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

Solène Derville, Leigh Gabriela Torres, Rémi Dodémont, Véronique Perard, Garrigue Claire

AQUATIC CONSERVATION
Marine and Freshwater Ecosystems

From land and sea, long-term data reveal persistent humpback whale breeding habitat in New Caledonia

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

Solène Derville[1,2,3,4*], Leigh G. Torres[3], Rémi Dodémont[4], Véronique Perard[4], Claire Garrigue[1,4]

[1]UMR ENTROPIE (IRD, Université de La Réunion, CNRS), New Caledonia.

[2]Sorbonne Université, Collège Doctoral, ED129, France.

[3]Geopsatial Ecology of Marine Megafauna Lab, Marine Mammal Institute, Department of Fisheries and Wildlife, Oregon State University, Newport, Oregon, USA.

[4]Opération Cétacés, New Caledonia.

*Corresponding author: solene.derville@ird.fr

1   **ABSTRACT**

2   1. Long-term monitoring is a prerequisite to understand and protect long-lived species such as
3   cetaceans. In New Caledonia, South Pacific, an endangered subpopulation of humpback whales
4   (*Megaptera novaeangliae*) seasonally congregates for mating and nursing during the austral
5   winter. For more than two decades, dedicated surveys have been conducted at sea and from land
6   to monitor humpback whale presence in a coastal breeding site, the South Lagoon.

7   2. Methods were developed to investigate space use patterns and their temporal variations over the
8   long term using a joint dataset of boat-based and land-based observations (1995 - 2017). A total
9   of 2,651 humpback whale groups were observed, including 1,167 from land and 1,484 at sea (of
10   which 30% were initially detected by the land-based observers).

11   3. Humpback whales displayed a persistent space use pattern over this 23 year period, consistent
12   social composition over the years, and an increase of the group encounter rates from land and at
13   sea. The core area of use by humpback whales was characterized in the austral winter by stable
14   and relatively low sea surface temperature (22°C). Whales consistently occupied nearshore
15   waters from 10 to 200 m deep and open to the ocean. Waters surrounded by dense coral reefs
16   were avoided.

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

KEYWORDS

Coastal, habitat mapping, lagoon, mammals, monitoring, recovery, recreation, shipping

INTRODUCTION

Industrial whaling of the 19th and 20th century greatly impacted humpback whale (*Megaptera novaeangliae*) populations worldwide (Rocha, Clapham, & Ivashchenko, 2015). Today, humpback whale populations globally show encouraging signs of recovery, yet are variable from one population to the other (Thomas, Reeves, & Brownell, 2015). As humpback whales are now facing the cumulative effects from threats of pollution, vessel traffic, entanglement, noise or tourism resulting from increasing anthropogenic activities (Avila, Kaschner, & Dormann, 2018), there is a need to monitor populations at a local scale. Understanding the trends in distribution, habitat use and dynamics of populations is essential to implementing appropriate local conservation measures, and ensure the species recovery as a whole.

The slow breeding rate (i.e. generation time 21.5 yr, Taylor, Chivers, Larese, & Perrin, 2007) and long life-span (i.e. 95 yr, Chittleborough 1965; Gabriele, Lockyer, Straley, Jurasz, & Kato, 2010) of humpback whales warrants long-term datasets in order to detect potential trends in distribution and population demographics. Thereby, monitoring programmes conducted over several decades have greatly contributed to the knowledge and protection of humpback whales, for example in Glacier Bay (Gabriele et al., 2017; Pierszalowski et al., 2016) or the Gulf of Maine (Robbins, 2007). However, such long-term datasets are rarely available (Sydeman, Poloczanska, Reed, & Thompson, 2015), as the high financial cost and challenging survey environment characterizing cetacean studies are obvious obstacles to the implementation of research projects over several decades (Simmonds & Eliott, 2009). Also, once actually collected, long-term datasets often constitute data processing and statistical challenges, particularly due to protocol mismatches (Ducklow, Doney, & Steinberg, 2009; Lindenmayer & Likens, 2010) regarding the extent of survey effort and the evolution of methods used across several years or decades.

46　The Oceania population of humpback whales is relatively small, has one of the slowest recovery rates

47　(Constantine et al., 2012; Jackson et al., 2015) and is still listed as "endangered" in the IUCN Red List

48　(Childerhouse et al., 2008). Humpback whales of the Oceania population feed during the austral summer

49　in the remote waters of the Southern Ocean, from the Balleny Islands to the Antarctic peninsula

50　(Albertson et al., 2018; Constantine et al., 2014; Riekkola et al., 2018; Steel et al., 2017). During the

51　austral winter, they migrate to breeding grounds in the South Pacific islands and reefs, where mating,

52　calving and nursing take place. Various degrees of subpopulation structuring have been identified across

53　this vast area (Constantine et al., 2012; Olavarría et al., 2007) and the International Whaling Commission

54　recognizes several breeding sub-stocks including BSE2 in New Caledonia, BSE3 in Tonga and BSF in

55　French Polynesia (IWC, 1998; Jackson et al., 2015). Among the widely dispersed breeding grounds

56　found across Oceania, humpback whale research has only been carried out in a few specific study sites.

57　New Caledonia is the most westerly archipelago visited by the endangered humpback whale population

58　of Oceania. Humpback whales found in this archipelago are demographically isolated and genetically

59　differentiated from the two neighbour breeding populations of eastern Australia and Tonga (Garrigue,

60　Dodemont, Steel, & Baker, 2004; Olavarría et al., 2007). The New Caledonia South Lagoon (Figure 1)

61　is historically considered one of the main humpback whale breeding grounds known to date for this

62　subpopulation (Garrigue, Greaves, & Chambellant, 2001). Humpback whales at this breeding site have

63　been the focus of a continuous long-term monitoring programme (Garrigue et al., 2001) initiated in the

64　mid-1990s, which has documented humpback whale presence in the South Lagoon during the austral

65　winter, with a peak of abundance after mid-August. Humpback whales in this coastal study site have

66　been consistently monitored for more than 20 years using an original protocol combining boat-based and

67　land-based observation.

68　The New Caledonia South Lagoon also concentrates several human activities that constitute liable threats

69　to whales. Active nickel mining on the mainland has induced increased maritime traffic of large cargo

70　ships, specifically in the Prony Bay where an industrial port was constructed in 2006 following the

71　development of a new hydrometallurgical process plant (Bourgogne, Derville, & Garrigue, 2018, Figure

72　1). New Caledonia also is a leading whale watching destination among the South Pacific Islands

73　(Schaffar, Garrigue, & Constantine, 2010; Schaffar et al., 2013; Figure 1). Since 2008, humpback whales

74　have been legally protected by the local environmental legislation that forbids deliberate disturbance,

75　specifically approaching whales closer than 50 m or observing whales within less than 200 m for over 2

76　hours (Province Sud, 2009). In addition, observations guidelines have been proposed to promote

77　responsible whale watching behaviour (Province Sud, 2018). Yet, increasing tourism and human

3

78 population density (www.isee.nc) is a cause of concern in terms of disturbance and collision risks (Currie,

79 Stack, & Kaufman, 2017; New et al., 2015; Senigaglia et al., 2016). In the South Lagoon, the number of

80 whale watching touristic operators has increased from 5 in 1995, to 24 in 2017 (Province Sud &

81 Opération Cétacés, unpublished data). An integral marine protected area, the Merlet Reserve, was created

82 in 1970 to prevent all human activities over a 170 km² area north-east of the South Lagoon (IUCN

83 category Ia, Figure 1). A great part of the South Lagoon is also classified as a UNESCO World Heritage

84 Zone (UNESCO, 2009), as well as a Province Park (roughly equivalent to IUCN category II, Figure 1)

85 but the level of protection provided by these zones is very low as it imposes few restrictions on human

86 activities. The management objective of the South Lagoon Province Park is to ensure the stability of

87 ecological processes and preserve the natural equilibrium by regulating the activities and needs of the

88 local population (Cleguer, Grech, Garrigue, & Marsh, 2015). In practice, the Province Park management

89 plan allows public use of the Park, including fishing and recreational activities, but prevents industrial

90 pollution and mining (Province Sud, 2013). The contribution of these protected areas to the conservation

91 of critical habitats for humpback whales has never been investigated.

92 In the context of a population recovering from industrial whaling and facing growing human pressure,

93 this study aims to assess the ecological value of the New Caledonia South Lagoon as a breeding site by

94 an endangered humpback whale subpopulation. This study is based on the long-term monitoring

95 occurring 30 years after commercial whaling of this species ended in the Southern Hemisphere. A dataset

96 of simultaneous boat-based and land-based surveys is used to evaluate humpback whale occurrence,

97 social composition, spatial distribution and habitat use in the New Caledonia South Lagoon, over more

98 than 20 years (a quarter of a humpback whale's maximum life span). Finally, the current level of

99 protection against potential threats is evaluated, and recommendations are provided to improve future

100 conservation of this endangered population.

METHODS

Study region and survey design

103 New Caledonia is an archipelago located in the south-west Pacific Ocean about 1,500 km north-east of

104 Australia (Figure 1). New Caledonia mainland, also called "Grande Terre", is surrounded by a large

105 lagoon delimited by a 1,500 km-long barrier reef. The South Lagoon is a large shallow area (about 50 m

106 deep) located south of the mainland, bounded by the Prony Bay and the Ouen Island to the north, and by

107 two reef complexes to the south-west ("Corne Sud") and the north-east (Isle of Pines, Figure 1). The

4

108   south-eastern part of this lagoon is open to the ocean and is characterized by deeper waters (reaching 600

109   m deep). New Caledonia is under the influence of two main currents: the highly unstable south-eastward

110   Vauban Current (VC) flows south through the Loyalty channel bringing warm waters in winter. In

111   contrast, the south-eastward Alis Current of New Caledonia (ACNC) carries colder waters into the area

112   from the west (Figure 1; Cravatte et al., 2015; Marchesiello, Lefèvre, Vega, Couvelard, & Menkes, 2010).

113   Surveys were part of a single monitoring program conducted in the South Lagoon of New Caledonia

114   from 1995 to 2017 (except for 2004 and 2008), between the beginning of July and the end of September.

115   Surveys were conducted in Beaufort sea-states ≤3 (and avoiding heavy rain) and were simultaneously

116   conducted at sea and from a land-based look-out located on top of the Cape N'Doua (altitude 189 m, >

117   270° visibility, Figure 2). Both teams could communicate at all times using Very High Frequency (VHF)

118   radios. A land-based team composed of one to five trained observers scanned the study area and detected

119   whales up to 36 km from the Cape. A few areas close to the coast and within the Prony Bay were masked

120   from the Cape (Schaffar et al. 2013; Figure 2b) and their extent was measured using a theodolite (a

121   rotating telescope for measuring vertical and horizontal angles to accurately locate positions at the sea

122   surface with a simple trigonometric calculation). The boat-based team was composed of three to five

123   trained observers in a 6 m rigid-hulled inflatable boat moving at 14 km.h^{-1} on average. Surveys followed

124   a haphazard sampling regime (Corkeron et al., 2011), with effort dependent on weather conditions and

125   focused on waters accessible on a daily basis from the Prony Bay.

Group occurrences and social composition

127   Data processing and statistical modelling was performed with the R software version 3.2.5 (R Core Team,

128   2016) and geographical data visualization was performed using QGIS v.2.14. (QGIS Development Team,

129   2016).

130   For each encounter, geographic position, time, social group type and minimum-maximum group size

131   were recorded. A whale group was defined by a unique detection source, (i.e. the team that first detected

132   the group, either land-based, boat-based or external source such as a whale-watching operator), and may

133   have been subsequently followed by both the land- and the boat-based teams. Encounters were

134   considered independent events, as repeated observations of the same individual whale within a survey

135   day rarely occurred (Derville, Torres, & Garrigue, 2018). The geographic position of groups followed at

136   sea was recorded in latitude-longitude using an on-board GPS, whereas groups only followed from land

137   were located either with a precise latitude-longitude position in years where a theodolite was used (51%

138   of observations), or using a grid of 1 nautical mile resolution (latitude-longitude was subsequently

5

139 extracted as the centre of the grid-cell the whale group was located in; 32% of observations), or by a
140 simple textual description of the location (latitude-longitude was subsequently extracted in a GIS
141 interface based on these descriptions: https://explorateur-carto.georep.nc/; 17% of observations).

142 The influence of external factors on the detection of whales from land and at sea was compared. Daily
143 rainfall (in mm) and mean wind conditions (in knots) recorded between 1995 and 2009 were retrieved
144 from a weather station based at the Cape N'Doua (22°23'24" 166°55'30", Meteo France). The effect of
145 rainfall and wind strength on the number of groups observed at sea or detected from land was assessed
146 with sequential GLMs. The daily number of groups observed or detected was modelled with a Poisson
147 GLM as a function of time on effort, year and Julian day of year. Then, the residuals from this regression
148 were modelled as a function of rainfall (square-root transformed) and wind strength using a linear
149 Gaussian regression.

150 The group encounter rates were calculated separately from land and at sea, as the number of groups of
151 whales observed per hour of survey effort conducted during each day. In addition, social group types
152 observed at sea were defined as: groups of three adults, groups of four adults, competitive groups, female
153 with calf, female with calf followed by a single escort, female with calf followed by a competitive group,
154 pairs, singletons, and singers. From land, solitary singers could not be differentiated from singletons, and
155 groups of three or more adults were pooled in the same category. The proportion of social group types
156 observed from land and at sea was calculated for each year. The effect of the observation platform (land
157 or sea) and time (breeding seasons from 1995 to 2017) on the proportion of social group types was tested
158 with beta regressions using the *betareg* R package (version 3.1-0).

Spatial distribution and habitat use

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

6

170 UTM coordinate system and a density surface of effort was estimated with a 2-dimension Local

171 Polynomial Regression (LOESS; span = 0.005).

172 From 1995 to 2002, research boats were not equipped to record GPS tracklines, a common limitation in

173 marine surveys prior to the mid-2000s. An original method was developed to assess the distribution of

174 survey effort for these seven years. GPS positions recorded over each day (end and start of focal follows,

175 and acoustical sampling positions) were compiled and connected together in a chronological order, thus

176 forming daily paths hereafter referred to as "pseudo-tracklines". These pseudo-tracklines were

177 considered a subsample of the real tracklines followed by the research boat over the course of a day.

178 Yearly maps of pseudo-effort were produced using a method similar to that applied to real GPS tracklines:

179 they were interpolated at one position/min, sections off-effort were removed, and the remaining positions

180 were smoothed with a LOESS applied with a varying bandwidth (i.e. span ranging from 0.002 and 0.02).

181 After evaluating the quality of each smoothed trackline in comparison to maps of effort after 2003, the

182 0.01 bandwidth was selected to provide the most realistic estimate of pseudo-effort distribution from

183 1995 to 2002 (for details see Supplement S1).

184 Finally, yearly maps of pseudo-effort from 1995 to 2002 and yearly maps of effort from 2003 to 2017

185 were concatenated, hence generating a time series of 21 yearly maps of boat-based effort. Yearly maps

186 were rescaled to [0-100], so that cells with maximum intensity across all years were attributed 100%

187 intensity values.

188 **Quantifying survey effort from land -** The effect of the number of observers on whale detectability

189 from land was tested with a sequential Generalized Linear Model (GLM, McCullagh & Nelder, 1989).

190 First, the number of groups detected from land per day was modelled as a Poisson variable, relative to

191 time on effort, year and Julian day of year. Residuals from this regression were modelled with a Gaussian

192 linear regression as a function of the number of observers, with values simplified to one for one observer,

193 and two for several observers, based on preliminary tests.

194 Daily land-based effort was modelled per grid cell of coordinates *(x, y)* as a logistic function of distance

195 to the coast:

196 $$Effort_{land}(x,y,t) = Nobs * Tobs_{land}(t) * \frac{100}{1 + e^{-\sqrt{d(x,y)} - 12}}$$

197

where *Nobs* reflected the number of observers on day t, $Tobs_{land}(t)$ was the time (in hours) spent on-effort at the Cape N'Doua on day *t,* and *d(x,y)* was the distance between the grid cell of coordinates *(x, y)* and the land-based observatory *(*in km; for more details see Supplement S2). The logistic curve midpoint was set to 12 km to approximate the average distance from the land-based look-out from which humpback whales were observed (11.3 km ± 5.9 SD). Effort was set to null for grid cells further than the maximum detection distance from the land-based look-out (36 km). Finally, daily maps of land-based effort were summed together per year to produce yearly maps of land-based effort, which were subsequently rescaled to [0,100], consistent with the boat-based survey effort maps.

Spatial distribution - For each year of survey, the geographic positions of humpback whale groups observed at sea were combined with that of groups observed from land but not at sea. Kernel Density Estimates (KDE, Worton, 1989) were applied to humpback whale group positions to model yearly areas of use in the South Lagoon. KDE were applied with weights associated to each group positions, to account for survey effort variability across breeding seasons. Values of survey effort intensity were extracted respectively from the yearly maps of sea- or land-based effort at the humpback whale group positions. These extracted values ranging from 0 to 100 were converted to weights ranging from 0 to 10 with an inverse function in order to downweight whale positions occurring in highly surveyed areas. Finally, weights at each whale group position were multiplied by group size to provide more weight to positions at which larger groups were observed. As group sizes were not always recorded precisely from land, weights were attributed as follows for land-based observations: 3 for a group of three of more individuals, 2 for a pair, and 1 for singletons and unidentified social group types. KDE were calculated with plug-in bandwidth selector (Hpi) then rescaled to [0-100], either with all years of data pooled together, or separately for each breeding season. In the latter case, yearly core areas of use were calculated as the 50 % contour of the yearly probability surfaces. The overlap of yearly core areas of use was calculated from 1995 to 2017 to illustrate the persistence of the humpback whale distribution pattern through time.

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

8

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

Habitat use model - The relationship between humpback whale distribution and environmental conditions was modelled with a Generalized Additive Model (GAM, Hastie & Tibshirani, 1990) using the R package *mgcv* (version 1.8-23). GAMs were applied to KDE values calculated for all years of survey from 1995 to 2017. The response variable was modelled with a beta-regression log link function. Explanatory variables included: depth, distance to the coast, distance to barrier and/or patch-reef complexes, slope, and aspect. Depth and slope were log-transformed to prevent an inflated influence of outliers as recommended by Wood (2006). Pearson coefficients were calculated between environmental variables to prevent collinearity (control that r <0.5 for all variables). Smoothed effects of explanatory variables in the GAM were optimized by Restrictive Maximum Likelihood (REML) and cubic smoothing splines with basis size limited to 5 to prevent overfitting. The descriptive performance of models was assessed through the computation of the proportion of deviance explained (Guisan & Zimmermann, 2000). The deviance explained (%) was calculated from the null deviance (deviance for a model with just a constant term) minus the residual deviance (deviance of the fitted model with explanatory terms). Partial dependence plots were produced to visualize the effect of one variable while all others were held constant at their mean (Friedman, 2001).

Sea Surface Temperature dynamic patterns - Monthly sea surface temperature (SST) was obtained to estimate the mean thermal conditions in the area during the austral winter. SST was obtained from the National Aeronautics and Space Administration (NASA) Multi-scale Ultra-high Resolution SST (MURSST) with a 1 km resolution from 2002 to 2017 (jplMURSST41, http://coastwatch.pfeg.noaa.gov/erdaap/). Average SST and associated coefficients of variation were calculated within and across seasons, and mapped over the study region.

RESULTS

Survey from two platforms

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

9

260 days of survey in common over the study period. As a result, the team at sea was assisted by the land

261 based observers during 88% of the days of survey.

262 The land-based team followed 2,021 groups of humpback whales (96.2 ± SD 60.2 per year), of which

263 1,167 (57.8%) were not followed by the boat-based team (Figure 2, Table 1). The boat-based team

264 followed 1,484 groups (70.7 ± SD 33.4 per year), of which 30.2 % were originally detected by the land-

265 based team who communicated the position through VHF.

266 The number of observers from land varied between 1 and 5 (mean = 2.0 ± SD 0.9, number reported for

267 737 survey days out of 790), and was greater than 1 in 64 % of survey days. The number of humpback

268 whale groups detected from the Cape N'Doua was significantly higher when more than one observer was

269 surveying. A null model was created to account for the effect of year, Julian day of year and duration of

270 survey effort, on the daily number of groups detected from land. The residuals of this null model were

271 significantly affected by the number of observers (GLM: t-value = 7.1, p < 0.001). On average, 2.0 ± SD

272 1.3 groups were observed when one observer was present, against 2.7 ± SD 2.6 with several observers.

273 Between 1995 and 2009, wind and rainfall were measured over 453 days of survey. Wind strength varied

274 from 4 to 27 knots (median = 13.6 knots; mean = 14.1 ± SD 4.8 knots) and daily rainfall varied from 0

275 to 61 mm (median = 0 mm; mean = 1.2 ± SD 4.0 mm). A null model was produced to relate the daily

276 number of groups detected from land, to year, Julian day of year and duration of survey effort. The

277 residuals of this null model were not significantly affected by rainfall (GLM: t-value = 0.4, p = 0.7) nor

278 wind strength (GLM: t-value = 1.6, p = 0.1). Among these 453 days, 412 days were surveyed at sea. A

279 null model was produced to relate the daily number of groups observed at sea, to year, Julian day of year

280 and duration of survey effort. The residuals of this null model were not significantly affected by rainfall

281 (GLM: t-value = 0.2, p = 0.8), but showed a small significant effect of wind strength (GLM: t-value = -

282 2.3, p = 0.02). The number of groups observed at sea decreased with stronger winds.

Occurrence and social composition

284 In total, 2,651 independent whale groups were observed from land and at sea (Figure 2), with a maximum

285 number of occurrences observed in 2007 (n = 264; Table 1). When accounting for survey effort per day,

286 the mean group encounter rates showed an increasing trend from 1995 to 2017, both at sea (Figure 3a),

287 and from land (Figure 3c). Both platforms showed a very similar trend, notably with a steeper increase

288 between 2005 and 2011, a low group encounter rate in 2014 (< 0.3 groups per hour of survey), and a

289 plateau with a slight decrease after 2012.

290   Social group types typical of a humpback whale breeding ground were observed at sea across all years:

291   maternal females with a calf, competitive groups and singers (Table 2, Figure 3b). A larger proportion

292   of group types remained unidentified by land-based observers (29.8 % ± 20.1) compared to observers at

293   sea (1.7 % ± 2.3, Figure 3d), as noted in a beta-regression relating the proportion of unidentified groups

294   to platform (z-value = 7.3, p < 0.0001).

295   Combined together, the proportion of social group types observed from both platforms did not show any

296   linear trends from 1995 to 2017. This analysis included groups with calf (mother-calf pairs, mother-calf

297   pairs with escort or competitive groups; beta-regression: z-value = 1.2, p = 0.2), groups of adults (beta-

298   regression: z-value = 1.7, p = 0.8), pairs (beta-regression: z-value = -0.2, p = 0.8), singleton (including

299   singers; beta-regression: z-value = -1.9, p = 0.05), and unidentified social types (beta-regression: z-value

300   = 1.9, p = 0.05).

Spatial distribution

302   A core area of use for humpback whales was identified outside the Prony Bay, between the two main

303   reef complexes of the South Lagoon, the Corne Sud to the south-west and the Merlet reserve to the north-

304   east (Figure 4a). Humpback whales were also found to display a noteworthy use of the inner waters of

305   the Prony Bay. Yearly core areas of use showed a strong overlap, in a zone located at the centre of the

306   study area (Figure 4b). Persistent use was found over a 77 km^2 zone that was included in yearly core

307   areas of use for at least 10 years (Figure 4b). There was no overlap between the core area of use and the

308   Merlet Reserve (0 % coverage, Figure 4a, Table 3), and only a limited overlap with the UNESCO World

309   Heritage zone (38 % coverage). On the other hand, the Province Park included 100 % of the core and

310   general areas of humpback whale use (Table 3).

Habitat use

312   Depth (edf = 3.8, Chi^2 = 575.7, p < 0.001), distance to coast (edf = 2.0, Chi^2 = 1081.2, p < 0.001), distance

313   to barrier and patch reef complexes (edf = 1.9, Chi^2 = 63.3, p < 0.001), and seabed slope (edf = 2.0, Chi^2

314   = 145.3, p < 0.001) were significant predictors of humpback whale habitat in the South Lagoon (GAM,

315   deviance explained = 36.6%). The occurrence of humpback whales increased with proximity to coast in

316   the South Lagoon. Humpback whales were less frequently found in close contact to coral reef complexes

317   (< 2 km from a reef). Seabed slopes of more than 2° were favoured, though there are few high values of

318   slope in the dataset. Humpback whale occurrence patterns displayed a complex relationship with respect

319   to depth: both very shallow waters (10 m) and relatively deep waters (50 - 100 m) were predicted to be

11

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

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

DISCUSSION

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

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

12

350 Jefferson, & Marsh, 1997; Giacoma, Papale, & Azzolin, 2013). They have been successfully applied to

351 monitor the impact of whale watching and maritime traffic (e.g. Avila, Correa, & Parsons, 2015; Schaffar

352 et al., 2013; Stamation, Croft, Shaughnessy, Waples, & Briggs, 2010; Sullivan & Torres, 2018). Here,

353 the land-based team had greater spatial and temporal detectability of whales than the boat-based

354 observers, as the team could survey a larger extent, and was capable of following several groups at the

355 same time. For instance, the Merlet integral reserve was consistently surveyed by the land-based team

356 throughout the study period, whereas the research boat was only permitted to enter the area during half

357 of the study years (1996-2008 and 2015, Figure 2). Similarly, land-based lookouts have been used in

358 support of boat-based survey teams in other parts of the world to increase the detection of smaller

359 cetacean species (e.g. Risso dolphin, *Grampus griseus*, Hartman et al., 2014). Considering the relatively

360 low cost of adding a team on land when a boat-based monitoring programme is already in place, this

361 study supports the synergic advantages of combining these two platforms of observation when a land-

362 based look-out is available in the study area.

363 In recent decades, ecological research methods have undergone tremendous technological advances. One

364 indirect drawback is the potential to alter the consistency of survey protocols used in long-term studies.

365 In the South Lagoon humpback whale monitoring program, as in many marine long-term studies, the

366 incorporation of onboard GPS tracking has greatly improved the quality of spatial data collected. Indeed,

367 tracklines represent an essential piece of information to spatially quantify survey effort (Derville, Torres,

368 Iovan, & Garrigue, 2018), but were only recorded from 2003 onwards in this study. In order to maintain

369 the integrity of the 20-year long dataset collected in the South Lagoon, survey effort at sea was

370 approximated using "pseudo-tracklines" (see Supplement S1). This method was based on acoustic

371 sampling and group locations, but it may be applied to any 'location data' recorded during a day of survey

372 at sea (e.g. environmental sampling locations). Using this approach on this long-term dataset, a general

373 trend of increasing group encounter rates was identified throughout the study period, both at sea and from

374 land. Anomalous years in the trend may be explained by slight changes in the seasonality of survey effort,

375 such as in 2014 when the mid-August breeding season peak was exceptionally not surveyed. Combining

376 several lines of evidence, this study supports the ongoing recovery of the New Caledonia endangered

377 humpback whale subpopulation.

378 Maternal females, competitive groups and singers were almost constantly observed across breeding

379 seasons, reflecting consistent mating and nursing activity in the South Lagoon. Although calving of

380 humpback whales has never been directly observed in the South Lagoon, as in the majority of the

381 breeding sites worldwide (Faria, DeWeerdt, Pace, & Mayer, 2013), it is assumed to occur within or close

13

382 to this breeding ground. Indeed, calves with newborn traits (pale flank pigmentation, small size and furled

383 dorsal fin; Cartwright & Sullivan, 2009; Irvine, Thums, Hanson, Mcmahon, & Hindell, 2017) are

384 regularly observed in the South Lagoon (Derville, Torres, & Garrigue, 2018). Overall, the core area of

385 humpback whale distribution was located at the centre of the study area, bounded by the coast and two

386 large reef complexes. Although humpback whales are observed sporadically in coastal waters and

387 lagoons all over the New Caledonian archipelago (Derville, Torres, Iovan, et al., 2018; Garrigue & Gill,

388 1994), the South Lagoon appears to be the most visited coastal breeding site (Garrigue et al., 2001). This

389 aggregation is likely to be at least partially driven by social factors (Clapham & Zerbini, 2015), but it

390 may also be linked to environmental conditions specific to this area. In the core area of humpback whale

391 distribution, SST averaged 22 - 22.5°C in the austral winter, a temperature that is well within the

392 preferential SST range identified by Rasmussen et al. (2007). The SST in the core area of use was also

393 relatively stable both within and between years, compared to the surrounding open ocean. Spatio-

394 temporal predictability of resources, or suitable environmental conditions, is an important driver of

395 spatial distribution in the ocean (Lambert et al., 2016; Scales et al., 2014). The persistence of temperature

396 conditions in the South Lagoon could contribute to its attractiveness for maternal females that can rely

397 on this area to provide suitable habitat to their calf.

398 Habitat models suggest a preference for nearshore shallow waters in accordance with other humpback

399 whale breeding grounds around the world (Bortolotto, Danilewicz, Hammond, Thomas, & Zerbini, 2017;

400 Cartwright et al., 2012; Lindsay et al., 2016; Martins et al., 2001; Oviedo & Solís, 2008; Smith et al.,

401 2012; Trudelle et al., 2018). However, the modelled habitat relationships also suggested that whales may

402 be found in the relatively deep waters in the southern part of the study area (about 200 m deep). The

403 modelled occurrence was relatively high in these conditions but was associated with a strong uncertainty.

404 Nevertheless, this result is consistent with satellite tracking of individual humpback whales from this

405 region that moved between the South Lagoon and several seamounts located south of the Isle of Pines

406 (i.e. Torch Bank and Antigonia seamount, Garrigue, Clapham, Geyer, Kennedy, & Zerbini, 2015).

407 Antigonia seamount is now known as an important breeding ground (Derville, Torres, & Garrigue, 2018;

408 Garrigue et al., 2017). Frequent movements between these hotspots (Garrigue et al., 2017; Orgeret,

409 Garrigue, Gimenez, & Pradel, 2014) may explain the relatively high occurrence of whales in the

410 southernmost part of the South Lagoon.

411 The relationship to coral reef complexes was not linear and showed that humpback whales occurred in

412 waters neighbouring reefs (3-4 km) but not directly next to them. In contrast, distance to coral reef was

413 not identified as a primary factor influencing humpback whale distribution in other breeding grounds that

14

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

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

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

ACKNOWLEDGMENTS

REFERENCES

Albertson, G. R., Friedlaender, A. S., Steel, D. J., Aguayo-Lobo, A., Bonatto, S. L., Caballero, S., … Baker, C. S. (2018). Temporal stability and mixed-stock analyses of humpback whales (Megaptera novaeangliae) in the nearshore waters of the Western Antarctic Peninsula. *Polar Biology*, *41*(2), 323–340. https://doi.org/10.1007/s00300-017-2193-1

Andréfouët, S., Chagnaud, N., Chauvin, C., & Kranenburg, C. J. (2008). *Atlas of French Overseas Coral Reefs*. http://umr-entropie.ird.nc/index.php/home/ressources/mcrmp. Accessed February

476   2016.

477   Aragones, L. V, Jefferson, T. A., & Marsh, H. (1997). Marine Mammal Survey Techniques Applicable
478   In Developing Countries. *Asian Marine Biology*, *14*, 15–39. Retrieved from
479   https://books.google.fr/books?hl=fr&lr=&id=rHVFBAAAQBAJ&oi=fnd&pg=PA15&dq=cetacea
480   n+whale+dolphin+abundance&ots=bXwaxYXhMf&sig=B8FaHSRBM4BKqAVWX1fZkClBm1s

481   Avila, I. C., Correa, L. M., & Parsons, E. C. M. (2015). Whale-Watching Activity in Bahía Málaga, on
482   the Pacific Coast of Colombia, and its Effect on Humpback Whale (Megaptera Novaeangliae)
483   Behavior. *Tourism in Marine Environments*, *11*(1), 19–32.
484   https://doi.org/10.3727/154427315X14398263718394

485   Avila, I. C., Kaschner, K., & Dormann, C. F. (2018). Current global risks to marine mammals: Taking
486   stock of the threats. *Biological Conservation*, *221*(February), 44–58.
487   https://doi.org/10.1016/j.biocon.2018.02.021

488   Bortolotto, G. A., Danilewicz, D., Hammond, P. S., Thomas, L., & Zerbini, A. N. (2017). Whale
489   distribution in a breeding area: spatial models of habitat use and abundance of western South
490   Atlantic humpback whales. *Marine Ecology Progress Series*, *585*, 213–227. Retrieved from
491   https://doi.org/10.3354/meps12393

492   Bourgogne, H., Derville, S., & Garrigue, C. (2018). *Étude du trafic maritime dans le Grand Lagon Sud*
493   *afin d'apprécier les risques de dérangement et de collision pour la population de baleines à bosse*
494   *de Nouvelle-Calédonie. Rapport non publié pour le CCCE.*

495   Cartwright, R., Gillespie, B., Labonte, K., Mangold, T., Venema, A., Eden, K., & Sullivan, M. (2012).
496   Between a Rock and a Hard Place : Habitat Selection in Female-Calf Humpback Whale
497   (Megaptera novaeangliae) Pairs on the Hawaiian Breeding Grounds. *PLOS One*, *7*(5), e38004.
498   https://doi.org/10.1371/journal.pone.0038004

499   Cartwright, R., & Sullivan, M. (2009). Behavioral ontogeny in humpback whale (Megaptera
500   novaeangliae) calves during their residence in Hawaiian waters. *Marine Mammal Science*, *25*(3),
501   659–680. https://doi.org/10.1111/j.1748-7692.2009.00286.x

502   Childerhouse, S., Jackson, J., Baker, C. S., Gales, N., Clapham, P. J., & Brownell, R. J. (2008).
503   Megaptera novaeangliae Oceania subpopulation. The IUCN Red List of Threatened Species 2008:
504   e.T132832A3463914. https://doi.org/10.2305/IUCN.UK.2008.RLTS.T132832A3463914.en.

505   Chittleborough, R. G. (1965). Dynamics of two populations of the humpback whale, Megaptera
506   novaeangliae (Borowski). *Marine and Freshwater Research*, *16*, 33–128.

507   Clapham, P. J., & Zerbini, A. N. (2015). Are social aggregation and temporary immigration driving
508   high rates of increase in some Southern Hemisphere humpback whale populations? *Marine
509   Biology*, *162*, 625–634. https://doi.org/10.1007/s00227-015-2610-3

510   Cleguer, C., Grech, A., Garrigue, C., & Marsh, H. (2015). Spatial mismatch between marine protected
511   areas and dugongs in New Caledonia. *Biological Conservation*, *184*, 154–162.
512   https://doi.org/10.1016/j.biocon.2015.01.007

513   Constantine, R., Jackson, J. A., Steel, D., Baker, C. S., Brooks, L., Burns, D., … Garrigue, C. (2012).
514   Abundance of humpback whales in Oceania using photo-identification and microsatellite
515   genotyping. *Marine Ecology Progress Series*, *453*, 249–261. https://doi.org/10.3354/meps09613

516   Constantine, R., Steel, D., Allen, J., Anderson, M., Andrews, O., Baker, C. S., … Ward, J. (2014).
517   Remote Antarctic feeding ground important for east Australian humpback whales. *Marine

17

518　　　*Biology*, *161*, 1087–1093. https://doi.org/10.1007/s00227-014-2401-2

519　Corkeron, P. J., Minton, G., Collins, T., Findlay, K., Willson, A., & Baldwin, R. (2011). Spatial models
520　　　of sparse data to inform cetacean conservation planning : an example from Oman. *Endangered*
521　　　*Species Research*, *15*, 39–52. https://doi.org/10.3354/esr00367

522　Cravatte, S., Kestenare, E., Eldin, G., Ganachaud, A., Lefevre, J., Marin, F., … Aucan, J. (2015).
523　　　Regional circulation around New Caledonia from two decades of observations. *Journal of Marine*
524　　　*Systems*, *148*, 249–271. https://doi.org/10.1016/j.jmarsys.2015.03.004

525　Currie, J. J., Stack, S. H., & Kaufman, G. D. (2017). Modeling whale-vessel encounters: the role of
526　　　speed in mitigating collisions with humpback whales (Megaptera novaeangliae). *Journal of*
527　　　*Cetacean Research and Management*, *17*, 57–63.

528　Derville, S., Torres, L. G., & Garrigue, C. (2018). Social segregation of humpback whales in contrasted
529　　　coastal and oceanic breeding habitats. *Journal of Mammalogy*, *99*(1), 41–54.
530　　　https://doi.org/10.1093/jmammal/gyx185

531　Derville, S., Torres, L. G., Iovan, C., & Garrigue, C. (2018). Finding the right fit: Comparative
532　　　cetacean distribution models using multiple data sources and statistical approaches. *Diversity and*
533　　　*Distribution*, *24*, 1657–1673. https://doi.org/10.1111/ddi.12782

534　Dransfield, a, Hines, E., McGowan, J., Holzman, B., Nur, N., Elliott, M., … Jahncke, J. (2014). Where
535　　　the whales are: using habitat modeling to support changes in shipping regulations within National
536　　　Marine Sanctuaries in Central California. *Endangered Species Research*, *26*(1), 39–57.
537　　　https://doi.org/10.3354/esr00627

538　DTSI. (2016). *Atlas bathymétrique de Nouvelle-Calédonie. Portail de l'information géographique de*
539　　　*Nouvelle-Calédonie*. http://www. geoportal.gouv.nc. Accessed February 2016.

540　Ducklow, H. W., Doney, S. C., & Steinberg, D. K. (2009). Contributions of long-term research and
541　　　time-series observations to marine ecology and biogeochemistry. *Annual Review of Marine*
542　　　*Science*, *1*, 279–302. https://doi.org/10.1146/annurev.marine.010908.163801

543　Faria, M. A., DeWeerdt, J., Pace, F., & Mayer, F. X. (2013). Observation of a humpback whale
544　　　(Megaptera Novaeangliae) birth in the coastal waters of Sainte marie Island, Madagascar. *Aquatic*
545　　　*Mammals*, *39*(3), 296–305. https://doi.org/10.1578/AM.39.3.2013.296

546　Friedman, J. H. (2001). Greedy Function Approximation: A gradient boosting machine. *The Annals of*
547　　　*Statistics*, *29*(5), 1189–1232. Retrieved from http://www.jstor.org/stable/2699986

548　Gabriele, C. M., Lockyer, C., Straley, J. M., Jurasz, C. M., & Kato, H. (2010). Sighting history of a
549　　　naturally marked humpback whale (Megaptera novaeangliae) suggests ear plug growth layer
550　　　groups are deposited annually. *Marine Mammal Science*, *26*(2), 443–450.
551　　　https://doi.org/10.1111/j.1748-7692.2009.00341.x

552　Gabriele, C. M., Neilson, J. L., Straley, J. M., Baker, C. S., Cedarleaf, J. A., & Saracco, J. F. (2017).
553　　　Natural history, population dynamics, and habitat use of humpback whales over 30 years on an
554　　　Alaska feeding ground. *Ecosphere*, *8*(1). https://doi.org/10.1002/ecs2.1641

555　Garrigue, C., Albertson, R., & Jackson, J. A. (2012). An anomalous increase in the New Caledonia
556　　　humpback whales breeding sub-stock E2. *Report to the Scientific Committee of the International*
557　　　*Whaling Commission*, *SC/64/SH6*, 25.

558　Garrigue, C., Bonneville, C., Derville, S., Dodemont, R., Oremus, M., & Pérard, V. (2017). Humpback
559　　　whale offshore breeding grounds in the South Pacific: unravelling the network. *22th Biennial*

18

560   *Conference on the Biology of Marine Mammals, Halifax, Canada*.

561   Garrigue, C., Clapham, P. J., Geyer, Y., Kennedy, A. S., & Zerbini, A. N. (2015). Satellite tracking
562   reveals novel migratory patterns and the importance of seamounts for endangered South Pacific
563   Humpback Whales. *Royal Society Open Science*, *2*, 150489. https://doi.org/10.1098/rsos.150489

564   Garrigue, C., Dodemont, R., Steel, D., & Baker, C. S. (2004). Organismal and "gametic" capture-
565   recapture using microsatellite genotyping confirm low abundance and reproductive autonomy of
566   humpback whales on the wintering grounds of New Caledonia. *Marine Ecology Progress Series*,
567   *274*, 251–262. https://doi.org/10.3354/meps274251

568   Garrigue, C., & Gill, P. (1994). Observations of humpback whales Megaptera novaeangliae in New
569   Caledonian waters during 1991-1993. *Biological Conservation*, *70*, 211–218.
570   https://doi.org/10.1016/0006-3207(94)90165-1

571   Garrigue, C., Greaves, J., & Chambellant, M. (2001). Characteristics of the New Caledonian
572   Humpback whale population. *Memoirs of the Queensland Museum*, *47*(2), 69–75.

573   Giacoma, C., Papale, E., & Azzolin, M. (2013). Are land based surveys a useful tool for managing
574   marine species of coastal protected areas? *Diversity*, *5*(1), 15–25.
575   https://doi.org/10.3390/d5010015

576   Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology.
577   *Ecological Modelling*, *135*, 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9

578   Hartman, K. L., Fernandez, M., & Azevedo, J. M. N. (2014). Spatial segregation of calving and nursing
579   Risso's dolphins (Grampus griseus) in the Azores, and its conservation implications. *Marine
580   Biology*, *161*(6), 1419–1428. https://doi.org/10.1007/s00227-014-2430-x

581   Hastie, T. J., & Tibshirani, R. J. (1990). *Generalized Additive Models, volume 43 of Monographs on
582   Statistics and Applied Probability*. London: Chapman and Hall/CRC. Retrieved from
583   http://books.google.com/books?hl=fr&lr=&id=qa29r1Ze1coC&pgis=1

584   Irvine, L. G., Thums, M., Hanson, C. E., Mcmahon, C. R., & Hindell, M. A. (2017). Evidence for a
585   widely expanded humpback whale calving range along the Western Australian coast. *Marine
586   Mammal Science*, (Lockyer 1981), 1–17. https://doi.org/10.1111/mms.12456

587   IWC. (1998). Report of the sub-committee on comprehensive assessment of Southern Hemisphere
588   humpback whales. Report of the Scientific Committee, Annex G. *Report of the International
589   Whaling Commission*, *Cambridge,* 170–182.

590   Jackson, J. A., Ross-Gillespie, A., Butterworth, D., Findlay, K., Holloway, S., Robbins, J., … Zerbini,
591   A. (2015). Southern Hemisphere Humpback Whale Comprehensive Assessment - A synthesis and
592   summary: 2005-2015. *Report to the Scientific Committee of the International Whaling
593   Commission*, *SC/66a/SH/*, 1–38.

594   Laist, D. W., Knowlton, A. R., Mead, J. G., Collet, A. S., & Podesta, M. (2001). Collisions Between
595   Ships and Whales. *Marine Mammal Science*, *17*(1), 35–75.

596   Lambert, C., Laran, S., David, L., Dorémus, G., Pettex, E., Van Canneyt, O., & Ridoux, V. (2016).
597   How does ocean seasonality drive habitat preferences of highly mobile top predators? Part I: the
598   north-western Mediterranean Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*.
599   https://doi.org/10.1016/j.dsr2.2016.06.012

600   Lammers, M. O., Pack, A., & Davis, L. (2007). Trends in whale/vessel collisions in Hawaiian waters.
601   *Report to the Scientific Committee of the International Whaling Commission*, *SC/59/BC14*.

19

602 Lindenmayer, D. B., & Likens, G. E. (2010). The science and application of ecological monitoring.
603   *Biological Conservation*, *143*(6), 1317–1328. https://doi.org/10.1016/j.biocon.2010.02.013

604 Lindsay, R., Constantine, R., Robbins, J., Mattila, D. K., Tagarino, A., & Dennis, T. (2016).
605   Characterising essential breeding habitat for whales informs the development of large-scale
606   Marine Protected Areas in the South Pacific. *Marine Ecology Progress Series*, *548*, 263–275.
607   https://doi.org/10.3354/meps11663

608 Marchesiello, P., Lefèvre, J., Vega, A., Couvelard, X., & Menkes, C. (2010). Coastal upwelling,
609   circulation and heat balance around New Caledonia's barrier reef. *Marine Pollution Bulletin*,
610   *61*(7–12), 432–448. https://doi.org/10.1016/j.marpolbul.2010.06.043

611 Martins, C. C. a, Morete, M. E., Engel, M. H., Freitas, a. C., Secchi, E. R., & Kinas, P. G. (2001).
612   Aspects of habitat use patterns of humpback whales in the Abrolhos Bank, Brazil, breeding
613   ground. *Memoirs of the Queensland Museum*, *47*(2), 563–570.

614 McCullagh, P., & Nelder, J. A. (1989). Generalized linear models. In *Monographs on statistics and
615   Applied Probability* (2nd. editi). London: Chapman and Hall/CRC. Retrieved from
616   http://www.popline.org/node/423879

617 Mercado III, E., & Frazer, L. N. (1999). Environmental constraints on sound transmission by
618   humpback whales. *Journal of the Acoustical Society of America*, *106*(5), 3004–3016.
619   https://doi.org/10.1121/1.423476

620 New, L. F., Hall, A. J., Harcourt, R., Kaufman, G., Parsons, E. C. M., Pearson, H. C., … Schick, R. S.
621   (2015). The modelling and assessment of whale-watching impacts. *Ocean and Coastal
622   Management*, *115*, 10–16. https://doi.org/10.1016/j.ocecoaman.2015.04.006

623 O'Connor, S., Campbell, R., Knowles, T., Cortez, H., & Grey, F. (2009). Whale Watching Worldwide:
624   Tourism numbers, expenditures and economic benefits - A special report from the International
625   Fund for Animal Welfare. *International Fund for Animal Welfare*, 295.
626   https://doi.org/10.2307/4444572

627 Olavarría, C., Baker, C. S., Garrigue, C., Poole, M., Hauser, N., Caballero, S., … Russell, K. (2007).
628   Population structure of South Pacific humpback whales and the origin of the eastern Polynesian
629   breeding grounds. *Marine Ecology Progress Series*, *330*, 257–268.
630   https://doi.org/10.3354/meps330257

631 Orgeret, F., Garrigue, C., Gimenez, O., & Pradel, R. (2014). Robust assessment of population trends in
632   marine mammals applied to the New Caledonia Humpback Whales. *Marine Ecology Progress
633   Series*, *515*, 265–273. https://doi.org/10.3354/meps10992

634 Oviedo, L., & Solís, M. (2008). Underwater topography determines critical breeding habitat for
635   humpback whales near Osa Peninsula, Costa Rica : implications for Marine Protected Areas. *Rev.
636   Bio. Trop.*, *56*, 591–602.

637 Pack, A. A., Herman, L. M., Craig, A. S., Spitz, S. S., Waterman, J. O., Herman, E. Y. K., … Lowe, C.
638   (2017). Habitat preferences by individual humpback whale mothers in the Hawaiian breeding
639   grounds vary with the age and size of their calves. *Animal Behaviour*, *133*, 131–144.
640   https://doi.org/10.1016/j.anbehav.2017.09.012

641 Pierszalowski, S. P., Gabriele, C. M., Steel, D. J., Neilson, J. L., Vanselow, P. B. S., Cedarleaf, J.
642   A., … Baker, C. S. (2016). Local recruitment of humpback whales in Glacier Bay and Icy Strait,
643   Alaska, over 30 years. *Endangered Species Research*, *31*, 177–189.
644   https://doi.org/10.3354/esr00761

20

645 Pirotta, E., New, L., & Marcoux, M. (2018). Modelling beluga habitat use and baseline exposure to
646   shipping traffic to design effective protection against prospective industrialization in the Canadian
647   Arctic. *Aquatic Conservation: Marine and Freshwater Ecosystems*, (July 2017), 1–10.
648   https://doi.org/10.1002/aqc.2892

649 Province Sud. (2009) Code de l'Environnement de la Province Sud. pp 322. Nouméa, Nouvelle-
650   Calédonie. Retrieved from www.province-sud.nc.

651 Province Sud. (2013). *Plan de gestion du Grand Lagon Sud 2013/2017*. Province Sud, Nouvelle-
652   Calédonie.

653 Province Sud. (2018). *Charte d'Observation des Cétacés*. https://www.province-
654   sud.nc/sites/default/files/CHARTE%20WW%202018.pdf. Accessed July 2018.

655 QGIS Development Team. (2016). QGIS Geographic Information System. Open Source Geospatial
656   Foundation Project. *Version 2.18 La Palma*. Retrieved from http://qgis.osgeo.org

657 R Core Team. (2016). *R: A language and environment for statistical computing*. R Foundation for
658   Statistical Computing, Vienna, Austria. Retrieved from http://www.r-project.org/.

659 Rasmussen, K., Palacios, D. M., Calambokidis, J., Saborío, M. T., Dalla Rosa, L., Secchi, E. R., …
660   Stone, G. S. (2007). Southern Hemisphere humpback whales wintering off Central America:
661   insights from water temperature into the longest mammalian migration. *Biology Letters*, *3*(3),
662   302–305. https://doi.org/10.1098/rsbl.2007.0067

663 Redfern, J. V., McKenna, M. F., Moore, T. J., Calambokidis, J., Deangelis, M. L., Becker, E. A., …
664   Chivers, S. J. (2013). Assessing the Risk of Ships Striking Large Whales in Marine Spatial
665   Planning. *Conservation Biology*, *27*(2), 292–302. https://doi.org/10.1111/cobi.12029

666 Riekkola, L., Zerbini, A. N., Andrews, O., Andrews-Goff, V., Baker, C. S., Chandler, D., …
667   Constantine, R. (2018). Application of a multi-disciplinary approach to reveal population structure
668   and Southern Ocean feeding grounds of humpback whales. *Ecological Indicators*, *89*(December
669   2017), 455–465. https://doi.org/10.1016/j.ecolind.2018.02.030

670 Robbins, J. (2007). *Structure and dynamics of the Gulf of Maine humpback whale population*. PhD
671   Thesis, School of Biology, University of St. Andrews.

672 Rocha, J. R. C., Clapham, P. J., & Ivashchenko, Y. (2015). Emptying the Oceans: A Summary of
673   Industrial Whaling Catches in the 20th Century. *Marine Fisheries Review*, *76*(4), 37–48.
674   https://doi.org/10.7755/MFR.76.4.3

675 Scales, K. L., Miller, P. I., Hawkes, L. A., Ingram, S. N., Sims, D. W., & Votier, S. C. (2014). On the
676   front line: Frontal zones as priority at-sea conservation areas for mobile marine vertebrates.
677   *Journal of Applied Ecology*, *51*(6), 1575–1583. https://doi.org/10.1111/1365-2664.12330

678 Schaffar, A., Garrigue, C., & Constantine, R. (2010). Exposure of humpback whales to unregulated
679   whalewatching activities in their main reproductive area in New Caledonia. *Journal of Cetacean
680   Research and Management*, *11*(2), 147–152.

681 Schaffar, A., Madon, B., Garrigue, C., & Constantine, R. (2013). Behavioural effects of whale
682   watching activities on an endangered population of humpback whales wintering in New
683   Caledonia. *Endangered Species Research*, *19*, 245–254. https://doi.org/10.3354/esr00466

684 Senigaglia, V., Christiansen, F., Bejder, L., Gendron, D., Lundquist, D., Noren, D. P., … Lusseau, D.
685   (2016). Meta-analyses of whale-watching impact studies: Comparisons of cetacean responses to
686   disturbance. *Marine Ecology Progress Series*, *542*(January), 251–263.

21

https://doi.org/10.3354/meps11497

Simmonds, M. P., & Eliott, W. J. (2009). Climate change and cetaceans: concerns and recent developments. *Journal of the Marine Biological Association of the United Kingdom*, *89*(01), 203–210. https://doi.org/10.1017/S0025315408003196

Smith, J., Grantham, H., Gales, N., Double, M., Noad, M., & Paton, D. (2012). Identification of humpback whale breeding and calving habitat in the Great Barrier Reef. *Marine Ecology Progress Series*, *447*(Harwood 2001), 259–272. https://doi.org/10.3354/meps09462

Stamation, K. A., Croft, D. B., Shaughnessy, P. D., Waples, K. A., & Briggs, S. V. (2010). Behavioral responses of humpback whales (Megaptera novaeangliae) to whale-watching vessels on the southeastern coast of Australia. *Marine Mammal Science*, *26*(1), 98–122. https://doi.org/10.1111/j.1748-7692.2009.00320.x

Steel, D., Anderson, M., Garrigue, C., Olavarría, C., Caballero, S., Childerhouse, S., … Baker, C. S. (2017). Migratory interchange of humpback whales (Megaptera novaeangliae) among breeding grounds of Oceania and connections to Antarctic feeding areas based on genotype matching. *Polar Biology*, *3*(0123456789), 1–10. https://doi.org/10.1007/s00300-017-2226-9

Stockin, K. A., Weir, C. R., & Pierce, G. J. (2006). Examining the importance of Aberdeenshire (UK) coastal waters for North Sea bottlenose dolphins (Tursiops truncatus). *Journal of Marine Biological Association of the United Kingdom*, *86*, 201–207.

Sullivan, F. A., & Torres, L. G. (2018). Assessment of vessel disturbance to gray whales to inform sustainable ecotourism. *Journal of Wildlife Management*, *82*, 896–905. https://doi.org/10.1002/jwmg.21462

Sydeman, W. J., Poloczanska, E. S., Reed, T. E., & Thompson, S. A. (2015). Climate change and marine vertebrates. *Science*, *350*(6262), 171–193. https://doi.org/10.1126/science.aac9874

Taylor, B. L., Chivers, S. J., Larese, J., & Perrin, W. F. (2007). Generation length and percent mature estimates for IUCN assessments of cetaceans. *Administrative Report LJ-07-01 National Marine Fisheries*, 24. https://doi.org/doi:10.1.1.530.4789

Thomas, P. O., Reeves, R. R., & Brownell, R. L. (2015). Status of the world's baleen whales. *Marine Mammal Science*, *32*(2), 682–734. https://doi.org/10.1111/mms.12281

Trudelle, L., Charrassin, J. B., Saloma, A., Pous, S., Kretzschmar, A., & Adam, O. (2018). First insights on spatial and temporal distribution patterns of humpback whales in the breeding ground at Sainte Marie Channel, Madagascar. *African Journal of Marine Science*, *40*(1), 75–86. https://doi.org/10.2989/1814232X.2018.1445028

UNESCO. (2009). *Lagoons of New Caledonia: Reef Diversity and Associated Ecosystems*. *U.W.H. Centre*. whc.unesco.org/en/list/1115/documents/ Accessed 2018-06-20. Retrieved from whc.unesco.org/en/list/1115/documents/

Wood, S. N. (2006). *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-Range studies. *Ecology*, *70*(1), 164–168.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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**

23

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 ± 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 ± 7.7	1.8 ± 1.6	1.1 ± 1.3	14.2 ± 5.0	24.5 ± 6.9	6.2 ± 4.1	32 ± 5.6	1.7 ± 2.3
Land-based observations	2.9 ± 3.6	0.2 ± 1.0	10.0 ± 6.3		35.0 ± 18.7		22.1 ± 8.3	29.8 ± 20.1

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 %

726

727

728

729

730

731

732

733

734

735

736

737

738

739

740

741

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

26

the group and the amount of survey effort. Land is shown in black and reefs 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.

Figure 5: Partial dependence plots modelling habitat selection of humpback whales from combined boat- and land-based surveys in the South Lagoon, New Caledonia between 1995 and 2017. Predicted habitat suitability is shown on the y-axis with varying scales. Rug plots illustrate the distribution of values in the modelled dataset in percentiles.

Figure 6: Sea Surface Temperature (SST) in the South Lagoon, New Caledonia, averaged from MURSST (jplMURSST41, http://coastwatch.pfeg.noaa.gov/erdaap/) between July and August, 2002-2017. (a) Mean austral winter SST averaged across 16 years. (b) Coefficient of variation of SST calculated across 16 years. (c) Coefficient of variation of SST calculated across 3 months of austral winter and averaged over 16 years. Land is shown in black and reefs in grey. White lines delineate contours of the SST patterns.

SUPPORTING INFORMATION

S1: Estimating boat-based survey effort without GPS tracklines

S2: Estimating land-based survey effort

Figure 1

168x72mm (300 x 300 DPI)

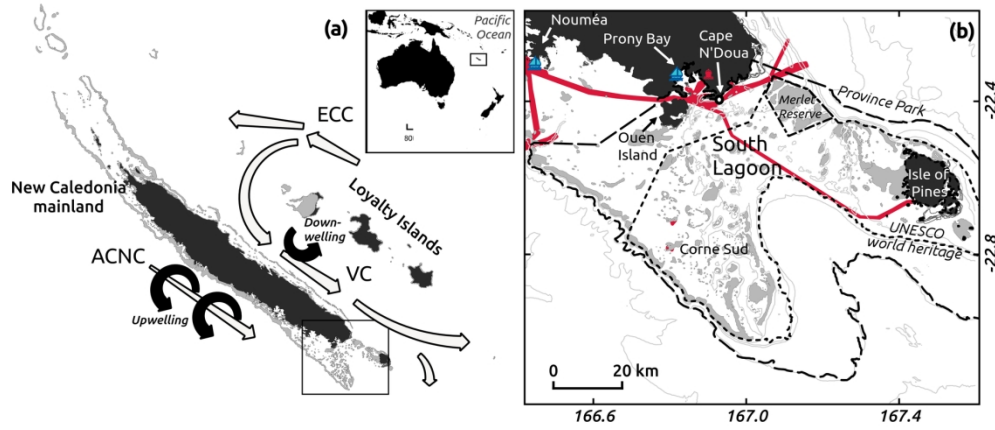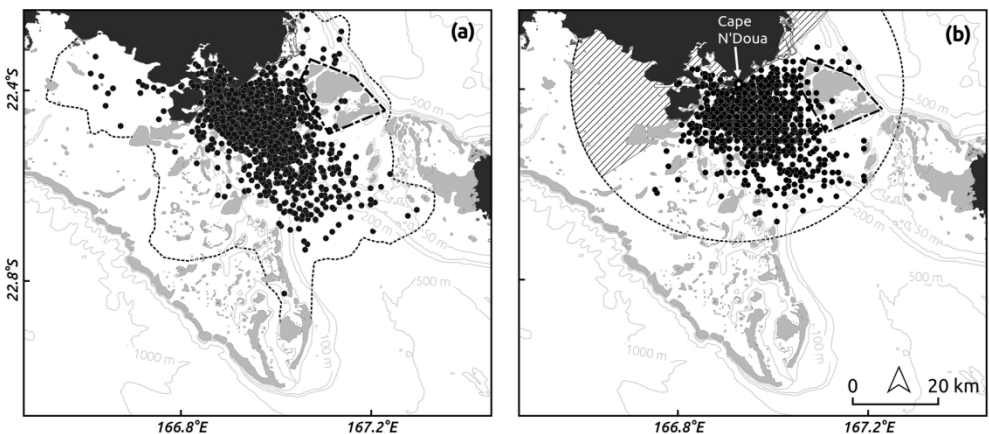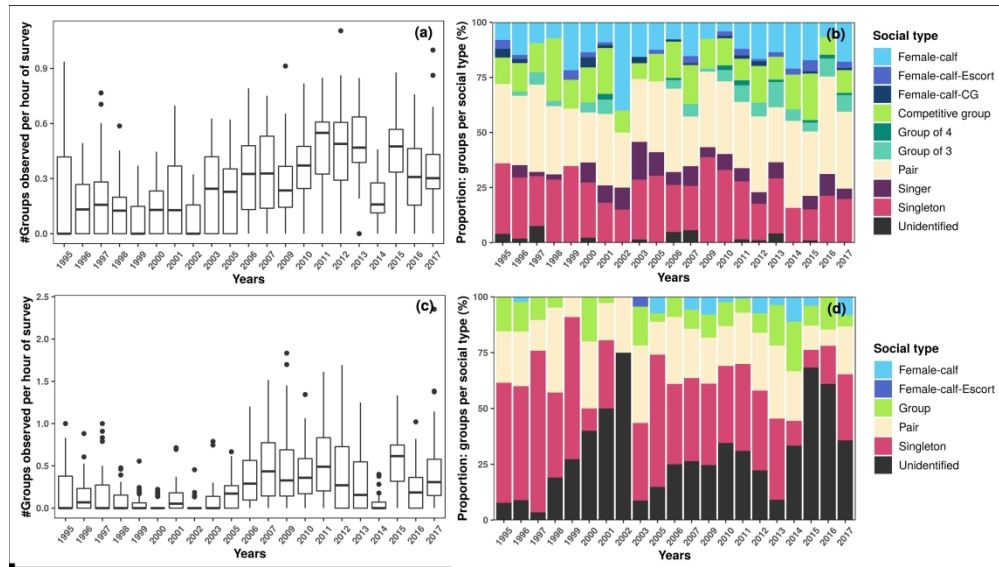Figure 2

168x74mm (300 x 300 DPI)

Figure 3

319x180mm (300 x 300 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
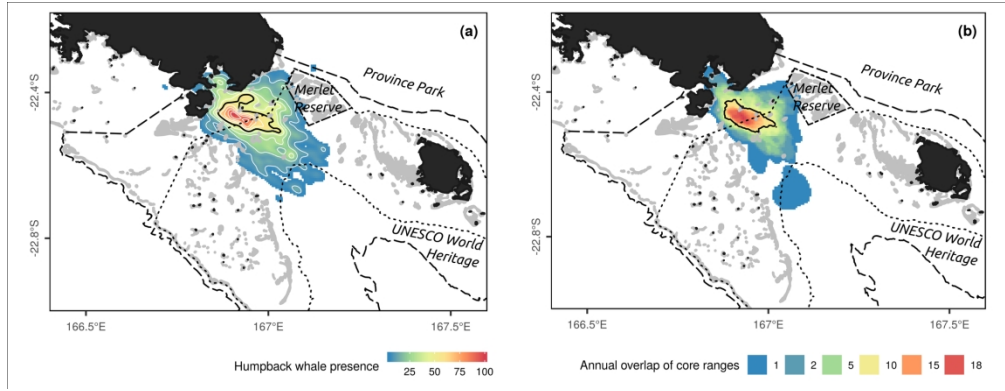50
51
52
53
54
55
56
57
58
59
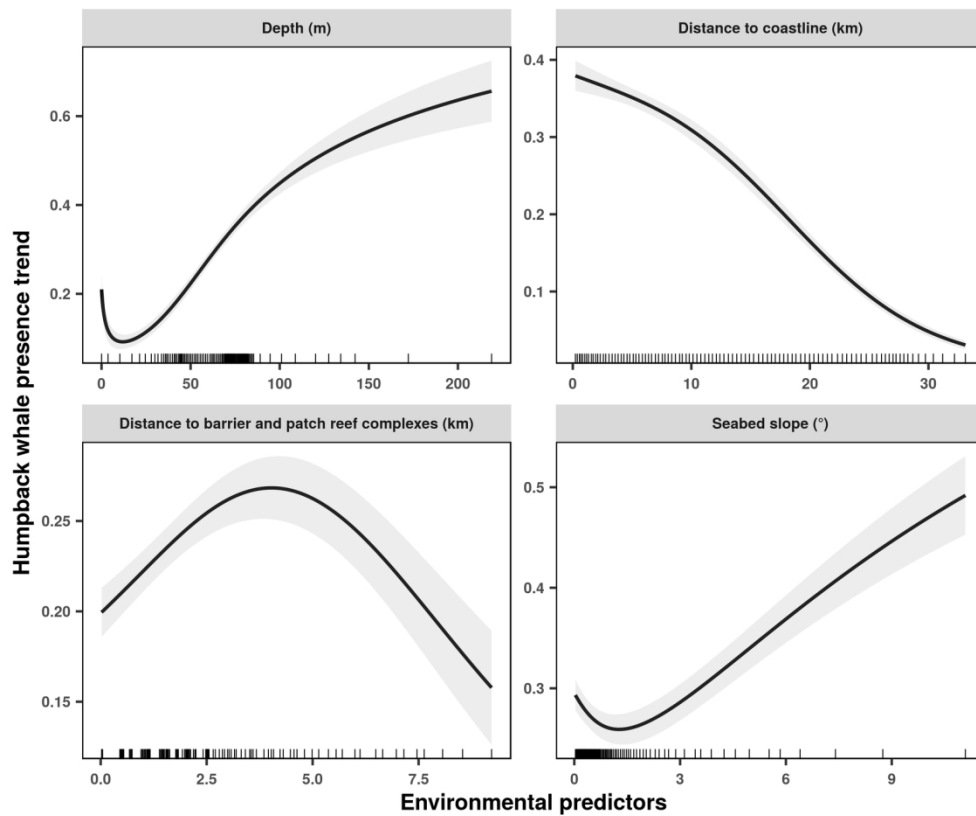60
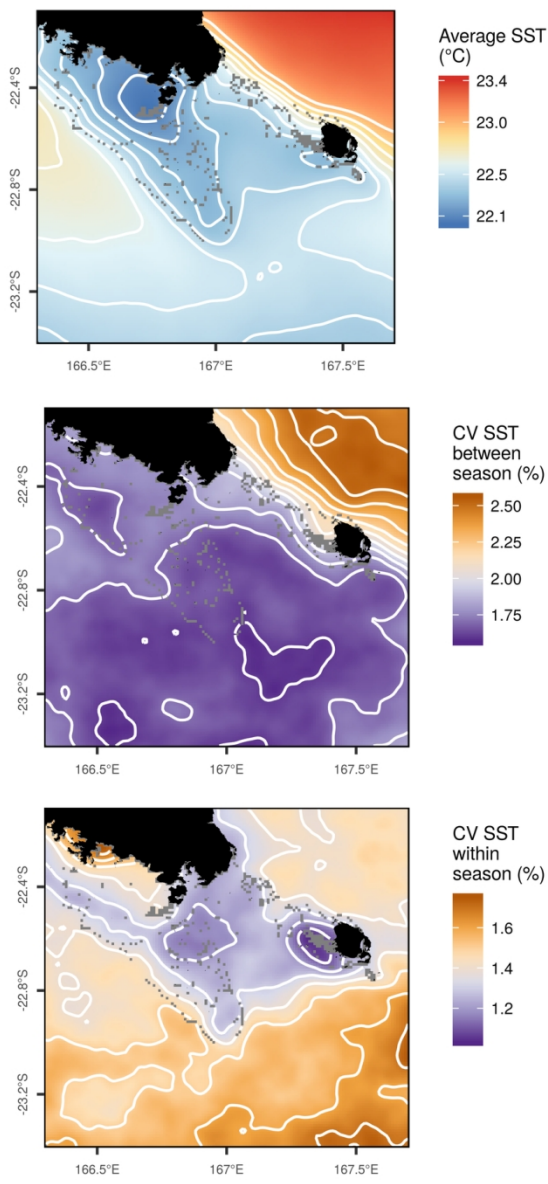

Figure 4

203x78mm (300 x 300 DPI)

Figure 5

152x127mm (300 x 300 DPI)

Figure 6

78x159mm (300 x 300 DPI)