

1 Geographical variation in the foraging behaviour of the 2 pantropical red-footed booby

3 Loriane Mendez^{1,2,*}, Philippe Borsa³, Sebastian Cruz⁴, Sophie de Grissac^{1,2}, Janos
4 Hennicke^{1,5}, Joëlle Lallemand¹, Aurélien Prudor^{1,2}, Henri Weimerskirch^{1,2}

5 ¹Centre d'Etudes Biologiques de Chizé (CEBC), UMR7372 CNRS, Université de La
6 Rochelle, 79360 Villiers-en-Bois, France

7 ²UMR 9220 UR CNRS IRD ENTROPIE, Faculté des Sciences et Technologies, Université de
8 la Réunion, 15 avenue René Cassin - CS 92003, 97744 Saint Denis Cedex 9, La Réunion

9 ³UMR 250 UR CNRS IRD ENTROPIE, 101 Promenade Roger Laroque, 98848 Nouméa,
10 Nouvelle-Calédonie

11 ⁴Department of Migration and Immuno-ecology, Max Planck Institute for Ornithology,
12 Radolfzell, 78315, Germany

13 ⁵Department of Ecology and Conservation, Institute of Zoology, University of Hamburg,
14 Martin-Luther-King-Platz 3, 20146-D Hamburg, Germany

15
16 **Running page head:** Geographical variation in foraging behaviour of RFB

17
18 **ABSTRACT:** While interspecific differences in foraging behaviour have attracted much
19 attention, less is known about how foraging behaviour differs between populations of a same
20 species. Here we compared the foraging strategy of a pantropical seabird, the red-footed
21 booby (*Sula sula*), in five populations breeding in contrasted environmental conditions. The
22 foraging strategy strongly differed between sites, from short trips strictly diurnal in Europa
23 Island (Mozambique channel) to long trips including up to 5 nights at sea in Genovesa Island
24 (Galapagos archipelago). The Expectation Maximisation binary Clustering (EMbC) algorithm
25 was used to determine the different behaviours of individuals during their foraging trips
26 (travelling, intensive foraging, resting and relocating). During the day, the activity budget was
27 similar for all the breeding colonies. During the night, birds were primarily on the water,
28 drifting with currents. At all sites, birds similarly performed intensive foraging in zones of
29 Area-Restricted Search (ARS), although the size and duration of ARS zones differed
30 markedly. Red-footed boobies foraged over deep oceanic waters, with chlorophyll-a
31 concentrations varying between sites. Birds did not appear to target areas with higher
32 productivity. We suggest that range differences between populations may be linked to other
33 factors such as intra- and interspecific competition.

34
35
36 **KEY WORDS:** *Sula sula*; tropical; GPS tracking; ARS; chlorophyll-a; EMbC

37 *corresponding author: loriane.mendez@cebc.cnrs.fr

39

INTRODUCTION

40

41 The concept of species-typical behaviour assumes that behavioural traits are common among
42 all members of a species (Greenberg & Haraway 1998). However, behavioural variation is
43 commonly observed within a species (Lott 1991). While interspecific differences in foraging
44 behaviour are well studied, less is known about how populations of the same species differ in
45 their foraging behaviour.

46 Seabirds are 'central-place foragers' during the breeding period, since they nest on land and
47 forage at sea (Orians & Pearson 1979). Foraging strategies are usually linked to the local
48 environmental conditions (e.g. Sims & Quayle 1998, Weimerskirch 1998, Burke &
49 Montevecchi 2009) and vary widely across seabird species (Shealer et al. 2002, Weimerskirch
50 2007). Some species search for unpredictable resources over wide areas covering large
51 distances during their foraging trips, while others specifically target oceanographic features
52 such as fronts, shelf edges or sea mounts to find prey (e.g. Schneider 1982, Haney 1986,
53 Weimerskirch 2007, Freeman et al. 2010). These oceanographic features play an essential role
54 in the dispersion and aggregation of nutrients and plankton, which attract both prey and
55 predators. Moreover, it has been found that mesoscale and sub-mesoscale structures (e.g.
56 eddies and filaments) can increase primary productivity and consequently concentrate
57 associated predators such as seabirds (Nel et al. 2001, Weimerskirch et al. 2004, Tew-Kai et
58 al. 2009). In tropical oligotrophic waters, resources are scarcer and more heterogeneously
59 distributed compared to temperate and polar waters (Longhurst & Pauly 1987, Ballance et al.
60 1997, Weimerskirch 2007). Several species of tropical seabirds feed in close association with
61 sub-surface predators, such as tuna and dolphins that bring prey to the surface in reach of
62 flying predators (Au & Pitman 1986, Hebshi et al. 2008).

63 The red-footed booby (*Sula sula*), hereafter RFB, is a non-migrant seabird species that lives
64 year-round in pantropical regions of the Atlantic, Pacific, and Indian Oceans (Nelson 1978).
65 During the breeding season, both partners of the pair take turns between nest-guarding and
66 foraging trips. The RFB mainly feeds on flying fishes (Exocoetidae) and flying squids
67 (Ommastrephidae) (Nelson 1978, Schreiber et al. 1996). Since these prey occupy a low
68 trophic position, the chlorophyll-a concentration (a common proxy of the water productivity)
69 could be an indicator of their spatial distribution. RFBs appear to target specific areas with
70 higher productivity in some sites (Ballance et al. 1997, Jaquemet et al. 2005, Weimerskirch et
71 al. 2005a) but not in others (Young et al. 2010).

72

73 Besides local productivity, competition between individuals may also affect the distribution of
74 the foraging zones around the colonies. Ashmole (1963) described the potential consequences
75 of intraspecific competition on the fitness of central-place foragers like seabirds. He
76 hypothesized that the more a colony hosts individuals, the more the surrounding waters can be
77 locally depleted. This 'Ashmole's halo' (Birt et al. 1987) could lead birds from large colonies
78 to travel further to find resources, inducing a decrease in reproductive success and thus a
79 regulation of the colony size. RFBs breeding in the presence of other tropical booby species

80 could reduce competition by partitioning resources, allowing for coexistence (Lack 1971). As
81 RFBs are known as the most pelagic booby species (Nelson 1978, Schreiber et al. 1996), we
82 expect them to have a longer foraging range in presence of other sulid species.

83

84 Few studies have compared the foraging behaviour of a seabird species between different
85 sites to better understand the factors affecting foraging strategies (e.g. Kappes et al. 2011,
86 Oppel et al. 2015). The wide distribution of RFB populations gives the opportunity to
87 examine the influence of contrasted biotic and abiotic conditions from different breeding sites
88 on foraging behaviour. The present study compares the foraging strategies of five different
89 populations of the RFB in the Indian and Pacific Oceans. Since the breeding sites have
90 contrasted local conditions, we predict that search strategies and foraging parameters will
91 differ between sites up to a certain level, constrained by the morphology and common habits
92 of the species. Knowing that the foraging strategy of the RFB varies substantially between the
93 stages of the breeding cycle (Mendez et al. 2016), we focused our study on the incubation
94 period only.

95

96

97

MATERIALS AND METHODS

98

99

Fieldwork

100 Data were collected from five sites: Europa Island (EU, Mozambique Channel), Christmas
101 Island (CI, Indian Ocean), Walpole Island (WA) and the Chesterfield Islands (CH, hereafter
102 ‘Chesterfield’) off New Caledonia, and Genovesa Island (GEN) in the Galapagos Archipelago
103 (Fig. 1). All five sites host important breeding colonies of RFBs (Table 1). Our study
104 examined the foraging behaviour of RFBs during the incubation period when male and female
105 alternate on the nest to incubate the egg (Nelson 1978). Timing of field work and numbers of
106 individuals studied on each breeding colony are given in Table 1. To study the movements of
107 birds at sea, incubating adults were selected randomly and fitted with 20 g (32 X 22 mm)
108 IGotU GPS loggers (Mobile Action Technology, Taipei). Depending on the site and date of
109 deployment, locations were recorded every 10 s, 30 s, 60 s, 120 s or 300 s. GPS loggers were
110 attached to a group of three or four central tail feathers using Tesa tape (Wilson et al. 1997).
111 Birds were captured on nests that were previously identified and mapped. They were marked
112 on the tail or the breast with labile dye to identify the individual rapidly and from a distance.
113 Individuals were captured by hand or, for birds nesting higher in the trees, with a 6 m
114 telescopic fishing pole fitted with a nylon noose. In a few cases, both partners at the same nest
115 were fitted with GPS loggers. Birds were weighed in a bag with a spring balance, at both the
116 deployment and the retrieval of the GPS logger to determine gain or loss of weight. The study
117 birds were also measured (culmen height and length, wing length) at the recovery of the GPS
118 logger. Birds were sexed by their voice when possible (males have a higher pitched voice than
119 females; Nelson 1978) or by measurements (females are larger than males; Nelson 1978;
120 Weimerskirch et al. 2006). Blood samples were also collected on a sub-sample of 15

121 individuals in Europa in 2003 to verify the sex using molecular markers (Weimerskirch et al.
122 2006).

123

124 **Track parameters and behaviour labelling**

125 A total of 199 tracks of birds leaving the island to go to the sea were analysed (Table 1).
126 These tracks represented 1 to 8 successive foraging trips of 123 birds. Complete tracks were
127 defined as trips for which GPS data were available from the departure of the bird from the
128 nest to its return (90% of the dataset). Incomplete tracks, e.g. due to battery failure of the GPS
129 device, were used only to estimate specific parameters when at least the beginning of the
130 return phase of the foraging trip was present. Duration of foraging trip (h), total distance
131 covered (km) and maximum range from the colony (km) were calculated for each track.

132 To determine the different behaviours of individuals during their foraging trips, we used the
133 Expectation Maximisation binary Clustering (EMbC) algorithm (Garriga et al. 2016), a
134 variant of the maximum likelihood estimation of Gaussian mixture models (Redner & Walker
135 1984). The EMbC algorithm is a robust, non-supervised multi-variate clustering algorithm
136 that considers correlation and uncertainty of variables giving a meaningful local labelling
137 easily linked to biological interpretations. The annotation of behaviours was based on two
138 input variables: the speed and the turning angle, obtained from successive locations. First, all
139 tracks were linearly interpolated with one location every 2 minutes and the maximum speed
140 was set to 90 km.h⁻¹ (Weimerskirch et al. 2005b). Each location was clustered by the
141 algorithm into four behaviour categories (Table 2): High velocity/Low turn (HL), High
142 velocity/High turn (HH), Low velocity/Low turn (LL), Low velocity/High turn (LH). A
143 behavioural mode was assigned to each cluster, as suggested by Louzao et al. (2014). The HL
144 and HH labels correspond respectively to travelling and relocating. Relocating reflects
145 important turns with a steady speed and can be interpreted as a displacement between
146 restricted areas of intensive foraging. The LL label corresponds to birds resting at the sea
147 surface, mostly sitting on water and drifting in a single direction induced by surface currents
148 (Weimerskirch et al. 2002). The LH label was interpreted as intensive foraging. A smoothing
149 procedure included in the package was applied to better accounts for the temporal
150 associations among behaviours. All trips from all breeding colonies were treated
151 simultaneously in the analysis conducted with the R package *EMbC* (Garriga et al. 2016).
152 Proportions of each behaviour along tracks were compared between sites and during daytime
153 or nighttime, i.e. when the sun was > 6° below the horizon. All analyses were conducted in R
154 3.1.2 (R Development Core Team 2014).

155 Area-restricted search (ARS) was defined as at least 3 successive locations (i.e. 4 minutes)
156 labelled as intensive foraging by the EMbC algorithm. To simplify the description of the
157 different behaviour along the trajectory, we merged ARS zones when ≤ 4 locations labelled
158 with other behaviours were observed between them (i.e. 10 minutes). The number of ARS
159 zones per hour and their duration were calculated. The area covered was estimated through
160 the minimum convex polygon around all the locations of a specific ARS zone. Each ARS was
161 summarized in one central location by taking the median latitude and longitude.

162

163

Foraging behaviour and environmental drivers

164 Kernel estimation (Worton 1989) was used to determine the utilization distribution (UD)
165 probability based on the locations of individuals. Kernel density estimates offer the
166 advantages of being widely used to identify population-level core habitat areas. We used the
167 function *kernelUD* implemented in the R package *adehabitatHR* (Calenge 2006) using the
168 reference bandwidth which produces contiguous cores without over-smoothing. Choosing a
169 secant projection and a narrow zone minimizes the distortions in a map generated from
170 projection. To estimate the size of general (95%) and core (50%) foraging areas, we used the
171 function *getverticeshr* with adapted local projections (Europa: Moznet / UTM zone 37S;
172 Genovesa: WGS 84 / UTM zone 16S; Christmas: RGNC91-93 / Lambert New Caledonia;
173 Chesterfield and Walpole: RGNC 1991 / Lambert New Caledonia). Depth was obtained from
174 the one arc-minute resolution GEBCO bathymetric dataset using the R package *marmap*
175 (Pante & Simon-Bouhet 2013). Monthly composites of chlorophyll-a concentration (chl-a, in
176 $\text{mg}\cdot\text{m}^{-3}$) were obtained at a spatial resolution of 4 km from Aqua MODIS satellite using the R
177 package *rerddap* (Chamberlain 2016). At a finer time-scale, we used a self-written script to
178 obtain 11-days composites of chl-a concentration at 4 km resolution (GlobColour, merged
179 sensor type and GSM algorithm) using the software GNA Octave (Eaton et al. 2014).

180 For each site, the accessible area was defined by a circle around the colony with a radius
181 corresponding to the maximum range recorded by GPS tracking. The foraging area was
182 delimited by the minimum convex polygon that included all ARS zones of all birds. The
183 accessible but not prospected area was defined as the accessible area to which the prospected
184 area was subtracted. Monthly chl-a concentration was compared between prospected areas
185 and non-prospected areas. Comparisons between travelling and ARS locations were made
186 using 11-day chl-a concentration. Prior to data analysis, travelling locations were resampled
187 with one location every 10 minutes to reduce autocorrelation and have a number of locations
188 in the same order of magnitude than the number of ARS zones.

189

190

Statistical analysis

191 As some individuals were tracked during several trips, linear mixed-effects models with
192 ‘individual’ as random factor were applied to avoid pseudoreplication. We used the function
193 *lmer* from the R package *lme4* (Bates et al. 2015) to test for differences in trip parameters
194 between breeding colonies. Tukey’s HSD test was used to calculate post-hoc comparisons on
195 each factor in the model using the function *glht* from the R package *multcomp* (Hothorn et al.
196 2008). When residuals were not normally distributed, variables were square-root transformed.
197 When the data still did not meet the assumptions, we used a Kruskal-Wallis rank sum test and
198 Tukey and Kramer (Nemenyi) test for pairwise comparisons with Tukey-Dist approximation
199 for independent samples from the R package *PMCMR* (Pohlert 2014). Data from Europa (in
200 years 2003 and 2013; Table 1) were pooled since no significant differences between years
201 were observed. Data from Genovesa (in years 2009 and 2014; Table 1) were analysed

202 separately to take into account the inter-annual effects. Males and females were pooled in all
203 analyses since no significant effect of the sex was observed when doing comparisons of track
204 parameters ($p > 0.05$). Generalized linear mixed model (GLMM) with binomial family and
205 logit link were applied to compare environmental parameters between ARS and travelling
206 with ‘individual’ and ‘track’ as random factors using the function *glmer* from the R package
207 *lme4* (Bates et al. 2015). Values of the dependent variables are given as mean \pm standard
208 deviation. The Marascuilo procedure (1966) was used to compare the pairwise proportions of
209 the behaviours defined according to the EMbC algorithm (Garriga et al. 2016) among
210 breeding colonies.

211

212

213

RESULTS

214

215

Trip parameters

216 Foraging parameters varied extensively between sites. Individuals from Europa undertook
217 short foraging trips exclusively, lasting on average less than 7 h, with a maximum range of 50
218 km, and never spent the night at sea (Fig. 2 and Fig. 3). At Walpole, apart from two trips that
219 lasted 60 h including three nights at sea, trips were only slightly longer than those of Europa
220 (mean duration 8 h, mean range 80 km). In Chesterfield, some trips were longer than 24 hours
221 and nights spent at sea were frequently observed, yielding a mean trip duration of 21 h and a
222 maximum range of 125 km. In contrast, overnight trips were common in Genovesa, with a
223 mean duration of 22 h and range of 122 km in 2009, and higher values in 2014 (37 h and 176
224 km). Four trips included 4 nights at sea and one trip included 5 nights at sea. The furthest
225 location was recorded 472 km away from the colony. Birds from Christmas Island made
226 significantly longer trips in duration than in the other sites (45 h on average), but the
227 maximum range recorded (164 km on average) was not greater. Four trips included 4 nights at
228 sea (Fig. 2 and Fig. 3).

229 All the foraging areas of RFB were over oceanic waters but their size clearly differed between
230 sites (Fig. 4). Europa had the smallest foraging area evenly distributed around the island (95%
231 and 50% kernels: 22 243 km² and 3 863 km² respectively; Fig. 4). The four other sites showed
232 directionality in foraging area. Birds foraged principally to the north-east of Walpole (54 988
233 km², 12 420 km²), to the west of Chesterfield (57 992 km², 14 422 km²), to the east of
234 Genovesa (2009: 60 438 km², 12 497 km²; 2014: 132 784 km², 28 206 km²) and to the east of
235 Christmas (111 900 km², 18 388 km²). The surface area covered by birds from Genovesa in
236 2014 was approximately six times larger when compared to birds from Europa. The direction
237 of all foraging areas was not related to the main wind direction (Table 1 and Fig. 4).

238 The multiple pairwise comparisons (Marascuilo procedure) showed that the percentages of
239 the different behaviours during the foraging trips were not significantly different between
240 sites during the day (Fig. 5). During the night, the high proportion of resting behaviour in

241 Christmas was significantly different from all the other sites. The proportion of resting
242 behaviour in Genovesa differed also from Europa and Chesterfield. The proportion of
243 relocating behaviour at Christmas was significantly different from Europa and Chesterfield.
244 After the sunset, individuals from Europa were mainly travelling for short periods until they
245 reached the colony. Foraging bouts occurred occasionally, and birds never rested on the sea
246 surface. In the other sites, the more the birds tended to spend entire nights at sea, the more a
247 resting behaviour was observed.

248 Only 2.5% of the dataset (5 tracks from 4 birds) did not contain ARS. The number of ARS
249 zones per hour was slightly different between breeding colonies ($F_{4,91} = 2.81$, $p = 0.03$), with
250 0.5-0.7 ARS.h⁻¹ on average (Fig. 6). Only Europa and Christmas differed significantly
251 (Tukey's HSD test, $p = 0.016$), with the highest values observed in Europa (up to 1.67 ARS.h⁻¹).
252 The mean duration of ARS differed between sites ($F_{4,91} = 5.91$, $p < 0.001$). ARS lasted on
253 average between 16 min and 28 min (Fig. 6). ARS from birds in Europa and Chesterfield,
254 doing relatively short trips, were significantly longer than in Genovesa (Tukey's HSD test, p
255 = 0.01 and $p = 0.04$ respectively) and Christmas (Tukey's HSD test, $p = 0.01$ and $p = 0.03$
256 respectively). Walpole was intermediate (Tukey's HSD test, $p > 0.05$). Long ARS lasting
257 more than one hour were occasionally observed at Europa but were rare at other sites. Mean
258 ARS surface ranged between 0.45 km² and 1.86 km² (Fig. 6), with often larger values for
259 Europa and Chesterfield which were statistically different from Christmas (Tukey's HSD test,
260 $p = 0.01$ and $p = 0.04$ respectively). No inter-annual effect was observed in Genovesa for the
261 three descriptive parameters (Tukey's HSD test, $p > 0.05$).

262

263 **Foraging areas and oceanographic conditions**

264 For Europa, Genovesa and Walpole, the incubation period occurred 2-3 months after the
265 annual peak of chl-a in the waters around each island, and 2-3 months before the peak at
266 Chesterfield and Christmas (Fig. 7). We observed a high variability in the concentration of
267 chl-a between study sites. Inside the foraging areas (Fig. 8), waters around Europa and
268 Walpole showed a particularly low concentration (mean 0.07 mg.m⁻³), significantly different
269 from the three other sites (Tukey's HSD test, $p < 0.05$). The chl-a concentration was
270 considerably higher in the foraging areas of birds from Genovesa and Christmas (more than
271 0.15 mg.m⁻³ on average). Chesterfield was intermediate (0.11 mg.m⁻³ on average) but not
272 significantly different from Genovesa and Christmas (Tukey's HSD test, $p > 0.05$).

273 Birds from Europa foraged in all directions with no specific orientation (Fig. 8). The foraging
274 areas of the four other sites were clearly oriented towards specific directions. RFB did not
275 seem to especially favour areas of higher chl-a concentration (Table 3). A slightly higher
276 monthly chl-a concentration in the prospected area was observed in Europa and was more
277 pronounced in Christmas. In the three other sites, the mean chl-a concentration was similar or
278 slightly but not significantly higher in the non-prospected area. Regarding the bathymetry,
279 birds foraged over relatively shallow oceanic waters at Europa, Chesterfield, Genovesa and
280 Walpole, with average depths ranging between 2 000 - 3 000 m (Table 3). Most birds from
281 Christmas moved over a deep oceanic trench during their foraging trips, leading to an average

282 depth of c. 5 000 m in the foraging area. Depending on the site, the bathymetry was
283 alternatively higher in the prospected or the non-prospected area (Table 3).

284 At a finer scale, the 11-day composite chl-a concentration and the bathymetry were compared
285 between ARS and travelling segments of a trip (Table 4). We found no significant differences
286 in chl-a for Europa (GLMM, $p = 0.50$) and Genovesa (GLMM, $p = 0.08$ and $p = 0.62$ in 2009
287 and 2014, respectively). Higher values were observed inside ARS than during travelling for
288 Christmas (GLMM, $p < 0.001$) and lower values for Chesterfield (GLMM, $p = 0.03$) and
289 Walpole (GLMM, $p=0.05$). No significant differences in bathymetry between ARS and
290 travelling were observed in Europa, Walpole and Chesterfield. ARS occurred in significantly
291 deeper waters than travelling in Genovesa (GLMM, $p = 0.01$ and $p < 0.0001$ in 2009 and
292 2014, respectively) and Christmas (GLMM, $p < 0.0001$).

293

294

295

296

DISCUSSION

297

298 This study is the first to compare the foraging behaviour and its relationship with
299 oceanographic conditions for a seabird species during a same breeding stage across breeding
300 colonies over a large extent of the species' pantropical range. We found significant inter-
301 colony differences in foraging behaviour, especially extensive differences in foraging
302 duration and range between sites. These differences were not directly explained by chl-a
303 concentration, a proxy of marine productivity. However, some similarities common to all sites
304 were observed at a fine spatio-temporal scale, as the proportion of the different behaviours
305 during the day and the main characteristics of area-restricted search (ARS) zones. Beyond
306 environmental conditions, we suggest that intra- and interspecific competition within a colony
307 and with adjacent colonies can explain the large diversity of foraging strategies used by the
308 red-footed booby.

309

310

311

Intraspecific differences in foraging behaviour

312 Our study confirms that RFBs are oceanic foragers throughout their range but also indicates
313 that the foraging behaviour differs substantially among colonies. Birds nesting on Europa
314 undertook relatively short and exclusively diurnal foraging trips. The foraging trips of the
315 birds from Walpole were similar to those from Europa, except for two trips including nights at
316 sea. The duration of trips was respectively higher in Chesterfield, Genovesa and Christmas,
317 where trips lasting more than a day were frequently observed. The longest durations and
318 ranges were observed in Genovesa but birds from Christmas made the longest trips on
319 average. Until the present study, red-footed boobies were thought to undertake diurnal
320 foraging trips exclusively based on preliminary results from GPS tracking (Weimerskirch et

321 al. 2005a, Young et al. 2010). The only locality where it was suggested from observation that
322 trips can last more than one day was in the Galapagos (Nelson 1978; Schreiber et al. 1996).
323 Here we confirmed the previous visual observations in the Galapagos, reporting birds leaving
324 the colony of Genovesa up to five days, and we showed that during these long trips birds can
325 forage at up to 472 km from the colony. At night, the percentages of the different behaviours
326 varied extensively across the five breeding colonies of RFB. At Europa, birds travelled
327 rapidly in order to return to the colony and rest on land. For the other breeding colonies, slow
328 and linear trajectories suggested that the birds floated on the water during the night, being
329 drifted by surface currents. Foraging activity was rare, occurring presumably during dawn and
330 dusk. Since RFBs are visual foragers with likely crepuscular vision, nocturnal foraging is
331 constrained by the lack of ambient light (Ashmole & Ashmole 1967). Weimerskirch et al.
332 (2005a) suggested that predation may be a reason for the RFBs from Europa to stay on land
333 during the night. RFBs from Genovesa, Chesterfield, Walpole and Christmas frequently
334 drifted on the sea surface at night, susceptible to attacks from below. Observations of foot
335 damage to Nazca Boobies *Sula granti* in the Galapagos indicated possible attacks from
336 toothed sub-surface predators (Zavalaga et al. 2012). Sharks are known to attack seabirds
337 (Johnson et al. 2006, Meyer et al. 2010) but since they are potentially present at all five
338 studied sites, predation risk may not be the main factor explaining the different foraging
339 behaviour observed. Sharks may rely on vision to detect seabirds on the surface, inducing that
340 resting at night may not be a high-risk behaviour. Birds could then afford nocturnal predation
341 risk for example in case of low prey encounter during the previous day (Zavalaga et al. 2012).

342

343

344

Similarities in diurnal foraging

345 Individuals of a species possess similar behaviours, even if discrete populations do not mix.
346 This ‘Species-Typical Behaviour’ is influenced by species genes and social-natural
347 environment (Haraway & Maples 1998). Many similarities appeared in the way RFBs used
348 their environment during the day. Generally, they left from and returned to the colony in a
349 straight trajectory. During the middle sections of the foraging trip, birds simultaneously
350 reduced their speed and increased their sinuosity, suggesting that they found a patch of prey
351 (Weimerskirch et al. 2005a). ARS frequency, size and duration showed large variability
352 within sites. This variability may reflect a fine adjustment of the time spent in a patch of food
353 according to its prey abundance and distribution, before moving to another. In order to
354 optimize their foraging trip, birds should minimise the travelling time between foraging areas
355 and their colonies (Charnov 1976). ARS were more variable at Europa, where trips were short
356 and strictly diurnal, with higher occurrence, larger sizes and longer durations than for the
357 other breeding colonies. Furthermore, the EMbC behaviour analysis of birds from Europa
358 showed a higher proportion of intensive foraging behaviour during trips, reflecting an
359 optimization of the daily trip. Overall similarity in foraging strategy might be related to the
360 fact that tropical seabirds generally feed in association with subsurface predators like tuna and
361 dolphins that make the preys available at the surface (Au & Pitman 1986). However, a study

362 reported that RFBs from Hawaii did not associate with any subsurface predator in greater
363 proportion than what would be expected by chance (Hebshi et al. 2008). Further research is
364 still needed to better understand the foraging strategies of tropical seabirds in oligotrophic
365 waters.

366

367

Foraging behaviour and productivity

368 Previous studies assumed that RFBs may forage in more productive areas (Ballance et al.
369 1997, Jaquemet et al. 2005, Weimerskirch et al. 2005a). However, Young et al. (2010) did not
370 find any major variation of chl-a concentration around a site that harbours a large RFB
371 colony, the Palmyra Atoll (Northern Pacific), that would support this hypothesis. After
372 examining the chl-a concentration inside prospected and non-prospected areas, we found that
373 birds from Christmas Island targeted productive areas with deep sea bed, but not birds from
374 the other colonies. At all the remaining sites, birds would have been able to reach more
375 productive waters within their range if they had flown in another direction. Top marine
376 predators such as cetaceans and seabirds target productive waters to increase their encounter
377 rate with prey patches in restricted areas (Jaquemet et al. 2005). At Europa, the feeding of
378 great frigatebirds *Fregata minor* is positively linked with dynamical fronts at the edge of
379 eddies (Weimerskirch et al 2004, Tew-Kai et al. 2009, De Monte et al. 2012, Jaquemet et al.
380 2014). However, the distribution of frigatebirds is negatively influenced by chl-a
381 concentration, suggesting that frigatebirds do not seem to directly target high primary
382 productivity (Thiers et al. 2014). Similarly, the productivity found in the foraging area of
383 masked boobies *Sula dactylatra* in the eastern tropical Pacific is not significantly different
384 from the non-prospected area within the foraging range of the population (Weimerskirch et al.
385 2008). As tropical waters are characterised by an overall lower productivity compared to
386 temperate or polar waters (Longhurst & Pauly 1987), the distribution and abundance of prey
387 is believed to be more unpredictable than in colder waters (Ashmole 1971). Here we see that
388 the chl-a concentration is not a good indicator of foraging areas of RFB in tropical
389 environments.

390 Time lags, physical forcings and food web processes can thwart the link between primary
391 productivity and the distribution of predators. Because seabirds do not feed directly on
392 primary producers, a natural delay due to energy transfer between phytoplankton, fish or
393 squid occurs. For example, in the Benguela current system, this phenomenon takes up to
394 several weeks (Grémillet et al. 2008). Moreover, seabird prey seems to be less uniformly
395 distributed than plankton (Piontkovski & Williams 1995). For top marine predators, long
396 time-series of chl-a may be better indicators of productive habitats than finer temporal-scale
397 measurements (Suryan et al. 2012). Static non-biological features, such as water depth and
398 distance to shore, can be better explanatory variables than chl-a (Nur et al. 2011). Since we
399 did not find a direct effect of the bathymetry nor the chl-a in four of the five sites, other
400 factors may account for the differences of foraging ranges observed between breeding
401 colonies.

402

403

404

Resource partitioning

405 Resource competition may lead to adaptations that reduce niche overlap (Gause 1934) and
406 thus explain differences in seabird foraging area and behaviour (Rome & Ellis 2004, Lance et
407 al. 2005). In mixed colonies, seabirds may have to cope with interspecific and intraspecific
408 competition. Birds from larger colonies could also have to forage further than birds from
409 smaller colonies because individuals foraging close to the colony may cause local prey
410 depletion (Ashmole 1963, Furness & Birkhead 1984, Jovani et al. 2015). The sizes of RFB
411 colonies differ extensively between study sites. The small population at Europa (2 800 - 3 800
412 pairs, Le Corre & Jouventin 1997) had the shortest foraging range while the large population
413 at Genovesa (140 000 pairs, Nelson 1978) had the longest foraging range, suggesting that
414 intraspecific competition may partly explain the differences in foraging range between
415 breeding colonies. In Genovesa, high intraspecific competition may lead birds to travel
416 several days including nights at sea and thus reach great distances. Grémillet et al. (2004)
417 studied two close colonies of Cape gannets *Morus capensis* in South Africa and found that
418 birds from the larger colony did longer foraging trips in duration and range. Similarly, mean
419 foraging trip duration of the northern gannet *Morus bassanus* from colonies in Britain and
420 Ireland was positively correlated with colony size (Lewis et al. 2001). In tropical ecosystems,
421 tracking of masked boobies from two islands differing in colony size, surrounded by similar
422 oligotrophic waters, was also consistent with Ashmole's hypothesis (Oppel et al. 2015). In
423 Clipperton (Pacific Ocean), masked boobies showed a particularly long foraging range
424 (average range of 103 km, maximum 242 km; Weimerskirch et al. 2008) and the huge colony
425 size (> 100 000 individuals) might explain that range.

426 Present or even previous competition could produce interspecific variation in foraging
427 behaviour (Trivelpiece et al. 1987). The RFB is the only booby species present in Europa,
428 while the four other sites host one or two other booby species. A little or no interspecific
429 competition could explain why foraging trips were almost evenly distributed in a short range
430 around Europa, and only during the day. The RFB is the smallest booby species and may fly
431 further in presence of other booby species because of lower flight costs. Incubating RFBs in
432 Johnston Atoll (central Pacific) made diurnal trips significantly longer than those made by
433 brown boobies *Sula leucogaster*, with a mean duration of 14 h and 6.7 h respectively (Lewis
434 et al. 2004). RFBs and masked boobies from Palmyra Atoll showed strong differences in their
435 foraging behaviour and ranges, with RFBs being again more pelagic than masked boobies
436 (Young et al. 2010). The two same species in Tromelin Island (Indian Ocean), surrounded by
437 more oligotrophic waters, demonstrated interspecific segregation at the level of core foraging
438 areas but not at the scale of the whole foraging region (Kappes et al. 2011). However, intra-
439 and interspecific competition did not explain the higher maximum ranges observed in Tern
440 Island (3 000 – 5000 RFB pairs) compared to Palmyra Atoll that hosts 25 000 RFB pairs and
441 one more tropical booby species (Young et al. 2015). However, the two islands have different
442 oceanographic contexts thus potential environmental effects may overshadow the competition
443 effect.

445 The exclusion by adjacent colonies is also known to potentially influence the directionality of
446 the foraging trips (Wakefield et al. 2013). The small foraging range observed in Europa may
447 be caused by a small competition since the island hosts a relatively small RFB colony, with
448 no other tropical boobies and no other island in the vicinity. Genovesa is one of the
449 Northeastern islands of the Galapagos archipelago. Since the foraging range was clearly
450 oriented in the east direction, birds may avoid competition with colonies from other species
451 that have shorter ranges (Anderson 1991). Lastly, no island is present in the vicinity of
452 Christmas Island, where the foraging area towards Java Island seems to be mainly driven by
453 the environment. Although resource partitioning between distant colonies is difficult to
454 evaluate, our data suggest that resource partitioning may also have an influence on the
455 foraging behaviour observed at the colony-scale.

456 To conclude, the environmental context and competition may affect the foraging behaviour of
457 the RFB, a central-place forager in tropical oligotrophic waters. To better understand the
458 patterns observed in infra-specific studies, multi-species studies and information about the
459 local environment seem essential to assess the impact of each effect resulting in the foraging
460 behaviour.

461

462

463 *Acknowledgments.* This research was supported by France's 'Iles Eparses' program (2011-
464 2013) managed by CNRS-Institut Ecologie et Environnement (InEE) with the financial
465 support of CNRS-InEE, CNRS- Institut National des Sciences de l'Univers (INSU), Institut
466 de recherche pour le développement (IRD), Agence des aires marines protégées (AAMP) and
467 the logistic support of Terres Australes et Antarctiques Françaises (TAAF). Research in the
468 Chesterfield Islands was during the MOMAlis cruise on board RV *Alis*, funded in part by
469 Commission nationale de la flotte côtière, IRD and AAMP. This work was also part of the
470 program EARLYLIFE, funded by a European Research Council Advanced Grant under the
471 European Community's Seven Framework Program FP7/2007–2013 (Grant Agreement ERC-
472 2012-ADG_20120314 to Henri Weimerskirch). We thank J.B. Pons, S. Jaquemet, M. Le
473 Corre and M. Bastien for their assistance in the field. We thank the Galapagos National Park
474 Service and the Ministry of the Environment of Ecuador for permission to work in the park,
475 and the Charles Darwin Research Station for logistical support. The work on Christmas Island
476 (Indian Ocean) was conducted within the framework of the Christmas Island Seabird Project
477 (www.seabirdproject.cx) which was supported by grants from the Universität Hamburg, Mini
478 Wunderland Hamburg, CI Island Trust, CI Territory Week Committee, CI Tourist
479 Association, and many private sponsors. Globetrotter Hamburg, Grube KG Hützel, Rische &
480 Herfurth Hamburg and The North Face Inc. USA provided in-kind support. Parks Australia
481 North Christmas Island provided accommodation and logistical support. M. Gant, M. Misso,
482 M. Orchard, M. Smith and their teams at CI National Park, as well as Prof. J. Ganzhorn and
483 his lab at the University of Hamburg, Germany, provided invaluable help and support. M.
484 Berlincourt and B. Holtmann helped in the field. During the fieldwork, J.C.H. was funded by

485 a Marie Curie Research Fellowship from the European Union (PIEF-GA-2009-236295).
486 Lastly, we thank the three anonymous reviewers whose suggestions helped improving the
487 manuscript.

488

489

LITTERATURE CITED

490

491 Anderson DJ (1991) Apparent predator-limited distribution of Galápagos Red-footed Boobies
492 *Sula sula*. *Ibis* 133:26–29

493 Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. *Ibis* 103:458–473

494 Ashmole NP (1971) Seabird ecology and the marine environment. In: Farner DS, King JR
495 (eds) *Avian Biology*, vol 1. New York: Academic Press, p 223-287

496 Ashmole NP, Ashmole MJ (1967) Comparative feeding ecology of sea birds of a tropical
497 oceanic island. *Peabody Mus Nat Hist Yale Univ Bull* 24:5-131.

498 Au DW, Pitman RL (1986) Seabird interactions with dolphins and tuna in the eastern tropical
499 Pacific. *Condor* 88:304–317

500 Ballance LT, Pitman RL, Reilly SB (1997) Seabird community structure along a productivity
501 gradient: importance of competition and energetic constraint. *Ecology* 78:1502–1518

502 Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using
503 lme4. *J Stat Softw* 67:48

504 Birt VL, Birt TP, Goulet D, Cairns DK, Montevecchi WA (1987) Ashmole’s halo: direct
505 evidence for prey depletion by a seabird. *Mar Ecol Prog Ser* 40:205–208

506 Borsa P, Pandolfi M, Andréfouët S, Bretagnolle V (2010) Breeding avifauna of the
507 Chesterfield Islands, Coral Sea: current population sizes, trends, and threats. *Pac Sci* 64:297–
508 314

509 Burke CM, Montevecchi WA (2009) The foraging decisions of a central place foraging
510 seabird in response to fluctuations in local prey conditions. *J Zool* 278:354–361

511 Calenge C (2006) The package “adehabitat” for the R software: a tool for the analysis of
512 space and habitat use by animals. *Ecol Model* 197:516–519

513 Chamberlain S (2016) rerddap: General purpose client for “ERDDAP” servers. R package.

514 Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor Popul Biol* 9:129–
515 136

516 De Monte S, Cotté C, d'Ovidio F, Lévy M, Le Corre M, Weimerskirch H (2012) Frigatebird
517 behaviour at the ocean–atmosphere interface: integrating animal behaviour with multi-satellite
518 data. *J R Soc Interface* 9:3351–3358

519 Eaton JW, Bateman D, Hauberg S, Wehbring R (2014) GNU Octave version 3.8.1 manual: a
520 high-level interactive language for numerical computations.

521 Freeman R, Dennis T, Landers T, Thompson D, Bell E, Walker M, Guilford T (2010) Black
522 Petrels (*Procellaria parkinsoni*) patrol the ocean shelf-break: GPS tracking of a vulnerable
523 procellariiform seabird. *PLoS One* 5:e9236

524 Furness RW, Birkhead TR (1984) Seabird colony distributions suggest competition for food
525 supplies during the breeding season. *Nature* 311: 655- 656

526 Garriga J, Palmer JR, Oltra A, Bartumeus F (2016) Expectation-maximization binary
527 clustering for behavioural annotation. *PloS One* 11:e0151984

528 Gause GF (1934) *The Struggle for Existence*. Williams and Wilkins, Baltimore, 163 p

529 Greenberg G, Haraway MM (1998) *Comparative Psychology: A Handbook*. Greenberg G,
530 Haraway MM (eds). Garland, New York

531 Grémillet D, Dell’Omo G, Ryan PG, Peters G, Ropert-Coudert Y, Weeks SJ (2004) Offshore
532 diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS
533 tracking of Cape gannets from neighbouring colonies. *Mar Ecol Prog Ser* 268:265–279

534 Grémillet D, Lewis S, Drapeau L, Der Lingen CD van, Huggett JA, Coetzee JC, Verheye
535 HM, Daunt F, Wanless S, Ryan PG (2008) Spatial match–mismatch in the Benguela
536 upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine
537 predator distributions? *J Appl Ecol* 45:610–621

538 Haney JC (1986) Seabird affinities for Gulf Stream frontal eddies: responses of mobile
539 marine consumers to episodic upwelling. *J Mar Res* 44:361–384

540 Haraway MM, Maples EG (1998) Species-typical behavior. In: Greenberg G, Haraway MM
541 (eds) *Comparative Psychology: A Handbook*. Garland, New York, p 191-197

542 Hebshi AJ, Duffy DC, Hyrenbach KD (2008) Associations between seabirds and subsurface
543 predators around Oahu, Hawaii. *Aquat Biol* 4:89–98

544 Hothorn T, Bretz F, Westfall P (2008) Simultaneous Inference in General Parametric Models.
545 *Biometrical Journal* 50:346-363

546 James DJ, McAllan IA (2014) The birds of Christmas Island, Indian ocean: A review. *Aust*
547 *Field Ornithol* 31:S1

548 Jaquemet S, Le Corre M, Marsac F, Potier M, Weimerskirch H (2005) Foraging habitats of
549 the seabird community of Europa Island (Mozambique Channel). *Mar Biol* 147:573–582

- 550 Jaquemet S, Ternon J-F, Kaehler S, Thiebot JB, Dyer B, Bemanaja E, Marteau C, Le Corre M
551 (2014) Contrasted structuring effects of mesoscale features on the seabird community in the
552 Mozambique Channel. *Deep Sea Res Part II Top Stud Oceanogr* 100:200–211
- 553 Johnson RL, Venter A, Bester MN, Oosthuizen WH (2006) Seabird predation by white shark
554 and Cape fur seal at Dyer Island. *South Afr J Wildl Res* 36(1): 23–32
- 555 Jovani R, Lascelles B, Garamszegi LZ, Mavor R, Thaxter CB, Oro D (2015) Colony size and
556 foraging range in seabirds. *Oikos* 125:968–974
- 557 Kappes MA, Weimerskirch H, Pinaud D, Le Corre M (2011) Variability of resource
558 partitioning in sympatric tropical boobies. *Mar Ecol Prog Ser* 441:281–294
- 559 Lack DL (1971) *Ecological isolation in birds*. Harvard University Press, Cambridge, MA,
560 United States, 416 p
- 561 Lance MM, Thompson CW, Burger AE (2005) Overlap in diets and foraging of Common
562 Murres (*Uria aalge*) and Rhinoceros Auklets (*Cerorhinca monocerata*) after the breeding
563 season. *Auk* 122:887–901
- 564 Le Corre M, Jouventin P (1997) Ecological significance and conservation priorities of Europa
565 Island (western Indian Ocean), with special reference to seabirds. *Rev Ecol Terre Vie* 52:205–
566 220
- 567 Lewis S, Schreiber EA, Daunt F, Schenk GA, Wanless S, Hamer KC (2004) Flexible foraging
568 patterns under different time constraints in tropical boobies. *Anim Behav* 68:1331–1337
- 569 Lewis S, Sherratt TN, Hamer KC, Wanless S (2001) Evidence of intra-specific competition
570 for food in a pelagic seabird. *Nature* 412:816–819
- 571 Longhurst ARP, Pauly D (1987) *Ecology of tropical oceans*. Academic Press, San Diego, CA.
- 572 Lott DF (1991) *Intraspecific variation in the social systems of wild vertebrates*. Cambridge
573 University Press, New York
- 574 Louzao M, Weigand T, Bartumeus F, Weimerskirch H (2014) Coupling instantaneous energy-
575 budget models and behavioural mode analysis to estimate optimal foraging strategy: an
576 example with wandering albatrosses. *Mov Ecol* 2:8
- 577 Marascuilo LA (1966) Large-sample multiple comparisons. *Psychol Bull* 65:280-290
- 578 Mendez L, Cotté C, Prudor A, Weimerskirch H (2016) Variability in foraging behaviour of
579 red-footed boobies nesting on Europa Island. *Acta Oecol* 72:87–97
- 580 Meyer CG, Papastamatiou YP, Holland KN (2010) A multiple instrument approach to
581 quantifying the movement patterns and habitat use of tiger (*Galeocerdo cuvier*) and
582 Galapagos sharks (*Carcharhinus galapagensis*) at French Frigate Shoals, Hawaii. *Mar Biol*
583 157:1857–1868

584 Nel DC, Lutjeharms JRE, Pakhomov EA, Ansorge IJ, Ryan PG, Klages NTW (2001)
585 Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche*
586 *chrysostoma* in the southern Indian Ocean. *Mar Ecol Prog Ser* 217:15–26

587 Nelson JB (1978) *The Sulidae—Gannets and Boobies*. Oxford University Press, Oxford

588 Nur N, Jahncke J, Herzog MP, Howar J, Hyrenbach KD, Zamon JE, Ainley DG, Wiens JA,
589 Morgan K, Ballance LT (2011) Where the wild things are: predicting hotspots of seabird
590 aggregations in the California Current System. *Ecol Appl* 21:2241–2257

591 Oppel S, Beard A, Fox D, Mackley E, Leat E, Henry L, Clingham E, Fowler N, Sim J,
592 Sommerfeld J (2015) Foraging distribution of a tropical seabird supports Ashmole’s
593 hypothesis of population regulation. *Behav Ecol Sociobiol* 69:915–926

594 Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Stairs
595 GR, Mitchell DR (eds) *Analysis of Ecological Systems*. Ohio State University Press,
596 Columbus, p 155–177

597 Pante E, Simon-Bouhet B (2013) Marmap: a package for importing, plotting and analyzing
598 bathymetric and topographic data in R. *PLoS One* 8:e73051

599 Piontkovski SA, Williams R (1995) Multiscale variability of tropical ocean zooplankton
600 biomass. *ICES J Mar Sci J Cons* 52:643–656

601 Pohlert T (2014) The pairwise multiple comparison of mean ranks package (PMCMR). R
602 Package. <http://CRAN.R-project.org/package=PMCMR>

603 R Development Core Team (2014) *R: A Language and Environment for Statistical*
604 *Computing*. R Foundation for Statistical Computing, Vienna, Austria

605 Rome MS, Ellis JC (2004) Foraging ecology and interactions between herring gulls and great
606 black-backed gulls in New England. *Waterbirds* 27:200–210

607 Schneider D (1982) Fronts and seabird aggregations in the southeastern Bering Sea. *Mar Ecol*
608 *Prog Ser* 10:101–103

609 Schreiber E, Schreiber R, Schenk G (1996) Red-footed booby (*Sula sula*). In: Poole A, Gill F
610 (eds) *The Birds of North America*, no. 241. The Academy of Natural Sciences, Philadelphia,
611 PA, and The American Ornithologists' Union, Washington, DC

612 Shealer DA, Schreiber EA, Burger J (2002) Foraging behavior and food of seabirds. *Biol Mar*
613 *Birds*. In: Schreiber EA, Burger J (eds) *Biology of Marine Birds*. CRC Press, Boca Raton, FL,
614 p 137–177

615 Sims DW, Quayle VA (1998) Selective foraging behaviour of basking sharks on zooplankton
616 in a small-scale front. *Nature* 393:460–464

617 Spaggiari J, Barré N, Baudat-Franceschi J, Borsa P (2007) New Caledonian seabirds. In:
618 Payri CE, Richer de Forges B (eds) *Compendium of Marine Species of New Caledonia*. Doc
619 Sci Techn IRD Nouméa Sér II 7:415–428

620 Suryan RM, Santora JA, Sydeman WJ (2012) New approach for using remotely sensed
621 chlorophyll a to identify seabird hotspots. *Mar Ecol Prog Ser* 451:213–225

622 Tew-Kai E, Rossi V, Sudre J, Weimerskirch H, Lopez C, Hernandez-Garcia E, Marsac F,
623 Garçon V (2009) Top marine predators track Lagrangian coherent structures. *Proc Natl Acad*
624 *Sci* 106:8245–8250

625 Thiers L, Louzao M, Ridoux V, Le Corre M, Jaquemet S, Weimerskirch H (2014) Combining
626 methods to describe important marine habitats for top predators: application to identify
627 biological hotspots in tropical waters. *PloS One* 9:e115057

628 Trivelpiece WZ, Trivelpiece SG, Volkman NJ (1987) Ecological segregation of Adélie,
629 gentoo, and chinstrap penguins at King George Island, Antarctica. *Ecology* 68:351–361

630 Wakefield ED, Bodey TW, Bearhop S, Blackburn J, Colhoun K, Davies R, Dwyer RG, Green
631 JA, Grémillet D, Jackson AL (2013) Space partitioning without territoriality in gannets.
632 *Science* 341:68–70

633 Weimerskirch H (1998) How can a pelagic seabird provision its chick when relying on a
634 distant food resource? Cyclic attendance at the colony, foraging decision and body condition
635 in sooty shearwaters. *J Anim Ecol* 67:99–109

636 Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Res Part*
637 *II Top Stud Oceanogr* 54:211–223

638 Weimerskirch H, Bonadonna F, Bailleul F, Mabile G, Dell’Omo G, Lipp H-P (2002) GPS
639 tracking of foraging albatrosses. *Science* 295:1259–1259

640 Weimerskirch H, Le Corre M, Bost CA (2008) Foraging strategy of masked boobies from the
641 largest colony in the world: relationship to environmental conditions and fisheries. *Mar Ecol*
642 *Prog Ser* 362:291–302

643 Weimerskirch H, Le Corre M, Jaquemet S, Marsac F (2005a) Foraging strategy of a tropical
644 seabird, the red-footed booby, in a dynamic marine environment. *Mar Ecol Prog Ser* 288:251–
645 261

646 Weimerskirch H, Le Corre M, Jaquemet S, Potier M, Marsac F (2004) Foraging strategy of a
647 top predator in tropical waters: great frigatebirds in the Mozambique Channel. *Mar Ecol Prog*
648 *Ser* 275:297–308

649 Weimerskirch H, Le Corre M, Ropert-Coudert Y, Kato A, Marsac F (2005b) The three-
650 dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment?
651 *Proc R Soc Lond B BiolSci* 272:53–61

652 Weimerskirch H, Le Corre M, Ropert-Coudert Y, Kato A, Marsac F (2006) Sex-specific
653 foraging behaviour in a seabird with reversed sexual dimorphism: the red-footed booby.
654 *Oecologia* 146:681–691

655 Wilson RP, Pütz K, Peters G, Culik B, Scolaro JA, Charrassin J-B, Ropert-Coudert Y (1997)
656 Long-term attachment of transmitting and recording devices to penguins and other seabirds.
657 *Wildl Soc Bull* 25:101–106

658 Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range
659 studies. *Ecology* 70:164–168

660 Young HS, Maxwell SM, Conners MG, Shaffer SA (2015) Pelagic marine protected areas
661 protect foraging habitat for multiple breeding seabirds in the central Pacific. *Biol Conserv*
662 181:226–235

663 Young HS, Shaffer SA, McCauley DJ, Foley DG, Dirzo R, Block BA (2010) Resource
664 partitioning by species but not sex in sympatric boobies in the central Pacific Ocean. *Mar*
665 *Ecol Prog Ser* 403:291–301

666 Zavalaga CB, Emslie SD, Estela FA, Müller MS, DELL’OMO G, Anderson DJ (2012)
667 Overnight foraging trips by chick-rearing Nazca Boobies *Sula granti* and the risk of attack by
668 predatory fish. *Ibis* 154:61–73

669

LEGEND TO TABLES

670
671
672
673
674
675
676

677

678
679

680

681
682
683
684
685

686

687
688
689
690
691

692

693

694

695

696

697

698

699

700

701

Table 1: Study sites and data collected on incubating red-footed boobies fitted with GPS loggers. EU = Europa, WA = Walpole, CH = Chesterfield, GEN = Genovesa, CI = Christmas. S= South, E = East. RFB = Red-footed booby *Sula sula*, BB = Brown booby *Sula leucogaster*, MB = Masked booby *Sula dactylatra*, AB = Abbott’s booby *Papasula abbotti*, NB = Nazca booby *Sula granti*

Table 2: Values of the delimiters of speed and turning angle of the four behaviours assigned by the EMbC algorithm

Table 3: Comparison of the chlorophyll-a concentration (chl-a, in mg.m^{-3}) and the bathymetry (bathy, in m) between the foraging area and the accessible but non-prospected area of red-footed boobies *Sula sula* from five different breeding colonies. Values expressed as mean \pm SD and significantly higher means are in bold for pairwise comparisons. EU = Europa, WA = Walpole, CH = Chesterfield, GEN = Genovesa, CI = Christmas

Table 4: Comparison of chlorophyll-a concentration (chl-a, in mg.m^{-3}) and bathymetry (bathy, in m) between travelling and area-restricted search (ARS) zones of red-footed boobies *Sula sula* from five different breeding colonies. Significantly higher values (mean \pm SD) generated from GLMM models are in bold. EU = Europa, WA = Walpole, CH = Chesterfield, GEN09 = Genovesa (2009), GEN14 = Genovesa (2014), CI = Christmas

702 Table 1:

Site	Island size	Colony location	Main wind direction	Study period	Number of RFB tracked	Number of tracks	RFB population size (pairs)	Other booby species (pairs)
EU	28 km ²	40.3°E 22.3°S	SE	2003: 09/08 - 09/23 2013: 09/23 - 10/16	9 13	9 34	2 800-3 800 ^a	/
WA	2 km ²	158.4°E 9.9°S	SE	2012: 05/27 - 06/02	17	25	c.1000 ^f	BB (100s) ^b
CH	< 10 km ²	168.9°E 22.6°S	SE	2014: 09/20 - 09/24	7	13	7 200-7 300 ^c	MB (280-500 ^c) BB (3 800-5 800 ^c)
GE N	14 km ²	105.6°E 10.5°S	S	2014: 07/29 - 08/22	15	39	140 000 ^e	NB (> 1000 ^f)
CI	135 km ²	-89.9°E 0.3°S	SE	2009: 11/13 - 11/25 2014: 11/10 - 11/25	26 36	37 42	12 000 ^d	AB (2 500 ^d) BB (5 000 ^d)

703

704 ^a Le Corre & Jouventin 1997, ^b Spaggiari et al. 2007, ^c Borsa et al. 2010, ^d James & McAllan 2014, ^e Nelson 1978,705 ^f H. Weimerskirch (pers. comm.)

706

707 Table 2:

708

Behaviour	Delimiter			
	Speed min (km.h ⁻¹)	Speed max (km.h ⁻¹)	Turn min (radians)	Turn max (radians)
Resting	0	4	0	0.30
Intense foraging	0	14	0.30	3.14
Travelling	4	90	0	0.31
Relocating	14	90	0.31	3.14

709

710

711 Table 3:

712

Breeding colony	Parameter	Area category	
		Non-prospectored	Foraging
EU	chl-a	0.149 ± 0.014	0.153 ± 0.018
	bathy	-2975 ± 554	-3023 ± 391
WA	chl-a	0.129 ± 0.033	0.111 ± 0.017
	bathy	-2290 ± 1481	-2634 ± 1383
CH	chl-a	0.111 ± 0.033	0.111 ± 0.027
	bathy	-2176 ± 1092	-2058 ± 797
GEN09	chl-a	0.207 ± 0.050	0.190 ± 0.036
	bathy	-2726 ± 709	-2268 ± 503
GEN14	chl-a	0.220 ± 0.049	0.203 ± 0.039
	bathy	-2763 ± 679	-2203 ± 512
CI	chl	0.182 ± 0.039	0.207 ± 0.043
	bathy	-4905 ± 1055	-5096 ± 1283

713

714

715 Table 4:
716

Breeding colony	Parameter	Behaviour		Test	
		Travelling	ARS	z	p-value
EU	chl-a	0.076 ± 0.059	0.069 ± 0.053	-0.669	0.5036
	bathy	-2828 ± 703	-2890 ± 631	-1.045	0.2961
WA	chl-a	0.077 ± 0.015	0.069 ± 0.017	-1.961	0.0499
	bathy	-2369 ± 1636	-3153 ± 1806	-0.869	0.3851
CH	chl-a	0.119 ± 0.028	0.112 ± 0.022	-2.179	0.0294
	bathy	-1894 ± 864	-1969 ± 853	-1.588	0.1122
GEN09	chl-a	0.111 ± 0.055	0.103 ± 0.038	-1.747	0.0806
	bathy	-1924 ± 507	-2029 ± 496	-3.195	0.014
GEN14	chl-a	0.190 ± 0.067	0.184 ± 0.061	-0.500	0.617
	bathy	-2154 ± 508	-2288 ± 463	-4.239	< 0.001
CI	chl-a	0.146 ± 0.063	0.156 ± 0.069	3.708	< 0.001
	bathy	-5297 ± 1221	-5503 ± 1104	-3.423	< 0.001

717

718

719

LEGEND TO FIGURES

720

721

722 Figure 1: Locations of the five breeding colonies of red-footed boobies *Sula sula* studied
723 during incubation

724 Figure 2: Boxplots of trip duration (h) and maximum range (km) for red-footed boobies *Sula*
725 *sula* from five different breeding colonies. Different letters above boxes indicate significant
726 differences (Tukey's HSD test). EU = Europa, WA = Walpole, CH = Chesterfield, GEN09 =
727 Genovesa (2009), GEN14 = Genovesa (2014), CI = Christmas

728 Figure 3: Distribution of trip duration (h) and maximum range (km) for red-footed boobies
729 *Sula sula* from five different breeding colonies. EU = Europa, WA = Walpole, CH =
730 Chesterfield, GEN09 = Genovesa (2009), GEN14 = Genovesa (2014), CI = Christmas

731 Figure 4: General (95% kernel density estimation, *light*) and core (50% kernel density
732 estimation, *dark*) foraging areas of red-footed boobies *Sula sula* from five different breeding
733 colonies superimposed on bathymetric maps. Colony sites are indicated by a yellow star

734 Figure 5: Mean proportion of each behaviour for red-footed boobies *Sula sula* from five
735 different breeding colonies. Behaviour was determined along tracks according to EMbC
736 analysis. Results are displayed in the form of pie charts according to the site and the period of
737 the day

738 Figure 6: Number per hour, mean duration (min) and mean surface (km²) of area-restricted
739 searches (ARS) zones for red-footed boobies *Sula sula* from five different breeding colonies.
740 Different letters above boxes indicate significant differences (Tukey's HSD test). EU =
741 Europa, WA = Walpole, CH = Chesterfield, GEN = Genovesa, CI = Christmas

742 Figure 7: Time series of the monthly chlorophyll-a concentration in the accessible area of red-
743 footed boobies *Sula sula* from five different breeding colonies. Grey boxes indicate
744 incubation periods

745 Figure 8: Foraging areas (red polygons) and accessible areas (black circles) of red-footed
746 boobies *Sula sula* from five different breeding colonies, superimposed on monthly
747 chlorophyll-a concentration maps. . Colony sites are indicated by a yellow star and grey dots
748 represent the centroid of each area-restricted search (ARS) zone.

749

750

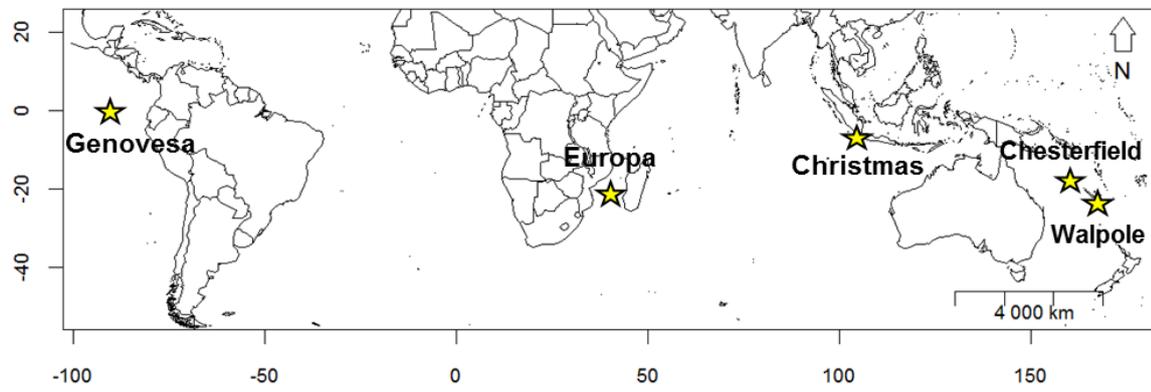
751

752

753

754 Figure 1:

755

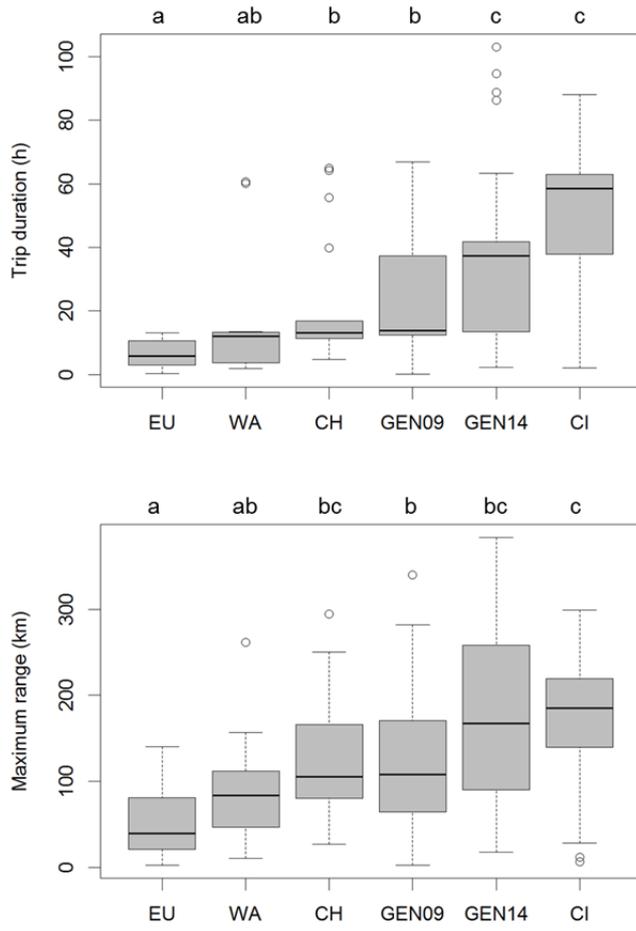


756

757

758

759 Figure 2:

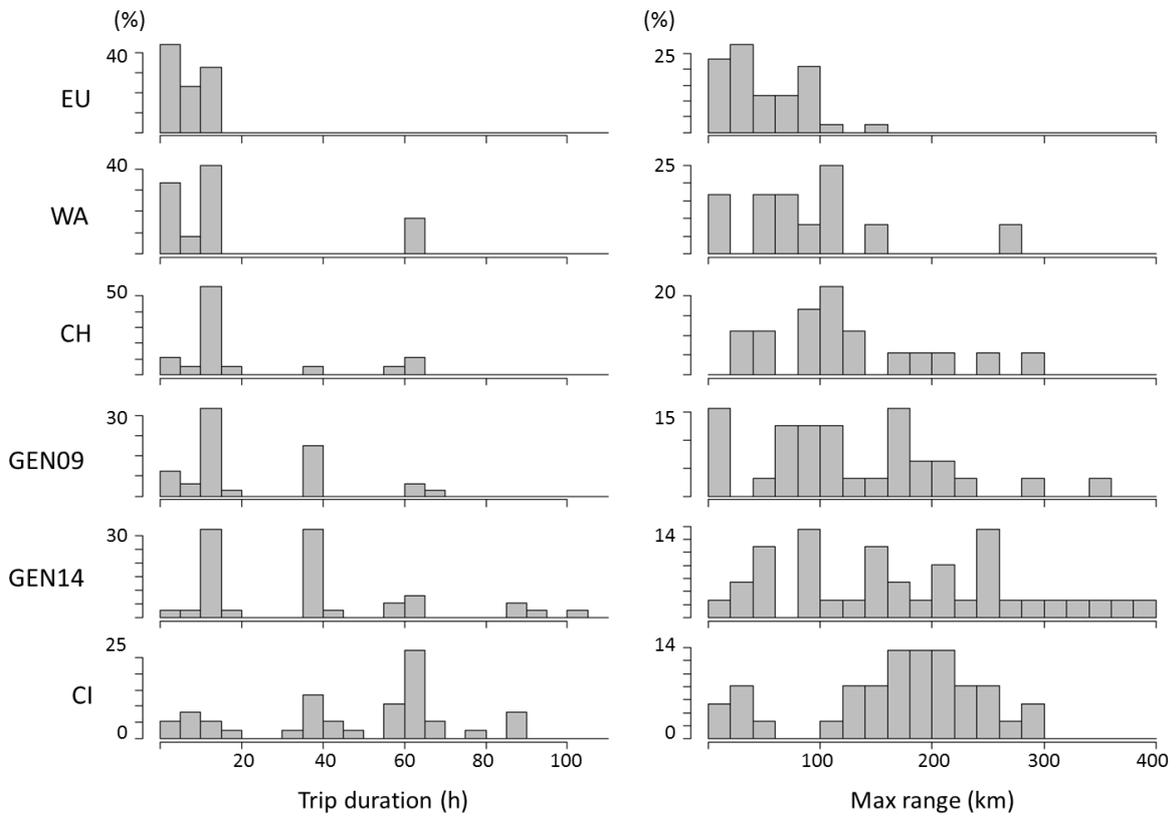


760

761

762 Figure 3:

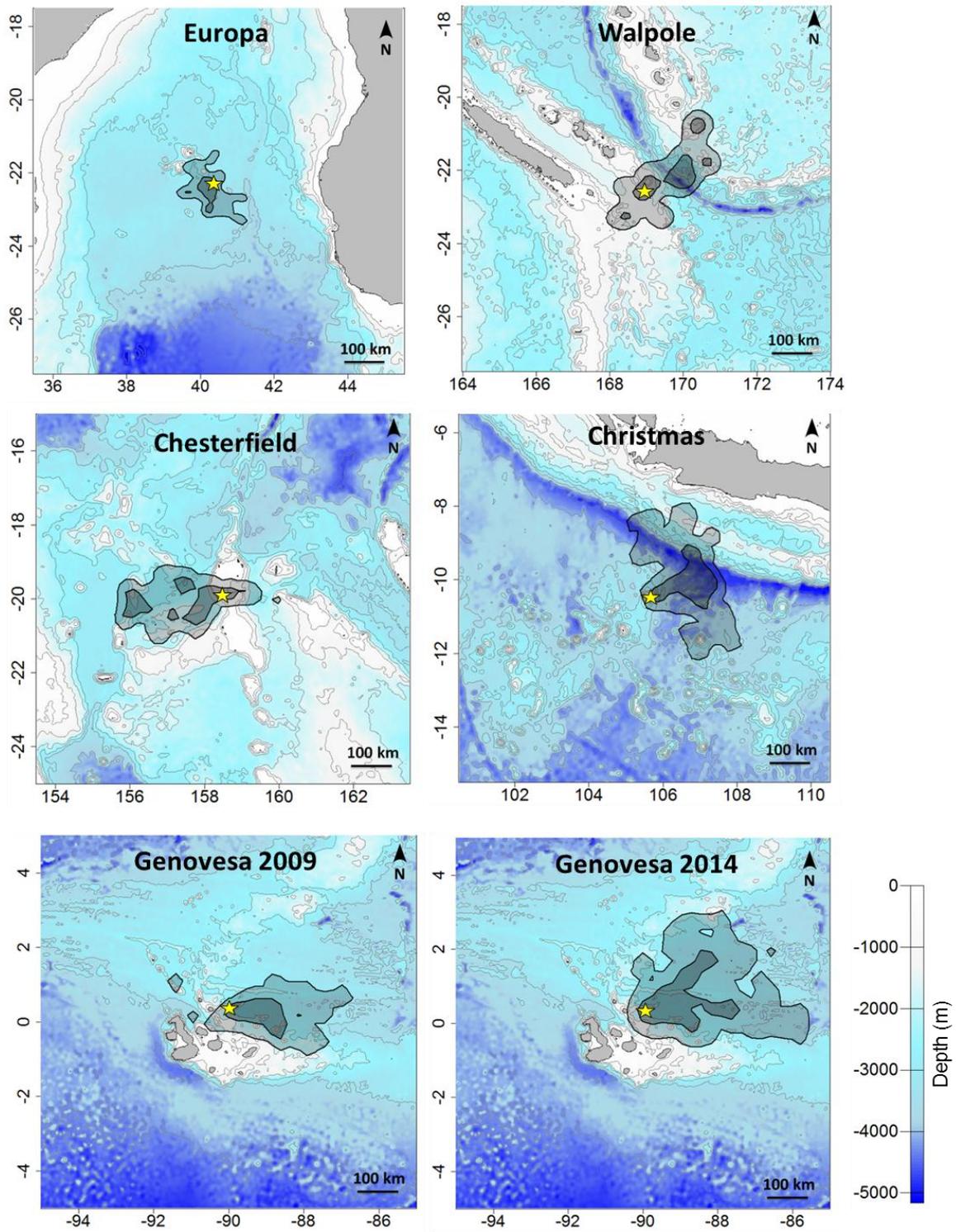
763



764

765

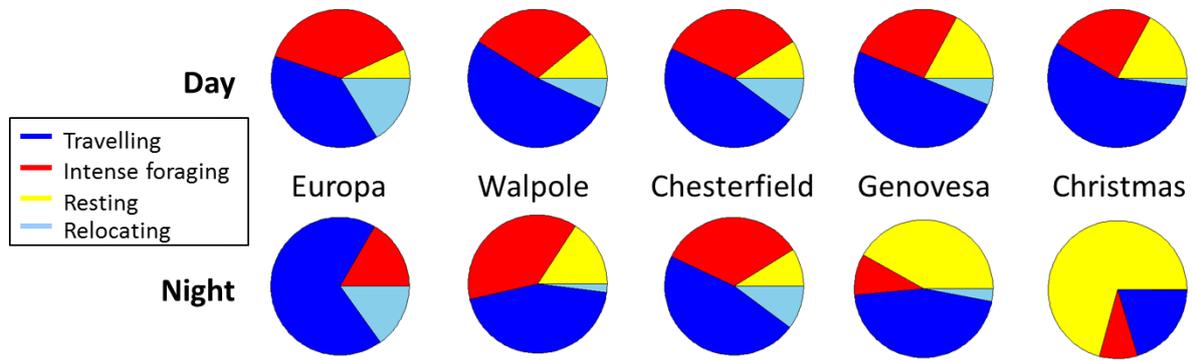
766 Figure 4:



767

768

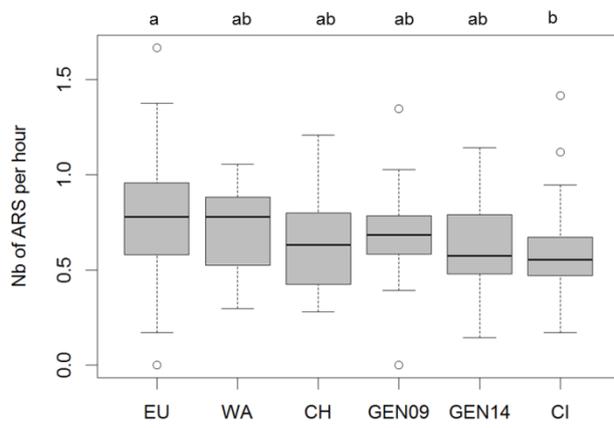
769 Figure 5:



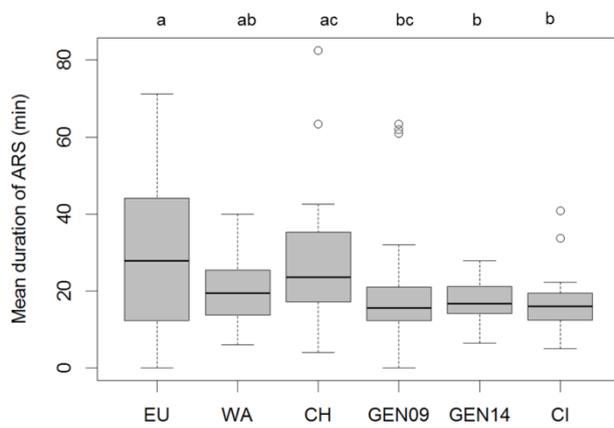
770
771

772 Figure 6:

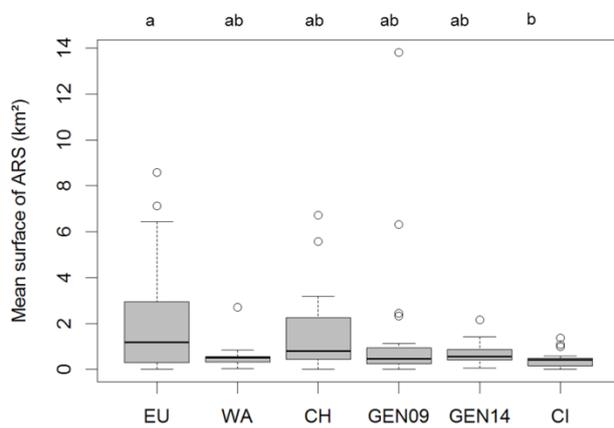
773



774



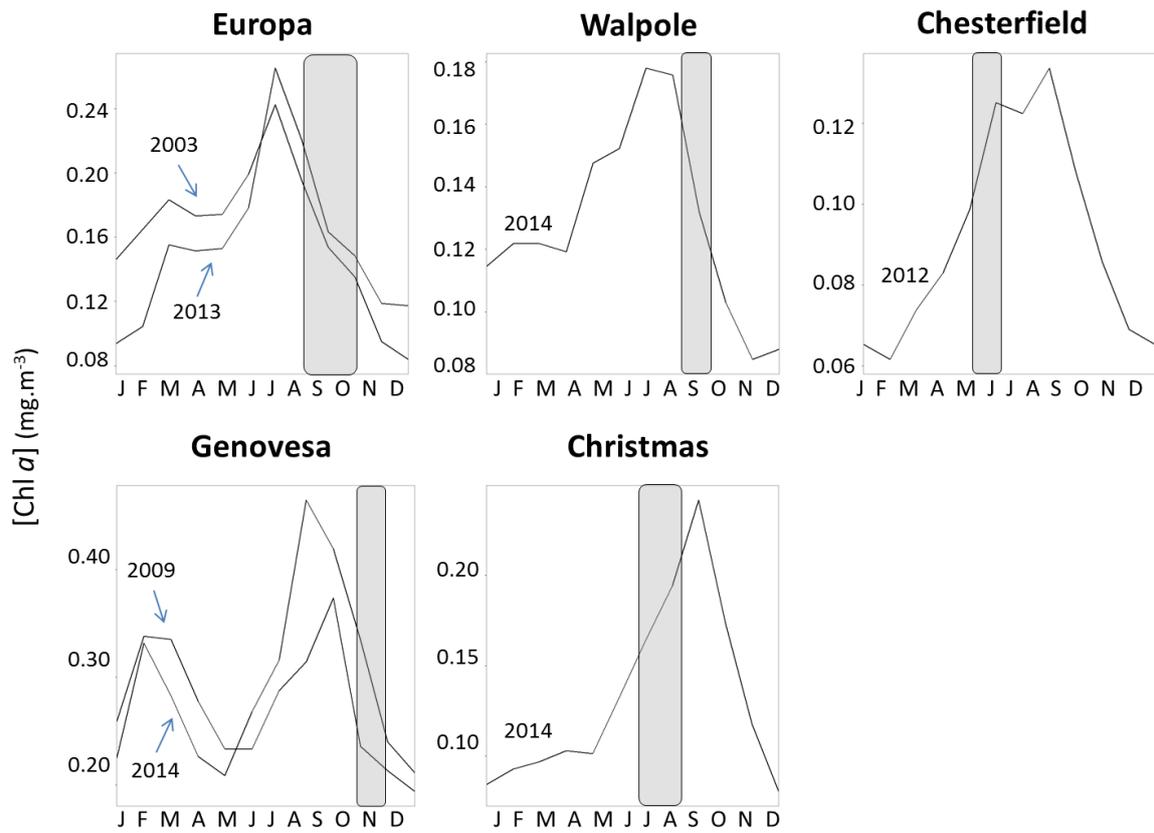
775



776

777

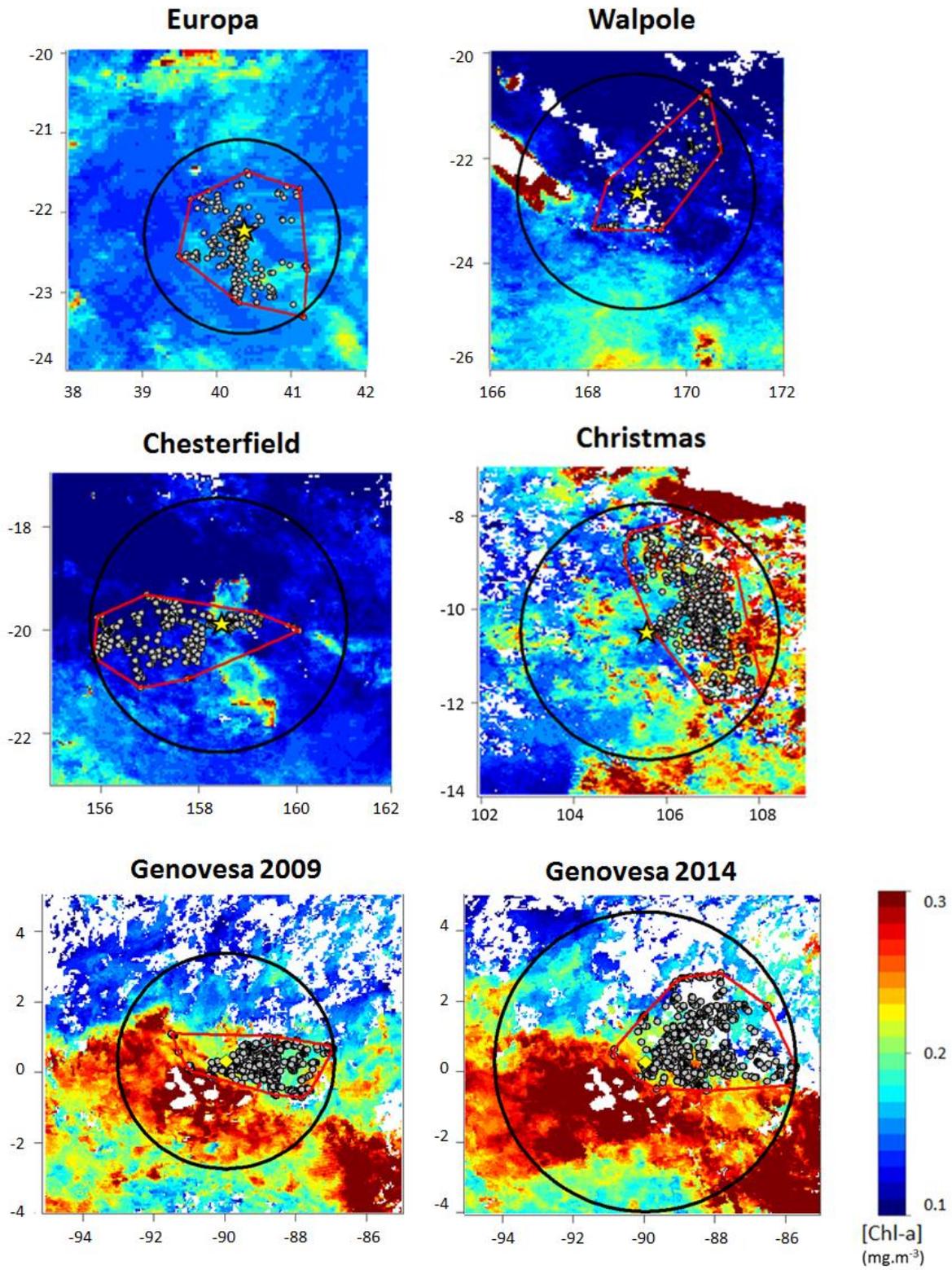
778 Figure 7:



779

780

781 Figure 8:



782