SC/66b/SH/03

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INTERNATIONAL
WHALING COMMISSION

FOR CONSIDERATION BY THE SCIENTIFIC COMMITTEE OF

THE INTERNATIONAL WHALING COMMISSION

Bled, Slovenia, June 2016

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

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ABSTRACT

Spatial segregation of humpback whale female and calf pairs has been observed in several breeding grounds around the world. These individuals tend to occupy shallow waters closer to the shore where other groups are less abundant. In New Caledonia, humpback whales seasonally visit two breeding grounds with very dissimilar environmental conditions: a large coastal reef complex (the South Lagoon) and an off-shore area of seamounts (the 'Southern Seamounts'), both located south of New Caledonia mainland. Boat-based observations of humpback whales collected between 1995 and 2015 (n=1,526) were combined to explore social segregation patterns in these two connected breeding grounds. Generalized Additive Models were applied to describe habitat relationships and Permissive Home Range Estimation were used to explicitly model spatial segregation resulting from these habitat preferences. In the South Lagoon, the number of groups with calves (n=206) increased throughout the season and these groups always preferred shallow waters close to the coast. On the contrary, no habitat segregation was observed between groups with (n=74) and without calf (n=140) in the Southern Seamounts. These habitat selection patterns resulted in a higher spatial overlap between groups with and without calf in the Southern Seamounts compared to the South Lagoon. Also, the proportion of groups with calf appeared higher in the Southern Seamounts (27%) than in the South Lagoon (16%). Photographs of the calves' dorsal flanks were analysed to compare age (based on unfurling of the dorsal and flank pigmentation) and ecological markers (scarring, fresh wounds and Cookiecutter shark bites) across sites at the end of the season. The dorsal fin of calves observed in the Southern Seamounts were significantly more unfurled, suggesting that females with older calves might be more likely to move to offshore, highly frequented areas. Nonetheless, no difference in scarring nor shark bites was found between the two sites, suggesting that calves observed in the South Lagoon and the Southern Seamounts have experienced similar lifestyles and might belong to a single population moving between off-shore and coastal waters south of New Caledonia mainland. This study highlights the behavioural plasticity of humpback whales in their habitat use patterns and raises new questions about the environmental and social factors driving the distribution of humpback whales in off-shore habitats.

KEYWORDS: HUMPBACK WHALES, PACIFIC OCEAN, BREEDING GROUND, HABITAT, MODELLING

INTRODUCTION

Space-use dynamics and habitat selection of mobile animals are driven by multiple needs 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 and this may result in changes in space-use patterns. These changes are very patent in migrating species such as humpback whales (*Megaptera novaeangliae*). Through their annual migrations from polar to tropical waters, the habitat of this species varies drastically (Clapham 2000). Calf survival currently appears as one of the primary drivers explaining the persistence of this behaviour through evolution. Given the lower predation rate due to a lesser killer whale abundance and the higher temperature of the water, calving in tropical to sub-tropical breeding grounds potentially increases the survival of the calves (Corkeron and Connor 1999). To date, many studies have focused on the behaviour of humpback whale females with calves in their breeding grounds. Due to their higher energy demand for calving, lactation and care for the young calf, they have a tighter energetic balance than other individuals (Chittleborough 1958) and are considered more at risk to human disturbance (Cartwright *et al.* 2012).

In several coastal or island breeding grounds of the world, female humpback whales with calves have been shown to avoid their con-specifics. This behaviour results in a spatial segregation of social groups, with mother-calf pairs preferentially occupying shallow waters <50m (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; Lindsay *et al.* 2016) and close to shore (around 1 to 2km in high islands: Hawaï, Frankel and Clark 2002; Antongil Bay, Madagascar, Ersts and Rosenbaum 2003; Osa Peninsula, Costa Rica, Oviedo and Solís 2008; and around 10km in low islands: Abrolhos Bank, Brazil, Martins et al. 2001; Ecuador, Félix and Botero-Acosta 2011) compared to other social groups.

However, less attention has been paid to oceanic breeding grounds in which no coastline nor reefs may constrain space-use. In the Coral Sea, such a breeding ground has been identified south of New Caledonia around Torch Bank and Antigonia Seamount (hereafter referred to as the 'Southern Seamounts'). These two seabed features are respectively located at 25 and 100km from the closest land (the Isle of Pines) along the Norfolk ridge. They are characterised by shallow depths (I.e. 30-60m) and rough sea state due to the lack of shelter from wind and currents. In austral winter, this area is used as a breeding ground by a small population of humpback whales connected to the well-known breeding ground of New Caledonia South Lagoon (Orgeret *et al.* 2014; Garrigue *et al.* 2015). This population has been monitored for more than two decades (Garrigue *et al.* 2001, 2015) and was recently reclassified as 'Endangered' in the IUCN Red List (Childerhouse *et al.* 2009). These seamounts seem to be used intensively by humpback whales moving from the South Lagoon, at least at the end of the breeding season, between the end of August and the end of September.

In this study, we focus on the space-use of humpback whale females with calf in two connected breeding grounds characterised by contrasting environmental conditions (coastal *vs* oceanic). We explore the patterns of geographical and environmental social segregation in the South Lagoon and in the Southern Seamounts throughout several breeding seasons. We hypothesise that social segregation will differ in these two breeding grounds and that age of calf and time of the season might influence their spatial behaviour.

METHODS

Study areas

New Caledonia is an archipelago located on the Norfolk Ridge, in the southwest Pacific Ocean about 1500km northeast of Australia (Fig. 1A). Unlike many Pacific islands, New Caledonia’s geography doesn’t result from recent volcanic activity but has a continental origin. Due to its geological history, this area displays original terrain and oceanographic features. Overall, the New Caledonian Economic Exclusive Zone (EEZ) spans over more than 1.4M km^2 and includes New Caledonia’s mainland, '*Grande Terre'*, several smaller islands (e.g. Isle of Pines, Loyalty Islands), remote reef complexes (e.g. Bellona-Chesterfield, Entrecasteaux) and seamounts (e.g. Antigonia seamount, Torch Bank). The mainland is surrounded by a large lagoon where depth averages 25m and is delimited by a barrier reef. Since 2014, 92% of the New Caledonian waters are included in the Natural Park of the Coral Sea, one of the largest Marine Protected Areas (MPA) in the world to date (Pala 2013).

New Caledonia South Lagoon – Located south of *Grande Terre,* the South Lagoon is a large shallow area (mean depth about 50m), bounded by the Prony bay and *Ile Ouen* to the north and by two reef complexes to the southwest and the northeast (Fig. 1B). The southeastern part of the lagoon is opened to the ocean and is characterized by deeper waters (reaching 600m deep under -22°54'S). This area constitutes the main humpback whale breeding ground known to date in the EEZ (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 two neighbour breeding sub-stocks of eastern Australia (E1) and Tonga (E3) (Olavarría *et al.* 2007). They visit the South Lagoon from the beginning of July to the end of September with a peak of abundance in mid-August (Garrigue *et al.* 2001, 2011).

Antigonia and Torch Bank – Antigonia seamount is located 170km from *Grande Terre*, on the Norfolk Ridge, in the continuity 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 60m deep and are surrounded by waters about 1500m deep. Presence of humpback whales in this area was first shown using satellite monitoring: many whales tagged in the South Lagoon between August and September visited the Southern Seamounts and remained there from several days to several weeks (Garrigue *et al.* 2015). Boat-based surveys conducted subsequently in the area confirmed the high density of humpback whales at the end of the breeding season (Garrigue *et al.* In Prep).

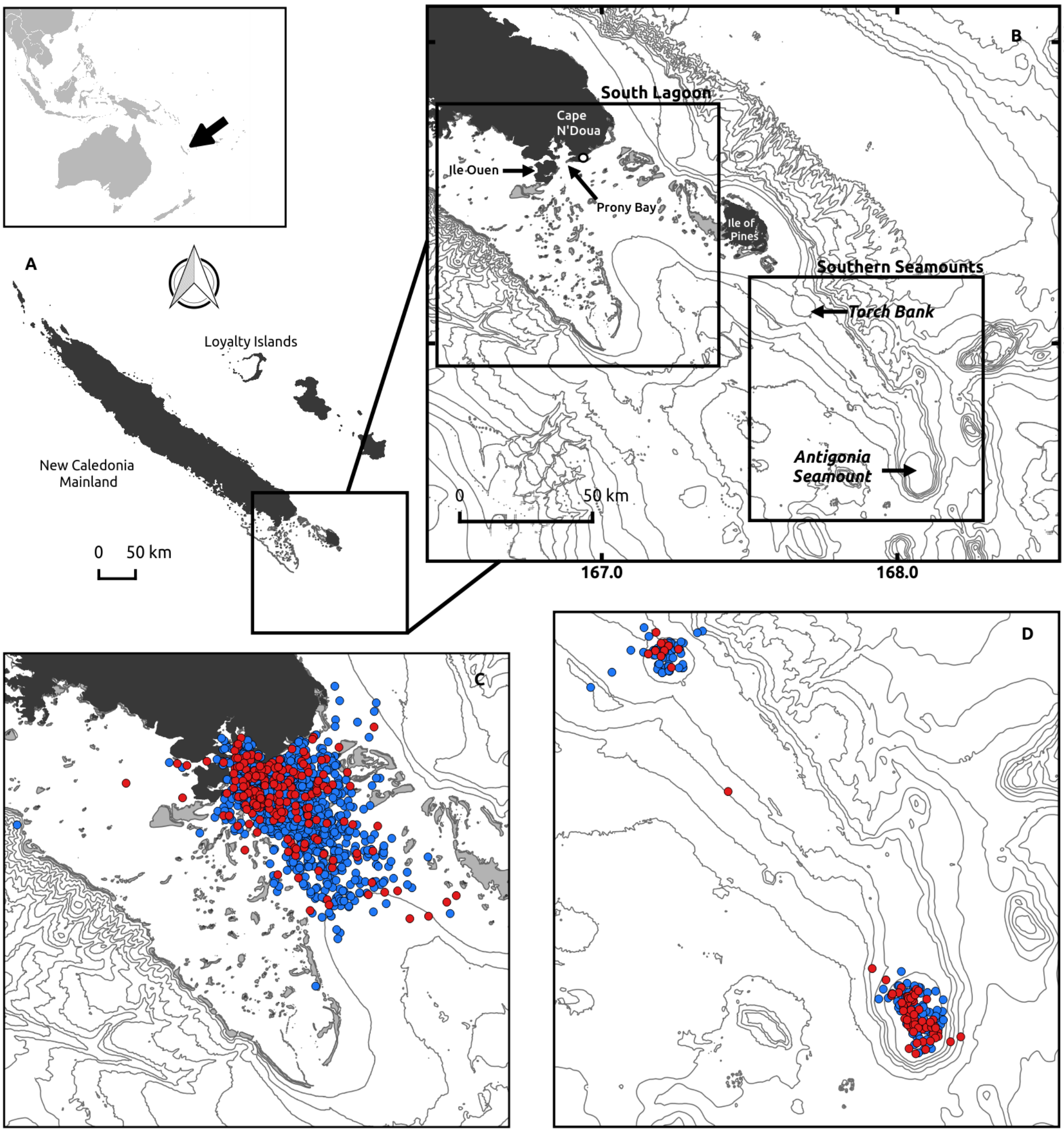

Figure 1: Map of New Caledonia (A), study areas (B) and positions of humpback whale encounters in the South Lagoon (C) and Southern Seamounts (D). Whale groups including a calf are shown in red and groups without calf are shown in blue. Light grey lines represent 200m isobaths. Land is shown in black and reefs in grey.

Data collection

Surveys were conducted from 1995 to 2015 in the South Lagoon and 2001 to 2011 in the Southern Seamounts (Table 1). They 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 six days of survey in Torch bank in July). For the purpose of this study, breeding seasons were therefore divided into two periods: the 'beginning of the season' from July to mid-August (i.e. calendar weeks 25 to week 32) and the 'end of the season' from mid-August to end of September (i.e. calendar weeks 33 to week 40).

Table 1: Total number of days of effort and total number of groups (#) observed in the South Lagoon and the Southern Seamounts. Gnocalf: groups without calf, Gcalf: groups with 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

Surveys did not follow a systematic or explicitly randomised sampling technique but rather a haphazard sampling regime (Corkeron *et al.* 2011). They were only initiated in Beaufort sea-states ≤3. In the South Lagoon, surveys were conducted from a 6m rigid-hulled inflatable boat and the search effort primarily focused on areas of known whale presence or logistically easier to survey. The team at sea was supported by a land-based team located at the Cape N'Doua, a 189m-high cape overlooking the study area (Fig. 1B). Teams could communicate at all times 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 rigid-hulled inflatable boat or a catamaran.

A group was defined as a spatial aggregation of whales characterised by a social type following the definitions of Clapham et al. (1992): competitive group (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 singleton (S). For each encounter, GPS position, time, social 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, especially in the Southern Seamounts where whales are densely aggregated. Yet, resighting rate was low enough for group encounters to be considered independent.

In the past decade, individuals were photographed with digital cameras CANON EOS 40D and 50D equipped with 70 X 300 mm lenses. For adults, photo-identification 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. They were therefore individually identified using the shape and markings of their dorsal fin. Insofar as possible, calves were photographed on both sides of their dorsal, with their body oriented perpendicular to the photographer. Tissue samples were collected on adult whales using a cross-bow with a specially adapted bolt (Lambertsen *et al.* 1994). Genomic DNA was extracted from these biopsy samples to identify sex (Gilson and Syvanen 1998).

Several environmental variables were collected in the study areas to characterise habitat use in grids at a 500m 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 500m*500m cell in the South Lagoon study area as the euclidean distance to the closest landmass (i.e. News Caledonia mainland, *Ile Ouen* or the Ile of Pines) and closest reef respectively. Bathymetry data was provided by the DTSI *'Service de la Géomatique et de la Télédetection'*, available on the *Georep* web depository (http://www.geoportal.gouv.nc [accessed Feb 2016]) at a 100m*100m resolution over both study areas. Two terrain features were derived from the bathymetry raster: slope and shading (metric combining orientation and inclination of the slope with respect to a southeast axis representing the dominant wind direction, Horn 1981).

Spatial analysis

Groups were classified into two categories: groups with calf (Gcalf) including MC, MC-E and MC-R social types, and groups without calf (Gnocalf) including R, P and S social types. Group encounters were georeferenced (Fig. 1C-D) and their positions were projected in a UTM coordinate system (UTM zone 58S).

Pairwise distance analysis - Euclidean distance was calculated between whale groups observed each day in the South Lagoon. The distributions of distance values were compared between groups with 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 use relationships – The probability of encountering a calf in a group was modeled with Generalized Additive Models (GAMs; Hastie and Tibshirani 1990) to assess the effect of distance to the coast (dist_coast), distance to reefs (dist_reef), bathymetry and seabed slope (see Supplement 1, Fig. S1A for more detail on predictor selection). First, this model was applied only to groups observed at the end of the season in the South Lagoon. Second, all observations recorded in the South Lagoon were combined to test for a potential effect of the time of season (i.e. included as calendar week of the year) on the space-use pattern of groups with calf. 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 top of the seamounts (dist_mount) and shading. GAMs were applied with a binomial response type (presence/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 penalises 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 categories may result in distinct patterns of spatial distribution. The core area of use for groups with or without 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 as in the GAM analysis were considered. Similarly to a traditional KDE, PHRE can be calculated with different smoothing parameters. Several methods exist to select the optimal bandwidth and three of them were tested: the plug-in bandwidth selector (*Hpi*), the least-square cross validation (*Hlscv*) and the smoothed cross-validation (*Hscv*) described in Duong (2007). The diagonal bandwidth matrix may also constrain the smoothing in directions parallel to the co-ordinate axes, thus two versions of each selector exists: unconstrained and diagonal. Here, the unconstrained smoothing was applied, as Duong (2007) reports better results with this method when data mass is largely oriented obliquely to the co-ordinate axes. Once the environmental hypervolume occupied by observations was identified, it was reprojected to latitude-longitude to create a map of relative probability of presence. We outlined 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 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 modelled using the *mgcv* R package and PHRE was based on a custom code by Tarjan and Tinker (2016).

Photographic analysis

Photographs of calves were used to detect eventual differences in age and ecological markers between the two study sites. Indeed, the approximative age of cetacean calves may be assessed from flank pigmentation (Hartman *et al.* 2015) and the degree of unfurling of the dorsal fin (Cartwright and Sullivan 2009b). A pale flank pigmentation (Chittleborough 1953) and a furled dorsal fin (Cartwright and Sullivan 2009b) are known neonate traits of humpback whales. As the calf grows, pigmentation darkens and the dorsal fin unfurls and these changes may be recorded within a breeding season (Cartwright and Sullivan 2009a). Also, scarring patterns are important ecological markers for cetaceans: they have been analysed in several species to study intraspecific interactions, predation, habitat use and migratory patterns (Heithaus 2001; 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 sp.*) 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 an indicator of pelagic habitat use (Wenzel and Suárez 2012; Towers *et al.* 2013; Best and Photopoulou 2016).

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 the pictures with fair quality were retained in the analysis (quality assessment being 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). Whenever a calf had been encountered on several occasions in a season, only the earliest encounter with best photographs was retained.

For each calf encounter, the following physical characteristics were recorded: flank pigmentation (very light/ light/ medium/ dark), unfurling of the dorsal fin (furled/ medium/ almost unfurled/ unfurled), scarring (none/ few scars/ medium/ many scars), presence/absence of fresh wounds, presence/absence of Cookiecutter shark bites, number of Cookiecutter shark bites. A manual describing and illustrating these characteristic was produced prior to the analysis and was used as a reference throughout the rating process (for more details on rating criteria, see Supplement 2). These physical characteristics were qualitatively rated “by eye” 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). Finally, physical characteristics were compared between South Lagoon and Southern Seamounts calves using Pearson's Chi-squared tests with simulated p-value (based on 2000 Monte-Carlo replicates).

RESULTS

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

Space-use in the South Lagoon

In the South Lagoon, the daily pairwise distances between groups with calf was significantly lower than between groups with calf and all other social groups without calf (Kruskal-Wallis test: Chi^2 = 12.45, df = 4, p-value = 0.01**, Fig. 2 left panel). Yet, when balancing these pairwise distances with the duration of the time interval between each observation, groups with calf no longer distinguished themselves from the rest of the population (Kruskal-Wallis test: Chi^2 = 3.55, df = 4, p-value = 0.47, Fig. 2 right panel). It appears that groups with calf spatially avoid all other groups, including other groups with calf.

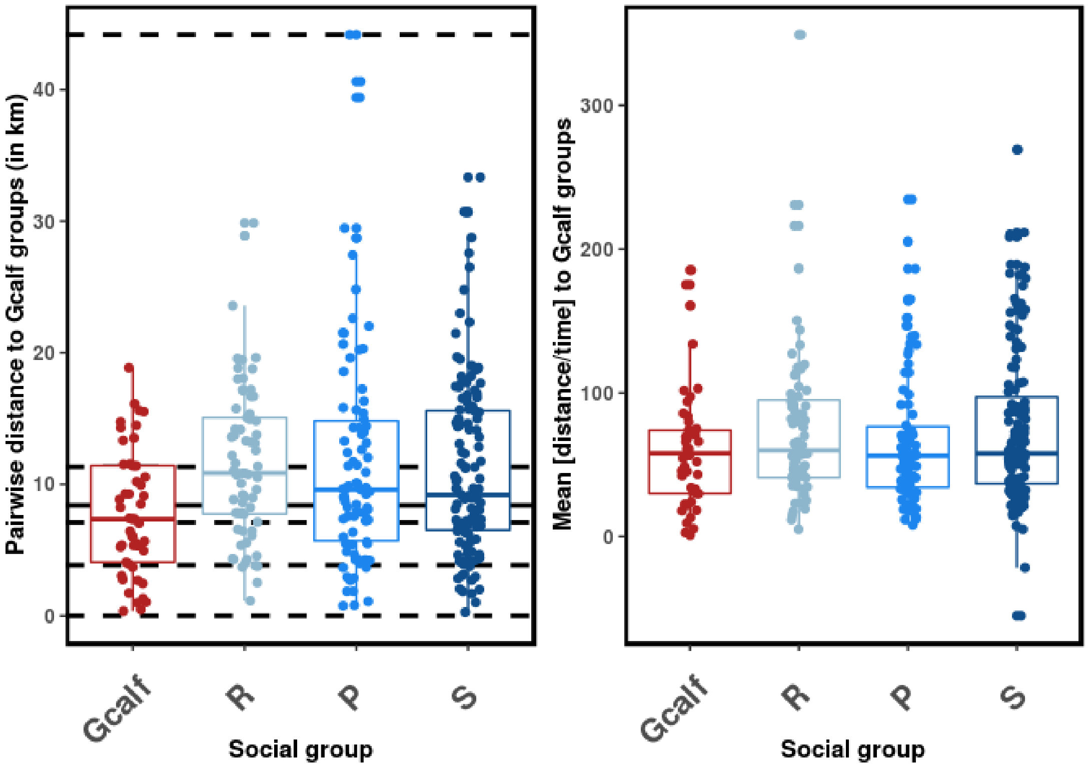

Figure 2: Daily pairwise distances (left panel) and spatio-temporal closeness (right panel) between groups with calf and other social types in the South Lagoon. Gcalf: groups with calf, R: Competitive groups, P: Pairs of adults, S: Singleton. G, P and S groups (in blue) don't include a calf. Black stripes in the background indicate the median pairwise distance (solid line) and quantiles (dashed lines) across the whole population.

Groups with calf observed at the end of the season were closer to the coast (Kruskal-Wallis test on dist_coast: Chi^2 = 13.21, p-value = 0.0003***) and in shallower waters (Kruskal-Wallis test on bathymetry: Chi^2 = 16.52, p-value = 4.82e-05***) compared to groups without calves in the South Lagoon (Fig. 3). This difference of habitat use relative to distance to the coast was also detected through the GAM analysis of group encounters at the end of the season (n = 646). The most simple 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 = -3.71, pvalue = 0.0002***). Bathymetry didn't appear like a significant predictor in either of the GAM models but this can be attributed to the strong correlation existing between dist_coast and bathymetry (Spearman coeff = -0.71, calculated on the full season sample n = 1,312).

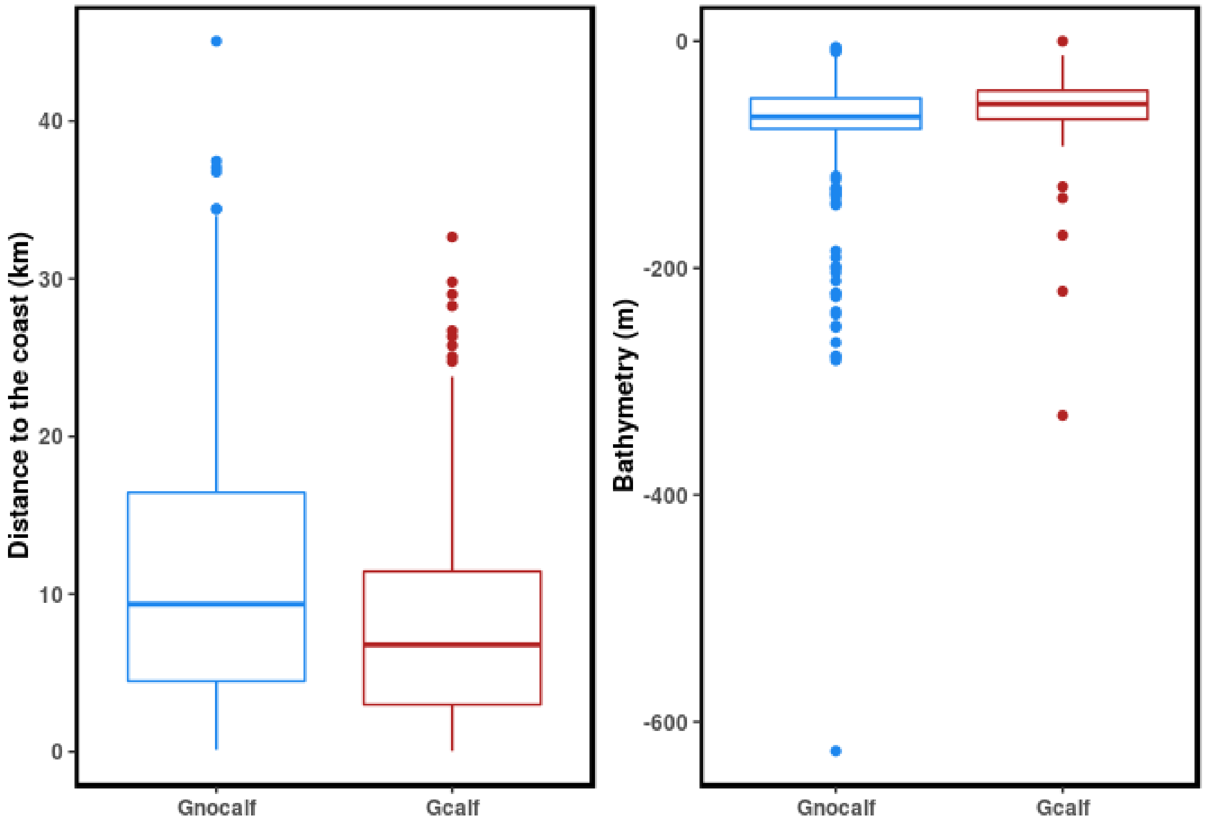

Figure 3: Distance to the coast and bathymetry extracted at the whale group positions in the South Lagoon at the end of the season (n = 646) Gcalf: groups with calf, Gnocalf: groups without calf.

Calf presence increased throughout the breeding season in the South Lagoon and closer to the coast. Indeed, in our 3-terms GAM analysis of group encounters over the whole season (n = 1,312), distance to the coast (Approximate significance of smooth terms: s(dist_coast) edf = 1,

Chi^2 = 19.54, p-value = 9.84e-06***) and week (Approximate significance of smooth terms: s(week) edf = 1, Chi^2 = 39.35, p-value = 3.55e-10***) were significant predictors of calf presence. The overall encounter rate peaked in the last week of August but the proportion of groups with calf and specifically of MC groups increased throughout the season and peaked in September (Fig. 4). Yet, calf presence was not driven by an interaction between dist_coast and week (Approximate significance of smooth terms: s(dist_coast,week) edf = 2.07e-05, Chi^2 = 0, p-value = 0.38), suggesting that despite the change in abundance of groups with calf along the breeding season, their habitat preferences remain the same.

Table 2: Summary of the Generalized Additive Models describing calf presence in the South Lagoon and Southern Seamounts 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. Shaded cells indicate best metric in each column. 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	BIC	Resid deviance	AUC	Z-stat	Delong's test p-value
South Lagoon	null	~ 1	652.4358	645.97	0.5	0	1
	1	dist_coast + dist_reef + bathy + slope	657.385	627.3	0.622	-4.49	6.98E-006
	2	dist_coast + dist_reef + bathy	654.093	628.21	0.62	-4.41	1.04E-005
	3	dist_coast + dist_reef	650.3508	630.94	0.615	-4.2	2.66E-005
	4	dist_coast + bathy	653.0492	633.64	0.61	-3.98	6.87E-005
	5	dist_coast	647.2078	634.26	0.603	-3.71	2.05E-004
Southern Seamounts	null	~1	281.3422	275.98	0.5	0	1
	1	bathy + dist_mount + slope + shade	297.1109	274.42	0.51	0.23	0.82
	2	bathy + dist_mount + slope	298.9733	268.68	0.607	-2.063	0.01
	3	bathy + dist_mount	298.971	268.68	0.607	-2.63	0.01
	4	dist_mount	290.9875	269.76	0.609	-2.64	0.01

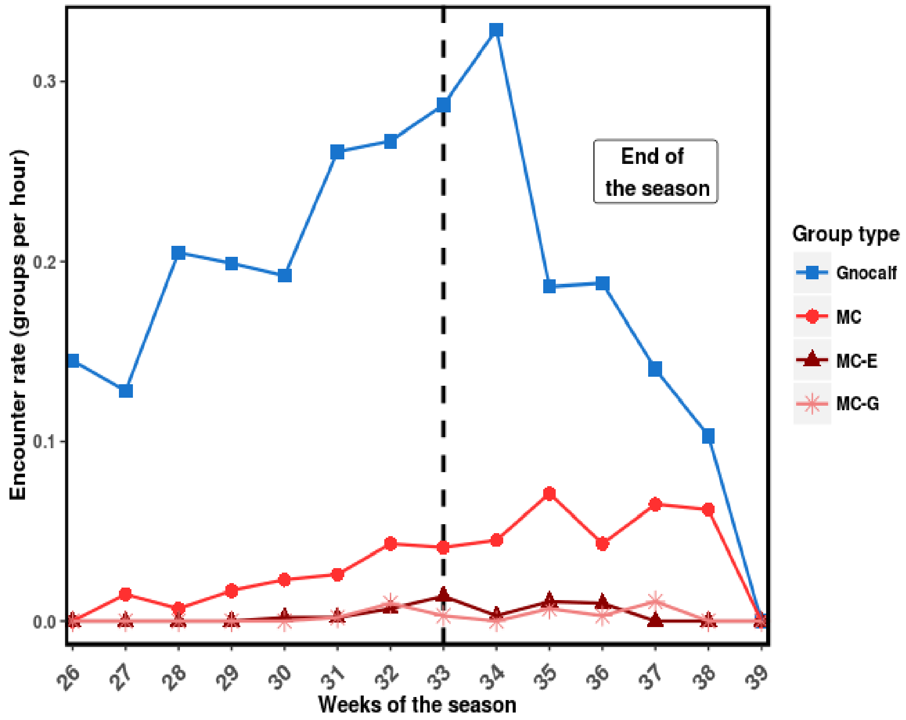

Figure 4: Encounter rate per social group in the South Lagoon (number of groups observed per hour of survey) along the breeding season. Calendar weeks are shown on the x-axis: August starts on week 31 and September starts on week 35.

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 = 281.34, 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 top of seamounts and shading.

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

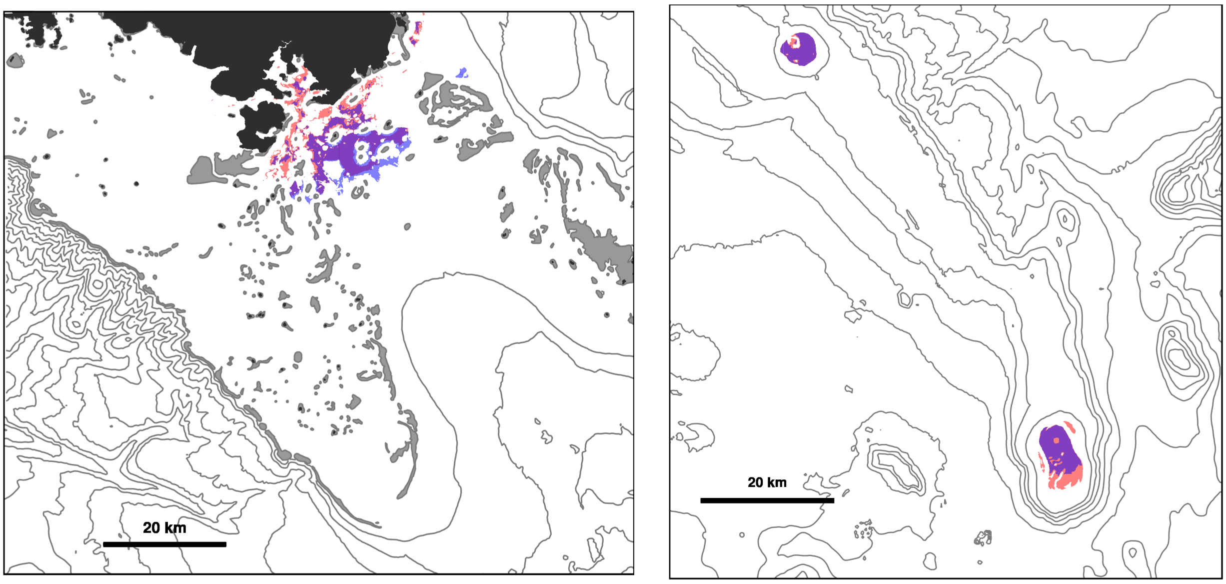

Figure 5: Permissive Home Range Estimate (PHRE) calculated for groups with (red) and without (blue) calf in the South Lagoon (A) and the Southern Seamounts (B). 50% contours of the PHRE are represented in transparent red and blue layers so that overlapping areas appear in purple. Light grey lines represent 200m isobaths. Land is shown in black and reefs in grey.

On average, groups with calf were more common in the Southern Seamounts than in the South Lagoon at the end of the season (South Lagoon: 26.9% +- SD 19.5, *vs* Southern Seamounts: 16.0% +- SD 8.5; Table 3) but this difference was not statistically significant (Kruskal-Wallis Chi^2 = 2.40, df = 1, p-value = 0.12). Groups with 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 (except for one female escort observed in 2007 in the South Lagoon).

Table 3: Mean proportions of social types encountered in the South Lagoon and in the Southern Seamounts 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		15.95	8.47	26.86	19.52
	MC	17.25	10.19	10	9.81
	MC-E	3.15	4.07	7.43	7.39
	MC-R	0.9	1.59	9.29	7.25
Gnocalf		84.05	8.47	73.14	19.52

Comparative photographic analysis between study sites

From a total of 180 encounters with groups with calf between 2007 and 2015, we selected a subset of 116 encounters that occurred at the end of the season. After deleting resights and poor pictures, the dataset was reduced to 40 calves in the South Lagoon and 47 in the Southern Seamounts. We found no significant difference in scarring, presence of fresh wounds, number of Cookiecutter shark bites, nor flank pigmentation between calves observed in the South Lagoon and the Southern Seamounts. Scarring also wasn't affected by the social group to which the calf belonged (MC, MC-E or MC-R; Pearson's Chi^2 test with 2000 Monte-Carlo simulations: Chi^2 = 6.12, p-value = 0.42). A significant difference was found in the degree of unfurling of the dorsal fin which was on average was more advanced in the Southern Seamounts (Pearson's Chi^2 test with 2000 Monte-Carlo simulations: Chi^2 = 8.25, p-value = 0.032*; Fig. 6).

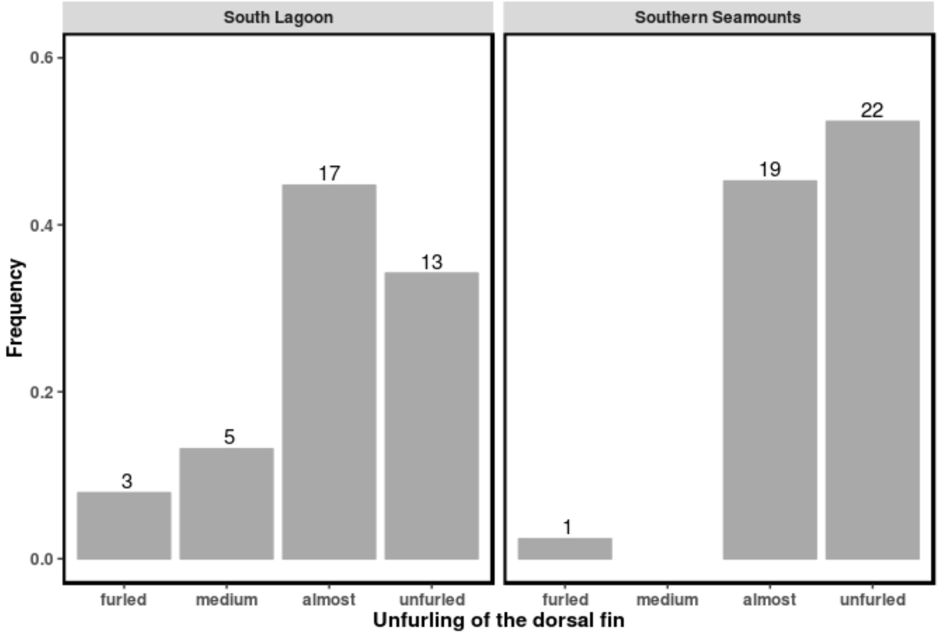

Figure 6: Degree of unfurling of the dorsal fin for calves observed in the South Lagoon and the Southern Seamounts at the end of the season. Sample sizes are indicated on top of the bars. Dorsals were classified in an increasing order of unfurling from left to right.

DISCUSSION

Photographic analysis showed that scarring and prevalence of wounds was not significantly different between calves from the two sites. Injuries to newborns are inflicted by males during reproduction in many species (Palombit 2015) but this has never been directly observed in humpback whales. Yet, there is proof for increased energy expenditure in the presence of adult males and increased strandings of calves in areas where the density of males is high (Cartwright and Sullivan 2009a; Craig *et al.* 2014). In New Caledonia, males have been observed trying to separate calves from their mother on several occasions (unpublished data). Despite the high density of whales in the Southern Seamounts, calves did not bear more scars there than in the South Lagoon. Interestingly, many females with calf observed in the Southern Seamounts were followed by a single escort. Females in oceanic habitats could therefore be avoiding male harassment and injuries to their calf by seeking the protection of an escort as stated in the 'bodyguard hypothesis' (Mesnick 1997). The prevalence of escorted mother-calf groups has actually been shown to increase with distance to the coast in several breeding grounds (Trudelle et al. In prep; Craig et al. 2014) and this change in social structure could be interpreted as an alternative strategy allowing the mother to protect her calf from harmful interactions when spatial avoidance of males is not possible (Cartwright *et al.* 2012). However, the relevance of the bodyguard hypothesis to humpback whales is debated (Craig *et al.* 2014) and in New Caledonia scarring of calves was not shown to decrease in presence of an escort.

In addition, prevalence of Cookiecutter shark bites was not significantly different between the two study sites. As Cookiecutter sharks are primarily found in tropical deep off-shore waters (*Isistius brasiliensis*, Jahn and Haedrich 1988), we would have expected a higher prevalence of these marks on calves which spent more time in oceanic habitats during their ontogeny (Wenzel and Suárez 2012; Best and Photopoulou 2016). Therefore, the fact that this ecological marker was similar between our two samples further suggests a similar life-history for calves observed in the South Lagoon and the Southern Seamounts. Photo-identification has already shown that many exchanges exist between these two breeding grounds (Orgeret *et al.* 2014). Satellite tracking also showed that towards the end of the breeding season many individuals, including mothers with calf, travelled between the South Lagoon and Antigonia seamount (Garrigue *et al.* 2015). These concordant results confirm that the humpback whales visiting the South Lagoon and the Southern Seamounts breeding grounds are likely part of the same population.

In the South Lagoon, groups with 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 which have found that mothers with calf favour shallow 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; Lindsay *et al.* 2016). This pattern has been observed in other cetaceans (i.e. southern right whale, Hartman et al. 2014; Risso's dolphin, Rayment et al. 2015)) 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 males (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 calf. Yet, we show that females with calf also occupy areas where none of these two needs are fulfilled. In the Southern Seamounts, groups with calf were found in greater proportion than in the South Lagoon, even if this area provides neither shelter nor the possibility to spatially avoid males. In this site, the core area used by groups with calf strongly overlapped with the area occupied by the rest of the population.

Our photographic analysis suggested that calves observed in the Southern Seamounts at the end of the season were older than the ones observed in the South Lagoon during the same period. It is not precisely known how long the dorsal fin of humpback whale calves takes to unfurl completely, and the rate of unfurling is likely to vary greatly between individuals. Also, our picture database is part of a long-term monitoring program and was not collected specifically for this purpose (Cartwright and Sullivan 2009b), thus caution is warranted in the interpretation of these results. Nonetheless, females could be less reluctant to visit unsheltered oceanic habitats such as the Southern Seamounts as their calf grows bigger and the risk of separation decreases.

Mothers with calf must find some form of benefit to using this inhospitable habitat. The Southern Seamounts are ecologically very different from most breeding grounds described over the world so far (Garrigue *et al.* 2015). Seamounts display peculiar oceanographic conditions such as internal waves, nutrient upwelling, eddies and frontal zones (Pitcher *et al.* 2008). This peculiar habitat might provide unexpected advantages for lactating females, at least towards the end of the breeding season. It is unlikely that whales use these seamounts as feeding spots since feeding behaviour has never been observed there (unpublished data) but eddies and currents formed around these seabed features might provide navigational cues connecting the South Lagoon to the southward migration routes. Antigonia and Torch Bank are the shallowest seamounts in the vicinity of the South Lagoon but this characteristic in itself is not sufficient to explain the high density of whales visiting these seamounts and their apparent absence in other seamounts of the region with similar bathymetric characteristics. A form of culture could be driving humpback whales to aggregate on the Southern Seamounts.

Aggregation is a commonly observed social behaviour which may occur independently from surrounding environmental conditions. In particular, humpback whales are not tied to resource constraints during their breeding season and their patterns of spatial distribution are likely to be constrained by social factors, for the most part (Clapham and Zerbini 2015). In the Southern Seamounts aggregations, humpback whales displayed intraspecific social interactions clearly linked to a reproductive behaviour (competition between males, escorting of females with calf etc.). Male songs were also very persistent in the area (Garrigue *et al.* In Prep). The Southern Seamounts could constitute a staging ground before departure to the southward migration and mothers with calves would aggregate there with the rest of the population before initiating their migration south. However, current knowledge is limited to the end of the breeding season and data is lacking to fully understand the role played by these oceanic habitats. The earliest known occurrence of a mother with calf in the seamounts comes from a female tagged 8 August 2010 in the South Lagoon and which reached Antigonia on 17 August. Future research should therefore focus on Southern Seamounts at the beginning of the breeding season in order to better understand the mysterious use of off-shore habitats by humpback whales in New Caledonia.

ACKNOWLEDGMENTS

We thank the volunteers for their technical support in the field and especially Rémi Dodemont, Marc Oremus and Véronique Pérard.

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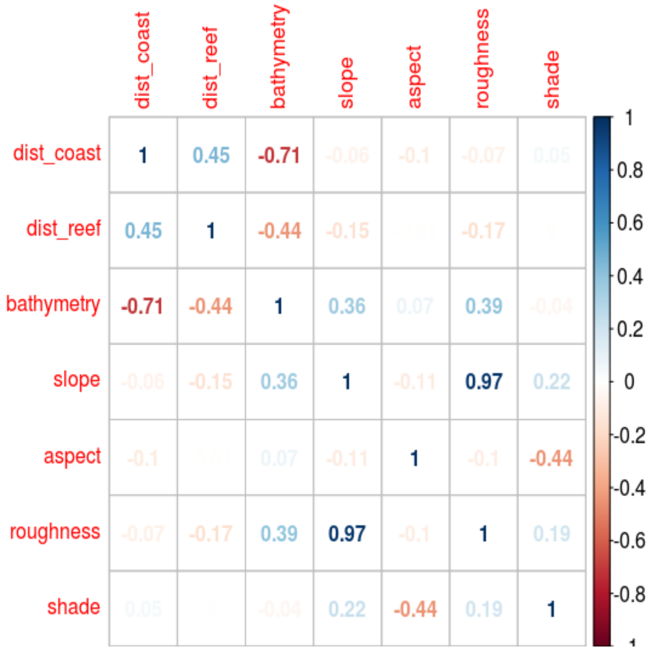
SUPPLEMENT 1: HABITAT USE

Correlation between environmental variables in the South Lagoon was assessed using the dataset composed of 1,312 positions. A correlation matrix was generated for all variables included in the GAM analysis (dist_coast, dist_reef, bathymetry and slope) as well as other variables derived from bathymetry: aspect (orientation of the slope in radians), roughness (difference between the maximum and the minimum value among the 8 surrounding cells) and shade (Fig. S1A). Due to the strong correlation between slope and roughness, we decided not to include the latter in the habitat use analysis for the South Lagoon. Moreover, aspect and shade where not strongly correlated to other variables in the South Lagoon, but they were extremely homogeneous over the study area and were therefore also pulled out of the analysis.



	dist_coast	dist_reef	bathymetry	slope	aspect	roughness	shade
dist_coast	1	0.45	-0.71	-0.06	-0.1	-0.07	0.05
dist_reef	0.45	1	-0.44	-0.15	-0.01	-0.17	0
bathymetry	-0.71	-0.44	1	0.36	0.07	0.39	-0.04
slope	-0.06	-0.15	0.36	1	-0.11	0.97	0.22
aspect	-0.1	-0.01	0.07	-0.11	1	-0.1	-0.44
roughness	-0.07	-0.17	0.39	0.97	-0.1	1	0.19
shade	0.05	0	-0.04	0.22	-0.44	0.19	1

Figure S1A: Correlation matrix between all environmental variables tested for inclusion in the Generalized Additive Models in the South Lagoon. Numbers correspond to Spearman correlation coefficient for each pair of environmental variables. dist_coast = distance to the coast, dist_reef = distance to the closest reef.

In the South Lagoon we tested several GAMs modelling calf presence (binomial response type) with time of the season (as calendar week) and distance to the coast. The aim of this analysis was to explore the potential changes in habitat selection throughout a breeding season. Week (s(week)) and distance to the coast (s(dist_coast)) were included as fixed effects to account for the average effect of week on calf presence and for their average habitat preference respectively. An interaction term (s(week,dist_coast)) was added to the model in order to account for an eventual change in the way calves distributed with respect to the coast along a season (e.g. if calves were preferentially found near the coast ONLY at the end of the season or ONLY at the beginning). Partial response plots (Fig. S1B) showed that calf presence increased with week and decreased with distance to the coast (top panels). However the interaction plot revealed that on average calves were positioned at the same distance to the coast all along the season (lower panel).

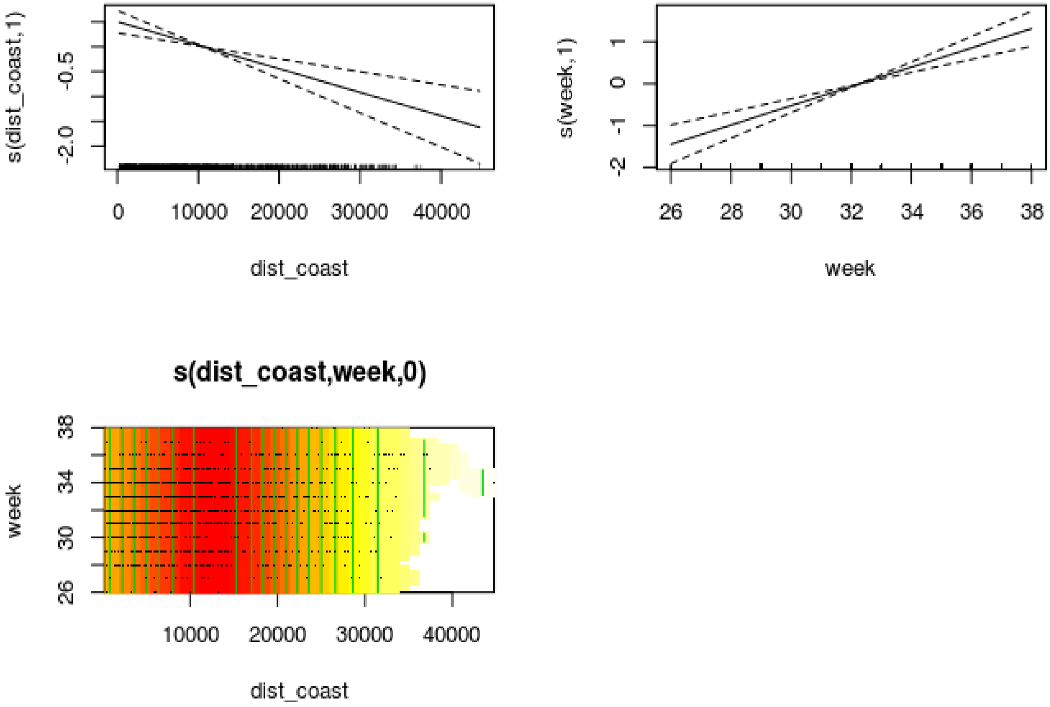


Figure S1B: Partial response for a GAM of calf presence relative to distance to the coast, week of the year and an interactive term. Probability of calf presence increases along the season and decreases with distance to the coast. The interaction plot shows no cross-effect of these two predictors on calf presence. Y-axis is on the logit scale.

SUPPLEMENT 2: PHOTOGRAPHIC ANALYSIS

Table S2A: Summary of parameters measured from the photographs of calves. We distinguish two types of parameters: characteristics used for age estimation (flank pigmentation and degree of unfurling of the dorsal fin: in increasing age order) and characteristics used to assess habitat use (scarring, presence of fresh wounds, presence of Cookiecutter shark bites).

Physical characteristics categorised as present or absent were only rated if both flanks of the calf had been photographed (presence of wounds and presence of Cookiecutter shark bites).

Age estimation				
flank pigmentation	dark	medium	light	very light
	entirely black/dark grey	light grey patches	entirely light grey or with white patches	entirely white or very light grey
furl of dorsal fin	unfurled	almost unfurled	medium	furled
	Angle 0°	Between 0° and 15°	Between 15° and 45°	Between 45° and 90°
Habitat use estimation				
scarring	none	few scars	medium	many scars
	no visible scars	<10 and superficial	>10 and <20, some scars may be deeper	>20, both sides are almost covered by scars, superficial and deep
wounds	present	absent		
	A wound is different from a simple scar in that it is deeper and th			
Cookie-cutter marks	present	absent		
	Circular marks as described in Best and Photopoulou 2016. If both sides of the dorsal are not visible, cookie-cuts are considered present but are not counted.			