Density-dependent changes in the distribution of southern right whales (*Eubalaena australis*) in the breeding ground Peninsula Valdés

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Background. Southern Right Whales (*Eubalaena australis*) population of the South-western Atlantic Ocean is recovering. In the breeding ground of Peninsula Valdés, as a consequence of the population growth, expansion to new areas by some types of groups and a change in the habitat use patterns at the coastal area were recorded.

Methods. We analyzed information gathered from aerial surveys conducted along the coast of Peninsula Valdés in 15 years of effective sampling in a 19-year span . These surveys were divided into 4 periods (1999-2000; 2004-2007; 2008-2012 and 2013-2016) and estimated the density of whales in a 620 km of coast divided into segments of 5 km.

Results. The density of the whales increased to near 3 whales per km2 (averaged over each period) in the high-density areas. When this mean number was reached, the significant changes in density in the adjacent areas were detected in the following period. These changes were a decrease in density in the high-density areas and an increase of density in the low-density areas.

Discussion. We propose that a threshold in density elicits a response in habitat use, with the *Mother-calf* pairs remaining in the area, while the *other* groups are displaced to new areas.

1 **Density-dependent changes in the distribution of southern**

2 **right whales (*Eubalaena australis*) in the breeding ground**

3 **Peninsula Valdés**

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Abstract

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Introduction

The Southern Right Whale (*Eubalaena australis*) has a circumpolar distribution in the southern hemisphere. This species was subjected to a commercial exploitation between the 19th and 20th centuries that put the species on the brink of extinction (Richards 2009). The species was protected for the first time in 1936 and additionally, in 1986, the moratorium on commercial catch established by the International Whaling Commission (IWC) came into force. By the mid-1970's several populations have shown evidence of recovery, with a doubling time of 10 to 12 years (Bannister 2001; Best et al. 2001; Cooke et al. 2001). However, there are other populations that are still very small and there is uncertainty about their recovery (Galletti Vernazzani et al. 2014). Even today, the geographical distribution of all breeding and feeding areas of the species prior to its exploitation are unknown (IWC 2001).

The estimated population size for the species in 1997 was 7,500 animals (including 547 mature females, from Argentina and 659 from South Africa), with an estimated average growth rate for all populations in the Southern Hemisphere of 7.5% (IWC 2012). The breeding population of Peninsula Valdés is one of the best studied, with a long-term research program carried out in the Peninsula Valdés area since 1970 (Payne 1986). The population size and other parameters

47 derived from capture-recapture models have been estimated, based on the individual recognition
48 of the whales. The population growth rate was estimated to be around 8% by the early 80's
49 (Payne 1986; Payne et al. 1981; Payne et al. 1990; Whitehead et al. 1986), and recent studies
50 estimate a 5.1% for 2010 (Cooke 2012) and 6.5% for 2012 (Cooke et al. 2015) using the same
51 techniques.
52 The process of gathering the information from photo-identification is time-consuming, and there
53 was a need for a quick assessment of the number of whales and population trend by the
54 authorities. In 1999 a protocol involving coastal aerial survey with the direct counting of marine
55 mammals in the Peninsula Valdés area was started (Crespo et al. 2018). Crespo and colleagues
56 estimated for the year 2007 an increasing rate of 6.22%. For the year 2014, the models indicated
57 that the population grew at a rate of 3.23% per year (Crespo et al. 2018). However, the reduction
58 in the rate of increase was not uniform across the different groups that comprise the population.
59 The estimate of the growth rate for offspring born in the Peninsula Valdés was 5.54% per year
60 between 1999 and 2014 (Crespo et al. 2018), almost doubling the rate of increase for the whole
61 population during the same period. The rate of increase of the other class groups (namely
62 *Solitary Individuals* and *Breeding groups*) is now close to 0% (Crespo et al. 2018). During the
63 first sampling seasons, all the types of groups were close to the coast. As the population grew the
64 *Mother-calf* pairs remained close to the shore, while the other types of groups were displaced
65 farther off from it. This change in Peninsula Valdés distribution could mean that the coastal zone
66 (within 2km from shore) is close to it carrying capacity (Crespo et al. 2018). Therefore, in spite
67 of the overall decrease in the population increasing rate observed in the sampling area, it is
68 proposed that the southern right whale stock of the south-western Atlantic is still growing at a
69 rate that would be the combination of its growth in the Peninsula Valdés area and the occupation
70 rate of other zones (Crespo et al. 2018). If this scenario is correct, whales should begin to move
71 to other less dense regions (*ie:*, sub-optimal habitats) where the growth rate should be higher
72 (Hobbs & Hanley 1990; Verner et al. 1986). There are different indicators supporting this
73 hypothesis for Peninsula Valdés as evidenced by the number of whales occupying areas with
74 deeper waters in Peninsula Valdés and the growing number of whales observed in Golfo San
75 Matías, Buenos Aires, Uruguay and Santa Catarina in southern Brazil (Crespo et al. 2018; Groch
76 et al. 2005; IWC 2011).

77   The expansion of whales to other areas may be determined by the priority occupation of mothers

78   with offspring in optimal habitat areas (Barendse & Best 2014; Carroll et al. 2014; Danilewicz et

79   al. 2016). If this is the case, there should be a threshold density in which the *Other* groups

80   increase their density in adjacent areas (*eg:* nonpreferred by *Mother-calf* pairs). Similar trends

81   have also been recorded in other southern right whale stocks from South Africa, New Zealand

82   and southern Brazil, where *Solitary Individuals* and *Breeding* Groups move to new sites, outside

83   the established breeding area (Barendse & Best 2014; Carroll et al. 2014; Danilewicz et al.

84   2016).

85   ## Methods

86   The censuses were carried out from a single-engine high-wing CESSNA B-182 aircraft, flying at

87   a constant height of 500 feet (152 m) and at 80/90 knots every 45 days from April to December

88   each year (Crespo et al. 2018). In each survey a distance of 620 km was covered in 5 hours of

89   flight, flying from south to north along the coast. The surveyed area (Figure 1) is located

90   between the mouth of the Rio Chubut and Puerto Lobos on the border with the province of Rio

91   Negro. The width of the strip is composed by 500 meters from the coast plus approximately 1000

92   meters from the plane to the open sea, composing a surveyed strip of 1500 meters (Crespo et al.

93   2018). This strip is set to cover the "whale-road" as described by Payne (1986), where more than

94   90% of the whales in the area concentrate near the coast in shallow waters.

95   The team comprised a pilot, a recorder sitting next to the pilot and two observers in the rear

96   seats, one on the left and one on the right side of the aircraft (Crespo et al. 2018). The

97   observations were made with the naked eye, and the information was recorded in spreadsheets or

98   tablet applications developed *ad-hoc* with Cyber Tracker ™. Information on the group

99   composition was recorded, including *Mother-calf* pairs, *Solitary Individuals* or *Breeding* groups

100   comprising a female and several males (Crespo et al. 2018). For the analysis in this work *Solitary*

101   *Individuals* and *Breeding* groups were pooled in *Other* groups, as a group category opposite to

102   the *Mother-calf* pairs. Along with the type of group we recorded the position registered with a

103   handheld GPS, the number of individuals and the sea state on the Beaufort scale. Flights were

104   suspended when the visibility conditions were not optimal, either because of fog or the sea state

105   exceeded the level 3 on the Beaufort scale. Data were entered into a database developed in

106   Access-Microsoft® specifically for this purpose. Fields in the database included time and

107   position, number of animals, side of the sighting, type of group, and other ancillary information.

108 The information was grouped into four periods, making each period as similar as possible

109 considering the number of flights. A total of 58 aerial surveys were clumped in four periods:

110 period 1 from 1999 and 2000 (8 flights) and the other 3 periods comprised from 2004 to 2007 for

111 period 2 (18 flights), period 3 from 2008 to 2012 (17 flights) and period 4 from 2013 to 2016 (15

112 flights). No flights were performed during the period 2001-2003.

113 The surveyed coast was divided into segments of 5 km in length, totalling 124 segments for the

114 620 km sampled in each flight, where the 0 km is the mouth of the Chubut River (Figure 2). The

115 densities were calculated by dividing the number of whales counted in each segment, weighted

116 by the number of flights performed per period and the area of each segment, calculated as the 5

117 km segment by 1.5 km (bandwidth), and thus each segment accounted for a 7.5 km^2. The length

118 of the segment was chosen following Rowntree et al. (2001), who divided the coast into 5 km

119 segments to evaluate the distribution of the Southern Right Whales.

120 Preliminary examination of data led us to define two high densities zones, one inside Golfo

121 Nuevo from Puerto Madryn to Punta Cormoranes and other inside Golfo San José, from Punta

122 Conos to Punta Tehuelche (Figure 3). These areas coincide with the ones defined previously by

123 Rowntree et al. (2001) for the areas selected by whales in the early 90's. We also defined the

124 low-density zones as those outside the high-density zones (*ie:* Chubut River mouth-Puerto

125 Madryn; Punta Cormoranes-Punta Conos; Punta Tehuelche-Puerto Lobos). Differences in

126 densities among the periods in these zones were assessed by Mann-Whitney U tests (Zar 2010).

127 The permit was granted by the Secretaría de Turismo y Áreas Protegidas of the Province of

128 Chubut, (issued for the last time under permit number 93-SsCyAP / 15).

129 ## Results

130 The overall density of both group categories for the whole surveyed area shows for the first

131 period a similar density for *Mother-calf* pairs and *Other* groups. For the second period, the

132 observed increase of density is similar for both categories (Figure 2). During the third and the

133 fourth period, the density of *Mother-calf* pairs slightly increases, while the *Other* group's density

134 decreases (Figure 2).

135 The coastal area defined as high densities zones are located between the segments 24 (Puerto

136 Madryn) and 49 (Punta Cormoranes) (*high-density 1*) within the Golfo Nuevo and between the

137 segments 90 (Punta Conos) and 101 (Punta Tehuelche) (*high-density 2*) within the Golfo San

138 José (Figure 3). The highest densities in any of the four periods were observed at the Doradillo

139   (segment 28 and 29) and Playa Fracaso (segment 97 and 98), reaching a maximum estimated of

140   3.15 whales per km^2 during the first period for all type of groups.

141   Figure 4 shows the density changes in the two areas of high density of animals. In the *high-*

142   *density 1*, the *Mother-calf* pairs increased their density in the second and third period with

143   respect to the first ($U_{1,2}$: 181.5/$U_{1,3}$: 157.5; p< 0.05) but a great variation was observed in the

144   fourth period. The density of the *Other* groups category increases, but with a subsequent

145   decrease ($U_{1,2}$: 179/$U_{2,4}$: 426; p< 0.05).

146   In the *high-density 2*, a similar pattern is observed, an increase in the density of *Mother-calf* pairs

147   ($U_{1,3}$: 41.5; p< 0.05) that is sustained in time. For the groups without calves or the Other groups,

148   the initial increase is followed by a marked decrease in the last period ($U_{2,4}$: 143/$U_{3,4}$: 147.5; p<

149   0.05).

150   Figure 5 shows the changes in the low-density zones. *Mother-calf* pairs in the *low-density 1*

151   increased their density during the third period ($U_{2,3}$: 215; p <0.05). Also, an increase in the

152   density of the *Other* groups from the first to the second period can be observed ($U_{1,2}$: 205;

153   p<0.05). Afterwards a decrease in the density from the second to the third ($U_{2,3}$: 540; p< 0.05)

154   was recorded to the groups without calves. In the *low-density 2* the *Mother-calf* pairs increased

155   their density only during the third period ($U_{1,3}$: 489/$U_{2,3}$: 437/$U_{3,4}$: 1054/ p <0.05) decreasing

156   afterwards. For the *Other* groups there was an increase in the second period and it remained

157   higher than the first period later ($U_{1,2}$: 372/$U_{1,3}$: 519.5/$U_{1,4}$: 511.5/$U_{2,4}$: 994.5; p <0.05). In the

158   *low-density 3* for the density of *Mother-calf* pairs increases during the whole period ($U_{1,2}$:

159   119/$U_{1,3}$: 109/$U_{1,4}$: 116; p <0.05). The *Other* groups show an increase in density in the second

160   period and a sharp decrease later on ($U_{1,2}$: 56/$U_{1,3}$: 82/$U_{1,4}$: 71/$U_{2,4}$: 308; p <0.05).

161   Overall, when in a particular period in a high-density area the mean density for the period

162   reaches around 3 whales per squared km^2, the next period is characterized by a decrease of

163   density in it. The process is also accompanied by an increase of density in the nearby low-density

164   areas.

165   ## Discussion

166   This is the first study that proposes that a threshold in whale´s density in breeding areas triggers

167   a density-dependent response, it has been observed in other species of smaller size and in its

168   majority of terrestrial environments (Matthysen 2005). This response includes the movement of

169   *Solitary Individuals* and *Breeding* Groups (*Other* Groups) to adjacent areas when the average

170 density in the area is close to 3 whales per km^2. This must be taken with caution since it is an

171 average from April to December for each period (Crespo et al. 2018). In any given season, as

172 much as 15,87 whales per km^2 can be found in the El Doradillo area for a few days (up to 15

173 days approximately) from the end of July until October. The inter-annual variation in the exact

174 moment the maximum of whales is present in the area precludes us to use the census near the

175 peak of the season because the surveys cannot always coincide with this peak in the number of

176 whales. Hence, the density-dependent process proposed here cannot be observed using only the

177 peak of the season but using the average of the density. Changes in the distribution of the

178 Southern Right Whales in Peninsula Valdés were reported by Rowntree et al. (2001) during the

179 late 80's. Rowntree et al. (2001) recorded a movement of whale breeding areas from the outer

180 coast of Peninsula Valdés into the gulfs (Golfo Nuevo and Golfo San José), but no mechanism

181 was proposed. The areas reported as new for the 1990s in Peninsula Valdés are the same as those

182 observed in this work for the first period (Figure 2). Rowntree et al. (2001) considered several

183 factors such as gull inflicted wounds or undetected changes in the environment and topography

184 of the area as the possible causation of the observed shift in distribution. Our data lead us to

185 propose that density changes (and probably related social causes) can be the main mechanism

186 that promotes the search for new areas and the expansion of the occupied coast in Peninsula

187 Valdés breeding ground. This mechanism might not have been the same mechanism that drove

188 the changes observed during the late 1980's. Other social interactions not previously described in

189 the area are being recorded. *Mother-calf* interactions and mating groups were almost exclusively

190 the only social interaction recorded, but nowadays is possible to observe adult individuals

191 without calves engaged in the same activities (e.g.: travelling together or socialize without

192 forming a *Breeding* group) (Arias et al. 2017). Also, cooperative feeding was recorded recently

193 (Argüelles 2017), and hence these new interactions never reported before may be shaping the

194 social behaviour of whales in the area. These social aspects of the whales may have not been

195 previously reported due to the low number of individuals until recent years.

196 *Mother-calf* pairs continue to select areas used in the late 1990s, the so-called high-density

197 zones (Figure 4). The density in these areas increased, but differentially by type of groups: while

198 *Mother-calf* increased their density, the *Other* groups continue to select this area until an average

199 threshold of 3 whales per km^2 is reached. In every considered period, this is mainly due to the

200 increase in density of *Mother-calf*. The only fraction of the population that is still growing, since

201 the other type of groups have not shown positive increasing rates in the last few years (Crespo et

202 al. 2018). During the first period, the average annual density reached near 3 whales per km^2 in

203 the area Puerto Madryn- El Doradillo. In the following period a change in the density of whales

204 occurred (Figure 4); not only was there an increase in the *Mother-calf* pairs density, but the

205 *Other* groups are more prone to be found in peripheral areas of less density (*eg. low-density 1*),

206 as shown in Figure 3. The same pattern can be found in Golfo San José high-density area during

207 the second period. After the mean density approached to 3 whales per km^2, the density of the

208 *Other* groups increased in the *low-density 3* (Figure 5).

209 In the fourth period, it is observed that the average annual density of whales in the Doradillo area

210 is close to 3 whales per km^2. If the same pattern is repeated in the next period, we could

211 hypothesize that an expansion of part of the whales to areas with physical and biological

212 conditions similar to those found in Peninsula Valdes will occur in the next few years, as well as

213 a new increase in the low-density areas.

214 In a context of population growth, the expansion into new areas is been driven by *Solitary*

215 *Individuals* and *Breeding* groups (Arias et al. 2018). The optimum areas are first occupied by the

216 *Mother-calf* pairs, as the density of this type group increases, the rest of the groups are displaced

217 to suboptimal zones, as observed in the San Matias Gulf where the first groups in the area were

218 the *Solitary Individuals* and *Breeding* groups (Svendsen 2013).

219 This kind of mechanism was recorded in other mammals. When the red deer (*Cervus elaphus*)

220 population of the island of Rum doubled its size, females presented on average a greater spatial

221 distance among them (Albon et al. 1992). In the case of roe deer (*Cupreolus capreolus*) their

222 increase in density caused a change in the habitat use of young males and later of adult males.

223 While females continue to use the habitat used by the population in the past (*ie*; optimal habitat),

224 younger males tended to move to other areas (Vincent et al. 1995). Our results indicate that the

225 recolonization process started at least in the mid-2000s when whales changed both the way they

226 use the habitat related to the type of groups and the areas where they could be found. The

227 expansion of these groups to other areas was observed in the province of Rio Negro with the

228 presence of whales in the area near the San Antonio Bay. In this area, more than 80% of whales

229 are *Solitary Individuals* and *Breeding* Groups (Arias et al. 2017; Crespo et al. 2018). These

230 movements of *Solitary Individuals* and *Breeding* Groups move to new sites, outside the

231 established breeding area has also been recorded in other southern right whale stocks from South

232 Africa, New Zealand and southern Brazil, but no mechanism was ever proposed (Barendse &
233 Best 2014; Carroll et al. 2014; Danilewicz et al. 2016).

Conclusion

235 The growth and expansion of the southern right whale population in Peninsula Valdés are
236 proposed to being modelled by density-dependent determinants. One proposed mechanism is
237 related to social mediated factors. It is important continuing to monitor the rate of increase in the
238 core areas as well as the densities in these areas. The rate of increase of the population is now the
239 combination of the increase recorded in Peninsula Valdés and the growth experienced while
240 probably recolonizing ancient habitat (Arias et al. 2018; Crespo et al. 2018). Also, it is important
241 to evaluate the habitat suitability of different areas, and to test if the mean density of around 3
242 individuals per km2 is an actual threshold that is also found outside Peninsula Valdés; and if so,
243 which are the social causes that trigger this density-dependent response.

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323
324

Figure 1

Sampling area

The thick black line along the coast represent the surveyed area
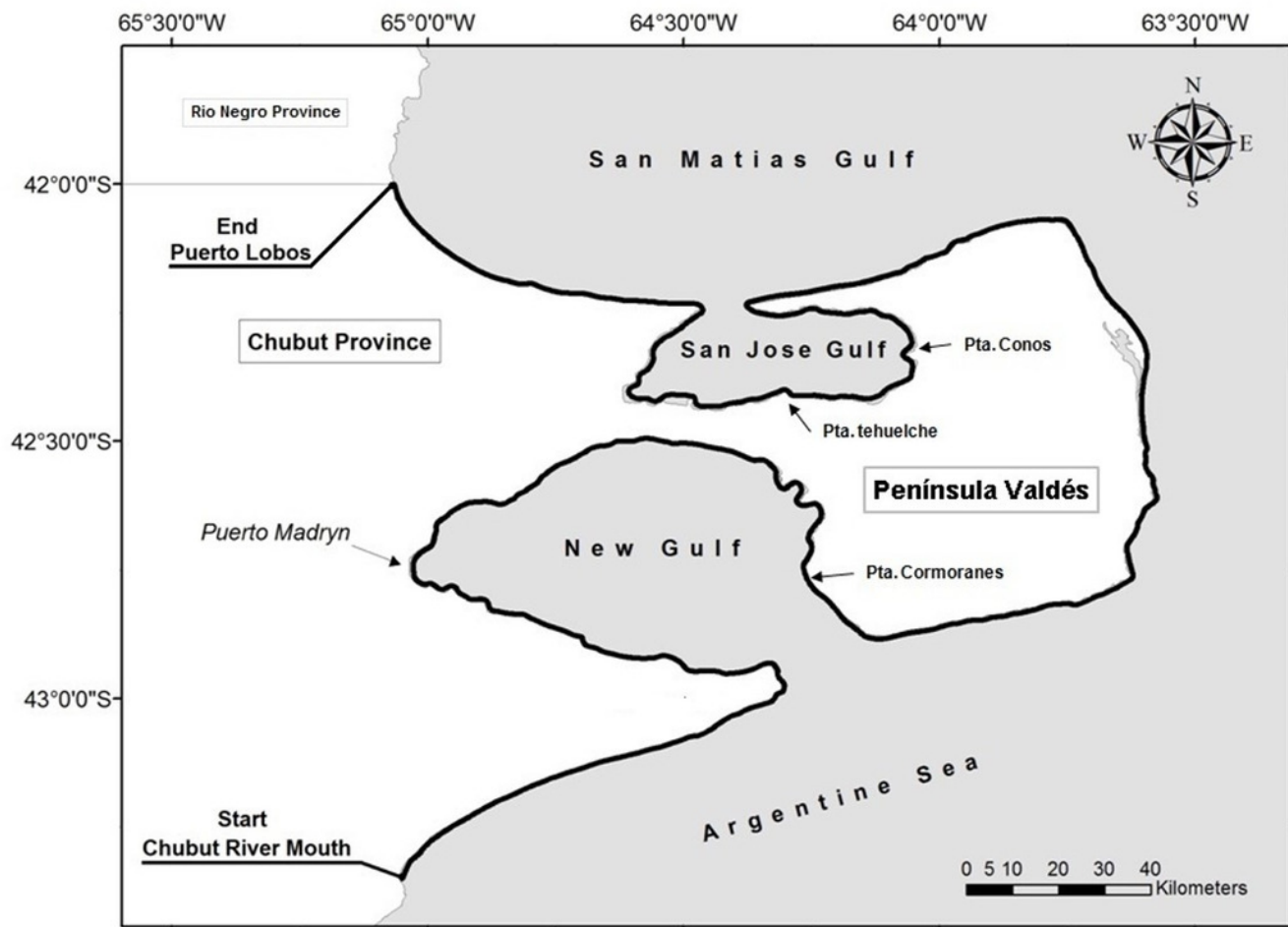
Figure 2

Variation of the average density of the sampling area for each established period.
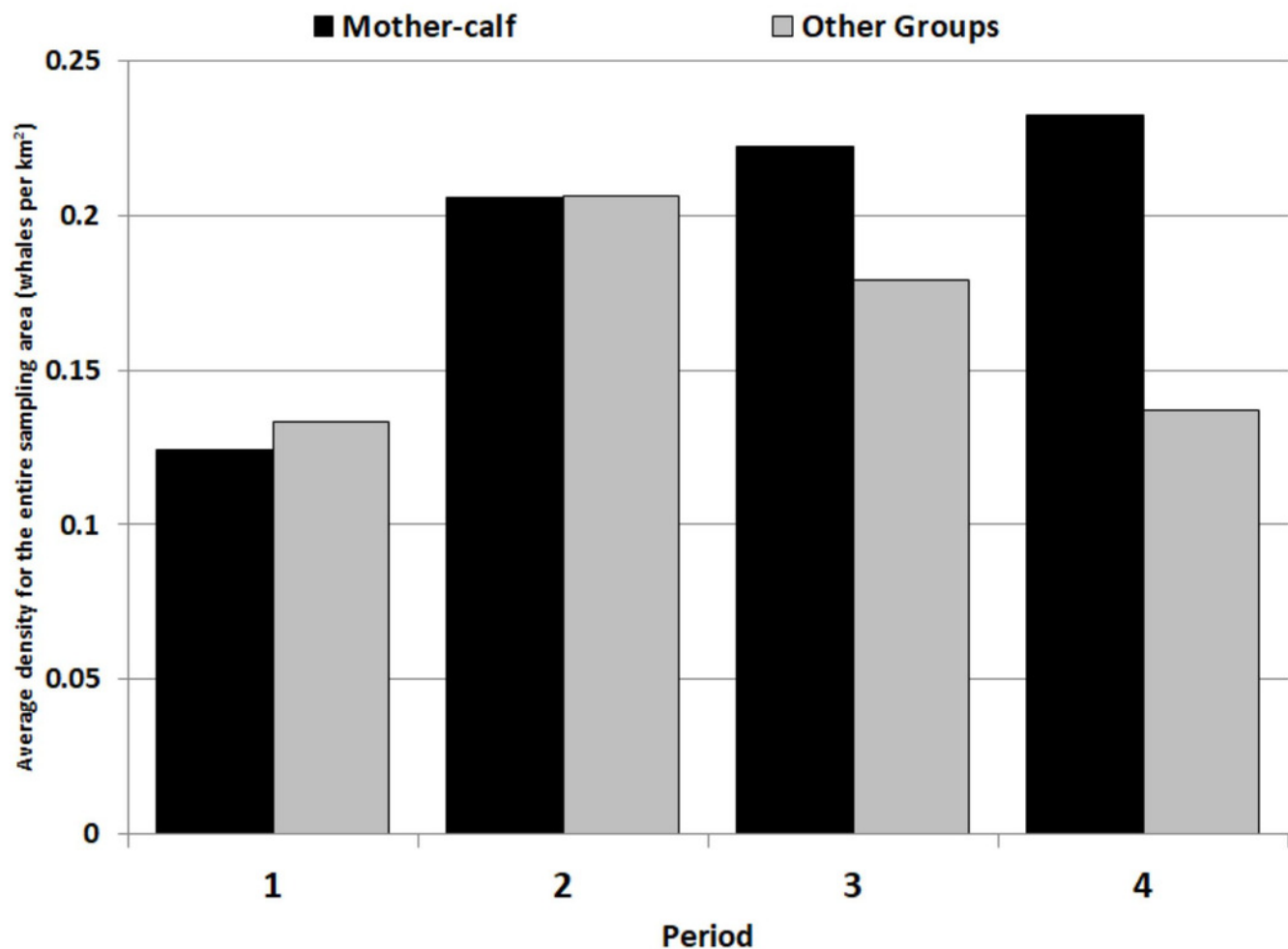
Figure 3

Density of the number of whales per km^2 in each segment of 5km performed in the 4 established periods for all the counted whales in the surveyed area.

Mother-calf pairs: white bars, *Other* groups: Black bar, All groups: gray continuous line.
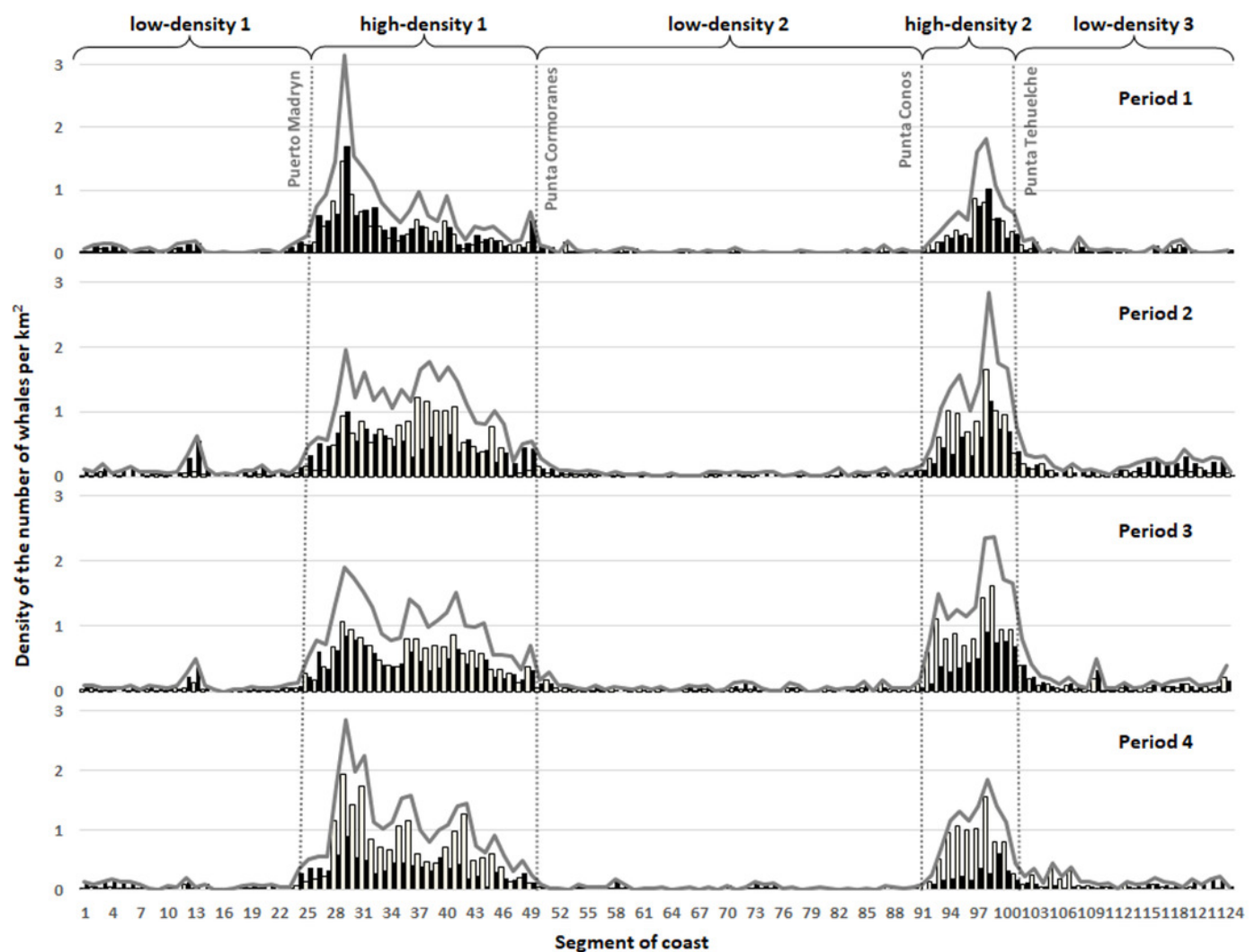
Figure 4

Variation of whale densities in the 4 periods for the three groups classified in the two high-density zones.

The brackets with the asterisk show the periods where there is a significant difference
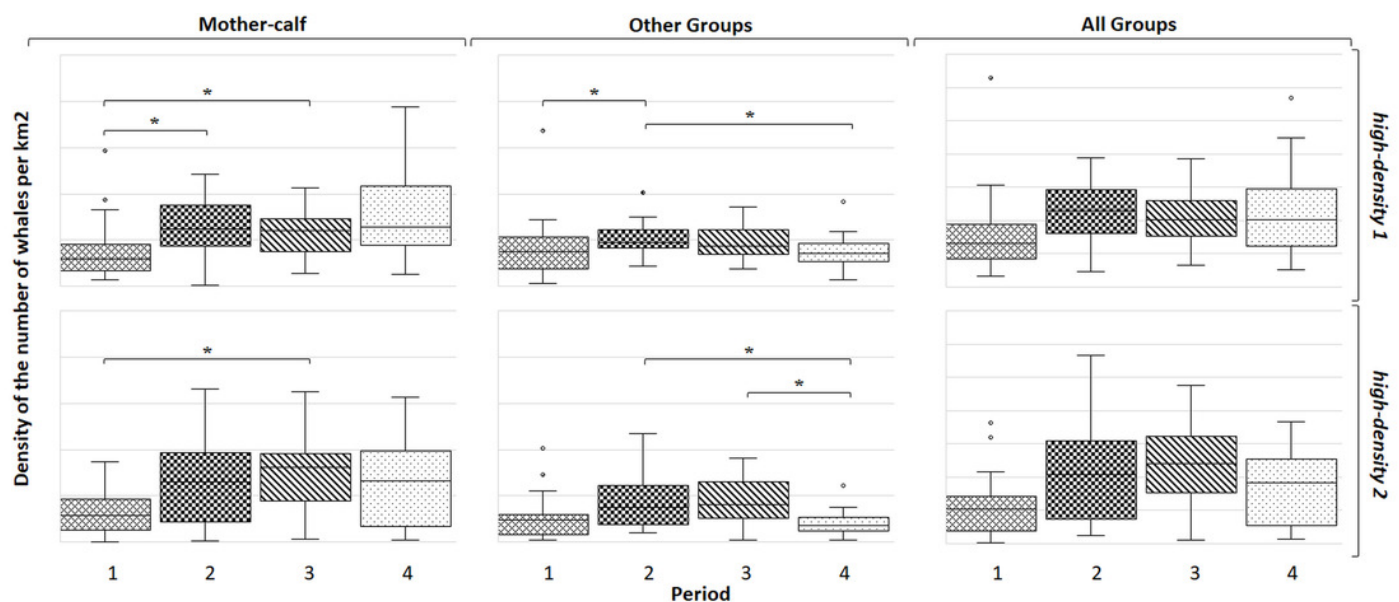
Figure 5

Mean densities of whales in the 4 periods for the three groups classified in the three low-density zones.

The brackets with the asterisk show the periods where there is a significant difference.