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Estimation of total population size of southern elephant seals (*Mirounga leonina*) on Kerguelen and Crozet Archipelagos using very high-resolution satellite imagery

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Southern elephant seals (*Mirounga leonina*) play a pivotal role in the Southern Ocean as wide-ranging marine predators and major prey consumers within Southern Ocean marine ecosystems. Due to their circumpolar distribution and the remoteness of their habitat, large uncertainties remain about their total population sizes. This is especially true for elephant seal populations in the French Southern Territories in the southern Indian Ocean (i.e. Crozet and Kerguelen Archipelagos) as many breeding sites are inaccessible for ground censuses. Here, we present a simple and efficient approach for estimating the total elephant seal populations of the Kerguelen and Crozet Archipelagos by using very high-resolution satellite imagery (<1m resolution). Twenty-eight satellite images taken during the breeding season to count female elephant seals in inaccessible areas were used and complemented the traditional annual ground counts in accessible areas. For Kerguelen Island sectors likely to host colonies and where no satellite images were available for the breeding season, a statistical predictive model was built to estimate the most likely number of breeding females to be present on a given beach according to its physiographic characteristics. Our results show the reliability of using very high-resolution satellite images, a relatively low-cost platform, to count pinniped populations and provide the first estimation of the total southern elephant seal population for both the Kerguelen 347,995 (s.e. = 4,950) and Crozet 13,065 (s.e. = 169) Archipelagos. The combined total represents over 35% of the global elephant seal population with the Kerguelen stock being numerically equivalent to the South Georgia stock. In addition, we re-examined the population trends since the last mid-century for Kerguelen and over the last five decades for Crozet.

The demographic trends of the southern Indian Ocean populations show marked growth over the last decade (5.1% and 1.6% annual growth rate for Crozet and Kerguelen respectively), particularly on Crozet where the elephant seal population has more than tripled.

KEYWORDS

marine mammals, pinnipeds, southern Elephant seals, Kerguelen and Crozet Islands, remote sensing, population size, census

1 Introduction

Effective monitoring using appropriate biodiversity indicators is critical to the surveillance of the natural environment, to detect changes and assess threats associated with natural or human-driven environmental changes (Johnson et al., 2017). Total population size data are critically important to improve ecological or trophic modeling studies such as estimations of the overall amount of food consumed by seabirds and marine top mammals and their contribution to ocean carbon and nutrients fluxes (Guinet et al., 1996; Moore, 2008). As such, long-term monitoring of population size along with demographic studies are essential to define the conservation status of species and implement conservation responses. Beyond conservation issues, long-term surveys are also essential for research purposes.

In this context, monitoring of the southern elephant seal (*Mirounga leonina*), an abundant marine top predator with a large circumpolar distribution (Ling and Bryden, 1992), is of particular interest. Southern elephant seals are major deep diving predators within the Southern Ocean. Monitoring their population changes could provide insights into the changes affecting the mesopelagic and bathypelagic fishes and squids they consume (Guinet et al., 1996; Cherel et al., 2008).

Four genetically distinct populations are identified: the Valdés Peninsula population in Argentina, the South Georgia population in the South Atlantic Ocean, the Kerguelen and Heard populations including the Crozet and Prince Edward Archipelagos in the South Indian Ocean, and the Macquarie population in the South Pacific Ocean (Slade et al., 1998; Rus Hoelzel et al., 2001). The number of breeding females ashore provides a reliable indicator of the total population size (Hindell and Burton, 1987). Available land censuses suggest that the three largest elephant seal breeding populations located in South Georgia, Kerguelen and Macquarie, hosted approximately 100,000, 60,000 and 20,000 breeding females respectively in 2010 (Hindell et al., 2016).

Monitoring studies of elephant seal populations have reported different population trends according to the breeding localities over the last sixty years. South Georgia, in the Atlantic population of the Southern Ocean, was the only breeding location where elephant seal numbers were reported to be stable (McCann and Rothery, 1988; Boyd et al., 1996; McMahon et al., 2005). Elsewhere, in Argentina, population size increased rapidly over the 1982-1995 period (Campagna and Lewis, 1992; Lewis et al., 1998). In contrast,

within the Pacific sector of the Southern Ocean, the number of elephant seal females breeding on Macquarie Island declined from a maximum of about 40,000 in the 1950s to a minimum of 18,300 in 2000, then increased slightly to 19,200 up to 2004 (van den Hoff et al., 2007) before initiating a new decline in recent years (Hindell et al., 2017).

Meanwhile, within the Southern Indian Ocean, large changes in elephant seal numbers have been observed since 1950 (Guinet et al., 1992; Guinet et al., 1999; Authier et al., 2011; Oosthuizen et al., 2015). On Marion Island, the population has declined by 83%, from approximately 3 700 breeding females in 1951, and an estimation of 1,200 females in 1970, to a low 450 breeding females in the late 1990s with the population declining by 5.8% per year between 1986 and around 1994 (McMahon et al., 2009; Oosthuizen et al., 2015). Since then the population has slightly increased (N. de Bruyn, personal communication and see <https://www.marionseals.com/elephantseals>). On the Crozet Archipelago, the Possession Island population has decreased at a rate of 5.4% per year between 1970 (with an estimation of ~1,700 breeding females) to 500 breeding females in 1990 (i.e. a decline of 73%) with no change in numbers detected between 1990 and 1997 (Barrat and Mougouin, 1978; Guinet et al., 1992; Guinet et al., 1999). At the Kerguelen Islands, the number of breeding females censused on the Courbet Peninsula declined from about 70,000 breeding females in 1952 (Pascal, 1981) to 37,400 in 1987 (Guinet et al., 1992) before starting to increase at a 1% annual rate over the 1987-2009 period (Guinet et al., 1999; Authier et al., 2011). However, within the Crozet and Kerguelen Archipelagos, population trends were estimated from only about 20% of the total coastlines, the remaining 80% of coastlines being inaccessible. On the Crozet Archipelago, censuses of elephant seals colonies are conducted annually on Possession Island only even though colonies also inhabit Cochons Island and Est Island (Despin et al., 1972; Barrat and Mougouin, 1978; Jouventin et al., 1982). Similarly, beaches located south, west and northeast of the Kerguelen Archipelago are inaccessible by land for censuses, resulting in annual censuses being conducted solely east of the Courbet Peninsula despite the fact that 1925-1931 sealing data revealed the harvesting of very large numbers of elephant seals south and west of Kerguelen Island (Savours, 2009).

Satellite images have been successfully used to census seabirds (Fretwell et al., 2017; Zhao et al., 2020), whales (Fretwell et al., 2014; Borowicz et al., 2019; Cubaynes et al., 2019; Guirado et al., 2019) and seals (LaRue et al., 2011; McMahon et al., 2014; Gonçalves et al., 2020).

However, most of these studies were small-scale, proof-of-concept investigations except for some studies that have shown the ability of satellites to survey animals at more regional scales (Fretwell et al., 2014; Weimerskirch et al., 2018; LaRue et al., 2020), and global scales (Lynch and LaRue, 2014; LaRue et al., 2021).

In view of using very high-resolution satellite imagery to expand data on population estimates, the global objective of this present study is to provide the first exhaustive census of southern elephant seals (i.e. breeding female) for both the Kerguelen and Crozet Archipelagos. To achieve this goal, very high-resolution (VHR) satellite images obtained during the breeding season were acquired to complement ground censuses. VHR images provided by earth-observation satellites such as Pleiades PHR-1B (panchromatic 0.50 m resolution), WorldView (WV) 2 and 3 (panchromatic 0.50 m, and 0.30 m resolution respectively) and GeoEye1 (panchromatic 0.50 m resolution) offer a means to overcome the challenge of censusing colonies of large seabirds and pinnipeds in difficult-to-access areas while limiting the impact of human presence on protected sites (disturbance, invasive species or habitat degradation).

Building on the new horizons opened up by satellite images, this present study aims to: (1) use satellite images taken during the breeding season to count seals on selected favorable breeding beaches on the Kerguelen and Crozet Islands; (2) assess the accuracy of the satellite-image census method compared to (3) ground counts and when available, (4) complement satellite counts with ground censuses in order to (5) construct and validate a predictive statistical model for estimating the number of breeding females according to the physiography of beaches, and implement this model for beaches where no direct censuses and/or satellite images were available during the elephant seal breeding season; and (6) reevaluate the importance of the Crozet and Kerguelen southern elephant seal populations with respect to the species' other populations. Finally, we aim to (7) assess recent population trends on the Kerguelen and Crozet Archipelagos.

2 Materials and methods

2.1 Study sites

This study was carried out in the Indian sector of the southern Indian Ocean, in the Crozet Archipelago (-46.4260°S, 51.7750°E) composed of five small main islands totaling 350 km², and the Kerguelen Archipelago (-49.3649°S, 69.3843°E, Figure 1) comprising more than 300 islands and islets covering a total area of more than 7,200 km². These islands are part of the National Nature Reserve of the French Southern Territories, listed as a UNESCO World Heritage area, and constitute a sanctuary for biodiversity, in particular for seabirds and marine mammals. Scientific monitoring studies have been performed in this sector for almost 70 years, with the first elephant seal census performed in 1952 on the Courbet Peninsula, Kerguelen Island (Pascal, 1981). On Possession Island within the Crozet Archipelago, the first census was conducted in 1966 and totaled about 2000 breeding females (Barrat and Mougin, 1978).

2.2 Satellite image acquisition

Three different sources of satellite images were used in this study. Firstly, we acquired a Pleiades PHR-1B (AIRBUS Defence & Space satellite) image taken on a relatively cloud-free day (28th October 2015). This image, acquired in 2015, covers a small part of the Courbet Peninsula for which ground censuses were also performed (Figure 2). Image processing was performed by the French National Center for Space Research (CNES) to produce a pan-sharpened orthorectified image. The resolution (pixel size) of this image, 0.5 meter per pixel, provides a potential density of approximately 4 pixels/m² allowing the detection of adult elephant seals present on the beaches during this period. Secondly, satellite images performed by the MAXAR satellites WV-1, WV-2, WV-3 and GeoEye-1 and by the French satellite Pleiades PHR-1B, providing a ground resolution varying from 30 to 50 cm per pixel with panchromatic images, were bought or freely available from Google Earth and Bing Maps. 26 VHR images were acquired for this study to perform elephant seal counts at inaccessible locations (one on Crozet and 25 on Kerguelen; Table 1; Figures 2, 3).

2.3 Satellite image counts

Counting on satellite images was carried out by visual inspection using GIMP 2.8 software (GIMP 2014) which allows counts to be made manually. Only females were counted during the breeding season. When, contrary to what might be observed during the molt, females tend to maintain some free space around themselves (Figure 2), reducing the probability of merging several females as one individual. Adult males and newborns, distinguishable from females by their size, were not counted, and the probability of confusion with females is low. Males (4 to 6 m) are two times longer and wider than females (2 to 3 m), while newborns and nearly weaned pups are much smaller (0.8 to 1.3 m) and have a black coat instead of the brown color of adults. McMahan et al. (2014) found one-to-one relationships with a $R^2 = 0.9062$, between harem counts performed by a naive observer on satellite images and those performed on the ground.

For each satellite image, three successive counts were performed by the same experienced observer at intervals of at least 6 months to estimate any census errors and to avoid biases introduced by prior knowledge. The observer's experience in land-based elephant seal surveys helped to facilitate detection of harems and to limit confusion with the different environmental elements of breeding sites (sexing, other species, rocks and vegetation). The mean of these three corrected counts was taken to represent the number of females per sector during the breeding season.

We prioritized the satellite image search for beaches with known historical sealing records (Savours, 2009) and for those where no ground census was available. Beaches were distinguished according to their physiographic characteristics (i.e. sandy versus boulder beaches, beach lengths, and beaches directly exposed to the open ocean versus beaches at the inner end of fjords). For this purpose, we used Geographic Information System (GIS) software QGIS (QGIS, 2020) with the OpenLayers extensions allowing access

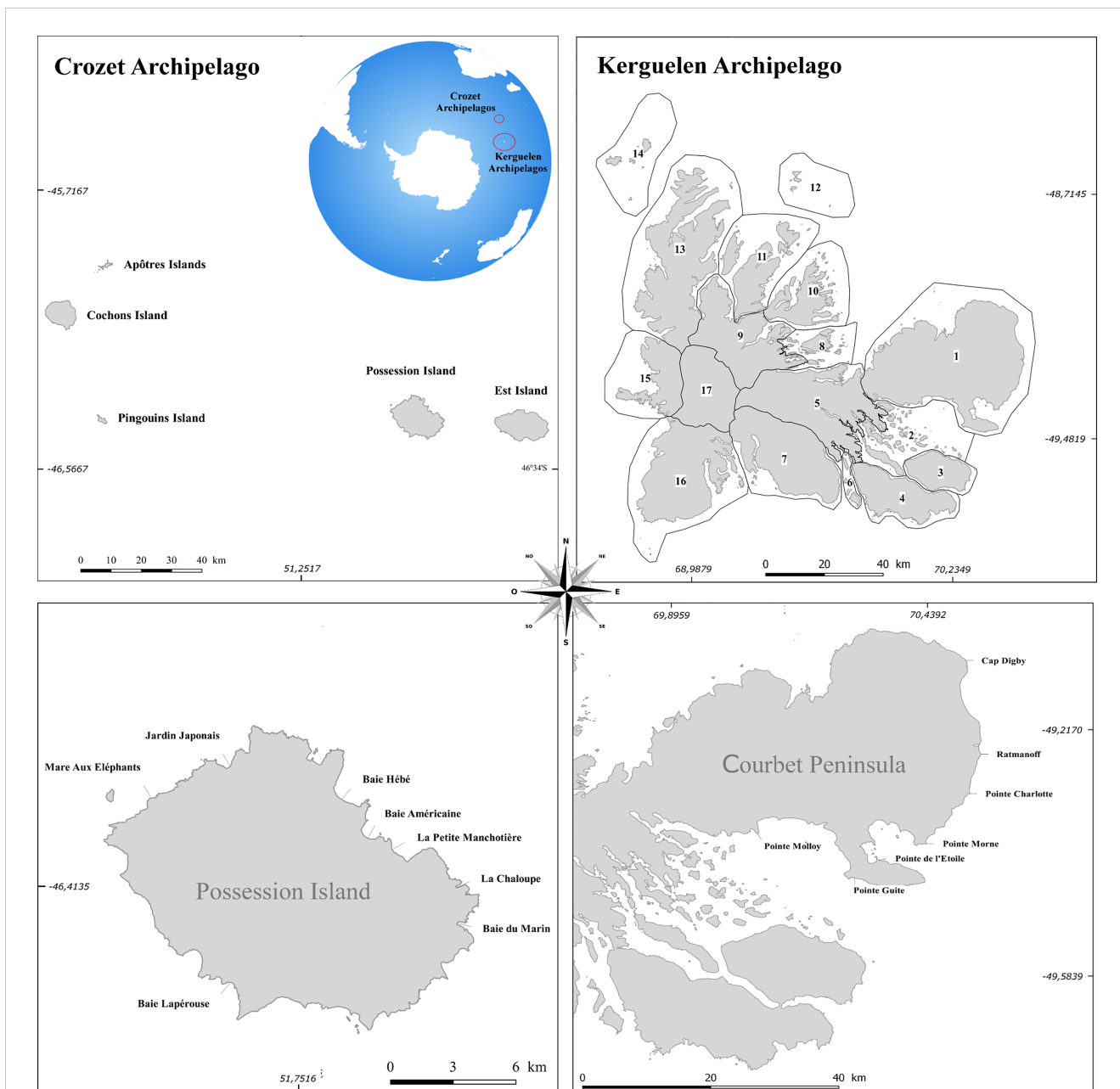


FIGURE 1 Location of the French Southern Islands with the Crozet (upper left panel) and Kerguelen Archipelagos divided into 17 sectors (upper right panel). For Kerguelen Island (top right), the count areas are 1) Péninsule Courbet, 2) Golfe du Morbilhan, 3) Presqu'île Ronarch, 4) Presqu'île Jeanne d'Arc, 5) Plateau central, 6) Ilots de la Baie des Swain, 7) Massif Galieni, 8) Ilots du Golfe des baleiniers, 9) Presqu'île de la Société de Géographie, 10) Presqu'île de Joffre, 11) Îles Foch, Howe, Saint-Lanne Grammont, 12) Îles Leygues, 13) Presqu'île du Loranchet, 14) Îles Nuageuses, Îles de l'Ouest, 16) Péninsule Ralier du Batty. The two lower panels represent the long-term monitoring study areas in Crozet and Kerguelen.

to Google Earth and Bing Maps public software for visualization of the Earth from space.

2.4 Ground counts

Males arrive in colonies earlier than females, and fight for control of harems upon their arrival (Jones, 1981). Large body size confers advantages in fighting, and the antagonistic relationships between bulls give rise to a dominance hierarchy, with access to harems and activity

within harems being determined by rank (McCann, 1981). The dominant bulls (harem masters) establish harems of several dozen females.

During the reproduction haul-out when pinnipeds spend time on land, females aggregate in dense colonies to give birth to a single pup, weaned 3 weeks later, then mate before returning to sea. While the timing of female return varies from mid-September until late October, each female only stays ashore for about four weeks (van Aarde, 1980) with a maximum number of breeding females present ashore in mid-October (Galimberti and Boitani, 1999; Galimberti

TABLE 1 Information from the 26 satellite images available for the estimation of the total population size of elephant seals in the Kerguelen and Crozet Archipelagos.

Id	satellite id	sector (Figure 1)	Island	area (km ²)	Satellite	subsidiary	Pan-reso (m)	acquisition date
1	1050010006A08100	15	Kerguelen	25.6	GeoEye1	DigitalGlobe	0.44	10/12/2016
2	104001002371F200	16	Kerguelen	25.2	WorldView3	DigitalGlobe	0.33	10/12/2016
3	103001000EBA6200	7	Kerguelen	25.2	WorldView2	DigitalGlobe	0.52	10/14/2011
4	1050010006A08100	16	Kerguelen	25.2	GeoEye1	DigitalGlobe	0.44	10/12/2016
5	1050010006A08100	16	Kerguelen	28.7	GeoEye1	DigitalGlobe	0.44	10/12/2016
6	104001000322CE00	16	Kerguelen	28.3	WorldView3	DigitalGlobe	0.38	10/17/2014
7	103001005E64E800	16	Kerguelen	41.5	WorldView2	DigitalGlobe	0.49	09/29/2016
8	1040010022D4D100	16	Kerguelen	25.8	WorldView3	DigitalGlobe	0.33	10/06/2016
9	1040010022D4D100	7	Kerguelen	30.5	WorldView3	DigitalGlobe	0.33	10/06/2016
10	103001000D806F00	7	Kerguelen	25.4	WorldView2	DigitalGlobe	0.55	10/14/2011
11	103001000EBA6200	8	Kerguelen	27.2	WorldView2	DigitalGlobe	0.52	10/14/2011
12	103001000EBA6200	10	Kerguelen	25.7	WorldView2	DigitalGlobe	0.52	10/14/2011
13	103001000EBA6200	10	Kerguelen	25.2	WorldView2	DigitalGlobe	0.52	10/14/2011
14	103001001CCDD700	11	Kerguelen	25.5	WorldView2	DigitalGlobe	0.55	10/20/2012
15	103001001CCDD700	11	Kerguelen	28.1	WorldView2	DigitalGlobe	0.55	10/20/2012
16	103001000D806F00	11	Kerguelen	25.8	WorldView2	DigitalGlobe	0.54	10/14/2011
17	10300100742C9900	13-15	Kerguelen	45	WorldView2	DigitalGlobe	0.48	10/16/2017
18	1030010007481F00	13	Kerguelen	25.8	WorldView2	DigitalGlobe	0.49	10/20/2010
19	1030010007481F00	13	Kerguelen	25.3	WorldView2	DigitalGlobe	0.49	10/20/2010
20	1030010007481F00	13	Kerguelen	25.8	WorldView2	DigitalGlobe	0.49	10/20/2010
21	1040010022D4D100	7-16	Kerguelen	31.8	WorldView3	DigitalGlobe	0.33	10/06/2016
22	1040010023AD0800	16	Kerguelen	26.7	WorldView3	DigitalGlobe	0.33	10/12/2016
23	PHR1B_MS_202010210510543_OR_T_5429583101-2	13	Kerguelen	205	Pléiades 1B	Pléiades CNES (2020) & AIRBUS DS	0.50	10/21/2020
24	PHR1B_MS_202010210510543_OR_T_5429582101-2	15	Kerguelen	213	Pléiades 1B	Pléiades CNES (2020) & AIRBUS DS	0.50	10/10/2020
25	DS_PHR1B_201510280509422_FR1_PX_E070S50_0516_01260	1	Kerguelen	212	Pléiades 1B	Pléiades CNES (2015) & AIRBUS DS	0.50	10/28/2015
26	06OCT19065632-P2AS-056816935030_01_P002	Cochons Island	Crozet	25.2	WorldView1	DigitalGlobe	0.60	10/19/2006

The satellite images indicated in bold are those with the highest resolution taken by the WorldView3 satellite.

et al., 2001; Authier et al., 2011). For this reason, no census can comprehensively encompass all females that may have come ashore.

The method for counting elephant seals on beaches is carried out as part of a standardized long-term monitoring protocol for the breeding populations of these pinnipeds in the French Southern Territories. At Kerguelen Island, such ground counts have been carried out annually since 1986 on the eastern part of the Courbet Peninsula (Figure 1). The method relies on an exhaustive count of all individuals present ashore on dates centered on 15 October (i.e. date of maximum haul-out). The counts are performed while walking along the coast, separately counting all females and males

ashore. For the breeding females, ideally three independent counts are conducted by different observers while one count is performed for both harem and peripheral males. If the difference between the 3 counts of females exceeds 10%, new counts are performed for this given area in order to limit detection bias by observers. A GPS point (latitude and longitude) is taken between each census sector's start and end, generally between each harem, in order to minimize the risks of differences between counts, but also to facilitate the location of abundance areas and the comparison with counts by satellite image. These data are collected and archived at the CEBC-CNRS long-term population monitoring database (program no. 109 of the

French Polar Institute Paul-Emile Victor) and the National Natural Reserve of the French Southern Territories.

The number of breeding females present ashore at any time during the breeding season varies according to a normal distribution model (McCann and Rothery, 1988). For both the Crozet and Kerguelen Archipelagos, the average date for the maximum haul-out is 15 October \pm 2 days, (Barrat and Mougin, 1978; Pascal, 1981; Guinet et al., 1992), a date identical to that of the Marion and Heard Islands breeding colonies (Condy, 1979; Wilkinson, 1992; Slip and Burton, 1999) with no change over time in this maximum haul-out date (Barrat and Mougin, 1978; Guinet et al., 1992; Slip and Burton, 1999; Authier et al., 2011). Following Rothery and McCann (1987) and Authier et al. (2011), we applied a correction factor to the counts according to the census date. The calculation of this correction factor takes into account: i) measurement error by the various observers; and ii) the date of the counts compared to the peak of female presence on the ground evaluated on 15 October when approximately 90% of breeding females are estimated to be present ashore (Authier et al., 2011).

For each census, an estimation of the total number of females breeding (\pm confidence interval) was calculated by implementing a Bayesian statistical approach combined with a Generalized Additive Model (GAM) and “Penalized B-Splines” (Eilers and Marx, 2010).

2.5 Comparison between ground and satellite counts

A Pleiades PHR-1B (ID 25; Table 1) satellite image with a 50 cm ground resolution was used to compare the number of breeding females provided by ground counts and those counted on the image. To this end, both counts were corrected according to Authier et al. (2011) to estimate the total number of females giving birth in a specific area. A linear regression model was constructed to compare the number of breeding females for the 18 different beaches encompassed by both the satellite and ground counts. To assess any possible bias in detection by satellite image resulting from the substrate on which the elephant seals reproduce (Laliberte and Ripple, 2003), the habitat was described for each counting area during the ground counts fieldwork (i.e. two categories: sand beach or vegetated area) and we compared the performances of the regression models for both conditions.

2.6 Estimation of the total elephant seal population size

An unknown proportion of elephant seal populations is always at sea, making accurate assessments of total population size is difficult. For this reason, the number of females is often used as an index of population size. Males on land during the breeding season represent a small part of the population and therefore do not provide a reliable indicator, in contrast to females and pups. As pups are more difficult to count during the peak of their presence on land and are smaller than females, to estimate the total population size, the number of breeding females should be multiplied by a correction factor estimated from

southern elephant seal life-table analyses (Laws, 1952; Harwood and Prime, 1978; McCann, 1985; McCann and Rothery, 1988). Based on Hindell and Burton (1987) and McCann and Rothery (1988), we chose a correction factor of 3.47.

2.7 Building a predictive model

In order to estimate a total elephant seal population size for the Kerguelen and Crozet Archipelagos and to overcome the absence of censuses for beaches likely to host elephant seal colonies according to their physiographic characteristics, a statistical predictive model was built to estimate the number of breeding females likely to be present on a given beach. VHR satellite images enabled characterization of each beach according to seven explanatory variables: 1) “Z” representing the 17 different geographical sectors of the Kerguelen Archipelago (see Figures 1, 2) “D” in order to make corrections according to the date of the counts of the known beaches used; 3) “SP” corresponding to the beaches’ surface area in m²; 4) “EP” corresponding to the beaches’ orientation (east, north, west, south); 5) “EM” corresponding to the orientation of the open sea area at the entrance of a fjord (east, north, west, south); 6) “DM” corresponding to the distance (m) of the beach from the entrance of a fjord; and 7) “DB50” corresponding to the distance (m) of the beach from the 50 m depth contour (i.e. shelf break, Table 2).

We were unable to include the nature of the beach substrate (sand, pebbles, or blocks) from the satellite images and that information was not collected when ground censuses were performed as nearly all Courbet Peninsula beaches are made of sand.

Some variables such as the rough number of females (not corrected by date) or the “surface area” of the beaches were log-transformed, in order to facilitate analysis of the models and comparison of the effects between them.

A data correlation test was carried out in order to eliminate the correlated variables, for which we used the function GGally: ggcorr, with the “pearson” method. The residues were also tested on each model with a Shapiro test. The statistical models used were Mixed Effects Linear Models (lmer) and Generalized Additive Models (GAM). We started with a full model and followed a stepwise procedure of removing non-significant variables with the threshold set at p-value < 0.05 (Zuur et al., 2009). We followed the standard procedure for model validation (Zuur et al., 2009). Best model selection was made by comparing Akaike information criterion (AIC). In addition to the selection by AIC, we verified the predictive capacity of the models by performing a cross-validation with the Leave-one-out (Loo) package, which randomly chose a beach and ignored the number of females counted on this beach to predict the number of females with all the models (Tab. II). The model giving the closest estimate to reality was used to estimate the number of breeding females on the uncensused beaches.

The best model was used to predict the most likely number of breeding females present on the unobserved beaches at the time of the peak presence of breeding females (i.e. 15 October). then this value was corrected according to Authier et al. (2011) to estimate the total number of elephant seal females which went to that beach to breed.

All the processing and analysis of statistical data were realized with R version.3.6.0 (R Core Team, 2019) and required the use of different specific packages such as “lme4,” “mgcv,” “tidyverse,” “mvtnorm,” “rstan,” “coda,” “ggplot2,” “ggthemes”.

2.8 Population trends in the Kerguelen and Crozet Archipelagos

Population trends for the Kerguelen and Crozet Archipelagos were established by a series of calculations performed on yearly censuses. Inter-annual changes in breeding elephant seal females were determined using the formula for mean annual percentage change:

$$\text{Mean annual percentage change} = (e^r - 1) \times 100$$

where $e = (\ln(N_t/N_0))/t$, and r = intrinsic rate of population change, N_t = population at time t , N_0 = original population size, and t = time elapsed between the two population estimates (Caughley, 1977; Slip and Burton, 1999; Bester et al., 2006).

For Kerguelen, the population trend was calculated from 40 annual censuses conducted over a 63-year period [1956: 2019] (on the Courbet Peninsula, no censuses were conducted between 1960 and 1977). Furthermore, incomplete censuses (1952, 1970 and 1984) were excluded, so as not to distort the trajectory of the population trend that was calculated between 1956 and 2018. These censuses were used to assess the Kerguelen elephant seal population on the Eastern and southern part of Courbet peninsula over the 1956-2019 period and shown in Figure 2.

Furthermore, over the 2010-2018 period, the usual Courbet Peninsula census area on Kerguelen Island was extended to breeding colonies located in the northwestern part of the Courbet Peninsula and around the Ronarc’h Peninsula (Figure 2). Beaches that were surveyed for at least four years between 2010 and 2018 provided data to estimate an observed growth rate over the same period. This growth rate was then used and implemented on the latest census available for a given beach to estimate the number of breeding females on that beach for the 2018 reference year, in order to estimate the total breeding female population sizes.

In this way, the Crozet population trend was assessed for nine beaches on Possession Island, using annual censuses since 1980 (Figure 3).

3 Results

3.1 Validation of seal counts from satellite images

Comparison between satellite and ground counts was conducted over a large sector, south-east of the Courbet Peninsula, shown in Figure 1. Ground counts yielded an estimated total number of $13,190 \pm 2,120$ breeding females

compared to $13,540 \pm 6,290$ females counted on satellite images, i.e. a 2.6% difference between the two approaches.

The type of substrate on which the harems are located influenced the quality of the relationship (Figures 4A, B). On beaches, the linear regression between satellite and ground counts were highly correlated ($R^2 = 0.98$, Figure 4A). On vegetated areas, in particular in the presence of vegetated mounds, the quality of the relationship decreased ($R^2 = 0.71$, Figure 4B).

3.2 Estimating total elephant seal population sizes in the Kerguelen and Crozet Archipelagos

3.2.1 Explorations and counts from satellite images

Over the 2010-2016 period, 25 VHR satellite images of the south and southwest part of the Kerguelen Islands, taken between 29 September at the earliest and 20 October at the latest, were acquired over the various sectors of the islands, where historical sealing activities had taken place (Figure 2). These images covered 218 beaches, representing a coastal line of 572 km, in other words, more than 80% of beaches favorable for elephant seal breeding colonies not yet counted. However, due to cloud cover during the elephant seal breeding season, no satellite images were available for 46 beaches (approximately 20% of the favorable beaches). A total of $21,046 \pm 2,470$ females were counted directly on the satellite images available (Table 3). When applying: i) corrections for the census date versus the maximum haul-out date; and ii) a mean annual growth rate of 1.6% over the 2010-2018 period (corresponding to the growth rate estimated from ground censuses for all areas combined), and taking account of the time elapsed (in years) between each satellite picture and 2018, we estimated a total of $27,600 \pm 5,300$ females breeding on those beaches in 2018 (Figure 5; Table 3).

In the Crozet Archipelago, four beaches were thus counted (two on each island) giving a total number of females of $1,370 \pm 160$ from rough censuses (Figure 6; Table 3). Application of the mean 5% annual growth rate from Possession Island considering the time elapsed (in years) between the date of the satellite picture and 2018 provided an estimate of $1,986 \pm 240$ breeding females.

3.2.2 Predictive models

Eight models were fitted with the different explanatory variables, but due to missing values for the distance (km) of the beach from the 500 m depth contour (Dist_Bathy_50), the first two models (mod0 and M0) could not be compared with the others using AIC. The number of breeding females on the beaches was best explained by four variables: the zone, the beaches’ surface area, and the distance to the sea (best model selected (M3); Table 2) and an interaction between the surface area and the beaches’ distance to the sea. The model also revealed high variability between the different zones amongst the selected beaches, with the uncertainty of prediction

TABLE 2 Comparison of different linear mixed-effect (MOD) and generalized additive models (M) and selection of the best predictive model of the number of breeding females on the ranges.

Models	Variables	R-sq.(adj)	DEV-Expl	AIC	loglik	I00
<u>mod-0</u>	Z+D+SP+EP+EM+DM+DB50			951.6	-466.8 (df=9)	
<u>m-0</u>		0.743	75.8%	901.1	-432.1 (df=18.4)	507.4
<u>mod-1</u>	Z+D+SP+EM+DM			969.2	-477.6 (df=7)	
<u>m-1</u>		0.747	76%	924.8	-445.9 (df=16.4)	482.3
<u>mod-2</u>	Z+D+SP+DM			971.2	-479.6 (df=6)	
<u>m-2</u>		0.747	75.8%	924.4	-446.7 (df=15.5)	481.2
<u>mod-3</u>	Z+D+SP+DM+SPxDM			967.9	-476.9 (df=7)	
<u>m-3</u>		0.752	76.4%	919.8	-443.4 (df=16.5)	475.2

Results in bold show the best model. 1) "Z" representing the 17 different geographical sectors of the Kerguelen Archipelago (see Figure 1); 2) "D" in order to make corrections according to the date of the counts of the known beaches used; 3) "SP" corresponding to the beaches' surface area in m²; 4) "EP" corresponding to the beaches' orientation (east, north, west, south); 5) "EMer" corresponding to the orientation of the open sea area at the entrance of a fjord (east, north, west, south); 6) "DM" corresponding to the distance (m) of the beach from the entrance of a fjord and 7) "DB50" corresponding to the distance (m) of the beach from the 50 m depth contour.

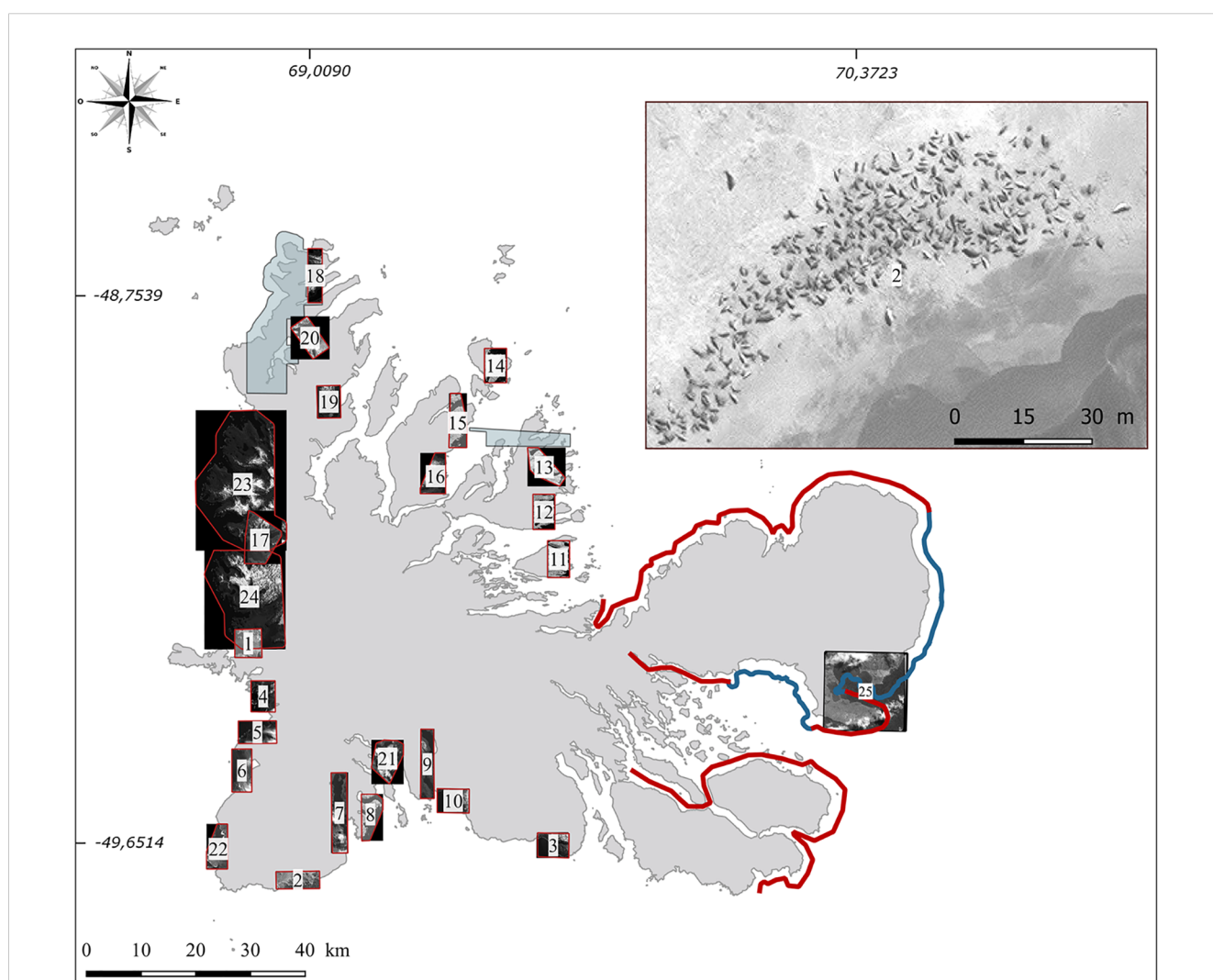


FIGURE 2 Locations of ground and satellite censuses in the Kerguelen Archipelago. Beaches annually censused are indicated with a blue line. The complementary ground census zone are indicated by a red line and encompass 37 breeding colonies. The black square corresponds to the validation satellite area. For all other areas (1 to 24), censuses were conducted on the basis of very high-resolution satellite images. The top right represents an example of a very high-resolution satellite image (0,30 m/pixel) of a beach. The blue areas represent the satellite images available in the opensource platform Google Earth during the peak presence of breeding females on land.

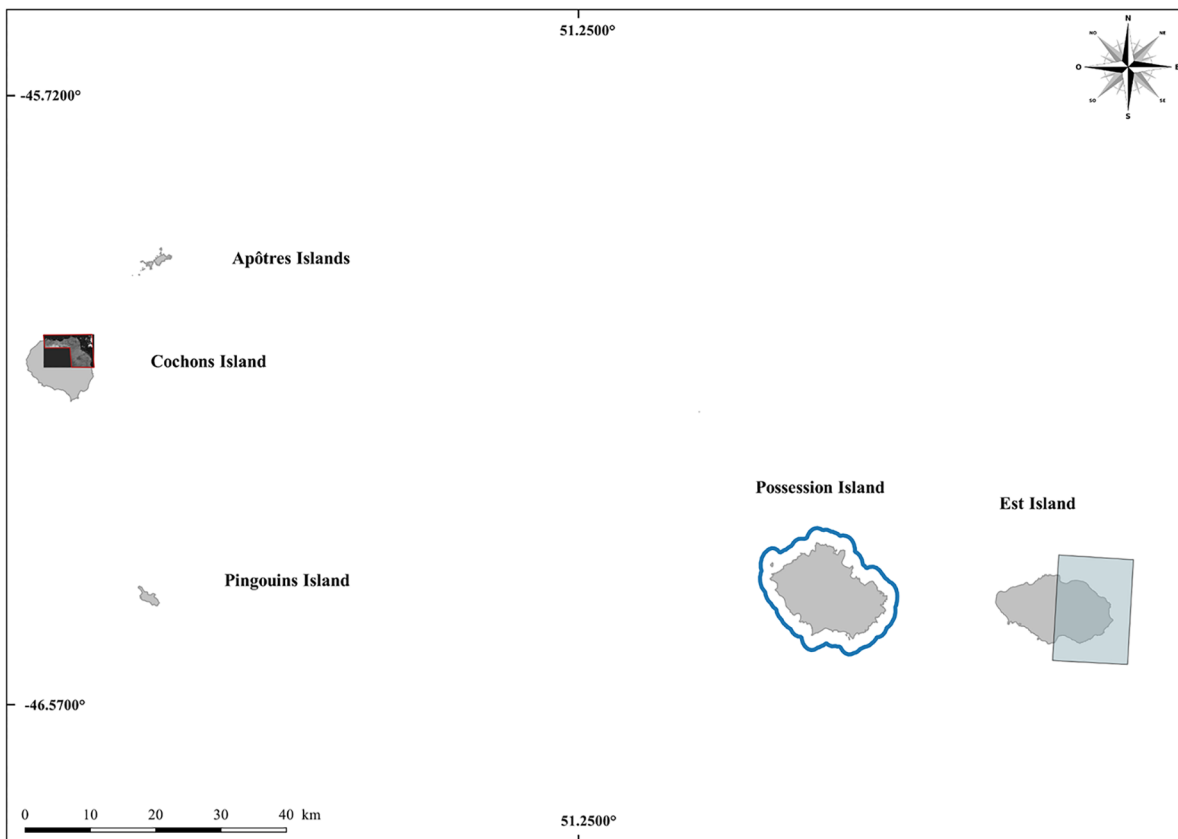


FIGURE 3
Locations of ground and satellite censuses in the Crozet Archipelago. Beaches annually censused are indicated by a blue line, and satellite images censuses for Cochons Island and Est Island are represented by red and blue polygons respectively.

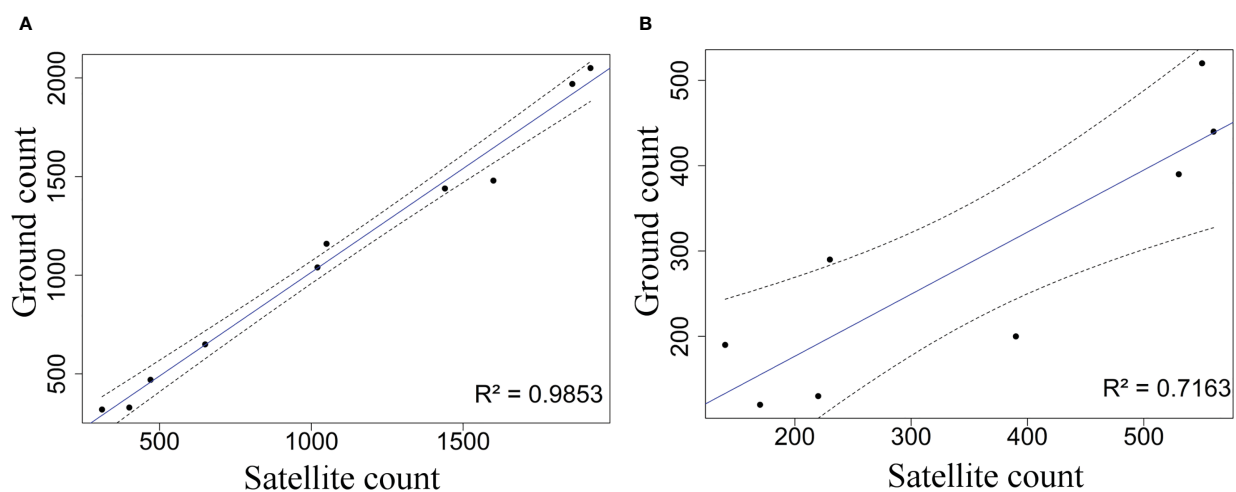


FIGURE 4
Correlation between counts performed based on very high-resolution satellite images and ground counts over the Baie Novégienne area, Kerguelen in 2015 (see Figure 1) over (A) sandy beaches or vegetated and (B) eroded areas with a presence of vegetation turradon. The black dots represent the relationship between the land-based counts and the satellite counts for each beach. The solid blue line represents the line of best fit and the dashed black lines indicate the 95% confidence limits of that line.

TABLE 3 The estimated population size (number of breeding females) of Kerguelen and Crozet Archipelagos elephant seals updated for the year 2018.

ISLAND	SECTOR (Figure 1)	METHOD	ESTIMATED NUMBER OF BREEDING FEMALES	IC	PROSPECTION %
CROZET	Possession	Ground	1 780	295	100%
	Est	Satellite	1 180	145	50%
	Cochons	Satellite	805	140	80%
	Sub-Total			3 765	580
Kerguelen	1	Ground	66 390	13 615	100%
	2	Ground	<10		100%
	3	Ground	1 325	180	100%
	4	Ground	2 510	490	100%
	5	Ground	868	150	100%
	6	Prediction	181	<i>1 007</i>	
	7	Satellite	7 025	805	90%
	8	Satellite	65	10	50%
	8	Prediction	15	<i>78</i>	
	9				
	10	Satellite	190	35	80%
	11	Satellite	3 330	645	70%
	11	Prediction	540	<i>1 869</i>	
	12				
	13	Satellite	1 660	360	60%
	13	Prediction	385	<i>1 597</i>	
14					
15	Satellite	2 310	380	90%	
15	Prediction	123	<i>498</i>		
16	Satellite	13 360	4 320	95%	
Sub-Total			100 287	20 990	
Kerguelen & CROZET	TOTAL		104 052	21 570	

The confidence intervals (IC) of predicted estimations (in italics) are not included in the total estimates because too many uncertainties surround them and this may result in an overestimation of the total number of elephant seals.

much higher for new areas than for those used by the model. The selected model estimated approximately 1,250 breeding females [6: 14,000] on the remaining 46 beaches of the Kerguelen Archipelago for which no ground or satellite image censuses are available.

3.2.3 Estimation of the total population size

When adding together ground censuses, satellite censuses and predictive model estimates, the total number of breeding females for the whole of the Kerguelen Archipelago in 2018 is about 100,300 ± 20,840 (Table 3).

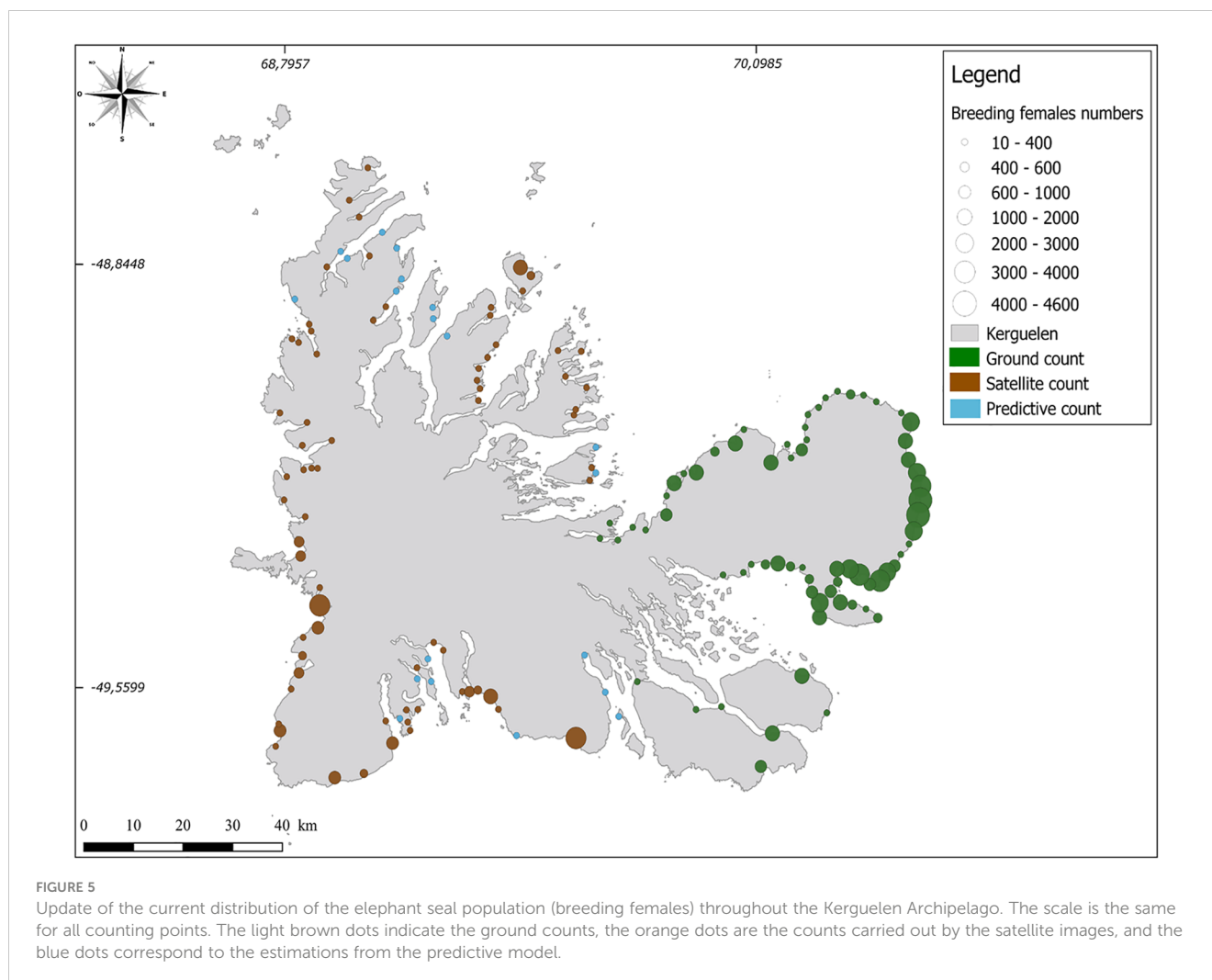
For the Crozet Archipelago in 2018, ground and satellite censuses total 3,765 ± 690 breeding females, which is likely to be an underestimation as some beaches are not yet censused (Table 3).

According to these new counts, the total southern elephant seal population sizes in 2018 for the Kerguelen and Crozet Archipelagos

respectively are estimated to be about 347,995 (s.e. = 4,950) and 13,064 (s.e. = 169) individuals.

3.3 Population trends for long-term monitoring areas

At Kerguelen, censuses conducted annually between Cap Digby and Pointe Molloy on the Courbet Peninsula (Figures 1, 2) reveal that the number of breeding females increased by about 13,000 females (Figure 7) from the minimum estimate of 37,000 breeding females in 1987 (Guinet et al., 1992) to a maximum of 50,020 ± 11,050 (95% confidence index) females in 2018. All ground counts (long-term monitoring and additional counts) led to a total estimated number of approximately 66,400 ± 14,000 breeding females in 2018 (Table 3).



Ground count areas were extended at Kerguelen Island with 37 new beaches over 400 km of coastline, located north-west and north of the Courbet Peninsula, Prince de Galles Peninsula, Ronarc'h Peninsula, and Jeanne d'Arc Peninsula, censused punctually over the 2010-2018 period for multiple years (Figure 2). For those additional beaches with multiple census years over that period, an overall growth rate of $2.7\% \cdot \text{yr}^{-1}$ was found, leading to an estimation of $16,500 \pm 4,000$ breeding females in 2018 for these 37 beaches. Meanwhile, over the 2010-2018 period, colonies located between Cap Digby and Pointe Molloy on the Courbet Peninsula (Figures 1, 2) grew at an annual growth rate of 0.9%.

At Crozet, on Possession Island, the minimum number of breeding females was observed over the 1990-1994 period with about 520 individuals coming ashore. In 2018, a total of $1,780 \pm 450$ females came to breed (Figure 8; Table 3), which represents a 5.1% annual growth rate over the 1994-2018 period.

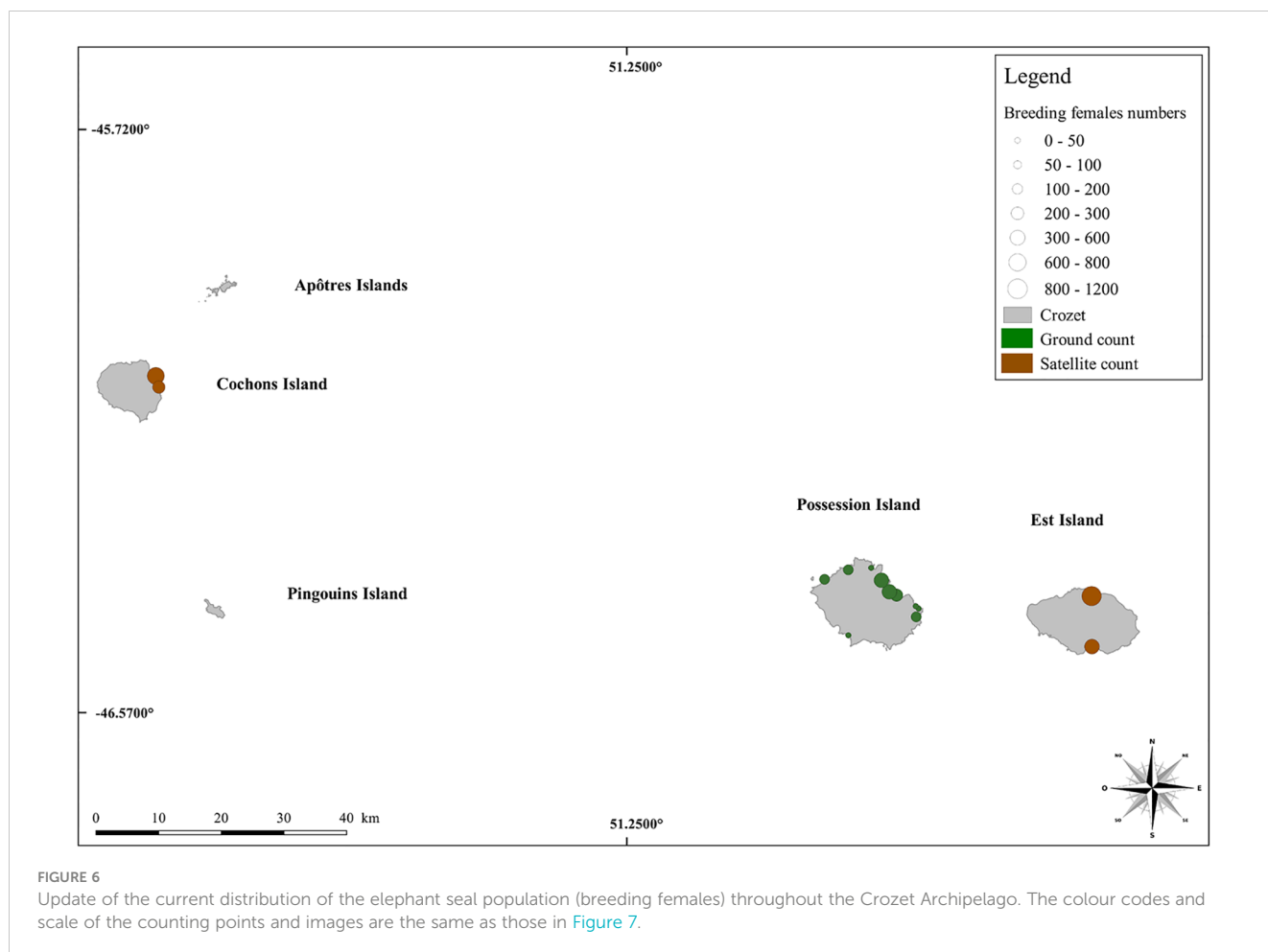
4 Discussion

Here, we sought to extend the census method from space to all areas that are inaccessible on foot for ground counts and not

previously counted on both the Kerguelen and Crozet Archipelagos. We provide the first estimates of the total breeding population of southern elephant seals at both these locations, which highlights the potential to conduct long-term population size monitoring. This study, thanks to satellite imagery, shows the importance of these two French Archipelagos at a global level for the southern elephant seal population. At both locations, the elephant seal populations have been increasing over the last two decades, particularly on the Crozet Archipelago.

4.1 Use of very high-resolution satellite images and estimate of total number of breeding elephant seal females

Satellite images have been successfully used to census wildlife (Fretwell et al., 2014; Fretwell et al., 2017; Weimerskirch et al., 2018; Cubaynes et al., 2019; Gonçalves et al., 2020; LaRue et al., 2020). Some more recent studies have also shown the ability of satellites to survey animals at more global scales (Lynch and LaRue, 2014; LaRue et al., 2021). As this field is still developing, most studies on southern elephant seal populations have been small-scale, proof-of-



concept investigations. [McMahon et al. \(2014\)](#) pioneered in showing that VHR satellite images could be used to accurately census elephant seals, indicating that good precision counts could be conducted despite the low color contrast between beaches and elephant seals. Similarly to [McMahon et al. \(2014\)](#), we found no difference in average between satellite and ground counts for the total number of seals on the beaches (but associated errors are different), demonstrating that remotely sensed images can be used reliably to census elephant seals on remote sub-Antarctic islands. However, [Dickens et al. \(2021\)](#) showed variation between ground and unmanned aerial vehicles (UAV) counts, aerial counts consistently recording higher numbers of animals, particularly on beaches with higher densities of animals, and confirms that the aerial method (satellite and UAV) provides reliable or better results for population monitoring. A recent study by [LaRue et al. \(2021\)](#) showed that Weddell seals (*Leptonychotes weddellii*) could also be accurately counted from space on a global population study area.

The present study yields similar results from ground and satellite image censuses, and allows distinguishing between females, males and pups. However, the substrate on which elephant seals were found tended to be a limiting factor in the method using panchromatic resolution, and detection appeared to be more difficult in vegetated areas, in contrast to ice, as shown in

LaRue's study in 2011, and sand in Hindell's study in 2014. Furthermore, due to the lack of successive satellite images, difference in resolution (30 vs 50cm/px) and/or consecutive ground counts for a given beach, we could not assess how the census error varied depending on the resolution of images and/or when departing from the optimal census date (i.e. 15 October).

This study joins others ([Fretwell et al., 2017](#); [LaRue et al., 2019](#)) that demonstrate the huge potential of VHR satellite images (i.e. up to 0.30 m), now readily available, to census and monitor large seal and seabird species breeding in very isolated and inaccessible sectors of the planet. Such an approach may be even more competitive and efficient than the use of new aerial images by kite aerial photography ([Delord et al., 2015](#)) or by UAVs ([Hodgson et al., 2018](#); [Fudala and Bialik, 2020](#); [Dickens et al., 2021](#); [Edney and Wood, 2021](#)), which often remain confined to restricted areas. The main constraint of satellite image censuses (particularly acute for subantarctic islands) lies in cloud cover, which limits visibility and hence prevents counts. We suggest experimenting with new accessible technologies imageries such as ICEYE satellite, based on X-band SAR sensors suitable for all-weather day and night Earth Observations with a resolution of 0.25 m. Although counts with standard resolution images (0.50 m) are relatively accurate, we recommend using the highest resolution (0.30 m) whenever

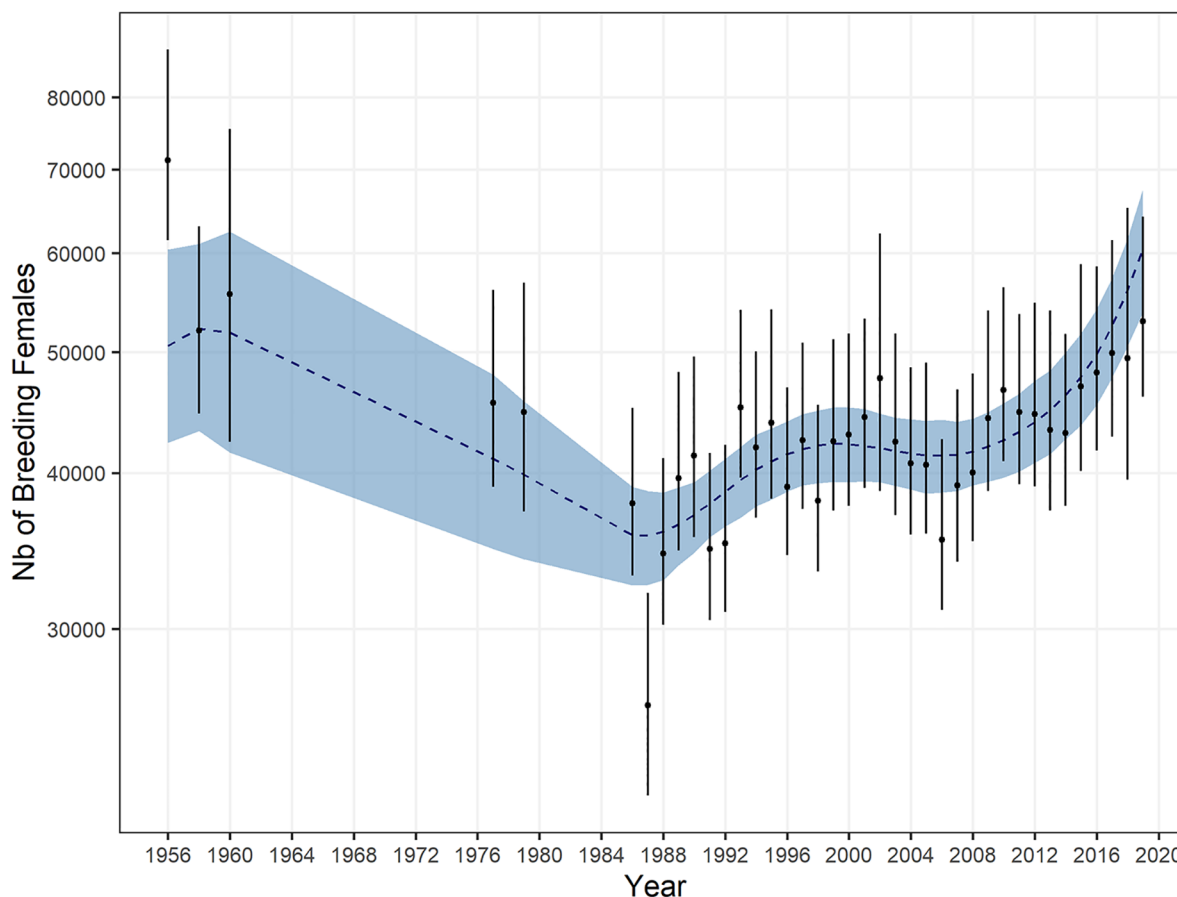


FIGURE 7

Population trend of female southern elephant seals breeding on the Courbet Peninsula, Kerguelen since the 1950s. Posterior medians of breeding female counts, corrected for census dates, along with their 95% CI, are depicted by the black dots and bars. The blue envelope and the dotted blue line represent a 95% CI and the posterior median value of the trend, respectively.

possible, as the latter makes counts much easier to perform and can limit detectability errors on vegetated areas.

4.2 Total elephant seal population size estimates for the Crozet and Kerguelen Archipelagos

By combining ground counts with censuses on satellite images, and predictions for beaches for which no data were available, this study allowed us to provide the first estimate of the total elephant seal population for the Kerguelen Archipelago.

Prior to this study, the Kerguelen Archipelago elephant seal population was considered the second largest in the world (~45,000 breeding females), after South Georgia Island (~110,000 breeding females). Our study shows that the Kerguelen stock share of the total elephant seal population has been underestimated. In fact Kerguelen hosts about 100,000 breeding females, which is more or less equivalent to the South Georgia figure (Boyd et al., 1996). Based on the updated counts from this study, the Kerguelen and South Georgia populations (i.e. totaling about 740,000 individuals) could

represent as much as 80% of the global southern elephant seal population (Hindell et al., 2016).

With a minimum estimate of about 4,000 breeding females, the Crozet Archipelago remains a relatively small population (Figure 6). Supplementary census efforts should be deployed to fill the gap on other beaches where additional seal colonies are likely to be present but where no satellite images are available to date due to cloud coverage. The use of a predictive model is however impossible on Crozet, as the beach characterization data are insufficient to be implemented.

These new total population size estimates have significant consequences for estimates of the biomass of marine organisms consumed by these predators, and their role in ecosystem models. In this way, the biomass consumed by these predators is very significantly higher than previously estimated for the area (Guinet et al., 1996), underlining the considerable ecological role that southern elephant seals may play in the marine ecosystem within the Indian sector of the Southern Ocean. The contribution of southern elephant seal predation to the ecosystem, using ecosystem models such as Ecopath (Christensen and Pauly, 1992; Whipple et al., 2000; Coll et al., 2015), will have to be revised in order to best sustainably manage the biological resources within

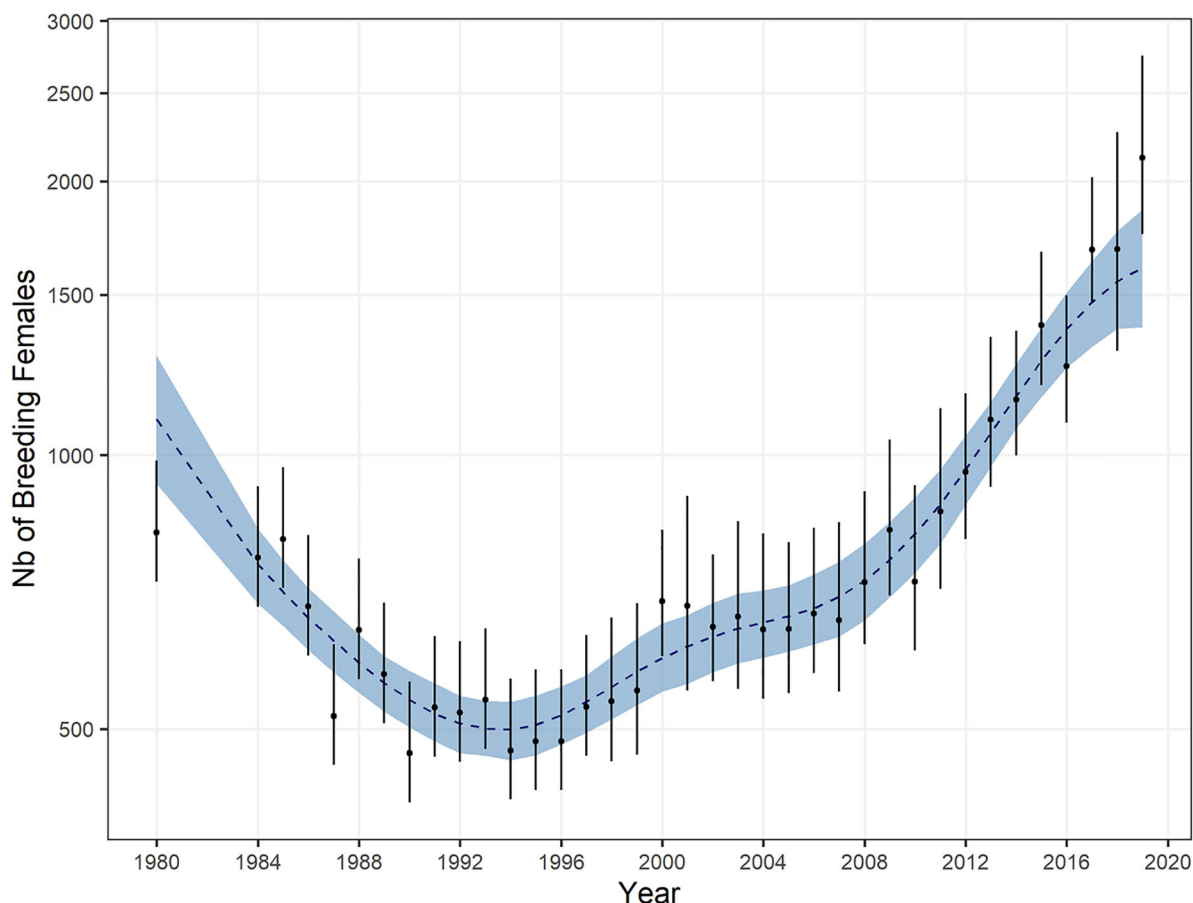


FIGURE 8

Population trend of female southern elephant seals breeding on Possession Island, Crozet since 1980. Posterior medians of breeding female count, corrected for census dates, along with their 95% CI are depicted by the black dots and bars. The blue envelope and the dotted blue line represent a 95% CI and the posterior median value of the trend, respectively.

those ecosystems as part of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) area.

4.3 Reassessment of Crozet and Kerguelen population trends over the last four decades

Another major result of this study is to highlight the changes in southern elephant seal population trends for both the Crozet and Kerguelen Archipelagos. Population trends provided by the current study complement those previously performed for the Crozet and Kerguelen Islands (Barrat and Mougouin, 1978; Pascal, 1981; Guinet et al., 1992; Guinet et al., 1999; Authier et al., 2011) but also the Marion and Heard Islands (van den Hoff et al., 2007; McMahon et al., 2009; Pistorius et al., 2011). These studies show that elephant seal foraging and breeding throughout the Indian sector of the Southern Ocean underwent a significant decline starting in the 1950s before stabilizing in the late 1980s-1990s and subsequently increasing. This common general pattern in the area's population trends suggests similar processes driving those demographic changes for at least the Marion, Crozet and Kerguelen Islands. However, large differences are

observed between the Crozet and Kerguelen populations, both in terms of the early rate of decrease and the current rate of increase. The annual rate of decrease as well as the overall decrease in percentage of the Crozet elephant seal population size were steeper in the Crozet Archipelago (i.e. ~80% of the population size was lost at Possession Island; Guinet et al., 1992; Guinet et al., 1999) compared to the Kerguelen Archipelago (i.e. 44%; Guinet et al., 1992). Population stabilized in the late 1980s on Kerguelen and about ten years later on Crozet. Since then, the Crozet population has been growing at a much faster rate ($+5.1\%.\text{yr}^{-1}$) compared to the Kerguelen one ($+1.6\%.\text{yr}^{-1}$, all ground censuses combined).

This general pattern, which is also shared by Marion Island's population (Oosthuizen, pers. comm), is most likely to be driven by a global change in productivity within the Indian sector of the Southern Ocean (McMahon et al., 2009). However, the differences in the extent of decline and growth rates between Crozet and Kerguelen suggest that local factors are also at work.

Elephant seal weaning mass, a strong predictor of juvenile survival (McMahon et al., 2000; McMahon et al., 2003), was found to be positively related to chlorophyll-*a* concentration within the main foraging region of adult female seals (Authier et al., 2012; Oosthuizen et al., 2015). This suggests that despite the

indirectness of the link between chlorophyll-*a* and elephant seal prey, phytoplankton biomass is a reasonable predictor of the foraging performances of elephant seals. Interestingly, chlorophyll-*a* concentration has been found to be increasing significantly over the whole Southern Ocean and in particular within the Indian sector (Castillo et al., 2019; Pinkerton et al., 2021), suggesting that primary production, and elephant prey availability, have been rising over the last two to three decades.

Local factors are also likely to drive the local differences in growth rates between the Crozet and Kerguelen pups. For instance, Mestre et al. (2020) showed that over the 2004–2018 period, post-molting females improved their body conditions more rapidly when foraging west of Kerguelen compared to the east, suggesting that foraging conditions varied according to longitude, and were more favorable over the Crozet and Marion sector than east of Kerguelen. Kerguelen females foraging westward overlap with the Marion Island females (Oosthuizen et al., 2015; Mestre et al., 2020), but unfortunately no tracking data are available so far for the Crozet individuals.

Currently, it is unknown if different population trends are observed within the Kerguelen Archipelago depending on the location of the breeding colonies. However, significant differences in the foraging locations of females have been found between colonies, with females breeding northwest of the Courbet Peninsula foraging, to a very large extent, west of Kerguelen, while females breeding east tend to forage mainly eastward (Mestre et al., 2020). The foraging locations of females breeding south and west of Kerguelen remain unknown. However, we can expect that at-sea distribution differences according to the location of the breeding colonies translate into local differences in population growth rate. This is suggested by the higher 2.7% annual growth rate observed for colonies located northwest of the Courbet, Ronarc'h and Jeanne d'Arc Peninsula compared to the 0.9% annual growth rate observed for colonies located east of Courbet Peninsula over the 2010–2018 period.

Changes in predation pressure, might also contribute to the differences in the rate of decrease and growth between Crozet and Kerguelen. Elephant seal population demographics could also be sensitive to killer whale predation (Reisinger et al., 2011). Killer whale (*Orcinus orca*) predation has been hypothesized to be the main factor driving the faster rate of decline of the Crozet compared to the Kerguelen population over the 1970–1980 period (Guinet et al., 1992). Killer whales preyed on as much as 20% of pups born on one beach and that figure was likely to be an underestimation (Guinet et al., 1992). However, due to the incidental mortality of Crozet killer whales interacting with illegal Patagonian toothfish (*Dissostichus eleginoides*) fisheries, the killer whale population was reduced by half from an estimated population size of 180 to 90 individuals over the 1996–2003 period (Poncelet et al., 2010; Guinet et al., 2015; Tixier et al., 2017). Therefore, the predation pressure exercised by killer whales on southern elephant seals was likely relaxed, and could have contributed to a higher population growth rate for the Crozet Archipelago colonies compared to the Kerguelen ones. It follows that the high Crozet elephant seal population growth

rate could be explained by the combination of improved foraging conditions and the easing of predation pressure exercised by the Crozet killer whale population, with a more relaxed density-dependence effect (i.e. better foraging conditions) compared to Kerguelen Island. We cannot however exclude that the emigration of seals from Kerguelen to Crozet could also contribute to this high growth rate, as elephant seal movements have been observed between Kerguelen, Crozet and Marion (Oosthuizen et al., 2011).

The growth rate exhibited by the Crozet population is among the highest observed for any southern elephant seal population in the world, with the exception of Valdés Peninsula in Patagonia (Ferrari et al., 2013). At the same time, the change in the Kerguelen elephant seal population, which does not appear to be significantly affected by killer whale predation (Guinet et al., 1999), suggests that trophic conditions are improving for elephant seals over the whole Indian sector of the Southern Ocean.

Conclusion

Our study shows the reliability of using VHR satellite images to count pinniped populations in a remote and inaccessible areas of the planet, at reasonable costs if these operations are repeated a few times every decade. Following the validation of this counting method, we found that the previous estimates of elephant seal populations breeding in the French Southern Territories were largely underestimated due to a deficit of counts in hard-to-access areas. This study confirms the major status of these populations, as they emerge as representing around 35% of the world southern elephant seal population.

In addition to conventional methods, VHR satellite images would be useful to define the locations of new breeding colonies of relatively large southern elephant seal aggregations similar to what has been done for emperor penguins (Fretwell et al., 2012). Such work is key to improving assessments of the impact of top marine predators on marine food webs and to understanding how these fauna are responding to the ongoing changes of the Southern Ocean environmental conditions (Weimerskirch et al., 2018).

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Ethics statement

Ethical review and approval was not required for the animal study because the satellite studies did not qualify for ethical review, given that the research did not involve the direct handling of animals. The project was approved by the head office of the French Southern and Antarctic Lands.

Author contributions

JL, CG and AC designed the study protocol and collected the data. JL and MA performed the analyses. JL and CG wrote the manuscript. AC, KD and HW significantly contributed to and revised the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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