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6 Running header: Social segregation of humpback whales

7 **Social segregation of humpback whales in contrasted coastal and oceanic breeding**

8 **habitats**

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19 Maternal habitat preferences of humpback whales (*Megaptera novaeangliae*) are well
20 documented from decades of coastal research but oceanic areas have received less attention.

21 Whales breeding in New Caledonia occupy both ecosystems: a coastal reef complex (South
22 Lagoon) and oceanic seamounts (Southern Seamounts). Generalized Additive Models were

23 applied to 20 years of boat-based whale observations ($n = 1,526$) to describe habitat preferences
24 and Permissive Home Range Estimations were used to explicitly model spatial segregation in

25 relation to social context. Groups with calves ($n = 206$) preferred shallow coastal waters
26 throughout the season in the South Lagoon, whereas no habitat segregation was observed

27 between groups with ($n = 74$) and without calves ($n = 140$) in the Southern Seamounts. As a
28 result, spatial overlap between groups with and without calves was more common in the
29 Southern Seamounts than the South Lagoon. Despite a lack of social segregation around
30 seamounts, mother-calf pairs were proportionally more frequent in the Southern Seamounts
31 (27%) than in the South Lagoon (16%). Photographs of the calves' dorsal flanks were analyzed
32 to compare age and ecological markers across sites. Calves appeared older in the Southern
33 Seamounts than in the South Lagoon but no difference in scarring nor shark bites was found
34 across sites, suggesting that calves experienced similar lifestyles and may move between off-
35 shore and coastal waters during the breeding season. This study highlights the flexible habitat
36 use patterns of breeding humpback whales and raises new questions about the environmental
37 and social drivers of their presence in off-shore breeding grounds.

38 Key words: breeding ground, habitat use, humpback whales, Pacific Ocean, seamounts, social
39 interactions

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48 Space-use dynamics and habitat selection of mobile animals are driven by multiple ecological
49 demands such as feeding, mating, or avoiding predators. The concept of 'ecological niche' relies
50 on the notion that individual fitness depends on space-use strategies and access to optimal
51 habitats. Yet, biological needs vary throughout an individual's lifetime, causing changes in
52 space-use patterns. These changes are very patent in migrating species, such as humpback
53 whales (*Megaptera novaeangliae*) whose habitat varies drastically during annual migrations
54 between polar and tropical waters (Clapham 2000a). Though still subject to an ongoing debate,
55 the primary driver explaining the evolutionary persistence of this behavior appears to be calf
56 development and survival. The warm waters in tropical and sub-tropical breeding grounds
57 (Clapham 2000b), and reduced risk of killer whale (*Orcinus orca*) predation in these regions
58 (Corkeron and Connor 1999), assumedly contribute to greater calf survival. Yet, even within
59 breeding grounds, survival is not guaranteed. Due to the higher energetic demand of calving,
60 lactation, and care for the young calf, mothers have a tighter energetic balance than other
61 individuals (Lockyer 1981) and are considered more at risk from environmental stressors,
62 including human disturbance (Lammers et al. 2007; Cartwright et al. 2012).

63 In several coastal and island breeding grounds across the oceans, female humpback
64 whales with calves have been shown to avoid their con-specifics. This behavior results in a
65 spatial segregation of social groups, with mother-calf pairs preferentially occupying waters
66 shallower than 50 m (Martins et al. 2001; Ersts and Rosenbaum 2003; Zerbini et al. 2004;
67 Oviedo and Solís 2008; Félix and Botero-Acosta 2011; Craig et al. 2014; Guidino et al. 2014;
68 Lindsay et al. 2016) and closer to shore (within 1 to 2 km of islands with steep seabed slopes:
69 Hawaiï, Frankel and Clark 2002; Antongil Bay, Madagascar, Ersts and Rosenbaum 2003; Osa
70 Peninsula, Costa Rica, Oviedo and Solís 2008; and within 10 km of low islands with gradual
71 slopes: Abrolhos Bank, Brazil, Martins et al. 2001; Ecuador, Félix and Botero-Acosta 2011)
72 compared to other social groups.

73 However, less scientific exploration has been dedicated to oceanic habitats where
74 coastlines and or reefs do not constrain space-use. Satellite tracking has recently uncovered that
75 humpback whales also occupy the high seas during the breeding season (Kennedy et al. 2014;
76 Garrigue et al. 2015; Dulau et al. 2017), but these offshore areas have rarely been directly
77 surveyed. In the Coral Sea, an oceanic breeding ground has been identified south of New
78 Caledonia around Torch Bank and Antigonina Seamount (hereafter referred to as the 'Southern
79 Seamounts'; Fig. 1). These 2 seabed features are respectively located at 25 and 100 km from
80 the closest land (the Isle of Pines) along the Norfolk Ridge. These features are totally submerged
81 and characterized by shallow depths (30–60 m) and rough sea state due to the lack of shelter
82 from wind and currents. In austral winter, a population of humpback whales congregates in the
83 New Caledonian breeding grounds such as these Southern Seamounts and the well-known
84 breeding ground of the South Lagoon (Orgeret et al. 2014; Garrigue et al. 2015). These whales
85 have been monitored for more than 2 decades (Garrigue et al. 2001, 2015) and photo-
86 identification of individual whales has revealed evidence of connectivity between the Southern
87 Seamounts and South Lagoon (Garrigue et al. 2013; Orgeret et al. 2014). Humpback whales
88 breeding in this region belong to the Oceanian population, classified as 'Endangered' in the
89 IUCN Red List (Childerhouse et al. 2009).

90 In this study, we examined the space-use of humpback whale females with a calf in 2
91 connected breeding grounds (Garrigue et al. 2013) characterized by contrasting environmental
92 conditions (coastal versus oceanic). We explored the patterns of geographical and
93 environmental social segregation in the South Lagoon and in the Southern Seamounts
94 throughout several breeding seasons using statistical habitat modeling. We predicted that social
95 segregation will differ in these 2 breeding grounds based on age of calf and time of the season.

96 **MATERIALS AND METHODS**

97 *Study areas.*— New Caledonia is located in the southwest Pacific Ocean about 1,500
98 km northeast of Australia, on the Norfolk Ridge (Fig. 1A). This area displays original terrain
99 and oceanographic features, including many banks and seamounts (e.g., Antigonía seamount,
100 Torch Bank). New Caledonia's mainland, '*Grande Terre*', is surrounded by a large lagoon
101 delimited by 1,600 km of barrier reef. Since 2014, 92% of the New Caledonian waters are
102 included in the Natural Park of the Coral Sea.

103 New Caledonia South Lagoon.— Located south of the mainland, the South Lagoon is
104 a large shallow area (mean depth about 50 m), including the Prony Bay and the Ouen Island to
105 the north and bounded by 2 reef complexes to the southwest and the northeast (Fig. 1B). The
106 southeastern part of the lagoon is open to the ocean and is characterized by deeper waters
107 (reaching 600 m deep below 22°54'S). The South Lagoon constitutes the main humpback whale
108 breeding ground known to date in New Caledonia (Garrigue et al. 2001). These whales belong
109 to the breeding stock E, as defined by the Scientific Committee of the International Whaling
110 Commission, and more specifically to the breeding sub-stock E2, which is demographically
111 isolated and genetically differentiated from the 2 neighboring breeding sub-stocks of eastern
112 Australia (E1) and Tonga (E3) (Garrigue et al. 2004; Olavarría et al. 2007). Humpback whales
113 visit the South Lagoon in austral winter with a peak of abundance in mid-August (Garrigue et
114 al. 2001, 2011).

115 Antigonía Seamount and Torch Bank.— Antigonía seamount is located 170 km from
116 the mainland, on the Norfolk Ridge, south of the South Lagoon, the Isle of Pines and Torch
117 Bank (Fig. 1B). Torch Bank (167°41'W 22°51'S) and Antigonía (168°4'W 23°24'S) respectively
118 culminate at 30 and 60 m deep, span about 48 km² and 98 km² (Gardes et al. 2014), and are
119 surrounded by waters about 1,500 m deep. Presence of humpback whales in this area was first
120 discovered using satellite monitoring: most whales tagged in the South Lagoon between August
121 and September visited the Southern Seamounts (males and females, including maternal

122 females) and remained there from several days to several weeks (see Garrigue et al. 2015 for
123 further details). Boat-based surveys conducted subsequently in the area at the end of the
124 breeding season confirmed the high density of humpback whales, compared to the South
125 Lagoon (Garrigue et al. 2013; Orgeret et al. 2014, Garrigue et al. 2017).

126 *Data collection.*— Surveys were conducted from 1995 to 2015 in the South Lagoon
127 and between 2001 and 2011 in the Southern Seamounts (Table 1). Surveys took place between
128 July and September in the South Lagoon and from the end of August to the end of September
129 in the Southern Seamounts (with the exception of 5 days of survey in Torch Bank in July). For
130 the purpose of this study, breeding seasons were divided into 2 periods: the 'beginning of the
131 season' from July to mid-August (calendar week 25 to week 32) and the 'end of the season' from
132 mid-August to end of September (calendar week 33 to week 40).

133 Surveys did not follow a systematic or explicitly randomized sampling technique but
134 rather a haphazard sampling regime (Corkeron et al. 2011) to maximize encounters with whales
135 (see maps of survey effort, Supplementary Data S1). Surveys were only initiated in Beaufort
136 sea-states ≤ 3 . In the South Lagoon, the search effort primarily focused on waters that could be
137 accessed with a 6-m rigid-hulled inflatable boat. The team at sea was supported by a land-based
138 team located at the Cape N'Doua, a 189-m-high cape overlooking the study area (Fig. 1B).
139 Teams could communicate continuously using Very High Frequency (VHF) radios and whale
140 groups could therefore be detected at sea or from the land, and subsequently approached by
141 boat. In the Southern Seamounts, surveys were only boat-based and were conducted with a
142 sailing or motor catamaran. Field surveys conformed to the guidelines of the American Society
143 of Mammalogists on use of live animals in research (Sikes et al. 2016).

144 A group was defined as a spatial aggregation of whales characterized by a social group
145 type following the definitions of Clapham et al. (1992): groups of 3 or more individuals,

146 involved in competitive behavior or not (R); mother with calf pair (MC); mother with calf
147 followed by a single escort (MC-E); mother with calf followed by a competitive group (MC-
148 R); pair of adults (P); and singletons (S). For each encounter, GPS position, time, social group
149 type, minimum group size, and maximum group size were recorded. Due to the fluid social
150 structure typically displayed by humpback whales in their breeding grounds (Clapham 1996),
151 a few individuals may have been encountered more than once per survey day, if they moved to
152 a new group with a different social type (for instance, a maternal female observed as a MC on
153 one occasion, and later on the same day as a MC-E or a MC-R).

154 In the past decade, individuals were photographed with digital cameras (CANON
155 EOS 40D and 50D; Canon Inc., Courbevoie, France) equipped with 70 X 300 mm lenses. For
156 adults, photo-identification of individuals is typically conducted using the unique markings on
157 the ventral surface of the tail fluke (Katona et al. 1979). Calves on the other hand rarely show
158 their fluke when diving. Calves were therefore individually identified using the shape and
159 markings of their dorsal fin, or of their mother's fluke and dorsal fin. Insofar as possible, calves
160 were photographed on both sides of their dorsal fin, with their body oriented perpendicular to
161 the photographer. Tissue samples were collected from both adult and calf whales using a
162 crossbow with a specially adapted bolt (Lambertsen et al. 1994), or a modified .22 caliber
163 capture veterinary rifle (Krutzen 2002). Genomic DNA was extracted from these biopsy
164 samples to identify sex (Gilson and Syvanen 1998) and individuals (see Garrigue et al 2004 for
165 further details). Photo-identification and genotyping allowed individual identification of whales
166 in each group encountered, allowing the estimation of daily resighting rates as the mean number
167 of times a given individual was observed during a given day of survey. Daily resighting rates
168 were compared between study sites and between group types to ensure that group encounters
169 did not suffer from spatial auto-correlation.

170 Several environmental variables were collected in the study areas to characterize
171 habitat at a 500-m resolution. Coastline and reef shapefiles were produced by the Millennium
172 Coral Reef Mapping Project (version 8, Andréfouët et al. 2008). Using these shapefiles,
173 distance to the coast and distance to reefs were calculated for each 500 x 500 m cell in the South
174 Lagoon study area as the euclidean distance to the closest landmass (i.e., New Caledonia
175 mainland, Ouen Island, or the Isle of Pines) and closest reef, respectively. Bathymetry data
176 (DTSI 2016) was provided at a 100 x 100 m resolution over both study areas. Raster gaps were
177 filled through extrapolation of satellite and aerial composite imagery (Lefèvre, French National
178 Research Institute for Sustainable Development, pers. comm., February, 2016). Two terrain
179 features were derived from the bathymetry raster: slope over both study areas, and shading only
180 at the Southern Seamounts, which is a metric combining orientation and inclination of the slope
181 with respect to a southeast axis that represents the dominant wind direction (Horn 1981).
182 Finally, distance to the center of the seamounts was calculated for the Southern Seamount study
183 area.

184 *Space-use analysis.*— Groups were classified into 2 categories: groups with a calf
185 (Gcalf) including MC, MC-E, and MC-R social types, and groups without a calf (Gnocalf)
186 including R, P, and S social types. Group encounters were georeferenced and their positions
187 were projected in a UTM coordinate system (UTM zone 58S). For this analysis, group
188 encounters were considered statistically independent within each study area at a daily scale.

189 *Pairwise distance analysis.* — For this analysis, a metric was developed to estimate
190 the spatio-temporal closeness between group encounters that was then used to assess potential
191 patterns of attraction or avoidance between whale groups. Euclidean distance was calculated
192 between whale groups observed each day in the South Lagoon. The distributions of distance
193 values were compared between groups with a calf and groups belonging to other social types.
194 Subsequently, these distances were divided by the time interval between each group encounter.

195 This metric, hereafter referred to as the spatio-temporal closeness, was calculated per social
196 type and compared using Kruskal-Wallis rank sum tests.

197 *Habitat preferences.* —The probability of encountering a calf in a group was modeled
198 with Generalized Additive Models (GAMs; Hastie and Tibshirani 1990). First, the GAM was
199 applied only to groups observed at the end of the season in the South Lagoon to assess the effect
200 of distance to the coast, distance to reefs, bathymetry, and seabed slope (see Supplementary
201 Data S1, for more detail on predictor selection). Second, all observations recorded in the South
202 Lagoon were combined to test for a potential effect of the time of season (included in the model
203 as calendar week of the year) on the space-use pattern of groups with a calf. A GAM was built
204 over all observations of groups with or without a calf and including distance to the coast, week,
205 and a linear interaction term between these 2 variables as predictors. Finally, encounter rate per
206 week of the year and per social types (Gnocalf, MC, MC-E, and MC-R) was calculated by
207 dividing the number of groups observed by the number of hours spent on-effort for each week
208 (sum of daily survey durations: from start to end of observations), all years pooled together.

209 In the Southern Seamounts, time of season was not tested because the great majority
210 of the data was collected at the end of the season. Distance to the coast and to the reefs were
211 also excluded and replaced by other environmental factors thought to be more relevant in this
212 off-shore area: bathymetry, seabed slope, distance to the center of the seamounts, and shading.

213 GAMs were applied with a binomial response type (presence or absence of a calf in
214 a group), *logit* link function and maximum likelihood (ML) smoothing selector. Several models
215 of decreasing complexity were fitted to our dataset and model selection was performed with a
216 stepwise approach using the Bayesian Information Criterion (BIC; Schwarz 1978). BIC is a
217 variant of the more commonly applied Akaike Information Criterion (AIC). It takes in account
218 the number of observations included in the model and penalizes model complexity more heavily

219 than AIC. The Receiver Operating Characteristic (ROC) curves were also calculated for each
220 model and the corresponding Area Under the Curve (AUC) was reported in order to compare
221 descriptive and predictive performance across models. AUC evaluates the model's capacity for
222 binary classification: a random model has an AUC of 0.5 and a perfect model an AUC of 1
223 (Swets 1988). Delong's Z-test was applied to compare models to the AUC of the null model
224 (Delong et al. 2016).

225 *Spatial overlap.* —Differences in habitat preferences between social types may result
226 in distinct patterns of spatial distribution. The core area of use for groups with or without a calf
227 was estimated using the Permissive Home Range Estimation (PHRE) method developed by
228 Tarjan and Tinker (2016). This method was initially developed to assess home ranges of
229 individual animals based on satellite tracking data. Here, it was applied to the positions of group
230 encounters, so that the term “home range” actually refers to the range of the overall population.
231 Instead of calculating home ranges using a Kernel Density Estimate (KDE, Worton 1989) in
232 geographical space, the PHRE applies a KDE to the positions in a multidimensional
233 environmental space and then reprojects the niche estimate to a 2-dimensions geographical
234 surface. The same environmental variables applied in the GAM analysis were considered.
235 Similar to a traditional KDE, PHRE can be calculated with different smoothing parameters.
236 Three methods were tested to optimize the KDE bandwidth: the plug-in bandwidth selector
237 (*H_{pi}*), the least-square cross validation (*H_{lscv}*), and the smoothed cross-validation (*H_{scv}*)
238 described in Duong (2007). Once the environmental hypervolume occupied by observations
239 was identified, it was reprojected to latitude-longitude to create a map of relative probability of
240 presence. The 50% contour of the probability surface was outlined and considered as the core
241 area of use. Then, the overlap of these areas was calculated between groups with or without a
242 calf.

243 All data manipulation and spatial analysis was conducted using R statistical software
244 v.3.2.5 (R Core Team 2016) and QGIS v.2.14. (QGIS Development Team 2016). More
245 specifically, GAMs were modeled using the *mgcv* R package and PHRE was based on a
246 modified version of a custom code by Tarjan and Tinker (2016).

247 *Photographic analysis.*— Photographs of calves were used to evaluate age and
248 ecological markers between the 2 breeding sites. Indeed, the approximate age of humpback
249 whale calves may be assessed from the degree of unfurling of the dorsal fin (Cartwright and
250 Sullivan 2009a). A pale flank pigmentation (Chittleborough 1953) and a furled dorsal fin
251 (Cartwright and Sullivan 2009a) are known traits of neonatal humpback whales. As the calf
252 grows, pigmentation darkens and the dorsal fin unfurls. These phenotypic changes may be
253 recorded within a breeding season (Cartwright and Sullivan 2009a). Also, scarring patterns are
254 important ecological markers for cetaceans: they have been analyzed in several species to study
255 intra-specific interactions, predation, habitat use, and migratory patterns (Heithaus 2001a;
256 Wenzel and Suárez 2012; Marley et al. 2013; Towers et al. 2013; Elwen et al. 2014; Best and
257 Photopoulou 2016). In particular, Cookiecutter sharks (*Isistius* spp.) primarily live in tropical
258 oceanic waters and are known to attack cetaceans, leaving distinctive crater-like wounds on
259 their body (Dwyer and Visser 2011; Best and Photopoulou 2016). Prevalence of Cookiecutter
260 shark bites on individual whales may therefore be interpreted as a rough indicator of pelagic
261 habitat use (Wenzel and Suárez 2012; Towers et al. 2013; Best and Photopoulou 2016). Finally,
262 scars, and occasionally observed fresh wounds, are assumed to be partially due to prolonged
263 antagonist interactions with competitive males as the barnacles on the fluke and pectoral fins
264 of the latter can injure the calf during contact.

265 Photographic analysis was performed on pictures of the dorsal fins of calves
266 encountered at the end of the season in the South Lagoon and in the Southern Seamounts,
267 between 2007 and 2015. Only pictures with fair or better quality were retained in the analysis

268 (quality assessment was based on focus, lighting conditions, proportion of the frame occupied
269 by the animal, and angle of the animal relative to the sensor plane; following Towers et al.
270 2013). If a calf was encountered on several occasions, only the earliest encounter among those
271 including good-quality pictures was retained.

272 For each calf encounter at the end of the season, the following physical characteristics
273 were recorded: flank pigmentation (very light, light, medium, dark), unfurling of the dorsal fin
274 measured by the angle between the dorsal fin and the flank (furled = 45-80°, medium = 15-45°,
275 almost unfurled = 0-15°, unfurled = 0°), scarring (none, few scars, medium, many scars),
276 presence or absence of fresh wounds, presence or absence of Cookiecutter shark bites, and
277 number of visible Cookiecutter shark bites over the left and right flanks (for more details on
278 rating criteria, see Supplementary Data S2). A manual that described and illustrated these
279 characteristic was produced prior to the analysis and was used as a reference throughout the
280 rating process. These physical characteristics were qualitatively rated visually by a single
281 researcher blind to the exact date of the encounter and to the identity of the calf in order to avoid
282 observer bias (Coomber et al. 2016). Physical characteristics were compared between South
283 Lagoon and Southern Seamounts calves using Pearson's Chi-square tests with simulated *P*-
284 values (based on 2,000 Monte-Carlo replicates). Finally, the independence between scarring
285 and social group type in which the calf was found (MC, MC-E, or MC-R) was tested over both
286 study sites pooled together using the same statistical test.

287 **RESULTS**

288 In the South Lagoon, a total of 1,312 whale groups were encountered over 20 years
289 of surveys (equivalent to 716 days of effort), of which 206 included a calf (16%, Fig 1.C). A
290 total of 646 groups were observed at the end of the season (517 without a calf versus 129 with

291 a calf). In the Southern Seamounts, 214 groups were observed over 7 years of surveys
292 (equivalent to 34 days of effort), from which 74 included a calf (35%, Table 1, Fig 1.D).

293 The number of daily resightings of an individual was close to 1 on average.
294 Individuals in groups without a calf were observed 1.19 times ($\pm SD$ 0.48) in the South Lagoon
295 and 1.15 times ($\pm SD$ 0.41) in the Southern Seamounts. Maternal females were resighted 1.07
296 times ($\pm SD$ 0.28) per day on average in the South Lagoon and 1.17 times ($\pm SD$ 0.42) in the
297 Southern Seamounts. Resights were significantly lower for maternal females than adults from
298 groups without a calf (2-way ANOVA: $F_{1, 2664} = 7.3$, $P = 0.007$), but did not vary across study
299 sites (2-way ANOVA: $F_{1, 2664} = 0.8$, $P = 0.4$).

300 *Space use in the South Lagoon.*— In the South Lagoon, the daily pairwise distances
301 ($n = 335$ distance values in total) between groups with a calf was significantly lower than
302 between groups with a calf and all other social group types without a calf (Kruskal-Wallis test:
303 $X^2_3 = 12.4$, $P = 0.01$, Fig. 2A). Indeed, Dunn's post-hoc test with a Bonferroni correction
304 showed significant differences between Gcalf and R ($Z = -3.36$, $P = 0.02$), Gcalf and P ($Z = -$
305 2.74 , $P = 0.02$), Gcalf and S ($Z = -2.91$, $P = 0.01$), but not between R, P, and S. Yet, when
306 balancing these pairwise distances with the duration of the time interval between each
307 observation, groups with a calf no longer distinguished themselves from the rest of the
308 population. The spatio-temporal closeness between groups with a calf was not significantly
309 different from that between groups with a calf and all other social group types without a calf
310 (Kruskal-Wallis test: $X^2_3 = 3.5$, $P = 0.32$, Fig. 2B). Therefore, groups with a calf were observed
311 in the same geographical areas as groups without a calf, but rarely at the same time of the day.
312 Groups with a calf avoided all other groups, including other groups with a calf.

313 In the South Lagoon, groups with a calf observed at the end of the season were
314 observed closer to the coast (Kruskal-Wallis test: $X^2_2 = 13.2$, $P < 0.001$) and in shallower waters

315 (Kruskal-Wallis test: $X^2_2 = 16.5$, $P < 0.001$) compared to groups without calves (Fig. 3). This
316 habitat-use relationship relative to distance to the coast was also detected through the GAM
317 analysis of group encounters ($n = 646$) at the end of the season. The simplest model including
318 only distance to the coast as a predictor of calf presence was selected as the best model based
319 on BIC (Table 2). Interestingly, this model did not maximize AUC compared to other models
320 including more predictors, but it provided the best trade-off between performance and
321 complexity. The predictive performance of this model measured through AUC was
322 significantly higher than that of a random model (DeLong's Z -test: $Z = -3.7$, $P < 0.001$). None
323 of the GAM models included a significant effect of depth (Table 2), which can be attributed to
324 the strong correlation between distance to the coast and bathymetry (Spearman coeff = -0.71,
325 calculated on the full season sample of sightings, $n = 1,312$).

326 The overall encounter rate peaked in the last week of August in the South Lagoon,
327 but the proportion of groups with a calf, and particularly of MC groups, increased throughout
328 the season and peaked in September (Fig. 4). Additionally, in our 3-term GAM analysis of
329 group encounters over the whole season ($n = 1,312$, see Supplementary Data S1), distance to
330 the coast (approximate significance of smooth terms: $s(\text{dist_coast})$ edf = 1, $X^2 = 19.54$, $P <$
331 0.001) and week (approximate significance of smooth terms: $s(\text{week})$ edf = 1, $X^2 = 39.35$, $P <$
332 0.001) were significant predictors of calf presence. Yet, the interaction between distance to the
333 coast and week had no significant effect on the probability of encountering a group with a calf
334 (approximate significance of smooth terms: $s(\text{dist_coast,week})$ edf = $2.07e-05$, $X^2 = 0$, $P =$
335 0.38), suggesting that despite the change in calf abundance throughout the breeding season,
336 their habitat preferences remain the same.

337 *Comparative habitat analysis between study sites.*— In the GAM analysis of calf
338 presence on the Southern Seamounts, none of the 5 models built with different combinations of

339 environmental predictors outperformed the null model (lowest BIC = 281.3, Table 2). This
340 indicates that there was no habitat segregation between groups with and without calf in the
341 Southern Seamounts with respect to bathymetry, slope, distance to the center of seamounts, and
342 shading.

343 After graphically comparing the maps of relative probability of presence generated
344 by the PHRE set at different bandwidths, the unconstrained *Hscv* method was selected as the
345 best candidate for our PHRE analysis. The relative probability of whale presence was mapped
346 in a geographical coordinate system and the 50% probability contours were separately retrieved
347 for each social type: Gcalf and Gnocalf (Fig. 5). The overlap of the PHRE core area between
348 groups with and without a calf was higher in the Southern Seamounts (75%) than in the South
349 Lagoon (59%). The core area of use for groups with a calf also was more than twice as small in
350 the Southern Seamounts (63 km²) than in the South Lagoon (139 km²).

351 On average, groups with a calf were proportionally more common in the Southern
352 Seamounts (26.9% ± SD 19.5) than in the South Lagoon (16.0% ± SD 8.5) at the end of the
353 season (Pearson's Chi-square test with 2,000 Monte-Carlo simulations: $X^2 = 19.0$, $P < 0.001$;
354 Table 3). The breeding site significantly affected the social group type of groups with a calf
355 (Pearson's Chi-square test with 2,000 Monte-Carlo simulations: $X^2 = 49.3$, $P < 0.001$). Groups
356 with a calf were predominantly MC pairs in the South Lagoon whereas in the Southern
357 Seamounts, MC-E and MC-R groups were more frequent (Table 3). Molecular analysis of tissue
358 samples confirmed that all escorts biopsied in MC-E groups were males.

359 *Comparative photographic analysis between study sites.*— From a total of 180
360 encounters with groups with a calf between 2007 and 2015, a subset of 116 encounters that
361 occurred at the end of the season for which pictures were available was selected for analysis.
362 After deleting resights and poor pictures, the dataset was composed of 40 calves in the South

363 Lagoon and 47 in the Southern Seamounts. No significant difference in scarring, presence of
364 fresh wounds, number of Cookiecutter shark bites, or flank pigmentation was found between
365 calves observed in the South Lagoon and the Southern Seamounts. Calf scarring also was not
366 related to its social group type (MC, MC-E, or MC-R; Pearson's Chi-square test with 2,000
367 Monte-Carlo simulations: $X^2 = 6.0$, $P = 0.44$). A significant difference was found in the degree
368 of unfurling of the dorsal fin, which was on average more advanced in the Southern Seamounts
369 (Pearson's Chi-square test with 2000 Monte-Carlo simulations: $X^2 = 8.25$, $P = 0.03$; Fig. 6).

370 **DISCUSSION**

371 In this study, maternal female humpback whales displayed different space-use
372 patterns with respect to other whales depending on whether they occupied coastal or oceanic
373 habitat. In the South Lagoon, groups with a calf avoided contact with other con-specifics and
374 occurred in higher proportion in waters nearest to the coast. This pattern of social segregation
375 is consistent with studies in other humpback whale breeding grounds of the world that also
376 found that mothers with a calf favor shallow coastal waters close to the coast or to reefs
377 (Smultea 1994; Martins et al. 2001; Ersts and Rosenbaum 2003; Oviedo and Solís 2008; Félix
378 and Botero-Acosta 2011; Craig et al. 2014; Guidino et al. 2014; Lindsay et al. 2016). This
379 pattern has been observed in other cetaceans (i.e., southern right whale, *Eubalaena australis*—
380 Rayment et al. 2015; Risso's dolphin, *Grampus griseus*— Hartman et al. 2014) and is thought
381 to result from a need to 1) shelter from wind and currents (Félix and Botero-Acosta 2011;
382 Rayment et al. 2015), and 2) avoid male harassment (Elwen and Best 2004; Craig et al. 2014).
383 Indeed, lactating females and their offspring are constrained by a tight energy balance on their
384 breeding ground and during the migration towards polar feeding grounds (Chittleborough
385 1958). Spatial segregation from other whales and sheltering are thought to be energy-saving
386 strategies for females with a calf. Yet, in this study we show that females with a calf also occupy

387 areas where neither of these 2 needs are fulfilled. In the Southern Seamounts, groups with a calf
388 were found in greater proportion than in the South Lagoon, despite this area's lack of shelter or
389 the possibility to spatially avoid adult males. In the Southern Seamount site, the core area used
390 by groups with a calf strongly overlapped with the area occupied by the other whale groups.

391 Our photographic analysis suggested that calves observed in the Southern Seamounts
392 at the end of the season were older than the calves observed in the South Lagoon during the
393 same period. It is not known precisely how long it takes the dorsal fin of humpback whale
394 calves to unfurl completely, and the rate of unfurling is likely to vary between individuals
395 (Cartwright and Sullivan 2009a). Our picture database also is part of a long-term monitoring
396 program and was not collected specifically for this purpose (Cartwright and Sullivan 2009a).
397 Thus, caution is warranted in the interpretation of these results. Nonetheless, maternal females
398 have been shown to use deeper waters as their calf grows larger during the breeding season
399 (Hawaii, Pack et al. 2017). Females could be more reluctant to visit unsheltered oceanic habitats
400 such as the Southern Seamounts until their calf grows large enough that the risk of exposure to
401 harsh environmental conditions and separation decreases, as suggested by Trudelle et al. (2016).

402 Photographic analysis showed that scarring and prevalence of wounds was not
403 significantly different between calves from the 2 sites. Injuries to newborns are inflicted by
404 males during reproduction in many species (Palombit 2015). Direct deadly injuring is rarely
405 observed in humpback whales, but there is proof for increased energy expenditure by calves in
406 the presence of adult males (Darling et al. 2006; Cartwright and Sullivan 2009b) and increased
407 strandings of calves in areas where the density of males is high (southern right whales, Elwen
408 and Best 2004). In New Caledonia, males have been observed trying to separate calves from
409 their mother in the South Lagoon and in the Southern Seamounts (C. Garrigue, personal
410 observation). Despite the high density of whales in the Southern Seamounts, calves did not bear
411 more scars there than in the South Lagoon. Interestingly, more females with a calf were

412 observed with a single escort in the Southern Seamounds than in the South Lagoon. Females in
413 oceanic habitats could therefore be avoiding male harassment and injuries to their calf by
414 seeking the protection of an escort as suggested in the 'bodyguard hypothesis' (Mesnick 1997).
415 However, the presence of a competitive group (MC-R) or an escort (MC-E) with the maternal
416 female did not seem to have an effect on the scarring of calves. As it is not possible to tell
417 whether the calves acquired scars from contacts with escorts, competitive males, or even
418 potentially from their mother, this study cannot provide further support in favor or against the
419 bodyguard hypothesis. Previous studies have demonstrated increased distance to the coast of
420 escorted mother-calf groups in several breeding grounds (Craig et al. 2014; Trudelle 2016).
421 Selecting a single escort (MC-E groups) in some contexts instead of remaining alone with her
422 calf (MC groups) could therefore be interpreted as an alternative strategy that allows the mother
423 to protect her calf from harmful interactions when the density of whales is high or the
424 environment does not include natural barriers to allow spatial avoidance of males (Cartwright
425 et al. 2012).

426 Prevalence of cookiecutter shark bites was not significantly different between the 2
427 study sites. Cookiecutter sharks are primarily found in tropical, deep off-shore waters (*Isistius*
428 *brasilensis*— Jahn and Haedrich 1988), though they may migrate vertically at night, moving
429 to the surface with the deep scattering layers (Heithaus 2001b). Despite the lack of ecological
430 data regarding the distribution of this ectoparasite, their predominant preference for waters
431 >1,000 m deep (Heithaus 2001b) has led to cookiecutter shark bites on cetacean being used as
432 proxies for time spent offshore (Wenzel and Suárez 2012; Best and Photopoulou 2016). Hence,
433 a higher prevalence of these marks is expected on calves that spent more time in oceanic habitats
434 during their ontogeny. The fact that this ecological marker was similar between our 2 sites
435 suggests a similar life-history for calves observed in the South Lagoon and the Southern
436 Seamounds. Photo-identification has indicated individual re-sights ($n > 30$) between these 2

437 breeding grounds within and between seasons (site fidelity indices, Garrigue et al. 2013;
438 probability of transitions, Orgeret et al. 2014). Satellite tracking also demonstrated that toward
439 the end of the breeding season many individuals (68% of tagged whales), including mothers
440 with a calf (50% of tagged maternal females), visited both the South Lagoon and Antigonina
441 seamount (Garrigue et al. 2015). These concordant results confirm that the humpback whales
442 observed in the South Lagoon and on the Southern Seamounts breeding grounds are part of the
443 same population.

444 Mothers with a calf must derive some form of benefit from using this relatively
445 inhospitable oceanic habitat. The Southern Seamounts are ecologically very different from most
446 humpback whale breeding grounds studied around the world (Garrigue et al. 2015). Similar
447 oceanic unsheltered breeding grounds have been described, namely Penguin Banks (Hawaii:
448 Baker and Herman 1981; Mobley et al. 1999) or Navidad Bank (Dominican Republic: Winn et
449 al. 1975; Mattila et al. 1989), but have been subject to less research due to their relative
450 inaccessibility. This peculiar habitat might provide unexpected advantages for maternal
451 females, at least towards the end of the breeding season. While predation is often considered a
452 major driver of species distributions, there is a paucity of data concerning the potential predators
453 of humpback whales in the area. Killer whales are known to attack calves of humpback whales
454 (Pitman et al. 2015), but the past and present intensity of this predation in breeding grounds is
455 debated (Clapham 2000b). Killer whales have been reported outside the New Caledonian
456 lagoon on 15 occasions since 1995 (Poupon 2010), and Mehta et al. (2007) have estimated that
457 31% of flukes photographed in New Caledonia bore killer whale rake marks. Killer whales have
458 never been observed in the South Lagoon nor in the Southern Seamounts, however, and never
459 in interaction with humpback whales. Avoidance of predation is therefore unlikely to be the
460 main factor driving the intense use of offshore seamounts by maternal females in New
461 Caledonia. Alternatively, 2 hypotheses may explain this space-use pattern: opportunistic

462 feeding grounds and staging grounds. Seamounts are known to be sites of large vertical water
463 excursions due to internal waves, together with vigorous turbulences and mixing, which in turn
464 leads to nutrient export or stimulation of biological production (Pitcher et al. 2008). These
465 enriched and dynamic waters trigger local trophic cascades (Morato et al. 2010) that humpback
466 whales could be using as opportunistic feeding spots (Stockin and Burgess 2005; Hann et al.
467 2016). Neither humpback whale feeding behavior nor defecation has ever been directly
468 observed in the Southern Seamounts to date, however (C. Garrigue, personal observation).
469 Alternatively, eddies and currents around these seamounts might provide navigational cues
470 connecting the South Lagoon to the southward migration routes. The Southern Seamounts could
471 constitute a staging ground before departure southward, where maternal females may
472 congregate with the rest of the population before initiating their migration south. In this
473 scenario, fewer whales would be found in the Southern Seamounts at the beginning of the
474 season than at the end. However, knowledge of use of the Southern Seamounts in the early
475 season is limited. Over the few days of survey conducted on the Southern Seamounts at the
476 beginning of July ($n = 5$), no females with a calf were observed (in 2001 and 2006, Table 1).
477 Additionally, as most whales were tagged in August and September, satellite tracking over the
478 Southern Seamounts only occurred at the end of the season (Garrigue et al. 2015). Though this
479 tracking showed movements in both directions between the South Lagoon and the Southern
480 Seamounts, it is not known whether females with a calf stop on the seamounts on their way to
481 the other breeding grounds, such as the South Lagoon, at the beginning of the austral winter.
482 Surveying the Southern Seamounts early in the breeding season is required to fill this data gap
483 in occurrence patterns of whales throughout the season, and acquire a more complete
484 perspective on use of these oceanic habitats by humpback whales.

485 Satellite tracking showed a marked preference by humpback whales for Antigonía
486 seamount and Torch Bank compared to other similar neighboring seabed structures (Garrigue

487 et al. 2015). Social interactions might partially drive this distribution (Clapham and Zerbini
488 2015) and the selection of the Southern Seamounts as congregation areas. Indeed, social
489 aggregation is commonly observed independently from surrounding environmental conditions.
490 The organization of humpback whales within their winter grounds has long been attributed to
491 a lekking system (Herman and Tavorga 1980), defined as a gathering of males engaged in
492 competitive or vocal and visual display to attract females. This concept has been elaborated on
493 by Clapham (1996) who suggested the term of a “floating lek” to reflect the absence of
494 territoriality in leks of humpback whales. There also can be more than one congregation spot
495 (referred to as “arenas”) for humpback whales within a given breeding ground (Herman 2016),
496 as observed in the New Caledonian region (Garrigue et al. 2017). However, the lek hypothesis
497 fails to explain why gravid and maternal females would also join the arenas, including the South
498 Lagoon and the Southern Seamounts. Natal philopatry has been put forward as an explanation
499 for movements of maternal females (Baker et al. 2013; Herman 2016), but the spatial scale of
500 this process is unknown: does it function across the arenas, such as the Southern Seamounts
501 versus South Lagoon, or the whole wintering ground, such as the New Caledonian region?
502 Furthermore, Dulau et al. (2017) suggested that the wandering behavior of maternal females,
503 who sometimes travel extensive distances with their newborn calf to visit several arenas, may
504 serve the maternal cultural transmission of breeding area geography. It is unlikely that this
505 reason alone could explain the large amount of time spent in the Southern Seamounts (Garrigue
506 et al. 2015) but it could partially drive transits between the South Lagoon and other breeding
507 locations in New Caledonian waters.

508 In conclusion, maternal female humpback whales displayed alternative and non-
509 exclusive space-use patterns: in coastal breeding grounds such as the South Lagoon, they
510 actively avoided other whales and specifically used shallow waters closer to the coast, whereas
511 in the oceanic habitat of the Southern Seamounts, they congregated with the rest of the

512 population and had no sheltered habitat available. Thus, maternal humpback whales
513 demonstrate flexible patterns of habitat use on their breeding grounds, contradicting the
514 paradigm that females obligatorily seek shelter from rough seas and males when nursing a
515 newborn calf. This finding has important conservation implications for spatial management
516 within the Natural Park of the Coral Sea, a large protected area covering most of New
517 Caledonia's economic exclusive zone. Further research into the mechanisms underlying
518 mother-calf presence around off-shore seamounts and shallow banks is needed to advise efforts
519 to protect these sensitive hot-spots.

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528 **SUPPLEMENTARY DATA**

529 **Supplementary data S1.** —R codes and additional information for PHRE and habitat modeling
530 of humpback whale distribution in New Caledonia.

531 **Supplementary data S2.** —Photographic analysis of humpback whale calves.

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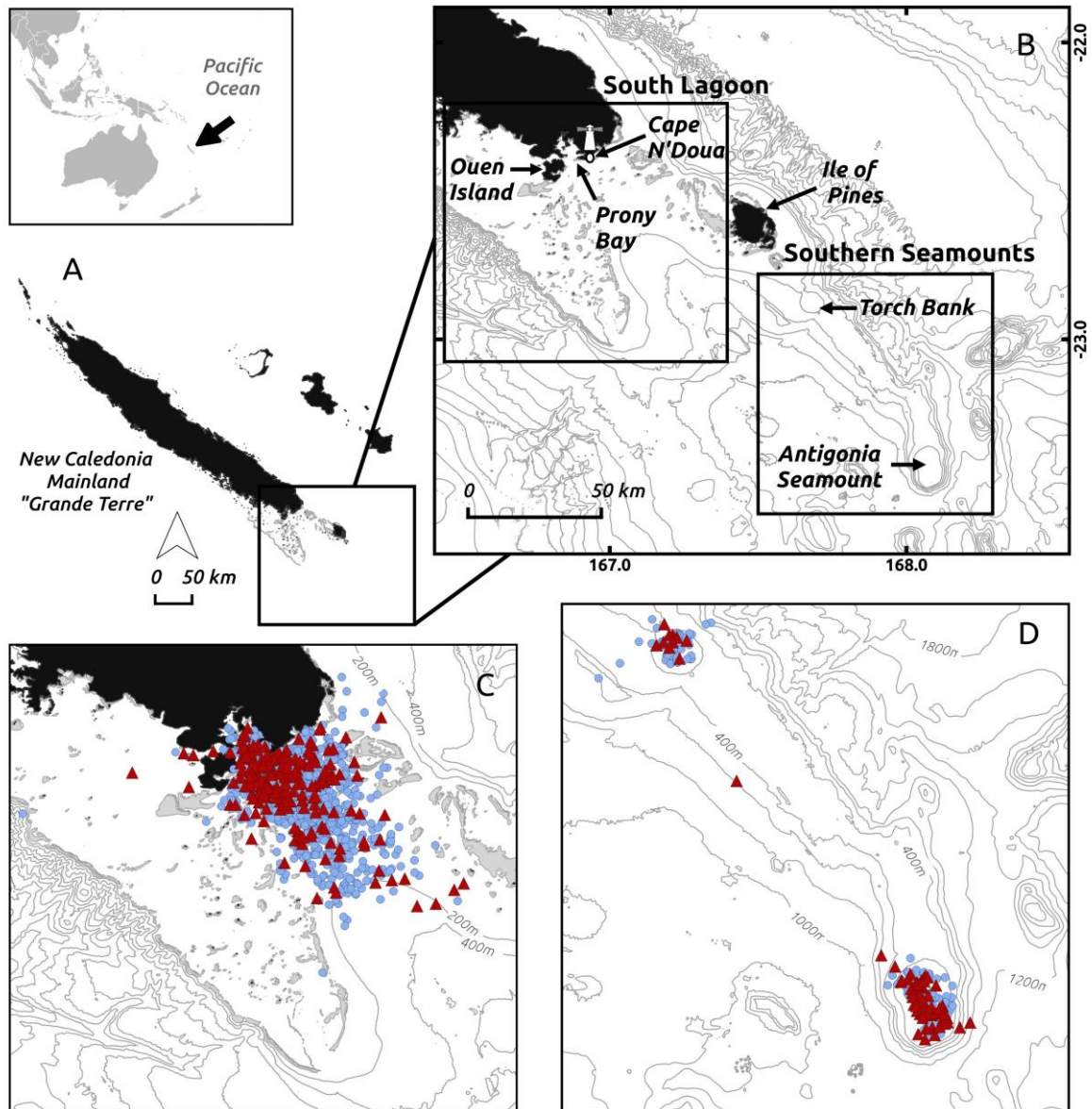
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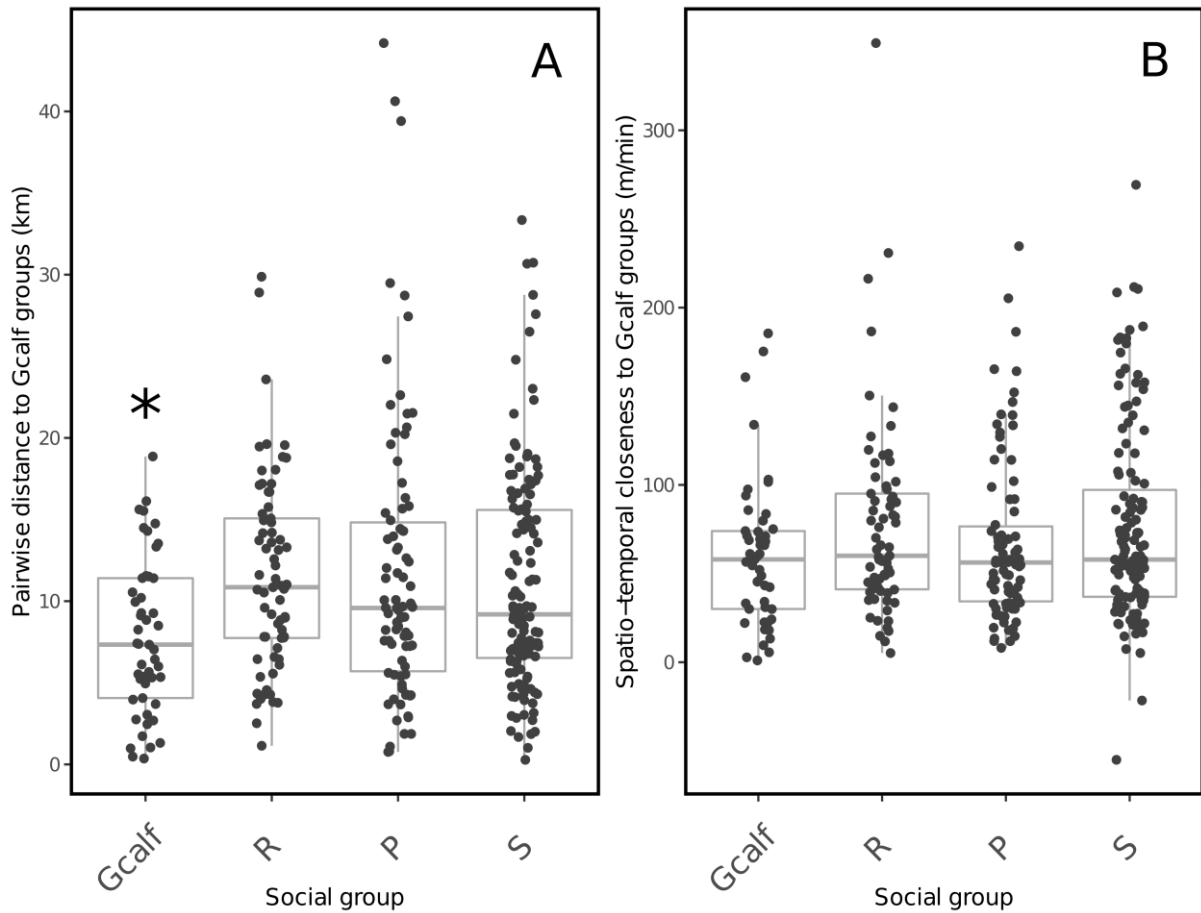
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782 **Fig. 1** Map of New Caledonia (A), study areas (B), and positions of humpback whale
783 (*Megaptera novaeangliae*) encounters in the South Lagoon (C) and Southern Seamounds (D).
784 Groups with a calf are shown with triangles and groups without a calf are shown with circles.
785 Light gray lines represent 200-m isobaths. Land is shown in black and reefs in gray.

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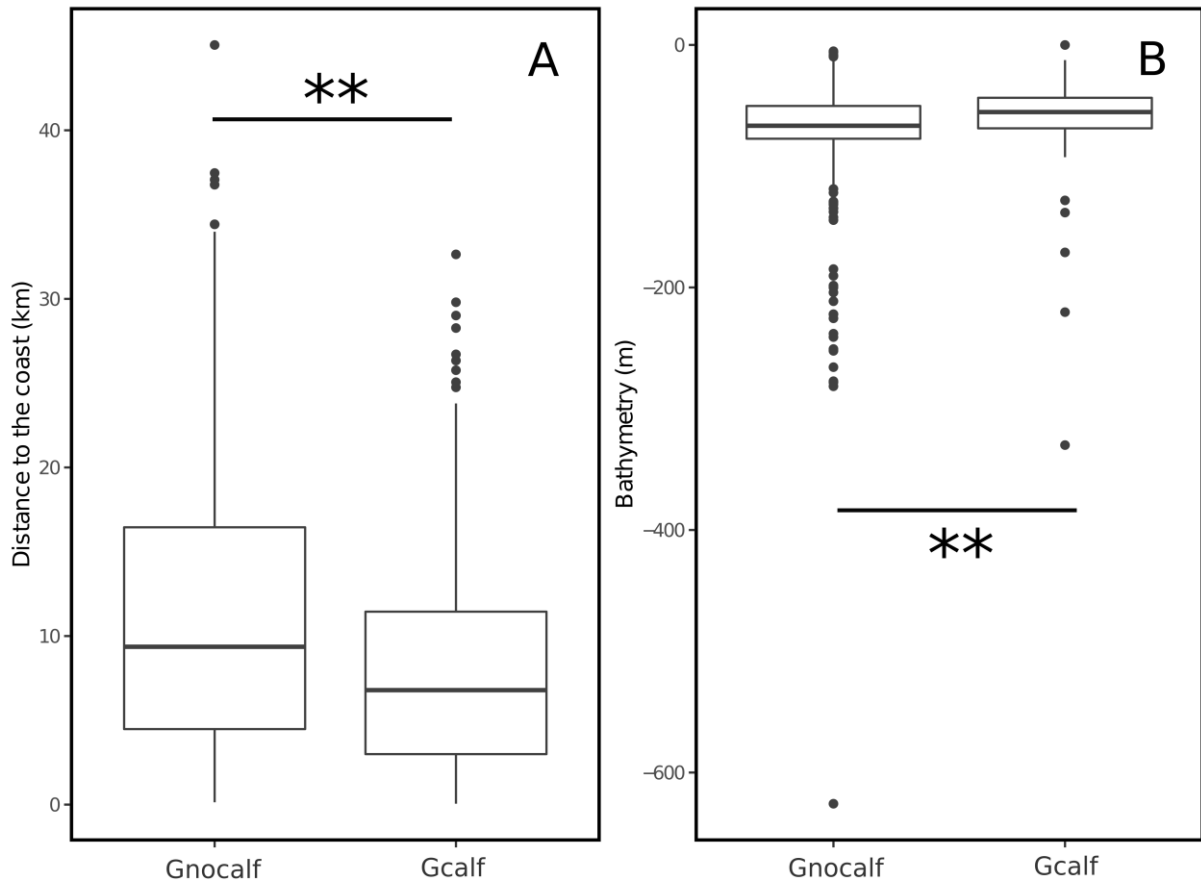
788 **Fig. 2** Daily pairwise distances (A) and spatio-temporal closeness (B) between humpback
 789 whale (*Megaptera novaeangliae*) groups with a calf and other social group types in the South
 790 Lagoon, New Caledonia ($n = 335$). Gcalf: groups with a calf, R: Competitive groups, P: Pairs
 791 of adults, S: Singletons. Raw distances are represented with jittered points directly on the
 792 boxes. Kruskal-Wallis tests show a significant difference across groups in (A) $X^2_3 = 12.4$, $P =$
 793 0.01 but not in (B) $X^2_3 = 3.5$, $P = 0.32$.

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799 **Fig. 3** Distance to the coast (A) and bathymetry (B) extracted at the humpback whale
 800 (*Megaptera novaeangliae*) group positions in the South Lagoon, New Caledonia, at the end of
 801 the season ($n = 646$) Gcalf: groups with a calf, Gnocalf: groups without a calf. Kruskal-Wallis
 802 tests show significant differences between groups in (A) $X^2_2 = 13.2$, $P < 0.001$ and (B) $X^2_2 =$
 803 16.5 , $P < 0.001$.

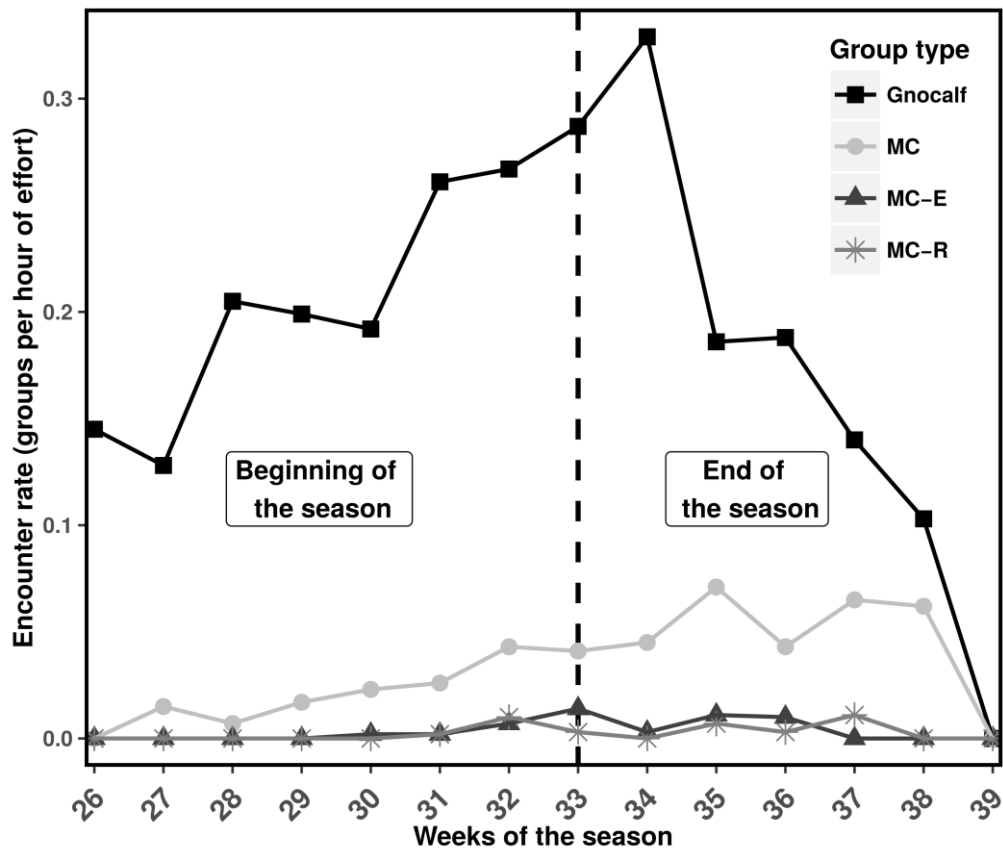
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810 **Fig. 4** Encounter rate (number of groups observed per hour of survey at sea, all years pooled
 811 together) by humpback whale (*Megaptera novaeangliae*) social group type in the South
 812 Lagoon, New Caledonia, across the breeding season. Calendar weeks are shown on the x-
 813 axis: August starts on week 31 and September starts on week 35.

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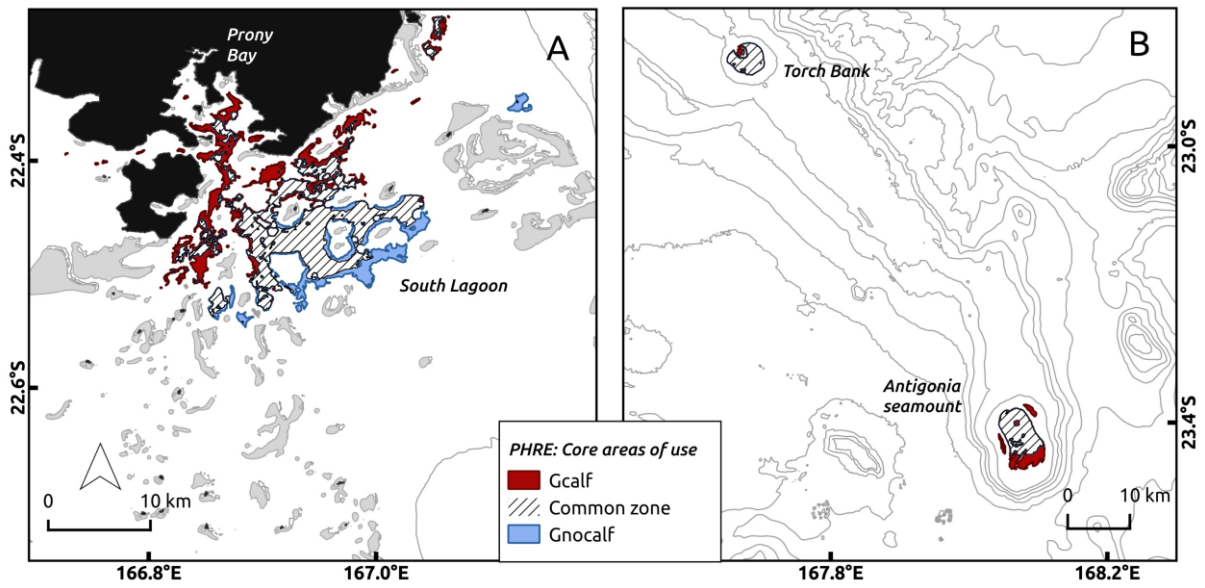
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821 **Fig. 5** Permissive Home Range Estimate (PHRE) calculated for humpback whale (*Megaptera*
 822 *novaeangliae*) groups with and without a calf in the South Lagoon (A) and the Southern
 823 Seamounts (B), New Caledonia. 50% contours of the PHRE are represented. The area of
 824 overlap between the 2 social group types is represented with black dashes. Light gray lines
 825 represent 200-m isobaths. Land is shown in black and reefs in gray.

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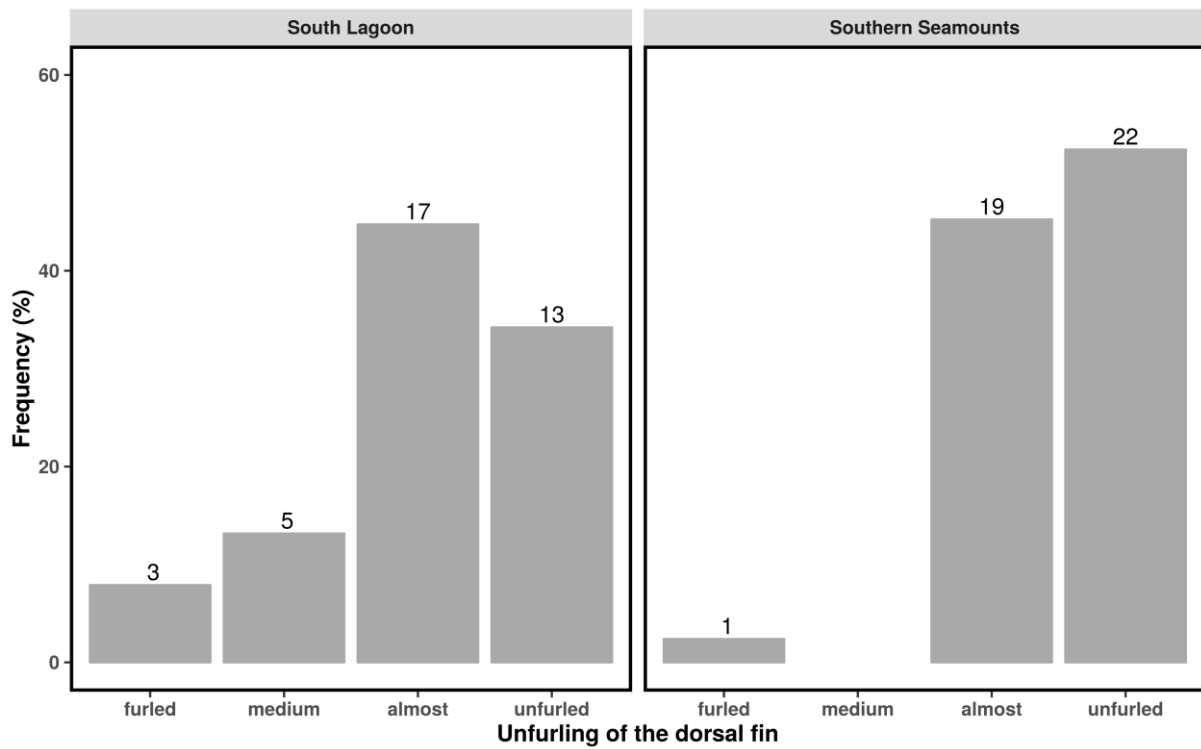
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835 **Fig. 6** Degree of unfurling of the dorsal fin for calves of humpback whales (*Megaptera*
 836 *novaeangliae*) observed in the South Lagoon ($n = 40$) and the Southern Seamounds ($n = 47$),
 837 New Caledonia, at the end of the season. Sample sizes are indicated on top of the bars. Dorsal
 838 fins are classified in an increasing order of unfurling from left to right. Pearson's Chi-square
 839 test shows significantly more advanced unfurling in the Southern Seamounds: $X^2 = 8.25$, $P =$
 840 0.03.

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848 **Table 1.** Survey effort and number (#) of groups of humpback whales (*Megaptera*
 849 *novaeangliae*) observed in the South Lagoon and the Southern Seamounts, New Caledonia.
 850 Gnocalf: groups without a calf, Gcalf: groups with a calf. *SD* = standard deviation.

	South Lagoon			Southern Seamounts		
	Days at sea	#Gnocalf	#Gcalf	Days at sea	#Gnocalf	#Gcalf
1995	27	20	4			
1996	55	46	10			
1997	44	46	5			
1998	50	41	3			
1999	46	18	8			
2000	45	34	8			
2001	40	47	3	1	2	0
2002	27	12	6			
2003	39	59	14			
2004	5	21	0			
2005	33	53	10	6	17	12
2006	41	92	9	3	14	0
2007	47	96	25			
2008				7	19	19
2009	32	65	5	5	22	9
2010	34	85	7	6	31	15
2011	38	110	22	6	35	19
2012	29	77	20			
2013	25	78	15			
2014	28	31	9			
2015	31	75	23			
Total	716	1106	206	34	140	74
Mean	35.8	55.3	10.3	4.5	20.0	10.6
<i>SD</i>	11.2	28.6	7.2	2.1	11.0	8.1

852 **Table 2.** Summary of the Generalized Additive Models describing presence of calves of
853 humpback whales (*Megaptera novaeangliae*) in the South Lagoon (SL) and Southern
854 Seamounts (SS), New Caledonia, at the end of the season. BIC: Bayesian Information
855 Criterion, Resid deviance = residual deviance, AUC = Area Under the ROC Curve, Z-stat =
856 Delong's Z-test statistic. Based on BIC, model 5 was selected as best model in the South
857 Lagoon. In the Southern Seamounts, no model outperformed the null model based on BIC.

Study site	Model	Predictors ^a	BIC	Res.dev	AUC	Delong's test Z-stat	Delong's test P-value
	Null	~1	652	646	0.500	0	1
SL	1	Dist_coast + dist_reef + bathy + slope	657	627	0.622	-4.49	<0.001
	2	Dist_coast + dist_reef + bathy	654	628	0.620	-4.41	<0.001
	3	Dist_coast + dist_reef	650	630	0.150	-4.20	<0.001
	4	Dist_coast + bathy	653	633	0.610	-3.98	<0.001
	5	Dist_coast	647	634	0.603	-3.71	<0.001
	Null	~1	281	276	0.500	0	1
SS	1	Bathy + dist_mount + slope + shading	297	274	0.510	0.23	0.82
	2	Bathy + dist_mount + slope	299	269	0.607	-2.06	0.01
	3	Bathy + dist_mount	299	269	0.607	-2.60	0.01

858 ^a dist_coast = distance to the coast, dist_reef = distance to the reef, bathy = bathymetric measure
859 of depth, dist_mount = distance to the center of the seamount, slope = seabed slope.

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865 **Table 3.** Mean proportions of social group types of humpback whales (*Megaptera*
866 *novaeangliae*) encountered in the South Lagoon and in the Southern Seamounts, New
867 Caledonia, at the end of the season. Gcalf: MC = mother-calf, MC-E = mother-calf-escort,
868 MC-R = mother-calf-competitive group. Gnocalf: groups with no calf (R, P, and S groups).
869 Mean proportions and the associated standard deviation (*SD*) are calculated on a sample of 20
870 years in the South Lagoon and 7 years in the Southern Seamounts.

	South Lagoon		Southern Seamounts	
	Mean %	<i>SD</i>	Mean %	<i>SD</i>
Gcalf	16.0	8.5	26.9	19.5
MC	17.3	10.2	10.0	9.8
MC-E	3.2	4.1	7.4	7.4
MC-R	0.9	1.6	9.3	7.3
Gnocalf	84.1	8.5	73.1	19.5

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