138	0.11 ± 0.17	0.617	0.540
Dunlin	54	1.09 ± 0.25	4.294	<0.001	0.28 ± 0.19	1.465	0.150	0.05 ± 0.22	0.240	0.812
Sanderling	62	-0.70 ± 0.25	-2.775	0.008	0.12 ± 0.19	0.645	0.522	0.03 ± 0.22	0.128	0.898
Little stint	20	-0.10 ± 0.18	-0.572	0.570	-0.02 ± 0.14	-0.154	0.879	0.01 ± 0.16	0.079	0.937
Eurasian curlew	35	0.51 ± 0.19	2.707	0.010	0.12 ± 0.14	0.870	0.389	0.03 ± 0.17	0.164	0.871
Spotted redshank	41	0.46 ± 0.15	3.168	0.003	-0.10 ± 0.11	-0.924	0.361	0.00 ± 0.13	0.022	0.983
Common redshank	51	1.12 ± 0.21	5.350	<0.001	-0.16 ± 0.16	-1.043	0.303	0.02 ± 0.19	0.116	0.908
Marsh sandpiper	21	0.02 ± 0.16	0.153	0.879	0.17 ± 0.12	1.468	0.149	-0.12 ± 0.14	-0.847	0.401
Common greenshank	26	0.00 ± 0.14	0.006	0.995	0.20 ± 0.10	1.994	0.052	-0.12 ± 0.12	-1.027	0.310
Ruddy turnstone	53	0.13 ± 0.06	2.424	0.019	0.08 ± 0.04	1.968	0.055	0.00 ± 0.05	0.032	0.975

DISCUSSION

The aim of this work was to assess the relevance of habitat features and human presence as predictors of the abundance of shorebirds and wading birds wintering in the Gulf of Gabès, a particularly important waterbird area in the southern Mediterranean (van Dijk et al. 1986, Spiekman et al. 1993, van der Have et al. 1997, Bos et al. 2001, Hamdi et al. 2008). In agreement with previous studies, our results confirmed once again the presence of important international populations of shorebirds and wading birds in the Gulf of Gabès (van Dijk et al. 1986, Isenmann et al. 2005). Indeed, for 5 species, namely the Eurasian spoonbill, greater flamingo, Kentish plover, grey plover and common redshank, the level of the 1% criterion according to the Ramsar Convention was exceeded.

As predicted, we found that the strength and direction of the relationships between bird abundance and both habitat and human parameters varied among species. With regard to the effects of habitat characteristics, most shorebird and wading bird species showed higher abundances in large mudflats compared to narrow sandy beaches, which is consistent with the findings of previous studies conducted in similar habitat systems in different geographic regions (e.g. Zwarts 1988, Goss-Custard & Yates 1992, Congdon & Catterall 1994). This trend seems to be largely due to higher food abundance and availability in large mudflats compared to narrow sandy beaches (Hamza 2011).

In our study area, large mudflats are generally crossed by tidal channels and pools which are constantly immersed, even at low tide, and covered by seagrass (Hamza et al. 2014). In these channels and pools, the sediment is muddy and charged with organic materials. All these parameters are likely to offer suitable habitat conditions for benthic invertebrates (Zweers et al. 1995, Rosa et al. 2003, Granadeiro et al. 2007, Liordos 2010, Miller & de Rivera 2014), increasing the diversity and biomass of prey sought by shorebirds and some wading birds, such as the flamingo and spoonbill. The fact that the sediment was constantly moistened with water likely maintained the activity of invertebrates close to the surface and increased the penetrability of the substrate for the bill, enhancing prey availability for birds (Spruzen et al. 2008). Tidal channels are also known to provide refuges and nursery grounds for many fish species during their early life stages (Shenker & Dean 1979, Reis & Dean 1981, Boesch & Turner 1984, Paterson & Whitfield 2000, Jensen et al.

2007). At low tides, these juvenile fishes are stranded in the tidal channels and pools, providing highly concentrated feeding opportunities for piscivorous wading birds, such as the great egret and spoonbill.

Unlike the other shorebird species, the sanderling was found to avoid large mudflats, occurring more abundantly on narrow sandy beaches. This observation is consistent with the findings of several previous studies in different geographic areas (e.g. Zwarts 1988, Clark et al. 1993, Summers et al. 2002, Granadeiro et al. 2004) and matches the known habitat requirements of this species. Indeed, the sanderling is recognized to be associated with tidal sandy beaches where it feeds on small invertebrates, such as larvae, insects and crustaceans, by pursuing receding waves and snatching items washed in by the tide along wave-break zones (Evans et al. 1980, Reneerkens et al. 2009). Moreover, the little egret, grey heron, Eurasian oystercatcher, Kentish plover, little stint, marsh sandpiper and common greenshank seemed to be less sensitive to habitat features and occurred in large mudflats as well as in small sandy beaches. This observation was expectable for the little egret, grey heron, Eurasian oystercatcher and Kentish plover, which are known to feed in a broad range of habitats (Zwarts 1988, Moreira 1999, Granadeiro et al. 2004, 2007, Ens et al. 2005, Liordos 2010). However, it was surprising that the little stint did not show increased abundance in large mudflats compared to sandy beaches, considering its preference for muddy sediments (Zwarts 1988).

Human presence had no significant effect on 17 species, suggesting that they were not perceived as a threat. Indeed, people encountered in our study area were mainly artisanal clam-harvesters completely indifferent to birds. Most of the waterbirds, notably small species, seemed to be habituated to their presence and did not appear to perceive them as predators. Previous studies have also shown that the disturbance of waterbirds was mainly due to people engaged in recreational activities and/or accompanied by domestic animals (Navedo & Herrera 2012, Lafferty et al. 2013, Martín et al. 2015). Furthermore, because birds mainly occurred on large mudflats, they could position themselves far away from humans, decreasing disturbance. Other studies have also shown that the disturbing effect of human presence mainly occurs on narrow beaches (Lafferty et al. 2013, Martín et al. 2015). In contrast, the abundance of the common ringed plover showed positive associations with the intensity of human presence. Similar but less significant trends were also observed for the common greenshank and ruddy turnstone. It seems

that these species benefitted from clam-harvesting activity, as sediment flipping may make invertebrates more available (Lunardi & Macedo 2014). Alternatively, it could be that these bird species simply shared habitats with clam harvesters, with little direct influence of clam harvesters on the birds.

Overall, the results of this study increase our understanding of the factors shaping the abundance of waterbirds wintering in the Gulf of Gabès. Large mudflats most likely represent key areas for wintering shorebirds and wading birds in this region. Within these sites, the birds seem to share habitats with clam harvesters without any noticeable prejudice. These particular sites should receive special priority and protection efforts if we are to preserve the diversity of waterbirds wintering in the Gulf of Gabès. However, other types of threats seem to be more critical for wintering waterbirds in this area, notably water and sediment pollution through the huge quantities of phosphogypsum released by the Gabès-Ghannouche factory complex for phosphate treatment for fertilizer and acid production. Indeed, during the first 20 yr following the installation of this factory complex (in the early 1970s), approximately 50 million tons of phosphogypsum were discharged into the sea (Guillaumont et al. 1995). According to Bejaoui et al. (2004), 1250 tons of phosphogypsum are released into the Gulf of Gabès per day. Recent studies have shown the accumulation of heavy metals in various invertebrates inhabiting this coastal area (Bouraoui et al. 2010, Rabaoui et al. 2014), which is likely to increase the risk of negative impact on waterbirds. However, further detailed investigations are needed to assess the impact of habitat pollution on waterbirds wintering in this area. Such investigations are essential for understanding the complexity of ecological and anthropogenic factors affecting waterbirds in this wintering area, which should allow setting up an effective management plan for the sustainable conservation of this avifauna.

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LITERATURE CITED

- Bejaoui B, Rais S, Koutitonsky V (2004) Modélisation de la dispersion du phosphogypse dans le golfe du Gabès. *Bull Inst Natl Sci Tech Mer Salammbô* 31:103–109
- BirdLife International (2015) Country profile: Tunisia. www.birdlife.org/datazone/country/tunisia (accessed on July 1, 2015)
- Boesch DF, Turner RE (1984) Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* 7: 460–468
- Bos JFP, van der Geest GM, Gilissen NLM, Pahlplatz R, Essetti I, Ayache F (2001) Waterbirds in the Gulf of Gabès and other wetlands in Tunisia, autumn 1999. WIWO Rep 74. Working Group International Waterbird and Wetland Research (WIWO), Zeist
- Bouraoui Z, Banni M, Chouba L, Ghedira J and others (2010) Monitoring pollution in Tunisian coasts using a scale of classification based on biochemical markers in worms *Nereis (Hediste) diversicolor*. *Environ Monit Assess* 164: 691–700
- Bryant DM (1979) Effects of prey density and site character on estuary usage by overwintering waders (Charadrii). *Estuar Coast Shelf Sci* 9:369–384
- Burger J, Howe M, Hahn D, Chase J (1977) Effects of tide cycles on habitat selection and habitat partitioning by migrating shorebirds. *Auk* 94:743–758
- Cayford J (1993) Wader disturbance: a theoretical overview. *Wader Study Group Bull* 68:3–5
- Clark KE, Niles LJ, Burger J (1993) Abundance and distribution of migrant shorebirds in Delaware Bay. *Condor* 95: 694–705
- Colwell MA, Landrum SL (1993) Nonrandom shorebird distribution and fine-scale variation in prey abundance. *Condor* 95:94–103
- Congdon BC, Catterall CP (1994) Factors influencing the Eastern Curlew's distribution and choice of foraging sites among tidal flats of Moreton Bay, south-eastern Queensland. *Wildl Res* 21:507–518
- Ens BJ, Brinkman AG, Dijkman EM, Meesters HWG, Kersten M, Brenninkmeijer A, Twisk F (2005) Modelling the distribution of waders in the Westerschelde: What is the predictive power of abiotic variables? Alterra Report, Wageningen
- Evans PR, Breary DM, Goodyer LR (1980) Studies on Sanderling at Teesmouth, NE England. *Wader Study Group Bull* 30:18–20
- Goss-Custard JD, Verboven N (1993) Disturbance and feeding shorebirds on the Exe estuary. *Wader Study Group Bull* 68:59–66
- Goss-Custard JD, Yates MG (1992) Towards predicting the effect of salt-marsh reclamation on feeding bird numbers on the wash. *J Appl Ecol* 29:330–340
- Granadeiro JP, Andrade J, Palmeirim JM (2004) Modeling the distribution of shorebirds in estuarine areas using generalized additive models. *J Sea Res* 52:227–240
- Granadeiro JP, Santos CD, Dias MP, Palmeirim JM (2007) Environmental factors drive habitat partitioning in birds feeding in intertidal flats: implications for conservation. *Hydrobiologia* 587:291–302
- Guillaumont B, Ben Mustapha S, Ben Moussa H, Zaouali J, Soussi N, Ben Mammou A, Cariou C (1995) Pollution impact study in Gabès Gulf (Tunisia) using remote sensing data. *Mar Technol Soc J* 29:46–58
- Hamdi N, Charfi-Cheikhrouha F, Moali A (2008) Le peuplement des oiseaux aquatiques hivernant du Golfe de Gabès (Tunisie). *Bull Soc Zool Fr* 133:267–275
- Hamza F (2011) Contribution à l'étude de l'hivernage du Flamant rose (*Phoenicopterus roseus*) dans le Golfe de Gabès. MSc thesis, Carthage University, Bizerte
- Hamza F, Hammouda A, Chokri MA, Bechet A, Selmi S (2014) Distribution et abondance du flamant rose *Phoenicopterus roseus* hivernant dans la zone centrale du golfe

- de Gabès, Tunisie. *Alauda* 82:135–142
- Hicklin PW, Smith PC (1984) Choice of foraging sites and invertebrate prey by migrant semi-palmated sandpipers *Calidris pusilla* (Pallas) in Minas Basin, Bay of Fundy. *Can J Zool* 62:2201–2211
 - Isenmann P, Gaultier T, El Hili A, Azafaf H, Dlensi H, Smart M (2005) Oiseaux de Tunisie. Birds of Tunisia. Société d'Études Ornithologiques de France, Muséum Naturelle d'Histoire Naturelle, Paris
 - Jensen SI, Kühl M, Priemé A (2007) Different bacterial communities associated with the roots and bulk sediment of the seagrass *Zostera marina*. *FEMS Microbiol Ecol* 62: 108–117
 - Kalejta B, Hockey PAR (1994) Distribution of shorebird at the Berg River estuary, South Africa, in relation to foraging mode, food supply and environmental features. *Ibis* 136:233–239
 - Kirwan ML, Megonigal JP (2013) Tidal wetland stability in the face of human impacts and sea-level rise. *Nature* 504: 53–60
 - Kissling WD, Carl G (2008) Spatial autocorrelation and the selection of simultaneous autoregressive models. *Glob Ecol Biogeogr* 17:59–71
 - Lafferty KD, Rodriguez DA, Chapman A (2013) Temporal and spatial variation in bird and human use of beaches in southern California. *SpringerPlus* 2:38
 - Liordos V (2010) Foraging guilds of waterbirds wintering in a Mediterranean coastal wetland. *Zool Stud* 49:311–323
 - Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH and others (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806–1809
 - Lourenço PM, Granadeiro JP, Palmeirim JM (2005) Importance of drainage channels for waders foraging on tidal flats: relevance for the management of estuarine wetlands. *J Appl Ecol* 42:477–486
 - Lourenço PM, Catry P, Lecoq M, Ramirez L, Granadeiro JP (2013) Role of disturbance, geology and other environmental factors in determining abundance and diversity in coastal avian communities during winter. *Mar Ecol Prog Ser* 479:223–234
 - Lunardi VO, Macedo RH (2014) Shorebirds can adopt foraging strategies that take advantage of human fishing practices. *Emu* 114:50–60
 - Lunardi VO, Macedo RH, Granadeiro JP, Palmeirim JM (2012) Migratory flows and foraging habitat selection by shorebirds along the northeastern coast of Brazil: the case of Baía de Todos os Santos. *Estuar Coast Shelf Sci* 96:179–187
 - Martín B, Delgado S, Cruz A, Tirado S, Ferrer M (2015) Effects of human presence on the long term trends of migrant and resident shorebirds: evidence of local population declines. *Anim Conserv* 18:73–81
 - Miller AK, de Rivera CE (2014) Small tidal channels improve foraging opportunities for *Calidris* shorebirds. *Condor* 116:113–121
 - Moreira F (1999) On the use by birds of intertidal areas of the Tagus estuary: implications for management. *Aquat Ecol* 33:301–309
 - Navedo JG, Herrera AG (2012) Effects of recreational disturbance on tidal wetlands: supporting the importance of undisturbed roosting sites for waterbird conservation. *J Coast Conserv* 16:373–381
 - Paterson AW, Whitfield AK (2000) Do shallow-water habitats function as refugia for juvenile fishes? *Estuar Coast Shelf Sci* 51:359–364
 - Pfister C, Harrington BA, Lavine M (1992) The impact of human disturbance on shorebirds at a migration staging area. *Biol Conserv* 60:115–126
 - Rabaoui L, Balti R, Zrelli R, Tlig-Zouari S (2014) Assessment of heavy metals pollution in the gulf of Gabes (Tunisia) using four mollusk species. *Mediterr Mar Sci* 15:45–58
 - Rangel TFLVB, Diniz-Filho JAF, Bini LM (2006) Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Glob Ecol Biogeogr* 15: 321–327
 - Reis RR, Dean JM (1981) Temporal variation in the utilization of an intertidal creek by the Bay Anchovy (*Anchoa mitchilli*). *Estuaries* 4:16–23
 - Rendón MA, Green AJ, Aguilera E, Almaraz P (2008) Status, distribution and long-term changes in the waterbird community wintering in Doñana, south-west Spain. *Biol Conserv* 141:1371–1388
 - Reneerkens J, Benhoussa A, Boland H, Collier M and others (2009) Sanderlings using African–Eurasian flyways: a review of current knowledge. *Wader Study Group Bull* 116:2–20
 - Rosa S, Palmeirim JM, Moreira F (2003) Factors affecting waterbird abundance and species richness in an increasingly urbanized area of the Tagus estuary in Portugal. *Waterbirds* 26:226–232
 - SAS Statistical Institute (1998) SAS/STAT user's guide, version 8. SAS Statistical Institute, Cary, NC
 - Shenker JM, Dean JM (1979) The utilization of an intertidal salt marsh creek by larval and juvenile fishes: abundance, diversity and temporal variation. *Estuaries* 2: 154–163
 - Spiekman HW, Keijl GO, Ruiters PS (1993) Waterbirds in the Kneiss area and other wetlands, Tunisia, Eastern Mediterranean Wader Project, Spring 1990. WIWO Rep 38. Working Group International Waterbird and Wetland Research (WIWO), Zeist
 - Spruzen FL, Richardson AMM, Woehler EJ (2008) Influence of environmental and prey variables on low tide shorebird habitat use within the Robbins Passage wetlands, North Tasmania. *Estuar Coast Shelf Sci* 78:122–134
 - Summers RW, Underhill LG, Simpson A (2002) Habitat preferences of waders (Charadrii) on the coast of the Orkney Islands. *Bird Study* 49:60–66
 - van der Have M, Baccetti N, Keijl O, Zenatello M (1997) Waterbirds in Kneiss, Tunisia February 1994. WIWO Rep 54. Working Group International Waterbird and Wetland Research (WIWO), Zeist
 - van Dijk AJ, van Dijk K, Dijksten LJ, Van Spanje TM, Wymenga E (1986) Wintering waders and waterfowls in the gulf of Gabes, Tunisia, January–March 1984. WIWO Rep 11. Working Group International Waterbird and Wetland Research (WIWO), Zeist
 - Wilson WH Jr (1990) Relationship between prey abundance and foraging site selection by semipalmated sandpipers on a Bay of Fundy mudflat. *J Field Ornithol* 61:9–19
 - Yates MG, Goss-Custard JD, McGrorty S, Lakhani KH and others (1993) Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. *J Appl Ecol* 30:599–614
 - Zwarts L (1988) Numbers and distribution of coastal waders in Guinee-Bissau. *Ardea* 76:42–55
 - Zweers G, De Jong F, Berkhoudt H, Vanden Berge JC (1995) Filter feeding in flamingos (*Phoenicopterus ruber*). *Condor* 97:297–324