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Running header: Social segregation of humpback whales

Social segregation of humpback whales in contrasted coastal and oceanic breeding habitats

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Maternal habitat preferences of humpback whales (*Megaptera novaeangliae*) are well documented from decades of coastal research but oceanic areas have received less attention. Whales breeding in New Caledonia occupy both ecosystems: a coastal reef complex (South Lagoon) and oceanic seamounts (Southern Seamounts). Generalized Additive Models were applied to 20 years of boat-based whale observations (n = 1,526) to describe habitat preferences and Permissive Home Range Estimations were used to explicitly model spatial segregation in relation to social context. Groups with calves (n = 206) preferred shallow coastal waters throughout the season in the South Lagoon, whereas no habitat segregation was observed between groups with (*n* = 74) and without calves (*n* = 140) in the Southern Seamounts. As a result, spatial overlap between groups with and without calves was more common in the Southern Seamounts than the South Lagoon. Despite a lack of social segregation around seamounts, mother-calf pairs were proportionally more frequent in the Southern Seamounts (27%) than in the South Lagoon (16%). Photographs of the calves' dorsal flanks were analyzed to compare age and ecological markers across sites. Calves appeared older in the Southern Seamounts than in the South Lagoon but no difference in scarring nor shark bites was found across sites, suggesting that calves experienced similar lifestyles and may move between off-shore and coastal waters during the breeding season. This study highlights the flexible habitat use patterns of breeding humpback whales and raises new questions about the environmental and social drivers of their presence in off-shore breeding grounds.

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

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

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

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

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

MATERIALS AND METHODS

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

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

Antigonia Seamount and Torch Bank.— Antigonia seamount is located 170 km from the mainland, on the Norfolk Ridge, south of the South Lagoon, the Isle of Pines and Torch Bank (Fig. 1B). Torch Bank (167°41'W 22°51'S) and Antigonia (168°4'W 23°24'S) respectively culminate at 30 and 60 m deep, span about 48 km^2 and 98 km^2 (Gardes et al. 2014), and are surrounded by waters about 1,500 m deep. Presence of humpback whales in this area was first discovered using satellite monitoring: most whales tagged in the South Lagoon between August and September visited the Southern Seamounts (males and females, including maternal females) and remained there from several days to several weeks (see Garrigue et al. 2015 for further details). Boat-based surveys conducted subsequently in the area at the end of the breeding season confirmed the high density of humpback whales, compared to the South Lagoon (Garrigue et al. 2013; Orgeret et al. 2014, Garrigue et al. 2017).

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

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

A group was defined as a spatial aggregation of whales characterized by a social group type following the definitions of Clapham et al. (1992): groups of 3 or more individuals, involved in competitive behavior or not (R); mother with calf pair (MC); mother with calf followed by a single escort (MC-E); mother with calf followed by a competitive group (MC-R); pair of adults (P); and singletons (S). For each encounter, GPS position, time, social group type, minimum group size, and maximum group size were recorded. Due to the fluid social structure typically displayed by humpback whales in their breeding grounds (Clapham 1996), a few individuals may have been encountered more than once per survey day, if they moved to a new group with a different social type (for instance, a maternal female observed as a MC on one occasion, and later on the same day as a MC-E or a MC-R).

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

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

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

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

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

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

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

GAMs were applied with a binomial response type (presence or absence of a calf in a group), *logit* link function and maximum likelihood (ML) smoothing selector. Several models of decreasing complexity were fitted to our dataset and model selection was performed with a stepwise approach using the Bayesian Information Criterion (BIC; Schwarz 1978). BIC is a variant of the more commonly applied Akaike Information Criterion (AIC). It takes in account the number of observations included in the model and penalizes model complexity more heavily than AIC. The Receiver Operating Characteristic (ROC) curves were also calculated for each model and the corresponding Area Under the Curve (AUC) was reported in order to compare descriptive and predictive performance across models. AUC evaluates the model's capacity for binary classification: a random model has an AUC of 0.5 and a perfect model an AUC of 1 (Swets 1988). Delong's *Z*-test was applied to compare models to the AUC of the null model (Delong et al. 2016).

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

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

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

Photographic analysis was performed on pictures of the dorsal fins of calves encountered at the end of the season in the South Lagoon and in the Southern Seamounts, between 2007 and 2015. Only pictures with fair or better quality were retained in the analysis (quality assessment was based on focus, lighting conditions, proportion of the frame occupied by the animal, and angle of the animal relative to the sensor plane; following Towers et al. 2013). If a calf was encountered on several occasions, only the earliest encounter among those including good-quality pictures was retained.

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

RESULTS

In the South Lagoon, a total of 1,312 whale groups were encountered over 20 years of surveys (equivalent to 716 days of effort), of which 206 included a calf (16%, Fig 1.C). A total of 646 groups were observed at the end of the season (517 without a calf versus 129 with a calf). In the Southern Seamounts, 214 groups were observed over 7 years of surveys (equivalent to 34 days of effort), from which 74 included a calf (35%, Table 1, Fig 1.D).

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

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

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

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

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

Comparative habitat analysis between study sites.— In the GAM analysis of calf presence on the Southern Seamounts, none of the 5 models built with different combinations of environmental predictors outperformed the null model (lowest BIC = 281.3, Table 2). This indicates that there was no habitat segregation between groups with and without calf in the Southern Seamounts with respect to bathymetry, slope, distance to the center of seamounts, and shading.

After graphically comparing the maps of relative probability of presence generated by the PHRE set at different bandwidths, the unconstrained *Hscv* method was selected as the best candidate for our PHRE analysis. The relative probability of whale presence was mapped in a geographical coordinate system and the 50% probability contours were separately retrieved for each social type: Gcalf and Gnocalf (Fig. 5). The overlap of the PHRE core area between groups with and without a calf was higher in the Southern Seamounts (75%) than in the South Lagoon (59%). The core area of use for groups with a calf also was more than twice as small in the Southern Seamounts (63 km^2) than in the South Lagoon (139 km^2).

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

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

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

DISCUSSION

In this study, maternal female humpback whales displayed different space-use patterns with respect to other whales depending on whether they occupied coastal or oceanic habitat. In the South Lagoon, groups with a calf avoided contact with other con-specifics and occurred in higher proportion in waters nearest to the coast. This pattern of social segregation is consistent with studies in other humpback whale breeding grounds of the world that also found that mothers with a calf favor shallow coastal waters close to the coast or to reefs (Smultea 1994; Martins et al. 2001; Ersts and Rosenbaum 2003; Oviedo and Solís 2008; Félix and Botero-Acosta 2011; Craig et al. 2014; Guidino et al. 2014; Lindsay et al. 2016). This pattern has been observed in other cetaceans (i.e., southern right whale, *Eubalaena australis*— Rayment et al. 2015; Risso's dolphin, *Grampus griseus*— Hartman et al. 2014) and is thought to result from a need to 1) shelter from wind and currents (Félix and Botero-Acosta 2011; Rayment et al. 2015), and 2) avoid male harassment (Elwen and Best 2004; Craig et al. 2014). Indeed, lactating females and their offspring are constrained by a tight energy balance on their breeding ground and during the migration towards polar feeding grounds (Chittleborough 1958). Spatial segregation from other whales and sheltering are thought to be energy-saving strategies for females with a calf. Yet, in this study we show that females with a calf also occupy areas where neither of these 2 needs are fulfilled. In the Southern Seamounts, groups with a calf were found in greater proportion than in the South Lagoon, despite this area's lack of shelter or the possibility to spatially avoid adult males. In the Southern Seamount site, the core area used by groups with a calf strongly overlapped with the area occupied by the other whale groups.

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

Photographic analysis showed that scarring and prevalence of wounds was not significantly different between calves from the 2 sites. Injuries to newborns are inflicted by males during reproduction in many species (Palombit 2015). Direct deadly injuring is rarely observed in humpback whales, but there is proof for increased energy expenditure by calves in the presence of adult males (Darling et al. 2006; Cartwright and Sullivan 2009b) and increased strandings of calves in areas where the density of males is high (southern right whales, Elwen and Best 2004). In New Caledonia, males have been observed trying to separate calves from their mother in the South Lagoon and in the Southern Seamounts (C. Garrigue, personal observation). Despite the high density of whales in the Southern Seamounts, calves did not bear more scars there than in the South Lagoon. Interestingly, more females with a calf were observed with a single escort in the Southern Seamounts than in the South Lagoon. Females in oceanic habitats could therefore be avoiding male harassment and injuries to their calf by seeking the protection of an escort as suggested in the 'bodyguard hypothesis' (Mesnick 1997). However, the presence of a competitive group (MC-R) or an escort (MC-E) with the maternal female did not seem to have an effect on the scarring of calves. As it is not possible to tell whether the calves acquired scars from contacts with escorts, competitive males, or even potentially from their mother, this study cannot provide further support in favor or against the bodyguard hypothesis. Previous studies have demonstrated increased distance to the coast of escorted mother-calf groups in several breeding grounds (Craig et al. 2014; Trudelle 2016). Selecting a single escort (MC-E groups) in some contexts instead of remaining alone with her calf (MC groups) could therefore be interpreted as an alternative strategy that allows the mother to protect her calf from harmful interactions when the density of whales is high or the environment does not include natural barriers to allow spatial avoidance of males (Cartwright et al. 2012).

Prevalence of cookiecutter shark bites was not significantly different between the 2 study sites. Cookiecutter sharks are primarily found in tropical, deep off-shore waters (*Isistius brasiliensis*— Jahn and Haedrich 1988), though they may migrate vertically at night, moving to the surface with the deep scattering layers (Heithaus 2001b). Despite the lack of ecological data regarding the distribution of this ectoparasite, their predominant preference for waters >1,000 m deep (Heithaus 2001b) has led to cookiecutter shark bites on cetacean being used as proxies for time spent offshore (Wenzel and Suárez 2012; Best and Photopoulou 2016). Hence, a higher prevalence of these marks is expected on calves that spent more time in oceanic habitats during their ontogeny. The fact that this ecological marker was similar between our 2 sites suggests a similar life-history for calves observed in the South Lagoon and the Southern Seamounts. Photo-identification has indicated individual re-sights (*n* > 30) between these 2 breeding grounds within and between seasons (site fidelity indices, Garrigue et al. 2013; probability of transitions, Orgeret et al. 2014). Satellite tracking also demonstrated that toward the end of the breeding season many individuals (68% of tagged whales), including mothers with a calf (50% of tagged maternal females), visited both the South Lagoon and Antigonia seamount (Garrigue et al. 2015). These concordant results confirm that the humpback whales observed in the South Lagoon and on the Southern Seamounts breeding grounds are part of the same population.

Mothers with a calf must derive some form of benefit from using this relatively inhospitable oceanic habitat. The Southern Seamounts are ecologically very different from most humpback whale breeding grounds studied around the world (Garrigue et al. 2015). Similar oceanic unsheltered breeding grounds have been described, namely Penguin Banks (Hawaii: Baker and Herman 1981; Mobley et al. 1999) or Navidad Bank (Dominican Republic: Winn et al. 1975; Mattila et al. 1989), but have been subject to less research due to their relative inaccessibility. This peculiar habitat might provide unexpected advantages for maternal females, at least towards the end of the breeding season. While predation is often considered a major driver of species distributions, there is a paucity of data concerning the potential predators of humpback whales in the area. Killer whales are known to attack calves of humpback whales (Pitman et al. 2015), but the past and present intensity of this predation in breeding grounds is debated (Clapham 2000b). Killer whales have been reported outside the New Caledonian lagoon on 15 occasions since 1995 (Poupon 2010), and Mehta et al. (2007) have estimated that 31% of flukes photographed in New Caledonia bore killer whale rake marks. Killer whales have never been observed in the South Lagoon nor in the Southern Seamounts, however, and never in interaction with humpback whales. Avoidance of predation is therefore unlikely to be the main factor driving the intense use of offshore seamounts by maternal females in New Caledonia. Alternatively, 2 hypotheses may explain this space-use pattern: opportunistic feeding grounds and staging grounds. Seamounts are known to be sites of large vertical water excursions due to internal waves, together with vigorous turbulences and mixing, which in turn leads to nutrient export or stimulation of biological production (Pitcher et al. 2008). These enriched and dynamic waters trigger local trophic cascades (Morato et al. 2010) that humpback whales could be using as opportunistic feeding spots (Stockin and Burgess 2005; Hann et al. 2016). Neither humpback whale feeding behavior nor defecation has ever been directly observed in the Southern Seamounts to date, however (C. Garrigue, personal observation). Alternatively, eddies and currents around these seamounts might provide navigational cues connecting the South Lagoon to the southward migration routes. The Southern Seamounts could constitute a staging ground before departure southward, where maternal females may congregate with the rest of the population before initiating their migration south. In this scenario, fewer whales would be found in the Southern Seamounts at the beginning of the season than at the end. However, knowledge of use of the Southern Seamounts in the early season is limited. Over the few days of survey conducted on the Southern Seamounts at the beginning of July ($n = 5$), no females with a calf were observed (in 2001 and 2006, Table 1). Additionally, as most whales were tagged in August and September, satellite tracking over the Southern Seamounts only occurred at the end of the season (Garrigue et al. 2015). Though this tracking showed movements in both directions between the South Lagoon and the Southern Seamounts, it is not known whether females with a calf stop on the seamounts on their way to the other breeding grounds, such as the South Lagoon, at the beginning of the austral winter. Surveying the Southern Seamounts early in the breeding season is required to fill this data gap in occurrence patterns of whales throughout the season, and acquire a more complete perspective on use of these oceanic habitats by humpback whales.

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

In conclusion, maternal female humpback whales displayed alternative and non-exclusive space-use patterns: in coastal breeding grounds such as the South Lagoon, they actively avoided other whales and specifically used shallow waters closer to the coast, whereas in the oceanic habitat of the Southern Seamounts, they congregated with the rest of the population and had no sheltered habitat available. Thus, maternal humpback whales demonstrate flexible patterns of habitat use on their breeding grounds, contradicting the paradigm that females obligatorily seek shelter from rough seas and males when nursing a newborn calf. This finding has important conservation implications for spatial management within the Natural Park of the Coral Sea, a large protected area covering most of New Caledonia’s economic exclusive zone. Further research into the mechanisms underlying mother-calf presence around off-shore seamounts and shallow banks is needed to advise efforts to protect these sensitive hot-spots.

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SUPPLEMENTARY DATA

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

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

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FIGURES

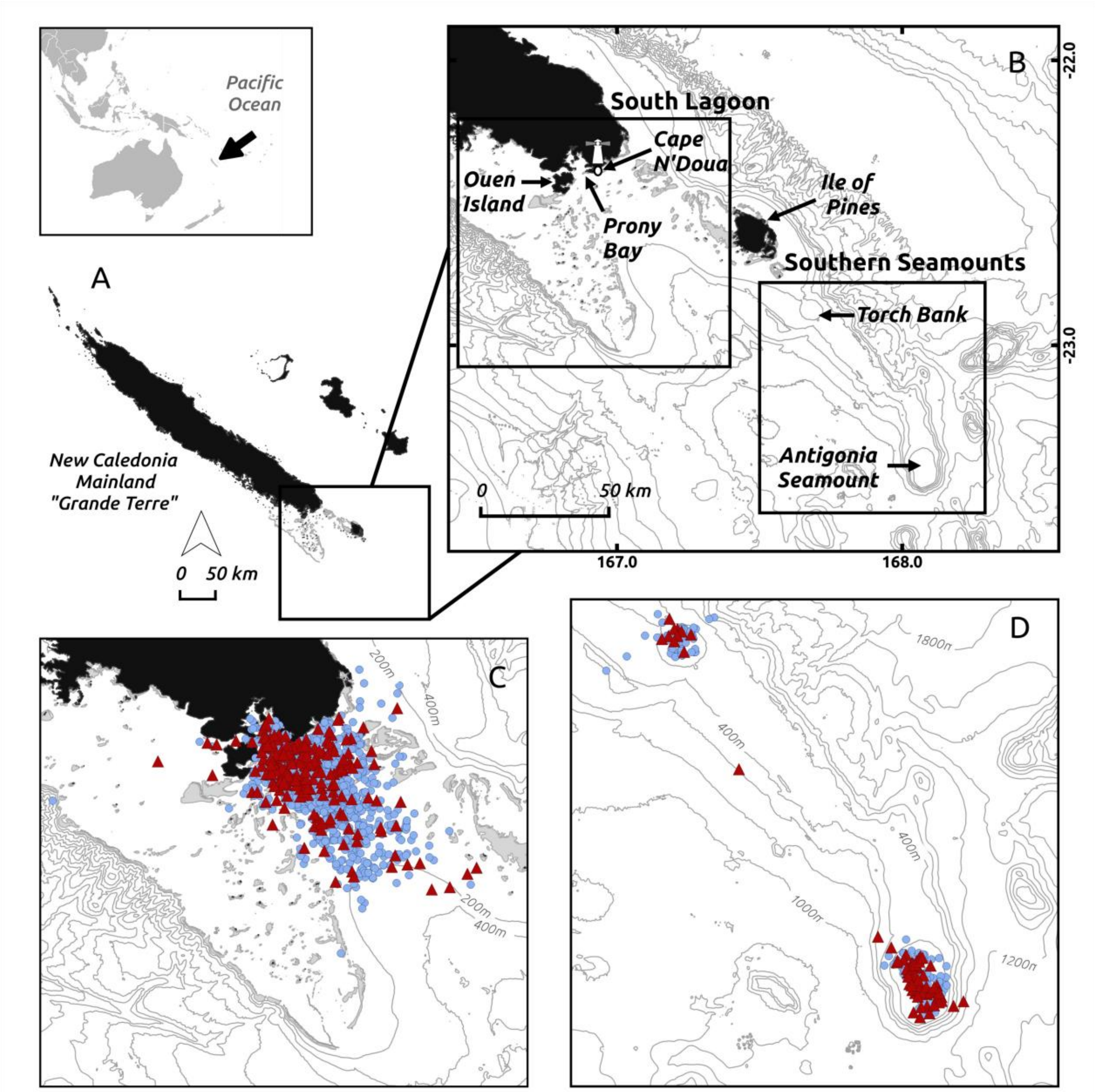

Fig. 1 Map of New Caledonia (A), study areas (B), and positions of humpback whale (*Megaptera novaeangliae*) encounters in the South Lagoon (C) and Southern Seamounts (D). Groups with a calf are shown with triangles and groups without a calf are shown with circles. Light gray lines represent 200-m isobaths.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

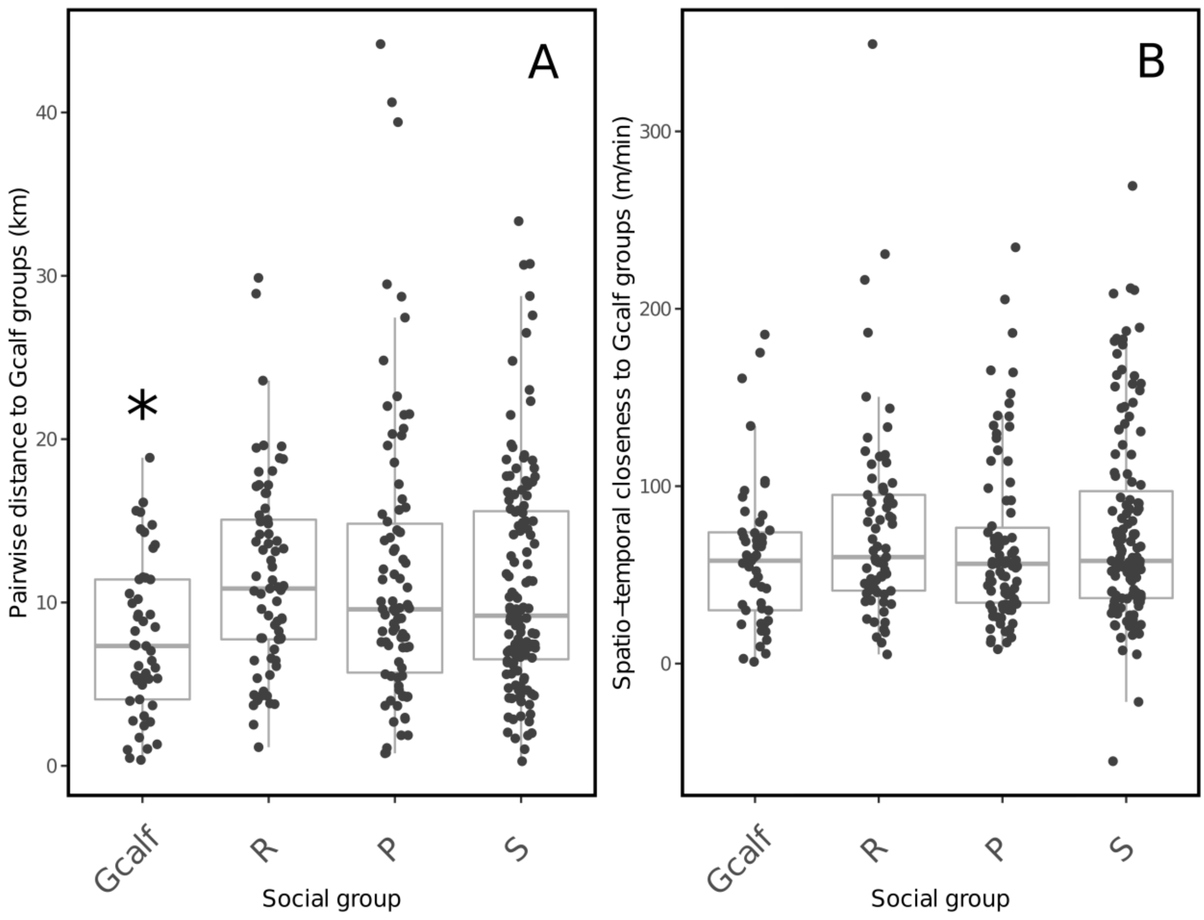

Fig. 2 Daily pairwise distances (A) and spatio-temporal closeness (B) between humpback whale (*Megaptera novaeangliae*) groups with a calf and other social group types in the South Lagoon, New Caledonia (*n* = 335). Gcalf: groups with a calf, R: Competitive groups, P: Pairs of adults, S: Singletons.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

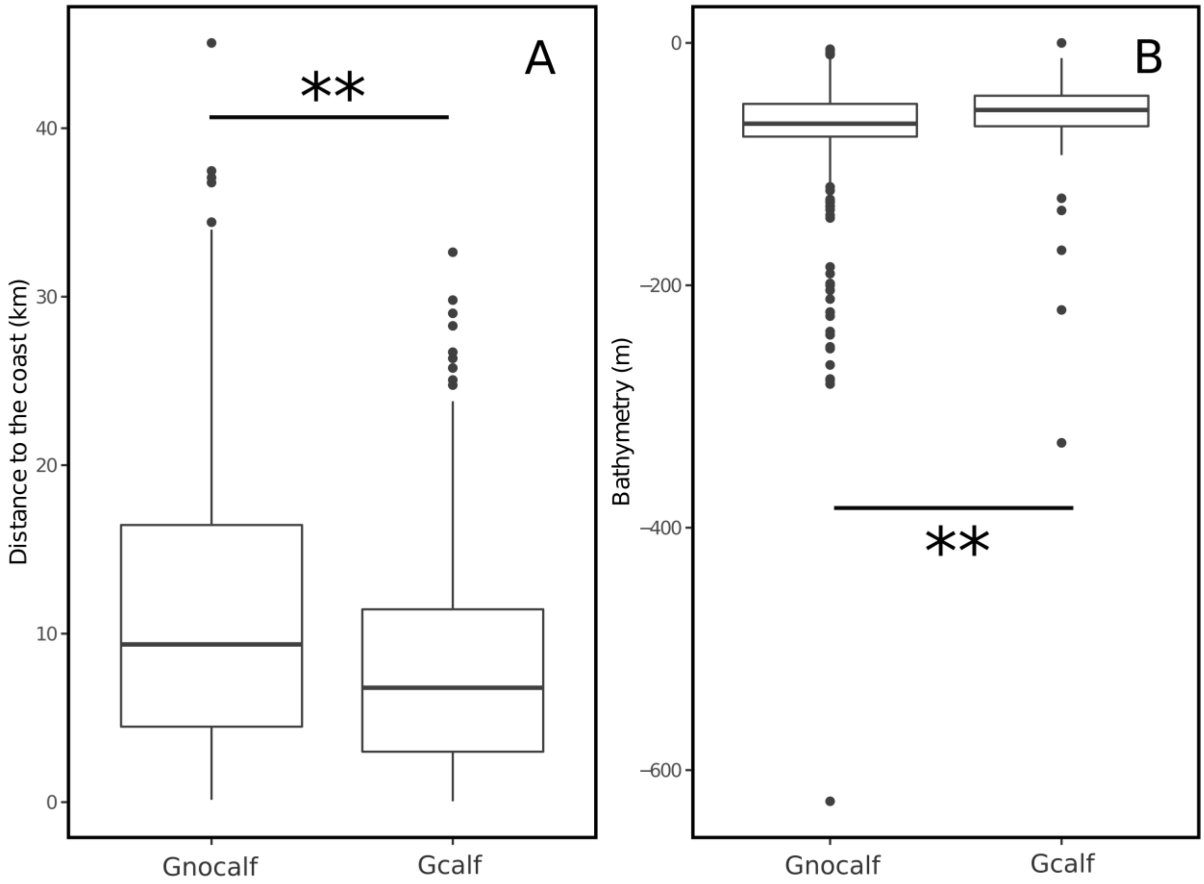

Fig. 3 Distance to the coast (A) and bathymetry (B) extracted at the humpback whale (*Megaptera novaeangliae*) group positions in the South Lagoon, New Caledonia, at the end of the season (n = 646) Gcalf: groups with a calf, Gnocalf: groups without a calf. Kruskal-Wallis tests show significant differences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

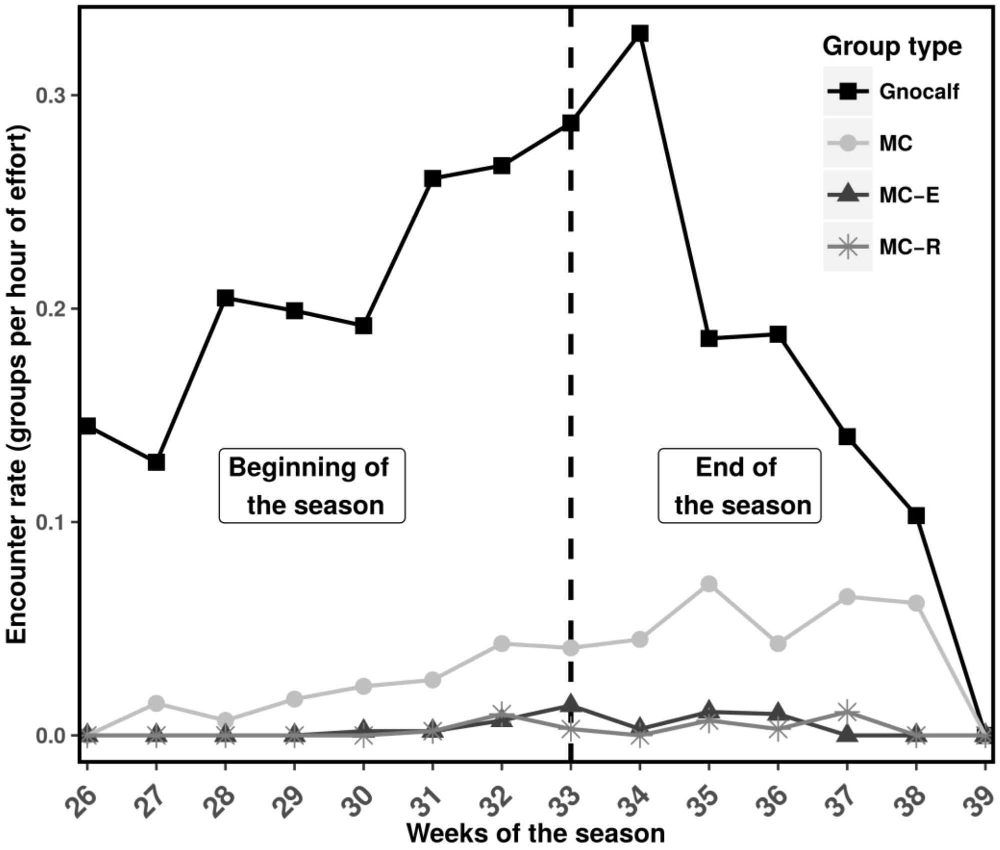

Fig. 4 Encounter rate (number of groups observed per hour of survey at sea, all years pooled together) by humpback whale (*Megaptera novaeangliae*) social group type in the South Lagoon, New Caledonia, across the breeding season. Calendar weeks are shown on the x-axis: August starts on week 31 and September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

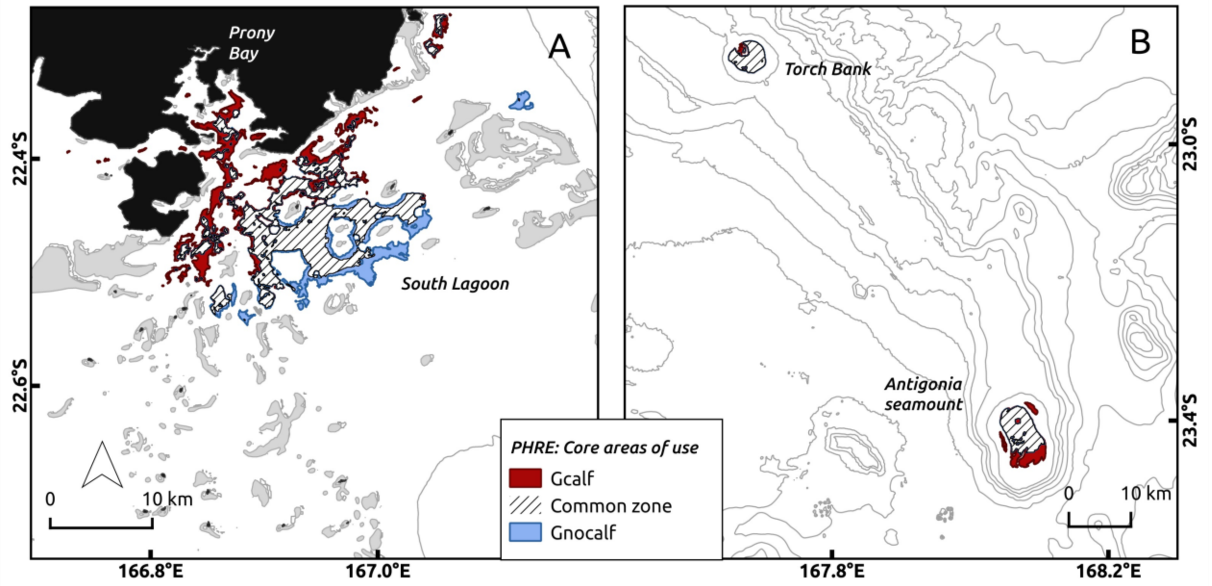

Fig. 5 Permissive Home Range Estimate (PHRE) calculated for humpback whale (*Megaptera novaeangliae*) groups with and without a calf in the South Lagoon (A) and the Southern Seamounts (B), New Caledonia. 50% contours of the PHRE are represented. The area of overlap between the 2 social group types is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

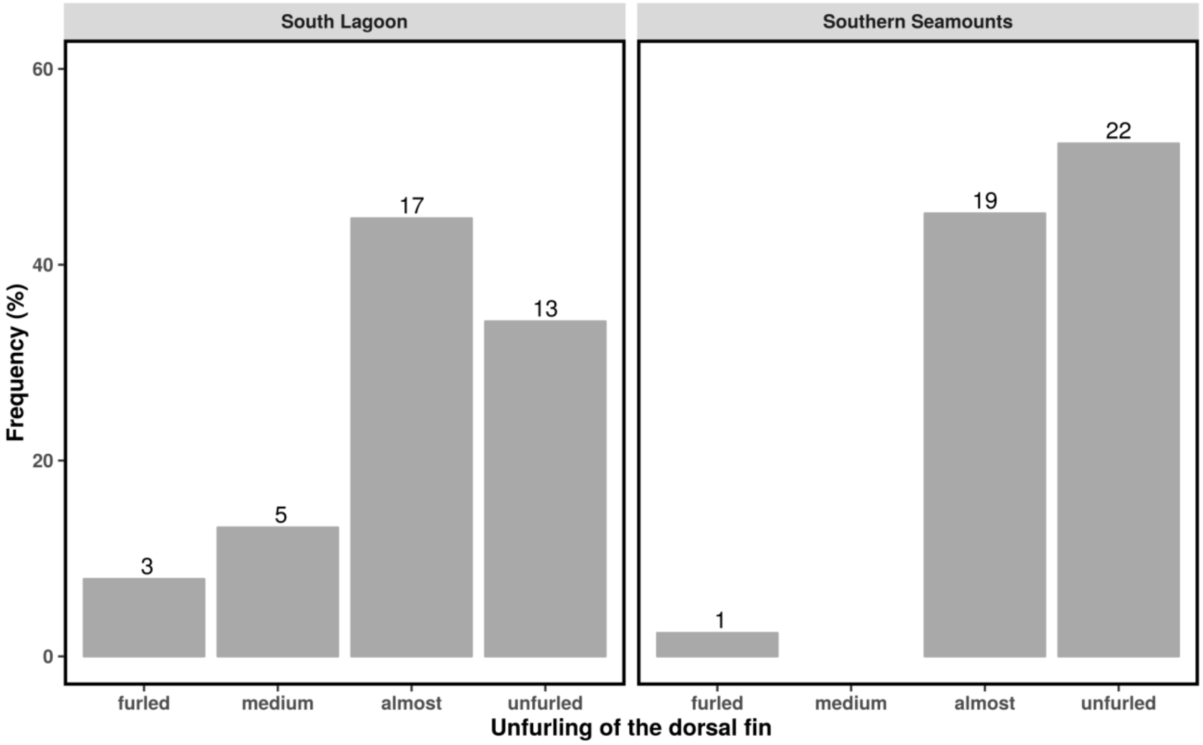

Fig. 6 Degree of unfurling of the dorsal fin for calves of humpback whales (*Megaptera novaeangliae*) observed in the South Lagoon (n = 40) and the Southern Seamounts (n = 47), New Caledonia, at the end of the season. Sample sizes are indicated on top of the bars. Dorsal fins are classified in an increasing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

TABLES

Table 1. Survey effort and number (#) of groups of humpback whales (*Megaptera novaeangliae*) observed in the South Lagoon and the Southern Seamounts, New Caledonia. 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
SD	11.2	28.6	7.2	2.1	11.0	8.1

Table 2. Summary of the Generalized Additive Models describing presence of calves of humpback whales (*Megaptera novaeangliae*) in the South Lagoon (SL) and Southern Seamounts (SS), New Caledonia, at the end of the season. BIC: Bayesian Information Criterion, Resid deviance = residual deviance, AUC = Area Under the ROC Curve, *Z*-stat = Delong's *Z*-test statistic. Based on BIC, model 5 was selected as best model in the South 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
SL	Null	~1	652	646	0.500	0	1
	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
SS	Null	~1	281	276	0.500	0	1
	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

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

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

		South Lagoon		Southern Seamounts	
		Mean %	*SD*	Mean %	*SD*
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