

Short-term prey field lability constrains individual specialisation in resource selection and foraging site fidelity in a marine predator

Courbin Nicolas ^{1,*}, Besnard Aurélien ¹, Péron Clara ², Saraux Claire ³, Fort Jérôme ⁴, Perret Samuel ¹, Tornos Jérémy ¹, Grémillet David ^{1,5}, Nathan Ran

¹ Centre d'Ecologie Fonctionnelle et Evolutive (CEFE); UMR 5175; Centre National de la Recherche Scientifique (CNRS); Université de Montpellier; Université Paul Valéry Montpellier; Ecole Pratiques des Hautes Etudes (EPHE); 1919 Route de Mende 34293 Montpellier Cedex 5, France

² Marine Biodiversity Exploitation and Conservation (MARBEC); UMR 248; Institut de Recherche pour le Développement (IRD); Université de Montpellier; Place Eugène Bataillon - bât 24 - CC093 34095 Montpellier Cedex 5, France

³ Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER); UMR 248 MARBEC; Avenue Jean Monnet CS 3017 34203 Sète, France

⁴ Littoral, Environnement et Sociétés (LIENSs); UMR 7266; Centre National de la Recherche Scientifique (CNRS); Université La Rochelle; 2 rue Olympe de Gouges 17000 La Rochelle, France

⁵ FitzPatrick Institute; DST/NRF Excellence Centre at the University of Cape Town; Rondebosch 7701, South Africa

* Corresponding author : Nicolas Courbin, email addresses : nicolas.courbin@cefe.cnrs.fr ; ncourbin@gmail.com

Abstract :

Spatio-temporally stable prey distributions coupled with individual foraging site fidelity are predicted to favour individual resource specialisation. Conversely, predators coping with dynamic prey distributions should diversify their individual diet and/or shift foraging areas to increase net intake. We studied individual specialisation in Scopoli's shearwaters (*Calonectris diomedea*) from the highly dynamic Western Mediterranean, using daily prey distributions together with resource selection, site fidelity and trophic-level analyses. As hypothesised, we found dietary diversification, low foraging site fidelity and almost no individual specialisation in resource selection. Crucially, shearwaters switched daily foraging tactics, selecting areas with contrasting prey of varying trophic levels. Overall, information use and plastic resource selection of individuals with reduced short-term foraging site fidelity allow predators to overcome prey field lability. Our study is an essential step towards a better understanding of individual responses to enhanced environmental stochasticity driven by global changes, and of pathways favouring population persistence.

Keywords : Behavioural consistency, *Calonectris diomedea*, foraging site fidelity, resource selection, Scopoli's shearwater, temporal resource dynamic, Western Mediterranean

51 **Introduction**

52 Individual specialization (i.e. consistent trait variations among individuals [Sutherland 1987;
53 Araújo *et al.* 2011]) shapes population-level behavioral diversity (Woo *et al.* 2008; Potier *et*
54 *al.* 2015), and has strong implications for evolutionary processes and ecological interactions,
55 affecting population and community dynamics (Araújo *et al.* 2011; Bolnick *et al.* 2011; Violle
56 *et al.* 2012; Wolf & Weissing 2012; Spiegel *et al.* 2017). Individual specialization is related to
57 differences in physiological, behavioral and ecological mechanisms (Sutherland 1987; Fortin
58 *et al.* 2008; Araújo *et al.* 2011; Bolnick *et al.* 2011; Spiegel *et al.* 2017) and is found across
59 terrestrial and marine taxa (Bell *et al.* 2009; Araújo *et al.* 2011; e.g. fish: Allgeier *et al.* 2017;
60 mammals: Duchesne *et al.* 2010; Leclerc *et al.* 2016; birds: Phillips *et al.* 2017). Studying the
61 mechanisms by which individual specialization arises is critical to test theoretical approaches
62 (Bolnick *et al.* 2011), and develop relevant conservation strategies (Duchesne *et al.* 2010;
63 Wakefield *et al.* 2011; Merrick & Koprowski 2017), especially in the context of rapid global
64 change.

65 Individual specialization in resource selection (ISRS) is the within-individual
66 consistency in selection of a subset within a range of available resources that differs from
67 selection by other individuals. Mechanistic models suggested that individual resource
68 specialization increases with intra-specific competition, to mitigate reduction in availability of
69 the preferred prey, and decreases in dense populations to yield low resource levels and high
70 fitness costs for specialists (Svanbäck & Bolnick 2005; Fortin *et al.* 2008). Empirical studies
71 confirmed these predictions (Araújo *et al.* 2011; e.g. fish: Svanbäck & Bolnick 2007; sea
72 otter: Tinker *et al.* 2012; seabirds: Navarro *et al.* 2017). For example, inter-individual
73 variations in resource selection within a red deer (*Cervus elaphus*) population on the Isle of
74 Rum (Scotland) reflected selective pressures for density- and frequency-dependent foraging
75 tactics (Fortin *et al.* 2008). Individual specialization in foraging was also related to spatio-

76 temporal changes in resource availability and prey predictability (Woo *et al.* 2008; Phillips *et*
77 *al.* 2017). Most empirical studies (e.g. reviewed for seabirds in Ceia & Ramos 2015) found
78 reduced individual specialization in diet and habitat use in years with lower resource
79 accessibility (Catry *et al.* 2014). In systems with rapid (day to week) changes in abiotic
80 conditions, high prey patchiness and low prey predictability (e.g. Weimerskirch 2007;
81 Fernandez *et al.* 2017), low ISRS is expected. Indeed, in such a situation, the costs of tracking
82 one elusive resource could outweigh foraging benefits of specialization related to predator
83 abilities and prey features.

84 ISRS offers a selective advantage if individuals increase foraging efficiency by
85 reducing search times, and this is related to their abilities to locate prey (Spiegel & Crofoot
86 2016) and to prey predictability (Phillips *et al.* 2017). When prey distributions are predictable,
87 predators can reduce search time using memory (Weimerskirch 2007; Wakefield *et al.* 2013)
88 and/or public information (Weimerskirch *et al.* 2010; Wells *et al.* 2016). In contrast, if prey
89 distributions are unpredictable, information cannot allow maintaining ISRS. Individuals may
90 overcome low spatio-temporal prey predictability by diversifying their diet, either through
91 generalist foraging tactics (no selection) or by alternating foraging tactics targeting specific
92 prey items (narrow short-term resource selection). In colonial species, this is promoted by the
93 breeding site functioning as an information centre (Harel *et al.* 2017). Previous studies
94 showed predator specialization on resources that are temporally dynamic but predictable in
95 space and/or time. For instance, Nile crocodiles (*Crocodylus niloticus*) prey on migrating
96 wildebeest (*Connochaetes taurinus*) at predictable times (Subalusky *et al.* 2017). However,
97 the relative effect of the two main contrasting drivers, intra-specific competition and prey
98 predictability, acting upon ISRS remains largely unknown.

99 To tackle such question, we must consider behaviours that distort the interplay
100 between resource selection, ISRS and prey predictability. Individual foraging site fidelity

101 (IFSF, i.e. consistent use of the same foraging areas by an individual, Wakefield *et al.* 2015)
102 is a widespread behaviour within colonial marine predator populations (Arthur *et al.* 2015;
103 Baylis *et al.* 2015; Wakefield *et al.* 2015), probably selected for the benefit of site familiarity
104 (Wakefield *et al.* 2015) or because predators go where their preferred prey usually occur.
105 IFSF increases with environmental stability (Switzer 1993) and should be positively
106 correlated with resource selection and ISRS when prey distribution is stable and not depleted
107 (Fig. 1). Accordingly, seabirds show both IFSF and individual specialization in habitat use
108 (reviewed in Ceia & Ramos 2015; e.g. Grémillet *et al.* 1999; Patrick *et al.* 2014; Wakefield *et*
109 *al.* 2015). The determinants of ISRS remain nevertheless unclear: Does individual
110 specialization on a given prey type occur because of IFSF, or do individuals track specific
111 prey types occurring systematically at the same place (ISRS as well as IFSF)? Theoretically,
112 prey predictability should enforce a trade-off between IFSF and ISRS. In environments with
113 rapidly changing spatio-temporal prey distribution, visits to the same foraging areas should
114 promote generalist foraging tactics (dietary diversification) and low ISRS, while low IFSF
115 allows specialized foraging tactics and high ISRS (Fig. 1). If specialization costs in prey type
116 (ISRS) or site (IFSF) are too high, individuals may use generalist or short-term specialized
117 foraging tactics and switch among foraging areas leading to low ISRS and low IFSF.
118 Understanding if and how ISRS arises in environments with low prey predictability thus
119 requires to simultaneously consider IFSF and ISRS in a dynamic habitat selection framework
120 including prey availability fluctuations (i.e. disproportionate use relative to resource
121 availability; Manly *et al.* 2002).

122 We studied the ecological drivers of ISRS in Scopoli's shearwaters (*Calonectris*
123 *diomedea*) using an analytical framework combining modelling of prey field lability, spatial
124 and trophic ecology of shearwaters (see Appendix S1). We tracked birds with GPS loggers
125 during four chick-rearing seasons within the Gulf of Lions (Western Mediterranean, Fig. 2), a

126 marine system associated with daily to yearly environmental stochasticity (Saraux *et al.* 2014;
127 Appendix S2, Fig. S2.1). We used hydro-acoustic estimations of biomass (summed individual
128 masses) and net sampling estimations of abundance (number of individuals) of prey targeted
129 by shearwaters, to develop dynamic prey habitat models and predict prey daily spatial
130 distributions according to shifting oceanographic conditions. We then assessed resource
131 selection for shearwaters, based on daily prey fields, to test the following predictions: 1)
132 Shearwaters show low ISRS and low IFSF at the individual level, and switch between
133 specialized foraging tactics (selection related to trophic level and/or prey type over the short-
134 term). 2) IFSF is uncoupled from ISRS and resource selection at the individual level. 3)
135 Information use for prey localization partly drives ISRS. Finally, we confronted our findings
136 with seabird trophic analyses. Overall, our study aimed at determining how short-term
137 predictability in prey distribution shapes ISRS and its mechanisms within foraging
138 populations.

139

140 **Material and Methods**

141 *Study system*

142 Our study was carried out during four chick-rearing seasons (in 2011, 2012, 2014 and 2015)
143 at two Marseille islands (Frioul and Riou, 43°11'00"N, 05°23'00"E) located in the Western
144 Mediterranean Sea (Fig. 2). Marseille's archipelago hosts one of the largest French breeding
145 colonies of Scopoli's shearwater (Anselme & Durand 2012), with approximately 520
146 breeding pairs. During the chick-rearing period, Scopoli's shearwaters are known to feed on a
147 wide range of prey, from zooplankton to small pelagic fish and squid (Sarà 1993; Ramos *et al.*
148 2009). The dynamic spatial distribution of these prey mainly relies on stochastic inputs of
149 nutrients associated with the Rhône River discharge, on coastal upwelling due to northerly
150 winds, and on the spatial extent of the Rhône freshwater plume induced by wind forcing.

151 Consequently, small pelagic fish show strong inter-annual heterogeneity in their summer
152 spatial distribution (Saraux *et al.* 2014). Additionally, we demonstrated high spatio-temporal
153 variations in fish and zooplankton distribution on a daily scale (Fig. S2.1).

154

155 *GPS tracking and feather sampling*

156 We tracked the foraging movements of 75 breeding Scopoli's shearwaters of both sexes
157 during the chick-rearing period using GPS loggers between the 29th July and the 18th August
158 in four years (n = 18, 27, 19 and 20 birds in 2011, 2012, 2014 and 2015, respectively; see
159 Appendix S3). Individuals were caught at the nest at night. We equipped birds with GPS
160 loggers (Perthold Engineering LCC) encapsulated in heat-shrink tubing and attached to back
161 feathers with Tesa tape. Tagged birds weighted 604g on average (range: 500 to 753g), and
162 tagging load (22.7g) represented ~3.8% of individual's body mass (range: 3.0 to 4.5%). GPSs
163 recorded a location every 1.5, 2 or 3 min depending on individuals and all GPS tracks were
164 interpolated to regular 2 min intervals. Birds were recaptured and loggers were retrieved after
165 1 to 5 days. At recapture, and before releasing birds, we collected the tip (1-2 cm) of the first
166 primary feather to assess their trophic position using stable isotopic analyses (see Appendix
167 S4). Through GPS-tracking, we thus had information on the foraging ecology of shearwaters
168 for periods of up to 5 days, and for approximately two-week periods (feather growth period)
169 through isotopic analyses. No effect of manipulation and instrumentation was found on the
170 breeding performance and divorce rate of shearwaters at this study site (Authier *et al.* 2013).
171 Also, device and exposure to stress potentially affecting short-term behavior was
172 standardized, as all birds were handled in exactly the same manner.

173

174 *Identification of foraging locations*

175 We considered a foraging trip as a round trip between colony/colony or colony/raft because
176 sometimes shearwaters stopped at rafts localized within 4 km of the colony before starting a
177 new trip. We identified the foraging locations of each trip using the residence in space and
178 time method (Torres *et al.* 2017). This method discriminates between behavioural states by
179 calculating the amount of space and time occupied by an individual in an area of constant
180 surface (a circle of radius r): Movement across long distances and protracted residency time
181 within an area reflect foraging behaviour; short movement distances and long residency time
182 reflect resting, and short distance and time correspond to travelling. The radius r was
183 determined with an automated dynamic scaling process for each foraging trip (Torres *et al.*
184 2017). Its average value was 0.52 ± 0.14 km (\pm SD). Foraging locations corresponding to
185 surface pecking behavior may have been omitted, yet previous studies showed that this
186 behavior is marginal in shearwaters (Camphuysen & Van Der Meer 2001).

187

188 *Prey field modelling*

189 To obtain daily shearwater prey distributions (zooplankton and pelagic fish; Sarà 1993;
190 Ramos *et al.* 2009) across our entire study area, we modelled biomasses (tonnes) of European
191 anchovies (*Engraulis encrasicolus*), sardines (*Sardina pilchardus*) and sprats (*Sprattus*
192 *sprattus*) of both juvenile and adult stages. We also modelled the abundance (ind.m^{-3}) of two
193 zooplankton groups: ‘preferred zooplankton prey’ (copepods, euphausiids, fish eggs and fish
194 larvae) and ‘others’, based on shearwater dietary preferences (Appendix S2). Empirical data
195 for potential prey were collected each year in July during PELMED oceanographic campaigns
196 (Appendix S2, Fig. S2.2). We used spatial generalized linear mixed models with a Horseshoe
197 prior in a Bayesian framework (Authier *et al.* 2017) and models were fitted with daily
198 dynamic oceanographic predictors (Fernandez *et al.* 2017, see Appendix S2). Such models
199 make robust and accurate predictions for fish biomass in the Gulf of Lions, including

200 extrapolations (Authier *et al.* 2017). We assessed zooplankton model robustness using leave-
201 one-out cross-validation (see Appendix S2). The ecological niches of small pelagic fish and
202 zooplankton are sustained across the summer period in the Gulf of Lions (Plounevez &
203 Champalbert 2000), and the slight temporal mismatch between prey field assessment and bird
204 tracking was not an issue.

205

206 *Resource selection of shearwaters*

207 We assessed Scopoli's shearwater resource selection functions (RSF; Manly *et al.* 2002)
208 based on daily prey distributions. Such analyses are rarely performed in marine ecology (but
209 see Wakefield *et al.* 2009; Raymond *et al.* 2015) because direct information on prey
210 availability is particularly difficult to obtain (Grémillet *et al.* 2004; Torres *et al.* 2008). RSF
211 compared the daily predictions for the six fish biomasses, the two zooplankton abundances
212 and their predictability (i.e. variance of biomasses or abundances calculated over the previous
213 seven days) at foraging locations and at available locations where birds could potentially
214 forage. Prey-related variables were standardized, and availability was determined in two
215 steps. First, for each observed foraging trip, we simulated 10 tracks that started at the same
216 location as the observed trip using a first-order vector autoregressive model (Raymond *et al.*
217 2015). Simulated tracks considered no habitat preference, while respecting constraints on trip
218 structure (duration and travel speed; Raymond *et al.* 2015). We then identified available
219 foraging locations for each simulated track using the residence in space and time method
220 described previously (Torres *et al.* 2017). Foraging locations and their associated available
221 locations occurred at the same spatio-temporal scale and we therefore controlled for short-
222 term variability in prey spatial distribution. Additionally, with simulated tracks being spatially
223 anchored to the colony, we used a non-uniform spatial distribution of availability adapted to

224 study central-place foragers that use areas close to the colony more frequently than elsewhere
 225 (Wakefield *et al.* 2009; Monsarrat *et al.* 2013).

226 We fitted one RSF for each of the 16 prey-related variables, and estimated RSF
 227 coefficients using mixed-effects logistic regressions (Gillies *et al.* 2006; Hebblewhite &
 228 Merrill 2008; Courbin *et al.* 2013). We used nested random intercepts to accommodate the
 229 three-level hierarchical structure of our data: foraging locations (n = 56945) within foraging
 230 trips (n = 182) within individuals (n = 75) (Hebblewhite & Merrill 2008). Random intercepts
 231 corrected for differences in sample size between foraging trips and individuals (Gillies *et al.*
 232 2006). We added random coefficients (one slope per individual and per trip) to assess
 233 differences in resource selection between individuals and trips (conditional estimates) in
 234 addition to estimate population-level responses (marginal estimate; Gillies *et al.* 2006;
 235 Hebblewhite & Merrill 2008; Leclerc *et al.* 2016; Carneiro *et al.* 2017). We tested the added
 236 value of using random coefficients based on the Akaike Information Criterion (AIC). RSF
 237 modelled for foraging location i , trip j and shearwater k took the form:

238

$$239 \quad w(\mathbf{x}_{ijk}) = \exp(\beta_0 + \mathbf{X}\boldsymbol{\beta} + \gamma_{0jk}^{(trip)} + \gamma_{0k}^{(bird)} + \gamma_{xjk}^{(trip)} x_{ijk} + \gamma_{xk}^{(bird)} x_{ijk}), \quad (1)$$

240

241 where $w(\mathbf{x}_{ijk})$ is the relative probability of selecting resources for shearwaters, \mathbf{x} is a
 242 vector, β_0 is the mean intercept, $\mathbf{X}\boldsymbol{\beta}$ is the vector of the fixed-effect resource selection
 243 coefficients for the set of covariate (i.e. the standardized fish biomasses, standardized
 244 zooplankton abundances or their standardized variances, year [four levels] and islands [two
 245 levels]), $\gamma_{0jk}^{(trip)}$ and $\gamma_{0k}^{(bird)}$ are the random intercepts at the trip and individual levels,
 246 respectively, $\gamma_{xjk}^{(trip)}$ is the random coefficient of prey-related variable x for trip j and
 247 shearwater k , and $\gamma_{xk}^{(bird)}$ is the random coefficient of x for shearwater k . No multicollinearity

248 between variables was detected (variance inflation factor being < 2 ; Dormann *et al.* 2013).
249 We accounted for multiple comparisons by adjusting the 95% confidence interval of RSF
250 coefficients with Benjamini-Yekutieli correction (Benjamini & Yekutieli 2001). RSFs were
251 performed with the *lme4* package (Bates *et al.* 2015) of the R software (R Development Core
252 Team 2016).

253

254 *Assessing individual specialization in resource selection (ISRS)*

255 We quantified ISRS, i.e. within-individual consistency in resource selection, by calculating an
256 adjusted repeatability index R_k for each shearwater k between its different trips (47 birds were
257 tracked for multiple trips) and each prey-related variable. We adapted the population-level
258 repeatability index R developed for logistic regression with random coefficients (Johnson
259 2014; Nakagawa *et al.* 2017) at the individual-level, by partitioning the global observation-
260 level (GPS location level) variance σ_ε^2 at the individual level, as usually done for linear
261 models (Potier *et al.* 2015; Wakefield *et al.* 2015; see Appendix S5). In a mixed RSF for
262 foraging location i , trip j and shearwater k , R_k took the form:

263

$$264 \quad R_k = \frac{\sigma_{x,between}^2}{\sigma_{x,between}^2 + \sigma_{x,within}^2 + \sigma_{\varepsilon k}^2}, \quad (2)$$

265

266 where $\sigma_{x,between}^2$ and $\sigma_{x,within}^2$ are the between- and within-individual variances (bird and trip
267 level, respectively) estimated from Eq. 1 with a random effect for the prey-related variable x ,
268 $\sigma_{\varepsilon k}^2$ is the partitioned observation-level variance for the k^{th} bird given a logit link.

269 R_k values range between 0 and 1, with 1 meaning high consistency in resource
270 selection for shearwater k between its different trips. Low R_k values arise from heterogeneous
271 resource selection among foraging trips or locations of shearwater k (i.e. high within-

272 individual and/or partitioned observation-level variance). Analyses were performed with the
273 *rptR* package (Stoffel *et al.* 2017) of the R software (R Development Core Team 2016).

274

275 *Assessing individual foraging site fidelity (IFSF)*

276 We quantified within-individual consistency in the use of space, an index of IFSF (Wakefield
277 *et al.* 2015). For each shearwater k in each year ($n = 47$ individuals and 154 trips), we
278 calculated the 95% utilization distributions (UDs) for each of its trips based on foraging
279 locations only, and assessed the mean overlap between all pairwise combinations of
280 consecutive UD's using Bhattacharyya's affinity (BA_k , Fieberg & Kochanny 2005). BA_k ranges
281 between 0 (no spatial overlap) and 1 (perfect spatial overlap). All UD's were calculated with a
282 fixed bandwidth (Wakefield *et al.* 2015) of 0.5 km that encompassed the extent of almost all
283 bandwidth estimations ($href$) calculated for a random sample of foraging areas and individuals
284 ($n = 32$, c.a. 93-quantile of $href = 0.5$ km), on a 0.3 km resolution grid.

285 We determined if overlap among foraging areas of different trips of a given individual
286 k (BA_k) differed from a random expectation, $BA_{k,random}$. $BA_{k,random}$ was the average overlap
287 between each UD for observed trips and each UD for the immediate previous and next
288 simulated tracks. We compared BA_k and $BA_{k,random}$ with a paired t-test. We also tested if BA_k
289 differed from overlap among foraging areas of different individuals, $BA_{k,between}$. $BA_{k,between}$ was
290 the average overlap for individual k between each of its UD and the UD's of other individuals
291 occurring within ± 1 day. We contrasted BA_k and $BA_{k,between}$ with a paired t-test. Analyses were
292 performed with the *adehabitat* package (Calenge 2006) of the R software (R Development
293 Core Team 2016).

294 Finally, we used Spearman rank correlation to investigate the relationships between
295 IFSF (BA_k) and ISRS (R_k), and between IFSF (BA_k) and individual selection coefficients

296 $(\gamma_{xk}^{(bird)})$ in Eq. 1) for each prey-related variable. P-values were adjusted with Benjamini-
297 Yekutieli correction (Benjamini & Yekutieli 2001).

298

299 *Identifying foraging trip tactics*

300 In order to identify the main foraging trip tactics within the shearwater population, reflecting a
301 potential gradient of specialization with respect to trophic level and/or prey type, we
302 discriminated between groups of trips (cluster) with similar resource selection. We conducted
303 the analysis at the trip level because of higher heterogeneity within, than between individuals
304 (Fig. 3). We ran a hierarchical cluster analysis with a Ward clustering method using selection
305 coefficients of 182 trips ($\gamma_{xjk}^{(trip)}$ in Eq. 1) for biomasses of adult anchovies, adult sprats and
306 abundances of both zooplankton groups. The selection coefficients for other variables of
307 biomass had low variations around 0 and were not considered in the cluster analysis (Fig. 3B).

308

309 **Results**

310 We collected 2.4 ± 1.8 trips per bird (mean \pm SD, ranging from 1 to 11 trips), characterized by
311 an average trip range of 59 ± 46 km from the colony, a total travelled distance of 218 ± 167
312 km, and a duration of 22.2 ± 11.9 hours (Appendix S6, Fig. S6.1). Foraging areas mostly
313 occurred within the continental shelf of the Gulf of Lions and along the continental slope,
314 generally within a 40 km-radius from the colony and over the -100m isobath (Fig. 2, Fig.
315 S6.2).

316

317 *Rapid changes in resource selection feature low ISRS*

318 Random coefficients for prey-related variables improved fit of RSFs ($\Delta AIC > 6652$ for all
319 models). RSFs including the variance of biomasses of all juvenile fish and adult sardines
320 failed to converge. At the population-level, shearwaters selected foraging areas with higher

321 abundances of both zooplankton groups and generally lower fish biomass than expected
322 randomly (Appendix S6, Table S6.1). However, this apparent habitat selection pattern
323 resulted from heterogeneous selection among individuals, and to a greater extent, from
324 heterogeneous selection across trips of the same individuals (Table S6.1, Fig. 3). The
325 relatively high within-individual variability in selection featured a low ISRS for each prey-
326 related variable ($R_k < 0.3$, Fig. 4A, Table S6.2).

327 At the trip level, clustering revealed two foraging trip tactics (Fig. S6.3). Shearwaters
328 selected different prey and trophic levels among their trips, which entailed rapid changes in
329 their resource selection (Table S6.3). During most trips (54%), shearwaters selected areas
330 with higher abundances of both zooplankton groups, as well as areas with higher biomasses of
331 adult anchovies and adult sprats, than expected randomly (Fig. 5A). The biomass of pelagic
332 fish increased along the shelf edge and at the Cassis canyon head close to the colony, while
333 zooplankton-preferred group was associated with coastal areas, the plume of the Rhône river,
334 and canyons (Appendix S2, Table S2.1, S2.5, S2.7, Fig. S2.3). Selection of high zooplankton-
335 other abundance required cautious interpretation due to the poor prediction ability of its
336 model, while zooplankton-preferred abundance was correctly predicted (Fig. S2.4).
337 Shearwaters used zooplankton-only specialist trips to a lesser extent (46%), selecting areas
338 with a higher zooplankton-preferred abundance and lower fish biomasses than randomly
339 expected (Fig. 5B). Birds always avoided the most coastal foraging areas with high biomass
340 of sardines and juvenile sprats (Fig. 5, Table S2.3, S2.4, S2.6, Fig. S2.3). Isotopic analyses
341 revealed that the trophic position of shearwaters was 3.30 ± 0.25 (median \pm IQR, Appendix
342 S4, Fig. S4.1), and confirmed that most birds used both foraging tactics and foraged on
343 different trophic levels including zooplankton (trophic position = 2) and small pelagic fish
344 (trophic position = 3, Fig. 6).

345

346 *Low individual foraging site fidelity*

347 Shearwaters showed low IFSF between consecutive trips, with values only slightly higher
348 than for a random process (mean $BA_k = 0.135$, mean $BA_{k,random} = 0.084$, t-test: $t_{46} = 5.43$, $P <$
349 0.001 , Fig. 4B). Different individuals shared some foraging areas, with similar BA index
350 found within and between birds (mean $BA_{k,between} = 0.131$, t-test: $t_{46} = 0.39$, $P = 0.70$, Fig. 4B).
351 IFSF was not related to the number of trips performed by single individuals ($r^2 < 0.01$, $P =$
352 0.51). IFSF was uncoupled from shearwater resource selection and its within-individual
353 consistency (ISRS).

354

355 *Prey predictability shapes search patterns in shearwaters*

356 Shearwaters used directional search to find fish as they selected foraging areas with high
357 predictability (i.e. lower variance) of biomasses of adult anchovies and sprats (Fig. 5A). In
358 contrast, they selected areas with high zooplankton abundance independently from their
359 predictability (Fig. 5). Interestingly, zooplankton abundances were less predictable than fish
360 biomasses and temporal autocorrelation in zooplankton abundances was low after only one
361 day, the mean trip duration (Fig. S2.1).

362

363 **Discussion**

364 As theoretically expected, our broad analytical framework allowed us to demonstrate that
365 short-term prey predictability induces low individual specialization in resource selection
366 (ISRS) and low individual foraging site fidelity (IFSF) within a predator population.

367 According to RSF and isotopic analyses, breeding Scopoli's shearwaters searched for
368 zooplankton and fish within the Gulf of Lions, where we showed daily changes in prey
369 distribution. To overcome prey field lability, we found that shearwaters searched for
370 zooplankton patches, which they detect remotely via olfactory cues (Dell'Araccia *et al.* 2014).

371 Such tactics do not require previous information on prey distributions. Indeed, RSFs showed
372 that shearwaters selected zooplankton patches independently from their predictability.
373 However, environmental variation (e.g. wind conditions, low prey availability) and lack of
374 luck (stochastic noise) may prevent shearwaters from detecting distant zooplankton patches.
375 Consequently, we found that shearwaters frequently switched between alternative foraging
376 tactics, and their selection of predictable fish patches may suggest memory/public information
377 use. Crucially, we demonstrated how low prey predictability shaped specialized foraging
378 tactics over the short-term and potentially information use, and resulted in the use of varied
379 foraging sites and diet items.

380

381 *Prey field lability constrains individual specialization in resource selection*

382 Costs associated with intra-specific competition and niche overlap favour individual
383 specialization (Araújo *et al.* 2011; Bolnick *et al.* 2011; Wolf & Weissing 2012; Wakefield *et*
384 *al.* 2013), and lead to the emergence of competing density-dependent foraging behaviours and
385 diet (Fortin *et al.* 2008; Tinker *et al.* 2012). This is true in stable environments, but when prey
386 distributions vary spatio-temporally and become temporarily inaccessible, fitness costs
387 associated with narrow resource selection can increase (Fortin *et al.* 2008; Woo *et al.* 2008).
388 To increase net intake when tracking highly mobile prey, predators can diversify their diet and
389 use selection patterns allowing them to exploit different prey simultaneously, as demonstrated
390 for wolves (*Canis lupus*; Courbin *et al.* 2013). Low ISRS is thus expected if behavioural
391 plasticity is not dramatically constrained (Sih *et al.* 2004, Hendry 2016) and if higher
392 encounter rates favoured by behavioural plasticity overcome the potential benefits of
393 specialization (improved search image and handling technique). As hypothesized, shearwaters
394 had low short-term ISRS, and isotopic analyses confirmed that most individuals consumed
395 various prey at different trophic levels (Fig. 6; median individual trophic position was 3.30;

396 Fig. S4.1). Zooplankton-based diets are common in seabirds (Savoca & Nevitt 2014) and, in
397 our study system, fish and zooplankton-preferred have close calorific contents (Harmelin-
398 Vivien *et al.* 2012). Hence, diet diversification and low ISRS should not be promoted by a
399 low zooplankton nutritional value. Overall, low spatio-temporal predictability in prey
400 distributions constrained predators to diversify their diet at the individual level, thereby
401 diminishing inter-individual differences. However, trophic position appeared more
402 heterogeneous among individuals in some years (2010 and 2011; Fig. S4.1), revealing that
403 competing foraging strategies may emerge (at low frequency) in dynamic systems.

404 Seabird populations can switch diets between years (Garthe *et al.* 2011; Tew Kai *et al.*
405 2013), ultimately limiting negative effects on population dynamics (Cury *et al.* 2011).
406 Whether such dietary plasticity arises from variability in prey availability, or from predator
407 behavioural changes is often unclear (Hunsicker *et al.* 2011). In our study system, we showed
408 that inter-annual dietary switches can arise from changes in resource selection, rather than in
409 prey availability (Table S6.5). Thereby, changes in prey distribution and availability occurring
410 at multiple temporal scales (day to year) shaped individual specialization: Short-term changes
411 prevented short- and long-term specialization, while long-term changes tended to favour
412 individual specialization in the shorter-term.

413

414 *Relaxing individual foraging site fidelity is not sufficient in dynamic prey fields*

415 In systems with low prey predictability, low ISRS should arise when individuals use a
416 generalist foraging tactic (no selection), or each individual uses different short-term
417 specialized foraging tactics. IFSF is common in colonial central-place predators (Arthur *et al.*
418 2015; Baylis *et al.* 2015; Ceia & Ramos 2015; Wakefield *et al.* 2015). When prey distribution
419 varies daily, as observed in our studied system, individuals have to balance ISRS and IFSF,
420 and IFSF should imply generalising of diet and habitat use, while preventing specialization

421 (Fig. 1). As theoretically expected, by relaxing IFSF only, Scopoli's shearwaters were able to
422 track daily changes in prey distribution, selecting foraging areas with high biomasses of adult
423 anchovies and adult sprats, and high zooplankton abundance. Antarctic fur seals
424 (*Arctocephalus gazella*) tracking changes in prey distribution during the winter also showed
425 low IFSF (Arthur *et al.* 2015).

426 Our dynamic study area and associated low predictability in prey distributions implied,
427 however, that shearwaters switched foraging tactics on a daily basis. This resulted in rapid
428 changes in individual resource selection. Birds used 1-day trips, either focusing on nearby
429 areas with high zooplankton abundance, or also searching more distant waters harbouring
430 adult anchovies or sprats. Short-term resource selection by shearwaters highlighted their
431 foraging plasticity when exposed to changes in prey distributions. This strategy, which could
432 allow predators to maintain their foraging efficiency, requires some capacity to predict prey
433 distributions (Pettex *et al.* 2010), and/or to reduce search time with the prospect of exploring
434 alternative prey patches.

435

436 *Linking prey predictability, information use and ISRS*

437 Our study emphasizes how the coupling between the frequency of prey redistribution and the
438 frequency at which information on prey location can be updated and reused by the predator
439 shapes search patterns of predators and ISRS. Thereby, it sheds light on the mechanisms
440 linking prey predictability and narrow resource selection. Shearwaters searched for
441 zooplankton-rich areas independently of their predictability. Autocorrelation in zooplankton
442 abundance was low after only one day and birds were unlikely to use memory/public
443 information on zooplankton distribution between daily trips. In this context, sensory cues
444 available over long distances seem a far more efficient way to locate shifting resources than
445 public information (Savoca & Nevitt 2014; Spiegel & Crofoot 2016). Recent investigations

446 confirm that shearwaters use long to medium-scale olfactory cues to find zooplankton
447 (Dell’Ariccia *et al.* 2014). However, combination of unstable olfactory landscapes and
448 quickly outdated information on zooplankton distribution limits ISRS and requires alternative
449 foraging tactics. Further investigations should verify if the increase of individual
450 specialization in the capacity to use sensory cues according to age and experience (Harel *et al.*
451 2016) is balanced by prey unpredictability.

452 During trips specialized on zooplankton and fish, shearwaters selected areas with the
453 most predictable biomasses of adult anchovies and sprats. Fish biomasses being
454 autocorrelated for longer periods than shearwater daily trips (Fig. S2.1), shearwaters may gain
455 information on prey locations using short-term memory (Wakefield *et al.* 2013; Spiegel &
456 Crofoot 2016) or public information (Weimerskirch *et al.* 2010; Spiegel & Crofoot 2016;
457 Wells *et al.* 2016). Our results confirm that both mechanisms can occur in parallel, as
458 shearwaters shared a limited number of foraging areas across their consecutive trips, and
459 different individuals shared some foraging areas at similar time. Although information on
460 patch location can reduce search times and could favour foraging efficiency and ISRS, we
461 found almost no ISRS. Prey predictability being generally low, individuals rather used public
462 information to locate prey patches independently of the species, probably following their
463 peers (Harel *et al.* 2017). We found low overlap values among birds but the small proportion
464 of tracked individuals probably led to underestimating shared space use. Additional sources of
465 information may also be involved, such as the visual detection of tuna chasing smaller pelagic
466 fish, or knowledge of the most predictable fishing areas through long-term memory
467 (Weimerskirch 2007; Monsarrat *et al.* 2013). Interestingly, moderate ISRS for predictable
468 anchovy patches revealed individual differences in bird ability to use available information
469 (Fig. 4A; Spiegel & Crofoot 2016).

470

471 **Conclusions**

472 Our study demonstrates that colonial predator populations preying on relatively unpredictable
473 prey are subjected to ecological drivers leading to contrasting effects on ISRS. Thereby, the
474 negative effect of prey unpredictability and patchiness on ISRS, overrides the positive effect
475 of intra-specific competition (Fortin *et al.* 2008; Araújo *et al.* 2011). Prey unpredictability
476 also seems to limit potential inter-sexual differences in individual specialization (both sexes
477 were tracked here). Prey variability may further constrain the expected enhancement of
478 individual specialization with age/experience due to longer sampling of environmental
479 variation and development of specific skills (see also Woo *et al.* 2008). Future work explicitly
480 considering age and sex of tagged birds should therefore quantify the opposite effects of low
481 prey predictability and internal states on individual specialization. Moreover, individual
482 specialization could vary among phases of the annual cycle, especially if birds migrate and/or
483 encounter different foraging conditions.

484 Importantly, our study shows how individual responses to enhanced environmental
485 stochasticity driven by global change could potentially impact population persistence. A
486 population requires some degree of non-specialization to overcome novel conditions, e.g.
487 generalist populations consisting of specialized individuals (Wolf & Weissing 2012; Merrick
488 & Koprowski 2017). Here, we reinforce the idea that individual plasticity in foraging
489 movements (low individual specialization and inter-annual variation in tactics used) could be
490 a globally important pathway to cope with changing conditions and maintain population
491 density, in the presence of limited behavioural plasticity (Dall *et al.* 2004, Sih *et al.* 2004,
492 Hendry 2016). Finally, individual foraging plasticity may prevent the use of apex predators as
493 ecological indicators of lower trophic levels (Grémillet & Charmantier 2010). This is
494 particularly relevant as seabird populations are being flagged as indicators of food supplies
495 within marine systems (Boyd *et al.* 2015, Brisson-Curadeau *et al.* 2017).

496

497 **Acknowledgements**

498 This study was funded by the French Agency for Biodiversity (AFB) within the program
499 PACOMM-Natura2000 en mer and INDEXPUF, and by the OSU OREME Montpellier.
500 Handling protocols for shearwaters were approved by the boards of the ‘Parc National des
501 Calanques’ (permit number: 2014-068, 2016-111), the French ‘Direction Départementale de
502 la Protection des Populations’ (permit number: 34-369, #A34-505), the French ‘Direction
503 Départementale des Territoires et de la Mer des Bouches-du-Rhône’ (permit number: 170-
504 0010, 184-0017) and the ‘Comité d’Ethique pour l’Expérimentation Animale Languedoc-
505 Rousillon’ (permit number: 1170). Thanks to O. Spiegel, R. Nathan and one anonymous
506 reviewer for their helpful comments. We are very grateful to M. Authier for his help with
507 Bayesian models for prey, S. Benhamou for our fruitful discussions and A. Kibler for revising
508 the manuscript. Thanks to all fieldworkers involved in this study: P. Giraudet, L. Martin, A.
509 Gaborit Loret, M. Kriloff, J.-B. Pons, C. de Franceschi. We also thank the agents from ‘Parc
510 National des Calanques’ of Marseille for providing support during the fieldwork (J.-P.
511 Durand, C. Pastorelli and A. Mante), N. El Ksabi for the preparation of feather samples,
512 Plateforme d’Analyses Chimiques en Ecologie at CEFÉ for logistic support, and Plateforme
513 ‘Spectrométrie isotopique’ (University of La Rochelle – LIENSs) for isotopic analyses of
514 feathers samples. Thanks to the staff of PELagic MEDiterranean oceanographic campaigns to
515 share with us empirical data on fish and zooplankton (doi: <http://dx.doi.org/10.18142/19>) and
516 to Directive Cadre Stratégie pour le Milieu Marin for providing fish isotopic values in 2015.
517 We are grateful to B. Raymond from the Australian Antarctic Division for sharing his track
518 simulation R package. We finally are very grateful to NASA (Ocean Color project), CNES
519 (Aviso+ project), IEDA (Marine Geoscience Data System), IFREMER, SHOM and Meteo

520 France (PREVIMER project), and EUSeaMap European project for sharing oceanographic
521 data and satellite images.

522

523 **References**

524 Allgeier, J.E., Adam, T.C. & Burkepile, D.E. (2017). The importance of individual and
525 species-level traits for trophic niches among herbivorous coral reef fishes. *Proc. R. Soc.*
526 *B*, 284, 20170307.

527 Anselme, L. & Durand, J.P. (2012). *Le puffin cendré Calonectris diomedea diomedea, Etat*
528 *des connaissances et de conservation actualisés, des populations nicheuses des petites îles de*
529 *Méditerranée*, pp 1-17.

530 Araújo, M.S., Bolnick, D.I. & Layman, C.A. (2011). The ecological causes of individual
531 specialization. *Ecol. Lett.*, 14, 948-958.

532 Arthur, B. *et al.* (2015). Return customers: Foraging site fidelity and the effect of
533 environmental variability in wide-ranging Antarctic fur seals. *PLoS ONE*, 10, e0120888.

534 Authier, M., Péron, C., Mante, A., Vidal, P. & Grémillet, D. (2013). Designing observational
535 biologging studies to assess the causal effect of instrumentation. *Methods Ecol. Evol.*, 4, 802-
536 810.

537 Authier, M., Saraux, C. & Péron, C. (2017). Variable selection and accurate predictions in
538 habitat modelling: a shrinkage approach. *Ecography*, 40, 549-560.

539 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects
540 Models Using lme4. *J. Stat. Softw.*, 67, 1-48.

541 Baylis, A.M.M. *et al.* (2015). Diving deeper into individual foraging specializations of a large
542 marine predator, the southern sea lion. *Oecologia*, 179, 1053-1065.

543 Bell, A.M., Hankison, S.J. & Laskowski, K.L. (2009) The repeatability of behaviour: a meta-
544 analysis. *Anim. Behav.*, 77, 771-783.

545 Benjamini, Y. & Yekutieli, D. (2001). The control of the false discovery rate in multiple
546 testing under dependency. *Ann. Stat.*, 29, 1165-1188.

547 Bolnick, D.I. *et al.* (2011). Why intraspecific trait variation matters in community ecology.
548 *Trends Ecol. Evol.*, 26, 183-192.

549 Boyd, C. *et al.* (2015). Predictive modelling of habitat selection by marine predators with
550 respect to the abundance and depth distribution of pelagic prey. *J. Anim. Ecol.*, 84, 575-1588.

551 Brisson-Curadeau, E., Patterson, A., Whelan, S., Lazarus, T. & Elliott, K.H. (2017). Tracking
552 cairns: Biologging improves the use of seabirds as sentinels of the sea. *Front. Mar. Sci.*, 4,
553 357.

554 Calenge, C. (2006). The package “adehabitat” for the R software: a tool for the analysis of
555 space and habitat use by animals. *Ecol. Modell.*, 197, 516-519.

556 Camphuysen, K. & Van Der Meer, J. (2001). Pelagic distribution, moult and (sub-)specific
557 status of Cory’s shearwaters *Calonectris [D.] diomedea/borealis* wintering off Southern
558 Africa. *Mar. Ornithol.*, 29, 89-96.

559 Carneiro, A.P.B., Bonnet-Lebrun, A.S., Manica, A., Staniland, I.J. & Phillips, R.A. (2017).
560 Methods for detecting and quantifying individual specialisation in movement and foraging
561 strategies of marine predators. *Mar. Ecol. Prog. Ser.*, 578, 151-166.

562 Catry, T., Alves, J.A., Gill, J.A., Gunnarsson, T.G. & Granadeiro, J.P. (2014) Individual
563 specialization in a shorebird population with narrow foraging niche. *Acta Oecol.*, 56, 56-65.

564 Ceia, F.R. & Ramos, J.A. (2015). Individual specialization in the foraging and feeding
565 strategies of seabirds: a review. *Mar. Biol.*, 162, 1923-1938.

566 Courbin, N., Fortin, D., Dussault, C., Fargeot, V. & Courtois, R. (2013). Multi-trophic
567 resource selection function enlightens the behavioural game between wolves and their prey. *J.*
568 *Anim. Ecol.*, 82, 1062-1071.

569 Cury, P.M. *et al.* (2011). Global seabird response to forage fish depletion – One-third for the

570 birds. *Science*, 334, 1703-1706.

571 Dall, S.R.X., Houston, A.I. & McNamara, M. (2004). The behavioural ecology of personality:
572 consistent individual differences from an adaptive perspective. *Ecol. Lett.*, 7, 734-739.

573 Dell'Araccia, G., Célérier, A., Gabirot, M., Palmas, P., Massa, B. & Bonadonna, F. (2014).
574 Olfactory foraging in temperate waters: sensitivity to dimethylsulphide of shearwaters in the
575 Atlantic Ocean and Mediterranean Sea. *J. Exp. Biol.*, 217, 1701-1709.

576 Dormann, C.F. *et al.* (2013). Collinearity: a review of methods to deal with it and a simulation
577 study evaluating their performance. *Ecography*, 36, 27-46.

578 Duchesne, T., Fortin, D. & Courbin, N. (2010). Mixed conditional logistic regressions for
579 habitat selection studies. *J. Anim. Ecol.*, 79, 548-555.

580 Fernandez, M., Yesson, C., Gannier, A., Miller, P.I. & Azevedo, J.M.N. (2017). The
581 importance of temporal resolution for niche modelling in dynamic environments. *J.*
582 *Biogeogr.*, 00, 1-12. <https://doi.org/10.1111/jbi.13080>.

583 Fieberg, J. & Kochanny, C.O. (2005). Quantifying homerange overlap: the importance of the
584 utilization distribution. *J. Wildlife Manage.*, 69, 1346-1359.

585 Fortin, D., Morris, D.W. & McLoughlin, P.D. (2008). Habitat selection and the evolution of
586 specialists in heterogeneous environments. *Israel J. Ecol. Evol.*, 54, 311-328.

587 Garthe, S., Montevecchi, W.A. & Davoren, G.K. (2011). Inter-annual changes in prey fields
588 trigger different foraging tactics in a large marine predator. *Limnol. Oceanogr.*, 56, 802-812.

589 Gillies, C. *et al.* (2006) Application of random effects to the study of resource selection by
590 animals. *J. Anim. Ecol.*, 75, 887-898.

591 Grémillet, D., Wilson, R.P., Storch, S. & Gary, Y. (1999). Three-dimensional space
592 utilization by a marine predator. *Mar. Ecol. Prog. Ser.*, 183, 263-273.

593 Grémillet, D. *et al.* (2004). Linking the foraging performance of a marine predator to local
594 prey abundance. *Funct. Ecol.*, 18, 793-801.

595 Grémillet, D. & Charmantier, A. (2010). Shifts in phenotypic plasticity constrain the value of
596 seabirds as ecological indicators of marine ecosystems. *Ecol. Appl.*, 20, 1498-1503.

597 Harel, R., Horvitz, N. & Nathan, R. (2016). Adult vultures outperform juveniles in
598 challenging thermal soaring conditions. *Sci. Rep.*, 6:27865.

599 Harel, R., Spiegel, O., Getz, W.M. & Nathan, R. (2017). Social foraging and individual
600 consistency in following behaviour: testing the information centre hypothesis in free-ranging
601 vultures. *Proc. R. Soc. B*, 284, 20162654.

602 Harmelin-Vivien, M., Mahé, K., Bodiguel, X. & Mellon-Duval, C. (2012). Possible link
603 between prey quality, condition and growth of juvenile hake (*Merluccius merluccius*) in the
604 Gulf of Lions (NW Mediterranean). *Cybium*, 36, 323-328.

605 Hebblewhite, M. & Merrill, E. (2008). Modelling wildlife-human relationships for social
606 species with mixed-effects resource selection models. *J. Appl. Ecol.*, 45, 834-844.

607 Hendry, A.P. (2016). Key questions on the role of phenotypic plasticity in eco-evolutionary
608 dynamics. *J. Hered.*, 107, 25-41.

609 Hunsicker, M.E. *et al.* (2011). Functional responses and scaling in predator-prey interactions
610 of marine fishes: contemporary issues and emerging concepts. *Ecol. Lett.*, 14, 1288-1299.

611 Johnson, P.C.D. (2014) Extension of Nakagawa & Schielzeth's R^2_{GLMM} to random slopes
612 models. *Methods Ecol. Evol.*, 5, 944-946.

613 Leclerc, M., Vander Wal, E., Zedrosser, A., Swenson, J.E., Kindberg, J. & Pelletier, F.
614 (2016). Quantifying consistent individual differences in habitat selection. *Oecologia*, 180,
615 697-705.

616 Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002).
617 *Resource selection by animals: statistical analysis and design for field studies*. Second
618 edition. Kluwer Academic Publishers, Dordrecht, pp. 1-221.

619 Meier, R.E. *et al.* (2017). Tracking, feather moult and stable isotopes reveal foraging

620 behaviour of a critically endangered seabird during the non-breeding season. *Divers. Distrib.*,
621 23, 130-145.

622 Merrick, M.J. & Koprowski, J.L. (2017). Should we consider individual behavior differences
623 in applied wildlife conservation studies. *Biol. Conserv.*, 209, 34-44.

624 Monsarrat, S., Benhamou, S., Sarrazin, F., Bessa-Gomes, C., Bouten, W. & Duriez, O.
625 (2013). How predictability of feeding patches affects home range and foraging habitat
626 selection in avian social scavengers? *PLoS ONE*, 8, e53077.

627 Nakagawa, S., Johnson, P.C.D. & Schielzeth, H. (2017). The coefficient of determination R²
628 and intra-class correlation coefficient from generalized linear mixed-effects models revisited
629 and expanded. *J. R. Soc. Interface*, 14, 20170213.

630 Navarro, J., Grémillet, D., Ramirez, F.J., Afán, I., Bouten, W. & Forero, M.G. (2017).
631 Shifting individual habitat specialization of a successful predator living in anthropogenic
632 landscapes. *Mar. Ecol. Prog. Ser.*, 578, 243-251.

633 Patrick, S.C. *et al.* (2014). Individual foraging specialisation and differences in searching
634 behaviour of a wide-ranging marine predator. *Oikos*, 123, 33-40.

635 Pettex, E., Bonadonna, F., Enstipp, M.R., Siorat, F. & Grémillet, D. (2010). Northern gannets
636 anticipate the spatio-temporal occurrence of their prey. *J. Exp. Biol.*, 213, 2365-2371.

637 Phillips, R.A., Lewis, S., González-Solís, J. & Daunt, F. (2017). Causes and consequences of
638 individual variability and specialization in foraging and migration strategies of seabirds. *Mar.*
639 *Ecol. Prog. Ser.*, 578, 117-150.

640 Plounevez, S. & Champalbert, G. (2000). Diet, feeding behaviour and trophic activity of the
641 anchovy (*Engraulis encrasicolus* L.) in the Gulf of Lions (Mediterranean Sea). *Oceanologica*
642 *Acta*, 23:175-192.

643 Potier, S., Carpentier, A., Grémillet, D., Leroy, B. & Lescroël, A. (2015). Individual
644 repeatability of foraging behaviour in a marine predator, the great cormorant, *Phalacrocorax*
645 *carbo*. *Anim. Behav.*, 103, 83-90.

646 R Development Core Team (2016). *R: A Language and Environment for Statistical*
647 *Computing*. R Foundation for Statistical Computing, Vienna.

648 Ramos, R., González-Solís, J. & Ruiz, X. (2009). Linking isotopic and migratory patterns in a
649 pelagic seabird. *Oecologia*, 160, 97-105.

650 Raymond, B. *et al.* (2015). Important marine habitat shift off east Antarctica revealed by two
651 decades of multi-species predator tracking. *Ecography*, 38, 121-129.

652 Sara, M. (1993) Feeding habits of Cory's shearwater (*Calonectris diomedea*) in the central
653 Mediterranean Sea. In: *Estatus y conservacion de aves marinas* {eds. Aguilar, J.S.,
654 Monbailliu, X.Y. & Paterson, A.M.}. Sociedad Espanola de Ornitologia, Madrid, pp. 213-
655 222.

656 Saraux, C. *et al.* (2014) Spatial Structure and Distribution of Small Pelagic Fish in the
657 Northwestern Mediterranean Sea. *PLoS ONE*, 9, e111211.

658 Savoca, M.S & Nevitt, G.A. (2014). Evidence that dimethyl sulfide facilitates a tritrophic
659 mutualism between marine primary producers and top predators. *Proc. Natl. Acad. Sci.*
660 *U.S.A.*, 111, 4157-4161.

661 Sih, A. Bell, A. & Johnson, J.C. (2004). Behavioral syndromes: an ecological and
662 evolutionary overview. *Trends Ecol. Evol.*, 19, 372-378.

663 Spiegel, O. & Crofoot, M.C. (2016). The feedback between where we go and what we know –
664 information shapes movement, but movement also impacts information acquisition. *Cur.*
665 *Opin. Behav. Sci.*, 12, 90-96.

666 Spiegel, O., Leu, S.T., Bull, C.M. & Sih, A. (2017). What's your move? Movement as a link
667 between personality and spatial dynamics in animal populations. *Ecol. Lett.*, 20, 3-18.

668 Stoffel, M.A., Nakagawa, S. & Schielzeth, H. (2017). rptR: Repeatability estimation and
669 variance decomposition by generalized linear mixed-effects models. *Methods Ecol. Evol.*, 8,
670 1639-1644.

671 Subalusky, A.L., Dutton, C.L., Rosi, E.J. & Post, D.M. (2017). Annual mass drownings of the
672 Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River.
673 *Proc. Natl. Acad. Sci. U.S.A.*, 114, 7647-7652.

674 Sutherland, W.J. (1987). Why do animals specialize? *Nature*, 32, 483-484.

675 Svanbäck, R. & Bolnick, D.I. (2005). Intraspecific competition affects the strength of
676 individual specialization: an optimal diet theory method. *Evol. Ecol. Res.*, 7, 993-1012.

677 Svanbäck, R. & Bolnick, D.I. (2007). Intraspecific competition drives increased resource use
678 diversity within a natural population. *Proc. R. Soc. B*, 274, 839-844.

679 Switzer, P.V. (1993). Site fidelity in predictable and unpredictable habitats. *Evol. Ecol.*, 7,
680 533-555.

681 Tew Kai, E. *et al.* (2013). Are Cape gannets dependent upon fishery waste? A multi-scale
682 analysis using seabird GPS-tracking, hydro-acoustic surveys of pelagic fish and vessel
683 monitoring systems. *J. Appl. Ecol.*, 50, 659-670.

684 Tinker, M.T. *et al.* (2012). Structure and mechanism of diet specialisation: testing models of
685 individual variation in resource use with sea otters. *Ecol. Lett.*, 15, 475-483.

686 Torres, L.G., Read, A.J. & Halpin, P. (2008) Fine-Scale Habitat Modeling of a Top Marine
687 Predator: Do Prey Data Improve Predictive Capacity. *Ecol. Appl.*, 18, 1702-1717.

688 Torres, L.G., Orben, R.A., Tolkova, I. & Thompson, D.R. (2017) Classification of Animal
689 Movement Behavior through Residence in Space and Time. *PLoS ONE*, 12, e0168513.

690 Violle, C. *et al.* (2012). The return of the variance: intraspecific variability in community
691 ecology. *Trends Ecol. Evol.*, 27, 244-252.

692 Wakefield, E.D., Phillips, R.A. & Matthiopoulos, J. (2009). Quantifying habitat use and
693 preferences of pelagic seabirds using individual movement data: a review. *Mar. Ecol. Prog.
694 Ser.*, 391, 165-182.

695 Wakefield, E.D. *et al.* (2011). Habitat preference, accessibility, and competition limit the
696 global distribution of breeding black-browed albatrosses. *Ecol. Monogr.*, 81, 141-167

697 Wakefield, E.D. *et al.* (2013). Space partitioning without territoriality in gannets. *Science*,
698 341, 68-70.

699 Wakefield, E.D. *et al.* (2015). Long-term individual foraging site fidelity – why some gannets
700 don't change their spots. *Ecology*, 96, 3058-3074.

701 Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep Sea Res.
702 Part 2 Top. Stud. Oceanogr.*, 54, 211-223.

703 Weimerskirch, H., Bertrand, S., Silva, J., Marques, C. & Goya, E. (2010). Use of social
704 information in seabirds: compass raft indicate the heading of food patches. *PLoS ONE*, 5,
705 e9928.

706 Wells, M.R., Angel, L.P. & Arnould, J.P.Y. (2016). Habitat-specific foraging strategies in
707 Australasian gannets. *Biol. Open*, 15, 921-927.

708 Wolf, M. & Weissing, F.J. (2012). Animal personalities: consequences for ecology and
709 evolution. *Trends Ecol. Evol.*, 27, 452-461.

710 Woo, K.J., Elliott, K.H., Davidson, M., Gaston, A.J. & Davoren, G.K. (2008). Individual
711 specialization in diet by a generalist marine predator reflects specialization in foraging
712 behaviour. *J. Anim. Ecol.*, 77, 1082-1091.

713 **Figure legends**

714 Figure 1. Theoretical outcomes for resource selection patterns (i.e. disproportionate use
715 relative to the availability of resources, from no selection [generalism] to positive selection) in
716 predators depending on individual foraging site fidelity (from low to high) and spatio-
717 temporal variability of prey distribution among days (from low to high). The intersection of
718 the three axes represents the lowest value along each axis.

719

720 Figure 2. Spatial distribution of foraging locations (black point) for Scopoli's shearwaters
721 breeding off Marseille (red triangle), Western Mediterranean during the chick-rearing period
722 in August 2011, 2012, 2014 and 2015. Foraging locations were determined using an
723 automatic process discriminating between different behavioural modes (travelling, resting and
724 foraging) along foraging trips (Torres *et al.* 2017).

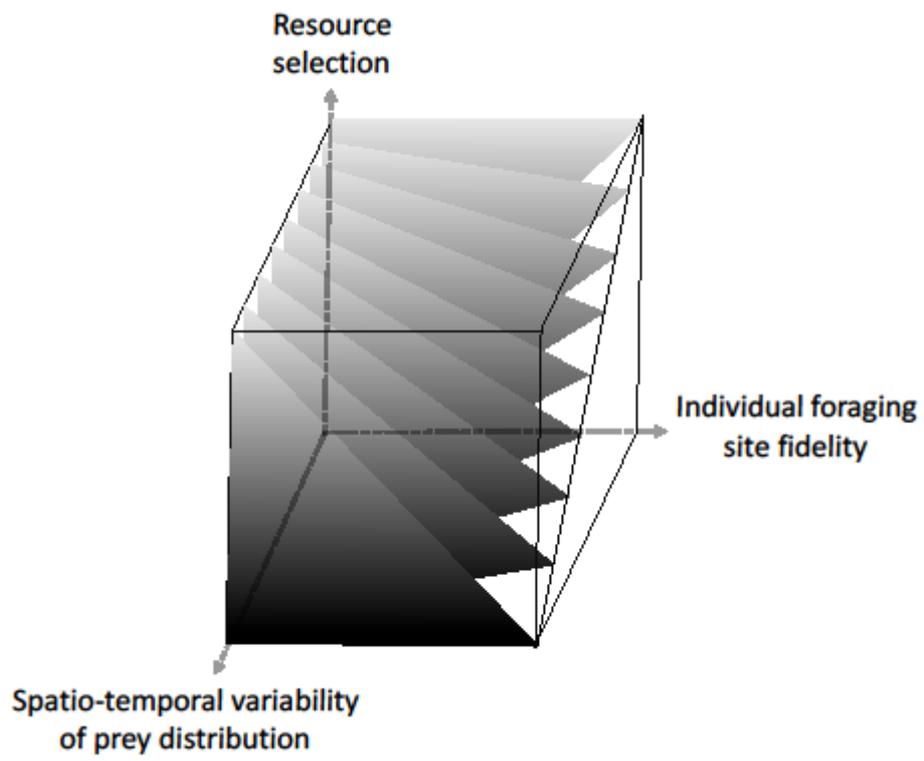
725

726 Figure 3. RSF coefficients of Scopoli's shearwaters at the individual (A) and trip (B) levels
727 (solid circle), in the Gulf of Lions (Western Mediterranean) during the chick-rearing period
728 between 2011 and 2015, estimated from three-level mixed-effects logistic regression models
729 (i.e. 75 individuals, 182 trips, 56945 GPS locations). Grey square represent the population-
730 level inference. Values are jittered and * mean values are divided by 10 to ease visualization.

731

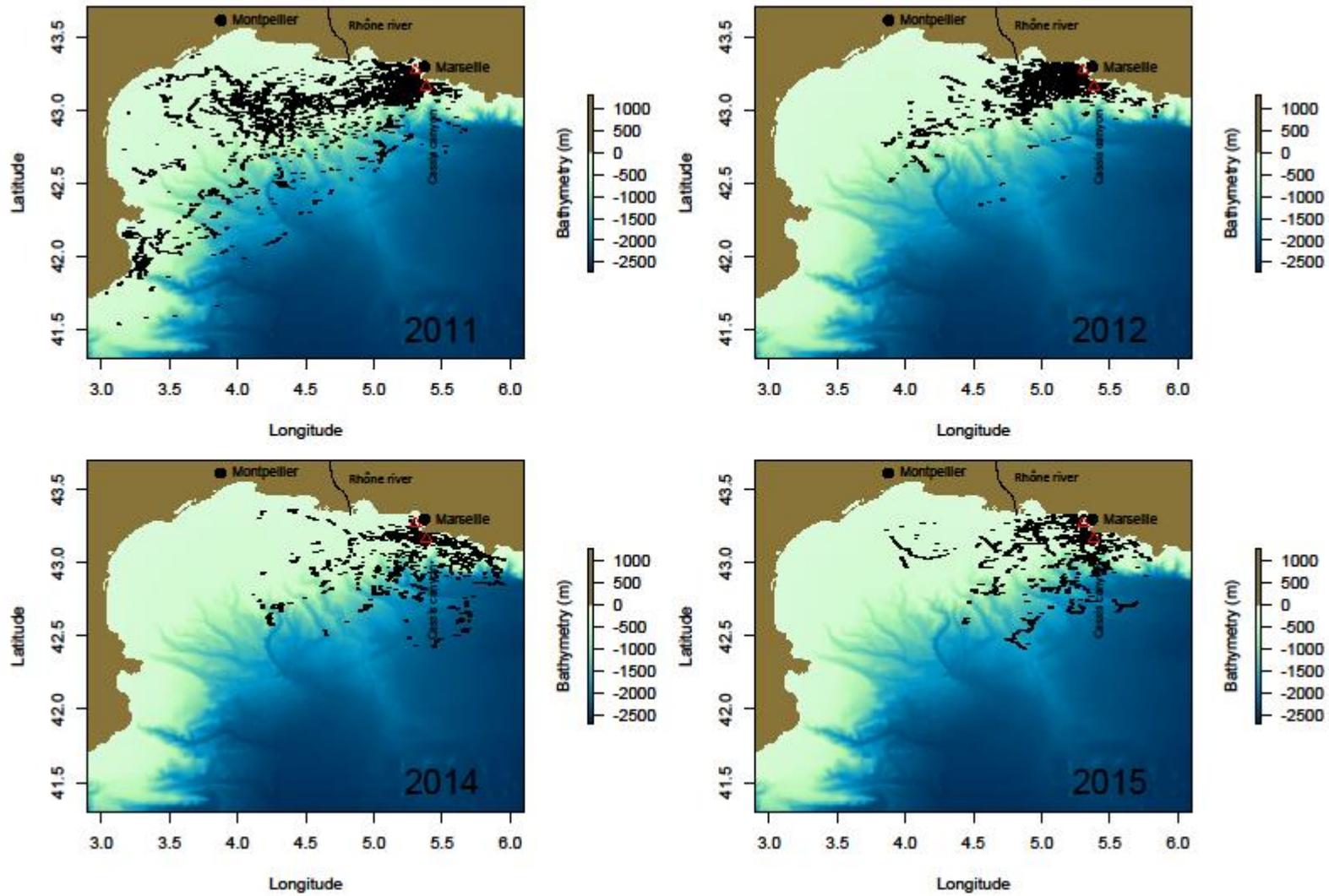
732 Figure 4. (A) Individual specialization in resource selection of Scopoli's shearwaters (n=47)
733 assessed with an index of repeatability R , varying between 0 and 1 (i.e. low to high selection
734 consistency). (B) Individual foraging site fidelity of Scopoli's shearwaters (n=47) among their
735 consecutive trips (BA), among trips of individuals foraging on the same day ($BA_{between}$) and
736 expected under a random space use without selection (BA_{random}), using a Bhattacharyya's

737 index ranging between 0 (no spatial overlap of UDs) and 1 (perfect spatial overlap of UDs).
738 Boxplot shows the median, 25th and 75th percentiles and solid circle represents the data.
739
740 Figure 5. RSF coefficients for (A) zooplankton-fish specialist trips and (B) zooplankton-only
741 specialist trips (n = 83 and 99 trips, respectively) used by Scopoli's shearwaters in the Gulf of
742 Lions (Western Mediterranean) during the chick-rearing period between 2011 and 2015.
743 Means (solid circle) are shown with their 95% confidence intervals. * mean values are divided
744 by 10 to ease visualization.
745
746 Figure 6. Stable isotope ratios representing the diet of Scopoli's shearwaters in the Gulf of
747 Lions (Western Mediterranean) during the chick-rearing period between 2010 and 2015. Due
748 to the molting pattern of shearwaters, isotopic signature of birds sampled at year *n* are
749 matched with isotopic signature of their prey at year *n*-1. Black points represent the stable
750 isotope ratios of each shearwater. We show the mean expected range (solid lines) and its
751 standard deviation (dotted lines) in prey isotopic values for shearwaters, based on shearwater
752 tissue. We used a diet-tissue discrimination factor of $\delta^{15}N$: 3.7 +/- 1‰ [mean +/- SD] as
753 recommended by Meier *et al.* (2017) for shearwaters. The mean stable isotope ratios with
754 their standard deviations assessed independently for prey are also shown: zooplankton,
755 copepods, euphausiids (empty squares), small pelagic fish (empty triangles) and squids
756 (empty circles). Isotopic signatures of small pelagic fish are year-specific, while considered
757 constant across years for the other prey (no data available). Inferences on diet of shearwaters
758 from $\delta^{15}N$ values were valuable because average $\delta^{15}N$ isotopic signatures in
759 zooplankton/copepods and fish species differed significantly and $\delta^{15}N$ remained stable over
760 space and time within the Gulf of Lions during our study (see details in Appendix S4).
761



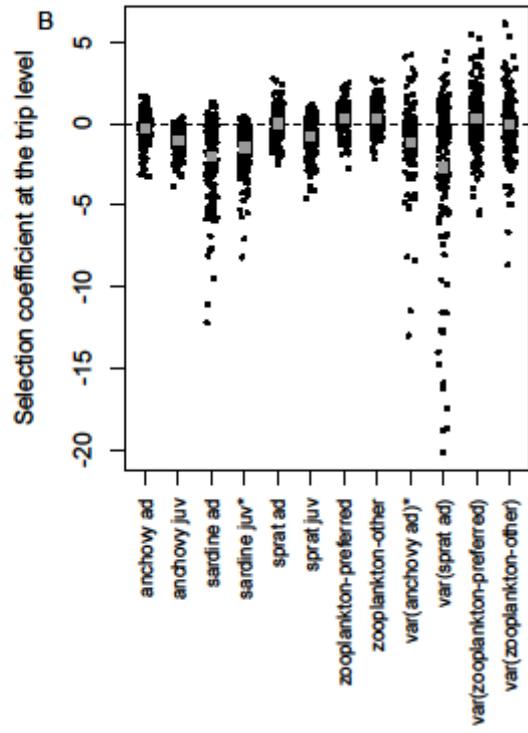
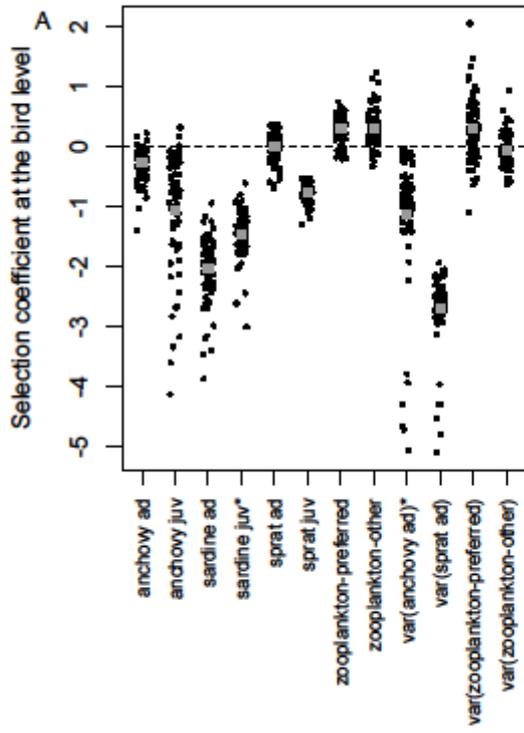
762

763 Figure 1.



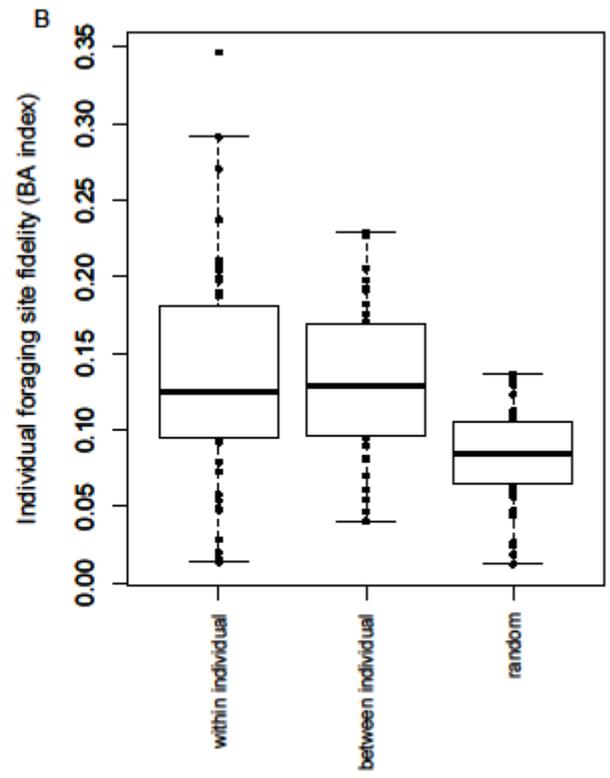
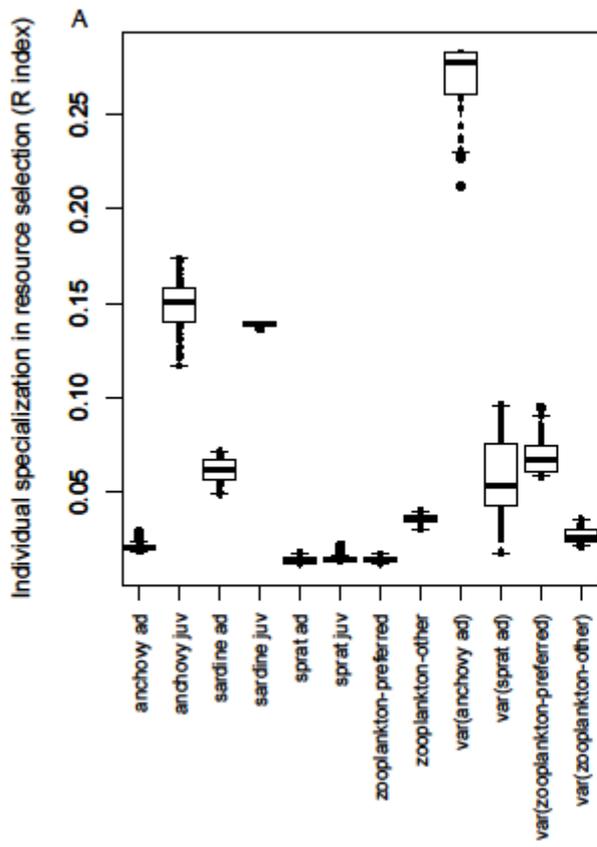
764

765 Figure 2.

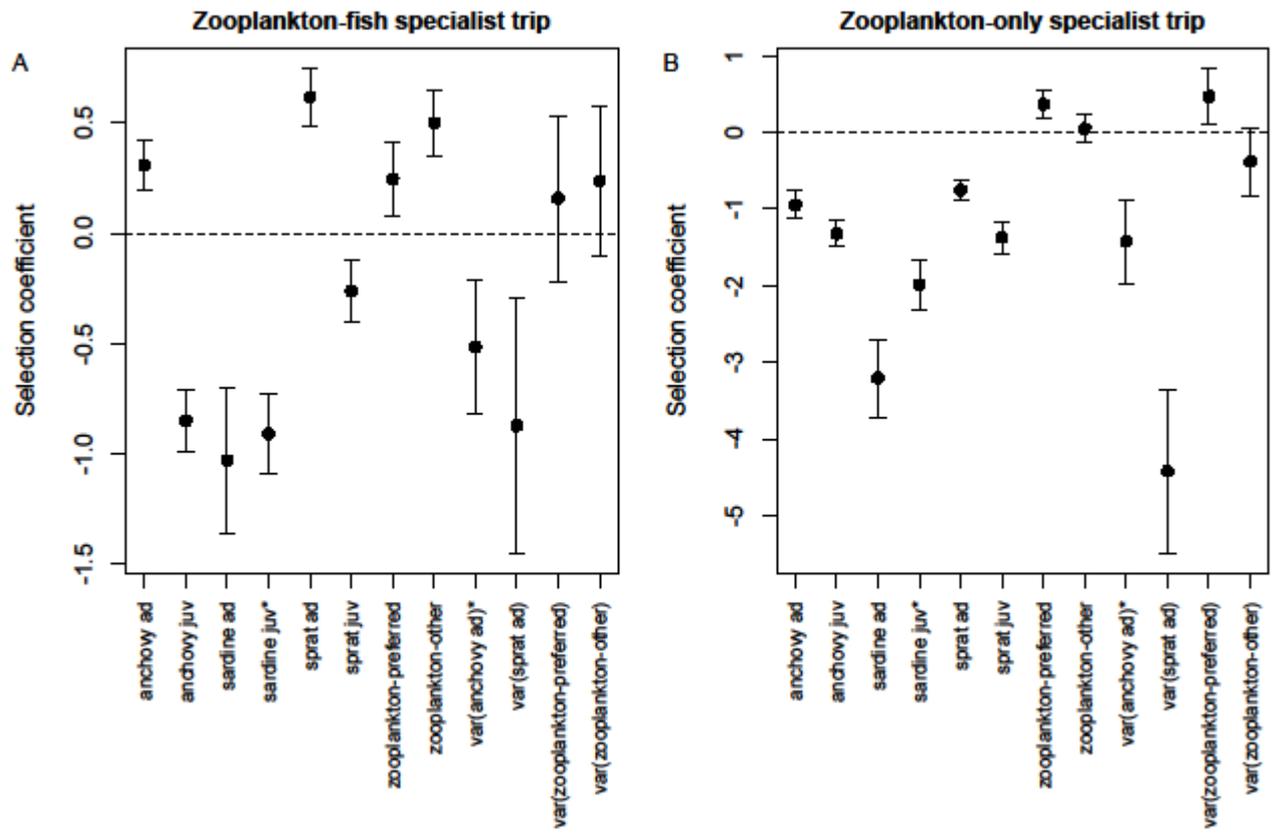


766

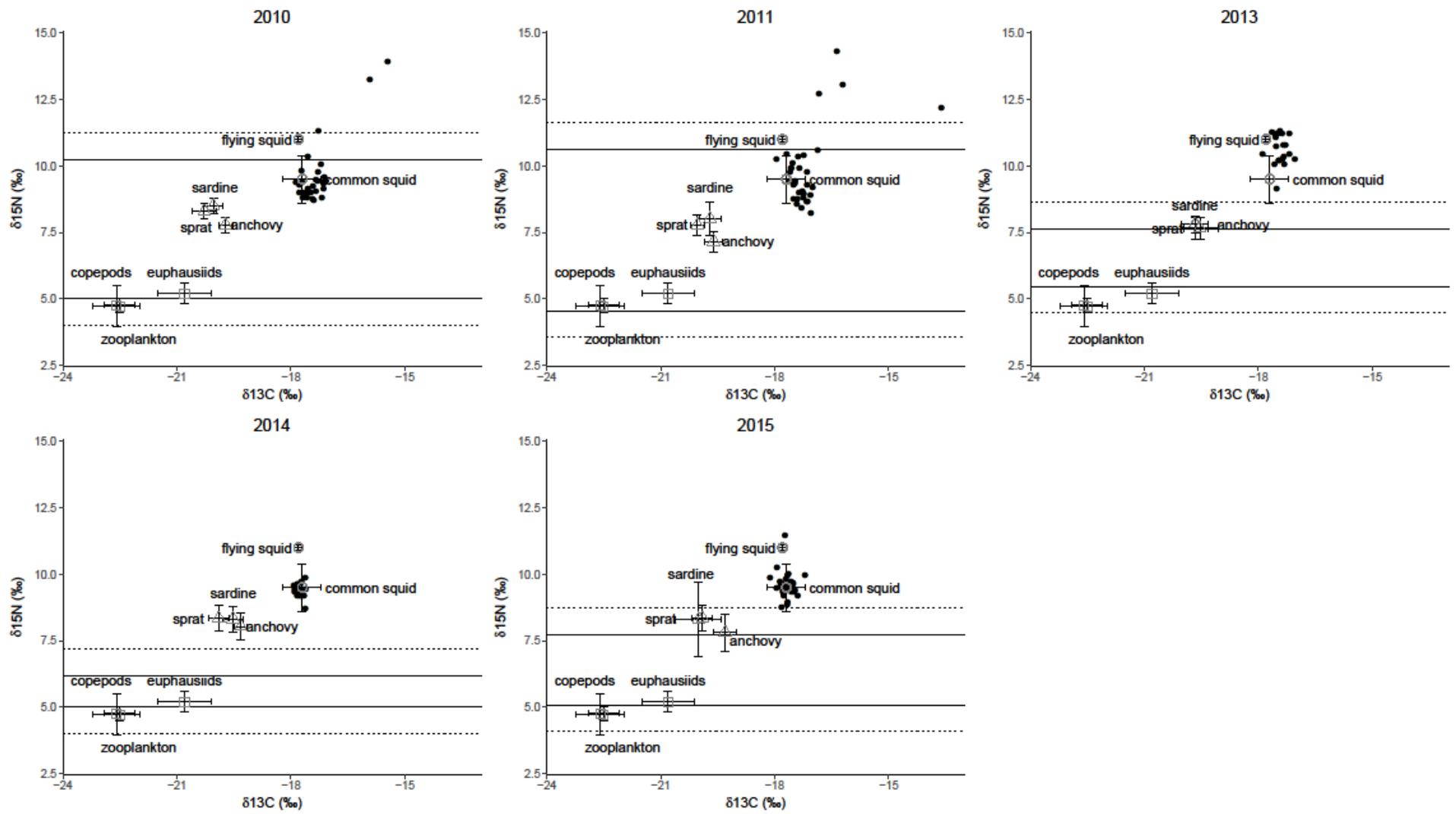
767 Figure3.



768
769 Figure 4.



770
771 Figure 5.



772
773 Figure 6.

1 Supporting Information for Ecology Letters

2

3 **Short-term prey field lability constrains individual resource specialization and foraging**

4 **site fidelity in a marine predator**

5

6 Nicolas Courbin¹, Aurélien Besnard¹, Clara Péron², Claire Saraux³, Jérôme Fort⁴, Samuel

7 Perret¹, Jérémy Tornos¹, David Grémillet^{1,5}

8

9 ¹ Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), UMR 5175, Centre National de la

10 Recherche Scientifique (CNRS), Université de Montpellier, Université Paul Valéry

11 Montpellier, Ecole Pratiques des Hautes Etudes (EPHE), 1919 Route de Mende, 34293

12 Montpellier Cedex 5, France

13 ² Marine Biodiversity Exploitation and Conservation (MARBEC), UMR 248, Institut de

14 Recherche pour le Développement (IRD), Université de Montpellier, Place Eugène

15 Bataillon - bât 24 - CC093, 34 095 Montpellier Cedex 5, France

16 ³ Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER), UMR 248

17 MARBEC, Avenue Jean Monnet CS 3017, 34203 Sète, France

18 ⁴ Littoral, Environnement et Sociétés (LIENSs), UMR 7266, Centre National de la Recherche

19 Scientifique (CNRS), Université La Rochelle, 2 rue Olympe de Gouges, 17000 La

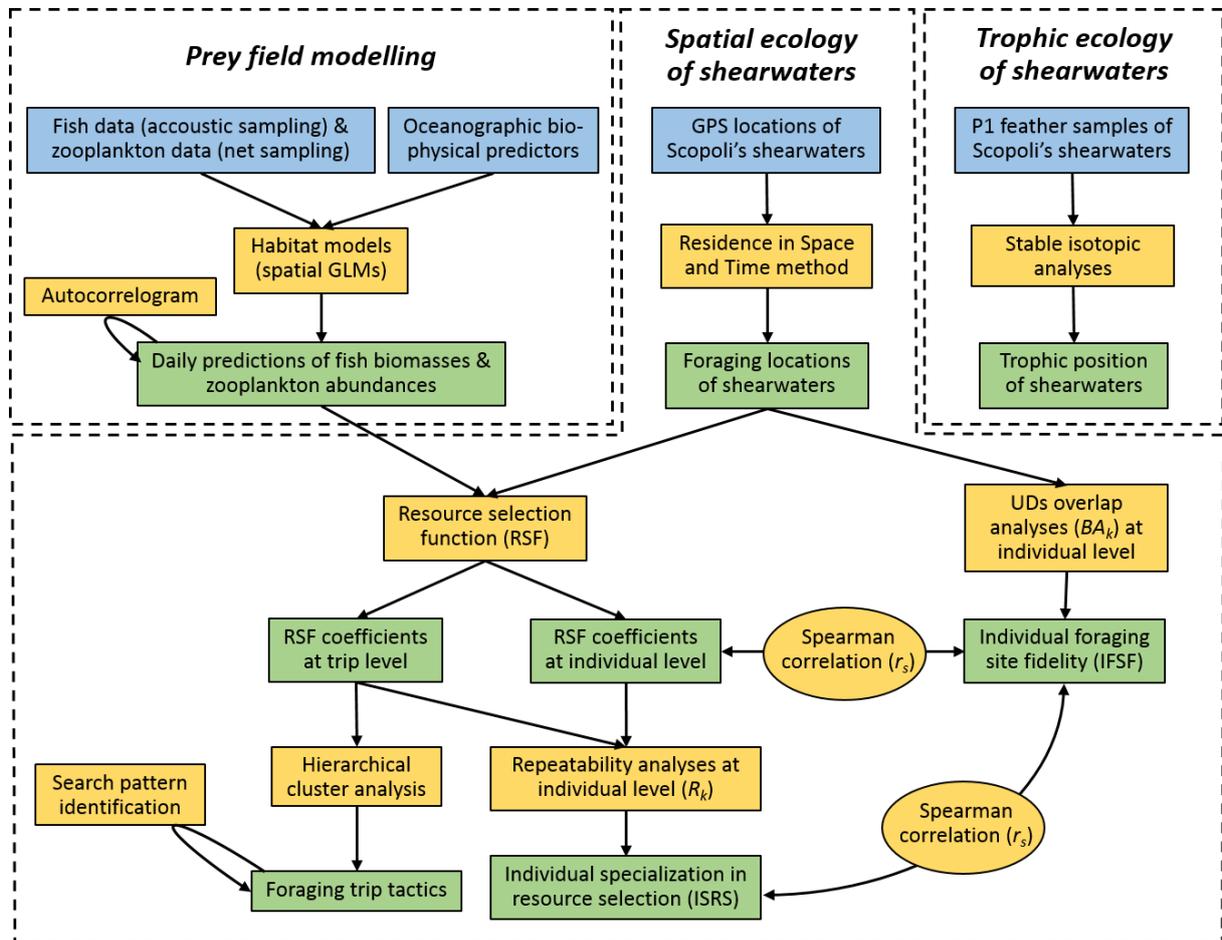
20 Rochelle, France

21 ⁵ FitzPatrick Institute, DST/NRF Excellence Centre at the University of Cape Town,

22 Rondebosch 7701, South Africa

23 **Supporting Information S1. Conceptual analytical framework.**

24



25

26 Figure S1.1. Analytical framework to study the foraging behavior of breeding Scopoli's
 27 shearwaters in the Gulf of Lions (Western Mediterranean) showing input empirical datasets
 28 (blue boxes), the statistical models and analyses (orange boxes) and outcomes (green boxes).

29 **Supporting Information S2. Modelling of daily spatial distribution of biomass and**
30 **abundance of prey of shearwaters**

31

32 In order to determine the resource selection of shearwaters at foraging locations, we built
33 dynamic habitat models predicting the daily spatial distribution of biomass of European
34 anchovies (*Engraulis encrasicolus*), sardines (*Sardina pilchardus*) and sprats (*Sprattus*
35 *sprattus*) in our study area. We distinguished between juvenile and adult fish based on their
36 length-at-maturity (9 cm, 11 cm, and 9 cm for anchovies, sardines and sprats, respectively,
37 Authier *et al.* 2017) because juveniles and adults are spatially segregated during the summer
38 (see Fig. S2.3). We used biomass data per species and per stage, estimated from yearly
39 standardized hydro-acoustic and trawl surveys of small pelagic fish carried out every July
40 between 2010 and 2015 in the Gulf of Lions by IFREMER during the PELagic
41 MEDiterranean (PELMED) at-sea campaigns (doi: <http://dx.doi.org/10.18142/19>). Biomass
42 data were systematically collected each nautical mile along 9 parallel hydro-acoustic transects
43 perpendicular to the coastline, 12 nautical miles apart, covering the continental shelf of the
44 Gulf of Lions (see more details on sampling design and biomass data estimation in Authier *et*
45 *al.* 2017).

46 We modelled fish biomass (tonnes) using zero-inflated spatial generalized linear
47 mixed models with a Horseshoe prior in a Bayesian framework (except we used a non-spatial
48 model for juvenile anchovies due to convergence issue). Such models have already
49 demonstrated their robustness to predict fish biomass in the Gulf of Lions and allow accurate
50 predictions, including extrapolations (Authier *et al.* 2017). Random spatial effects were
51 modelled with a stationary Gaussian process of mean 0, an isotropic Matèrn covariance
52 function of order 3/2 and a year-specific sill parameter. The Horseshoe prior favours a
53 parsimonious variable selection by shrinking toward 0 small regression coefficient effects, yet

54 leaving larger regression coefficient effects unshrunk, while avoiding overfitting (see
55 statistical details in Authier *et al.* 2017). We used a set of dynamic predictors on a daily basis
56 and 1.2 km-resolution: sea surface salinity (g.kg^{-1} , PREVIMER-MARS3D model), sea surface
57 temperature ($^{\circ}\text{C}$, MODIS satellite data) and its variance describing the spatio-temporal
58 dynamic of water mass features, and chlorophyll a concentration (mg.m^{-3} , MODIS satellite
59 data) and its variance used as proxies of primary productivity dynamics. Variance was
60 calculated from the previous 15 days. We considered sea level anomaly (m) and Eddy kinetic
61 energy ($\text{cm}^2.\text{s}^{-2}$) on a daily basis and 14km-resolution (AVISO satellite data) reflecting
62 hydrodynamic movements and turbulences occurring at the meso-scale within the Gulf of
63 Lions. Bathymetry with a 180 m-resolution (m, Marine Geoscience Data System), its gradient
64 and seabed substrate (four levels: sands, muddy sands, sandy muds and muds; EUSeaMap)
65 were used as static predictors in the models. Year was finally considered as a random effect to
66 control for the inter-annual variation in fish biomasses. Models were fitted by initializing four
67 chains with random starting values and running at least 3000 iterations to get the posterior
68 sample distributions. Convergence was assessed based on the Gelman-Rubin potential scale
69 reduction factor \hat{r} . We used the *RStan* package (Stan Development Team 2016) of R software
70 (R Development Core Team 2016).

71 Similarly, we modelled mesozooplankton (thereafter ‘zooplankton’) abundance
72 (ind.m^{-3}) using data collected with vertical WP2 plankton-net (200 μm mesh size) during the
73 PELMED survey conducted in July 2015 (data were not available for previous years) at 37
74 stations (Fig. S2.2). Zooplankton samples ($n = 37$) were identified and classified in two
75 groups based on shearwater diet. The first group, ‘zooplankton-preferred’, included copepods,
76 euphausiids, fish eggs and fish larvae already found in stomach contents or regurgitates of
77 shearwaters (Beaubrun *et al.* 2013), and the rest of zooplankton formed the ‘zooplankton-
78 other’ group. We fitted a spatial GLM with a Horseshoe prior, and considered a bivariate

79 normal distribution for the dependent variable (both zooplankton groups) and the same set of
80 environmental predictors as for fish biomass models. Model was fitted by initializing four
81 chains with random starting values and running at least 3000 iterations to get the posterior
82 sample distributions. Convergence was assessed based on the Gelman-Rubin potential scale
83 reduction factor \hat{r} . We used the *RStan* package (Stan Development Team 2016) of R software
84 (R Development Core Team 2016). We finally assessed the robustness and predictive power
85 of the zooplankton model using leave-one-out cross-validation and compared the predicted
86 abundance to the observed abundance within the range of abundance used by shearwaters.

87 All parameters converged (Gelman-Rubin potential scale reduction factor $\hat{r} < 1.2$) for
88 fish and zooplankton models. The zooplankton model significantly predicted observed
89 abundances of zooplankton-preferred group within the range of abundance used by
90 shearwaters [0-800 ind.m⁻³] ($r^2 = 0.24$, $P < 0.005$) (Fig. S2.4). The zooplankton model
91 performed poorly to predict observed abundances of zooplankton-other group within the
92 range of abundance used by shearwaters [0-600 ind.m⁻³] ($r^2 = 0.02$, $P = 0.44$) (Fig. S2.4).
93 Sardines and juvenile sprats were coastal and their biomasses mainly decreased with
94 bathymetry (Table S2.3, S2.4 and S2.6, Fig. S2.3). Juvenile anchovies were more widely
95 distributed across the Gulf of Lions and were related to the plume of the Rhône river (Table
96 S2.2, Fig. S2.3). Biomass of adult sprats was higher at the center of the Gulf than along the
97 coast (Table S2.5, Fig. S2.3). Adult anchovies were the most pelagic prey category and their
98 biomasses increased along the edge of the continental shelf, and also in some coastal areas
99 (Table S2.1, Fig. S2.3). Both biomasses of adult anchovies and adult sprats increased near the
100 Cassis canyon head close to the colony (Fig. S2.3). Abundance of zooplankton-preferred was
101 related to coastal areas, the plume of the Rhône river and canyon areas (Table S2.7, Fig.
102 S2.3). Zooplankton-other abundance was widely distributed across the Gulf of Lions (Table
103 S2.7, Fig. S2.3).

104 We found high spatio-temporal variations in zooplankton abundances with a strong
105 decrease of their temporal autocorrelation after only 1 day (Fig. S2.1). Autocorrelation of
106 biomasses of adult anchovies and sprats strongly declined after 2-3 days, particularly in the
107 eastern part of the Gulf of Lions where most foraging locations occurred (Fig. S2.1B).
108 Autocorrelation of other fish biomasses vanished in less than 5 days.

109

110 **References**

111 Authier, M., Saraux, C. & Péron, C. (2017). Variable selection and accurate predictions in
112 habitat modelling: a shrinkage approach. *Ecography*, 40, 549-560.

113 Beaubrun, P. *et al.* (2012). *Etat de l'art des connaissances sur les distributions spatiales des*
114 *oiseaux marins et des petits poissons pélagiques dans le golfe du Lion*. Rapport final du
115 Contrat DREAL-LR / IFREMER n°11/3211726/F, 1-580 pp.

116 Stan Development Team (2016). *RStan: the R interface to Stan*. *R package version 2.14.1*.
117 <http://mc-stan.org/>.

118 Table S2.1. Zero-inflated spatial generalized linear mixed model with Horseshoe priors
 119 predicting the spatial distribution of adult anchovies in the Gulf of Lions (Western
 120 Mediterranean) between 2010 and 2015. Model parameters (β) are shown with their standard
 121 deviation (SD) and 95% confidence intervals (CI) for both the absence (zero-inflated part
 122 modelling the probability of being absent) and biomass models of fish.
 123

Variable	Absence (zero-inflated part)			Biomass		
	β	SD	95% CI	β	SD	95% CI
<i>Fixed effects</i>						
Intercept	-6.07	2.28	-11.87;-3.37	1.31	0.20	0.90;1.71
Bathymetry (m)	0.10	0.48	-0.54;1.35	-0.01	0.04	-0.10;0.07
G(bathymetry)	-0.18	0.61	-1.87;0.31	-0.04	0.04	-0.12;0.01
Sea surface salinity (g.kg ¹)	0.15	0.54	-0.42;1.63	-0.04	0.05	-0.16;0.03
Sea surface temperature (°C)	-0.002	0.33	-0.77;0.75	-0.01	0.04	-0.10;0.07
Var(sea surface temperature)	-0.05	0.42	-1.22;0.63	-0.01	0.03	-0.09;0.05
Chlorophyll a (mg.m ⁻³)	-0.13	0.39	-1.26;0.27	-0.02	0.03	-0.09;0.05
Var(chlorophyll a)	-0.20	0.62	-2.02;0.22	-0.01	0.02	-0.06;0.04
Eddy kinetic energy (cm ² .s ⁻²)	-0.06	0.43	-1.20;0.62	-0.02	0.04	-0.12;0.05
Sea level anomalies (m)	-0.03	0.41	-0.96;0.73	0.01	0.04	-0.06;0.12
<i>Seabed substrate</i>						
Muds	-0.08	0.78	-1.87;1.02	-0.02	0.10	-0.28;0.15
Muddy sands	-0.09	0.88	-2.42;1.33	-0.17	0.18	-0.59;0.05
Sandy muds	-0.20	0.85	-2.51;0.75	0.05	0.12	-0.13;0.38
Sands	-0.16	0.79	-2.37;0.91	0.44	0.15	0.16;0.79
<i>Random effect</i>						

2010	-6.14	2.37	-12.33;-3.27	1.28	0.17	0.92;1.60
2011	-6.17	2.38	-12.13;-3.33	1.27	0.18	0.91;1.62
2012	-6.11	2.42	-12.33;-3.22	1.41	0.18	1.05;1.76
2013	-6.14	2.41	-12.15;-3.14	1.01	0.23	0.58;1.42
2014	-6.13	2.36	-12.10;-3.29	1.38	0.18	0.99;1.72
2015	-6.17	2.49	-12.71;-3.15	1.56	0.20	1.16;1.96
<i>Spatial effect</i>						
Rho				6.73	0.87	5.24;8.61
Sill in 2010				0.78	0.10	0.61;0.98
Sill in 2011				0.79	0.10	0.63;0.99
Sill in 2012				0.89	0.10	0.73;1.08
Sill in 2013				0.95	0.11	0.76;1.18
Sill in 2014				0.90	0.12	0.69;1.14
Sill in 2015				0.95	0.12	0.73;1.19
<i>Horseshoe (global)</i>	0.26	0.26	0.03;0.96	0.07	0.07	0.01;0.27

125 Table S2.2. Zero-inflated generalized linear mixed model with Horseshoe priors predicting
 126 the spatial distribution of juvenile anchovies in the Gulf of Lions (Western Mediterranean)
 127 between 2010 and 2015. Model parameters (β) are shown with their standard deviation (SD)
 128 and 95% confidence intervals (CI) for both the absence (zero-inflated part modelling the
 129 probability of being absent) and biomass models of fish.
 130

Variable	Absence (zero-inflated part)			Biomass		
	β	SD	95% CI	β	SD	95% CI
<i>Fixed effects</i>						
Intercept	-3.91	0.71	-5.55;-2.95	0.01	0.01	-0.002;0.03
Bathymetry (m)	-0.04	0.14	-0.35;0.26	0.015	0.002	0.010;0.018
G(bathymetry)	-0.21	0.38	-1.27;0.16	0.007	0.002	0.003;0.010
Sea surface salinity (g.kg ¹)	-0.62	0.11	-0.85;-0.42	-0.05	0.003	-0.06;-0.05
Sea surface temperature (°C)	0.39	0.37	-0.05;1.26	0.005	0.002	0.001;0.009
Var(sea surface temperature)	0.17	0.19	-0.14;0.54	-0.008	0.002	-0.011;-0.004
Chlorophyll a (mg.m ⁻³)	-0.06	0.09	-0.28;0.06	-0.007	0.002	-0.011;-0.002
Var(chlorophyll a)	-0.07	0.19	-0.60;0.18	-0.001	0.001	-0.003;0.002
Eddy kinetic energy (cm ² .s ⁻²)	-0.76	0.47	-1.77;-0.003	0.002	0.002	-0.001;0.006
Sea level anomalies (m)	-0.06	0.24	-0.68;0.36	-0.001	0.002	-0.005;0.002
<i>Seabed substrate</i>						
Muds	0.07	0.37	-0.47;1.01	-0.001	0.004	-0.009;0.009
Muddy sands	-0.38	1.50	-4.37;0.61	-0.01	0.01	-0.03;0.002
Sandy muds	-0.01	0.37	-0.63;0.83	0.002	0.004	-0.006;0.011
Sands	-0.94	3.21	-15.01;0.70	0.003	0.007	-0.007;0.021
<i>Random effect</i>						

2010	-4.12	0.84	-6.10;-2.97	0.01	0.005	-0.002;0.02
2011	-3.99	0.81	-5.84;-2.87	0.01	0.005	-0.002;0.02
2012	-4.03	0.82	-5.90;-2.91	0.01	0.005	0.001;0.02
2013	-3.71	0.71	-5.40;-2.59	0.02	0.005	0.01;0.03
2014	-3.91	0.68	-5.49;-2.90	0.03	0.005	0.02;0.04
2015	-3.87	0.74	-5.57;-2.79	0.01	0.005	-0.002;0.02
<i>Horseshoe (global)</i>	0.32	0.22	0.08;0.87	0.009	0.005	0.003;0.240

131 Table S2.3. Zero-inflated spatial generalized linear mixed model with Horseshoe priors
 132 predicting the spatial distribution of adult sardines in the Gulf of Lions (Western
 133 Mediterranean) between 2010 and 2015. Model parameters (β) are shown with their standard
 134 deviation (SD) and 95% confidence intervals (CI) for both the absence (zero-inflated part
 135 modelling the probability of being absent) and biomass models of fish.
 136

Variable	Absence (zero-inflated part)			Biomass		
	β	SD	95% CI	β	SD	95% CI
<i>Fixed effects</i>						
Intercept	-5.61	1.99	-9.73;-1.41	1.32	0.22	0.89;1.78
Bathymetry (m)	2.09	0.78	0.96;3.91	0.63	0.07	0.50;0.76
G(bathymetry)	-0.07	0.74	-1.90;1.10	0.16	0.05	0.07;0.26
Sea surface salinity (g.kg ¹)	0.22	0.71	-0.27;1.81	-0.01	0.04	-0.09;0.07
Sea surface temperature (°C)	0.16	0.26	-0.18;0.80	-0.04	0.05	-0.17;0.04
Var(sea surface temperature)	-0.03	0.19	-0.44;0.34	0.02	0.04	-0.06;0.13
Chlorophyll a (mg.m ⁻³)	0.02	0.16	-0.37;0.32	-0.05	0.06	-0.18;0.03
Var(chlorophyll a)	0.05	0.08	-0.07;0.22	-0.06	0.06	-0.19;0.04
Eddy kinetic energy (cm ² .s ⁻²)	0.04	0.26	-0.52;0.61	0.01	0.04	-0.06;0.11
Sea level anomalies (m)	0.01	0.18	-0.38;0.40	-0.01	0.05	-0.12;0.07
<i>Seabed substrate</i>						
Muds	-0.49	1.51	-4.59;0.60	-0.02	0.10	-0.29;0.18
Muddy sands	-0.03	0.36	-0.83;0.89	-0.01	0.10	-0.27;0.19
Sandy muds	0.31	0.47	-0.27;1.60	-0.03	0.07	-0.20;0.10
Sands	-1.22	3.63	-8.00;0.28	0.07	0.09	-0.06;0.28
<i>Random effect</i>						

2010	-4.56	2.06	-8.54;-2.37	1.10	0.14	0.81;1.38
2011	-8.49	5.69	-19.18;-4.23	1.03	0.14	0.75;1.30
2012	-8.27	5.43	-19.44;-4.10	1.26	0.15	0.95;1.55
2013	-4.51	1.44	-7.97;-2.41	1.71	0.20	1.31;2.10
2014	-8.04	3.82	-18.76;-4.20	1.47	0.16	1.17;1.78
2015	-8.16	5.01	-18.55;-4.05	1.35	0.16	1.02;1.68
<i>Spatial effect</i>						
Rho				4.92	0.73	3.71;6.53
Sill in 2010				0.71	0.10	0.52;0.91
Sill in 2011				0.70	0.11	0.49;0.92
Sill in 2012				0.79	0.10	0.61;1.00
Sill in 2013				1.00	0.13	0.78;1.27
Sill in 2014				0.89	0.11	0.69;1.11
Sill in 2015				0.92	0.11	0.71;1.16
<i>Horseshoe (global)</i>	0.33	0.25	0.06;0.97	0.09	0.07	0.02;0.26

138 Table S2.4. Zero-inflated spatial generalized linear mixed model with Horseshoe priors
 139 predicting the spatial distribution of juvenile sardines in the Gulf of Lions (Western
 140 Mediterranean) between 2010 and 2015. Model parameters (β) are shown with their standard
 141 deviation (SD) and 95% confidence intervals (CI) for both the absence (zero-inflated part
 142 modelling the probability of being absent) and biomass models of fish.
 143

Variable	Absence (zero-inflated part)			Biomass		
	β	SD	95% CI	β	SD	95% CI
<i>Fixed effects</i>						
Intercept	-0.76	0.62	-2.08;0.44	0.81	0.17	0.47;1.16
Bathymetry (m)	-1.80	0.18	-2.16;-1.47	0.92	0.08	0.77;1.06
G(bathymetry)	-0.62	0.18	-1.04;-0.32	0.19	0.08	0.03;0.33
Sea surface salinity (g.kg ¹)	0.11	0.11	-0.08;0.34	-0.005	0.03	-0.07;0.06
Sea surface temperature (°C)	0.01	0.07	-0.14;0.16	-0.03	0.05	-0.17;0.05
Var(sea surface temperature)	-0.002	0.08	-0.19;0.15	0.01	0.04	-0.06;0.11
Chlorophyll a (mg.m ⁻³)	-0.08	0.13	-0.40;0.13	0.002	0.03	-0.06;0.07
Var(chlorophyll a)	0.21	0.10	-0.001;0.40	0.01	0.03	-0.04;0.07
Eddy kinetic energy (cm ² .s ⁻²)	0.03	0.07	-0.10;0.18	-0.0001	0.04	-0.08;0.09
Sea level anomalies (m)	-0.03	0.09	-0.23;0.13	-0.03	0.06	-0.20;0.05
<i>Seabed substrate</i>						
Muds	0.10	0.24	-0.28;0.79	-0.004	0.10	-0.24;0.22
Muddy sands	-0.14	1.29	-1.12;0.78	-0.002	0.08	-0.19;0.17
Sandy muds	0.05	0.17	-0.30;0.42	0.003	0.06	-0.13;0.14
Sands	-0.19	0.21	-0.67;0.09	-0.005	0.06	-0.15;0.12
<i>Random effect</i>						

2010	-0.66	0.24	-1.13;-0.17	0.92	0.15	0.64;1.25
2011	0.63	0.24	0.19;1.14	0.61	0.23	0.16;1.07
2012	-2.12	0.35	-2.87;-1.44	1.12	0.17	0.81;1.42
2013	-2.67	1.27	-6.54;-1.35	0.78	0.15	0.49;1.05
2014	0.26	0.24	-0.18;0.76	0.63	0.14	0.36;0.92
2015	-0.81	0.27	-1.33;-0.28	0.87	0.15	0.56;1.17
<i>Spatial effect</i>						
Rho				4.02	0.83	2.69;5.93
Sill in 2010				0.97	0.13	0.71;1.23
Sill in 2011				1.28	0.17	0.99;1.64
Sill in 2012				0.96	0.11	0.77;1.18
Sill in 2013				0.74	0.09	0.57;0.93
Sill in 2014				0.56	0.14	0.31;0.84
Sill in 2015				0.74	0.12	0.52;0.98
<i>Horseshoe (global)</i>	0.24	0.15	0.07;0.62	0.07	0.05	0.01;0.21

145 Table S2.5. Zero-inflated spatial generalized linear mixed model with Horseshoe priors
 146 predicting the spatial distribution of adult sprats in the Gulf of Lions (Western Mediterranean)
 147 between 2010 and 2015. Model parameters (β) are shown with their standard deviation (SD)
 148 and 95% confidence intervals (CI) for both the absence (zero-inflated part modelling the
 149 probability of being absent) and biomass models of fish.
 150

Variable	Absence (zero-inflated part)			Biomass		
	β	SD	95% CI	β	SD	95% CI
<i>Fixed effects</i>						
Intercept	-4.41	1.82	-7.92;-0.30	1.17	0.28	0.60;1.78
Bathymetry (m)	2.39	0.41	1.76;3.31	0.11	0.06	-0.01;0.23
G(bathymetry)	0.45	0.72	-0.83;1.65	-0.03	0.04	-0.11;0.03
Sea surface salinity (g.kg ¹)	0.08	0.12	-0.11;0.38	0.02	0.04	-0.04;0.11
Sea surface temperature (°C)	0.29	0.25	-0.04;0.84	-0.02	0.04	-0.14;0.05
Var(sea surface temperature)	-0.03	0.13	-0.33;0.19	-0.03	0.04	-0.14;0.05
Chlorophyll a (mg.m ⁻³)	0.03	0.10	-0.16;0.26	-0.001	0.04	-0.09;0.09
Var(chlorophyll a)	0.03	0.08	-0.12;0.19	0.04	0.06	-0.06;0.18
Eddy kinetic energy (cm ² .s ⁻²)	0.14	0.17	-0.13;0.50	-0.002	0.03	-0.08;0.07
Sea level anomalies (m)	0.05	0.16	-0.27;0.40	-0.05	0.06	-0.21;0.04
<i>Seabed substrate</i>						
Muds	-0.04	0.38	-0.87;0.66	0.02	0.08	-0.14;0.23
Muddy sands	-0.04	0.28	-0.69;0.49	-0.12	0.18	-0.61;0.07
Sandy muds	-0.08	0.22	-0.68;0.26	-0.03	0.10	-0.26;0.15
Sands	0.07	0.21	-0.28;0.65	0.22	0.14	-0.01;0.49
<i>Random effect</i>						

2010	-3.48	0.65	-5.02;-2.42	0.72	0.17	0.40;1.08
2011	-8.40	3.66	-19.01;-4.91	1.11	0.21	0.72;1.55
2012	-6.84	2.70	-14.71;-4.01	1.34	0.21	0.92;1.76
2013	-1.36	0.44	-2.33;-0.67	1.78	0.31	1.15;2.33
2014	-8.47	3.07	-16.93;-5.27	1.06	0.19	0.69;1.44
2015	-7.65	3.72	-18.21;-4.16	0.81	0.15	0.50;1.13
<i>Spatial effect</i>						
Rho				6.92	1.31	4.63;9.66
Sill in 2010				0.65	0.08	0.50;0.81
Sill in 2011				1.05	0.11	0.85;1.28
Sill in 2012				1.00	0.10	0.81;1.20
Sill in 2013				1.16	0.15	0.90;1.48
Sill in 2014				1.00	0.14	0.76;1.31
Sill in 2015				0.57	0.07	0.43;0.72
<i>Horseshoe (global)</i>	0.26	0.18	0.05;0.72	0.07	0.05	0.01;0.21

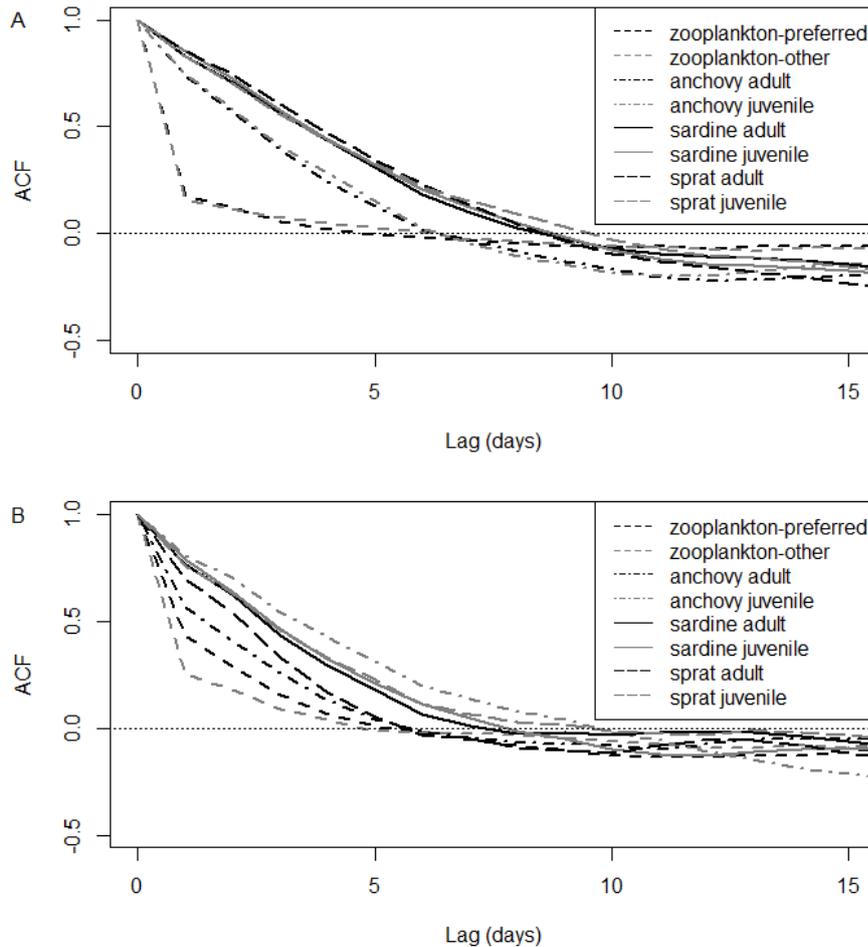
152 Table S2.6. Zero-inflated spatial generalized linear mixed model with Horseshoe priors
 153 predicting the spatial distribution of juvenile sprats in the Gulf of Lions (Western
 154 Mediterranean) between 2010 and 2015. Model parameters (β) are shown with their standard
 155 deviation (SD) and 95% confidence intervals (CI) for both the absence (zero-inflated part
 156 modelling the probability of being absent) and biomass models of fish.
 157

Variable	Absence (zero-inflated part)			Biomass		
	β	SD	95% CI	β	SD	95% CI
<i>Fixed effects</i>						
Intercept	-2.43	1.98	-6.11;2.68	0.73	0.25	0.31;1.25
Bathymetry (m)	-1.31	0.13	-1.62;-1.07	0.19	0.08	0.03;0.34
G(bathymetry)	-0.18	0.17	-0.58;0.07	0.03	0.04	-0.02;0.12
Sea surface salinity (g.kg ¹)	0.08	0.18	-0.16;0.61	0.02	0.03	-0.02;0.08
Sea surface temperature (°C)	0.15	0.20	-0.09;0.65	-0.04	0.05	-0.15;0.03
Var(sea surface temperature)	-0.17	0.14	-0.50;0.02	-0.003	0.05	-0.13;0.08
Chlorophyll a (mg.m ⁻³)	0.02	0.10	-0.17;0.24	-0.02	0.03	-0.09;0.02
Var(chlorophyll a)	-0.02	0.06	-0.18;0.08	-0.01	0.02	-0.06;0.04
Eddy kinetic energy (cm ² .s ⁻²)	-0.02	0.06	-0.17;0.10	-0.03	0.04	-0.12;0.04
Sea level anomalies (m)	0.01	0.08	-0.16;0.24	-0.04	0.06	-0.18;0.04
<i>Seabed substrate</i>						
Muds	0.07	0.45	-0.87;1.04	-0.02	0.08	-0.26;0.11
Muddy sands	1.33	0.58	0.01;2.24	-0.10	0.13	-0.42;0.05
Sandy muds	-0.01	0.16	-0.39;0.32	0.02	0.07	-0.10;0.18
Sands	-0.11	0.21	-0.70;0.15	0.14	0.10	-0.01;0.35
<i>Random effect</i>						

2010	-7.84	3.37	-18.38;-4.24	0.48	0.18	0.13;0.86
2011	-0.01	0.25	-0.46;0.52	0.65	0.26	0.17;1.15
2012	-6.41	3.33	-13.18;-2.96	0.77	0.28	0.15;1.26
2013	0.82	0.24	0.43;1.42	1.11	0.42	0.40;1.96
2014	-5.74	3.06	-13.20;-2.21	0.38	0.15	0.09;0.66
2015	-5.06	2.18	-11.13;-2.78	0.67	0.20	0.31;1.07
<i>Spatial effect</i>						
Rho				11.97	1.49	9.45;15.62
Sill in 2010				0.72	0.10	0.53;0.93
Sill in 2011				0.96	0.16	0.68;1.33
Sill in 2012				1.13	0.13	0.90;1.46
Sill in 2013				1.51	0.27	1.04;2.09
Sill in 2014				0.49	0.07	0.36;0.65
Sill in 2015				0.81	0.11	0.61;1.04
<i>Horseshoe (global)</i>	0.25	0.21	0.04;0.81	0.07	0.06	0.01;0.19

159 Table S2.7. Spatial generalized linear mixed model with Horseshoe priors predicting the
 160 spatial distribution of zooplankton abundance in the Gulf of Lions (Western Mediterranean)
 161 in 2015. Model parameters (β) are shown with their standard deviation (SD) and 95%
 162 confidence intervals (CI).
 163

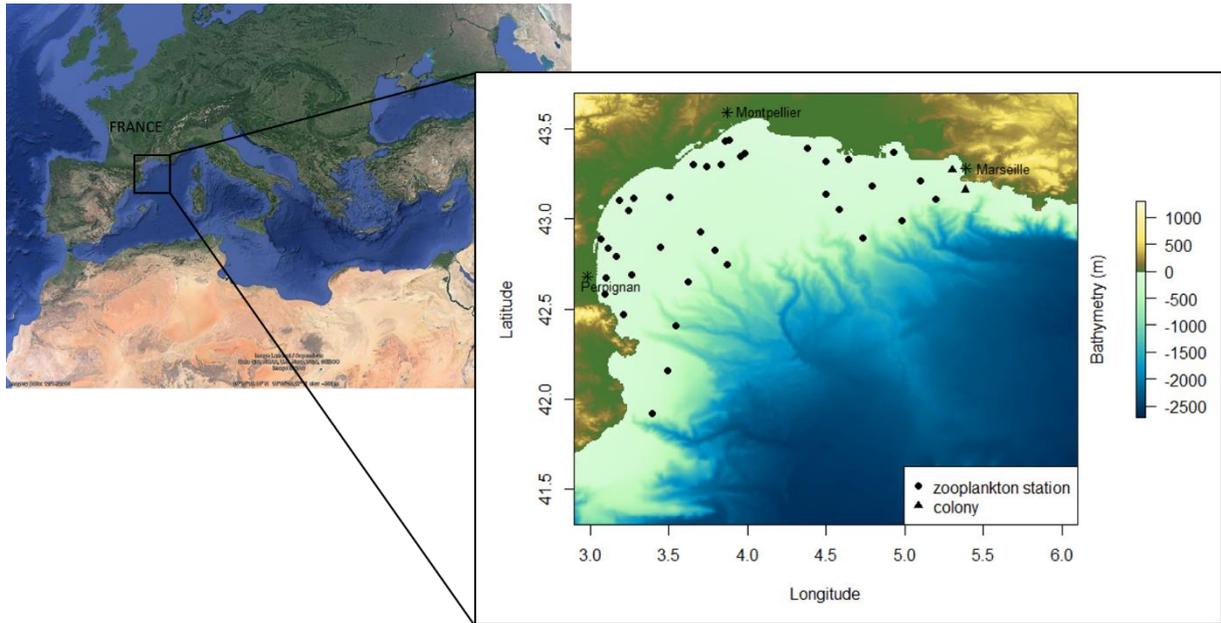
Variable	Zooplankton-preferred			Zooplankton-other		
	β	SD	95% CI	β	SD	95% CI
<i>Fixed effects</i>						
Intercept	5.46	0.80	3.32;6.57	5.53	0.62	3.98;6.54
Bathymetry (m)	0.001	0.06	-0.14;0.15	0.03	0.09	-0.12;0.26
G(bathymetry)	0.02	0.07	-0.08;0.21	-0.07	0.11	-0.35;0.08
Sea surface salinity (g.kg ¹)	-0.01	0.06	-0.17;0.11	0.16	0.15	-0.03;0.48
Sea surface temperature (°C)	0.005	0.06	-0.11;0.15	-0.01	0.08	-0.19;0.17
Var(sea surface temperature)	-0.04	0.09	-0.28;0.08	-0.02	0.08	-0.23;0.12
Chlorophyll a (mg.m ⁻³)	0.03	0.07	-0.07;0.21	-0.003	0.07	-0.16;0.14
Var(chlorophyll a)	-0.08	0.11	-0.36;0.04	-0.04	0.10	-0.30;0.09
Eddy kinetic energy (cm ² .s ⁻²)	-0.01	0.06	-0.18;0.10	-0.01	0.08	-0.20;0.14
Sea level anomalies (m)	-0.01	0.06	-0.18;0.10	0.05	0.10	-0.10;0.31
<i>Seabed substrate</i>						
Muds	0.03	0.11	-0.12;0.35	-0.09	0.18	-0.61;0.12
Muddy sands	-0.01	0.09	-0.25;0.16	0.11	0.20	-0.12;0.68
Sandy muds	-0.02	0.14	-0.39;0.19	0.02	0.18	-0.31;0.48
Sands	-0.03	0.18	-0.55;0.22	-0.001	0.22	-0.44;0.44
<i>Spatial effect (Rho)</i>	112.71	57.42	3.87;197.20	89.73	59.84	4.35;194.25
<i>Horseshoe (global)</i>	0.06	0.05	0.003;0.20	0.09	0.08	0.01;0.30



164

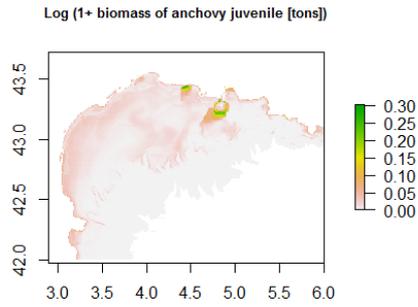
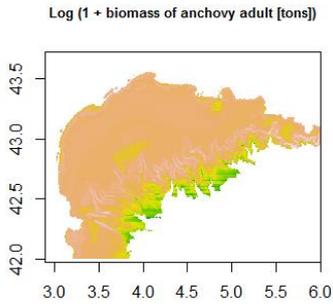
165 Figure S2.1. Temporal autocorrelation in the zooplankton abundances (ind.m^{-3}) and small
 166 pelagic fish biomasses (tonnes) (A) in the entire the Gulf of Lions (Western Mediterranean)
 167 and (B) in its eastern part where most foraging locations occurred (longitude $> 4.5^\circ$), during
 168 the chick-rearing period of Scopoli's shearwater (August). We considered three fish species
 169 (anchovy, sardine and sprat) at two stages (adult or juvenile) and zooplankton in two distinct
 170 categories: zooplankton-preferred that includes mesozooplankton already found in the diet of
 171 shearwater (copepods, euphausiid, fish eggs and fish larvae) and zooplankton-other that
 172 includes the rest of holoplankton and meroplankton. We assessed an autocorrelogram for each
 173 prey abundance/biomass daily predicted between the 20 July and 20 August 2015 at 900
 174 locations randomly distributed in the Gulf of Lions. For each prey type, values were averaged
 175 among the 900 autocorrelograms at each lag and the mean values are presented. Abundances

176 and biomasses data are predicted based on habitat models estimated from data collected on
177 July 2015 using plankton-net and hydro-acoustic survey (PELagic MEDiterranean campaigns,
178 IFREMER), respectively.

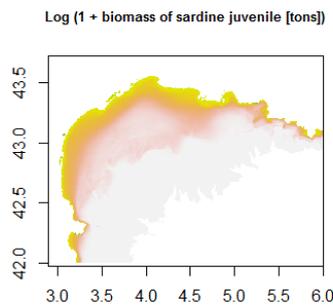
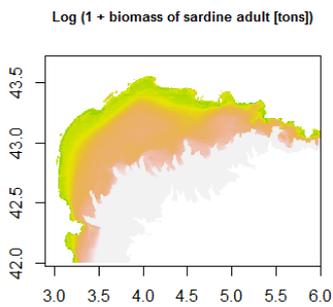


179

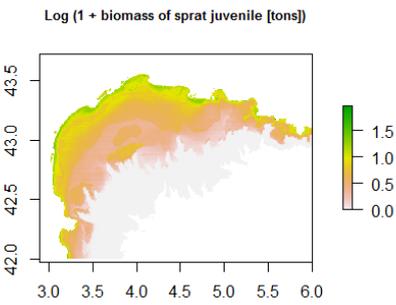
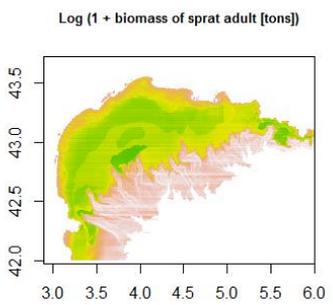
180 Figure S2.2. Spatial distribution of the 37 stations where zooplankton abundance was sampled
181 during the PELMED campaign in July 2015, within the Gulf of Lions (Western
182 Mediterranean).



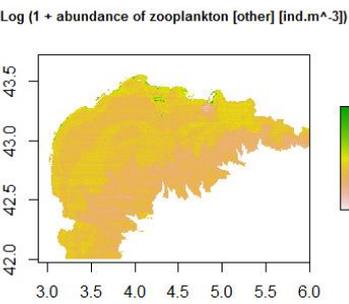
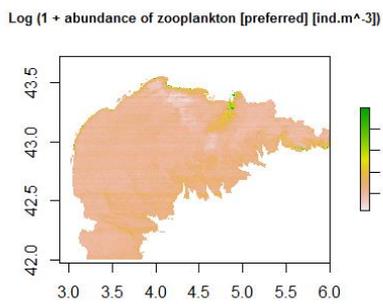
183



184

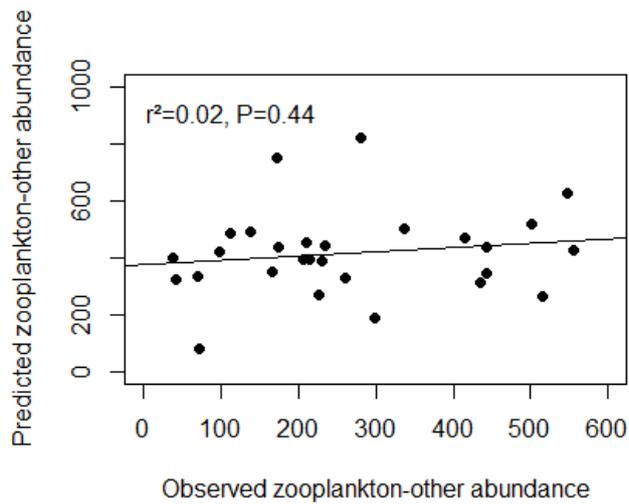
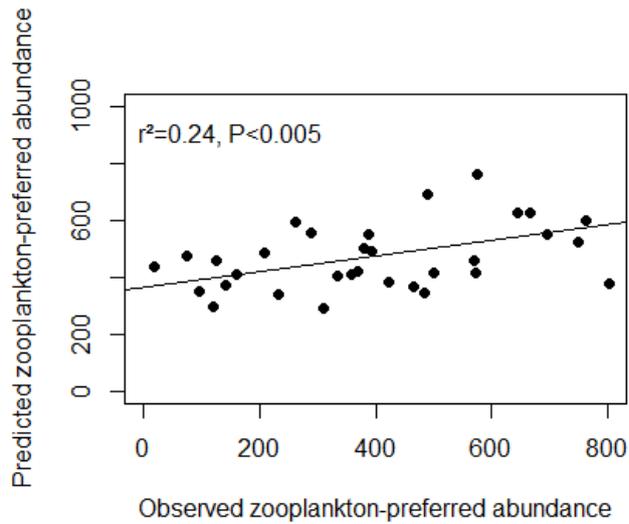


185



186

187 Figure S2.3. Example of predictions of fish biomasses and zooplankton abundances in our
 188 study area (Gulf of Lions, Western Mediterranean) for the August 17th 2014.



189

190 Figure S2.4. Relationship between observed and predicted zooplankton-preferred and
 191 zooplankton-other abundances within the range of abundances used by shearwaters, between
 192 0 and 800 ind.m⁻³ for zooplankton-preferred group and between 0 and 600 ind.m⁻³ for
 193 zooplankton-other group. A significant positive correlated relationship represents the ability
 194 of the model to correctly predict zooplankton abundance. Predicted abundances were
 195 estimated using a leave-one-out cross-validation. Note that an exceptional low salinity or deep
 196 bathymetry or type of seabed substrate found at three samples stations produced unrealistic
 197 predictions (>3000 ind.m⁻³) and we removed these outliers before determining the correlation
 198 between observed and predicted abundances.

199 **Supporting Information S3. Summary of the features of foraging trips of the GPS-**
200 **tracked Scopoli's shearwaters in the Gulf of Lions (Western Mediterranean) during the**
201 **chick-rearing period between 2011 and 2015.**

202

ID	Island	Year	Trip ID	Number of foraging locations	Duration (h)	Total travelled distance (km)	Trip range (km)
EA536869	Riou	2015	1	301	17.26667	130.3072	37.24427
EA537115	Frioul	2012	1	169	17.83333	95.32814	33.77627
EA537115	Frioul	2012	2	527	23.86667	150.7962	44.54079
EA537115	Frioul	2012	3	262	22.9	235.3361	81.88775
EA537119	Frioul	2012	1	352	17.86667	77.92335	21.20606
EA537119	Frioul	2012	2	386	21.16667	161.5663	44.26024
EA537119	Frioul	2012	3	402	22.66667	112.9971	41.98626
EA537314	Riou	2014	1	362	17.96667	197.3995	66.18423
EA537342	Riou	2015	1	431	21.23333	202.8944	46.61669
EA574518	Frioul	2012	1	392	18.63333	81.73911	10.45051
EA574518	Frioul	2012	2	406	17.03333	67.91646	12.91926
EA575316	Frioul	2012	1	134	17.8	158.9419	19.47904
EA575316	Frioul	2012	2	309	17.6	174.6852	32.09053
EA575316	Frioul	2012	3	279	17.43333	129.372	21.23269
EA583455	Riou	2014	1	202	20.13333	272.5217	107.4334
EA583462	Riou	2011	1	1077	90.2	1041.618	187.9398
EA583462	Riou	2012	1	400	22.36667	102.2403	26.37054
EA583462	Riou	2014	1	123	22.36667	195.9221	57.64454
EA583471	Riou	2011	1	185	17.96667	112.6837	22.71272
EA583471	Riou	2011	2	163	18.6	151.9209	48.85248
EA583471	Riou	2011	3	267	17.66667	255.0441	81.3694
EA583471	Riou	2012	1	171	16.93333	56.63242	10.74711
EA583471	Riou	2012	2	297	16.86667	119.7053	35.72179
EA583471	Riou	2012	3	399	21.9	91.69251	20.61444
EA583471	Riou	2012	4	288	16.66667	62.78475	15.29072
EA583473	Riou	2011	1	267	20.03333	217.588	59.64424
EA583473	Riou	2011	2	422	23.3	204.8924	23.58706
EA583473	Riou	2011	3	380	22.53333	247.112	101.1507
EA583473	Riou	2011	4	777	47.1	478.3253	117.6529
EA583473	Riou	2011	5	221	25.6	227.249	59.64342
EA583473	Riou	2014	1	510	26.1	251.4774	52.51986
EA583473	Riou	2014	2	330	20.2	144.4306	28.60502
EA583515	Riou	2014	1	224	25	369.067	61.83389
EA583515	Riou	2014	2	299	21.03333	170.5801	38.05091
EA583521	Riou	2011	1	735	47.9	654.1349	166.7566
EA583521	Riou	2011	2	310	18.96667	177.8097	52.61471
EA583521	Riou	2011	3	836	52.76667	674.7173	231.5562
EA584082	Frioul	2012	1	278	17.2	140.4598	52.02414
EA584082	Frioul	2012	2	437	22.2	153.8898	44.59631
EA584082	Frioul	2012	3	283	17.13333	135.7145	47.14116
EA587492	Riou	2012	1	197	19.76667	163.0775	37.56865
EA587492	Riou	2012	2	204	22.2	116.4792	29.6461
EA587494	Riou	2015	1	119	18.6	302.4084	117.0496
EA587495	Riou	2012	1	215	21.66667	322.8619	132.7221
EA587495	Riou	2012	2	420	19.4	89.86135	29.49951
EA588706	Frioul	2012	1	312	16.96667	109.8093	24.28834
EA588706	Frioul	2012	2	328	18.06667	176.1783	34.26667
EA588706	Frioul	2012	3	453	23.4	240.9952	62.65067
EA591287	Frioul	2012	1	225	18.1	147.6267	34.95949
EA591287	Frioul	2012	2	192	17.33333	211.9506	83.03631
EA591287	Frioul	2012	3	318	20.3	174.3363	52.14879
EA591293	Frioul	2011	1	214	17.9	301.16	90.29346
EA591293	Frioul	2011	2	371	18.63333	341.9844	110.5827
EA591293	Frioul	2011	3	140	19.93333	439.2692	201.86
EA591293	Frioul	2011	4	358	24.03333	344.7705	130.0115
EA591293	Frioul	2012	1	220	19.76667	106.7811	22.414
EA591293	Frioul	2012	2	239	17.53333	146.2526	56.44107

EA591293	Frioul	2012	3	365	17.33333	68.91761	11.27812
EA591317	Riou	2011	1	117	17.8	274.1575	112.9897
EA591317	Riou	2011	2	135	19.1	257.104	85.67987
EA591317	Riou	2011	3	114	17.16667	213.4884	89.32922
EA591396	Riou	2011	1	253	19.33333	254.674	106.3596
EA591396	Riou	2011	2	534	41.93333	558.7664	178.8871
EA591396	Riou	2011	3	443	22.1	205.4152	30.0629
EA591396	Riou	2011	4	238	22.6	105.0809	17.01076
EA591603	Frioul	2012	1	232	17.26667	85.05565	21.20548
EA591603	Frioul	2012	2	242	17.1	246.9954	109.9167
EA591604	Frioul	2011	1	242	19.5	312.323	117.5258
EA591643	Frioul	2011	1	496	25.16667	170.1195	22.71646
EA591643	Frioul	2011	2	564	46	737.3911	216.5993
EA591643	Frioul	2012	1	177	21.93333	158.3072	46.2028
EA591643	Frioul	2012	2	498	23.43333	134.9211	34.51857
EA593790	Riou	2014	1	290	22.26667	323.6014	58.25641
EA593790	Riou	2014	2	224	19.7	88.61498	17.1535
EA593791	Riou	2011	1	960	45.6	442.3402	125.0831
EA593791	Riou	2011	2	311	17.8	156.4401	38.93911
EA593793	Riou	2011	1	281	19.73333	345.7348	144.5087
EA593793	Riou	2011	2	527	41.63333	595.6626	185.988
EA593793	Riou	2011	3	59	5.866667	34.50492	6.127479
EA593793	Riou	2011	4	403	22.93333	181.4883	14.81019
EA593793	Riou	2011	5	41	5.3	53.00642	22.24902
EA593793	Riou	2011	6	311	21.63333	110.9618	17.80161
EA593793	Riou	2012	1	238	17.16667	125.5197	37.19858
EA593793	Riou	2012	2	177	17.66667	323.8028	133.3971
EA593793	Riou	2012	3	270	23.23333	148.8923	39.52289
EA593793	Riou	2014	1	130	13.6	159.055	23.17425
EA593793	Riou	2014	2	33	3.533333	19.12922	5.73451
EA593798	Riou	2012	1	270	19.66667	79.77859	13.90533
EA593798	Riou	2012	2	193	17.13333	86.4203	16.60192
EA593798	Riou	2012	3	420	25.83333	275.3548	48.85784
EA593798	Riou	2012	4	164	16.33333	135.0189	52.13851
EA595979	Riou	2015	1	336	17.66667	173.7901	71.66334
EA621014	Riou	2011	1	770	69.26667	682.8429	146.2361
EA621014	Riou	2011	2	587	47.36667	755.6292	259.5073
EA621029	Riou	2014	1	61	19.9	185.4475	35.27625
EA621030	Riou	2014	1	230	16.33333	210.5041	73.7311
EA621030	Riou	2014	2	455	29	248.8434	44.4035
EA621030	Riou	2014	3	305	21.06667	212.2364	36.69691
EA621030	Riou	2014	4	460	22.83333	130.2794	33.13248
EA621030	Riou	2014	5	322	17.16667	175.1493	35.69736
EA621030	Riou	2014	6	216	19.16667	191.0858	53.17421
EA621053	Riou	2011	1	1252	112.7333	1290.359	131.7114
EA621081	Riou	2014	1	71	17.8	172.1036	47.827
EA621083	Riou	2012	1	246	18.33333	136.6396	32.34254
EA621083	Riou	2012	2	183	16.66667	273.245	108.3758
EA621085	Riou	2011	1	186	21.43333	222.1787	19.29173
EA621085	Riou	2011	2	814	48.86667	452.8178	69.15876
EA621124	Frioul	2012	1	229	19.96667	278.0153	118.5711
EA621124	Frioul	2012	2	186	21.13333	155.2585	33.80452
EA621124	Frioul	2012	3	574	26.33333	182.9879	31.47239
EA621252	Riou	2012	1	381	21.2	220.8059	23.32588
EA621252	Riou	2012	2	246	16.66667	120.7745	32.78243
EA621254	Riou	2015	1	227	19.1	31.38855	9.478269
EA621282	Frioul	2012	1	359	19.66667	131.3543	19.99216
EA621282	Frioul	2012	2	269	20.8	185.2309	42.75986
EA621282	Frioul	2012	3	219	17.26667	137.758	34.19235
EA621347	Riou	2011	1	96	16.66667	133.4084	25.11375
EA621347	Riou	2011	2	258	16.73333	159.0478	18.94242
EA621379	Riou	2011	1	455	25.53333	282.486	48.67823
EA621379	Riou	2011	2	355	24.3	229.622	85.31952
EA621379	Riou	2011	3	267	20.6	240.5288	78.12428
EA621379	Riou	2011	4	368	21.03333	99.82077	27.36082
EA621673	Frioul	2012	1	167	17.43333	237.5918	61.14044
EA621673	Frioul	2012	2	266	18.4	309.4056	112.24
EA621673	Frioul	2012	3	181	17.56667	251.4703	100.8403
EA621673	Frioul	2012	4	304	22.76667	362.6366	141.9427
EA621683	Frioul	2012	1	392	17.83333	120.8243	17.21523

EA621683	Frioul	2012	2	217	19.3	143.1574	33.86665
EA621683	Frioul	2012	3	437	20.8	138.6181	24.19683
EC100001	Riou	2011	1	185	15.36667	109.4745	25.37992
EC100001	Riou	2011	2	134	11.43333	172.7164	58.56319
EC100002	Riou	2012	1	228	17.83333	169.9823	57.03959
EC100002	Riou	2012	2	307	22.76667	259.0814	95.54314
EC100002	Riou	2014	1	544	42.36667	560.7254	115.1856
EC100054	Frioul	2012	1	317	22.46667	335.7444	118.0449
EC100054	Frioul	2012	2	223	23.33333	102.0563	17.26958
EC100054	Frioul	2012	3	379	21.83333	123.5627	43.27236
EC100104	Riou	2015	1	347	22.7	344.462	90.98925
EC100104	Riou	2015	2	279	18.93333	237.5836	76.64678
EC100156	Riou	2012	1	107	18.16667	74.70529	26.8197
EC100156	Riou	2012	2	218	19.16667	116.7197	31.65386
EC100156	Riou	2012	3	336	21	138.7979	50.91555
EC100160	Riou	2012	1	423	22.4	99.63473	26.54514
EC100160	Riou	2012	2	258	17.1	168.0411	34.38288
EC100183	Riou	2015	1	310	16.73333	150.7264	60.51673
EC100253	Riou	2015	1	264	17.03333	174.5967	68.18407
EC102691	Riou	2014	1	433	21.86667	158.9545	34.90184
EC102692	Riou	2014	1	636	46.96667	495.5599	84.38068
EC102698	Riou	2014	1	259	18.73333	152.3522	49.09335
NB02	Riou	2011	1	211	19.76667	145.5024	23.07429
NB02	Riou	2011	2	22	6.766667	13.02388	2.097616
NB02	Riou	2011	3	269	16.93333	138.1201	42.86953
NB06	Riou	2012	1	230	18.2	162.8009	37.6337
NB06	Riou	2012	2	319	21.13333	126.9835	28.01322
NB06	Riou	2012	3	418	22.4	88.22749	18.16903
NB07	Riou	2014	1	471	18.2	83.71739	21.39259
NB08	Riou	2014	1	108	26.46667	294.8945	47.0458
NB08	Riou	2014	2	362	20.33333	101.7575	23.6823
NB09	Riou	2014	1	326	20.13333	140.1232	49.31408
NB10	Riou	2014	1	279	20.66667	159.4168	41.84232
NB11	Riou	2014	1	243	25.23333	298.2127	96.93353
NB11	Riou	2014	2	94	17.86667	102.0556	23.6134
NB12	Riou	2015	1	329	18.66667	280.2737	124.3417
NB13	Riou	2015	1	171	19	162.264	60.2429
NB13	Riou	2015	2	102	4.166667	9.352807	3.394749
NB13	Riou	2015	3	335	22.4	98.93079	19.69591
NB13	Riou	2015	4	277	17.33333	330.5388	94.25448
NB14	Riou	2015	1	277	17.8	176.8317	53.54744
NB15	Riou	2015	1	80	17	255.3445	102.2782
NB16	Riou	2015	1	405	21.7	203.2518	29.24086
NB16	Riou	2015	2	423	24.1	272.6973	29.55321
NB17	Riou	2015	1	349	21.7	320.6357	73.82406
NB17	Riou	2015	2	269	20.06667	230.7422	82.62435
NB17	Riou	2015	3	171	23.46667	204.3194	59.18303
NB18	Riou	2015	1	313	23.5	270.2717	58.78955
NB18	Riou	2015	2	25	3.2	8.57647	1.871632
NB19	Riou	2015	1	359	21.8	215.4816	46.68042
NB20	Riou	2015	1	292	17.06667	55.43941	13.44915
NB21	Riou	2015	1	237	17.16667	230.0234	49.71648
NB22	Riou	2015	1	284	21.53333	305.2421	59.42231
NB23	Riou	2015	1	266	16.96667	157.3242	38.13538
NB23	Riou	2015	2	426	24.26667	253.7867	53.44138

203 **Supporting Information S4. Stable isotope analyses and trophic position of shearwaters**

204

205 To corroborate the degree of trophic specialization found in the resource selection patterns
206 and their inter-annual variations, we assessed the individual trophic position of shearwaters
207 using stable isotope analyses of the first primary feather (P1) of each individual. Considering
208 the moult pattern of Scopoli's shearwaters, P1 feathers collected in August reflect diet during
209 the previous chick-rearing period (Ramos *et al.* 2009). Therefore, feathers collected on GPS-
210 tracked shearwaters during chick-rearing at year n described their diet during the chick-
211 rearing period of year $n-1$. A total of 134 P1 feathers were collected during the biotelemetry
212 fieldwork ($n = 31$ in 2011, $n = 33$ in 2012, $n = 20$ in 2014, $n = 20$ in 2015 and $n = 30$ in 2016).
213 We collected both GPS data and P1 samples in 2016, but did not considered GPS data
214 collected in 2016 in our analyses. Relative abundance of stable isotopes of nitrogen ($^{15}\text{N}:^{14}\text{N}$,
215 thereafter ' $\delta^{15}\text{N}$ ') and carbon ($^{13}\text{C}:^{12}\text{C}$, thereafter ' $\delta^{13}\text{C}$ ') were determined on about 0.4 mg
216 subsamples of P1 feathers by continuous-flow isotope-ratio spectrometry (see Péron *et al.*
217 [2013] for more details on sample preparation and calculation of isotopic ratios). $\delta^{15}\text{N}$ values
218 measured in predators reflect their trophic status and $\delta^{13}\text{C}$ values reflect the characteristics of
219 their foraging location (Ramos *et al.* 2009; Cardona *et al.* 2012; Péron *et al.* 2013). We
220 estimated and compared the trophic position (TP) between individuals using the following
221 equation as described by Hobson and Bond (2012) for seabirds:

222

$$223 \quad TP_i = 3 + (\delta^{15}N_i - \Delta d_{feather} - \delta^{15}N_{copepods})/3.4 \quad (1)$$

224

225 where $\delta^{15}N_i$ is the stable nitrogen isotope ratio for individual i in its P1 feather, $\Delta d_{feather}$ is
226 the mean diet-tissue discrimination factor between feather and prey muscle protein for
227 comparable species because no data is available for adult Procellariiforms (3.7‰ for $\delta^{15}N$,

228 Meier *et al.* 2017), $\delta^{15}N_{copepods}$ (4.7‰) is the average value measured on copepods in the
229 Gulf of Lions based on samples collected during the PELMED campaign in 2014, with an
230 assumed trophic level of 2. We found a similar value for the $\delta^{15}N_{copepods}$ than in 2008 in the
231 Gulf of Lions (4.5‰; Costalago *et al.* 2012). We considered a constant trophic enrichment
232 factor of 3.4‰ (Post 2002).

233 To gain additional insights into diet specialization of Scopoli's shearwaters, we related
234 the isotopic signature of individuals to those of their potential prey. The isotopic signatures of
235 European anchovy, sardine and sprat were determined yearly between 2010 and 2015 based
236 on sample collected during PELMED surveys covering our study area (n ranged between 18
237 and 61 for anchovies, n ranged between 36 and 51 for sardines, n ranged between 32 and 57
238 for sprats; Brosset *et al.* 2016; Mialet *et al.* 2017). No data was available for sprat in 2015 and
239 we used the isotopic values found in 2014 for this species in 2015. We also considered
240 isotopic values estimated for zooplankton in 2014 (n = 174 samples, Brosset *et al.* 2016) and
241 copepods only (calanoids) in 2014 ($\delta^{15}N = 4.74 \pm 0.77$ [mean \pm SD], $\delta^{13}C = -22.59 \pm$
242 0.63, n = 134 samples, unpublished data) in the Gulf of Lions by IFREMER. Finally, isotopic
243 signatures of European common squids (*Loligo vulgaris*), European flying squids (*Todarodes*
244 *sagittatus*) and euphausiids (*Meganyctiphanes norvegica*) were taken from oceanographic
245 surveys carried out in 2006-2007 in the Western Mediterranean (Cardona *et al.* 2012).

246 Importantly, inference on diet of shearwaters from $\delta^{15}N$ values were valuable because
247 1) the average $\delta^{15}N$ isotopic signatures in zooplankton/copepods (4.75‰/4.74‰) were clearly
248 different (at least ~ 3.3 ‰, i.e. about one trophic level) from $\delta^{15}N$ in the three fish species
249 (anchovy: 8.03‰, sardine: 8.31‰ and sprat: 8.34‰) in 2014 and standard deviation was
250 small for each prey type, 2) the isotopic landscape is relatively homogeneous in space and
251 time (Fig. S4.2). We found a low spatial variability among $\delta^{15}N$ values within the Gulf of
252 Lion for fish species and zooplankton in 2014 and for fish species in other years (Fig. S4.2).

253 We fitted a linear mixed model assessing the relationship between $\delta^{15}\text{N}$ values for each prey
254 type (response variable) and a set of independent variables: longitude, latitude, fish length or
255 zooplankton size class, and added a nested random intercept for fish (year/station) or a
256 random intercept for zooplankton (station) to control for non-independence among multiple
257 samples from the same year and/or the same station. Models indicated a slight decrease in
258 isotopic values from West to East for anchovy (beta_longitude = -0.36, 95%CI = -0.54;-0.17)
259 and sardine (beta_longitude = -0.21, 95%CI = -0.36;-0.05), but $\delta^{15}\text{N}$ values remained very
260 different between fish and zooplankton throughout the longitudinal gradient. No longitudinal
261 trend was found for sprat and zooplankton and no latitudinal trend occurred for any species.
262 These results were supported by the low standard deviation in $\delta^{15}\text{N}$ for any species at each
263 year. Similarly, we also found a very low inter-annual variability among the $\delta^{15}\text{N}$ values for
264 any fish species in our study, with average values ranging between 7.15‰ and 8.03‰ for
265 anchovy, 7.81‰ and 8.5‰ for sardines, and 7.65‰ and 8.34‰ for sprats (see also Brosset *et al.*
266 *al.* 2016). We have no multi-year data for zooplankton/copepod but we expect that if $\delta^{15}\text{N}$
267 values for zooplankton/copepod changed significantly among years, small pelagic fish
268 (anchovy, sardine and sprat) preying on zooplankton/copepod should have also changed in
269 their $\delta^{15}\text{N}$ values among years, which is not the case. We thus are confident with the fact
270 that $\delta^{15}\text{N}$ values for zooplankton/copepod should be relatively stable during our study period.
271 This is reinforced by the fact that $\delta^{15}\text{N}$ values remained stable over time (2004, 2005 and
272 2014) in the Gulf of Lion (Brosset *et al.* 2016).

273 We found heterogeneity in the trophic position of individuals within and across years,
274 while most birds had low trophic position, with a mean trophic position of 3.39 +/- 0.03
275 (mean +/- SE, Fig. S4.1). In 2010 and 2011, shearwaters showed individual dietary
276 specialization with their trophic position ranging from 2.9 to 4.7, corresponding to a diet
277 exclusively based on zooplankton, euphausiids and copepods, or on small pelagic fish and

278 squid (Fig. S4.1, Fig. 6 in the main text). The following years had lower individual
279 heterogeneity. The trophic position and contribution of fish in the diet in 2013 seemed to
280 increase related to other years ($P < 0.02$), but we have to be cautious with this interpretation
281 because $\delta^{15}N_{copepods}$ was considered constant among years based on an estimation in 2014
282 (i.e. constant baseline). An increase of the $\delta^{15}N_{copepods}$ value in 2013 could imply higher
283 trophic position values for shearwaters in 2013. However, $\delta^{15}N_{copepods}$ seemed to be
284 relatively stable over years with similar values in 2008 and 2014, and isotopic signature of
285 shearwaters well matched isotopic signature of small pelagic fish in 2013 (Fig. 6 in the main
286 text). Shearwaters became more specialized on prey of lower trophic levels in 2014 with few
287 variations among individuals (Fig. S4.1, Fig. 6 in the main text). Mean trophic position of
288 individuals was not related to sex and age ($F_{6,93} = 2.24$, $r^2 = 0.07$, $P < 0.05$).

289

290 **References**

- 291 Brosset, P. *et al.* (2016). Linking small pelagic dietary shifts with ecosystem changes in the
292 Gulf of Lions. *Mar. Ecol. Prog. Ser.*, 554, 157-171.
- 293 Cardona, L., Álvarez de Quevedo, I., Borrell, A. & Aguilar, A. (2012). Massive Consumption
294 of Gelatinous Plankton by Mediterranean Apex Predators. *PLoS ONE*, 7, e31329.
- 295 Costalago, D., Navarro, J., Álvarez-Calleja, I. & Palomera, I. (2012). Ontogenic and seasonal
296 changes in the feeding habits and trophic levels of two small pelagic fish species. *Mar. Ecol.
297 Prog. Ser.*, 460, 169-181.
- 298 Hobson, K.A. & Bond, A.L. (2012). Extending an indicator: year-round information on
299 seabird trophic ecology from multiple-tissue stable-isotope analyses. *Mar. Ecol. Prog. Ser.*,
300 461, 233-243.
- 301 Meier, R.E. *et al.* (2017). Tracking, feather moult and stable isotopes reveal foraging
302 behaviour of a critically endangered seabird during the non-breeding season. *Divers. Distrib.*,

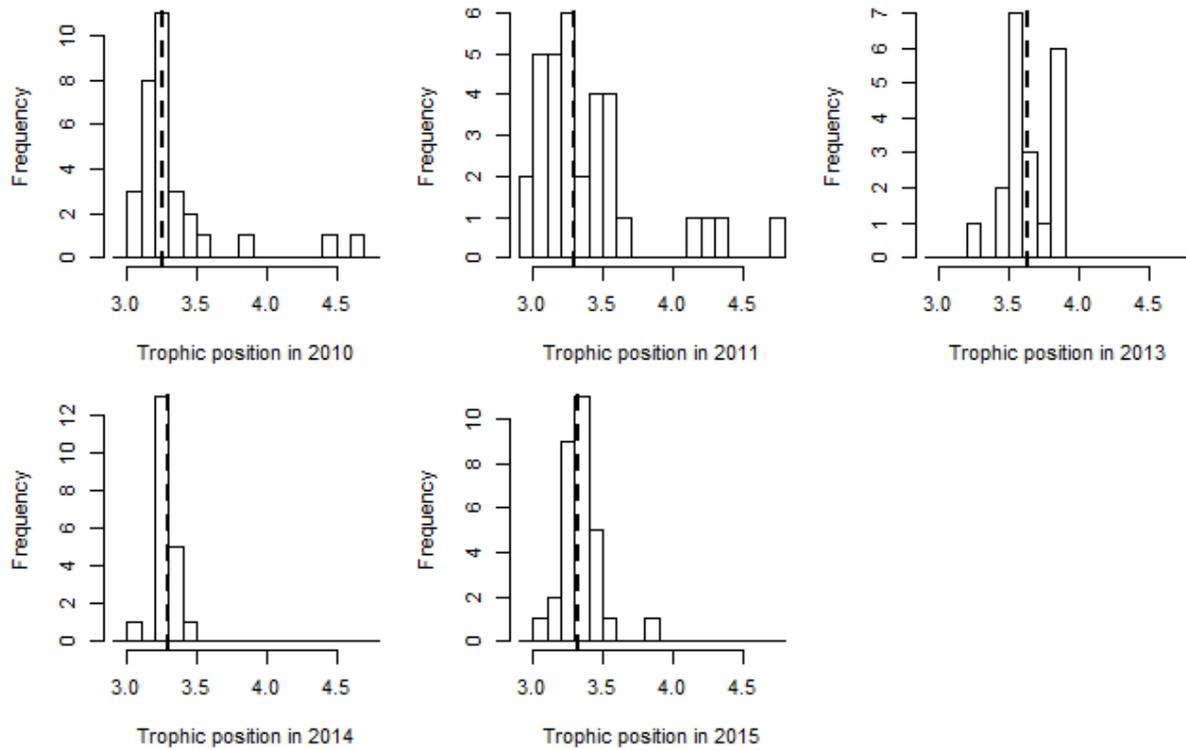
303 23, 130-145.

304 Mialet, B. (2017). Bilan des essais et optimisation du suivi mutualisé « réseaux trophiques et
305 contaminants » sur les campagnes halieutiques DCF 2014- 2015. Rapport pour le projet
306 DCSMM. <http://archimer.ifremer.fr/doc/00373/48447/>

307 Péron, C. *et al.* (2013). Importance of coastal Marine Protected Areas for the conservation of
308 pelagic seabirds: the case of vulnerable yelkouan shearwaters in the Mediterranean Sea. *Biol.*
309 *Conserv.*, 168, 210-221.

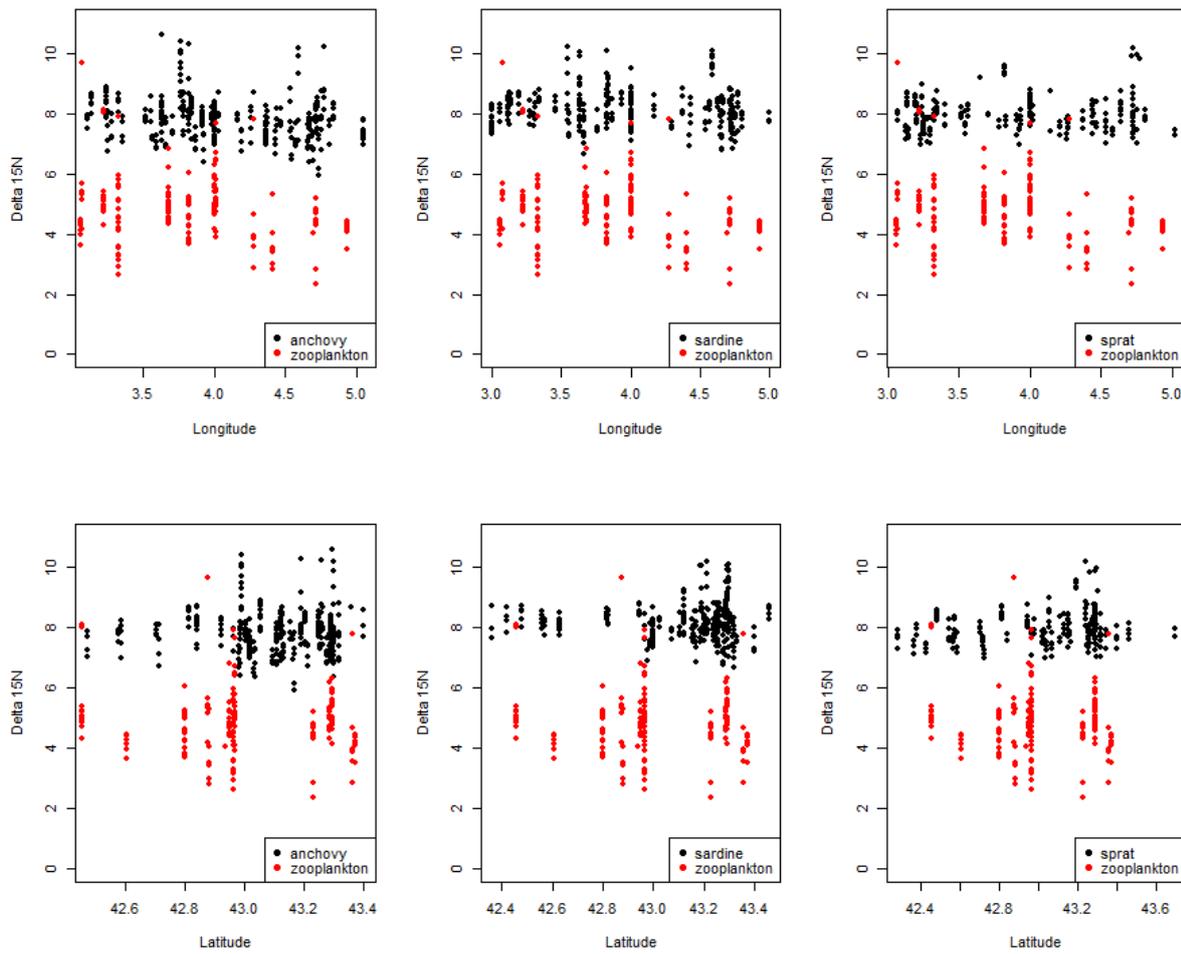
310 Post, D.M. (2002) Using stable isotopes to estimate trophic position: models, methods, and
311 assumptions. *Ecology*, 83,703-718.

312 Ramos, R., González-Solís, J. & Ruiz, X. (2009). Linking isotopic and migratory patterns in a
313 pelagic seabird. *Oecologia*, 160, 97-105.



314

315 Figure S4.1. Annual distributions of inter-individual heterogeneity of trophic position of
 316 Scopoli's shearwaters in the Gulf of Lions (Western Mediterranean) during the chick-rearing
 317 period between 2010 and 2015. Dotted lines represent median values within distributions.



318

319 Figure S4.2. Spatial trends in the $\delta^{15}\text{N}$ isotopic values along longitudinal and latitudinal

320 gradients for three pelagic fish species (black circles) in July 2010 to 2015 and for

321 zooplankton in July 2014 (red circles) within the Gulf of Lion (Western Mediterranean). $\delta^{15}\text{N}$

322 values for zooplankton higher than 7‰ correspond to anchovy eggs.

323 **Supporting Information S5. Determining within-individual consistency in resource**
 324 **selection**

325

326 We quantified individual specialization in resource selection (i.e. within-individual
 327 consistency in resource selection) with an adjusted repeatability index R_k for each shearwater
 328 k . We adapted the population-level repeatability index R developed for logistic regression
 329 with random coefficients (Johnson 2014; Nakagawa *et al.* 2017) that took the form:

330

$$331 \quad R = \frac{\sigma_{x,between}^2}{\sigma_{x,between}^2 + \sigma_{x,within}^2 + \sigma_\varepsilon^2}, \quad (1)$$

$$332 \quad \sigma_{x,between}^2 = (\sum_k \sum_i \text{var}(\gamma_{0k}^{(bird)} + \gamma_{xk}^{(bird)} x_{ijk}))/n, \quad (2)$$

$$333 \quad \sigma_{x,within}^2 = (\sum_{jk} \sum_i \text{var}(\gamma_{0jk}^{(trip)} + \gamma_{xjk}^{(trip)} x_{ijk}))/n, \quad (3)$$

$$334 \quad \sigma_\varepsilon^2 = \frac{1}{p(1-p)}, \quad (4)$$

$$335 \quad p \sim \text{logit}^{-1} \left(\beta_0 \sqrt{1 + \left(\frac{16\sqrt{3}}{15\pi} \right)^2 \times (\sigma_{x,between}^2 + \sigma_{x,within}^2 + \sigma_\varepsilon^2)}^{-1} \right), \quad (5)$$

336

337 where $\sigma_{x,between}^2$ and $\sigma_{x,within}^2$ are the between- and within-individual variances (bird and trip
 338 level, respectively) estimated within resource selection function with a random effect for the
 339 prey-related variable x , σ_ε^2 is global observation-level (GPS location level) variance at the
 340 individual level given a logit link, $\gamma_{0k}^{(bird)}$ and $\gamma_{xk}^{(bird)}$ are the random intercepts and the
 341 random coefficients of x , respectively, for shearwater k at the individual level, $\gamma_{0jk}^{(trip)}$ and
 342 $\gamma_{xjk}^{(trip)}$ are the random intercepts and the random coefficients of x , respectively, for trip j and
 343 shearwater k at the trip level, n the total number of observations, p is the expected proportion
 344 of successes on the observed scale, and σ_ε^2 is the fixed-effect variance.

345 We adapted the population-level index R with an individual-level index R_k by
 346 partitioning σ_ε^2 at the individual level, as usually done for linear models (Potier *et al.* 2015;
 347 Wakefield *et al.* 2015). In a mixed RSF for foraging location i , trip j and shearwater k , R_k took
 348 the form:

$$350 R_k = \frac{\sigma_{x,between}^2}{\sigma_{x,between}^2 + \sigma_{x,within}^2 + \sigma_{\varepsilon k}^2}, \quad (6)$$

$$351 \sigma_{\varepsilon k}^2 = \frac{1}{p_k(1-p_k)}, \quad (7)$$

$$352 p_k \sim \text{logit}^{-1} \left(\beta_0 \sqrt{1 + \left(\frac{16\sqrt{3}}{15\pi} \right)^2 \times (\sigma_{xk,between}^2 + \sigma_{xk,within}^2 + \sigma_{\varepsilon k}^2)}^{-1} \right), \quad (8)$$

353
 354 where $\sigma_{\varepsilon k}^2$ is the partitioned observation-level variance for the k^{th} bird, p_k is the expected
 355 proportion of successes on the observed scale for the k^{th} bird, $\sigma_{xk,between}^2$ and $\sigma_{xk,within}^2$ are
 356 the between- and within-individual variance attributable to the k^{th} bird, respectively, and $\sigma_{\varepsilon k}^2$
 357 is the fixed-effect variance for the k^{th} bird.

358 R_k values range between 0 and 1. R_k values close to 1 imply high specialization (i.e.
 359 consistency) in resource selection for shearwater k . Low R_k values can arise from a relatively
 360 high heterogeneity in resource selection among foraging trips or locations of shearwater k (i.e.
 361 high within-individual or partitioned observation-level variance). Analyses were performed
 362 with the *rptR* package (Stoffel *et al.* 2017) of the R software (R Development Core Team
 363 2016).

364
 365 **References**

366 Johnson, P.C.D. (2014) Extension of Nakagawa & Schielzeth's R^2_{GLMM} to random slopes
 367 models. *Methods Ecol. Evol.*, 5, 944-946.

368 Nakagawa, S., Johnson, P.C.D. & Schielzeth, H. (2017). The coefficient of determination R²
369 and intra-class correlation coefficient from generalized linear mixed-effects models revisited
370 and expanded. *J. R. Soc. Interface*, 14, 20170213.

371 Potier, S., Carpentier, A., Grémillet, D., Leroy, B. & Lescroël, A. (2015). Individual
372 repeatability of foraging behaviour in a marine predator, the great cormorant, *Phalacrocorax*
373 *carbo*. *Anim. Behav.*, 103, 83-90.

374 R Development Core Team 2016. R: A Language and Environment for Statistical Computing.
375 R Foundation for Statistical Computing, Vienna.

376 Stoffel, M.A., Nakagawa, S. & Schielzeth, H. (2017). rptR: Repeatability estimation and
377 variance decomposition by generalized linear mixed-effects models. *Methods Ecol. Evol.*, 8,
378 1639-1644.

379 Wakefield, E.D. *et al.* (2015). Long-term individual foraging site fidelity – why some gannets
380 don't change their spots. *Ecology*, 96, 3058-3074.

381 **Supporting Information S6. Supplementary figures and tables.**

382

383 Table S6.1. Mixed-effects logistic regression models for the resource selection of Scopoli's
 384 shearwater in the Gulf of Lions (Western Mediterranean) during the chick-rearing period
 385 between 2010 and 2015, estimated with GPS foraging locations (n = 56,945 locations) with
 386 random intercepts and coefficients for trip (n = 182 trips) and bird levels (n = 75 shearwaters).
 387 We showed the marginal selection coefficients (β) with their standard errors (SE) and 95%
 388 confidence intervals (CI), the variance of random effects at the bird (VAR_{bird}) and trip levels
 389 (VAR_{trip}). Models were assessed independently for each prey-related variable (12 models
 390 have converged) and summarized in the table. We accounted for multiple comparisons by
 391 adjusting our 95% CI with a Benjamini-Yekutieli correction at alpha = 0.0014 and z-value =
 392 3.19.

Variable	B	SE	Adjusted 95% CI	VAR_{bird}	VAR_{trip}
<i>Anchovy adult biomass</i>					
Intercept	-2.45*	0.11	-2.80;-2.10	0.02	0.20
Biomass	-0.26	0.10	-0.58;0.06	0.22	1.02
<i>Anchovy juvenile biomass</i>					
Intercept	2.34*	0.09	2.05;2.63	0.14	0.25
Biomass	-1.07*	0.10	-1.39;-0.75	1.31	0.96
<i>Sardine adult biomass</i>					
Intercept	-2.34*	0.10	-2.66;-2.02	0.12	0.29
Biomass	-2.04*	0.09	-2.33;-1.75	0.67	5.65
<i>Sardine juvenile biomass</i>					
Intercept	-3.03*	0.08	-3.29;-2.77	0.32	0.81
Biomass	-14.70*	0.09	-14.98;-14.41	34.41	210.43

Sprat adult biomass

Intercept	-2.59*	0.09	-2.88;-2.30	0.06	0.22
Biomass	-0.01	0.07	-0.23;0.21	0.12	0.94

Sprat juvenile biomass

Intercept	-2.22*	0.08	-2.48;-1.96	0.08	0.27
Biomass	-0.77*	0.07	-0.99;-0.55	0.06	1.06

Zooplankton-preferred abundance

Intercept	-3.02*	0.17	-3.56;-2.48	0.06	0.42
Abundance	0.30*	0.09	0.01;0.59	0.16	0.82

Zooplankton-other abundance

Intercept	-2.31*	0.15	-2.79;-1.83	0.15	0.34
Abundance	0.29*	0.09	0.003;0.58	0.22	0.79

Anchovy adult predictability

Intercept	-8.29*	0.30	-9.25;-7.33	0.63	3.40
Var(biomass)	-11.36*	0.69	-13.56;-9.15	171.90	430.57

Sprat adult predictability

Intercept	-7.80*	0.15	-8.28;-7.32	2.35	1.16
Var(biomass)	-2.70*	0.12	-3.08;-2.32	0.90	24.89

Zooplankton-preferred predictability

Intercept	-2.15*	0.11	-2.50;-1.80	0.02	0.20
Var(abundance)	0.29	0.18	-0.28;0.86	0.85	3.97

Zooplankton-other predictability

Intercept	-2.21*	0.12	-2.59;-1.83	0.01	0.34
Var(abundance)	-0.06	0.16	-0.57;0.45	0.32	4.04

393 * Benjamini-Yekutieli corrected 95% CI exclude 0.

394 Table S6.2. Variance components used to estimate the within-individual consistency in
 395 resource selection of shearwaters within the Gulf of Lions (Western Mediterranean) during
 396 the chick-rearing period between 2011 and 2015. We show the between-individual variance
 397 ($\sigma_{x,between}^2$), the within-individual variance ($\sigma_{x,within}^2$) and the distribution (mean \pm SE) of all
 398 the partitioned observation-level variance of each bird k ($\sigma_{\epsilon k}^2$) used in the analyses.
 399

Model	$\sigma_{x,between}^2$	$\sigma_{x,within}^2$	$\sigma_{\epsilon k}^2$
Anchovy adult biomass	0.234	1.224	9.589 \pm 0.102
Anchovy juvenile biomass	1.449	1.217	7.200 \pm 0.110
Sardine adult biomass	0.784	5.936	3.139 \pm 0.145
Sardine juvenile biomass	34.726	211.235	4.671 \pm 0.127
Sprat adult biomass	0.175	1.163	11.245 \pm 0.136
Sprat juvenile biomass	0.139	1.331	7.980 \pm 0.079
Zooplankton-preferred abundance	0.223	1.239	13.930 \pm 0.148
Zooplankton-other abundance	0.369	1.133	8.735 \pm 0.072
Anchovy adult predictability	172.535	433.963	36.178 \pm 5.766
Sprat adult predictability	3.249	26.049	49.715 \pm 4.830
Zooplankton-preferred predictability	0.868	4.173	7.557 \pm 0.197
Zooplankton-other predictability	0.319	4.378	7.114 \pm 0.192

400

401 Table S6.3. Resource selection for the two foraging trip tactics of shearwaters within the Gulf
 402 of Lions (Western Mediterranean) during the chick-rearing period between 2011 and 2015.

403 Mean selection coefficient ($\bar{\beta}$) are shown with their 95% confidence interval (CI).

404

Variable	Zooplankton-fish trips	Zooplankton-only trips
Anchovy adult biomass	0.31 [0.20;0.42]*	-0.95 [-1.13;-0.76]*
Anchovy juvenile biomass	-0.85 [-0.99;-0.71]*	-1.32 [-1.49;-1.15]*
Sardine adult biomass	-1.03 [-1.36;-0.70]*	-3.21 [-3.71;-2.70]*
Sardine juvenile biomass	-9.08 [-10.91;-7.25]*	-19.85 [-23.16;-16.54]*
Sprat adult biomass	0.62 [0.49;0.75]*	-0.75 [-0.89;-0.62]*
Sprat juvenile biomass	-0.26 [-0.40;-0.12]*	-1.37 [-1.58;-1.16]*
Zooplankton-preferred abundance	0.24 [0.08;0.41]*	0.37 [0.19;0.54]*
Zooplankton-other abundance	0.50 [0.35;0.65]*	0.05 [-0.13;0.23]
Anchovy adult predictability	-5.17 [-8.19;-2.14]*	-14.20 [-19.67;-8.74]*
Sprat adult predictability	-0.87 [-1.45;-0.29]*	-4.42 [-5.49;-3.36]*
Zooplankton-preferred predictability	0.16 [-0.22;0.53]	0.47 [0.11;0.84]*
Zooplankton-other predictability	0.24 [-0.10;0.57]	-0.38 [-0.83;0.06]

405 *95% CI exclude 0.

406 Table S6.4. Spearman rank correlations (r_s) and their significance (P) in parentheses between
 407 individual foraging site fidelity (IFSF) and individual specialization in resource selection
 408 (ISRS), and between IFSF and resource selection for Scopoli's shearwater (n = 47
 409 individuals), in the Gulf of Lions (Western Mediterranean) during four chick-rearing periods
 410 between 2011 and 2015 and each prey-related variable. P-values are adjusted with Benjamini-
 411 Yekutieli correction to account for the 24 multiple comparisons.

412

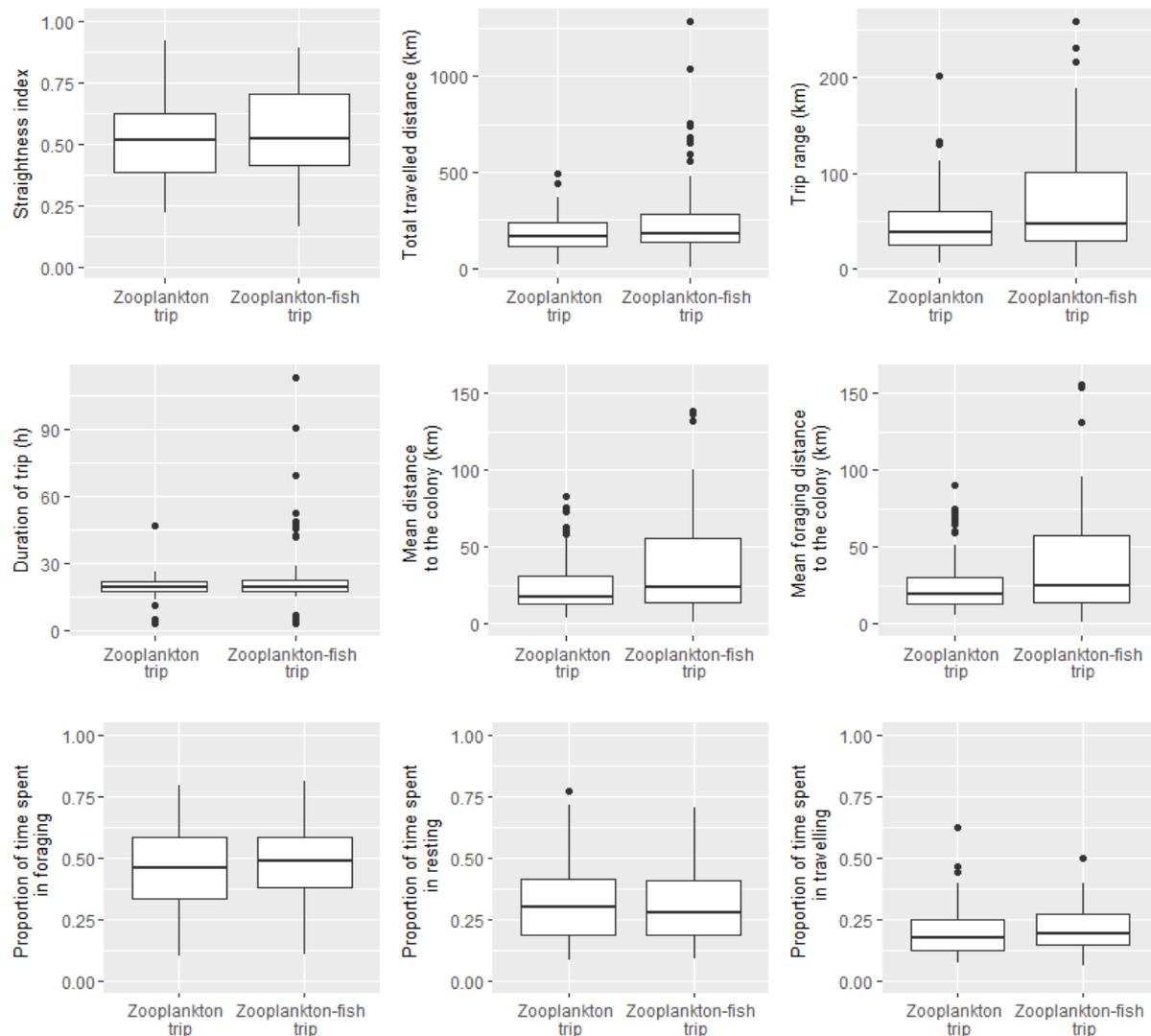
Model	IFSF versus ISRS	IFSF versus resource selection
Anchovy adult biomass	-0.04 (1.00)	-0.08 (1.00)
Anchovy juvenile biomass	0.17 (1.00)	-0.10 (1.00)
Sardine adult biomass	0.13 (1.0)	0.26 (1.00)
Sardine juvenile biomass	-0.03 (1.0)	0.27 (1.00)
Sprat adult biomass	-0.11 (1.0)	0.07 (1.00)
Sprat juvenile biomass	0.02 (1.00)	0.33 (1.00)
Zooplankton-preferred abundance	-0.27 (1.0)	-0.17 (1.00)
Zooplankton-other abundance	-0.43 (0.90)	-0.16 (1.00)
Anchovy adult predictability	-0.13 (1.0)	0.14 (1.00)
Sprat adult predictability	0.28 (1.0)	0.24 (1.00)
Zooplankton-preferred predictability	-0.17 (1.00)	0.13 (1.00)
Zooplankton-other predictability	-0.14 (1.00)	-0.002 (1.00)

413

414 Table S6.5. Proportions of the different foraging trip tactics of GPS-tracked shearwaters each
 415 year within the Gulf of Lions (Western Mediterranean) during the chick-rearing period. We
 416 tested for annual variations in the relative importance of selection tactics (n = 182 trips) using
 417 mixed logistic regression with individuals (n = 75 shearwaters) as random intercept and year
 418 as predictor. We found inter-annual variability in the probability to use zooplankton-fish over
 419 zooplankton-only trips. In 2011, shearwaters mainly (66%) used zooplankton-fish specialist
 420 trips, while zooplankton-only specialist trips became predominant (63%) in 2014. The
 421 probability to use a zooplankton-fish trip over a zooplankton-only trip was significantly
 422 higher in 2011 than in 2014 (z-test = -2.508, P = 0.01). Interestingly, isotopic analyses
 423 confirmed that shearwaters had low individual trophic position in 2014, relatively
 424 homogeneous among birds, and that their individual dietary specialization were poorly based
 425 on small pelagic fish this year (Supporting Information S4, Fig. S4.1, S4.2). Contrary to other
 426 years, selection patterns were more balanced among trips in 2012 and 2015 and the
 427 probability to use a zooplankton-fish trip over a zooplankton-only trip did not differ
 428 statistically from other years.

429

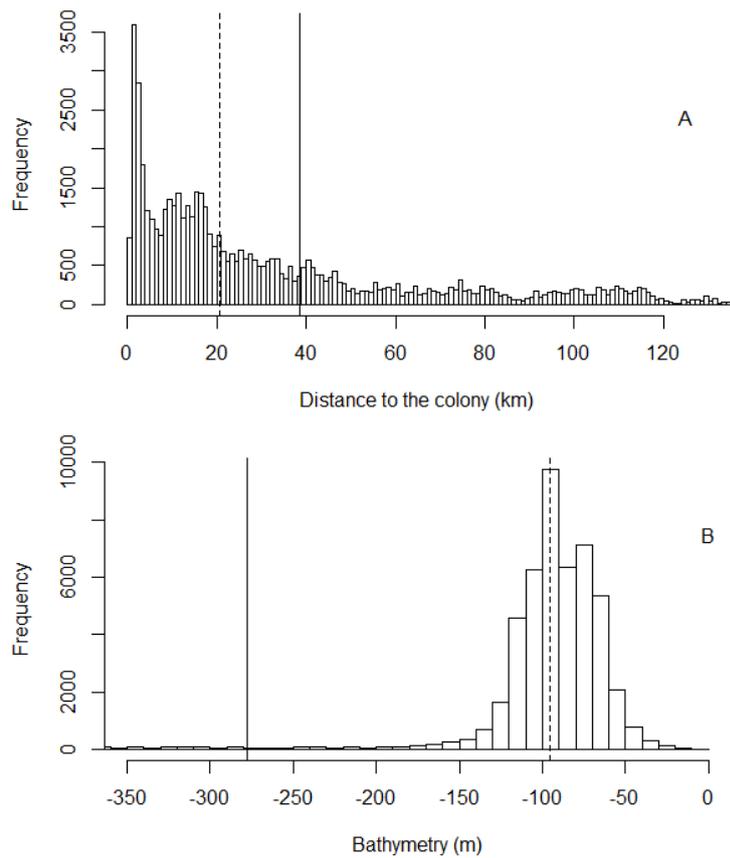
Year	Zooplankton-fish trip	Zooplankton-only trip	Nb trip
2011	0.66	0.34	50
2012	0.55	0.45	73
2014	0.37	0.63	30
2015	0.52	0.48	29



430

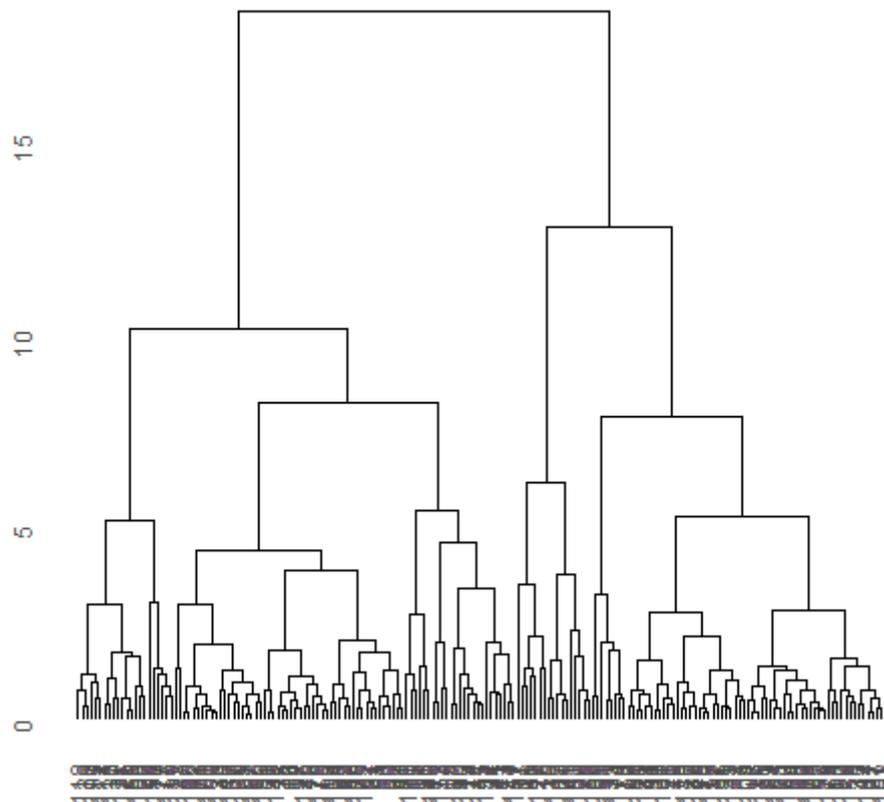
431 Figure S6.1. Foraging trip features of the different foraging trip tactics (zooplankton-only
 432 specialist trip and zooplankton-fish specialist trip) of Scopoli's shearwaters within the Gulf of
 433 Lions (Western Mediterranean) during the chick-rearing period between 2011 and 2015. We
 434 characterized differences between features of trip tactics considering tortuosity with a
 435 straightness index (i.e. $[2 \times \text{trip range}] / \text{total travelled distance}$), trip duration, mean distance
 436 to the colony, mean distance to the colony for foraging, and proportion of time spent in
 437 foraging, resting or travelling. We fitted linear or logistic mixed models depending the
 438 dependent variable with the trip tactics (i.e. groups of trips from the cluster analysis) and year
 439 as predictors. We used individuals as random intercept to accommodate for multiple trips. We
 440 calculated 95% confidence intervals with a bootstrap procedure. Relative to zooplankton-only

441 specialist trips, zooplankton-fish specialist trips had higher trip duration (24.2h versus 19.8h,
442 t-test = 2.106, $P < 0.03$), total travelled distance (247km versus 183km, t-test = 2.237, $P <$
443 0.03), trip range (67km versus 49km, t-test = 2.221, $P < 0.03$), mean distance to the colony
444 (36km versus 25km, t-test = 2.654, $P < 0.01$), mean distance to the colony for foraging
445 locations (38km versus 26km, t-test = 2.401, $P < 0.02$), but tortuosity (mean straightness
446 index = 0.55 versus 0.52, z-test = -0.031, $P = 0.98$) and proportion of time spent in resting
447 (0.30 versus 0.32, z-test = -0.685, $P = 0.49$), foraging (0.48 versus 0.46, z-test = 1.556, $P =$
448 0.12) or travelling (0.21 versus 0.21, z-test = -0.303, $P = 0.76$) were similar between trip
449 tactics.



450

451 Figure S6.2. Distribution of foraging locations as a function of distance to the colony (A) and
 452 bathymetry (B). The distributions are truncated at 130 km (95% of data are shown, the tail of
 453 the distribution reach 260 km) and -350 m (84% of data are shown, the tail of the distribution
 454 reach -2380 m). Mean (solid line) and median (dashed line) values of the distributions are
 455 showed.



456

457 Figure S6.3. Dendrogram for the cluster analysis based on selection coefficients for 182
458 foraging trips of shearwaters in the Gulf of Lions (Western Mediterranean) occurring during
459 the chick-rearing period between 2011 and 2015. We considered two different clusters
460 corresponding to two foraging trip tactics.