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From land and sea, long-term data reveal persistent humpback whale (*Megaptera novaeangliae*) breeding habitat in New Caledonia

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ABSTRACT

1. Long-term monitoring is a prerequisite to understand and protect long-lived species such as cetaceans. In New Caledonia, South Pacific, an endangered subpopulation of humpback whales (*Megaptera novaeangliae*) seasonally congregates for mating and nursing during the austral winter. For more than two decades, dedicated surveys have been conducted at sea and from land to monitor humpback whale presence in a coastal breeding site, the South Lagoon.
2. Methods were developed to investigate space use patterns and their temporal variations over the long term using a joint dataset of boat-based and land-based observations (1995 - 2017). A total of 2,651 humpback whale groups were observed, including 1,167 from land and 1,484 at sea (of which 30% were initially detected by the land-based observers).
3. Humpback whales displayed a persistent space use pattern over this 23 year period, consistent social composition over the years, and an increase of the group encounter rates from land and at sea. The core area of use by humpback whales was characterized in the austral winter by stable and relatively low sea surface temperature (22°C). Whales consistently occupied nearshore waters from 10 to 200 m deep and open to the ocean. Waters surrounded by dense coral reefs were avoided.

- 1 17 4. Although humpback whale distribution patterns were persistent and occurrence was found to
2 18 increase over two decades, a mismatch between humpback whale critical habitat and marine
3 19 protected areas was revealed. In the context of growing anthropogenic pressure from tourism and
4 20 industrial development, these findings should be incorporated into local management efforts to
5 21 protect the endangered Oceania humpback whale in one of its main breeding sites.
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10 **KEYWORDS**

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13 23 Coastal, habitat mapping, lagoon, mammals, monitoring, recovery, recreation, shipping
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17 **INTRODUCTION**

18 24
19 25 Industrial whaling of the 19th and 20th century greatly impacted humpback whale (*Megaptera*
20 26 *novaeangliae*) populations worldwide (Rocha, Clapham, & Ivashchenko, 2015). Today, humpback
21 27 whale populations globally show encouraging signs of recovery, yet are variable from one population to
22 28 the other (Thomas, Reeves, & Brownell, 2015). As humpback whales are now facing the cumulative
23 29 effects from threats of pollution, vessel traffic, entanglement, noise or tourism resulting from increasing
24 30 anthropogenic activities (Avila, Kaschner, & Dormann, 2018), there is a need to monitor populations at
25 31 a local scale. Understanding the trends in distribution, habitat use and dynamics of populations is
26 32 essential to implementing appropriate local conservation measures, and ensure the species recovery as a
27 33 whole.
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35 34 The slow breeding rate (i.e. generation time 21.5 yr, Taylor, Chivers, Larese, & Perrin, 2007) and long
36 35 life-span (i.e. 95 yr, Chittleborough 1965; Gabriele, Lockyer, Straley, Jurasz, & Kato, 2010) of humpback
37 36 whales warrants long-term datasets in order to detect potential trends in distribution and population
38 37 demographics. Thereby, monitoring programmes conducted over several decades have greatly
39 38 contributed to the knowledge and protection of humpback whales, for example in Glacier Bay (Gabriele
40 39 et al., 2017; Pierszalowski et al., 2016) or the Gulf of Maine (Robbins, 2007). However, such long-term
41 40 datasets are rarely available (Sydeman, Poloczanska, Reed, & Thompson, 2015), as the high financial
42 41 cost and challenging survey environment characterizing cetacean studies are obvious obstacles to the
43 42 implementation of research projects over several decades (Simmonds & Elliott, 2009). Also, once actually
44 43 collected, long-term datasets often constitute data processing and statistical challenges, particularly due
45 44 to protocol mismatches (Ducklow, Doney, & Steinberg, 2009; Lindenmayer & Likens, 2010) regarding
46 45 the extent of survey effort and the evolution of methods used across several years or decades.
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1 46 The Oceania population of humpback whales is relatively small, has one of the slowest recovery rates
2 47 (Constantine et al., 2012; Jackson et al., 2015) and is still listed as “endangered” in the IUCN Red List
3 48 (Childerhouse et al., 2008). Humpback whales of the Oceania population feed during the austral summer
4 49 in the remote waters of the Southern Ocean, from the Balleny Islands to the Antarctic peninsula
5 50 (Albertson et al., 2018; Constantine et al., 2014; Riekkola et al., 2018; Steel et al., 2017). During the
6 51 austral winter, they migrate to breeding grounds in the South Pacific islands and reefs, where mating,
7 52 calving and nursing take place. Various degrees of subpopulation structuring have been identified across
8 53 this vast area (Constantine et al., 2012; Olavarria et al., 2007) and the International Whaling Commission
9 54 recognizes several breeding sub-stocks including BSE2 in New Caledonia, BSE3 in Tonga and BSF in
10 55 French Polynesia (IWC, 1998; Jackson et al., 2015). Among the widely dispersed breeding grounds
11 56 found across Oceania, humpback whale research has only been carried out in a few specific study sites.

12 57 New Caledonia is the most westerly archipelago visited by the endangered humpback whale population
13 58 of Oceania. Humpback whales found in this archipelago are demographically isolated and genetically
14 59 differentiated from the two neighbour breeding populations of eastern Australia and Tonga (Garrigue,
15 60 Dodemont, Steel, & Baker, 2004; Olavarria et al., 2007). The New Caledonia South Lagoon (Figure 1)
16 61 is historically considered one of the main humpback whale breeding grounds known to date for this
17 62 subpopulation (Garrigue, Greaves, & Chambellant, 2001). Humpback whales at this breeding site have
18 63 been the focus of a continuous long-term monitoring programme (Garrigue et al., 2001) initiated in the
19 64 mid-1990s, which has documented humpback whale presence in the South Lagoon during the austral
20 65 winter, with a peak of abundance after mid-August. Humpback whales in this coastal study site have
21 66 been consistently monitored for more than 20 years using an original protocol combining boat-based and
22 67 land-based observation.

23 68 The New Caledonia South Lagoon also concentrates several human activities that constitute liable threats
24 69 to whales. Active nickel mining on the mainland has induced increased maritime traffic of large cargo
25 70 ships, specifically in the Prony Bay where an industrial port was constructed in 2006 following the
26 71 development of a new hydrometallurgical process plant (Bourgogne, Derville, & Garrigue, 2018, Figure
27 72 1). New Caledonia also is a leading whale watching destination among the South Pacific Islands
28 73 (Schaffar, Garrigue, & Constantine, 2010; Schaffar et al., 2013; Figure 1). Since 2008, humpback whales
29 74 have been legally protected by the local environmental legislation that forbids deliberate disturbance,
30 75 specifically approaching whales closer than 50 m or observing whales within less than 200 m for over 2
31 76 hours (Province Sud, 2009). In addition, observations guidelines have been proposed to promote
32 77 responsible whale watching behaviour (Province Sud, 2018). Yet, increasing tourism and human

1 78 population density (www.isee.nc) is a cause of concern in terms of disturbance and collision risks (Currie,
2 79 Stack, & Kaufman, 2017; New et al., 2015; Senigaglia et al., 2016). In the South Lagoon, the number of
3 80 whale watching touristic operators has increased from 5 in 1995, to 24 in 2017 (Province Sud &
4 81 Opération Cétacés, unpublished data). An integral marine protected area, the Merlet Reserve, was created
5 82 in 1970 to prevent all human activities over a 170 km² area north-east of the South Lagoon (IUCN
6 83 category Ia, Figure 1). A great part of the South Lagoon is also classified as a UNESCO World Heritage
7 84 Zone (UNESCO, 2009), as well as a Province Park (roughly equivalent to IUCN category II, Figure 1)
8 85 but the level of protection provided by these zones is very low as it imposes few restrictions on human
9 86 activities. The management objective of the South Lagoon Province Park is to ensure the stability of
10 87 ecological processes and preserve the natural equilibrium by regulating the activities and needs of the
11 88 local population (Cleguer, Grech, Garrigue, & Marsh, 2015). In practice, the Province Park management
12 89 plan allows public use of the Park, including fishing and recreational activities, but prevents industrial
13 90 pollution and mining (Province Sud, 2013). The contribution of these protected areas to the conservation
14 91 of critical habitats for humpback whales has never been investigated.

15 92 In the context of a population recovering from industrial whaling and facing growing human pressure,
16 93 this study aims to assess the ecological value of the New Caledonia South Lagoon as a breeding site by
17 94 an endangered humpback whale subpopulation. This study is based on the long-term monitoring
18 95 occurring 30 years after commercial whaling of this species ended in the Southern Hemisphere. A dataset
19 96 of simultaneous boat-based and land-based surveys is used to evaluate humpback whale occurrence,
20 97 social composition, spatial distribution and habitat use in the New Caledonia South Lagoon, over more
21 98 than 20 years (a quarter of a humpback whale's maximum life span). Finally, the current level of
22 99 protection against potential threats is evaluated, and recommendations are provided to improve future
23 100 conservation of this endangered population.

44 101 **METHODS**

47 102 **Study region and survey design**

48 103 New Caledonia is an archipelago located in the south-west Pacific Ocean about 1,500 km north-east of
49 104 Australia (Figure 1). New Caledonia mainland, also called "Grande Terre", is surrounded by a large
50 105 lagoon delimited by a 1,500 km-long barrier reef. The South Lagoon is a large shallow area (about 50 m
51 106 deep) located south of the mainland, bounded by the Prony Bay and the Ouen Island to the north, and by
52 107 two reef complexes to the south-west ("Corne Sud") and the north-east (Isle of Pines, Figure 1). The

1 108 south-eastern part of this lagoon is open to the ocean and is characterized by deeper waters (reaching 600
2 109 m deep). New Caledonia is under the influence of two main currents: the highly unstable south-eastward
3 110 Vauban Current (VC) flows south through the Loyalty channel bringing warm waters in winter. In
4 111 contrast, the south-eastward Alis Current of New Caledonia (ACNC) carries colder waters into the area
5 112 from the west (Figure 1; Cravatte et al., 2015; Marchesiello, Lefèvre, Vega, Couvelard, & Menkes, 2010).

11 113 Surveys were part of a single monitoring program conducted in the South Lagoon of New Caledonia
12 114 from 1995 to 2017 (except for 2004 and 2008), between the beginning of July and the end of September.
13 115 Surveys were conducted in Beaufort sea-states ≤ 3 (and avoiding heavy rain) and were simultaneously
14 116 conducted at sea and from a land-based look-out located on top of the Cape N'Doua (altitude 189 m, >
15 117 270° visibility, Figure 2). Both teams could communicate at all times using Very High Frequency (VHF)
16 118 radios. A land-based team composed of one to five trained observers scanned the study area and detected
17 119 whales up to 36 km from the Cape. A few areas close to the coast and within the Prony Bay were masked
18 120 from the Cape (Schaffar et al. 2013; Figure 2b) and their extent was measured using a theodolite (a
19 121 rotating telescope for measuring vertical and horizontal angles to accurately locate positions at the sea
20 122 surface with a simple trigonometric calculation). The boat-based team was composed of three to five
21 123 trained observers in a 6 m rigid-hulled inflatable boat moving at 14 km.h⁻¹ on average. Surveys followed
22 124 a haphazard sampling regime (Corkeron et al., 2011), with effort dependent on weather conditions and
23 125 focused on waters accessible on a daily basis from the Prony Bay.

34 126 **Group occurrences and social composition**

36 127 Data processing and statistical modelling was performed with the R software version 3.2.5 (R Core Team,
37 128 2016) and geographical data visualization was performed using QGIS v.2.14. (QGIS Development Team,
38 129 2016).

43 130 For each encounter, geographic position, time, social group type and minimum-maximum group size
44 131 were recorded. A whale group was defined by a unique detection source, (i.e. the team that first detected
45 132 the group, either land-based, boat-based or external source such as a whale-watching operator), and may
46 133 have been subsequently followed by both the land- and the boat-based teams. Encounters were
47 134 considered independent events, as repeated observations of the same individual whale within a survey
48 135 day rarely occurred (Derville, Torres, & Garrigue, 2018). The geographic position of groups followed at
49 136 sea was recorded in latitude-longitude using an on-board GPS, whereas groups only followed from land
50 137 were located either with a precise latitude-longitude position in years where a theodolite was used (51%
51 138 of observations), or using a grid of 1 nautical mile resolution (latitude-longitude was subsequently

1 139 extracted as the centre of the grid-cell the whale group was located in; 32% of observations), or by a
2 140 simple textual description of the location (latitude-longitude was subsequently extracted in a GIS
3 141 interface based on these descriptions: <https://explorateur-carto.georep.nc/>; 17% of observations).
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7 142 The influence of external factors on the detection of whales from land and at sea was compared. Daily
8 143 rainfall (in mm) and mean wind conditions (in knots) recorded between 1995 and 2009 were retrieved
9 144 from a weather station based at the Cape N'Doua (22°23'24" 166°55'30", Meteo France). The effect of
10 145 rainfall and wind strength on the number of groups observed at sea or detected from land was assessed
11 146 with sequential GLMs. The daily number of groups observed or detected was modelled with a Poisson
12 147 GLM as a function of time on effort, year and Julian day of year. Then, the residuals from this regression
13 148 were modelled as a function of rainfall (square-root transformed) and wind strength using a linear
14 149 Gaussian regression.
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18 150 The group encounter rates were calculated separately from land and at sea, as the number of groups of
19 151 whales observed per hour of survey effort conducted during each day. In addition, social group types
20 152 observed at sea were defined as: groups of three adults, groups of four adults, competitive groups, female
21 153 with calf, female with calf followed by a single escort, female with calf followed by a competitive group,
22 154 pairs, singletons, and singers. From land, solitary singers could not be differentiated from singletons, and
23 155 groups of three or more adults were pooled in the same category. The proportion of social group types
24 156 observed from land and at sea was calculated for each year. The effect of the observation platform (land
25 157 or sea) and time (breeding seasons from 1995 to 2017) on the proportion of social group types was tested
26 158 with beta regressions using the *betareg* R package (version 3.1-0).
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38 159 **Spatial distribution and habitat use**

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41 160 **Quantifying survey effort at sea** - The distribution of survey effort was estimated annually and
42 161 separately for boat-based and land-based teams. From 2003 to 2017, effort was estimated from boat GPS
43 162 tracklines recorded at one position per minute (about one position every 230 m for a boat moving at 14
44 163 km.h⁻¹). Tracklines were segmented into on-effort (times when the boat-based team was actively
45 164 searching for whales) and off-effort sections (times when the boat was engaged in a focal follow and was
46 165 not vigilant to the detection of another group). Effort was estimated seasonally over 500 × 500 m
47 166 resolution grids. Time spent on-effort per grid cell was calculated, rather than distance travelled, to
48 167 account for variable boat speed. To account for detection distance spanning further than the dimensions
49 168 of a grid cell (average detection distance 2 nm, Garrigue pers. obs.), a density surface of effort was
50 169 derived from discrete boat GPS on-effort positions. Per breeding season, GPS tracks were projected in a
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1 170 UTM coordinate system and a density surface of effort was estimated with a 2-dimension Local
 2 171 Polynomial Regression (LOESS; span = 0.005).

5 172 From 1995 to 2002, research boats were not equipped to record GPS tracklines, a common limitation in
 6 173 marine surveys prior to the mid-2000s. An original method was developed to assess the distribution of
 7 174 survey effort for these seven years. GPS positions recorded over each day (end and start of focal follows,
 8 175 and acoustical sampling positions) were compiled and connected together in a chronological order, thus
 9 176 forming daily paths hereafter referred to as “pseudo-tracklines”. These pseudo-tracklines were
 10 177 considered a subsample of the real tracklines followed by the research boat over the course of a day.
 11 178 Yearly maps of pseudo-effort were produced using a method similar to that applied to real GPS tracklines:
 12 179 they were interpolated at one position/min, sections off-effort were removed, and the remaining positions
 13 180 were smoothed with a LOESS applied with a varying bandwidth (i.e. span ranging from 0.002 and 0.02).
 14 181 After evaluating the quality of each smoothed trackline in comparison to maps of effort after 2003, the
 15 182 0.01 bandwidth was selected to provide the most realistic estimate of pseudo-effort distribution from
 16 183 1995 to 2002 (for details see Supplement S1).

17 184 Finally, yearly maps of pseudo-effort from 1995 to 2002 and yearly maps of effort from 2003 to 2017
 18 185 were concatenated, hence generating a time series of 21 yearly maps of boat-based effort. Yearly maps
 19 186 were rescaled to [0-100], so that cells with maximum intensity across all years were attributed 100%
 20 187 intensity values.

21 188 **Quantifying survey effort from land** - The effect of the number of observers on whale detectability
 22 189 from land was tested with a sequential Generalized Linear Model (GLM, McCullagh & Nelder, 1989).
 23 190 First, the number of groups detected from land per day was modelled as a Poisson variable, relative to
 24 191 time on effort, year and Julian day of year. Residuals from this regression were modelled with a Gaussian
 25 192 linear regression as a function of the number of observers, with values simplified to one for one observer,
 26 193 and two for several observers, based on preliminary tests.

27 194 Daily land-based effort was modelled per grid cell of coordinates (x, y) as a logistic function of distance
 28 195 to the coast:

$$Effort_{land}(x,y,t) = Nobs * Tobs_{land}(t) * \frac{100}{1 + e^{-\sqrt{d(x,y) - 12}}}$$

1 198 where N_{obs} reflected the number of observers on day t , $T_{obs_{land}}(t)$ was the time (in hours) spent on-effort
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3 199 at the Cape N'Doua on day t , and $d(x,y)$ was the distance between the grid cell of coordinates (x, y) and
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5 200 the land-based observatory (in km; for more details see Supplement S2). The logistic curve midpoint was
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7 201 set to 12 km to approximate the average distance from the land-based look-out from which humpback
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9 202 whales were observed ($11.3 \text{ km} \pm 5.9 \text{ SD}$). Effort was set to null for grid cells further than the maximum
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11 203 detection distance from the land-based look-out (36 km). Finally, daily maps of land-based effort were
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13 204 summed together per year to produce yearly maps of land-based effort, which were subsequently rescaled
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15 205 to $[0,100]$, consistent with the boat-based survey effort maps.

16 206 **Spatial distribution** - For each year of survey, the geographic positions of humpback whale groups
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18 207 observed at sea were combined with that of groups observed from land but not at sea. Kernel Density
19
20 208 Estimates (KDE, Worton, 1989) were applied to humpback whale group positions to model yearly areas
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22 209 of use in the South Lagoon. KDE were applied with weights associated to each group positions, to
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24 210 account for survey effort variability across breeding seasons. Values of survey effort intensity were
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26 211 extracted respectively from the yearly maps of sea- or land-based effort at the humpback whale group
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28 212 positions. These extracted values ranging from 0 to 100 were converted to weights ranging from 0 to 10
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30 213 with an inverse function in order to downweight whale positions occurring in highly surveyed areas.
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32 214 Finally, weights at each whale group position were multiplied by group size to provide more weight to
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34 215 positions at which larger groups were observed. As group sizes were not always recorded precisely from
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36 216 land, weights were attributed as follows for land-based observations: 3 for a group of three or more
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38 217 individuals, 2 for a pair, and 1 for singletons and unidentified social group types. KDE were calculated
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40 218 with plug-in bandwidth selector (Hpi) then rescaled to $[0-100]$, either with all years of data pooled
41
42 219 together, or separately for each breeding season. In the latter case, yearly core areas of use were calculated
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44 220 as the 50 % contour of the yearly probability surfaces. The overlap of yearly core areas of use was
45
46 221 calculated from 1995 to 2017 to illustrate the persistence of the humpback whale distribution pattern
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48 222 through time.

49 223 **Habitat variables** - Several topographic environmental variables were collected in the study areas to
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51 224 characterize habitat at a 100 m resolution. Coastline and reef shapefiles were produced by the Millennium
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53 225 Coral Reef Mapping Project (version 8, Andréfouët, Chagnaud, Chauvin, & Kranenburg, 2008). Fringing
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55 226 reefs (in contact with the coastlines) were removed in order to focus on barrier and intermediate patch-
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57 227 reef complexes. Using these shapefiles, distance to the coast and distance to non-fringing reefs were
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59 228 calculated for each 100×100 m cell in the South Lagoon study area as the Euclidean distance to the
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61 229 closest landmass (i.e. New Caledonia mainland, Ouen Island, or the Isle of Pines) and closest barrier or

1 230 patch reef complexes, respectively. Bathymetry data (DTSI, 2016) were provided at a 100×100 m
2
3 231 resolution and gaps in the depth raster were subsequently filled through extrapolation of satellite and
4
5 232 aerial composite imagery (J. Lefèvre, IRD, pers. comm.). Two terrain features were derived from the
6
7 233 bathymetry raster: seabed slope (in degrees) and seabed aspect (the orientation of the slope, in degrees).

8
9 234 **Habitat use model** - The relationship between humpback whale distribution and environmental
10
11 235 conditions was modelled with a Generalized Additive Model (GAM, Hastie & Tibshirani, 1990) using
12
13 236 the R package *mgcv* (version 1.8-23). GAMs were applied to KDE values calculated for all years of
14
15 237 survey from 1995 to 2017. The response variable was modelled with a beta-regression log link function.
16
17 238 Explanatory variables included: depth, distance to the coast, distance to barrier and/or patch-reef
18
19 239 complexes, slope, and aspect. Depth and slope were log-transformed to prevent an inflated influence of
20
21 240 outliers as recommended by Wood (2006). Pearson coefficients were calculated between environmental
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23 241 variables to prevent collinearity (control that $r < 0.5$ for all variables). Smoothed effects of explanatory
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25 242 variables in the GAM were optimized by Restrictive Maximum Likelihood (REML) and cubic smoothing
26
27 243 splines with basis size limited to 5 to prevent overfitting. The descriptive performance of models was
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29 244 assessed through the computation of the proportion of deviance explained (Guisan & Zimmermann,
30
31 245 2000). The deviance explained (%) was calculated from the null deviance (deviance for a model with
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33 246 just a constant term) minus the residual deviance (deviance of the fitted model with explanatory terms).
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35 247 Partial dependence plots were produced to visualize the effect of one variable while all others were held
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37 248 constant at their mean (Friedman, 2001).

38
39 249 **Sea Surface Temperature dynamic patterns** - Monthly sea surface temperature (SST) was obtained to
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41 250 estimate the mean thermal conditions in the area during the austral winter. SST was obtained from the
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43 251 National Aeronautics and Space Administration (NASA) Multi-scale Ultra-high Resolution SST
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45 252 (MURSST) with a 1 km resolution from 2002 to 2017 (<http://coastwatch.pfeg.noaa.gov/erdaap/>). Average SST and associated coefficients of variation were
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47 253 calculated within and across seasons, and mapped over the study region.
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50 254 **RESULTS**

51 255 **Survey from two platforms**

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53 256 Across 21 years of study from 1995 to 2017, 807 days were spent on survey at sea and 790 from land
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55 257 (Table 1). On average, seasonal surveys covered $38.4 \pm \text{SD } 9.5$ days at sea and $37.6 \pm \text{SD } 9.9$ from land.
56
57 258 Most of the survey effort was conducted simultaneously by both teams, on land and at sea, totalling 714

1 260 days of survey in common over the study period. As a result, the team at sea was assisted by the land
2 261 based observers during 88% of the days of survey.

3 262 The land-based team followed 2,021 groups of humpback whales ($96.2 \pm \text{SD } 60.2$ per year), of which
4 263 1,167 (57.8%) were not followed by the boat-based team (Figure 2, Table 1). The boat-based team
5 264 followed 1,484 groups ($70.7 \pm \text{SD } 33.4$ per year), of which 30.2 % were originally detected by the land-
6 265 based team who communicated the position through VHF.

7 266 The number of observers from land varied between 1 and 5 (mean = $2.0 \pm \text{SD } 0.9$, number reported for
8 267 737 survey days out of 790), and was greater than 1 in 64 % of survey days. The number of humpback
9 268 whale groups detected from the Cape N'Doua was significantly higher when more than one observer was
10 269 surveying. A null model was created to account for the effect of year, Julian day of year and duration of
11 270 survey effort, on the daily number of groups detected from land. The residuals of this null model were
12 271 significantly affected by the number of observers (GLM: $t\text{-value} = 7.1$, $p < 0.001$). On average, $2.0 \pm \text{SD}$
13 272 1.3 groups were observed when one observer was present, against $2.7 \pm \text{SD } 2.6$ with several observers.

14 273 Between 1995 and 2009, wind and rainfall were measured over 453 days of survey. Wind strength varied
15 274 from 4 to 27 knots (median = 13.6 knots; mean = $14.1 \pm \text{SD } 4.8$ knots) and daily rainfall varied from 0
16 275 to 61 mm (median = 0 mm; mean = $1.2 \pm \text{SD } 4.0$ mm). A null model was produced to relate the daily
17 276 number of groups detected from land, to year, Julian day of year and duration of survey effort. The
18 277 residuals of this null model were not significantly affected by rainfall (GLM: $t\text{-value} = 0.4$, $p = 0.7$) nor
19 278 wind strength (GLM: $t\text{-value} = 1.6$, $p = 0.1$). Among these 453 days, 412 days were surveyed at sea. A
20 279 null model was produced to relate the daily number of groups observed at sea, to year, Julian day of year
21 280 and duration of survey effort. The residuals of this null model were not significantly affected by rainfall
22 281 (GLM: $t\text{-value} = 0.2$, $p = 0.8$), but showed a small significant effect of wind strength (GLM: $t\text{-value} = -$
23 282 2.3 , $p = 0.02$). The number of groups observed at sea decreased with stronger winds.

23 283 **Occurrence and social composition**

24 284 In total, 2,651 independent whale groups were observed from land and at sea (Figure 2), with a maximum
25 285 number of occurrences observed in 2007 ($n = 264$; Table 1). When accounting for survey effort per day,
26 286 the mean group encounter rates showed an increasing trend from 1995 to 2017, both at sea (Figure 3a),
27 287 and from land (Figure 3c). Both platforms showed a very similar trend, notably with a steeper increase
28 288 between 2005 and 2011, a low group encounter rate in 2014 (< 0.3 groups per hour of survey), and a
29 289 plateau with a slight decrease after 2012.

1 290 Social group types typical of a humpback whale breeding ground were observed at sea across all years:
2 291 maternal females with a calf, competitive groups and singers (Table 2, Figure 3b). A larger proportion
3 292 of group types remained unidentified by land-based observers ($29.8 \% \pm 20.1$) compared to observers at
4 293 sea ($1.7 \% \pm 2.3$, Figure 3d), as noted in a beta-regression relating the proportion of unidentified groups
5 294 to platform (z-value = 7.3, $p < 0.0001$).

6 295 Combined together, the proportion of social group types observed from both platforms did not show any
7 296 linear trends from 1995 to 2017. This analysis included groups with calf (mother-calf pairs, mother-calf
8 297 pairs with escort or competitive groups; beta-regression: z-value = 1.2, $p = 0.2$), groups of adults (beta-
9 298 regression: z-value = 1.7, $p = 0.8$), pairs (beta-regression: z-value = -0.2, $p = 0.8$), singleton (including
10 299 singers; beta-regression: z-value = -1.9, $p = 0.05$), and unidentified social types (beta-regression: z-value
11 300 = 1.9, $p = 0.05$).

12 301 **Spatial distribution**

13 302 A core area of use for humpback whales was identified outside the Prony Bay, between the two main
14 303 reef complexes of the South Lagoon, the Corne Sud to the south-west and the Merlet reserve to the north-
15 304 east (Figure 4a). Humpback whales were also found to display a noteworthy use of the inner waters of
16 305 the Prony Bay. Yearly core areas of use showed a strong overlap, in a zone located at the centre of the
17 306 study area (Figure 4b). Persistent use was found over a 77 km² zone that was included in yearly core
18 307 areas of use for at least 10 years (Figure 4b). There was no overlap between the core area of use and the
19 308 Merlet Reserve (0 % coverage, Figure 4a, Table 3), and only a limited overlap with the UNESCO World
20 309 Heritage zone (38 % coverage). On the other hand, the Province Park included 100 % of the core and
21 310 general areas of humpback whale use (Table 3).

22 311 **Habitat use**

23 312 Depth (edf = 3.8, $\text{Chi}^2 = 575.7$, $p < 0.001$), distance to coast (edf = 2.0, $\text{Chi}^2 = 1081.2$, $p < 0.001$), distance
24 313 to barrier and patch reef complexes (edf = 1.9, $\text{Chi}^2 = 63.3$, $p < 0.001$), and seabed slope (edf = 2.0, Chi^2
25 314 = 145.3, $p < 0.001$) were significant predictors of humpback whale habitat in the South Lagoon (GAM,
26 315 deviance explained = 36.6%). The occurrence of humpback whales increased with proximity to coast in
27 316 the South Lagoon. Humpback whales were less frequently found in close contact to coral reef complexes
28 317 (< 2 km from a reef). Seabed slopes of more than 2° were favoured, though there are few high values of
29 318 slope in the dataset. Humpback whale occurrence patterns displayed a complex relationship with respect
30 319 to depth: both very shallow waters (10 m) and relatively deep waters (50 - 100 m) were predicted to be

1 320 suitable habitats. The modelled probability of presence reached a plateau when depth was greater than
2 321 100 m indicating that deeper waters may also be suitable, although there were little data collected at such
3 322 depth within the South Lagoon, as revealed by the rug plot associated to this variable (Figure 5).

6
7 323 SST patterns averaged over the study area from 2002 to 2017 revealed that waters located in the north-
8 324 western limit of the study area near Ouen Island were consistently colder during the winter (Figure 6).
9 325 The core area of use for humpback whales was characterized by average temperatures between 22°C and
10 326 22.4°C. Moreover, SST in the core area of use for humpback whales was the most stable in the winter
11 327 (within and between breeding seasons), in contrast with the eastern coast of New Caledonia and the Isle
12 328 of Pines under influence of the Vauban current (Figure 1). Indeed, standard deviation of the MURSST
13 329 in winter was highest in the north-eastern part of the study area (Figure 6).

21 22 330 **DISCUSSION**

23
24 331 This study provides information on the long-term occurrence patterns of an endangered population of
25 332 humpback whales seasonally present in the New Caledonia South Lagoon. Occurrence of humpback
26 333 whales in the South Lagoon was found to have increased between 1995 and 2017. The distribution and
27 334 social composition of the population visiting the area in the austral winter, between July and September,
28 335 was stable across years. Females with a calf were observed every year, as well as other social group types
29 336 typical of humpback whale breeding grounds, such as competitive groups. Persistent habitat use patterns
30 337 were robustly modelled using two complementary long-term datasets extending over more than two
31 338 decades. However, a mismatch was found between habitats favoured by humpback whales and currently
32 339 existing marine protected areas in the South Lagoon.

33 340 Although many of the most studied cetacean species live in coastal waters, the use of land-based lookouts
34 341 for the purpose of scientific research is uncommon. Indeed, many cetacean studies favour the collection
35 342 of biological samples and photographs that cannot be collected from land but that provide valuable
36 343 information on individuals (e.g. Garrigue et al., 2004) for studying behaviour, life history and
37 344 demography. In addition, unless the cetaceans are very close to shore (e.g. Stockin, Weir, & Pierce, 2006),
38 345 group sizes and behaviours are generally more accurately measured during focal follows at sea than from
39 346 land. Here, many of the groups observed only from land were not ascribed a social type, and groups of
40 347 more than three individuals were all pooled in the same category, with no distinction of group size or
41 348 competitive behaviour. On the other hand, compared to surveys at sea, land-based surveys have the great
42 349 advantages of being cheaper, less technically challenging and not impactful for animals (Aragones,

1 350 Jefferson, & Marsh, 1997; Giacoma, Papale, & Azzolin, 2013). They have been successfully applied to
2 351 monitor the impact of whale watching and maritime traffic (e.g. Avila, Correa, & Parsons, 2015; Schaffar
3 351 et al., 2013; Stamation, Croft, Shaughnessy, Waples, & Briggs, 2010; Sullivan & Torres, 2018). Here,
4 352 the land-based team had greater spatial and temporal detectability of whales than the boat-based
5 352 observers, as the team could survey a larger extent, and was capable of following several groups at the
6 353 same time. For instance, the Merlet integral reserve was consistently surveyed by the land-based team
7 353 throughout the study period, whereas the research boat was only permitted to enter the area during half
8 354 of the study years (1996-2008 and 2015, Figure 2). Similarly, land-based lookouts have been used in
9 354 support of boat-based survey teams in other parts of the world to increase the detection of smaller
10 355 cetacean species (e.g. Risso dolphin, *Grampus griseus*, Hartman et al., 2014). Considering the relatively
11 356 low cost of adding a team on land when a boat-based monitoring programme is already in place, this
12 356 study supports the synergic advantages of combining these two platforms of observation when a land-
13 357 based look-out is available in the study area.
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24 363 In recent decades, ecological research methods have undergone tremendous technological advances. One
25 363 indirect drawback is the potential to alter the consistency of survey protocols used in long-term studies.
26 364 In the South Lagoon humpback whale monitoring program, as in many marine long-term studies, the
27 364 incorporation of onboard GPS tracking has greatly improved the quality of spatial data collected. Indeed,
28 365 tracklines represent an essential piece of information to spatially quantify survey effort (Derville, Torres,
29 366 Iovan, & Garrigue, 2018), but were only recorded from 2003 onwards in this study. In order to maintain
30 366 the integrity of the 20-year long dataset collected in the South Lagoon, survey effort at sea was
31 367 approximated using “pseudo-tracklines” (see Supplement S1). This method was based on acoustic
32 367 sampling and group locations, but it may be applied to any ‘location data’ recorded during a day of survey
33 368 at sea (e.g. environmental sampling locations). Using this approach on this long-term dataset, a general
34 368 trend of increasing group encounter rates was identified throughout the study period, both at sea and from
35 369 land. Anomalous years in the trend may be explained by slight changes in the seasonality of survey effort,
36 370 such as in 2014 when the mid-August breeding season peak was exceptionally not surveyed. Combining
37 370 several lines of evidence, this study supports the ongoing recovery of the New Caledonia endangered
38 371 humpback whale subpopulation.
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51 378 Maternal females, competitive groups and singers were almost constantly observed across breeding
52 378 seasons, reflecting consistent mating and nursing activity in the South Lagoon. Although calving of
53 379 humpback whales has never been directly observed in the South Lagoon, as in the majority of the
54 380 breeding sites worldwide (Faria, DeWeerd, Pace, & Mayer, 2013), it is assumed to occur within or close
55 380 to the study area.

1 382 to this breeding ground. Indeed, calves with newborn traits (pale flank pigmentation, small size and furled
2 383 dorsal fin; Cartwright & Sullivan, 2009; Irvine, Thums, Hanson, McMahon, & Hindell, 2017) are
3 384 regularly observed in the South Lagoon (Derville, Torres, & Garrigue, 2018). Overall, the core area of
4 385 humpback whale distribution was located at the centre of the study area, bounded by the coast and two
5 386 large reef complexes. Although humpback whales are observed sporadically in coastal waters and
6 387 lagoons all over the New Caledonian archipelago (Derville, Torres, Iovan, et al., 2018; Garrigue & Gill,
7 388 1994), the South Lagoon appears to be the most visited coastal breeding site (Garrigue et al., 2001). This
8 389 aggregation is likely to be at least partially driven by social factors (Clapham & Zerbini, 2015), but it
9 390 may also be linked to environmental conditions specific to this area. In the core area of humpback whale
10 391 distribution, SST averaged 22 - 22.5°C in the austral winter, a temperature that is well within the
11 392 preferential SST range identified by Rasmussen et al. (2007). The SST in the core area of use was also
12 393 relatively stable both within and between years, compared to the surrounding open ocean. Spatio-
13 394 temporal predictability of resources, or suitable environmental conditions, is an important driver of
14 395 spatial distribution in the ocean (Lambert et al., 2016; Scales et al., 2014). The persistence of temperature
15 396 conditions in the South Lagoon could contribute to its attractiveness for maternal females that can rely
16 397 on this area to provide suitable habitat to their calf.

17 398 Habitat models suggest a preference for nearshore shallow waters in accordance with other humpback
18 399 whale breeding grounds around the world (Bortolotto, Danilewicz, Hammond, Thomas, & Zerbini, 2017;
19 400 Cartwright et al., 2012; Lindsay et al., 2016; Martins et al., 2001; Oviedo & Solís, 2008; Smith et al.,
20 401 2012; Trudelle et al., 2018). However, the modelled habitat relationships also suggested that whales may
21 402 be found in the relatively deep waters in the southern part of the study area (about 200 m deep). The
22 403 modelled occurrence was relatively high in these conditions but was associated with a strong uncertainty.
23 404 Nevertheless, this result is consistent with satellite tracking of individual humpback whales from this
24 405 region that moved between the South Lagoon and several seamounts located south of the Isle of Pines
25 406 (i.e. Torch Bank and Antigonía seamount, Garrigue, Clapham, Geyer, Kennedy, & Zerbini, 2015).
26 407 Antigonía seamount is now known as an important breeding ground (Derville, Torres, & Garrigue, 2018;
27 408 Garrigue et al., 2017). Frequent movements between these hotspots (Garrigue et al., 2017; Orgeret,
28 409 Garrigue, Gimenez, & Pradel, 2014) may explain the relatively high occurrence of whales in the
29 410 southernmost part of the South Lagoon.

30 411 The relationship to coral reef complexes was not linear and showed that humpback whales occurred in
31 412 waters neighbouring reefs (3-4 km) but not directly next to them. In contrast, distance to coral reef was
32 413 not identified as a primary factor influencing humpback whale distribution in other breeding grounds that

1 414 include large reef extents (e.g. Great Barrier Reef, Smith et al. 2012), except when considering maternal
2 415 females only (e.g. Vava'u, Tonga, Lindsay et al. 2016). In Vava'u, females with a calf preferentially used
3 416 the sheltered waters inside the reef complexes, whereas groups with no calf occupied deeper waters on
4 417 the external slope. In the South Lagoon, groups with and without a calf do not segregate with respect to
5 418 reef habitats but rather relative to proximity to the coastline (Derville, Torres, & Garrigue, 2018). Dense
6 419 reef complexes of the South Lagoon appeared to be avoided by all social group types. Indeed, dense and
7 420 shallow reef areas form intricate networks that have the potential to trap large whales. Also, seabed terrain
8 421 and depth are known to affect sound propagation (Mercado III & Frazer, 1999), hence potentially
9 422 constraining the spatial distribution of singing males. Rugged (Pack et al., 2017) and/or shallow habitats
10 423 (Mercado III & Frazer, 1999), such as that of the South Lagoon reef complexes could be less suitable for
11 424 acoustic communication, and therefore less attractive for singers and their audience. Based on these
12 425 distributional preferences, the Merlet integral reserve (IUCN category Ia) was rarely used by humpback
13 426 whales in the New Caledonia South Lagoon. The UNESCO World Heritage Zone also mostly
14 427 mismatched the humpback whale core area of use. The Province Park did include the area of humpback
15 428 whale use, but only offers a very low level of protection. As human activities such as maritime traffic
16 429 and tourism are not regulated within the Park, humpback whales potentially remain at risk of disturbance
17 430 and collisions. There is no marine protected area specifically dedicated to the mitigation of anthropogenic
18 431 impacts on cetaceans in New Caledonia. Moreover, it appears that the existing conservation areas with
19 432 high levels of protection in the South Lagoon do not overlap with critical habitats of this endangered
20 433 subpopulation of humpback whales.

21 434 Group encounter rates measured per year from both platforms of observations support the increase in the
22 435 population sizes that was independently estimated from capture-recapture using photo-identification and
23 436 genotype data (C. Garrigue, Albertson, & Jackson, 2012; Jackson et al., 2015; Orgeret et al., 2014).
24 437 However, this encouraging sign of recovery of a humpback whale subpopulation in Oceania should be
25 438 put in perspective with emerging threats in the region. Coastal breeding grounds are particularly exposed
26 439 to increasing anthropogenic threats resulting from touristic and industrial activities. Whale watching
27 440 activities are growing in popularity (O'Connor, Campbell, Knowles, Cortez, & Grey, 2009), and are an
28 441 increasing source of income in the Pacific Islands. Although observation guidelines exist for the region
29 442 (Province Sud, 2018), the ever increasing number of boats in the area during the winter is a current cause
30 443 of concern (Bourgogne et al., 2018). Land-based whale watching exists in a few regions of the world
31 444 (e.g. Cook Islands, South Africa, Australia, O'Connor et al. 2009) and could be further promoted in New
32 445 Caledonia as an alternative to boat-based tours. Moreover, the identification of the core area of humpback

1 446 whale use in the South Lagoon constitutes a first step towards the mitigation of collision risks around
2 447 shipping lanes (Dransfield et al., 2014; Pirotta, New, & Marcoux, 2018; Redfern et al., 2013). As the
3 448 New Caledonian subpopulation of humpback whales progressively recovers, private and public boat
4 449 drivers should be educated about risks to whales and where they are likely to be distributed to anticipate
5 450 increased collision risks in the areas of greatest humpback whale use. Efforts to prevent collisions should
6 451 particularly target females with a calf as these groups are most vulnerable to disturbance and ship strikes
7 452 (Cartwright et al., 2012; Laist, Knowlton, Mead, Collet, & Podesta, 2001; Lammers, Pack, & Davis,
8 453 2007), and also favour the sheltered waters closest to the coast where maritime traffic is the most intense
9 454 in the South Lagoon (Derville, Torres, & Garrigue, 2018). Finally, as humpback whale conservation was
10 455 identified as one of the main objectives for the South Lagoon Province Park (Province Sud, 2013), we
11 456 suggest that future management plans and zoning explicitly incorporate seasonal regulations of boat
12 457 traffic and recreational activities within their core area of use. Hence, by using a long-term monitoring
13 458 approach, this study provides important information to ensure the continued recovery of an endangered
14 459 subpopulation of humpback whales.

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29
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TABLES

Table 1: Summary of survey effort and observations of humpback whales at sea and from land in the South Lagoon, New Caledonia, from 1995 to 2017. (#) indicates the number of humpback whale groups. “# unique groups observed” is the sum of all the groups observed at sea and the groups observed from land only.

year	boat-based effort (days)	land-based effort (days)	# groups observed at sea	# groups detected from land	# groups observed from land only	# unique groups observed
1995	27	18	25	24	13	38
1996	55	48	54	82	45	99
1997	44	41	53	54	29	82
1998	50	52	42	50	21	63
1999	46	43	23	22	11	34
2000	50	43	44	25	10	54
2001	55	47	77	56	36	113
2002	33	38	20	6	4	24
2003	39	42	70	28	23	93
2005	33	25	56	35	27	83
2006	41	47	103	124	100	203
2007	48	49	124	162	140	264
2009	32	48	67	126	126	193
2010	36	38	97	138	84	181
2011	39	38	133	154	113	246
2012	29	30	96	105	81	177
2013	25	27	96	112	55	151
2014	29	23	38	28	9	47
2015	31	29	99	131	101	200
2016	26	25	61	50	41	102
2017	39	38	106	73	98	204
Total	807	789	1,484	1,585	1,167	2,651
Mean	38.4	37.6	70.7	75.5	55.6	126.2
SD	9.5	9.9	33.4	49.5	43.5	74.2

Table 2: Average proportion of humpback whale social group types observed across years at sea and from land in the South Lagoon, New Caledonia, from 1995 to 2017. Average proportion are indicated with \pm standard deviations. CG - represents Competitive Groups. From land, groups of more than 3 individuals with or without a calf were not distinguished, neither were singers from non-singing singletons.

	Female-calf	Female-calf-escort	Group		Solitary		Pair	Unidentified
			Female-calf-CG	CG	Singleton	Singer		
Boat-based observations	13.9 \pm 7.7	1.8 \pm 1.6	1.1 \pm 1.3	14.2 \pm 5.0	24.5 \pm 6.9	6.2 \pm 4.1	32 \pm 5.6	1.7 \pm 2.3
Land-based observations	2.9 \pm 3.6	0.2 \pm 1.0	10.0 \pm 6.3		35.0 \pm 18.7		22.1 \pm 8.3	29.8 \pm 20.1

For Peer Review

Table 3: Percentage of coverage of the humpback whale area of use by Marine Protected Areas in the New Caledonia South Lagoon. The area of use is estimated from the Kernel Density Estimates (KDE) presented in Figure 2a.

	Province Park	UNESCO Heritage Zone	Merlet Reserve
50 % KDE contour (core area of use)	100 %	38 %	0 %
95 % KDE contour (general area of use)	100 %	55 %	2 %

For Peer Review

FIGURES

Figure 1: Map of New Caledonia (a) and the South Lagoon study area (b). Main currents are illustrated on the map based on Marchesiello et al. (2010) and Cravatte et al. (2015): ECC = East Caledonian Current; VC = Vauban Current; ACNC = Alis Current of New Caledonia. The ECC is a local branch of the larger scale South Equatorial Current. Upwellings and downwellings are represented with black curved arrows. Land is shown in black. Barrier and patch reef complexes in grey. The Province Park is shown with a black dashed line, the UNESCO World Heritage Zone with a black dotted line, and the Merlet Reserve with a black dashed and dotted line. Blue sail boats logos locate the harbours from which whale watching boat operators depart for daily trips (in Nouméa, and also mostly in Prony Bay). The mining Port of Goro inside the Prony Bay is shown with a red cargo logo. The zones with the most intense maritime traffic interpreted from records of the Automatic Identification System (AIS, www.marinetraffic.com) are delineated by a red polygon.

Figure 2: Map of humpback whale groups observed in the South Lagoon, New Caledonia, between 1995 and 2017: groups observed at sea (a; $n = 1,484$) and groups observed from land only (b; $n = 1,167$). The dotted lines represents the study area at sea and from land respectively. In panel (b), areas filled with dashes could not be observed from the land-based lookout, and represent 29% of encircled study area. Land is shown in black, barrier and patch reef complexes in grey. Isobaths are represented with light grey lines. The limits of the Merlet Reserve are indicated with a black dashed and dotted line.

Figure 3: Breeding season group encounter rates and social group types measured in the South Lagoon, New Caledonia, between 1995 and 2017. (a) Group encounter rates at sea ($n = 1,484$ groups observed over 807 days), and (c) from land only ($n = 1,150$ groups observed over 752 days during which survey effort duration was recorded), per hour of survey effort and per day. The lower and upper hinges of the boxplot correspond to the first and third quartiles. Proportions of social group types observed per year (%) using each platform is represented in stacked colour bars: (b) at sea, and (d) from land.

Figure 4: Kernel density estimates (KDE) of humpback whale distribution in the South Lagoon, New Caledonia, between 1995 and 2017. (a) KDE based on unique observations at sea and from land over the whole study period ($n = 2,651$). KDE values below 5% are not shown. White lines delineate 10% contours of the KDE from 10% to 100%. The 50 % contour, or core area of use, is represented with a black line. (b) Overlap between 50% contours of annual KDE (colours represent the numbers of years over which the grid cell was included in a 50% contour). The black line delineates the area where more than 10 years of core areas overlap (77 km^2). Observations are weighted proportionally to the number of individuals in

1 the group and the amount of survey effort. Land is shown in black and reefs in grey. The Province Park
2 is shown with a black dashed line, the UNESCO World Heritage Zone with a black dotted line, and the
3 Merlet Reserve with a black dashed and dotted line.
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7 Figure 5: Partial dependence plots modelling habitat selection of humpback whales from combined boat-
8 and land-based surveys in the South Lagoon, New Caledonia between 1995 and 2017. Predicted habitat
9 suitability is shown on the y-axis with varying scales. Rug plots illustrate the distribution of values in the
10 modelled dataset in percentiles.
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14 Figure 6: Sea Surface Temperature (SST) in the South Lagoon, New Caledonia, averaged from MURSST
15 (jplMURSST41, <http://coastwatch.pfeg.noaa.gov/erdaap/>) between July and August, 2002-2017. (a)
16 Mean austral winter SST averaged across 16 years. (b) Coefficient of variation of SST calculated across
17 16 years. (c) Coefficient of variation of SST calculated across 3 months of austral winter and averaged
18 over 16 years. Land is shown in black and reefs in grey. White lines delineate contours of the SST patterns.
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25 **SUPPORTING INFORMATION**

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28 S1: Estimating boat-based survey effort without GPS tracklines
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30 S2: Estimating land-based survey effort
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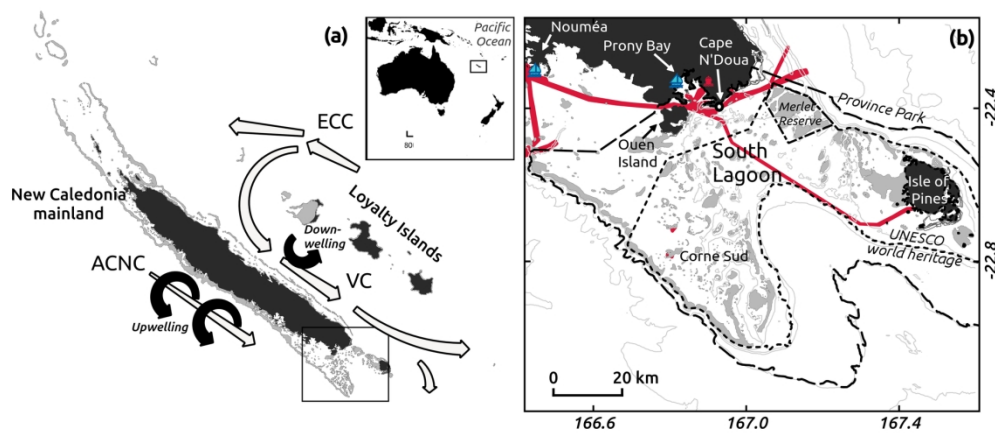


Figure 1

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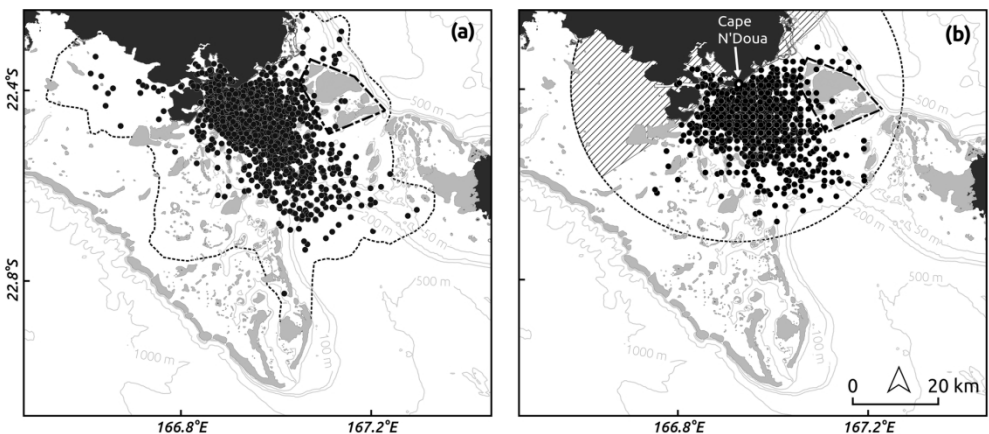


Figure 2

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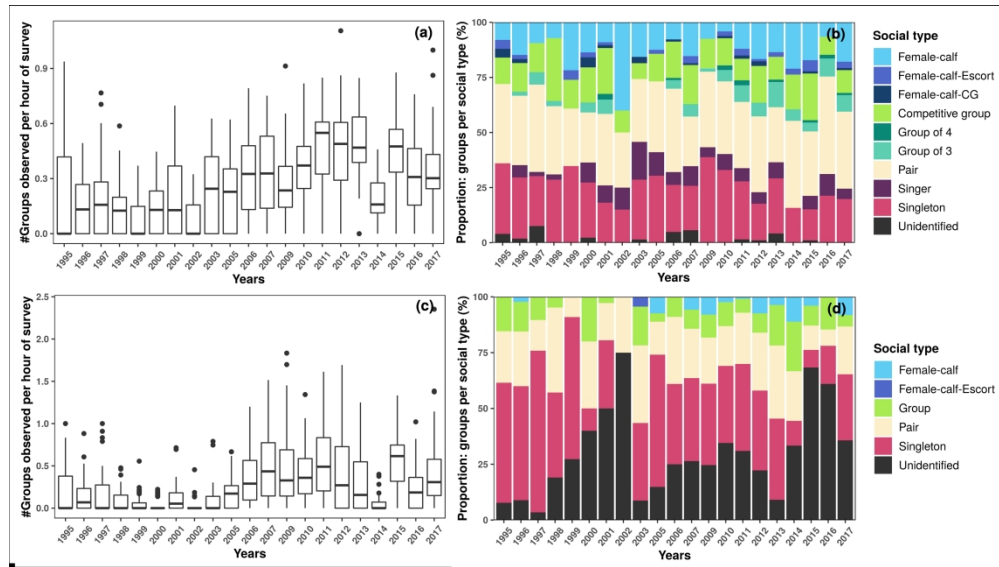


Figure 3

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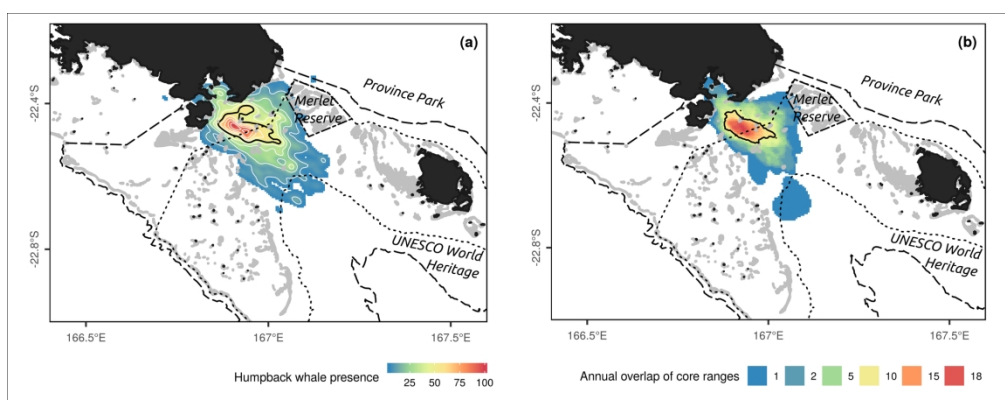


Figure 4

203x78mm (300 x 300 DPI)

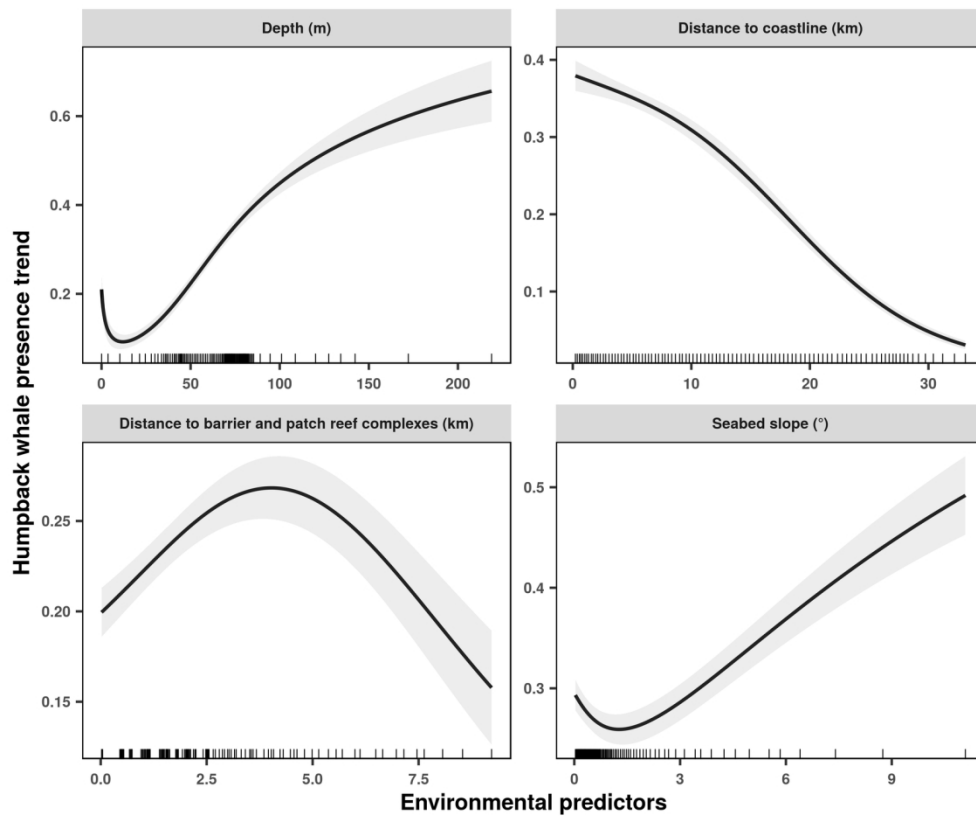


Figure 5

152x127mm (300 x 300 DPI)

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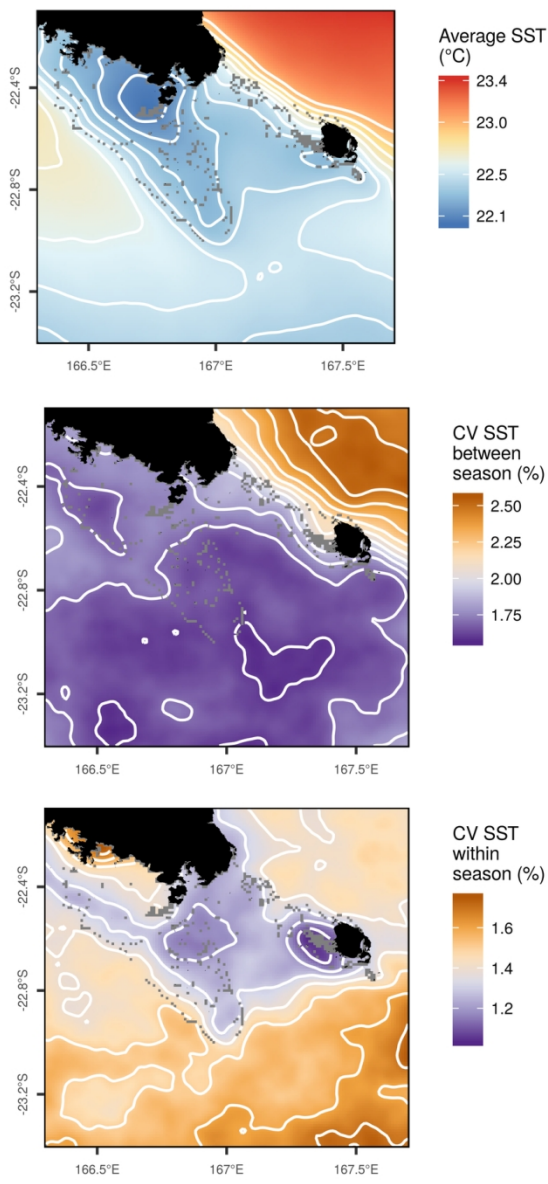


Figure 6

78x159mm (300 x 300 DPI)