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Searching for humpback whales two centuries post-whaling: what is left in the Chesterfield-Bellona archipelago?

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Searching for humpback whales two centuries post-whaling: what is left in the Chesterfield-Bellona archipelago?

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ABSTRACT

Humpback whales were severely depleted by commercial whaling, and understanding key factors of their recovery is a crucial step for their conservation worldwide. In Oceania, the Chesterfield-Bellona archipelago was identified as one of the primary humpback whale whaling sites of the 19th century. However, given its remoteness, it has remained almost unaffected by anthropogenic activities since then. In this study, we report on the first large-scale multidisciplinary dedicated surveys conducted in the Chesterfield-Bellona breeding area to assess the current status of its humpback whale population, two centuries post-whaling. In 2016 and 2017, two surveys were conducted, totalizing 24 days of effort and 57 groups encountered, among which 13 whales were identified though photo-id, 16 through genotyping and 22 with both methods. A total of 6 whales were equipped with satellite tracking devices. Though humpback whales still appear to visit the area during austral winter, especially the inner shallow waters of the reef complex and the neighbouring off-shore shallow banks, their density was relatively low (0.041 whales/km surveyed on average). Surprisingly for a breeding area, the sex ratio was very skewed towards females (1:2.8). A large proportion of the groups encountered included a mother and calf (45%), especially in the most sheltered waters south of the Chesterfield plateau. Photo-IDs and genetic comparisons suggest a strong connectivity with the New Caledonian South Lagoon breeding area. Although no match was detected to-date with the Australian Great Barrier Reef, a connectivity with the South East Australian migratory corridor is suggested by the tracking of three females (including one with calf).

INTRODUCTION

Large whales have been severely depleted by commercial whaling in the 19th and 20th centuries (Clapham 2016). Among them, humpback whale populations of the South Hemisphere have been decimated to reach only 1% of their pre-exploitation population sizes (more than 210,000 whales taken between 1904 and 1972 (Baker & Clapham 2002); The whaling moratorium and the local conservation efforts have allowed the partial recovery of most populations, with the exception of the Arabian Sea and the Oceanian breeding stocks that remain endangered under the IUCN red list (Childerhouse et al. 2009). Indeed, the humpback whale breeding population of Oceania was estimated to be the least abundant of the Southern Hemisphere by (Constantine et al. 2012).

The Chesterfield-Bellona plateaus are located about halfway between the East Australian coast and the New Caledonia mainland, in the Coral Sea. Along with Tonga, this area has been identified as one the two hotspots targeted by 19th century commercial whaling of humpback whales in the South Pacific (Townsend 1935). Logbooks (Townsend 1935), wrecks (http://museemaritime.nc/fortunesdemer/naufrages) and remains of whaling stations (Guillou 1983) attest to an intense whaling activity (Oremus & Garrigue 2014), hence suggesting that humpback whales were abundant in these reefs at the time. Though scientific surveys and opportunistic sightings have reported the presence of humpback whales in the area (Gill et al. 1995, Oremus & Garrigue 2014), the current status of the population visiting the Chesterfield-Bellona plateau is unknown. To date, there is no estimate of the number of whales still using this breeding area. Also, conservation actions greatly depend on whether the Chesterfield-Bellona humpback whales belong to the New Caledonia endangered sub-stock, to the healthy East Australian one or form a largely separate breeding population.

Moreover, while humpback whales are known worldwide for their coastal distribution during the breeding season, satellite tracking has recently highlighted the use of oceanic shallow seabed features, far from any land (Kennedy et al. 2014, Garrigue et al. 2015, Dulau et al. 2017). Offshore breeding areas have also been reported (Dominican Republic - Navidad bank, (Mattila et al. 1989); Hawaii -Penguin Bank, (Mobley et al. 1999), especially in New Caledonia, one of the only places where dedicated surveys have been conducted on remote seamounts and banks (Garrigue et al. 2017, Derville et al. 2018). Satellite tracking, genetics and photo-identification conducted in the region all suggest that humpback whales move between different breeding spots, over one or multiple seasons (Orgeret et al. 2014, Garrigue et al. 2015, Garrigue et al. 2017). At a larger scale, population dynamics and genetics analysis conducted in the Oceanian and East Australian regions also highlighted potential exchanges and longitudinal migrations across Oceania and Australia (Valsecchi et al. 2010, Garrigue et al. 2011, Clapham & Zerbini 2015, Steel et al. 2017). In this context, studying the connectivity between the Chesterfield-Bellona archipelago and the neighbouring coastal and oceanic breeding areas would fill in a knowledge gap in our understanding of the population structure and trends as well as of the South Pacific migratory system.

Finally, New Caledonia has recently created the Natural Park of the Coral Sea, which covers 1.3 million km^2, equivalent to 95% of New Caledonian waters (Decree GNC:2014-1063). This decision was taken in concert with Australia, as an international effort following a recent trend in marine conservation which aims at protecting both coastal and pelagic ecosystems within giant Marine Protected Areas (giant MPAs; Pala, 2013). Describing preferential habitats and space use patterns of species are key steps towards the management of protected areas, yet there is a paucity of data in remote and pristine waters of the Park, such as the Chesterfield-Bellona archipelago.

Estimating the current status of humpback whales in the Chesterfield-Bellona plateaus therefore appears both a local conservation challenge, and a key step towards better understanding the habitat use and regional movement patterns of humpback whales within breeding latitudes. Using a multidisciplinary approach combining photo-identification, genetic analysis, acoustics, habitat modelling and satellite telemetry, this study aims at 1) estimating whether humpback whales still occupy the Chesterfield-Bellona archipelago during the breeding season, 2) exploring the habitats and activities of humpback whales in this offshore reef complex, and 3) investigating the connectivity between the Chesterfield-Bellona whales and neighbouring stocks of New Caledonia and East Australia.

METHODS

Study area

The Chesterfield-Bellona archipelago lies in the Coral Sea between the East Australian coast and New Caledonia (Figure 1). It is approximately dated to 25 Mya (Missègue & Collot 1987) and constitutes one of the largest atolls in the world (Ceccarelli et al. 2013), covering about 16,000 km^2. The shallow plateaus (0-80m) are surrounded by reefs, small islets and sand cays that form sheltered lagoons, though most of the area remains

largely open to the Coral Sea. Several shallow banks (0-30 m) are found between the two plateaus, as well as along the Lord Howe seamount chain extending south of Bellona. For the purpose of this analysis, the study area is divided in three ecoregions: the Bellona plateau, the Chesterfield plateau and the banks located between the two plateaus (Figure 1).

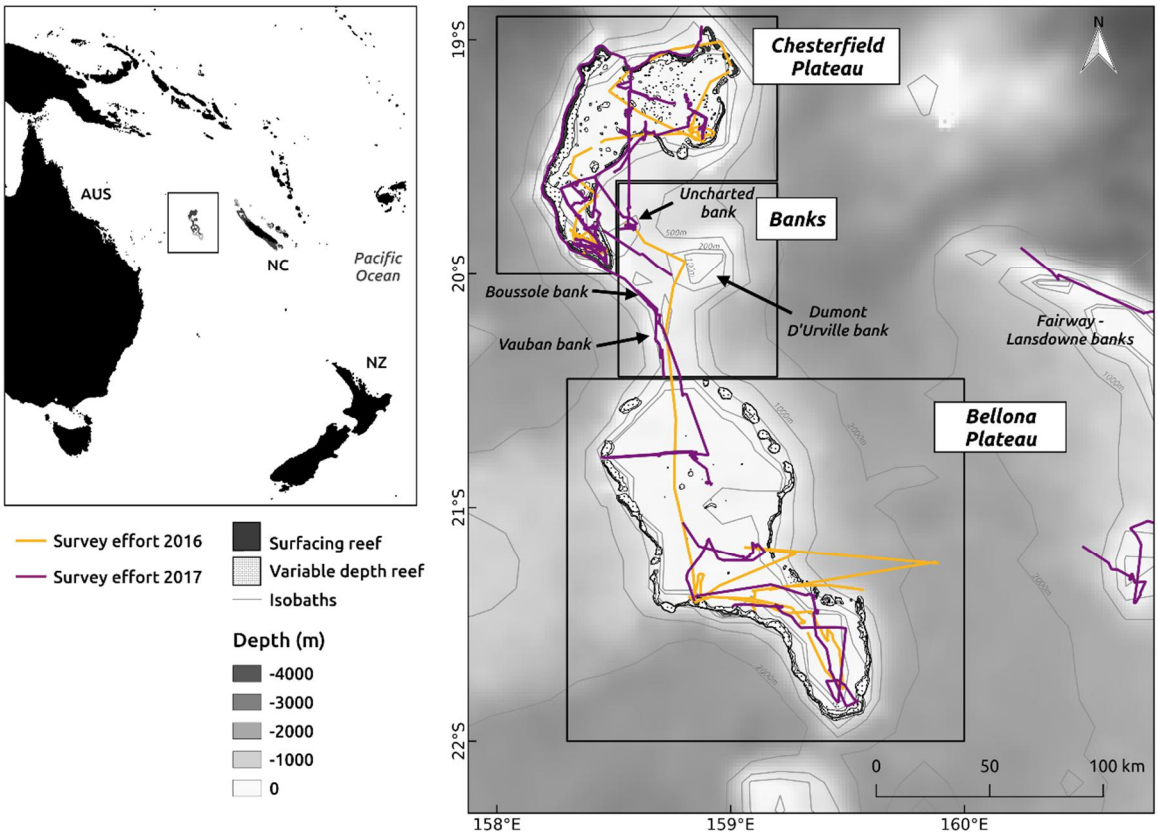

Figure 1: Map of the Chesterfield-Bellona archipelago in the Coral Sea with survey effort (2016-2017) and ecoregions defined for the purpose of this study. AUS = Australia, NZ = New Zealand, NC = New Caledonia.

Data collection

Surveys were conducted in the Chesterfield-Bellona plateaus in 2016 (August 24th – September 1^{rst}) and 2017 (August 10th – 24th) aboard two oceanographic vessels. Survey effort followed a non-systematic closing-mode protocol. Transect lines were determined on a daily basis and surveyed aboard the oceanographic vessels by two trained observers searching with naked-eye. When a group of humpback whales was detected and weather conditions allowed, a semi-inflatable boat was launched to conduct a focal follow. Once in close distance to the group, the GPS position, time, group size and social group type (as defined by (Clapham et al. 1992): singleton, pair, competitive group, mother with calf, mother with calf and escort, mother with calf in competitive group) were recorded.

During the focal follow, individual humpback whale encountered were photographed using digital camera Canon 40D and 50D equipped with lens 70X300mm or 100X200 mm with magnifier 1.4. Both sides of the dorsal fin and the underside of the caudal fluke were photographed when possible. Tissue samples were collected from both adult and calf whales using a crossbow with a specially adapted bolt (Lambertsen et al. 1994), a modified 0.22 caliber capture veterinary rifle (Krützen 2002) or from collecting sloughed skin at the water surface after intense surface activities. Finally, a hydrophone was deployed opportunistically on 49 occasions in August 2016 to detect acoustic activities of singing males in the study area.

Encounter rates

The distribution of humpback whales in the study area was estimated using an index accounting for the number of observations and the intensity of survey effort. The number of whales observed per kilometre of survey effort

was calculated (here after "Nw/km") as the sum of group sizes observed per day of survey divided by the distance surveyed per day (km).

Photographic analysis

Individual identification was performed through photo-identification of the underside of the fluke (Katona et al. 1979). The best photo-ID of each individual was added to the catalogue of humpback whales collected in the Chesterfield-Bellona archipelago. Within the same season, photographs of dorsal fins were also compared together to differentiate individuals and prevent undetected resights of whales that did not show their caudal fluke. Indeed, the comparison of dorsal fins between photo-identified and non photo-identified animals minimized the risk of double-counting in the total number of distinct whales during a season.

Photographs of caudal flukes were processed and were subsequently compared to the New Caledonian catalogue (N = 1282) using the Fluke Matcher software, a computer-assisted matching program (Kniest et al. 2010). When no match was detected by this program, visual manual comparison was performed on a pair-wise basis with the New Caledonian catalogue to confirm the identification of new individuals. The photographs of caudal flukes were also compared on a pairwise basis to the Great Barrier Reef catalogue collected during surveys conducted in 2016 and 2017 (Marine 2018) in order to reveal potential connections with the East Australian breeding stock E1 (Jackson et al. 2015).

Molecular analysis

Genomic DNA was isolated from skin tissue by digestion with ProK, followed by phenol/chloroform extraction and ethanol precipitation, according to (Sambrook et al. 1989), as modified for small samples (Baker et al. 1994). DNA was then quantified with Nanodrop 2000 (ThermoScientific).

The sex of each whale sampled was identified by the amplification of a male-specific SRY marker, with a ZFX positive control, using primers couples P15-EZ/P23-EZ (Aesen & Medrano 1990) and Y53-3c/Y53-3d (Gilson & Syvanen 1998). Results were visualized on agarose gel 2%.

Up to sixteen published microsatellite loci were screened for genotyping using previously published primers, GATA28, GATA417, (Palsboll et al. 1997), 464/465, (Schlötterer et al. 1991) EV1, EV14, EV21, EV37, EV94, EV96, EV104, Valsecchi & Amos 1996), GT211, GT23, GT575, (Bérubé et al. 2000), rw31, rw4-10, rw48 (Waldick et al. 1999). Amplifications followed protocols previously described by (Steel et al. 2008). The software GENEMAPPER V3.7 (Applied Biosystems) was used to size alleles: peaks were visually assessed and bins manually checked. Only those samples that amplified at a minimum of 10 microsatellites were retained for further analyses. Replicates samples were identified using CERVUS software (Kalinowski et al. 2007). The probability of identity (PID) was calculated using GenAlEX (Peakall & Smouse 2006) and corresponds to the probability that two randomly samples will have matching genotypes. Because of some incomplete genotypes, we consider a minimum overlap of 8 matching loci to decide that two samples will be replicates of the same individual. Genetic diversity was estimated on mtDNA and nuDNA. The program DnaSP 5.10 (Librado & Rozas 2009) was used to determine polymorphic sites (s), haplotypes (h), and haplotypic diversity (Hd) on mtDNA. Expected heterozygoties (He) observed heterozygoties (Ho) by locus and overall loci were estimated with Arlequin 3.5. (Excoffier & Lischer 2010). The significance of deviation from Hardy-Weinberg expectation in microsatellite allele frequencies by locus and overall loci (F_{IS}, (Weir & Cockerham 1984) were estimated with FSTAT (Goudet 2002).

A fragment of the mtDNA control region (approximately 800 base-pair bp) was amplified via the polymerase chain reaction (PCR) and sequenced using the primers, light-strand tPro-whale Dlp-1.5 (Baker et al. 1998) and heavy strand Dlp-8G (Lento et al. 1997). Sequencing was performed on a 3130xl Genetic Analyzer (Applied Biosystem). Haplotypic sequences were visualized and manually edited with Geneious R7. A Clustal W alignment using sequences from Chesterfield-Bellona Archipelago and sequences from (Olavarría et al. 2007) was performed in order to highlight polymorphic sites and name haplotypes with nomenclature known in the South Pacific. Sequences presenting indecision on polymorphic site (contamination or heteroplasmy[1] (Baker et al. 2013) were removed from the dataset.

Population structure and regional differentiation were performed with the available dataset from the New Caledonian South Lagoon study site, using microsatellites genotypes (N= 810) and mitochondrial control region haplotypes (N= 767). Comparison between these areas (F_{ST} on mtDNA and nuDNA; ϕ_{ST} on mtDNA) were

[1]Presence of a secondary peak at greater than 30 % of the primary peak confounding the resolution of a single haplotype

calculated using Arlequin 3.5. (Excoffier & Lischer 2010). The significance of regional differentiation was tested with 1,000 random permutations.

Habitat modeling

Humpback whale habitat preferences were modelled using a use/availability framework based a binomial regression of environmental conditions at the position of group encounters vs in the area surveyed in 2016-2017 in the Chesterfield-Bellona archipelago. Survey GPS tracklines were processed following the method described in (Derville et al. in review): 10 km stripwidth buffers were created around tracklines, within which 1,209 background points were sampled. Background and presence positions were pooled together and a series of environmental variables was extracted based on known habitat use patterns of humpback whales in breeding areas (e.g., (Rasmussen et al. 2007, Smith et al. 2012, Lindsay et al. 2016, Trudelle et al. 2016, Bortolotto et al. 2017).

Distance to the closest island or reef was calculated using shapefiles of coral reef contours obtained from the UNEP World Conservation Monitoring Center (UNEP-WCMC et al. 2010) and shapefiles of land contours obtained from OpenStreetMap. Seabed slope (in degrees) and depth (in meters) were deduced from the General Bathymetric Chart of the Oceans (GEBCO) at 1 km resolution. These three topographic variables were log-transformed prior to being included in the model. Serial correlation was used to remove collinearity between depth and distance to the nearest reef or coast. Within the presence-background point dataset, a linear regression was conducted between depth and distance, then the residuals of this regression were used to represent the effect of distance to the coast/reef while accounting for the effect of depth. Finally, sea surface temperature (SST in °C) was extracted from an average raster calculated over 1-km resolution remotely sensed data (MURSST, NOAA) winter months (early May to early December) of 2003 to 2014. This climatology of SST over the last decade represents the usual temperature conditions found in a given place, at a given day of the year.

Humpback whale habitat preferences were modelled with a binomial Generalized Additive Model (GAMs; (Hastie & Tibshirani 1990) using the mgcv R package (Wood 2017). A ‘cloglog’ link function and weights were used to account for the high zero prevalence (corresponding to the background positions). Penalized thin plate regression splines optimized with a Restricted Maximum Likelihood (REML) approach were used to model the effect of environmental variables: depth, seabed slope, distance to reef/islands (residuals), day of year and an isotropic interaction smooth of latitude and longitude with basis size equal to 100.

Satellite tracking

Satellite tags were deployed on adult whales aboard the semi-inflatable boat using a modified pneumatic line-thrower (ARTS, Restech) set to pressure 10 bars (Heide-Jorgensen et al. 2001). ARGOS location and dive recording tags, SPLASH10 (© Wildlife Computers, Redmond, WA 98052, USA) were implanted next to the dorsal fin. Biopsy sampling and caudal fluke photographs allowed the identification of the sex and identity of the tagged individuals. Tags were duty-cycled to transmit every day, every other hour, with a maximum daily number of transmissions set to 400.

ARGOS locations were filtered to remove invalid locations of class Z, locations on land and locations implying unrealistically rapid movements (speed > 18 km/h). Whenever a track was interrupted for more than 70 hours, the track was considered to be constituted by several segments, which were modelled separately. Furthermore, track segments were projected in a Pacific-centered Mercator coordinate system and were interpolated at one position every half-an-hour with a Continuous-time correlated random walk model using the R crawl package version 2.1.1 (Johnson et al. 2008). The error on ARGOS positions was incorporated as the ellipses semi-minor and semi-major axis error, with deployment GPS positions included with ellipses logarithmic error set to 0. The beta parameter (representing velocity autocorrelation) was constrained between [-3, 4] bounds and was optimized using a Normal distribution prior with mean -0.15 and standard deviation 1.5. The sigma parameter was left unconstrained.

RESULTS

Local distribution and density

In total, 13 humpback whale groups were observed in 2016 and 44 in 2017 (Fig. 2), with a majority in Chesterfield (53%) and Bellona (32%, Table 1). Numerous groups were observed in the southern part of the Chesterfield plateau, and the central part of the Bellona plateau. The encounter rate was calculated by year over group sizes, Nw/km and averaged. The highest encounter rate was found for the off-shore banks on average over

the two years (0.041 whales/km) despite low effort in this ecoregion. The values were comparable between Chesterfield and Bellona plateaus with a slightly higher number of whales per kilometre surveyed in Chesterfield (0.038 whales/km) compared to Bellona (0.035 whales/km). In general over the archipelago, the encounter rate was larger in 2017 (0.051 whales/km) than in 2016 (0.025 whales/km; Table 1).

Table 1: Survey effort and observation summary per year and per ecoregion. Nw: number of whales observed (summed over all groups observed).

		Distance surveyed (km)	Hours surveyed	Number of groups observed	Nw	Nw/km
Chesterfield	2016	378	34.2	4	7	0.019
	2017	858	81.8	26	48	0.056
Bellona	2016	611	35.9	8	18	0.030
	2017	550	46.9	10	22	0.040
Banks	2016	89	5.3	1	2	0.022
	2017	216	17.9	8	13	0.060
Total per year	**2016**	**1079**	**75.4**	**13**	**27**	**0.025**
	2017	**1624**	**146.4**	**44**	**83**	**0.051**
Total		**2702**	**221.8**	**57**	**110**	**0.041**

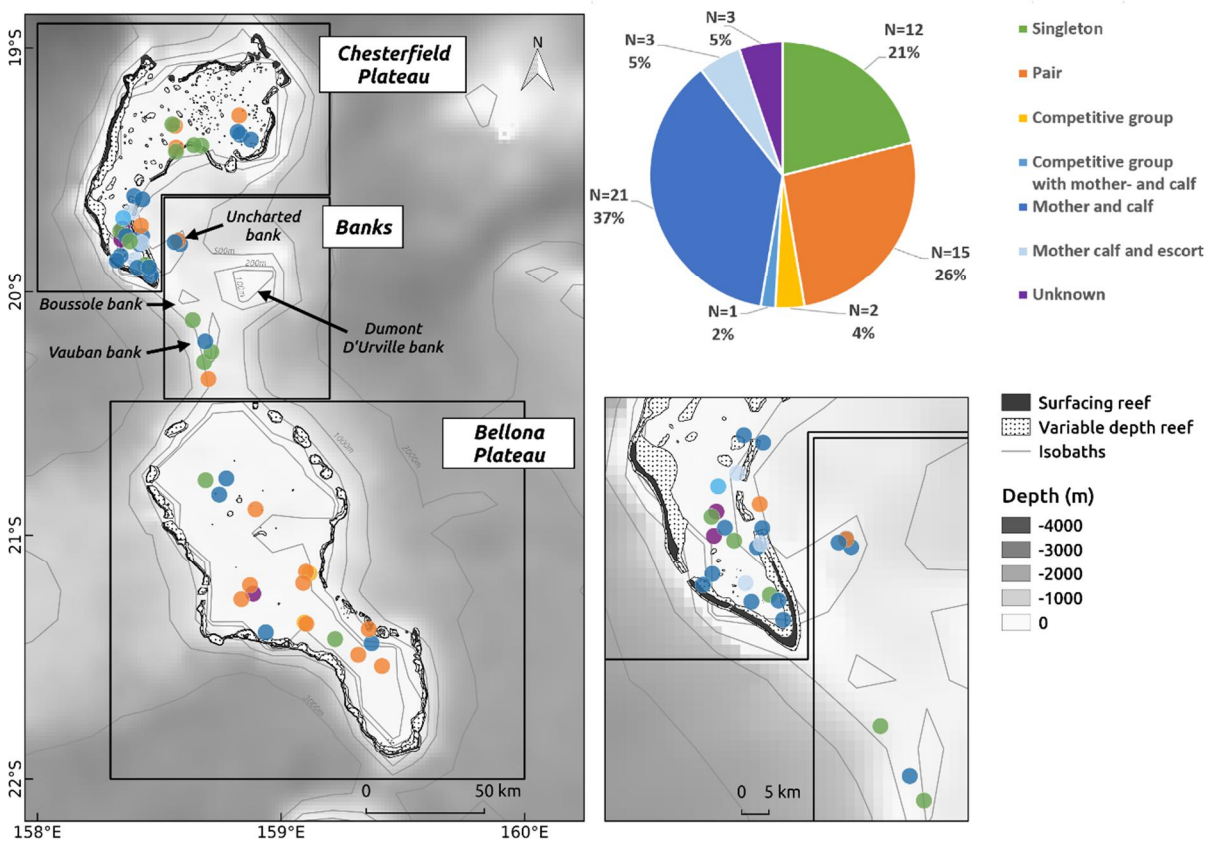

Figure 2: Positions of humpback whale groups and social group types observed during 2016-2017 surveys in the Chesterfield-Bellona archipelago (F/c = female with a calf).

Genetic diversity

Out of 16 microsatellite loci, 15 were used for analysis. Allele sizing of locus Ev104 (Valsecchi & Amos 1996) failed. All the samples collected were genotyped with up to 10 successful loci, so no genotype was removed from analysis. The Probability of Identity (PID) calculated for a minimum of 8 loci was less than 1 x 10-9, which is small enough to consider that two similar genotypes would belong to a same individual and two different

genotypes would belong to two different individuals (Baker et al. 2013). Success rate in genotyping samples from Chesterfield-Bellona varied between 93% and 100% depending on the locus analysed. The genotype catalogue of humpback whales from Chesterfield-Bellona archipelago was formed of 38 individuals from 40 samples, with 10 males and 28 females (Table 2). The sex ratio of 1:2.8 is in favour of females

Table 2: Number of skin samples collected in Chesterfield-Bellona study area, number of individual whales, number of males and females.

Year	# samples	# distinct individuals (M/F)	# new genotyped individuals	# individuals already known by genotype (M/F)
2016	8	3/4	5	1/1
2017	32	7/24	23	0/8
Total	40	10/28	28	1/9

Diversity of microsatellite loci was high, with an average of 9.13 alleles per locus and average observed heterozygosity of 0.735. No loci showed a significant expectation from Hardy-Weinberg equilibrium (F_{IS} by locus, $p > 0.05$). The fixation index F_{IS}, calculated for all loci, showed a slight excess of homozygosity (F_{IS}= 0.024) but this value was not significant.

A total of 37 haplotypic sequences from different individuals were obtained, including 6 inferred sequences already known. Clustal W alignment realized on 460 bp characterized 20 haplotypes defined by 45 polymorphic sites in Chesterfield-Bellona Archipelago (Figure 3). Five haplotypes were common between 2016 and 2017, one haplotype was only encountered in 2016 and 12 haplotypes were only found in 2017 (Figure 3). All but one haplotype were known from (Olavarría et al. 2007). This last one (NEW) corresponded to a sequence found in 2016. Haplotypic diversity calculated on Chesterfield-Bellona was Hd= 0.9640.

Haplotype	Variable sites	2016	2017
	48 55 61 68 77 90 92 94 109 110 114 116 119 128 129 140 155 156 161 177 190 234 240 241 242 247 251 255 257 258 259 260 262 263 267 278 279 280 300 311 341 374 431 441 442		
NEW	G C C T T C C A G _ T T C A G C T T T T T T T T C A T A G T T T T T A C C T A T T C G T T	1	0
SP13	. . . . . _ . C . . . . . C	1	1
SP14	. . . . . _ . C . . . . . C C	0	3
SP27	. . . . T . . . _ _ C . . . . C . . . . C C T . . G . . . . . T	0	3
SP3	A T T . . T . . . _ _ C . . . T . . C . . . . C . G . . . . C . C . . T . . . . . T . . C	1	3
SP36	. . . . . T . . . _ _ C . G . T . . . . . C . . . . . C C . . . T	0	1
SP52	. T . . . T . . . _ _ C T . A . . . C . . . C C . . . . . C . . . G T . C G . . . . C .	0	3
SP57	. T . . C T . . . T _ C T . . T . . C . . C . C . . . . . C . . . G T . C . C . . . C .	0	1
SP64	. T . . . T . . . _ _ C T . . . . . C . C . . . . . A . . C . . G T . . . . . T A . .	1	1
SP71	. T . . . T . . . _ _ C T . . T . C C C . . C C . . . . . C . C . C G T	1	2
SP73	. T . . . T . . . _ _ C T . . T . C C . . . C C . . C . . C C C . C G T	0	2
SP78	. T . . . T . . . _ _ C T . . T . C C . . . . C . . . . . C . . G T . . . . . T . . .	0	1
SP88	. T . . C T A . . . _ _ C T . . . . C C . . . C C . . . . . C . . G T	1	1
SP87	. T . . . T A . . . _ _ C T . . . . C C . . . C C . . C . . . . C . . G T	1	0
SP85	. T . . . T A . . . _ _ C T . A . . C C . . . . C . . . . . C . . G T . C . C C . . .	0	1
SP96	. T . . C T A . A _ _ C T . A . C . C . . . C C . . . . . T	0	2
SP99	. T . . C T A . . . _ _ C T . A . . . C . . . . C . . . . . G T	0	2
SP94	. T . C . T A . . . _ _ C T . . . . C C . . . C C . . . . . G T	0	1
SP89	. T . . C T A G . . _ _ C T . . . . C C . . . C C . . . . . C . . G T	0	1
SP10	. . . . . _ . C . . . . . C . . . . . T	0	1

Figure 3: Relative position of variable nucleotides defining 20 mtDNA control region haplotypes in humpback whales from Chesterfield-Bellona archipelago. The name of haplotypes is defined from Olavarria et al 2007. Dots (.) indicate matches with reference sequence (NEW), dashes (_) indicate insertion or deletion. Frequency of each haplotypes is indicated for each collecting years.

Local space use

Behavior

Only one competitive group was encountered in 2016, the other groups were mother with calf (n = 4), mother with calf and escort (n= 1), pairs of two adults (n= 4) and three un-identified group types (Fig. 2). In 2017, only one competitive group was observed, the other groups were mother with calf (n= 17), mother with calf and escort (n= 2), mother with calf within competitive group (n= 1), pairs of two adults (n= 11) and singleton (n= 12). In total, mothers with calf were present in 45% of the groups encountered. Finally, humpback whale songs were heard in 61% of the hydrophone deployments (n= 49) performed in 2016 over the Chesterfield-Bellona whole archipelago.

Habitat

Model explained 24% of the deviance in the binomial presence-background dataset. Only depth (approximate significance: edf= 2.4, Chi2= 9.2, p-value= 0.008**) and SST (approximate significance: edf= 2.3, Chi2= 9.6, p-value= 0.006**) significantly affected humpback whale probability of presence. The model revealed a preferential use of shallow waters (50 m deep) and averaging 23°C. Preferential areas were predicted at the South-East of Chesterfield and North of Bellona, as well as in the shallow waters of the unsheltered banks of La Boussole, Vauban, Dumont D'Urville and an uncharted bank (Fig. 4). External slopes and deep waters surrounding the plateaus were found to be relatively unsuitable.

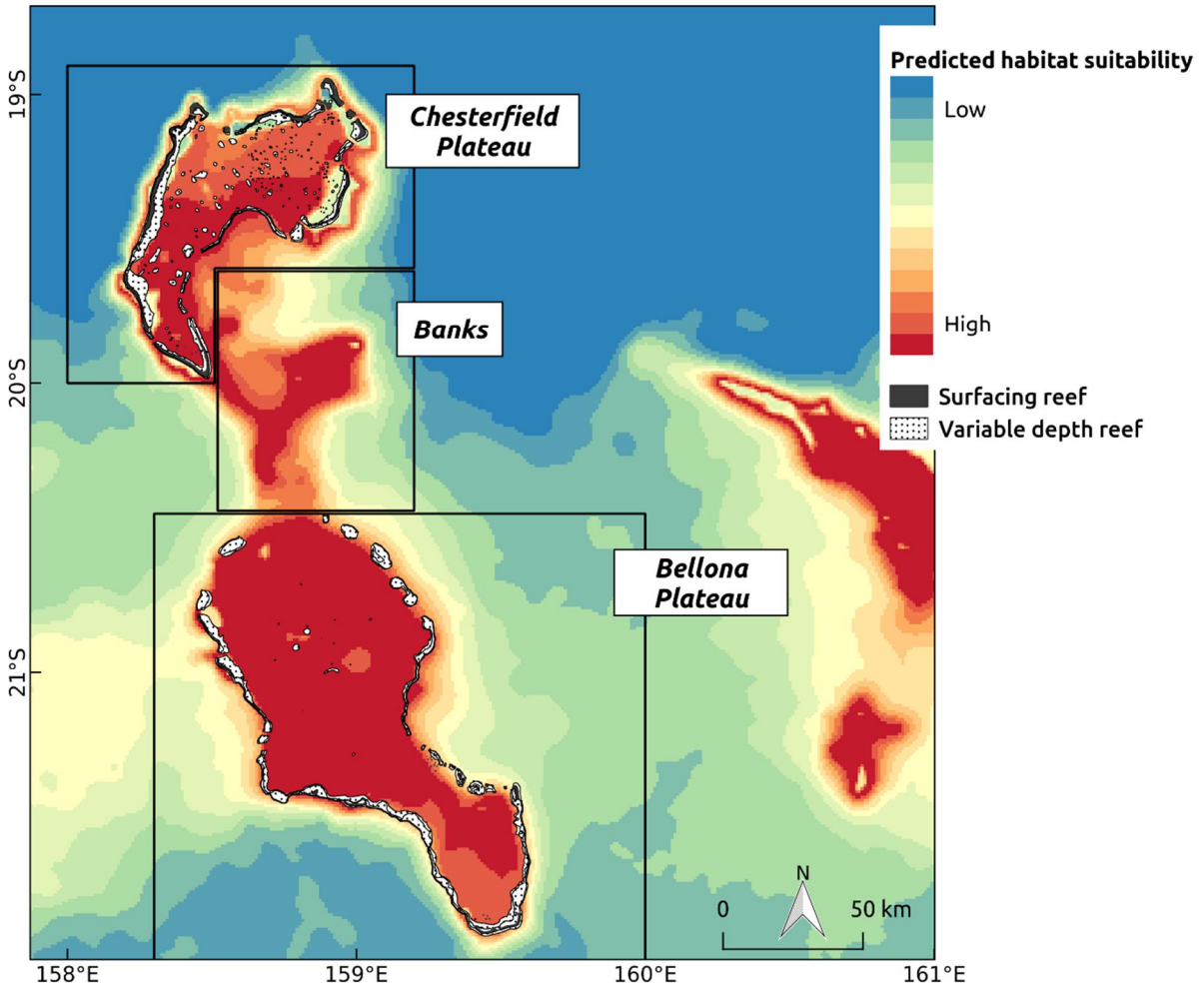

Figure 4: Map of predicted habitat suitability for humpback whales in the Chesterfield-Bellona archipelago. Predictions are based on Generalized Additive Models using observations from 2016 and 2017.

Movement

Six whales were equipped with satellite tags in 2017 (Fig. 5 and 6). Five of them were females from which three were accompanied by a calf. The satellite tags emitted between 5 and 70 days during which the whales covered

between 390 and more than 5,000 km (Table 3). Tagged whales showed a preference for shallow waters inside the plateaus, in contrast with the surrounding deeper waters that were only occupied during transiting periods (Fig. 5). Specifically females with a calf tagged in Chesterfield (n= 2) and the off-shore banks (n= 1) spent time in the sheltered waters south of the Chesterfield (PTT 34227) and Bellona (PTT 34222) plateaus. Half of the tagged whales (n = 3) also visited the off-shore unsheltered banks, and moved between the Chesterfield and Bellona plateaus as well. This preference for shallow waters outside lagoon areas is also emphasized by the stop-overs of two whales on the Kelso and Capel seamounts during their southward migration, including one with a calf (PTT 34226 and 34222, Fig. 5).

Table 3: Summary of satellite tracking for six tags deployed in 2017 in the Chesterfield-Bellona archipelago. Abbreviations: unk = 'unknown', F = 'female', P = 'Pair', F/c = 'Female with calf', S = 'Singleton'.

PTT	Start	End	sex	Social category	Duration of emissions (days)	Raw locations	Filtered locations	Track length (km)
34221	12/08/2017	19/08/2017	F	P	5.8	6	6	496
34222	22/08/2017	25/09/2017	F	F/c	33.8	204	187	1,907
34223	17/08/2017	23/08/2017	unk	P	6	43	35	390
34226	22/08/2017	08/10/2017	F	S	46.7	333	261	5,034
34227	18/08/2017	28/10/2017	F	F/c	70.5	451	386	4,858
34228	20/08/2017	25/08/2017	F	F/c	4.8	26	24	279

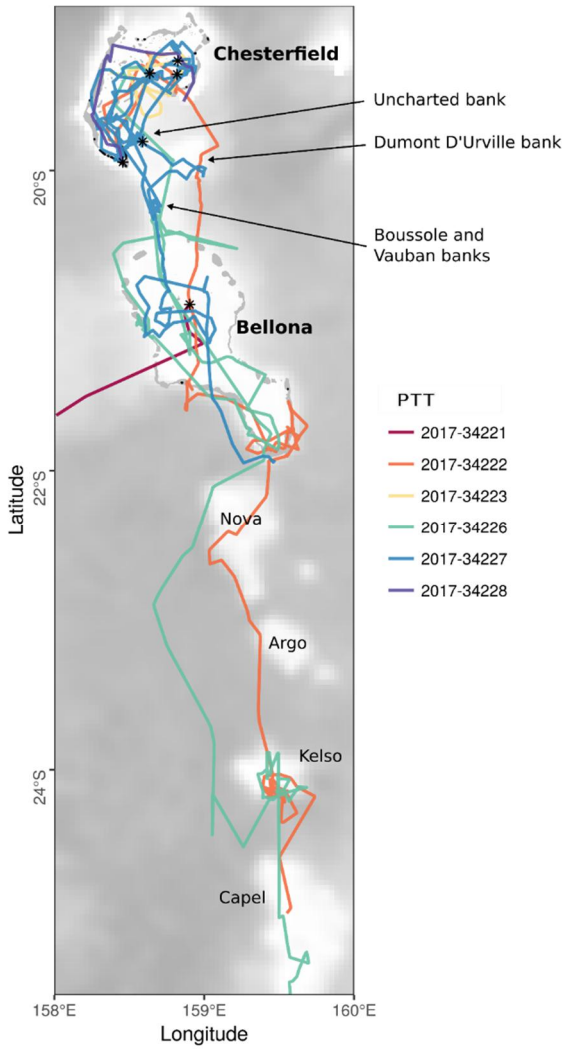

Figure 5: Satellite tracking of six humpback whales tagged in Chesterfield (n=4), Bellona (n=1), off-shore bank (n=1) in 2017. Interpolated tracks processed with *crawl* are represented in color. Deployment positions are shown with black stars.

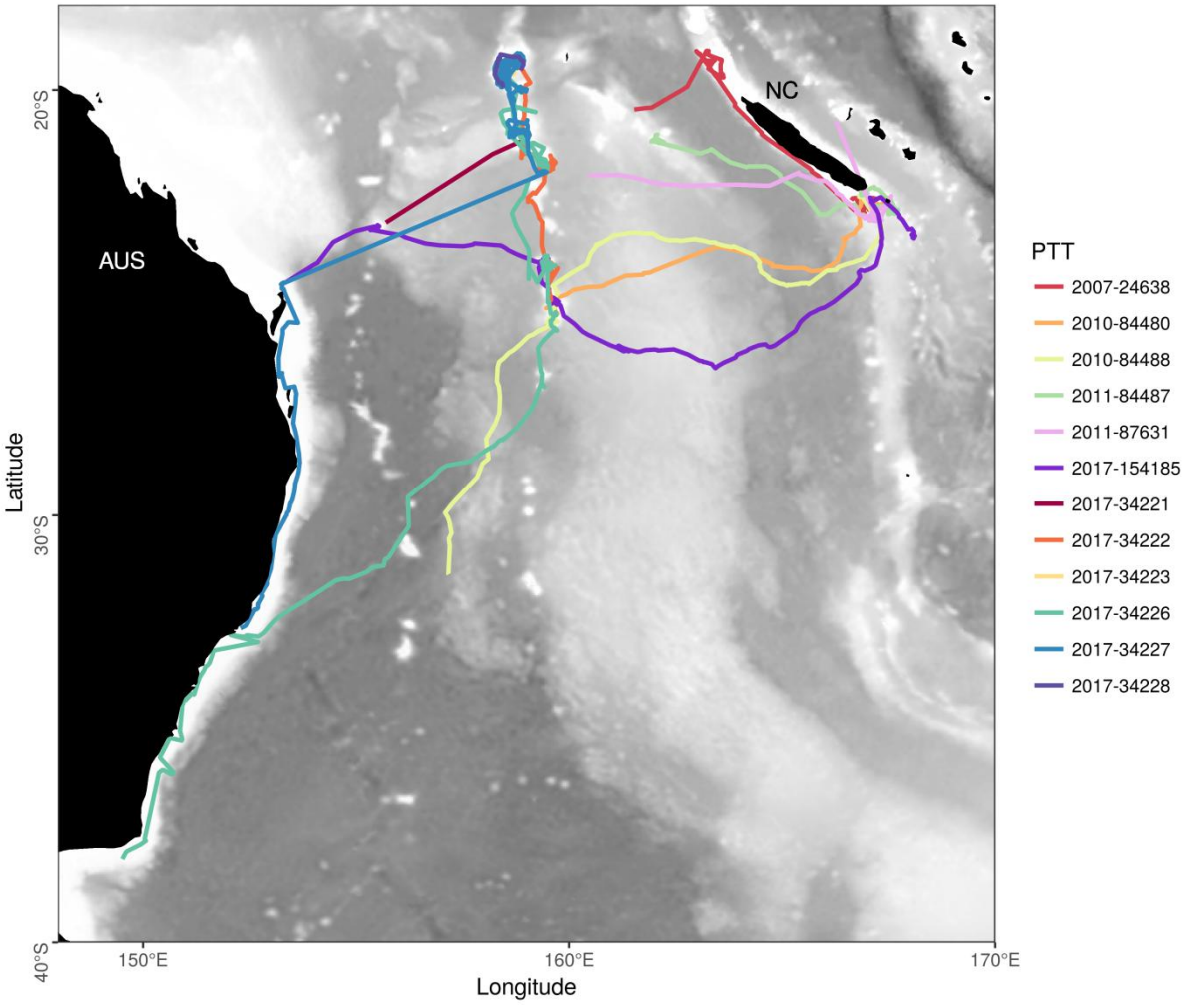

Figure 6: Satellite tracking of seven humpback whales tagged in Chesterfield (n=4), Bellona (n=1), off-shore bank (n=1) and Antigonia seamount (n=1) in 2017, and of five humpback whales tagged in previous years (2007 to 2011) suggesting a connection between New Caledonia and Chesterfield-Bellona or the Lord Howe seamount chain. Tracks from 2017 were interpolated with a *crawl* algorithm, whereas tracks from 2007 to 2011 were only filtered.

Regional connectivity

In 2016, 18 individuals were differentiated with photos of their caudal and/or dorsal fin, from which 7 could be catalogued using a photo-identification of the fluke caudal. In 2017, 62 individuals were differentiated, of which 28 could be catalogued.

To date the Chesterfield-Bellona humpback whale fluke catalogue contains 35 whales and the genetic catalogue contains 38 genotypes (Table 4) of which 61% are also known by photo-ID.

Table 4: Number of groups, count of distinct individuals, number of whale photo-identified including resighted and new ones.

Year	# groups	# distinct individuals	# whales identified by dorsal fin only	# individuals photo-identified	# new photo-identified individuals	# individuals already known by photo-identification
2016	13	18	11	7	4	3
2017	44	62	33	28	20	8
Total	57			35	24	11

A total of 11 out of 35 whales (31%) photo-identified, and 10 out of 38 genotyped whales (26%) in Chesterfield-Bellona archipelago has already been observed in other years (Tables 2 & 4) with 8 whales resighted by both methods. All of the resighted whales were first observed in the South Lagoon of New Caledonia between 1997 and 2017, one was also observed in the eastern lagoon but none of them were observed in other areas of the EEZ (e.g., southern seamounts). Most of these are females (n = 10), from which 90% have been observed at least once with a calf during the 2016-2017 expedition or on previous years. The only recaptured male was observed on the plateau as a pair member.

Pairwise comparison calculated on nuDNA (F_{ST}= -0.00121) showed no significant difference between whales sampled in the South Lagoon and in the Chesterfield-Bellona archipelago (p> 0.05). Likewise, pairwise comparison calculated on mtDNA at both haplotype (F_{ST}= 0.00164) and nucleotide (ϕ_{ST}= -0.00080) levels were not significant (p> 0.05): no genetic differentiation is highlighted between Chesterfield-Bellona archipelago and the South Lagoon of New Caledonia.

Finally, no match was found between the individuals identified in the Chesterfield-Bellona archipelago and those recently photographed in the Great Barrier Reef in 2016 and 2017. However, three of the whales tagged in the Chesterfield-Bellona archipelago migrated towards (n = 1) or along the East Australian Coast (n = 2, Fig. 6).

DISCUSSION

Presence post-whaling era

Encounter rates exceeded by far previous estimates made in 2002 and 2010 in the study area (Nw/km surveyed 0.020 and 0.003 (Oremus & Garrigue 2014). Although these surveys also occurred in August, they differed in the extent of the area surveyed and time on-effort. Indeed, the preliminary surveys conducted in 2002 and 2010 were for the most, restricted to the southern part of the Chesterfield plateau and spread over 41h and 26h respectively due to the limited logistics available for these expeditions. Aside from a potential survey effort bias, this observed increase in encounter rate could be attributed to an increase of the population visiting the Chesterfield-Bellona archipelago during the breeding season. Such an augmentation would be in line with the recovery of the Australian stocks, and to a lesser extent to the slower recovery of the Oceanian breeding stocks (Jackson et al. 2015).

Encounter rates measured in the Chesterfield-Bellona archipelago in 2016 and 2017 are comparable with those found in the South Lagoon breeding area located south of New Caledonia mainland (0.045 ± 0.018 whales/km from 2002 to 2010; (Oremus & Garrigue 2014) and subject to a long-term monitoring program since 1995 (Garrigue et al. 2001). While these figures suggest that humpback whales are still present in Chesterfield-Bellona in decent numbers, it does not seem to be enough to have sustained intense whaling activity in the 19th century. Did whalers use to hunt despite these low densities? Or were the densities higher at that time? Or is the peak of the season not the same in Chesterfield-Bellona and the South Lagoon, hence humpback whales could be found in greater numbers earlier in the season than mid-August-September? One last hypothesis concerns the spatial extent of surveys conducted so far in the region. Whalers could use to go in areas that have not been surveyed enough to date. The few data available from the whaling era do not provide any accurate location of the catches (Lund et al. 2018), but rather rough descriptions of the places where they occurred. Bourne et al (2005) noted "they (humpback whales) apparently occurred all around the islands although they were commonest off the south end of the Bellona reefs". Indeed, several whales tagged in 2017 and in previous years (Fig. 6) have spent time on the Lord Howe seamount chain located south of the Bellona plateau. Could these seamounts actually be the whaling sites logbooks were referring to? Considering that the American whalers were using sailing boats, they were more likely to work in the so-called "South of Bellona" waters, referring to the Lord Howe seamount chain, rather than inside the southern part of the Bellona plateau, a shallow and reef enclosed area where navigation by sail would be perilous.

Habitat use

Surprisingly, only two competitive groups were encountered during the expeditions in this area suitable for reproduction. Nevertheless, songs were extensively heard on the plateaus highlighting some reproductive activity. Moreover the sex ratio was in favor of females, hence the reverse of the typical breeding ground population structure. A majority of females with calf was encountered, especially in 2017 despite the fact that the 2017 expedition was conducted earlier in the reproductive season than the one undertaken in 2016. As a consequence, we should, in theory, have encountered even less mothers in 2017 than in 2016. The high occurrence of this social group compared to the few competitive groups encountered is usually expected at the end of the breeding season, but not at the peak. Yet, the timing of the expeditions was planned to be in synchrony with the peak of the reproductive season in the South Lagoon of New Caledonia, at a time where high

agonistic activities should be observed. The high proportion of females, and specifically mothers with a calf in the 2016-2017 expeditions could be explained by a shift of the season peak earlier in the season in the Chesterfield-Bellona compared to the South Lagoon of New Caledonia. Alternatively, the prevalence of mothers with a calf could be explained by a space use pattern heterogeneity between males and females, resulting from a slow recovery post-whaling. Indeed, males could be less inclined to remain within an area of low density presenting few breeding opportunities. On the contrary, mothers with a calf are more likely to stay in these plateaus, no matter what the whale densities are, as they include all types of suitable habitats for them, and are free from any anthropogenic disturbance. In fact, the geography of Chesterfield-Bellona archipelago provides relatively sheltered habitats open to the ocean and some potential stop-over shallow waters on the Lord Howe seamounts chain on the way to the southward migration. Telemetry highlighted the use of Kelso and Capel, the shallower seamounts of this chain. This geography, which is not unlike that of the southern part of New Caledonia (South Lagoon and seamounts on the Norfolk ridge), provides both shallow sheltered and shallow unsheltered areas, which are known to be appreciated by mothers with a calf (Derville et al. 2018). Hence, maternal females would have a higher probability of being observed within the plateaus, whereas the few males visiting the area would be more transient. Surveying the seamounts of the Lord Howe seamount chain could provide a better understanding of this demographically-biased spatial distribution pattern.

Regional connectivity

Photo-id and genotype comparisons suggest connectivity to the New Caledonian breeding sub-stock E2. Regional differentiation, both with mtDNA and nuDNA, highlighted no significant genetic differentiation between Chesterfield-Bellona archipelago and the South Lagoon of New Caledonia. Resight rate between the Chesterfield-Bellona archipelago and the South Lagoon is of the same order than the resight rate within the South Lagoon. While no resights have been observed between Chesterfield-Bellona archipelago and New Caledonia within the same season to date, previous studies have shown that six whales tagged in the southern part of New Caledonia travelled in a westerly direction aiming to the central part of the Coral Sea (Garrigue et al. 2010, Garrigue et al. 2015). One female with calf tagged in 2007 stopped at Lansdowne and Fairway Banks (Tag #34228, Fig. 6) as did one (Tag #84487) of the two adult males tagged at the end of August in 2011. The second male was going straight to Bellona plateau (Tag #87631, Fig. 6) but unfortunately, satellite tag stopped emitting before it reached it. Furthermore, three whales tagged in the south of New Caledonia, one female adult (Tag #84480) and one male (Tag #84488) within the South Lagoon (mid of August 2010) and one male (Tag #154185) on Antigonia Seamount (end of July 2017) travelled in the direction of the seamounts located on the Lord Howe ridge south of Chesterfield-Bellona archipelago, where they spend some time on the shallow seamount of Capel (Fig. 6). Then one of the two males travelled west and entered Hervey bay whereas the second one undertook its southern migration following the Lord Howe ridge. The tracks of these whales followed during the second part of the breeding season, from end of July to mid-October, suggest first a within-year connection with the breeding ground of New Caledonia and second that adult males could wander between several reproductive areas at large scale.

To-date no match has been found between Chesterfield-Bellona archipelago and the whales photo-identified in the Great Barrier Reef. However, the great majority of the GBR and the Chesterfield-Bellona catalogues were constituted in 2017. Therefore, the lack of match between these two reproductive areas is not surprising as it would imply a longitudinal movement within season. These events are thought to be rare in the light of previous studies using different methodology (Olavarría et al. 2006, Anderson et al. 2010, Garrigue et al. 2011, Franklin et al. 2014, Garrigue et al. 2015, Bonneville et al. 2017). However, this result does not imply that the absence of connectivity across years. Finally satellite tracks suggest a connection with the south east Australian migratory corridor as several whales travelled to the east Australian coast including one between New Caledonia and Hervey Bay in Australia. We could hypothesise that the whale inhabiting Chesterfield-Bellona archipelago use the Australian coast, but only as a migratory corridor and not as a reproductive destination. The genetic comparison between whales sampled in Chesterfield-Bellona and those samples on the Great Barrier Reef will bring more light on this hypothesis.

CONCLUSION

Whales are still inhabiting the Chesterfield-Bellona archipelago two centuries post-whaling but the currently observed density is probably weaker than that of the whaling time. Nevertheless, encounter rates are of the same order of magnitude than in the South Lagoon of New Caledonia. Chesterfield-Bellona archipelago provide suitable habitat for reproduction, but displays atypical population characteristics, namely a preponderance of mothers with a calf and a reversed sex-ratio. More data will be necessary to understand the reason for this female-biased sex-ratio. Though evidence are currently too sparse to decide to what population the whales

encountered in the Chesterfield-Bellona archipelago belong to, but genetic analysis suggest a connection to the New Caledonian population, whereas the tracking data indicates movements towards the east Australian coast and use of the south east migratory corridor. Data recently collected within the reproductive area of the GBR should help resolve this question.

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