Interspecific variations in shorebird responses to management practices on protected Mediterranean saltpans

Jean-Yves J.-Y. Barnagaud, Julien Papaix, Aurélien Audevard, Matthieu Lascève, Stanislas Wroza, David Geoffroy

HAL Id: hal-02625913
https://hal.inrae.fr/hal-02625913

Submitted on 25 Oct 2021

Interspecific variations in shorebird responses to management practices on protected

Mediterranean saltpans.

Authors

Jean-Yves Barnagaud[1]

Julien Papaïx[2]

Aurélien Audevard [3]

Matthieu Lascève[4]

Stanislas Wroza[1]

David Geoffroy[5]

[1] Centre d'Écologie Fonctionelle et Évolutive – UMR 5175 CEFE, CNRS, PSL Research

University, EPHE, UM, SupAgro, IND, INRA, 1919 route de Mende, Montpellier, France.

[2]Biostatistiques et Processus Spatiaux, INRA, Avignon, France.

[3]Ligue pour la Protection des Oiseaux PACA, 6 Avenue Jean Jaurès, 83400 Hyères, France

[4]Métropole Toulon Provence Méditerranée, site des Salins d'Hyères, 1746 Route de Giens,

Hyères, France

[5]Parc national de Port-Cros, 181 allée du Castel Sainte Claire, BP 70220, Hyères, France.

Corresponding author: jean-yves.barnagaud@cefe.cnrs.fr

1   **Interspecific variations in breeding waterbird responses to management practices on**

2   **protected Mediterranean saltpans.**

3

4   **Keywords:**

5   bayesian hierarchical model, gulls, population dynamics, Ramsar convention, salinity, water

6   levels, waterbirds, wetlands

7

8 **Abstract**

9

10 Tidal habitats sustain fragile ecosystems, undergoing pressures from coastal artificialization

11 and rising sea levels. Saltpans are a substitution habitat for birds that breed, winter or stop-

12 over along coastlands where most pristine tidal habitats have been removed. Balancing the

13 economical, patrimonial and biodiversity values of former saltpans is thus needed to

14 mitigate the threats posed by global changes on waterbirds. In this study, we scrutinized the

15 influence of management practices on waterbirds on two isolated saltpans located on the

16 French Mediterranean shore, several tens of kilometres apart from other suitable habitats.

17 We analysed three years of bird counts for nine protected species that breed, forage and

18 roost on these saltpans. We used a multispecies hierarchical model to relate variations in

19 bird counts to water levels, oxygenation and salinity, the three parameters targeted by the

20 saltpans management plan to promote bird settlement. We showed that the hypersaline

21 conditions that dominate in these saltpans are suboptimum to most species, suggesting that

22 waterbird concentrations are dictated by the lack of alternatives in the surrounding

23 landscape rather than by habitat suitability. Intraspecific variations in species' responses to

24 these variables should orient towards the creation of a habitat mosaic within the saltpans.

25 Eventually, between-site differences in bird responses to water conditions pointed the

26 effects of disturbance, predation and other landscape-level features. Our results reveal that

27 high waterbird numbers on isolated saltpans may be a misleading measure of their

28 ecological suitability, and that management on these sites needs to incorporate conflicts and

29 complementarity in species' habitat use.

30

31 **Introduction**

32

33 Wetlands, among the most biodiverse ecosystems on earth, sustain a wide range of essential

34 ecosystem services such as harvesting and fishing, water purification, floods buffering and

35 mitigation of catastrophic climatic events (Zedler & Kercher, 2005; Gardner *et al.*, 2015;

36 Montanarella *et al.*, 2018; Ramsar Convention on Wetlands, 2018). They also provide habitat

37 and resources for a high diversity of organisms organized into trophically complex

38 ecosystems. Although considered as foreground habitats for conservation and human

39 welfare, the global surface of wetlands has been reduced by 35% between 1970 and 2015

40 under various pressures, among which climate change and human land use are especially

41 prominent (Barbier *et al.*, 2011; Gardner *et al.*, 2015; Ramsar Convention on Wetlands,

42 2018). Wetlands are restricted in surface, highly unstable due to variations in water levels

43 and quality, and thus vulnerable to even small levels of disturbance (Adam, 2002; Kirwan &

44 Megonigal, 2013). Appropriate conservation effort is therefore needed to warrant the

45 maintenance of wetland-related ecosystems, and requires in-depth studies to evaluate the

46 effects of water management practices on targeted species (Clausen *et al.*, 2013).

47

48 Coastal wetlands are highly productive, yet unstable ecosystems with site-specific dynamics

49 tied to variations in sea levels, balance of freshwater and saltwater, and human usage

50 (Adam, 2002). The vulnerability of coastal wetlands facing rising sea levels as a result of

51 ongoing climate change is listed as one of the most severe threats to coastal biodiversity in

52 the coming decades (Boesch, 2000; Craft *et al.*, 2009; Hoegh-Guldberg & Bruno, 2010).

53 However, coastal wetlands are more immediately threatened by human land use, which

54   accounts for 25-50% of the decrease in their global surface cover during the past centuries

55   through direct destruction, draining for agriculture or urbanization, eutrophication, invasive

56   species and water pollution (Gedan *et al.*, 2009; Deegan *et al.*, 2012; Kirwan & Megonigal,

57   2013). As a result, many coastal wetlands are now restricted to small isolated patches of

58   marshy habitats within deeply man-modified seashores, some of which are maintained

59   artificially by conservation-oriented management, especially in northern America, western

60   Europe, and locally elsewhere (Hughes & Paramor, 2004).

61

62   Most waterbirds (mainly Charadriidae, Scolopacidae, Laridae and a few other related

63   families ; Burger & Olla, 1984) are strict invertebrate eaters or piscivores, and thus occupy a

64   top-position in trophic networks that make them suitable indicators to monitor the

65   functioning of coastal wetland ecosystems (Piersma *et al.*, 2004). Because most waterbirds

66   are migratory, the preservation of their breeding, stop-over and wintering habitats all along

67   migration routes is critical to their regional or global population persistence (Piersma *et al.*,

68   2006), for instance along the Pacific north-american coast (Velasquez, 1992), in southeastern

69   Asia (Sripanomyom *et al.*, 2011; Xia *et al.*, 2017) or on Mediterranean shores (AEWA, 2018;

70   Giosa *et al.*, 2018). Along these coasts, suitable wetlands are small and rare due to

71   topographic constraints and intense human land use (Myers, 1983; Piersma *et al.*, 2006). As

72   a consequence of climate change-induced erosion of coastal marshes and habitat loss

73   (Ramírez *et al.*, 2018), waterbird conservation thus largely benefits from the maintenance of

74   appropriate resources in artificial wetlands such as fishponds and saltpans (Velasquez, 1992;

75   Takekawa *et al.*, 2006; Giosa *et al.*, 2018). It is therefore of paramount importance to assess

76 carefully the conservation value of saltpan management practices in relation to waterbird

77 habitat and trophic requirements.

78

79 Mudflat-feeding waders (Charadriidae and Scolopacidae) account for a large proportion of

80 waterbirds biomass and thus bear a strong role on tidal trophic networks, in addition to their

81 high patrimonial value associated with hunting, conservation status and legal use as

82 indicator species (Colwell, 2010). These small-bodied species cannot cope with large

83 variations in water depth, which therefore determine habitat availability. Furthermore, the

84 abundance and quality of their invertebrate preys peaks in mesohaline waters with high

85 oxygenation levels (Velasquez, 1992; Takekawa *et al.*, 2006; Dias, 2009; Athearn *et al.*, 2012).

86 These conditions are specifically met in saltpans, in which water levels, variations in

87 physiochemical conditions and other sources of disturbance are buffered artificially by

88 hydraulic control, rendering these artificial saltmarshes suitable for high waterbird

89 concentrations (Velasquez, 1992; Sánchez *et al.*, 2006; Takekawa *et al.*, 2006).

90

91 Because waterbird numbers and diversity decrease in hypersaline conditions, the suitability

92 of saltpans to birds is conditioned to the maintenance of optimum physicochemical

93 conditions (Warnock *et al.*, 2002). Gulls (Laridae) and terns (Sternidae) breeding on saltpans

94 nest on small islets or dykes, as a substitution to sandpits or other coastal habitats subjected

95 to erosion and human disturbance (Catry *et al.*, 2004). By contrast with waders, these birds

96 benefit from higher water levels that isolate their breeding sites from predators (Warnock *et*

97 *al.*, 2002; Bluso-Demers *et al.*, 2016), although gulls also require mudflats for feeding.

98 Waterbird conservation on saltpans therefore need to accommodate conflicts in species'

99   habitat and resource requirements, which, in most instances, can only be done through

100   hydraulic management of water level and flow.

101

102   A major axis of the western Palearctic migration flyway crosses the western Mediterranean

103   on the French coast between the Rhône river and the foothills of the French Alps (Newton,

104   2003). Wetlands located in this area are therefore enlisted in the Ramsar convention among

105   priority sites for the conservation of migrating and breeding waterbirds at the scale of

106   Western Europe (Sadoul & Walmsley, 2000). Most suitable habitats have, however, been

107   eliminated by land artificalization. The two remaining significant wetlands along this stretch

108   of coast are the Camargue and, 120 km farther east, a small complex of two former saltpans

109   located three kilometers apart of each other on the highly urbanized Hyères peninsula. This

110   small isolated site has therefore become the only substantial habitat patch for waterbirds at

111   the eastern limit of the French Mediterranean shore and is an important breeding area for

112   several species of conservation concern at the national or regional scale, such as Kentish

113   Plover (Charadrius alexandrinus) and Black-headed Gull (Chroicocephalus ridibundus).

114   However, in spite of the essential role of these saltpans for bird conservation, an evaluation

115   of management practices still needs to determine whether local water management

116   adequately balances the species' ecological requirements according to their various habitat

117   uses.

118

119   We therefore framed a study on the following question: how do breeding shorebirds

120   respond to management practices in this isolated protected coastal wetland? The critical

121   importance of this site for coastal wetland breeders and migrants, the lack of any alternative

122   habitat for breeding birds around this point of the Mediterranean coast, and the strong

123   pressure from surrounding urbanization, are exemplary to evaluate the conservation value

124   of local saltpan management practices. Additionally, the absence of any substantial patch of

125   alternative habitat within a 100 km radius of dry and artificialized coast concentrates birds

126   inside this specific site, ensuring that once accounted for seasonal phenology, their

127   abundance variations are dictated by local conditions only. However, breeding species have

128   conflicting requirements, since colonial nesters (such as terns and gulls) favour high water

129   levels to ensure protection against predation pressure and feed on water, while waders

130   require large extents of emerged mudflats to forage on ground.

131

132   We specifically addressed three questions: (i) are bird counts high because water levels and

133   physiochemical properties encompass species' optimum values, or because of the lack of

134   alternative sites? (ii) do species with different habitat and trophic requirements respond

135   synchronically or idiosyncratically to variations in water physiochemical parameters? (iii) to

136   what extent are species' responses dictated by the way birds use these two saltpans? We

137   addressed these questions through a three-years monitoring based on decadal bird counts,

138   concentrating on nine breeding species prioritized by the site management plan. We

139   focused on variations in water levels, salinity and oxygen concentration, which are identified

140   as the most limiting physicochemical variables for waterbirds frequenting saltpans (Warnock

141   *et al.*, 2002; Takekawa *et al.*, 2006, 2015).

142

143   **Material and methods**

144

145   *Study area*

146

147   The study site comprises two former saltpans (hereafter "Pesquiers" and "Vieux Salins")

148   located three kilometres apart in a small peninsula of the eastern French Mediterranean

149   coast (43°05'N ; 006°11'E , Fig. 1), property of the Conservatoire du Littoral, a French agency

150   for the protection of coastal habitats. It is enlisted in the Ramsar convention (criterion 2:

151   supports vulnerable species ; criterion 3: supports populations of animal species important

152   for maintaining the biological diversity of the biogeographic region ; criterion 4: supports

153   animal species at a critical stage in their life cycles, or provides refuge during adverse

154   conditions ; Ramsar Convention, 1971).

155

156   The closest substantial site offering permanently suitable conditions for waterbirds is the

157   Camargue (>19000 ha of protected area, 120 km to the west). Our study site is therefore a

158   small islet of protected wetlands which warrants a resting, breeding and feeding area to

159   waterbirds throughout the year in an otherwise unsuitable landscape matrix formed by low

160   dry mountains and a heavily urbanized coast. Both saltpans are strictly closed to the public

161   and are protected as part of Port Cros National Park, which prevents any kind of exploitation

162   or human activities unrelated to biodiversity protection. Management is largely dedicated to

163   bird breeding and is ensured by fieldworkers from the municipality.

164

165   The Pesquiers (Fig. 1c) are a 650 ha saltpan located on a narrow sandy peninsula and used

166   for commercial exploitation from 1848 to 1995. It consists in a single large unit comprising

167   32 ponds (average surface 14.9 ha ± 22.3 ha, all uncertainties in standard deviation units

168   unless otherwise stated), close to or below the sea level (-1.19 to +0.6 m depending on

169   ponds). Hydraulic pumps and sluice gates distribute water across the ponds from a belt canal

170   connected to the adjacent sea, and the saltpan is encircled by a road. Dykes separating the

171   ponds are covered by sparse herbaceous vegetation and scattered bushes.

172

173   The Vieux Salins (Fig. 1d) are located inland in a less urbanized area bordered by vineyards

174   and fields at its northern end; the southern end is separated from the coast by a tree hedge

175   and a track. They cover a smaller extent (350 ha) with 34 ponds that result from the

176   grouping of several old familial units exploited from the 13rd century to 1995 (7.19 ha ± 5.46

177   ha). The ponds are mostly above the sea level (from -0.7 to +1.7 m); hydraulic pumps are

178   used to supply and distribute water from the adjacent sea, and sluice gates regulate water

179   flow inside ponds. The dykes and immediate surroundings are covered by a continuous

180   herbaceous cover with scattered bushes and small woods.

181

182   Modulations of water levels and flow are decided by the site manager on a day-to-day basis

183   and operated by local technicians. These controlled variations aim to secure the settlement

184   of breeding birds, trying to balance the requirements of foraging waders and those of other

185   species, with a specific focus on gull-tern colonies and Kentish Plover (Charadrius

186   alexandrinus, listed as vulnerable at a national level, Appendix S1, Table S1.1). On both sites,

187   the control of water levels is mainly limited by pump flow and tide ; desired levels are usually

188   reached within a few hours, up to a day. Shallow water enters the circuit only through

189   infiltrations, precipitations and casual drainage from surrounding hills after floods.

190

191   *Bird data*

192

193   Standardized bird counts have been performed on all the ponds of the two saltpans since

194   2005, but we restricted the dataset to the 12 ponds (7 on Vieux Salins and 5 on Pesquiers)

195   and three years (2014-2016) with complete physicochemical records (Fig. 1); these ponds

196   account for 62% of all bird counts for the species and years considered (from 32%, Little Tern

197   to 82%, Kentish Plover). Counts were performed by a trained ornithologist, on a weekly

198   (April-September) or ten-days (October-March) basis, at strategic locations maximizing

199   coverage along a standardized 77 km track covering all ponds within the two sites. Counts

200   started at sunrise and the whole track was sampled in a single day, usually in five hours. All

201   birds seen or heard were recorded, except flyovers or birds flying from a pond to another.

202   Bird flocks usually stayed together and remained well identifiable, allowing the observer to

203   minimize the risk of double counts. Counts were not replicated, but all species considered in

204   the studies feed on well-visible bare ground, mudflats or low waters, ensuring near-

205   exhaustive detection and counts. Identification errors were unlikely given the commonness

206   and overall low diversity of targeted species.

207

208   We focused on nine protected waterbird species specifically targeted by the saltpans

209   management plan due to their French and regional conservation status (species list,

210   conservation status, mean counts per site and number of pairs in Appendix S1, Table S1.1).

211   All but Greater Flamingo breed on at least one of the two saltpans, and all are regularly

212   present and forage onsite, although terns also fish at sea. All the species are at least partly

213   migratory or erratic in winter : for each species, we therefore limited our study to the period

214   corresponding to 95% of its annual counts to distinguish absences due to species' phenology

215   from temporary absences resulting from local environmental conditions (Appendix S1, Table

216   S1.1: "Period of inclusion"). So doing, we also eliminated casual counts of late or early

217   migrants.

218

219   *Physicochemical variables*

220

221   Three physicochemical variables have been monitored since 2014 by the reserve's

222   fieldworkers every 15 days at 14 fixed sampling points (nine on Pesquiers, five on Vieux

223   Salins, Fig. 1c,d), alternating each saltpan on a weekly basis (quantitative summary in

224   Appendix S1, Table S1.2 and Fig.S1.1). Some sampling events were offset by a few days in

225   case of bad weather, and 2% of the recordings could not be performed due to persisting

226   unsuitable weather or device breakdowns. Water level (cm) corresponded to the height of

227   the water column and was measured to the nearest cm using permanent limnimetric scales.

228   Salinity was measured to the nearest $g.L^{-1}$ with a probe (Consort C562, probe SK23T) up to its

229   saturation level (120 $g.L^{-1}$). Higher concentrations (20% of the recordings) needed to be

230   measured by a mechanical densimeter which was not systematically used by field

231   technicians for practical reasons: we therefore truncated all salinity measurements to 120

232    $g.L^{-1}$. Oxygen concentration was measured with a probe (Consort C562, probe SZ10T-PB) to

233   the nearest 10^{-4} mg.L^{-1}. These three variables were uncorrelated (R^2 from 0.08 to 0.05).

234   Physicochemical measurements and bird counts were not performed simultaneously; we

235   therefore matched each bird count with the closest measurement event (mean offset = 0 ± 2

236   days, from -6 (1 sample) to +6 (1 sample) days).

237

238   *Statistical Analyses*

239

240   We related species' abundances to variations in water levels, salinity and oxygen

241   concentration with a hierarchical autoregressive generalized linear model implemented in a

242   bayesian framework (Royle & Dorazio, 2008; Kery & Royle, 2015). We modelled species

243   counts $N_{i,t,k,s}$ of species (s) at monitoring event (t), year (k) and pond (i) as a Poisson

244   distribution with mean $\lambda_{i,t,k,s}$:

245    $N_{i,t,k,s} \sim Poisson\left(\lambda_{i,t,k,s}\right)$ (1)

246   We predicted λ with a pond-varying intercept (α), saltpan-specific linear (β) and quadratic (Υ)

247   effects of water level (WAL), salinity (SAL) and Oxygen concentration (OXY), plus a temporal

248   overdispersion term (ε). The effects of salinity > 120 g.L^{-1} was modelled by the saltpan-

249   specific conditional intercept α^{120}. All terms were species-specific :

250    $log\left(\lambda_{i,t,k,s}\right) = \alpha_{i,s} + \beta_{1,site(i),s} \times WAL_{i,t} + \gamma_{1,site(i),s} \times WAL_{i,t}^2 + \left(1 - \mathrm{I}_{SAL_{i,t}<120}\right) \times$

251    $\alpha_{site(i),s}^{120} + \mathrm{I}_{SAL_{i,t}<120} \times \left(\beta_{2,site(i),s} \times SAL_{i,t} + \gamma_{2,site(i),s} \times SAL_{i,t}^2\right) + \beta_{3,site(i),s} \times OXY_{i,t} +$

252    $\gamma_{3,site(i),s} \times OXY_{i,t}^2 + \varepsilon_{t,k,s}$ (2)

253   Where $\mathrm{I}_{SAL_{i,t}<120}$ indicates whether salinity is above the censoring threshold of 120g.L^{-1}:

254 $$I_{SAL_{i,t}<120} = \begin{cases} 1 & \text{if the salinity of the pond } i \text{ at time } t \text{ is } < 120 \text{ g.L}^{-1} \\ 0 & \text{otherwise} \end{cases} . (3)$$

255 Since data for water levels, salinity or oxygen were missing in 14% of the recordings, we

256 modelled missing values assuming that all variables were normally distributed around the

257 observed mean and with the observed standard deviation.

258

259 We nested pond-level intercepts $\alpha_{i,s}$ within the two saltpans for each species to reflect

260 saltpan-dependent suitability to birds:

261 $$\alpha_{i,s} \sim Norm(\mu_{site(i)}, \tau) \ (4)$$

262 We also imposed species-level priors to regression coefficients $\beta_{k,site(i),s}$:

263 $$\beta_{k,site(i),s} \sim Norm(B_s, T) \ (5)$$

264 Although we were interested in saltpan-level coefficients, these hyperpriors were necessary

265 to model species-level responses to variations in physico-chemical variables. This

266 hierarchical formulation is equivalent to a mixed model with nested pond and site random

267 effects on α and with a species random effect on β_k (Zuur, 2011).

268

269 We divided the overdispersion term $\varepsilon_{t,k,s}$ into a within-year error (ε_1) reflecting species'

270 seasonal phenology and a between-years error (ε_2) accounting for temporal autocorrelation

271 across consecutive breeding seasons :

272 $$\varepsilon_{t,k,s} = \varepsilon_{1,t,s} + \varepsilon_{2,k,s} \ (5)$$

273   We assumed that ε₁ and ε₂ were normally distributed first-order autoregressive terms (Zuur,

274   2011) :

275    $\varepsilon_{1,t,s} \sim Norm\left(\varphi_{1,s} \times \varepsilon_{1,t-1,s}, \tau_1\right)$ (6)

276    $\varepsilon_{2,k,s} \sim Norm\left(\varphi_{2,s} \times \varepsilon_{2,k-1,s}, \tau_2\right)$ (7)

277   In these equations, φ₁ and φ₂ quantify respectively the magnitude of intra- and inter-annual

278   autocorrelations.

279

280   We specified flat gaussian priors for all higher-level hyperparameters and ran three Monte-

281   Carlo Markov chains under JAGS 4.3.0 (Plummer, 2003), each with 10^6 burn-in iterations and

282   10^6 iterations for inference, thinned by 1000. The script of the model in BUGS language is

283   provided in Appendix S3. We computed the Gelman-Rubin statistics (Gelman *et al.*, 2004) for

284   all parameters and considered that a value below 1.1 indicated adequate convergence. We

285   assessed model fit with a Bayesian posterior predictive check based on a comparison of

286   observed and modelled species' abundances (Gelman & Hill, 2007).

287 **Results**

288

289 *Model fit and convergence*

290

291 The Bayesian posterior predictive check indicated varying fits according to species, from p =

292 0.26 to p = 0.7 (p = 0.5 indicates perfect fit; all results in Appendix S2, Fig S2.1). The poorest

293 fits corresponded to gregarious species that form large flocks (Black-headed Gull and

294 Greater Flamingo) or to semi-colonial species that aggregate in space (Stilt and Avocet). All

295 parameters converged adequately according to Gelman-Rubin's statistics (Appendix S2,

296 Table S2.1) and visual checks of chain stability. Autocorrelation was non-significant at both

297 intra- and inter-annual scales for most species (Appendix S1, Table S1.1), indicating that

298 temporal variations in counts were well captured by the variables considered.

299

300 *Site effect*

301

302 Species-level raw counts were lower in the smaller inland Vieux Salins than in the wide

303 coastal Pesquiers (Appendix S1, Table S1.1, which also displays the average number of pairs

304 per year on the two sites). This difference persisted once water level, salinity and dissolved

305 oxygen concentration were fixed to their average value over the two sites (Appendix S2, Fig.

306 S2.2). Species-specific variations unrelated to physiochemical parameters were not

307   explained by pond size only (maximum Pearson's R^2 between counts and pond area = 0.33 in

308   Greater Flamingo).

309

310   *Responses to physiochemical variables*

311

312   All physiochemical variables were non-linearly related to variations in species counts. Counts

313   varied by 0 to 100% along the range of variation of the three variables, with strong

314   interspecific variation (Fig. 2-4 : estimated marginal variation in species' counts against a

315   given physiochemical variable, holding all other fixed to their average value). Hence, none of

316   the variables considered had an unambiguously higher influence than the others, which

317   implies that species' responses to management practices were dictated by a balance of

318   multiple physiochemical features rather than merely by water levels.

319

320   Water level is the only lever available to the reserve managers to modulate water conditions

321   on the two saltpans, and the most integrative of the three variables considered. Waders,

322   which nest and forage on emerged ground, exhibited a bell-shaped response to variations in

323   water level on at least one of the two sites (Fig. 2), with flatter responses in four of the five

324   islet-breeding species (Slender-billed Gull, Fig. 2d and Terns, Fig. 2g, h, i, but not Black-

325   headed Gull, Fig. 2f). This result is explained by the need of these species to preserve their

326   nests from predators, but also by the fact that they tend to forage more frequently on open

327   waters. Leaving aside credible intervals, maximum counts were attained within the range of

328   water level variations for eight and five out of nine species in Pesquiers and Vieux Salins,

329   respectively (Appendix S2, Table S2.2, range of covariates in Appendix S1, Table S1.2 for

330   comparison). However, response curves differed sharply between the two saltpans without

331   any systematic pattern (compare blue and black curves in Fig. 2). For instance, Flamingo's

332   optimum was close to 22 cm in Vieux Salins, while its counts increased monotonically in

333   Pesquiers all over the water levels range (Fig. 2c and Table S2.2). These site-dependent

334   optimums imply that species-dependent factors unrelated to the tested variables contribute

335   to these response curves.

336

337   Responses to salinity were monotonically negative for six large islet-breeding species

338   (Avocet, Stilt, Slender-billed Gull, Kentish Plover, Black-headed Gull and Little Tern), the

339   three others exhibiting non-linear curves (Fig. 3). Estimates of species' abundances when

340   salinity exceeded the 120g.L^{-1} threshold imposed by our probe were consistent with these

341   curves in all species (Fig. 3). Interestingly, seven out of nine species reached a minimum

342   abundance within the salinity range observed in the Pesquiers, the main foraging site for

343   most of them, but only three in Vieux Salins, which birds use more for roosting (Table S3.2).

344   This pattern was reversed for Flamingo (maximum counts for 51 g.L^{-1}), which however uses

345   little Vieux Salins in the breeding season. Conversely, response curves were negative or flat

346   for three species which breed and feed on the two saltpans although usually more tied to

347   less saline waters, Black-headed Gull (Fig.3f), Little Tern (Fig. 3h) and Common Tern (Fig. 3i).

348   Most species' responses to salinity were flatter in Vieux Salins, and even positive for Stilt

349   (Fig. 3b) and Black-headed Gull (Fig. 3f), although salinity varied within the same range in

350   both saltpans (Table S3.2).

351

352   The effect of dissolved oxygen concentration was also species- and saltpan-dependent with

353   no general pattern, although response curves were flatter in Vieux Salins than in Pesquiers

354   (Fig. 4). Species' optimums were inconsistent across the two saltpans, except for Avocet

355   which peaked around 7 mg.L-1 in both (Fig. 4a and Appendix S2, Table S2.2). Flamingo

356   exhibited similar monotonic decreases with increasing oxygen concentrations in the two

357   saltpans (Fig. 4c), suggesting that this particular parameter might act as a strong limiting

358   factor to this species.

359

360   **Discussion**

361

362   Most species exhibited strong non-linear responses to at least one of the three variables

363   investigated, supporting the hypothesis that water level, salinity and dissolved oxygen

364   concentration are relevant parameters to control saltpans suitability to waterbirds, in line

365   with previous studies in other biogeographic areas (Velasquez, 1992; Warnock *et al.*, 2002;

366   Giosa *et al.*, 2018). As a general pattern, macroinvertebrate species diversity peak at mid-

367   salinity (Britton & Johnson, 1987), which in turn forces a decrease in bird occurrence

368   towards hypersaline waters due to a lack of prey and osmoregulation stress (Gutiérrez *et al.*,

369   2011). Salinity is thus crucial for waterbird assemblages through its direct influence on

370   trophic resources fluctuations (Warnock *et al.*, 2002; Takekawa *et al.*, 2006; Ramírez *et al.*,

371   2018). In our study, all species tied to saltpans for foraging, except flamingo (*i.e.*, all but

372   terns, which also fish at sea), exhibited negative response curves to salinity at least on

373   Pesquiers, which points that water on this saltpan is overly saline to most breeding

374   waterbirds. Accordingly, the levels of salinity recorded in our study site were well above the

375 range found in comparable protected saltpans elsewhere in the world (e.g. in San Francisco

376 bay, Warnock *et al.*, 2002). In line with studies on other artificial marshes (Takekawa *et al.*,

377 2006; Bellio *et al.*, 2009; Giosa *et al.*, 2018), these patterns imply that our study site is a

378 suboptimum and stressful habitat which waterbirds are forced to use by the lack of more

379 suitable marshes in the vicinity, the closest coastal wetland to our study site being the

380 Camargue, 120 km to the west.

381

382 While increasing salinity had clearly detrimental effects on most species, the effects of water

383 levels and dissolved oxygen were more species-specific, reflecting both species' habitat

384 preferences and site use. Waders and gulls peaked at low to intermediate water levels,

385 consistent with their need of mudflats for foraging (Piersma *et al.*, 2004), while terns, which

386 fish on open waters, exhibited flatter responses explained by the fact that they breed on

387 ponds where water levels are maintained permanently high. At the other extreme, the

388 particular ecology of flamingo, a large-bodied specialist of highly saline waters relying on

389 saltpans as up to 60% of its habitat (Béchet *et al.*, 2009), explains its maximum counts at

390 lower oxygenation, higher salinity and higher water levels than most other species. Its

391 unexpected apparent reluctance to high salinity in Vieux Salins can be explained by the

392 confusing fact that the few sufficiently large and deep ponds on this saltpan also happen to

393 be the least saline. In sum, waterbirds' responses to changes in water physicochemical

394 parameters were highly asynchronic across species and consistent with their differential use

395 of the saltpans, either for breeding, foraging or both.

396

397   Although species' responses to the three studied variables were generally well explained by

398   breeding and feeding behaviours, we observed marked differences between the two studied

399   saltpans suggesting the interplay of additional factors not accounted for in our study. Most

400   notably, responses to all tested variables were more marked, and abundances were higher,

401   on the barren Pesquiers saltpans than on the more vegetalized Vieux Salins, reflecting the

402   tendency of shorebirds to forage and breed preferentially in open habitats (Tavares *et al.*,

403   2015; Żmihorski *et al.*, 2016). This discrepancy between the two sites may also imply that

404   breeding waterbirds limit distances between breeding and foraging areas to reduce energy

405   expenditure and predation risk. Among undesired effects which may also contribute to inter-

406   site differences, herbaceous cover and wooded areas can increase predation pressure by

407   wild boar, red fox, yellow-legged gull, falcons and sparrowhawk (Żmihorski *et al.*, 2016), and

408   the small size of Vieux Salins exposes birds more to external disturbance (in particular the

409   proximity of an airport), although both sites are permanently closed to the public. These

410   speculations based on field experience demand formal testing with dedicated data, which

411   were not available during our study. Our results suggest, however, that waterbirds'

412   responses to water parameters interact with landscape and habitat-level determinants,

413   calling for an ecosystem-based management approach (Ma *et al.*, 2010; Clausen *et al.*,

414   2013), which would account for habitat complementation behaviours in the species under

415   focus.

416

417   The restoration of a natural connexion between the sea and inland waters is the most

418   efficient option to create vast expands of suitable wetlands to waterbirds and the associated

419   trophic network. This solution is however out of reach where dykes warrant protection

420   against coastal erosion and secure human land use : saltpans then become the only

421   substitution habitat for waterbirds in highly artificialized matrices, such as in our study site,

422   elsewhere in the Mediterranean basin (Paracuellos *et al.*, 2002), in western United States

423   (Takekawa *et al.*, 2006; Athearn *et al.*, 2012) or in south-eastern Asia (Lei *et al.*, 2018). To

424   ensure the efficiency of this artificial conservation solution, our results suggest that saltpans

425   management choices should be based on the ecological preferences of functional guilds

426   rather than, as is often favoured by managers for practical or communication reasons, on

427   flagship species. Distinguishing ponds matching the requirements of mudflat-feeding birds,

428   including shorebirds and gulls, from others dedicated to water-feeding species (here only

429   terns) or to flamingo (due to its specific ecology) would likely capture most of this ecological

430   variability. However, this segregation might need to be adjusted seasonally to account for

431   the requirements of passing-through migrants and wintering species (Bellio *et al.*, 2009;

432   Tavares *et al.*, 2015). Based on our results, a viable strategy to promote the simultaneous co-

433   occurrence of these two guilds would be to maintain a mosaic involving low-salinity (20 to 40

434   g.L^{-1}) ponds with water levels below 20 cm and emerged mudflats (shorebirds and gulls),

435   mid-salinity (40-80 g.L^{-1}) ponds with 20 cm of water (mainly flamingo) and ponds with higher

436   water levels protecting colonies from predation and offering foraging areas to terns.

437

438   Furthermore, contrary to Athearn et al (2012), we found no evidence that hypersaline

439   conditions above 40 g.L^{-1} favour any of the functional guilds present on our study site. This

440   discrepancy suggests regional and intra-guild species-specific variations in the range of

441   suitable water properties. Any reduction of salinity should furthermore be applied reversibly

442   to avoid undesired cascading effects on the trophic network through eutrophication and

443   competition induced by local invaders (Takekawa *et al.*, 2015). Our results additionally

444   suggest that birds' sensitivity to salinity is exacerbated on foraging sites due to its structuring

445   impact on trophic networks, while water levels are more critical on roosting and breeding

446   sites. This pattern implies that species' optimum responses to water physico-chemical

447   parameters are not just explained by trophic requirements and physiological stress, but also

448   by contextual effects associated with habitat complementation behaviours, landscape,

449   predation pressure and disturbance, calling for management decisions based on local

450   estimations of species' requirements rather than on external results.

451

452   It is tempting to believe that a more complete assessment of water physico-chemical

453   characteristics, including direct measurements of photosynthetic activity, evaluation of prey

454   resources, and a finer spatial resolution in water level measurements would yield a more

455   biologically realistic model and more precise management recommendations. These data

456   are, however, rarely available and the required sampling effort may not be sustainable for

457   managers over the long-term at a frequency compatible with the rapid environmental

458   changes observed in saltpans (a few days to a few weeks). Our dataset is therefore

459   representative of the actual data available in practice to decide on management options,

460   which are largely tied to a single lever, water levels. The resulting water flow modulates

461   directly salinity and oxygen, which in turn determine prey availability to waterbirds

462   (Velasquez, 1992; Athearn *et al.*, 2012) and can thus be considered suitable proxies of the

463   dynamics of the trophic chains (Takekawa *et al.*, 2015). We suggest however that a two-tier

464   monitoring of environmental variables on saltpans, coupling regular measurements of these

465   synthetic proxies with more spaced exhaustive analyses of water and geolocated bird

466   records, would substantially improve model-based assessments of management practices

467   and subsequent choices.

468

469   As pressure on coastal wetlands increases worldwide under the effects of sea level rise and

470   artificialization (Ma *et al.*, 2009; Traill *et al.*, 2011; Osland *et al.*, 2016), decommissioned

471   saltpans appear as a cost-effective way to preserve breeding and stopping-over habitats for

472   waterbirds and their associated trophic network (Green *et al.*; Masero, 2003; Athearn *et al.*,

473   2012). Although their small size cannot compensate the loss of large extents of wetlands,

474   they serve as essential stepping stones in connectivity networks (Volenec & Dobson, 2019)

475   and can sustain viable populations of vulnerable species (Márquez-Ferrando *et al.*, 2014),

476   making the protection of these artificial habitats central to preserve waterbirds along coastal

477   landscapes undergoing strong human pressure. Our study showed however that in such

478   isolated contexts, waterbirds may be forced to use saltpans by the absence of any

479   alternative habitat, in spite of the stress implied by hypersaline conditions. Balancing water

480   levels and flow aimed to match the preferences of functional guilds instead of focusing on

481   flagship species may be an effective way to solve this issue, but this local-level management

482   also needs to consider supplementary factors which influence waterbirds' behaviour, such as

483   site size, vegetation and direct disturbance. Implementing multi-species, multi-scale

484   management schemes is therefore likely the key to sustain the role of saltpans as

485   substitution habitats facing anthropogenic pressure on coastal wetlands.

486

488

489 *Acknowledgements blinded for double-blind peer review.*

490

491 **References**

492

493 Adam, P. (2002) Saltmarshes in a time of change. *Environmental Conservation*, **29**, 39–61.
494 AEWA (2018) *Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA) As*
495   *amended at the 7 th Session of the Meeting of the Parties to AEWA*, Durban, South Africa.
496 Athearn, N.D., Takekawa, J.Y., Bluso-Demers, J.D., Shinn, J.M., Brand, L.A., Robinson-Nilsen, C.W. &
497   Strong, C.M. (2012) Variability in habitat value of commercial salt production ponds:
498   implications for waterbird management and tidal marsh restoration planning. *Hydrobiologia*,
499   **697**, 139–155.
500 Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C. & Silliman, B.R. (2011) The value of
501   estuarine and coastal ecosystem services. *Ecological Monographs*, **81**, 169–193.
502 Béchet, A., Germain, C., Sandoz, A., Hirons, G.J.M., Green, R.E., Walmsley, J.G. & Johnson, A.R. (2009)
503   Assessment of the impacts of hydrological fluctuations and salt pans abandonment on
504   Greater flamingos in the Camargue, South of France. *Biodiversity and Conservation*, **18**,
505   1575–1588.
506 Bellio, M.G., Kingsford, R.T. & Kotagama, S.W. (2009) Natural versus artificial- wetlands and their
507   waterbirds in Sri Lanka. *Biological Conservation*, **142**, 3076–3085.
508 Bluso-Demers, J.D., Ackerman, J.T., Takekawa, J.Y. & Peterson, S.H. (2016) Habitat Selection by
509   Forster's Terns (Sterna forsteri) at Multiple Spatial Scales in an Urbanized Estuary: the
510   Importance of Salt Ponds. *Waterbirds*, **39**, 375–387.
511 Boesch, D.F.; F., John C.;. Scavia, Donald ;.U.S. Global Change Research Program National Assessment
512   Synthesis Team (2000) *The potential consequences of climate variability and change on*
513   *coastal areas and marine resources : report of the Coastal Areas and Marine Resources Sector*
514   *Team, U.S. National Assessment of the Potential Consequences of Climate Variability and*
515   *Change, U.S. Global Change Research Program*, U.S. Dept. of Commerce, National Oceanic
516   and Atmospheric Administration, National Ocean Service, National Centers for Coastal Ocean
517   Science, Coastal Ocean Program.
518 Britton, R.H. & Johnson, A.R. (1987) An ecological account of a Mediterranean salina: The Salin de
519   Giraud, Camargue (S. France). *Biological Conservation*, **42**, 185–230.
520 Burger, J. & Olla, B.L. eds. (1984) *Shorebirds: Breeding Behavior and Populations*, Springer US.
521 Catry, T., Ramos, J.A., Catry, I., Allen-Revez, M. & Grade, N. (2004) Are salinas a suitable alternative
522   breeding habitat for Little Terns Sterna albifrons?: Salinas as breeding habitat for Little Terns.
523   *Ibis*, **146**, 247–257.
524 Clausen, K.K., Stjernholm, M. & Clausen, P. (2013) Grazing management can counteract the impacts
525   of climate change-induced sea level rise on salt marsh-dependent waterbirds. *Journal of*
526   *Applied Ecology*, **50**, 528–537.
527 Colwell, M. (2010) *Shorebird Ecology, Conservation, and Management*, University of California Press,
528   Berkeley.

529 Craft, C., Clough, J., Ehman, J., Joye, S., Park, R., Pennings, S., Guo, H. & Machmuller, M. (2009)
530   Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services.
531   *Frontiers in Ecology and the Environment*, **7**, 73–78.
532 Deegan, L.A., Johnson, D.S., Warren, R.S., Peterson, B.J., Fleeger, J.W., Fagherazzi, S. & Wollheim,
533   W.M. (2012) Coastal eutrophication as a driver of salt marsh loss. *Nature*, **490**, 388-+.
534 Dias, M.P. (2009) Use of Salt Ponds by Wintering Shorebirds throughout the Tidal Cycle. *Waterbirds:*
535   *The International Journal of Waterbird Biology*, **32**, 531–537.
536 Dias, M.P., Granadeiro, J.P., Lecoq, M., Santos, C.D. & Palmeirim, J.M. (2006) Distance to high-tide
537   roosts constrains the use of foraging areas by dunlins: Implications for the management of
538   estuarine wetlands. *Biological Conservation*, **131**, 446–452.
539 Gardner, R.C., Barchiesi, S., Beltrame, C., Finlayson, C., Galewski, T., Harrison, I., Paganini, M.,
540   Perennou, C., Pritchard, D., Rosenqvist, A. & Walpole, M. (2015) *State of the World's*
541   *Wetlands and Their Services to People: A Compilation of Recent Analyses*, Social Science
542   Research Network, Rochester, NY.
543 Gedan, K.B., Silliman, B.R. & Bertness, M.D. (2009) Centuries of Human-Driven Change in Salt Marsh
544   Ecosystems. *Annual Review of Marine Science*, **1**, 117–141.
545 Gelman, A. & Hill, J. (2007) *Data Analysis Using Regression and Multilevel/Hierarchical Models*,
546   Cambridge University Press.
547 Gelman, A., J.B., C., H.S., S. & D.B., R. (2004) *Bayesian data analysis, 2nd Edition*, Chapman and Hall ⁄
548   CRC, New York, NY, USA.
549 Giosa, E., Mammides, C. & Zotos, S. (2018) The importance of artificial wetlands for birds: A case
550   study from Cyprus. *Plos One*, **13**, e0197286.
551 Green, J.M.H., Sripanomyom, S., Giam, X. & Wilcove, D.S. The ecology and economics of shorebird
552   conservation in a tropical human-modified landscape. *Journal of Applied Ecology*, **52**, 1483–
553   1491.
554 Gutiérrez, J.S., Masero, J.A., Abad-Gómez, J.M., Villegas, A. & Sánchez-Guzmán, J.M. (2011)
555   Understanding the energetic costs of living in saline environments: effects of salinity on basal
556   metabolic rate, body mass and daily energy consumption of a long-distance migratory
557   shorebird. *Journal of Experimental Biology*, **214**, 829–835.
558 Hoegh-Guldberg, O. & Bruno, J.F. (2010) The Impact of Climate Change on the World's Marine
559   Ecosystems. *Science*, **328**, 1523–1528.
560 Hughes, R.G. & Paramor, O. a. L. (2004) On the loss of saltmarshes in south-east England and
561   methods for their restoration. *Journal of Applied Ecology*, **41**, 440–448.
562 Kery, M. & Royle, J.A. (2015) *Applied Hierarchical Modeling in Ecology: Analysis of distribution,*
563   *abundance and species richness in R and BUGS: Volume 1:Prelude and Static Models by Marc*
564   *Kery*, Academic Press.
565 Kirwan, M.L. & Megonigal, J.P. (2013) Tidal wetland stability in the face of human impacts and sea-
566   level rise. *Nature*, **504**, 53–60.
567 Lei, W., Masero, J.A., Piersma, T., Zhu, B., Yang, H.-Y. & Zhang, Z. (2018) Alternative habitat: the
568   importance of the Nanpu Saltpans for migratory waterbirds in the Chinese Yellow Sea. *Bird*
569   *Conservation International*, **28**, 549–566.
570 Ma, Z., Cai, Y., Li, B. & Chen, J. (2010) Managing Wetland Habitats for Waterbirds: An International
571   Perspective. *Wetlands*, **30**, 15–27.
572 Ma, Z., Li, B., Li, W., Han, N., Chen, J. & Watkinson, A.R. (2009) Conflicts between Biodiversity
573   Conservation and Development in a Biosphere Reserve. *Journal of Applied Ecology*, **46**, 527–
574   535.
575 Márquez-Ferrando, R., Figuerola, J., Hooijmeijer, J.C.E.W. & Piersma, T. (2014) Recently created man-
576   made habitats in Doñana provide alternative wintering space for the threatened Continental
577   European black-tailed godwit population. *Biological Conservation*, **171**, 127–135.
578 Masero, J.A. (2003) Assessing alternative anthropogenic habitats for conserving waterbirds: salinas as
579   buffer areas against the impact of natural habitat loss for shorebirds. *Biodiversity &*
580   *Conservation*, **12**, 1157–1173.

581 Montanarella, L., Scholes, R. & Brainich, A. (2018) *The IPBES assessment report on land degradation*
582 *and restoration.*, Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity
583 and Ecosystem Services, Bonn, Germany.
584 Myers, J.P. (1983) Conservation of migrating shorebirds: staging areas, geographic bottlenecks, and
585 regional movements. *American Birds*, **37**, 23–25.
586 Newton, I. (2003) *The speciation and biogeography of birds*, Academic Press, Oxford.
587 Osland, M.J., Enwright, N.M., Day, R.H., Gabler, C.A., Stagg, C.L. & Grace, J.B. (2016) Beyond just sea-
588 level rise: considering macroclimatic drivers within coastal wetland vulnerability assessments
589 to climate change. *Global Change Biology*, **22**, 1–11.
590 Paracuellos, M., Castro, H., Nevado, J.C., Ona, J.A., Matamala, J.J., Garcia, L. & Salas, G. (2002)
591 Repercussions of the abandonment of Mediterranean saltpans on waterbird communities.
592 *Waterbirds*, **25**, 492–498.
593 Piersma, T., Boere, G.C., Galbraith, C.A. & Stroud, D.A. (2006) Migration in the balance: tight
594 ecological margins and the changing fortunes of shorebird populations.
595 Piersma, T., Ens, B. & Zwarts, L. (2004) *Shorebirds: An illustrated Behavioural Ecology*, 2nd Revised
596 edition edition. KNNV Uitgeverij, Utrecht.
597 Plummer, M. (2003) *JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs*
598 *Sampling.* Vienna, Austria.
599 Ramírez, F., Rodríguez, C., Seoane, J., Figuerola, J. & Bustamante, J. (2018) How will climate change
600 affect endangered Mediterranean waterbirds? *PLOS ONE*, **13**, e0192702.
601 Ramsar Convention (1971) *Convention on Wetlands of International Importance especially as*
602 *Waterfowl Habitat. Ramsar (Iran), 2 February 1971. UN Treaty Series No. 14583. As amended*
603 *by the Paris Protocol, 3 December 1982, and Regina Amendments, 28 May 1987.*
604 Ramsar Convention on Wetlands (2018) *Global Wetland Outlook: State of the World's Wetlands and*
605 *their Services to People.*, Ramsar Convention Secretariat, Gland, Switzerland.
606 Royle, J.A. & Dorazio, R.M. (2008) *Hierarchical modeling and inference in ecology*, Academic Press,
607 London.
608 Sadoul, N. & Walmsley, J.G. (2000) *Salinas and nature conservation in the Mediterranean*, (ed. by
609 R.M. Geertman) Elsevier Science Bv, Amsterdam.
610 Sánchez, M.I., Green, A.J. & Castellanos, E.M. (2006) Spatial and temporal fluctuations in presence
611 and use of chironomid prey by shorebirds in the Odiel saltpans, south-west Spain.
612 *Hydrobiologia*, **567**, 329–340.
613 Sripanomyom, S., Round, P.D., Savini, T., Trisurat, Y. & Gale, G.A. (2011) Traditional salt-pans hold
614 major concentrations of overwintering shorebirds in Southeast Asia. *Biological Conservation*,
615 **144**, 526–537.
616 Takekawa, J.Y., Ackerman, J.T., Brand, L.A., Graham, T.R., Eagles-Smith, C.A., Herzog, M.P., Topping,
617 B.R., Shellenbarger, G.G., Kuwabara, J.S., Mruz, E., Piotter, S.L. & Athearn, N.D. (2015)
618 Unintended Consequences of Management Actions in Salt Pond Restoration: Cascading
619 Effects in Trophic Interactions. *Plos One*, **10**, e0119345.
620 Takekawa, J.Y., Miles, A.K., Schoellhamer, D.H., Athearn, N.D., Saiki, M.K., Duffy, W.D., Kleinschmidt,
621 S., Shellenbarger, G.G. & Jannusch, C.A. (2006) Trophic structure and avian communities
622 across a salinity gradient in evaporation ponds of the San Francisco Bay estuary.
623 *Hydrobiologia*, **567**, 307–327.
624 Tavares, D.C., Guadagnin, D.L., de Moura, J.F., Siciliano, S. & Merico, A. (2015) Environmental and
625 anthropogenic factors structuring waterbird habitats of tropical coastal lagoons: Implications
626 for management. *Biological Conservation*, **186**, 12–21.
627 Traill, L.W., Perhans, K., Lovelock, C.E., Prohaska, A., McFallan, S., Rhodes, J.R. & Wilson, K.A. (2011)
628 Managing for change: wetland transitions under sea-level rise and outcomes for threatened
629 species. *Diversity and Distributions*, **17**, 1225–1233.
630 Velasquez, C.R. (1992) Managing Artificial Saltpans as a Waterbird Habitat: Species' Responses to
631 Water Level Manipulation. *Colonial Waterbirds*, **15**, 43–55.
632 Volenec, Z.M. & Dobson, A.P. (2019) Conservation value of small reserves. *Conservation Biology*, **0**.

633 Warnock, N., Page, G.W., Ruhlen, T.D., Nur, N., Takekawa, J.Y. & Hanson, J.T. (2002) Management
634   and conservation of San Francisco bay salt ponds: Effects of pond salinity, area, tide, and
635   season on Pacific flyway waterbirds. *Waterbirds*, **25**, 79–92.
636 Xia, S., Yu, X., Millington, S., Liu, Y., Jia, Y., Wang, L., Hou, X. & Jiang, L. (2017) Identifying priority sites
637   and gaps for the conservation of migratory waterbirds in China's coastal wetlands. *Biological
638   Conservation*, **210**, 72–82.
639 Zedler, J.B. & Kercher, S. (2005) Wetland resources: Status, trends, ecosystem services, and
640   restorability. *Annual Review of Environment and Resources*, **30**, 39–74.
641 Żmihorski, M., Pärt, T., Gustafson, T. & Berg, Å. (2016) Effects of water level and grassland
642   management on alpha and beta diversity of birds in restored wetlands. *Journal of Applied
643   Ecology*, **53**, 587–595.
644 Zuur, A. (2011) *Mixed Effects Models and Extensions in Ecology with R*, Softcover reprint of hardcover
645   1st ed. 2009 edition. Springer, New York, NY.

646

647

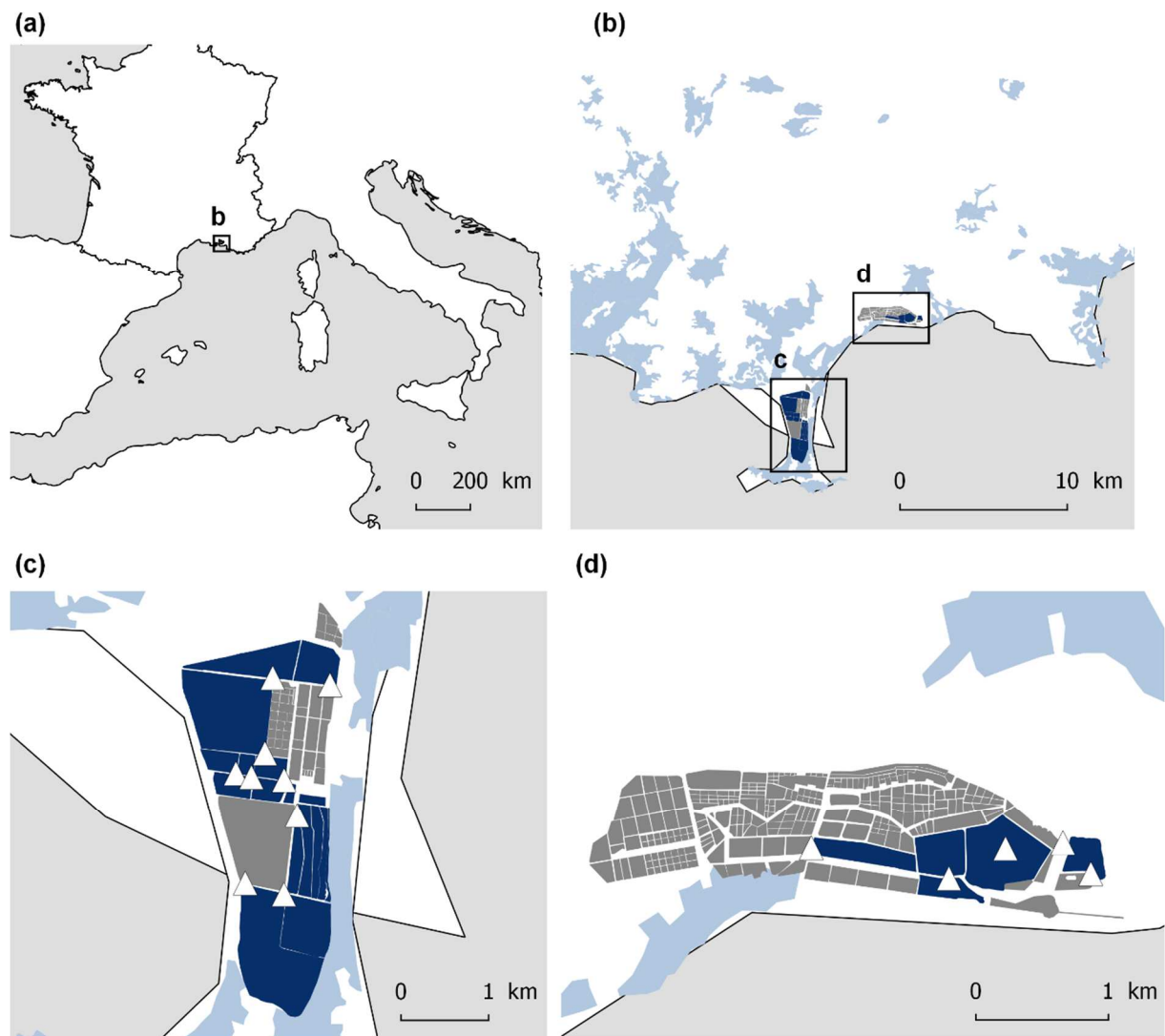648 **Supplementary Materials**

649

650 Appendix S1: Complementary information on the data set

651 Appendix S2: Complementary results on the model

652 Appendix S3: Script of the multispecies model in BUGS language

653

654   **Figures.**

(a)

(b)

(c)

(d)

655

656   **Figure 1. Location and configuration of the study area.** The site is located on the French

657   Mediterranean coast (a) and comprises two distinct saltpans located 3 km apart in a heavily

658   urbanized seashore (b, urban areas in light blue). The two saltpans consist in mosaics of

659   contiguous ponds that are connected together or to a belt canal (Pesquiers: c, Vieux Salins:

660   d). The ponds included in the study are shown in dark blue, other ponds in grey. The white

661   triangles indicate the location of the 14 measurement points for physico-chemical
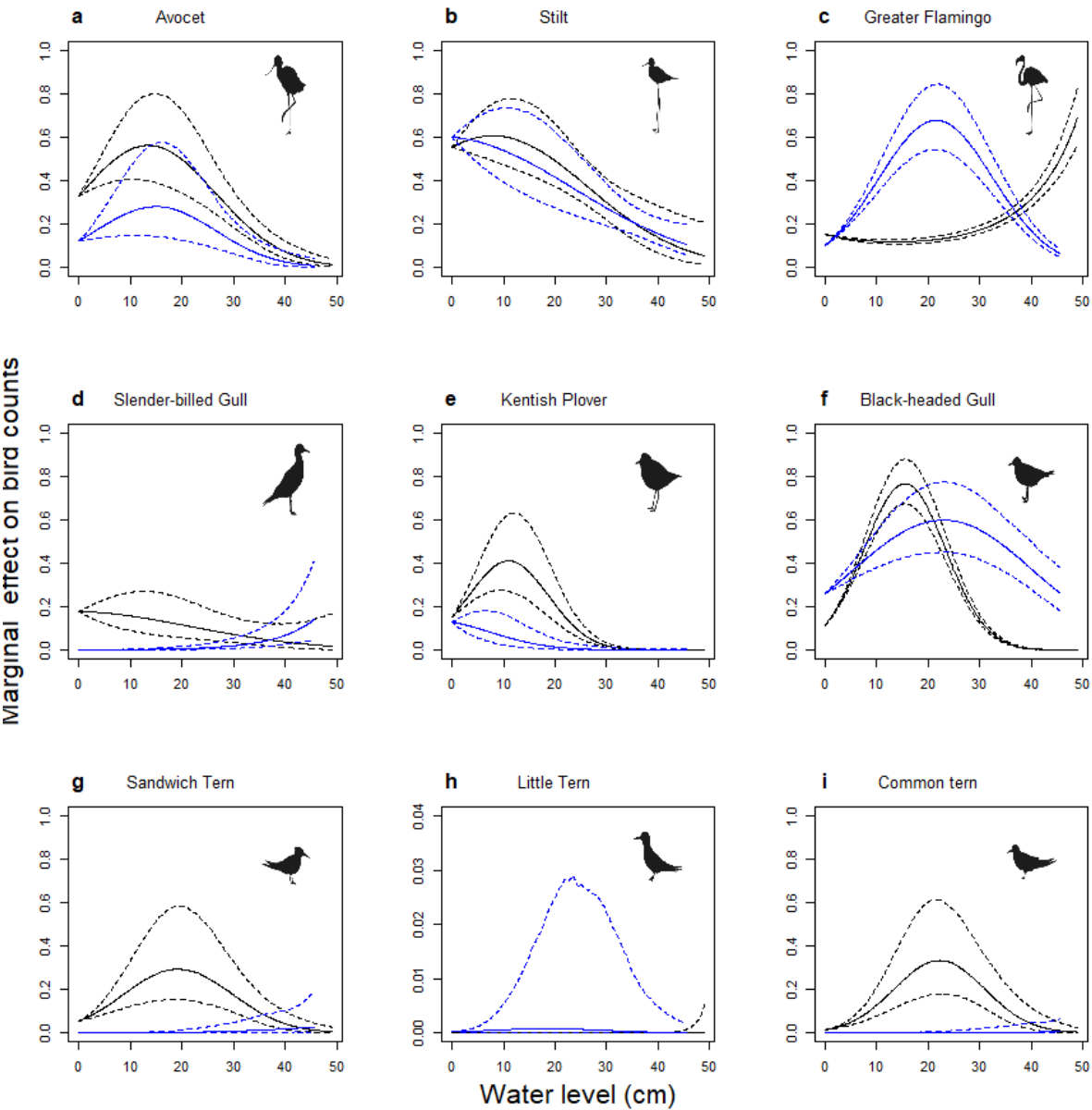
662   parameters and water levels.

663

664

Figure 2. Waterbird responses to variations in water levels in Pesquiers (black) and Vieux

Salins (blue). Curves depict marginal variations in species' counts on the two sites, as

predicted by a hierarchical model, holding all other variables in the model constant.

Responses are standardized by their maximum to ease comparisons (plain line = median,

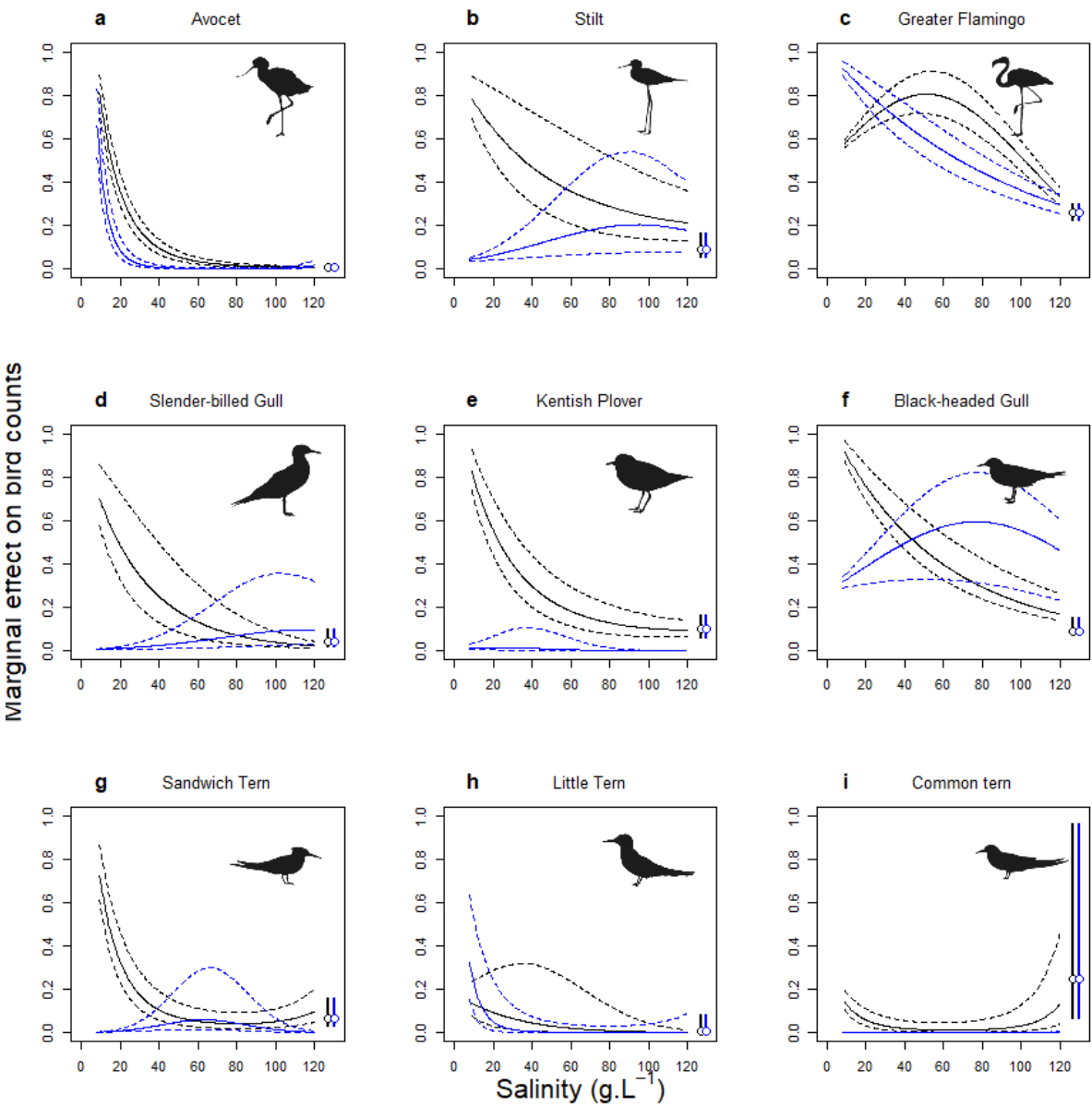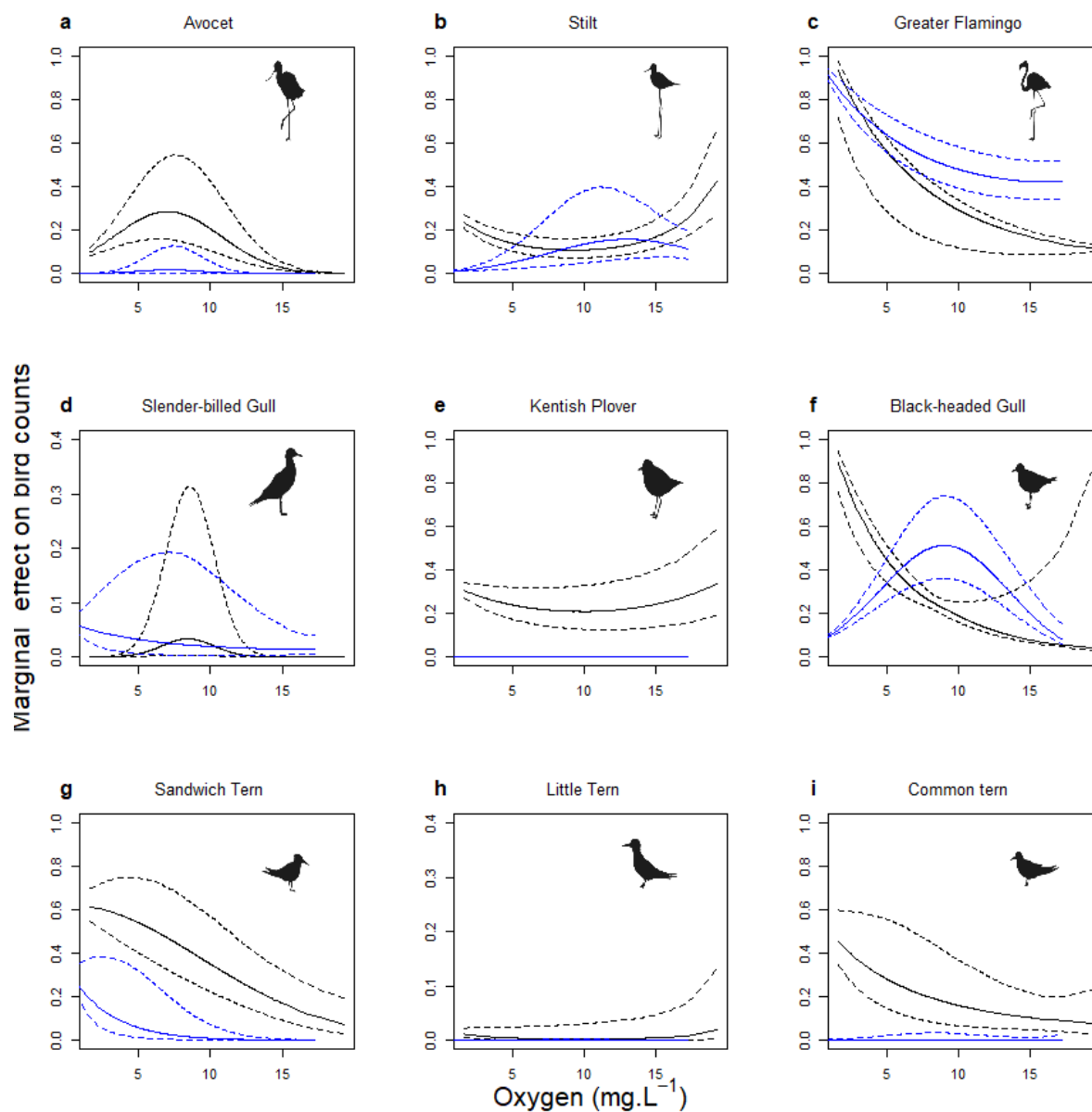dashed line = 95% credible interval). Vertical scale magnified in h.

671

672

673

674   **Figure 3.** Waterbird responses to variations in salinity (censored at 120 g.L^{-1}) in Pesquiers

675   (black) and Vieux Salins (blue). Curves depict marginal variations in species' counts on the

676   two sites, as predicted by a hierarchical model, holding all other variables in the model

677   constant. Responses are standardized by their maximum to ease comparisons (plain line =

678   median, dashed line = 95% credible interval). The bars on the right indicate the estimate and

679   95% credible interval of relative marginal species' abundance when salinity is above 120 g.L^{-1}

680   (α_{120} in equation 2).

681

682

683

684   **Figure 4.** Waterbird responses to variations in oxygen concentration (mg.L^{-1}) in Pesquiers

685   (black) and Vieux Salins (blue). Curves depict marginal variations in species' counts on the

686   two sites, as predicted by a hierarchical model, holding all other variables in the model

687   constant. Responses are standardized by their maximum to ease comparisons (plain line =

688   median, dashed line = 95% credible interval). Vertical scale magnified in d and h.

689