# 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*) is experiencing a population growth in the South-western Atlantic Ocean. In the breeding ground of Peninsula Valdés, as a consequence of the population increase, expansion to new areas and a change in the habitat use of the coastal area were recorded. Also, as a consequence of population increase changes in distribution and density in the core area are suspected.

**Methods.** We analyzed information that was gathered from aerial surveys developed along the coast of Peninsula Valdés for 19 years. These surveys were divided into 4 periods. A geographical analysis of 620 km of coast revealed that in 5 km-length segments.

**Results.** the density of whales increased to a maximum near to 3 whales per $km^2$.

**Discussion.** This figure is proposed as a threshold that elicits a density dependence response, where the *Mother-calf* pairs remain in the area, while the *other* groups decreased their density, forcing them to move to other areas.

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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 the object of a commercial exploitation between the XVIII and XX 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 derived from capture-recapture models have been estimated, based on the individual recognition of the whales. The population growth rate was estimated to be around 8% at that time (Payne

1986; Payne et al. 1981; Payne et al. 1990; Whitehead et al. 1986), and recent studies estimate a 5.1% for 2010 (Cooke 2012) and 6.5% for 2012 (Cooke et al. 2015) using the same techniques. Each year, between August and September, the number of whales reaches its maximum in the area (Crespo et al. 2018). The authors estimated for the year 2007 an increasing rate of 6.22%. For the year 2014, the models indicated that the population grew at a rate of 3.23% per year. This is an indication of a decrease at a rate of -0.45% per year in the rate of population increase (Crespo et al. 2018). However, the reduction in the rate of increase was not uniform across the different groups that comprise the population. The estimate of the growth rate for the number of offspring born in the Peninsula Valdés was 5.54% per year between 1999 and 2014 (Crespo et al. 2018), almost doubling the rate of increase for the whole population during the same period. However, the rate of increase of the other class groups (namely *Solitary Individuals* and *Breeding* groups) is now close to 0% (Crespo et al. 2018). *Mother-calf* pairs have displaced the *Other* groups from the shore, and the *Solitary Individuals* and the *Breeding* groups are now, or in deeper waters far away from the coast, or have moved away from the area. This change in Peninsula Valdés distribution could mean that the coastal zone (within 2km from shore) is close to its carrying capacity (Crespo et al. 2018). Therefore, in spite of the overall decrease in the rate of increase observed in the sampling area, it is proposed that the population of the south-western Atlantic is still growing at a rate that would be the combination of its growth in the Peninsula Valdés area and the rate occupation of new zones (Crespo et al. 2018). If this scenario is correct, whales should begin to move to other less dense regions (*ie:*, sub-optimal habitats) where the growth rate should be higher (Hobbs & Hanley 1990; Verner et al. 1986). There are different indicators support this hypothesis for Peninsula Valdés as evidenced by the number of whales occupying areas with deeper waters in Peninsula Valdés and the growing number of whales observed in Golfo San Matías, Buenos Aires, Uruguay and Santa Catarina in the southern Brazil (Crespo et al. 2018; Groch et al. 2005; IWC 2011).

The expansion of whales to other areas may be determined by the priority occupation of mothers with offspring in optimal habitat areas (Barendse & Best 2014; Carroll et al. 2014; Danilewicz et al. 2016). If this is the case, there should be a threshold density in which the *Other* groups increase their density in adjacent areas (*eg:* nonpreferred by *Mother-calf* pairs).

## Methods

The censuses were carried out from a single-engine high-wing CESSNA B-182 aircraft, flying at a constant height of 500 feet (152 m) and at 80/90 knots every 45 days from April to December each year (Crespo et al. 2018). In each survey a distance of 620 km was covered in 5 hours of flight, flying from south to north along the coast. The surveyed area (Figure 1) is located between the mouth of the Rio Chubut and Puerto Lobos on the border with the province of Rio Negro. The width of the strip is composed by 500 meters from the coast plus approximately 1000 meters from the plane to the open sea, composing a surveyed strip of 1500 meters (Crespo et al. 2018). This strip is set to cover the "whale-road" as described by Payne (1986), where more than 90% of the whales in the area concentrate near the coast in shallow waters.

The team comprised a pilot, a recorder sitting next to the pilot and two observers in the rear seats, one on the left and one on the right side of the aircraft (Crespo et al. 2018). The observations were made with the naked eye, and the information was recorded in spreadsheets or tablet applications developed *ad-hoc* with Cyber Tracker ™. Information on the on the group composition was recorded, including *Mother-calf* pairs, *Solitary Individuals* or *Breeding* groups comprising n-1 males and one female (Crespo et al. 2018). *Solitary Individuals* and *Breeding* groups were pooled in *Other* groups, as a group category opposite to the *Mother-calf* pairs.

Along with the type of group we recorded the position registered with a handheld GPS, the number of individuals and the sea state on the Beaufort scale. Flights were suspended when the visibility conditions were not optimal, either because of fog or the sea state exceeded the level 3 of Beaufort scale. The information was introduced into a database developed specifically for this purpose.

The information was clumped into four periods, making each period as similar as possible considering the number of flights. A total of 58 air surveys were clumped in four periods: period 1 from 1999 and 2000 (8 flights) and the other 3 periods comprised from 2004 to 2007 for period 2 (18 flights), period 3 from 2008 to 2012 (17 flights) and period 4 from 2013 to 2016 (15 flights). For each period, the average density per group type was calculated for the entire sampling area.

Later the coast of the surveyed coast was divided into segments of 5 km in length, totalling 124 segments for the 620 km sampled in each flight, where the 0 km is the mouth of the Chubut River (Figure 1). The densities were calculated by dividing the number of whales counted in each segment, weighted by the number of flights performed per period and the area of each segment, calculated as the 5 km segment by 1.5 km (bandwidth), and thus each segment accounted for a 7.5 $km^2$. The length of the segment was chosen following Rowntree et al. (2001), who divided the coast into 5 km segments to evaluate the distribution of the Southern Right Whales.

We defined two high densities zones, one inside Golfo Nuevo from Puerto Madryn to Punta Cormoranes and other inside Golfo San José, from Punta Conos to Punta Tehuelche (Figure 1). We also defined the low-density zones as the ones outside the high-density zones (*ie:* Chubut River mouth-Puerto Madryn; Punta Cormoranes-Punta Conos; Punta Tehuelche-Puerto Lobos). Differences in densities among the periods in these zones were assessed by Mann-Whitney *U* tests (Zar 2010).

The permit was granted by the Secretaría de Turismo y Áreas Protegidas of the Province of Chubut, (issued for the last time under permit number 93-SsCyAP / 15).

## Results

The overall density of both groups for the whole surveyed area shows for the first period a similar density for *Mother-calf* pairs and *Other* groups. For the second period, the observed increase is similar for both categories (Figure 2). During the third and the fourth period, there is a slight increase in the density of *Mother-calf* pairs, while the *Other* group's density decreases (Figure 2).

Numbering the 5 km segments consecutively from the Chubut river mouth (Figure 1), the coastal areas defined as high densities zones are located between the segment 24 (Puerto Madryn) and segment 49 (Punta Cormoranes) inside Golfo Nuevo and between the segment 90 (Punta Conos) and the segment 101 (Punta Tehuelche) inside Golfo San José (Figure 3).

The highest densities in any of the four periods are observed in the Doradillo (segment 28 and 29) and Playa Fracaso (segment 97 and 98), these two regions are the ones with the highest densities. The maximum mean density was calculated in 3.15 whales per $km^2$.

Figure 4 shows the density changes in the two areas of high density of animals. For the area between Puerto Madryn and Punta Cormoranes the *Mother-calf* pairs increased their density in the second period and third period with respect to the first period ($U_{1,2}$: 181.5/$U_{1,3}$: 157.5; $p< 0.05$) but a great variation was observed in the fourth period. In the case of *Other* groups there is an increase in density, but with a subsequent decrease ($U_{1,2}$: 179/$U_{2,4}$: 426; $p< 0.05$).

In the area between Punta Conos and Punta Tehuelche, a similar situation is observed. An increase in the density by the *Mother-calf* pairs ($U_{1,3}$: 41.5; $p < 0.05$) that is sustained in time. In the case of *Other* groups, the initial increase is followed by a marked decrease in the last period ($U_{2,4}$: 143/$U_{3,4}$: 147.5; $p < 0.05$).

Figure 5 shows the changes in the low-density zones. *Mother-calf* pairs from Chubut River Mouth to Puerto Madryn increased their density during the third period ($U_{2,3}$: 215; $p < 0.05$). Also, an increase in the density of the *Other* groups from the first to the second period can be observed ($U_{1,2}$: 205; $p < 0.05$). Afterwards a decrease in the density from the second to the third ($U_{2,3}$: 540; $p < 0.05$) was recorded. In the zone defined from Punta Cormoranes to Punta Conos the *Mother-calf* pairs increased their density only during the third period ($U_{1vs3}$: 489/$U_{2vs3}$: 437/$U_{3vs4}$: 1054/ $p < 0.05$) decreasing afterwards. For the *Other* groups the was an increase after the first period that remained higher than the first period ($U_{1vs2}$: 372/$U_{1vs3}$: 519.5/$U_{1vs4}$: 511.5/$U_{2vs4}$: 994.5; $p < 0.05$). In the area defined from Punta Tehuelche to Puerto Lobos for the *Mother-calf* pairs the increse is obly noticed between the first period and the rest ($U_{1vs2}$: 119/$U_{1vs3}$: 109/$U_{1vs4}$: 116; $p < 0.05$). The *Other* groups show an increase in density after the first period, but there is also a decrease in density from the second to the fourth period ($U_{1vs2}$: 56/$U_{1vs3}$: 82/$U_{1vs4}$: 71/$U_{2vs4}$: 308; $p < 0.05$).

## Discussion

This is the first study that proposes that a threshold in whale´s density in the core areas triggers a density-dependent response (Matthysen 2005). This response includes the movement of *Solitary Individuals* and *Breeding* Groups (*Other* Groups) to adjacent areas when the average density in the area is close to 3 whales per $km^2$. This figure must be taken with caution since it is an average from April to December, and the number of whales in the area peak only during August-September (Crespo et al. 2018). During the peak of the season, as much as 15,87 whales per $km^2$ can be found in the El Doradillo area but the description of the process can be better viewed using the average. This kind of changes in the distribution of southern right whale in Peninsula Valdés was reported by Rowntree et al. (2001) during the late 80's. Rowntree et al. (2001) propose a movement of whale breeding areas from the outer coast of Peninsula Valdés into the gulfs (Golfo Nuevo and Golfo San José), but no mechanism was proposed. The areas reported as new for the 1990s in Peninsula Valdés are the same as those observed in this work for the first period (Figure 3). Rowntree et al. (2001) considered several factors as gull inflicted wounds or undetected changes in the environment and topography of the area as the possible causation of the observed shift in distribution. Our data lead us to propose that density changes (and hence social causes) can be the main mechanism that promotes the search for new areas and the expansion of the occupied coast in Peninsula Valdés breeding ground, even though this might not have been the same mechanism that drives the changes observed during the late 1980's.

Other social interactions are being recorded in the area, besides the already described *Mother-calf* pairs. Solitary individuals engaged in the same activities and cooperative feeding were recorded recently, and hence new interactions never reported before may be shaping the behavior of whales in the area (Argüelles 2017; Arias et al. 2017).

*Mother-calf* pairs continue to select areas used in the late 1990s, the so-called high-density zones (Figure 4). The density in these areas increased, but differentially by type of groups: while *Mother-calf* increased their density, the *Other* groups continue to select this area until an average threshold of 3 whales per $km^2$ is reached. In every considered period, this is mainly due to the increase in density of *Mother-calf* (the only fraction of the population that is still growing- Crespo et al. (2018)). During the first period, the average annual density reached near 3 whales per $km^2$ in the area Puerto Madryn- El Doradillo. In the following period a change in the density of whales occurs (Figure 4); not only there is an increase in the *Mother-calf* pairs density, but the *Other* groups are more prone to be found in peripheral areas of less density (*eg.* Chubut River Mount-Puerto Madryn) in the second period, as shown in Figure 3. The same pattern can be found in Golfo San José high-density area during the second period. After the mean density approached to 3 whales per $km^2$, the density of the *Other* groups increased in the low-density area Punta Tehuelche-Puerto Lobos (Figure 5).

In the fourth period, it is observed that the average annual density of whales in the Doradillo area is close to 3 whales per $km^2$. If the same pattern is repeated in the next period, we could hypothesize that an expansion of part of the whales to areas with physical and biological conditions similar to those found in Peninsula Valdes will occur in the next few years, as well as a new increase in the low-density areas.

In a context of a population growth, the expansion into new areas has been recorded, mainly driven by *Solitary Individuals* and *Breeding* groups (Arias et al. 2018). The optimum areas are first occupied by the *Mother-calf* pairs, as the density of this type group increases, the rest of the groups are a move to suboptimal zones (Svendsen 2017).

This kind of mechanisms were recorded in other mammals. When the red deer (*Cervus elaphus*) population of the island of Rum doubled its size, females presented on average a greater spatial distance among them (Albon et al. 1992). The authors propose that in mammals with fission/fusion societies, dispersal is a gradual process and that it does not necessarily involve the total abandonment of the natal area by individuals as they disperse. Through a mechanism that involves the increase of the distance between mothers and daughters, of new matrilineal lines can establish in time new breeding areas. In the case of the roe deer (*Cupreolus capreolus*) the increase in density in the area caused a change in habitat use by young males and later by adult males. While  females continue to use the habitat used by the population in the past (*ie*; optimal habitat), younger males tend to move to other areas (Vincent et al. 1995). Our results indicate that the recolonization process started at least in the mid-2000s when whales change both, the way they use the habitat related to the type of groups (Crespo et al. 2018) and the areas where they could be found. The expansion of these groups to other areas was observed in the province of Rio Negro with the presence of whales in the area near the San Antonio Bay. In this area, more than 80% of whales are *Solitary Individuals* and *Breeding* Groups (Arias et al. 2017; Crespo et al. 2018). This process has also been recorded in other southern right whale stocks from South Africa, New Zealand and southern Brazil, where *Solitary Individuals* and *Breeding* Groups move to new sites, outside the established breeding area (Barendse & Best 2014; Carroll et al. 2014; Danilewicz et al. 2016).

## Conclusion

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

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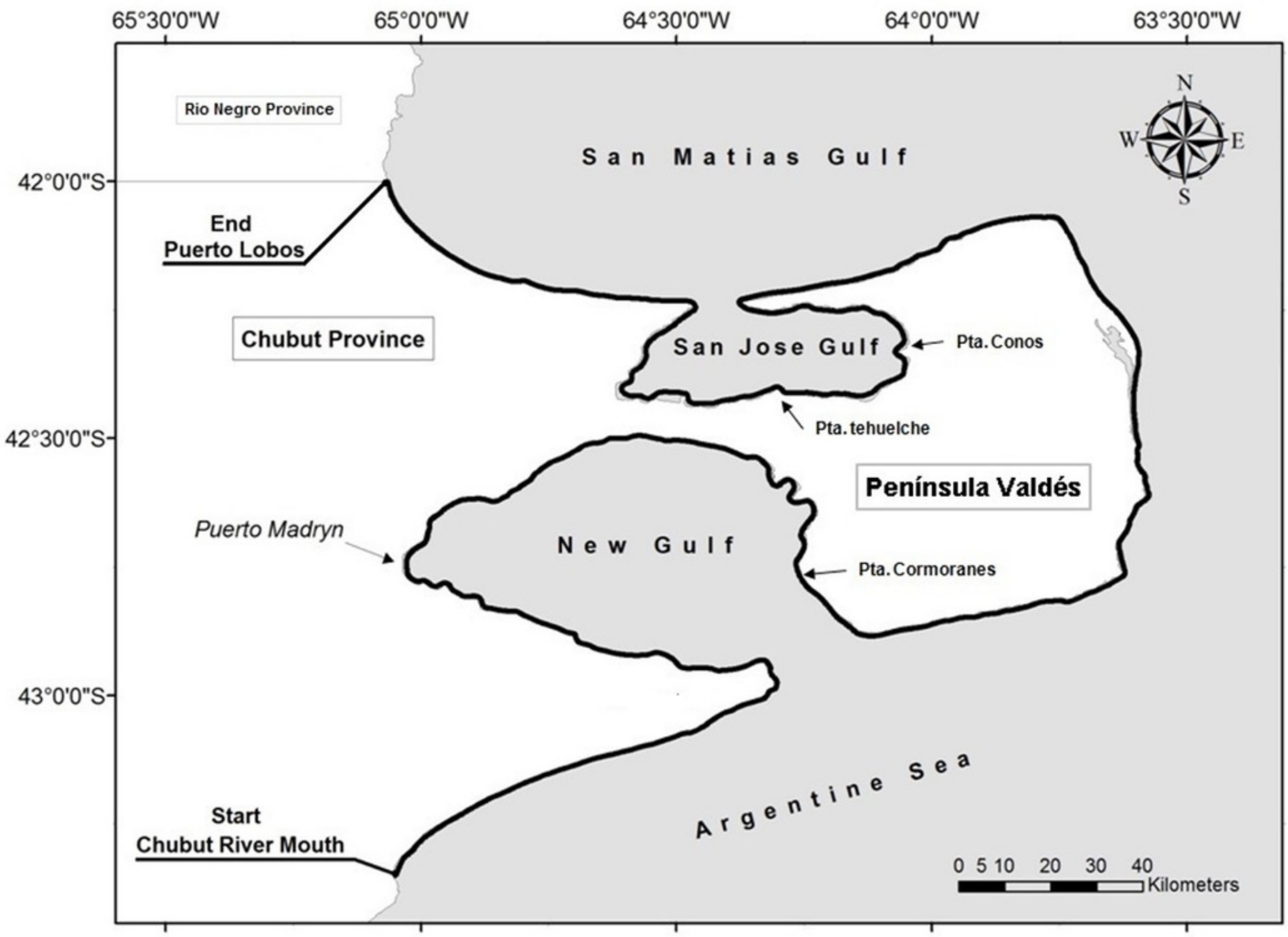
# Figure 1

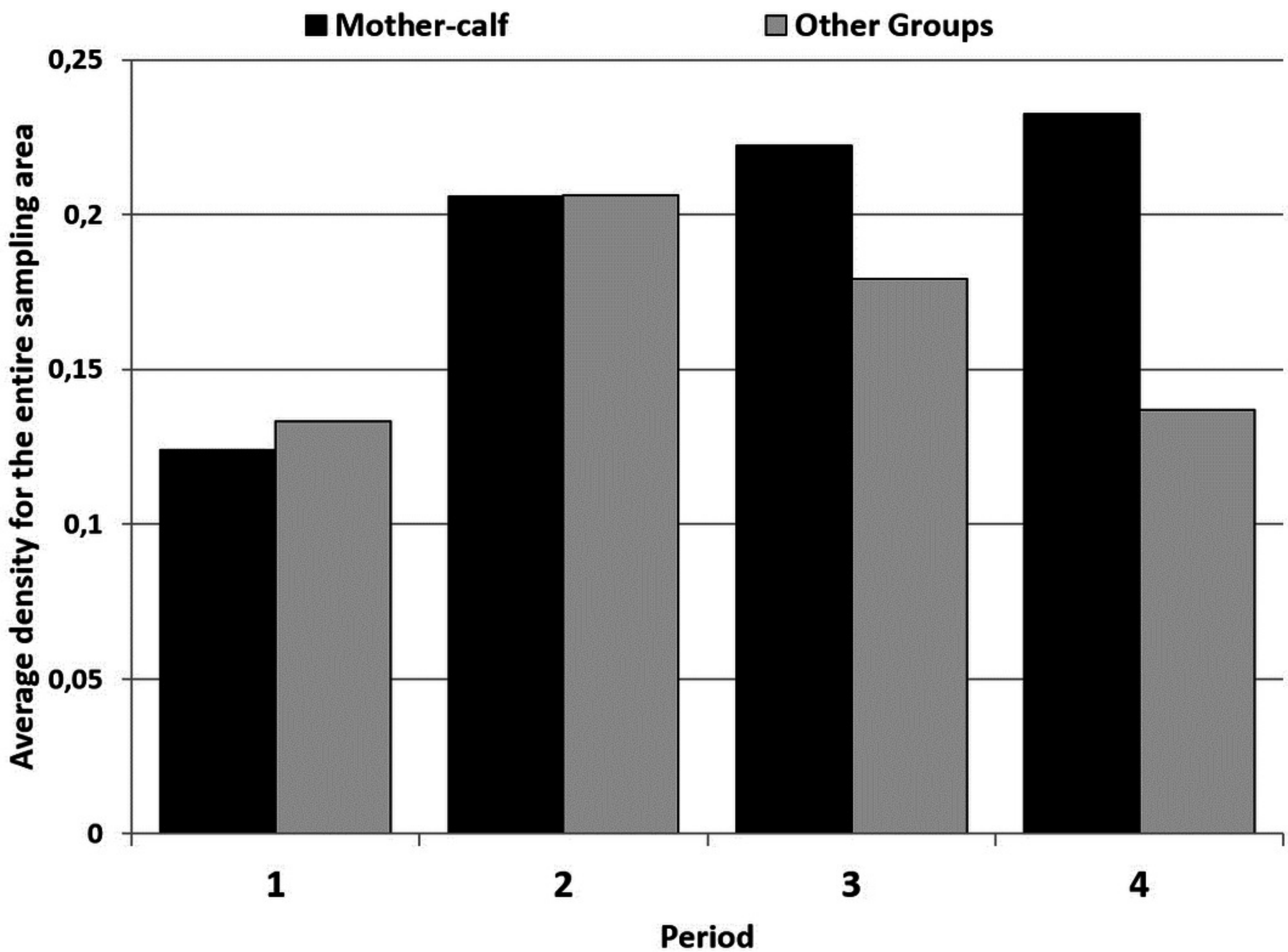
Sampling area

The thick black line along the coast represent the surveyed area



# Figure 2

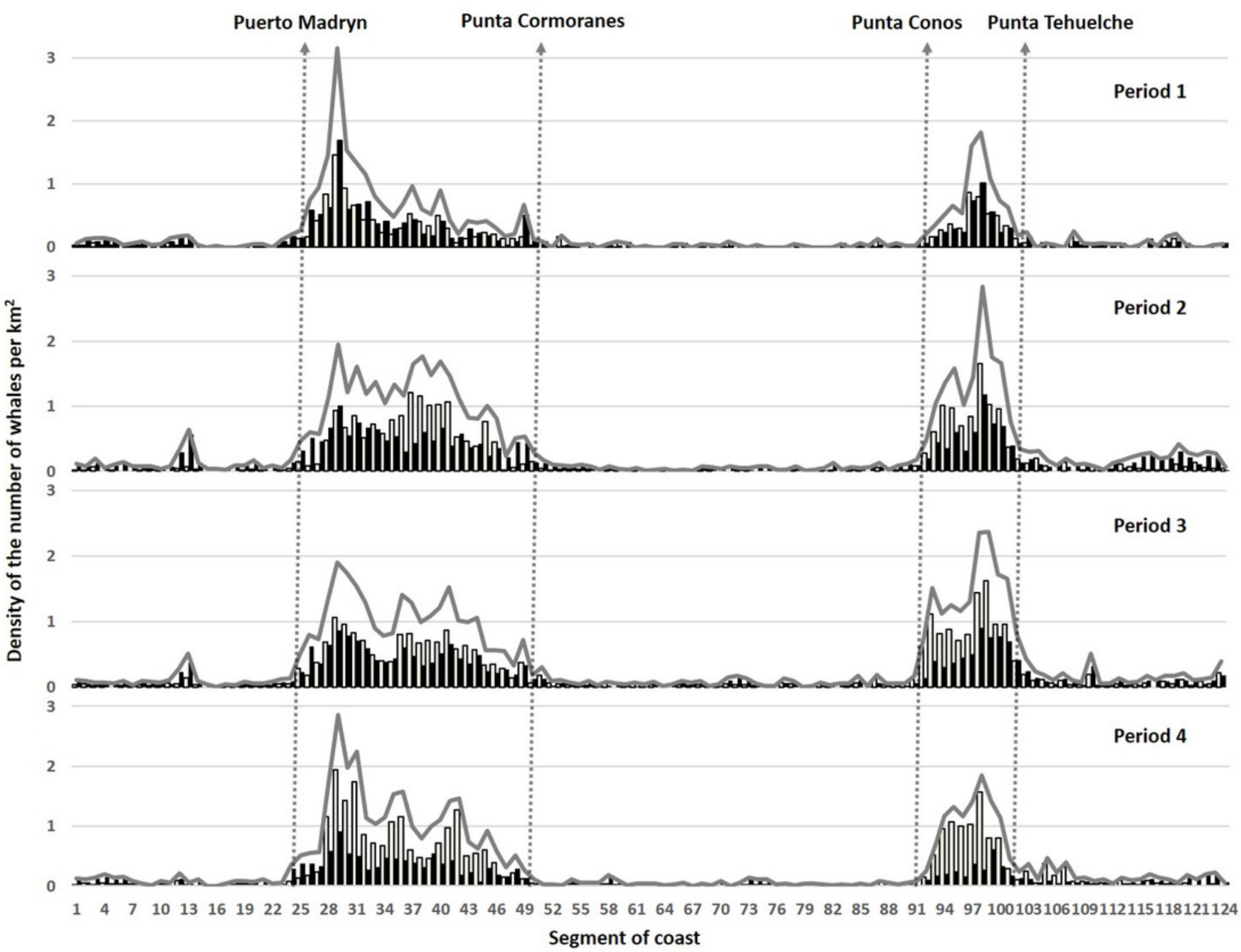
Variation of the average density of the sampling area for each established period



# Figure 3

Density of the number of whales per km² in each segment of 5 km performed in the 4 established periods for all the counted whales in the surveyed area without discriminating the group type

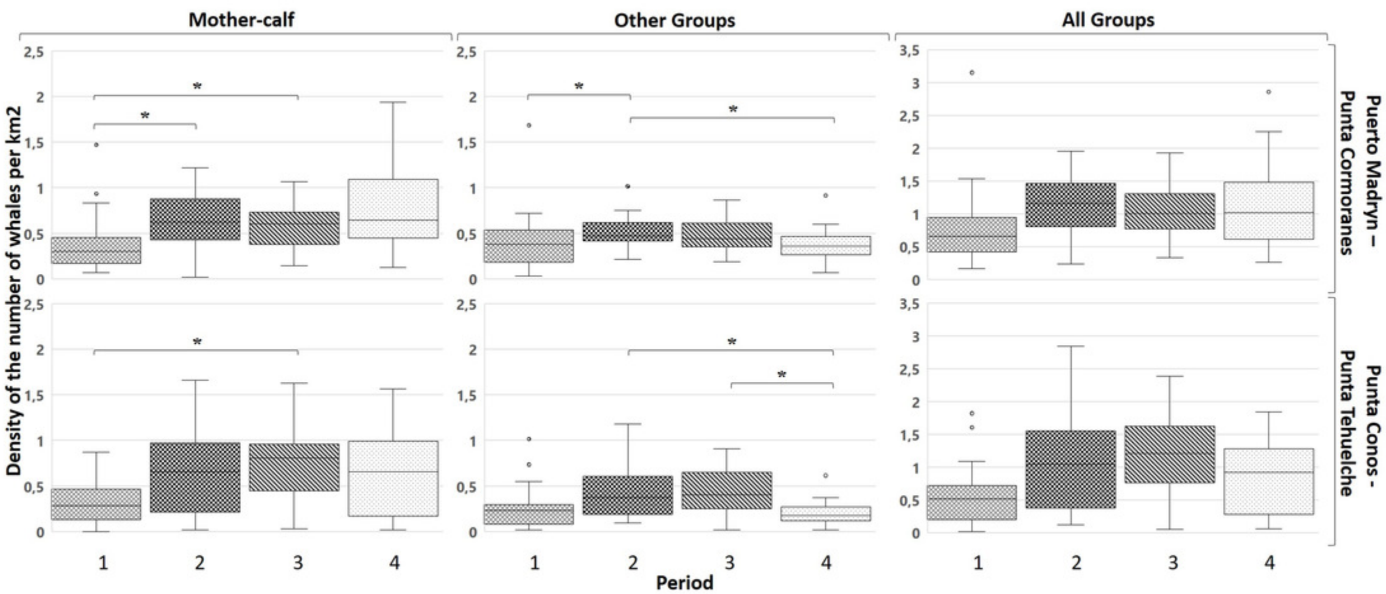
*Mother-calf* pairs: white bars, *Other* groups: Black bar, All groups: gray continuous line



# 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