Trends in sympatric otariid populations suggest resource limitations in the Peruvian Humboldt Current System

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HIGHLIGHTS

- Limitations in population growth of Peruvian sympatric otariid populations
- Sea lions are the current 'dominating' otariid species in Peru
- Decrease in juveniles contributes towards population decline
- Resource partitioning between otariids needs to be further explored in Humboldt Current System

ABSTRACT

Sympatric species evolve mechanisms to avoid competition and coexist. In the Humboldt Current System (HCS), populations of South American sea lions (SASL, *Otaria byronia*) and South American fur seals (SAFS, *Arctocephalus australis*) fluctuate mostly due to ENSO events and prey availability. We evaluate population trajectories of Peruvian sympatric otariids and discuss mechanisms for competition and/or resource limitation. For this purpose, we analyzed population trajectories of SASL and SAFS in a sympatric breeding site in Punta San Juan, Peru between 2001-2019. Wavelet analysis was used to extract trends and derivatives to estimate rates and turning points. Age-class proportions and biomass times series were constructed from weekly counts and evaluated. Both populations show a growth phase and subsequent decline. SAFS started decline ~2.25 years before and at a rate 1.5 times faster than SASL. Decrease in juvenile age-class suggests that resource limitation is the main contributing factor for current population decline.

KEYWORDS

Peru; Punta San Juan; population decline; competition; fur seal; sea lion; *Otaria byronia*; *Arctocephalus australis*

CREDIT AUTHOR STATEMENT

Cárdenas-Alayza, Susana: Conceptualization, Methodology, Analysis, Data handling, Writing –initial version, Review, Editing. **Gutiérrez, Dimitri:** Supervision, Writing – Review and Editing. **Tremblay, Yann:** Methodology, Supervision, Writing – Review and Editing.

1 INTRODUCTION

Understanding how species coexist is an important theme in ecology. Coexistence theory is a framework to understand how competitor traits can maintain species diversity and prevent competitive exclusion, even among similar species in ecologically similar habitats (Chesson and Kuang, 2008). Competition can compromise the fitness of one of the species involved, and may ultimately lead to its exclusion (Pacala and Roughgarden, 1985). Under the resource-utilization niche concept, two species cannot occupy the same ecological niche without exerting strong competition on each other (Schoener, 1974). The Lotka–Volterra competition model states that coexistence of two species is possible when the competitive effect that a species has on another species (interspecific competition) is less than the competitive effect that it has on its own species (intraspecific competition) (Chase et al., 2002; Chesson and Warner, 1981; Schoener, 1983). Furthermore, competitive interactions are known to be stronger between morphologically and phylogenetically closely related sympatric species (Di Bitetti et al., 2009; Loveridge and Macdonald, 2003; Schoener, 1983).

Otariids, composed of fur seals and sea lions, occur in sympatry in a number of upwelling regions in the world and have many similar life-history traits and foraging habits (Bailleul et al., 2005; Dellinger and Trillmich, 1999; Franco-Trecu et al., 2012; Jeglinski et al., 2013; Page et al., 2005; Villegas-Amtmann et al., 2013; Waite et al., 2012). Coexisting species are expected to develop strategies for niche differentiation when resources become scarce, to mitigate the reduction in population attributes, such as growth, survival or fecundity (Begon et al., 2006). The duration of coexistence in sympatric otariid seals is not known, and it is possible that sympatry has resulted from recent population recoveries posterior to the period of commercial sealing (Arnould and Costa, 2006). If sympatry is a result of recent events, it is possible that divergence is not yet evident or that competitive exclusion is now occurring.

In sympatric fur seals and sea lions, past research have found mixed results with regards to competition and segregation. Contrary to the situation in Peru, in many locations fur seal populations are typically larger and they appear to outcompete sea lions (Wickens and York, 1997). Researchers studying sympatric otariids have found trophic segregation, differing foraging strategies and contrasting population trends as mechanisms that explain coexistence (Franco-Trecu et al., 2014; Pablo-Rodríguez et al., 2016; Páez-Rosas et al., 2012). More recent studies demonstrate that intraspecific segregation, driven by interindividual specialization, takes place in colonial species (such as otariids) that are constrained to limited foraging ranges that overlap with conspecifics in similar niches (Jeglinski et al., 2013; Villegas-Amtmann et al., 2013; Schwarz et al., 2021).

Some authors suggest that trophic segregation between sea lions and fur seals is associated with the observed divergent trends in epipelagic and benthic foraging characteristic of each group (Arnould and Costa, 2006) and argue that body size is a central feature that characterizes foraging modes between larger sized benthic foraging sea lions and smaller epipelagic foraging fur seals. In those studies, sea lions showed greater oxygen storage capabilities; enabling them to aerobically dive longer and deeper resulting in higher metabolic and reproductive outputs (Costa et al., 1998). However, other studies have also demonstrated that sea lions of different age-classes (Jeglinski et al., 2013; Villegas-Amtmann et al., 2013) and within the same age-class (Schwarz et al., 2021) display specialized types of benthic, pelagic and nocturnal epipelagic foraging. Other studies have shown that foraging modes can vary regionally in the same species, therefore demonstrating the importance of prey availability as a driver for foraging mode (Hückstädt et al., 2016).

The Humboldt Current System (HCS) in Peru is recognized as the most productive of the Eastern Boundary Upwelling Systems in the world (Bakun and Weeks, 2008). As other upwelling ecosystems, cold nutrient rich water rises to the euphotic layer by a combination of the South east trade winds and the Coriolis force that fuel Ekman transport, giving rise to primary productivity in the upper pelagic and nearshore areas. Peru's coast is characterized by a narrow continental shelf, shallow productive upwelling waters and a relatively shallow thermocline related to an upper minimum oxygen layer at similar depths of approximately 50-80m, on average (Bertrand et al., 2010; Demarcq, 2009; Echevin et al., 2008). These features limit the potential habitat for otariid prey to be linked to the benthos. Thus, in this productive shallow environment foraging on highly patchy, but dense prey resources near the surface, may preclude the advantages of searching for more evenly distributed, but less dense, prey resources on the benthos (Arnould and Costa, 2006), which are also constrained by bottom water hypoxia.

Furthermore, HCS is characterized by recurring El Niño Southern Oscillation (ENSO) events, which can vary in intensity and duration. ENSO is known as a cycle of alternating warm El Niño and cold La Niña events and is the most prominent climate signal on Earth (McPhaden et al., 2006). When HCS is affected by an ENSO, increments of sea surface temperature and reduction of primary productivity occur in the marine environment, altering distribution of habitats and associated prey biomass. The ENSO events that occurred in 1982-83 and 1997-98, were categorized as ‘Extraordinary’ and are well documented for dramatically altering species composition and reducing marine biomass (Barber and Chavez, 1983; Tam et al., 2008). These climatic signals were strong and felt worldwide, changing the availability of prey items and causing declines in reproduction and survival of top marine predator populations around the globe (Arias-Schreiber and Rivas, 1998; Bond and Lavers, 2014; Cárdenas-Alayza, 2012; Forcada et al., 2006; Oliveira et al., 2006; Sprogis et al., 2018; Trathan et al., 2007).

In Peru two species of otariids coexist that have breeding colonies along the coast, the South American sea lion (SASL) and South American fur seal (SAFS). Analysis of population trends of coexisting species helps understand population status and response to ecosystem conditions. Otariid surveys for the coast of Peru exist from mid 1960s, providing information on the abundance of these populations, but had heterogeneous sampling effort. Since the mid 1990s, systematic annual surveys are conducted at main colonies and during each species breeding season (February/March for SASL and November/December for SAFS) by scientists from Instituto del Mar del Peru (IMARPE) to monitor their status and fluctuations (Arias-Schreiber and Rivas, 1998; Oliveira et al., 2006). Regardless, variability in Peru otariid continues to be observed (Figure 1). In the 1970s and early 1980s, historical records show a similar abundance for SASL and SAFS of ~ 20-25,000 individuals. However, in the late 1980s and 1990s SASL were more numerous than SAFS. Furthermore, a decline of 75% and 80% is documented for both SAFS and SASL, respectively due to the 1997-98 ENSO (Oliveira et al., 2006, 2012). Surveys post ENSO reflect population recoveries for both species but with a larger SASL abundance. Similar fluctuations are observed until 2014, after which, there is a decline in SAFS.

Existence of sympatric colonies of SAFS and SASL implies that some mechanism currently operates (or has in the past), to permit interspecific coexistence in the HCS ecosystem. Sympatry of SAFS and SASL occur at only a few locations along the distribution ranges of our study species in the HCS. Punta San Juan (PSJ), a peninsula on the south coast of Peru is a sympatric site and is considered a historically important breeding center for otariids in Peru. The effects of the 1997-98 ENSO also impacted this breeding site, with local reductions of ~87% in both species. In PSJ, abundance declined from 2,751 to 345 in SAFS from November 1996 to November 1999 and from 12,415 to 1,495 in February 1997 to February 1999 in SASL (Arias-Schreiber and Rivas, 1998). Since the decline, weekly counts of otariids were conducted to monitor population recovery. Although high resolution time series of marine megafauna populations are scarce; at this location, weekly counts permit to study fluctuations in abundance, which can help understand interspecific and intraspecific interactions in a common ecological context. Thus, we consider that the long time series collected at PSJ (which accounts roughly for 10-50% of the total Peruvian populations in both species in this only site) provide an adequate setting to study the coexistence of SAFS and SASL and is representative of their dynamics in Peru.

The main goal of this study is to describe population trajectories over the last 20 years, in a sympatric otariid colony in Peru and secondly, to discuss mechanisms (e.g. competition and/or resource limitation), possibly explaining these trends. In terms of the population trajectories, we expect a first phase of fast population recovery post 1997-98 ENSO, followed by a subsequent stabilization in populations' size. Given the larger body size and population size of SASL on the coast of Peru we hypothesize that the abundance and biomass of SASL dominates over SAFS, in PSJ during our study period. By using a combination of abundance time series, age-class proportions and biomass time series within and between species, we consider this is a first step towards exploring if larger body mass (SASL), a proxy for higher consumption of prey resources, can offer a greater competitive advantage in comparison to a smaller species (SAFS) to sustain population abundance in a common environmental setting.

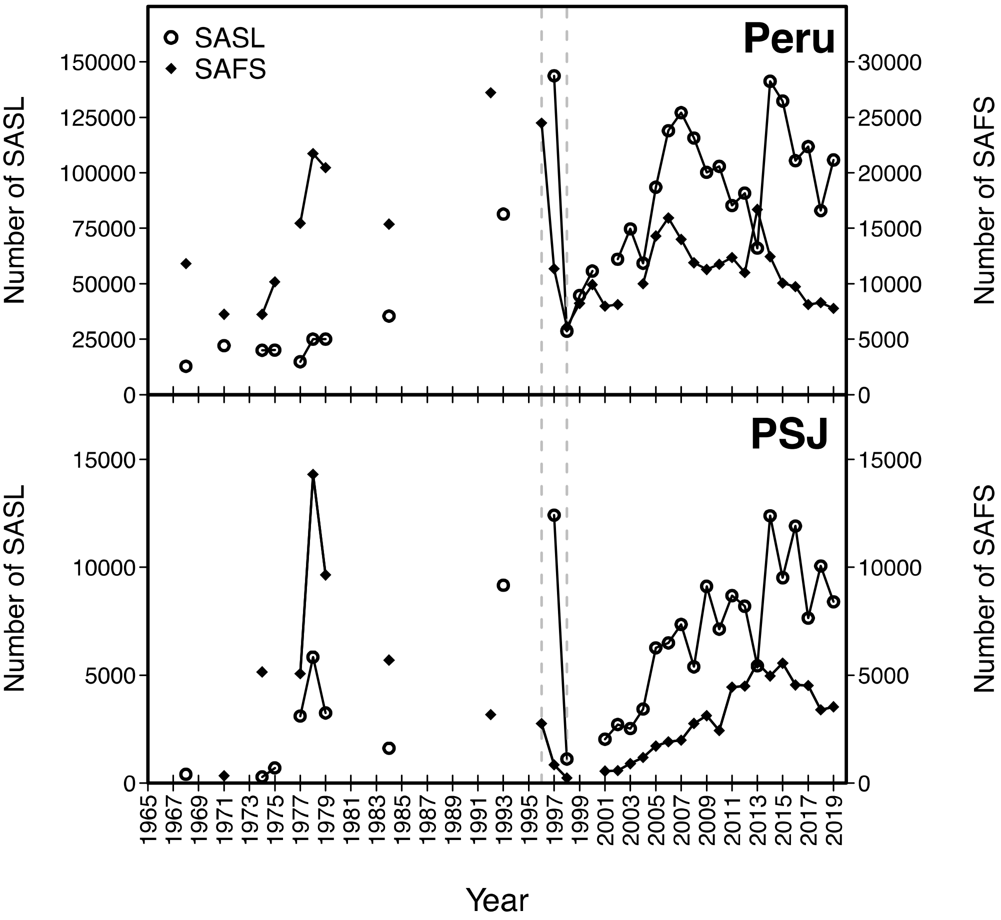

Figure 1. Time series of the total number South American sea lions (SASL, open circles) and South American fur seals (SAFS, filled diamonds) counted on the coast of Peru (top) and Punta San Juan study site (bottom) between 1965-2019. Dashed grey vertical lines delimit the population decline caused by the 1997-98 ENSO. Time series were constructed with official counts from surveys obtained from various sources (Arias-Schreiber and Rivas, 1998; IMARPE, 2018, 2017, 2016, 2015, 2014, 2013, 2012; Majluf and Trillmich, 1981; Muck and Fuentes, 1987; SERNANP, 2016; Tovar and Fuentes, 1984).

2 METHODS

2.1 Study site and data collection

Punta San Juan (15°22'S, 75°12'W) is a peninsula protected from land by a 1.2 km concrete wall that is part of a marine coastal national reserve system called 'Reserva Nacional Sistema de Islas, Islotes y Puntas Guaneras' (RNSIIPG, Spanish acronym). The PSJ coastline consists of 20 sites, which are beaches and coves all used for breeding and/or as haul-out sites by SASL and SAFS. In PSJ operates the Punta San Juan Program, a long-term research program that monitors otariid and seabird populations *in-situ*. Access to the PSJ Program database was granted for purpose of this study. At PSJ, land-based counts of accessible otariid sites are conducted at least once per week since 2001 to monitor population dynamics. For this study we accessed the count data during years 2001 to 2019, which have a minimum frequency of once per week. Counts took place between 0600-0900 hours by observers with 10x50 binoculars and tally counters on top of 8 – 30 meter cliffs overlooking otariid sites. Accessible sites are counted for total abundance and age-class categories, for each species. Gaps in count data occurred when roosting seabirds made it impossible to access the cliff-edge to view beaches and coves. More frequent counts available during the breeding seasons (January thru March for SASL and October thru December for SAFS) at selected breeding sites, were also included to enhance time series. Due to the long-term nature of this dataset (19 years), counters changed over time and beaches were counted by different observers. Standard error of the mean count between three simultaneous observers ranges between 3-4% for SAFS and 3-13% for SASL. Satellite images with 2.8m resolution (image courtesy of CNES/Airbus 31 October 2019 via Google Earth) were used to estimate the area of the main breeding sites for each species. SAFS main breeding site was estimated through *in-situ* measurements collected during low tide in 1999 when animal abundance was zero and used to validate use of satellite images. Finally, a time series of mean monthly density was estimated during the breeding season (January – March for SASL and October – December for SAFS) by dividing mean monthly number of otariids by the area of the site where animals were counted on land and reported as number of individuals per square meter (ind /m^2).

2.2 Abundance time series

In otariid breeding sites, the ratios of age-classes change throughout the year. Most evident shifts occur during the breeding season when territorial males, adult females and pups increase and subadult males and juveniles decrease. Breeding season for SAFS and SASL last for approximately 3 months (SAFS: October – December; SASL: January - March). Early in the breeding season males arrive to compete and hold territories; subsequently females arrive to give birth and there is rise in female and pup numbers. Females generally stay with the pup for 5-13 days, depending on the species. After females complete their post-partum fasting period, they will be at sea for varying periods and return to land to nurse the pup. Intra-annual dynamics in each species and age-class was examined (Appendix A). Due to the intra-annual dynamics due to breeding and non-breeding seasons as well as the long-term population fluctuations, we detrended the abundance time series with the goal to extract an annual trend of abundance for analysis and remove all the high-frequencies' signal in the data.

Total abundance for PSJ was estimated from the sum of all sites individually counted on a given date between 2001 and 2019, for each species. We verified that interannual dynamics of study sites was the same as dynamic of the sum of all sites. Because counts varied on a daily to weekly scale, these were linearly interpolated to generate a time series with an equal sampling interval of every 3 days. To detrend the abundance time series and be able to extract the values we used a wavelet trend decomposition with a "morlet" mother wavelet, since it overcomes the problems of non-stationarity in a time series by performing a local time-scale decomposition of the signal. This method gives the possibility to investigate the temporal evolution of a times series with different rhythmic components.

We identified the wavelength scale corresponding to one year using wavelet analysis in WaveletComp R package v. 1.1 to extract the trend of abundance for both species. To test the study hypothesis, the trend of abundance time series, density and ratios of abundance will be compared between both species. Increasing or decreasing phase of trends, were determined with first order derivatives. Turning points will permit to detect when the date of change in direction of a species population trajectory occurred. Difference of first order derivatives was used to understand which species was increasing over the other.

2.3 Age-class proportions

Time series for the proportion of each age-class were constructed using counts available for the main breeding sites of PSJ for SASL and SAFS, respectively. For this, we selected data sets from the main breeding sites in PSJ that are exclusive to one of the two species year-round. Age-class counts from beach site S3 were collected for SAFS between November 2003 to December 2019 (n = 977 observations). For SASL, there was a change in the beach site used to estimate age-classes in years 2012-2013 to improve the number of times the sea lion breeding site could be accessed over the year by observers. Therefore, we constructed a single time series combining counts from beach site S7.S8 for years 2003-2013 and beach N7 for years 2012-2019 (n = 666 observations), including a mean proportion between the two sites for overlapping dates. The pattern in the proportions was inspected carefully to verify that age-classes did not vary abruptly due to site change.

Age-class categories for this study includes: pups, juveniles, adult females, subadult males and territorial males. These are based on the categories used in the field at PSJ for counting animals, based on distinguishable anatomical features and behaviors (Vaz-Ferreira and Ponce de León, 1987). A 'juvenile' category was created in this study to group the 'yearling' (1 year old) and 'immature' (2-5 years old) categories used in the field. To estimate age-class proportions we only used the dates that considered all the beforementioned categories. Median proportions and interquartile range (IQR) were estimated .

Mean mass ± SD of otariids according to age classes were estimated using PSJ Program database. Mass was collected at PSJ between during otariid tagging and health assessment fieldwork that involved weighing live animals during the study period. Mass of adult age classes were collected during the breeding season while pupping was taking place. Meanwhile, pup mass was collected during pup round-ups, approximately 2 months after the peak of pupping occurs in each species (April for SASL and January for SAFS). Mass for the SAFS subadult male age-class was obtained from the PSJ Program necropsy records of individuals that stranded dead in PSJ due to interactions with longline fisheries, and is reported here. These animals were confirmed to have died from interaction with fishing gear, carcasses were in good body condition and therefore we consider their mass accurately represents their age-class. The only records of mass for dead juveniles available in PSJ were in emaciated body condition, probably due to nutritional stress, thus we do not consider they represent mass of healthy live individuals.

If values for the mean mass of an age-class were not available from PSJ, these were obtained from literature from conspecific or similar sized age-class otariids. We used reported mass of juveniles (Hückstädt et al., 2016) and territorial males (George-Nascimento et al., 1985) SASL collected in Chile. To our knowledge, no published values exist for mass of juvenile SAFS in the Pacific Ocean and in the Atlantic, studies either report captive animals or small sample sizes (<5) for an class that represents many ages and high variance. We therefore applied the reported mass of conspecific Northern fur seals (*Callorhinus ursinus*) from a study involving live captures and grouped mass of animals of ages 1-2, 2-3, 3-4 and 4-5 years old for the juvenile age class (Baker et al., 1994).

To verify our hypothesis about body size, we tested for differences between mean mass of age-classes between species. To evaluate if there is a source of competition between age-classes during breeding and non-breeding season (e.g., overlap in the proportion of territorial males and adult females in non-breeding season) we tested for independence between the weighted age-class proportions (product of proportion and mean mass for each age-class) within each species and season. This was done by applying a t-test or Mann Whitney Wilcoxon Test ($p < 0.05$) after verifying data distribution. Finally, we describe any shifts in the trends of age-class proportion time series to explain the mechanisms behind the population trajectory for each species.

2.4 Biomass times series

Biomass time series were constructed for each species in tons (t) by calculating the product of the abundance time series trend, the median age-class proportion and the mean mass per age-class. A time series for total otariid biomass was created from the sum of the SASL and SAFS biomass time series to determine the proportion of biomass that pertains to each species. To test our hypothesis, the percentages of each of the species biomass over time are used to describe interspecific competition and evaluate if SASL are dominating over SAFS. All analysis were done using R software version 3.6.2.

3 RESULTS

3.1 Abundance time series

After removing high frequency signal from count data, annual trends of abundance were extracted for each species. This revealed population trajectories in PSJ that vary between a range of 829 - 4,550 individuals for SASL (Figure 2A) and 291 – 3,443 individuals for SAFS (Figure 2B) between 2001 to 2019. During this study period mean density of individuals during breeding was 0.40 ± 0.23 ind /m^2 for SASL (January-March) and 0.12 ± 0.08 ind /m^2 for SAFS (October-December).

Throughout the abundance time series, there is always a higher abundance of SASL in comparison to SAFS, with a median ratio of 1.65 SASL : 1 SAFS. The ratio of SASL to SAFS starts at a maximum ratio of 2.84 SASL : 1 SAFS, followed by decreasing phase that hits a minimum of 1.23 SASL : 1 SAFS in October 2012. Then, a final increase phase that rises until a ratio of 2.75 SASL : 1 SAFS in December 2019.

In general, both species started with a positive increasing phase and then both declined toward a negative phase, with differing dates at each turning point. Turning points were detected as the date when a change from positive to negative phases occurred. First, SAFS changed its phase from positive to negative in November 2014. Then, 2.25 years after (in March 2017), SASL changed its phase and started to decline. Linear regressions ($p<0.05$) were adjusted to standardized data of the (negative) declining phase for each species. Slopes were significantly different from zero in both species ($R^2 = 0.99$, $p<0.05$); being slope incline of SAFS ($B_0 = -179.35 \pm SE\ 0.21$) steeper than SASL slope ($B_0 = -97.33 \pm SE\ 0.23$).

The difference between first orders derivatives describes which of the species had a higher growth rate, at a given time, in comparison to the other. We used these values to organize the time series into three different periods. Sea lions had a greater growth rate in comparison to SAFS, during the first period (January 2001 - June 2007) and in the third period (March 2012 - December 2019). SAFS had a stronger growth rate in comparison to SASL during the second period (June 2007 - March 2012).

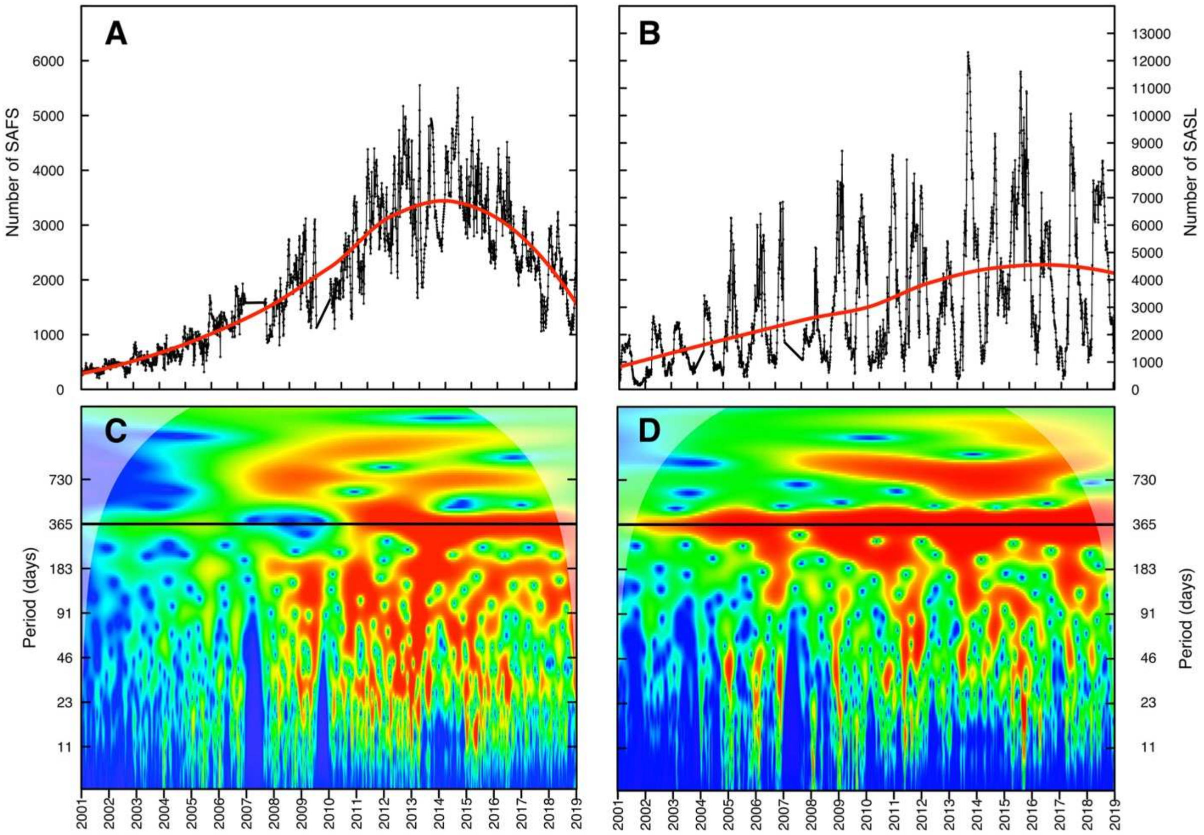

Figure 2. Top panel shows 3-day interpolated counts (black line) with trend of abundance (red line) for A) SAFS and B) SASL collected in Punta San Juan, Peru. Bottom panel shows wavelet spectrum with horizontal line indicating the annual signal at 365 days for C) SAFS and D) SASL abundance time series.

3.2 Age-class proportions

Median age-class proportions (Median, IQR) and mean mass (Mean ± SD) estimated for the entire time series are reported in Table 1. Due to the non-normal distribution of datasets, we applied the Mann Whitney Wilcoxon Test ($p<0.05$) with Bonferroni p-adjustment. Significant differences were found between mean mass of all age-class proportions within species and between species ($p<0.05$), with SASL being of a significant larger size (x1.5 larger) than SAFS (Table 1). Between the adult sexes, territorial male SAFS are 2.23 larger than adult female SAFS and territorial male SASL are 3.74 times larger than adult female SASL.

Significant differences were found between weighted age-class proportions (product of mean mass and number of individuals) of each species between breeding and non-breeding seasons (Mann Whitney Wilcoxon Test, $p<0.05$), during the final period of the study (March 2012 - December 2019) (Figure 3), suggesting low intraspecific competition between age-classes at this scale.

Time series of age-class proportions with smooth loess curve and 95% CI were compared during November 2003 – December 2019 (Figure 4). Evident shifts in proportion of age-classes include i) increase in adult females (+0.2 SASL and +0.1 SAFS) between 2016 - 2018; ii) decrease in juveniles (-0.40 SASL and -0.30 SAFS) from 2015 – 2019; iii) decrease in sub adult males (-0.10 SASL and -0.05 SAFS) between 2007 - 2015; iv) decrease in territorial males (-0.10 SASL) between 2008 - 2013. All the other ages class proportions are relatively stable. These trends suggest that the population decline in recent years in both species is associated to a decrease in the juvenile and, to a lesser extent, the sub-adult male age-classes at PSJ.

3.3 Biomass time series

Total otariid biomass time series was in the range of 83.16 – 506.72 t with a mean of 335.26 ± 139.95 t and reached its maxima in March of 2016. Throughout the time series 82.61 % ± 3.75 of total biomass is composed on average by SASL (range: 77.72 - 88.97 %), and 17.39 % ± 3.75 by SAFS (range: 11.03 – 22.28 %). This trend continues until the end of the study period, with 88.63 % of otariid biomass comprised by SASL and 11.36% by SAFS in the end of 2019. SASL occupy a biomass in the range of 73.99 – 406.25 t with a mean 272.97 ± 108.61 t, reaching its maxima in March 2017. Whereas SAFS occupy a biomass of 9.17 – 108.41 t with a mean of 62.30 ± 33.21 t, reaching its maxima in November 2014 (Figure 5).

Table 1. Median proportion of age-class per species with inter-quartile range (IQR). Mean mass and standard deviation (± SD) in kilograms. Sample size and source used for each age-class.

Species	**Age-class**	**Proportion of age-class**		**Mass of age-class (kg)**		
		Median	*IQR*	*Mean ± SD*	*n*	*Source*
SASL	Pups	0.16	0.18	13.98 ± 0.62	77	This study
	Juveniles	0.23	0.17	78.88 ± 17.68	9	Hückstädt et al 2016
	Adult females	0.38	0.19	82.74 ± 11.31	23	This study
	Subadult males	0.12	0.16	173.78 ± 40.96	44	This study
	Territorial males	0.05	0.08	310	-	George-Nascimento et al 1985
SAFS	Pups	0.36	0.13	8.75 ± 0.65	171	This study
	Juveniles	0.26	0.10	24.88 ± 14.4	5606	Baker et al 1994
	Adult females	0.33	0.09	48.56 ± 8.08	91	This study
	Subadult males	0.03	0.02	66.53 ± 8.56	6	This study
	Territorial males	0.04	0.03	108.64 ± 14.20	26	This study

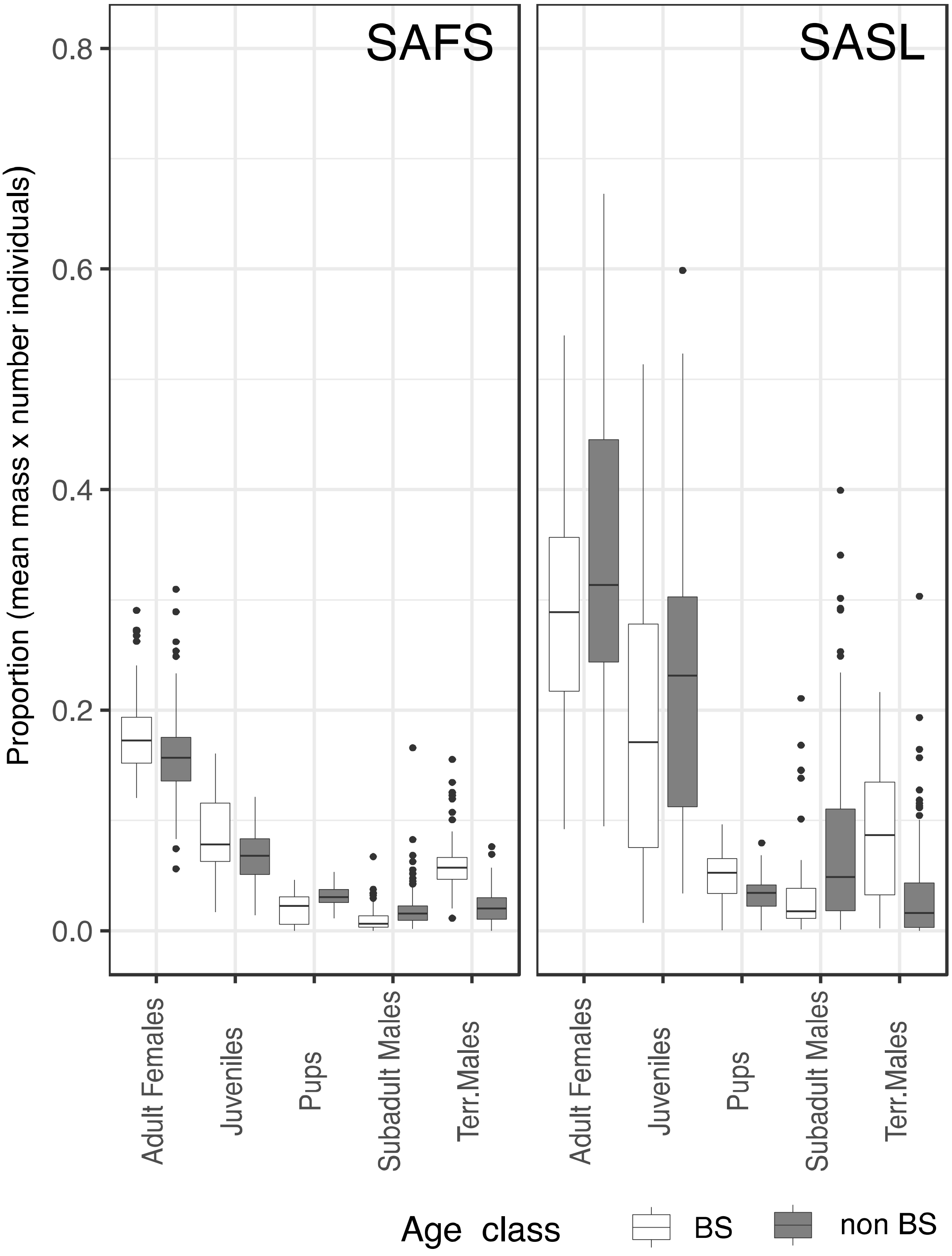

Figure 3. Boxplots of the weighted proportion (product of mean mass and number of individuals) of each age-class for SAFS and SASL during breeding season (BS, white) and non-breeding season (non BS, grey) during March 2012 - December 2019.

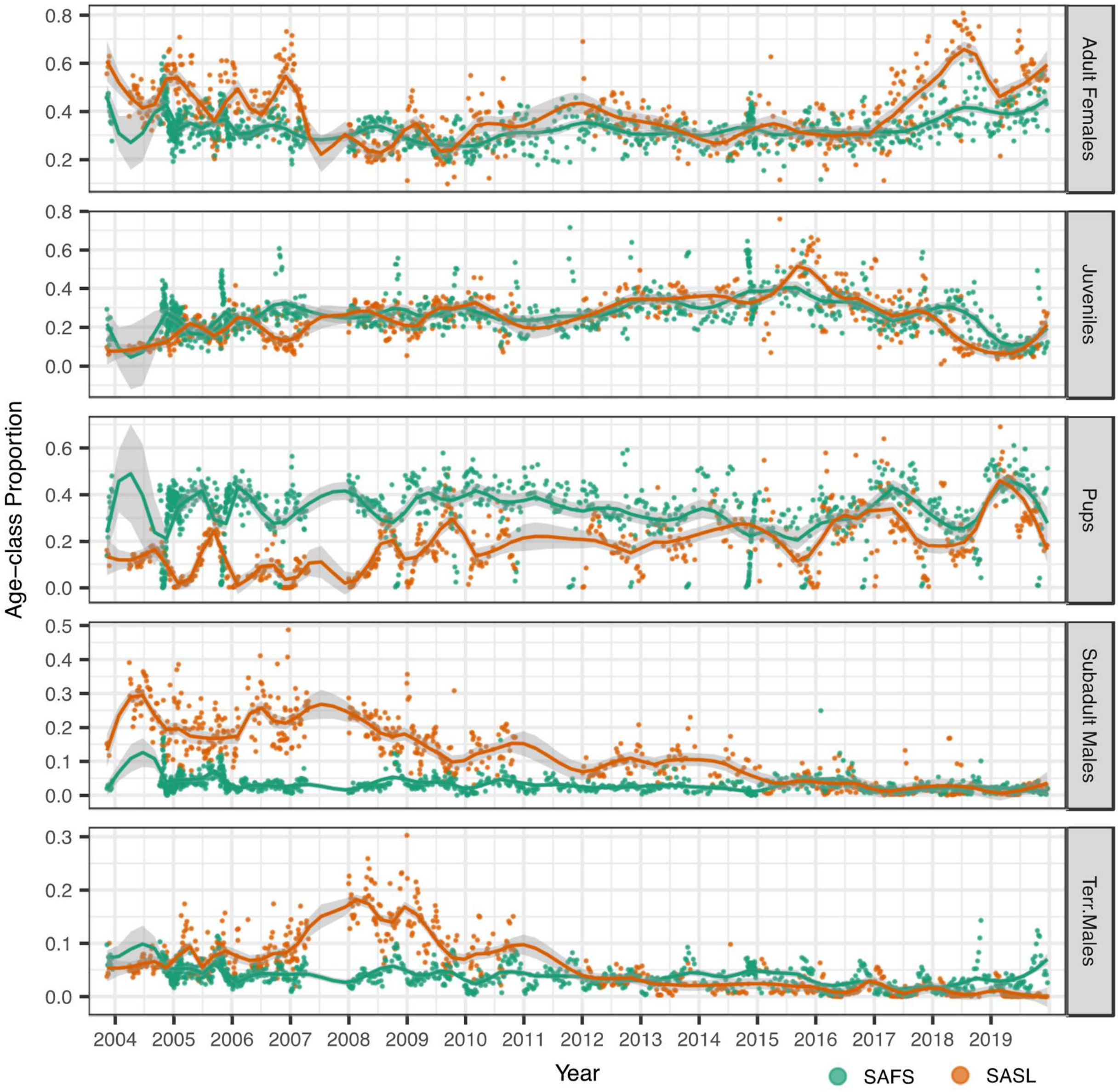

Figure 4. Time series of the proportion of age-classes for SAFS (green) and SASL (orange) constructed from weekly counts (circles) with smooth curve (line) with 95% CI (grey area). Age-class counts collected at Punta San Juan otariid breeding sites between November 2003 - December 2019.

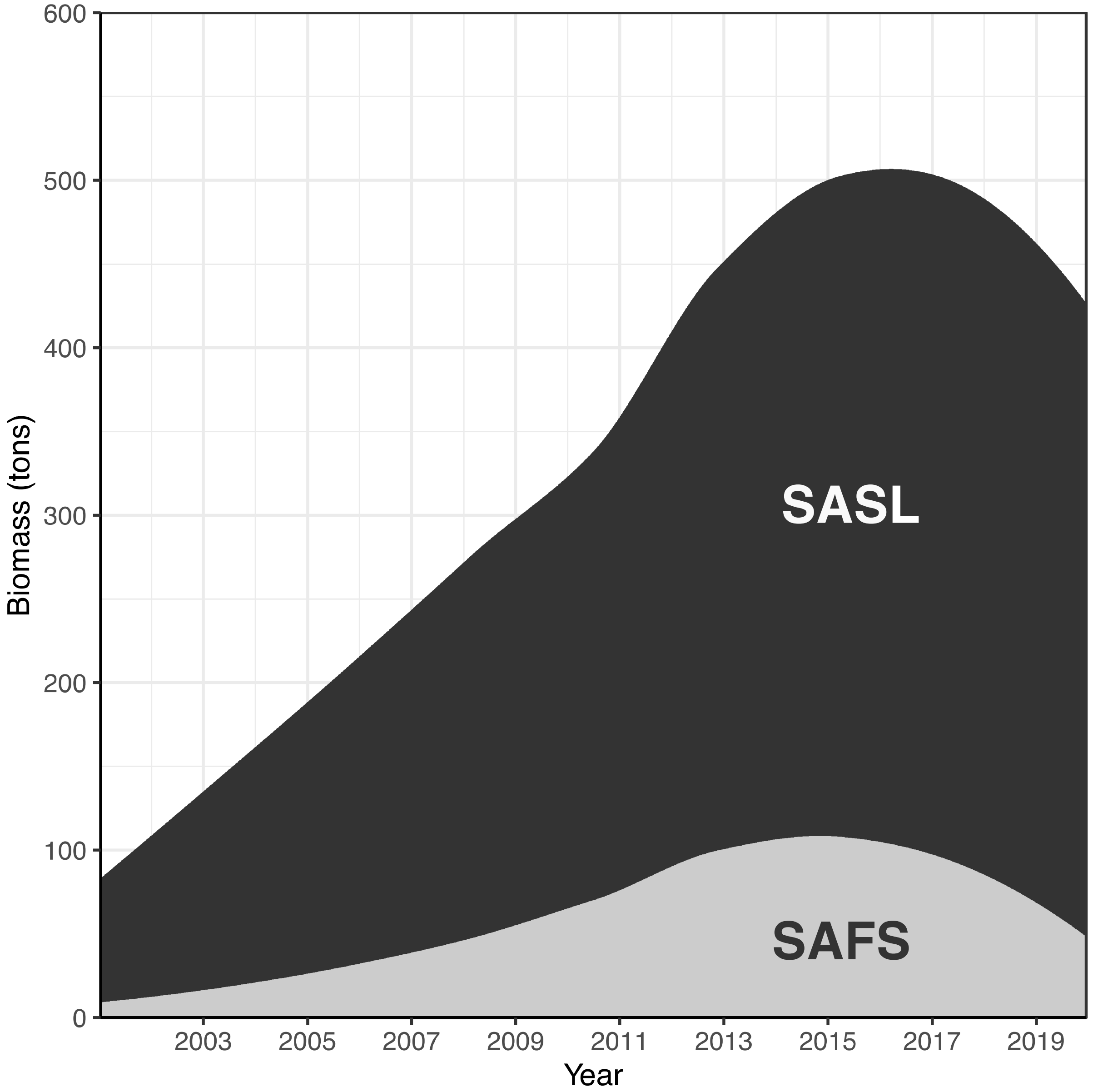

Figure 5. Stacked area chart of constructed biomass time series in tons (t) estimated from otariid abundance in Punta San Juan for SAFS (light gray) and SASL (dark grey) during years 2001-2019.

4 DISCUSSION

4.1 Changes in abundance, density and population trajectories

Since the effects of the Extraordinary ENSO in 1997-98 that caused otariid mortality and dispersal, it took SAFS 13 years and SASL 15 years to reach peak abundances similar to levels in 1980s and 1990s. Decomposition of time series of counts and biomass during years 2001-2019 shows that both species had a growth phase, a turning point and are currently in a declining phase. Our analyses reveal that SAFS abundance began to decline ~2.25 years before SASL and at a rate 1.5 times faster than SASL. The current phase of decline in SASL was unexpected and was only detectable with an in-depth analysis of the population trajectories and associated variables. In this study we also found a decrease in the juvenile and (to a lesser extent) in subadult male age-class proportions in both SASL and SAFS that is contributing to the recent decline detected in both species (Figure 4). Decrease in juveniles and subadult males can be attributed to an increase in mortality or dispersal of these age-classes, exacerbating failure of recruitment in PSJ. Unfortunately, we do not have information to adequately address mortality or dispersal. Furthermore, in our study we did not find any evidence for intraspecific competition at population level (Table 1, Figure 3). However it is possible that intraspecific competition can be operating at another scale, such as in the overlap of resource utilization or in use of foraging grounds, that should be further explored.

The trend in biomass in this study between species shows that, on average, 83% of all otariid biomass is composed by SASL and 17% by SAFS, making SASL the current ‘dominating’ species, as hypothesized. In the final phase of the time series 89% of total otariid biomass belongs to SASL, marking a large difference in the current composition between the two sympatric otariid species that inhabit the PSJ study site. Total SASL abundance is 1.23 - 2.84 times larger in comparison to SAFS, with an median ratio of 1.65 throughout the entire time series. We think this can be related to the different mechanisms of congregation employed by each species, evidenced at PSJ. The aggregation of individuals on land is different when we examine raw counts of otariids at PSJ over time (Figure 2A-B). Following recolonization, raw counts show that SAFS increments with what appears to be an exponential rate at PSJ (Cárdenas-

Alayza, 2012) that grows accumulating individuals at PSJ. Meanwhile, SASL shows pulse-like increments with seasonal peaks of abundance that can vary widely between years. However, as SAFS abundance increments plateau and then decrease, populations pulses of SASL have been up to four times the abundance of SAFS (Figure 2A-B). This variability in the recruitment of individuals in a given breeding season has played an important role in the population growth of SASL at PSJ.

A model for male dispersal proposed by Giardino et al. (2016) developed in the Atlantic population of SASL shows that male sea lions disperse between winter haulouts and breeding sites. Haulouts can be spatially segregated from central breeding areas during the non-breeding season, and are followed by male dispersal towards breeding sites in consecutive years. Males tend to have strong site fidelity to both breeding and haul-out sites maintaining functional connectivity and gene flow throughout their range (Giardino et al., 2016). This same phenomenon contributes towards the recruitment of new individuals at breeding sites and can also be occurring in Peru, with PSJ being a reproductive site where individuals that haul-out at different sites congregate to breed. Furthermore, as evidenced from the raw counts and intra-annual dynamics (Appendix A), SASLs leave the PSJ breeding rookery decreasing their abundance during non-breeding months. In contrast, SAFS female, juveniles and pups are found year-round at PSJ to complete extended lactation periods (up to 36 months), during which females, juveniles and pups show site fidelity towards lactation sites (Majluf, 1989). Thus, high dispersal rates in SASL seem to be key for augmenting population growth in a given breeding season permitting the recruitment of more individuals for breeding. However, the decline in juvenile and subadult age-classes suggests that PSJ is not a successful site for the recruitment of these age-class in both otariid species in recent years.

Otariid breeding sites tend to show seasonal age-class proportions that reflect the roles of age-classes and sexual segregation in their polygynous mating system (Bartholomew 1970). In this study we found that PSJ breeding sites are occupied by different proportions of age-classes during breeding and non-breeding season in both species, with females, pups and juveniles being the most important age-classes throughout the year. Intra-annual dynamics show that from July until December, the abundance of all SASL age-classes decrease to very low and can reach zero abundance in PSJ. In contrast to SAFS, which is present year round, and has a slight decrease in July-August (Appendix A). The wide variability in SASL in comparison to SAFS over the study period is promoted by the arrival of larger number of animals in a given season and the higher density at the breeding sites. Interestingly SAFS show a higher proportion of pups : female ratio than SASL (Figure 4), which suggests that female condition may be better in SAFS. However, this can be explained by the high site fidelity of breeding female SAFS at this site, where experienced breeders return to pup (Majluf, 1989). Whereas in SASL, it is possible that a bulk of the SASL females are young females.

In this study we found that SASL density (0.40 ± 0.23 ind / m^2) at PSJ during breeding was 3-4 times SAFS density (0.12 ± 0.08 ind / m^2). This can be explained by the difference in the social tactics intrinsic to each species. Soto and Trites (2011) reported a lek-like mating system in SASL with the highest female : male ratio recorded for this species in Ballestas Islands in Peru, about 250km from our study site. Large abundances of females congregate to breed at what some authors identify as population “hotspots”. These high density aggregations have been explained as a means to enhance mate selection (Soto and Trites, 2011). Territorial males line up at the tide line to display themselves to reproductive females. Females benefit from male competition and avoid subadult male harassment while remaining in close proximity to foraging sites (Bradbury and Gibson, 1983, Soto and Trites, 2011). Although there are no studies on the SASL mating system at PSJ, we suppose that the social tactics described above also occurs and PSJ is an important site for SASL breeding (S. Cárdenas-Alayza, personal observation).

We know from historical records that the SAFS population ranged between 9,644 - 14,303 and SASL between 3,249 – 5,836 at the PSJ study site in 1978-79 (Figure 1). This shows that PSJ is able to support larger abundances of these species on land and in the surrounding marine environment. Interestingly, during the post 1997-98 ENSO recolonization process, SAFS gathered in lower densities than SASL. Pre ENSO density of SAFS at PSJ was reported between 0.5 - 1 ind /m^2 (Majluf, 1989), considerably higher than average current density of 0.12 ± 0.08 ind / m^2 found in this study. In the 1980s and 1990s, 48% pup mortality was recorded in SAFS in

PSJ. This was caused by maladaptive aggression of females towards pups, attributed to the high density aggregations (Harcourt, 1992a, 1992b; Majluf, 1992). Furthermore, SAFS currently occupies many more beaches for breeding in PSJ in lower density, in comparison to the pre 1997-98 ENSO era (Cárdenas-Alayza, 2007). Other studies have demonstrated that habitat selection for breeding sites by SAFS and SASL varies in Peru, and is driven by access to water or shade for thermoregulation (Stevens and Boness, 2003). Therefore, availability of suitable habitat features will also play a role in the occupation of breeding sites in a given area so that each species can efficiently operate mating tactics characteristic of species social system.

4.2 Contributing factors of population fluctuations in Peruvian otariids

All species of otariid seals throughout the world were once subject to extensive and, in most cases, excessive hunting pressure during the eighteenth, nineteenth and twentieth centuries. By the late 1800s, however, most species had acquired total legislative protection or were subject to only regulated managed harvests (Wickens and York, 1997). Despite this protection, populations of various sea lion species have experienced very little recovery, and in some cases, are declining, and fur seal species have generally experienced rapid population recovery rates (Costa et al., 2007; Wickens and York, 1997). In Peru, we have the opposite case, a smaller fur seal population and a more abundant sea lion population. The current lack of recovery of SAFS in Peru may be explained in part by little time for SAFS population to recover from historical commercial exploitation, in synergy with recurring ENSO events and competition with fisheries and other predators (Majluf, 1991; Oliveira, 2011).

In Peru, SAFS were under more exploitation pressure due to the interest driven by the higher value of their pelts in the international fur trade market. By early 1900s, fur seal colonies in Peru were reported as small and isolated, describing this species as “close to the brink of extinction” (Murphy, 1925). The first commercial ban for otariids was legislated in Peru in 1946, prohibiting culling of adult female and pup SAFS (Majluf and Reyes, 1989). In 1950s fur seal abundance continued to be low which resulted in an extension of this ban to include all SAFS age-classes and also female SASL. Exploitation of otariids was reactivated in 1967 until early 1970s.

Finally, in 1976 commercial exploitation of both species was banned in Peru (Tovar and Fuentes, 1984).

In mid 1950s began the development of the industrial fishery for Peruvian anchovy (*Engraulis ringens*) in Peru, and has turned into the largest monospecific fishery in the world capturing between 4-12 million tons of fish annually (Chavez et al., 2008). Direct links have been found between anchoveta biomass and population abundance of other top marine predators in HCS, such as seabirds, that rely almost exclusively on this marine resource for growth, reproduction and survival (Barbraud et al., 2018; Bertrand et al., 2012; Passuni et al., 2016). In synergy with ENSO conditions, overfishing can have acute effects on the survival of predator populations in HCS (Oliveira, 2011). After the effects of the 1997-98 ENSO, a mere abundance of 6,257 SAFS was recorded on the coast of Peru from a previous count of 24,481 in 1996 (Arias-Schreiber and Rivas, 1998). After some time, nationwide 2006 survey showed that the population had recovered to an abundance of 15,137 SAFS (IMARPE, 2006). However, the SAFS population recovery was also limited geographically. Of the entire current abundance, 80% resides at five sites on the entire coast of Peru (IMARPE, 2013). In comparison, 44,725 SASL were counted in Peru in 1999 after the 1997-98 ENSO, from a previous abundance of 143,713 in early 1997 (Arias-Schreiber and Rivas, 1998; Oliveira, 2011). In 2006, recovery of SASL was documented with a count of 118,220 (IMARPE, 2006). In these years, SASL, breeding colonies and haulouts were already widespread along the coast compared to SAFS. For both species, authors suggest that recovery is due to the re-establishment of prey populations, the lack of strong ENSO events and migration from individuals in the colonies in northern Chile (Cárdenas-Alayza, 2012; Oliveira et al., 2012), but the fact that SASL was not reduced to such a small abundance seems fundamental to their recovery potential.

Our results show that SAFS recently declined at a rate 1.5 faster than SASL. The steeper decline in SAFS, is possibly linked to reduced recruitment in breeding adults at PSJ in recent years in combination with juvenile dispersal and mortality from this site. In our study, the sympatric otariids are exposed to the same environmental conditions, reason why the difference in this response can also be linked to intrinsic species traits that respond differently to the changes in the environment. A populations risk of extinction will depend both on the deterministic (harvest, commercial exploitation, natural selection, etc.) and stochastic (environmental, genetic, etc.) processes. The latter are more pronounced at small population sizes and can accelerate extinction process started by deterministic factors (Palstra and Ruzzante, 2008). Previous studies have shown that the effective population (Ne) is used as a tool to evaluate viable populations. High Ne values retain high levels of genetic diversity and reduce probability of effects from inbreeding depression (Oliveira et al., 2006, 2012; Wright, 1990). Whereas a population with a low Ne, is susceptible to genetic drift and less apt to respond to selection (Oliveira, 2011).

After the 1997-98 ENSO, SAFS have a critical Ne value of 2,153 (Oliveira et al., 2006) while SASL Ne is 7,715 (Oliveira et al., 2012). According to Oliveira et al (2009) population reductions after the 1997-98 ENSO, may have caused a significant genetic bottleneck in the Pacific population of SAFS and SASL, with loss of genetic diversity and presumably some loss of evolutionary potential for the species (Oliveira et al., 2009; 2012). Furthermore, the rate of loss of genetic diversity via genetic drift is greater in populations where Ne is small and migration is limited, as is the case for SAFS. This can be evidenced in the information gathered through Peru´s nationwide surveys, where >90% of SAFS breeding population is mostly restricted to latitude 15 -17° South, with PSJ supporting at least 40% of entire Peru SAFS population. Meanwhile, SASL population is distributed continuously along the coast, with important breeding sites in several latitudes (6, 13-14, 15 and 17° South) (IMARPE, 2018, 2017, 2016). Wider distribution of breeding sites with high density aggregations of SASL, suggest that migration and dispersal rates in SASL are higher than SAFS, resulting in higher connectivity. Therefore, even if there was genetic loss due to a bottleneck from a strong ENSO event, SASL has mechanisms to counterbalance loss of genetic diversity with temporal gene flow through migration. The difference in gene flow between these two species in HCS can be a key factor explaining the limited response to achieve population growth under scenarios of environmental change in SAFS in comparison to SASL suggested in this study, and should be further studied.

4.3 Natural history traits that influence interspecific competition in otariids

Body size of SASL is overall 1.5 larger in all age-classes compared to SAFS. In this study, although we hypothesize that a larger body size (SASL) could serve as advantageous to consume larger/ more prey, the decline in population abundance of both SAFS and SASL suggests that a resource limitation is affecting trajectories of both species. Between the sexes, territorial male SAFS are 2.23 larger than adult females and SASL males are 3.74 times larger than adult SASL females. Although at population level we did not find evidence for segregation between age-classes and sex, mechanism to avoid competition may be operating at a different scale. To elucidate differences and how these species are exploiting the environment, further studies need to be conducted to test intra and interspecific trophic niche segregation to understand how these sympatric otariid species exploit the HCS.

In our study we compared otariid biomass as a possible outcome of interspecific competition in PSJ and found that 83 % of total average biomass is composed by SASL throughout our time series. This can be explained by a the difference of 1.6 - 3.3 in mass between SASL and SAFS; in combination with a high density mating system in SASL versus lower density aggregations in SAFS. Researchers have examined potential competition between sympatric fur seal and sea lions at other locations and have found in some cases that trophic segregation is a mechanism to explain differing foraging strategies and contrasting population trends (Franco-Trecu et al., 2014; Pablo-Rodríguez et al., 2016; Páez-Rosas et al., 2012). Some authors suggest that difference in divergent trends is explained thru epipelagic and benthic foraging, being the latter characteristic of sea lions that have larger body size and diving capacity (Arnould and Costa, 2006). Other studies have also demonstrated that different age-classes within the same sea lion population have specialized benthic and epipelagic foraging modes (Jeglinski et al., 2013; Villegas-Amtmann et al., 2013). Therefore, otariid foraging ecology in PSJ needs to be evaluated at interspecific and intraspecific level to understand how the different groups are exploiting the local environment.

In the coast off PSJ, the continental shelf is extremely narrow limiting the access to benthic habitat. Furthermore, previous studies in Chile have demonstrated that SASL are epipelagic foragers with mean dives of 29.0 ± 34.8m, when they are in an upwelling environment

(Hückstädt et al., 2014, 2016). Therefore, we expect that competition for similar prey items may be taking place within the upper limit of the oxygen minimum zone off the Peru coast, which is usually located ~50 m in depth (Bertrand et al., 2010) making the foraging habitat of pelagic prey readily available for both otariid species diving capacity, independent of differences in body size.

It is well documented that the HCS in Peru holds a world-leading monospecific forage fishery in terms of landings of Peruvian anchovy, sustaining >5 million tons per year on average since 1960s (Bakun and Weeks, 2008; Chavez et al., 2008). In Peruvian otariids, the number of pups born, mean birth dates and anchovy biomass were found to have direct relationships in SASL and SAFS reproductive success, demonstrating that anchovy is a key resource in fulfilling the energetic demands of both species (Cárdenas-Alayza, 2012; Soto et al., 2004). Other studies have evaluated diet composition between these sympatric otariids in the decades of 1980s and late 1990s in south Peru, but conclusions for resource partitioning are not clear. Vásquez (1995) reported that otariid diets were both based on fish and cephalopods; with Peruvian anchovy (*Engraulis ringens*) and Jack Mackerel (*Trachurus murphyi*) as the main consumed species. Afterwards, Arias-Schreiber (2000) found that Peruvian anchovy, squids and a crustacean, the Red squat lobster (*Pleuroncodes monodon*), were ranked as important prey items shared by the sympatric species. Based on this, we understand that anchovy is an important prey shared by both otariids during these study periods, but mechanisms for trophic segregation are not clearly explained. Furthermore, prey availability may have changed in the last 20 years. Therefore, resource partitioning research needs to be updated and further explored in these sympatric species to disentangle current resource utilization in relation to population trajectories.

4.4 Current and future trends

In the final 5 years of our time series, both sympatric otariid populations were found to be in a state of decline. SAFS were the first to decline in 2014, which coincides with a decrease in the anchovy biomass estimated for the coast of Peru during this period. Anchovy biomass dropped from 11,201 tons in 2013 to 3,799 tons in 2014 (Zavala et al., 2019). In 2014 anchovy landings summed 1,302 tons, leaving an available biomass of 2,497 tons for all predators and other fisheries to consume, which may have posed limitations for growth and maintenance of predator populations. Warmer oceanographic conditions in HCS persisted and coincided with a reduced anchovy biomass from 2014 to 2017 (Zavala et al., 2019). Changes in oceanographic conditions can shrink and expand available habitat for prey items forcing new competition scenarios between coexisting species. Thus, under a scenario of reduced anchovy biomass we consider it is possible that prey availability is limiting population sizes at PSJ and can be responsible for the declines observed in the juvenile and subadult age-class for both SAFS and SASL; as younger individuals do not possess full diving capabilities.

Predictions for the future of HCS include scenarios with shoaling of the oxycline (Brochier et al., 2013), compressing the pelagic habitat that sustains the abundant biomass of small pelagic fish currently in the system (Bertrand et al., 2011). If this occurs, it will increase competition between all the predators that depend on pelagic resources, unless they adapt foraging strategies under new conditions. Under this hypothetical predicted scenario and our findings, we suspect SASL will be the more resilient of the two sympatric otariid species that will thrive in HCS, given its population recovery in the past 20 years. Therefore, to propose adequate management for the future of these species, it is important to better understand current underlying foraging strategies used by otariids of HCS and determine if trophic competition rules over space and time between species. These studies are key to tease apart the underlying mechanisms behind the current population trajectories revealed by the present study.

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Appendix A. Supplementary data.

Intra-annual dynamics of South American fur seals and South American sea lions by age-class.

Multimedia Component 1.

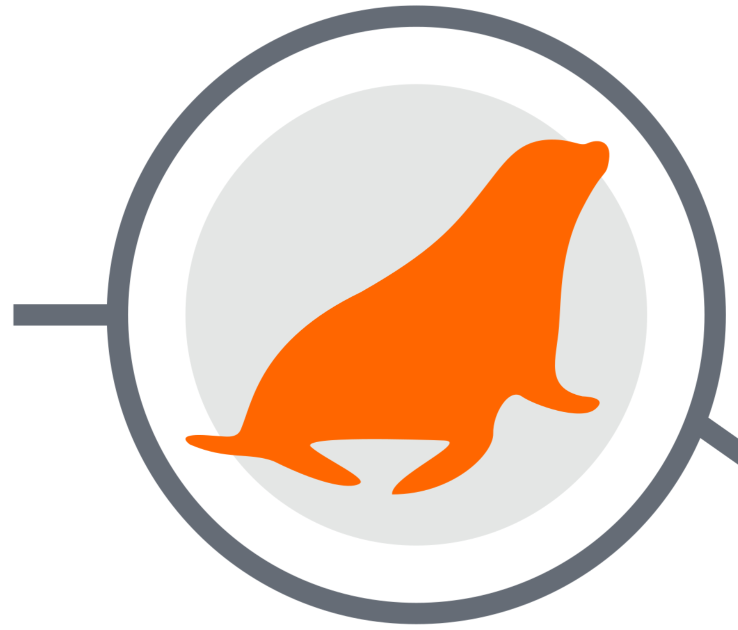
Multi-panel plot of South American fur seals counts by age-class according to day of year collected at the main breeding site S3 in Punta San Juan, Peru. Classes include: Adult Females, Juveniles, Pups, Subadult Males and Territorial Males. Total is the sum of all the age-classes. Blue line is a fitted loess model to depict the trend in abundance throughout the year. Data points include all study years available for site.

Multimedia Component 2.

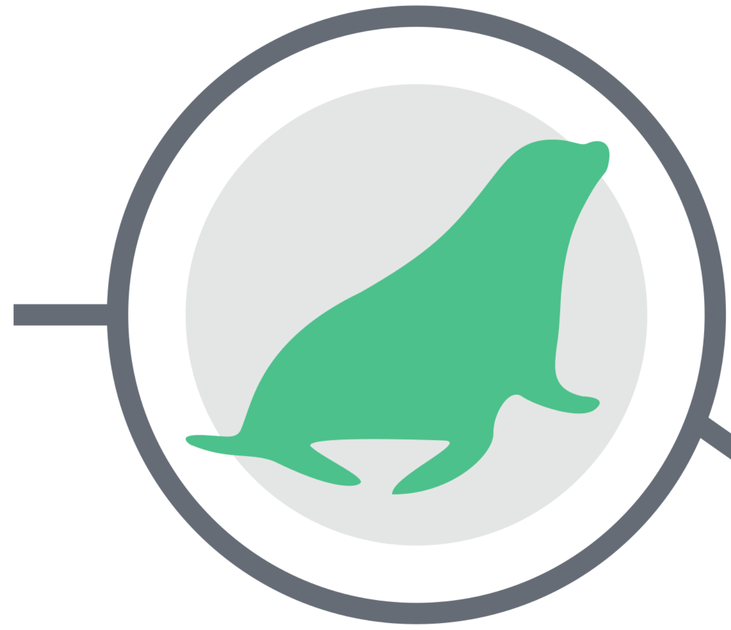
Multi-panel plot of South American sea lions counts by age-class according to day of year collected at the main breeding site N7 in Punta San Juan, Peru. Classes include: Adult Females, Juveniles, Pups, Subadult Males and Territorial Males. Total is the sum of all the age-classes. Blue line is a fitted loess model to depict the trend in abundance throughout the year. Data points include all study years available for site.

Information collected for 19 years in Punta San Juan, Peru. An important sympatric breeding site for pinnipeds of the Humboldt Current System.

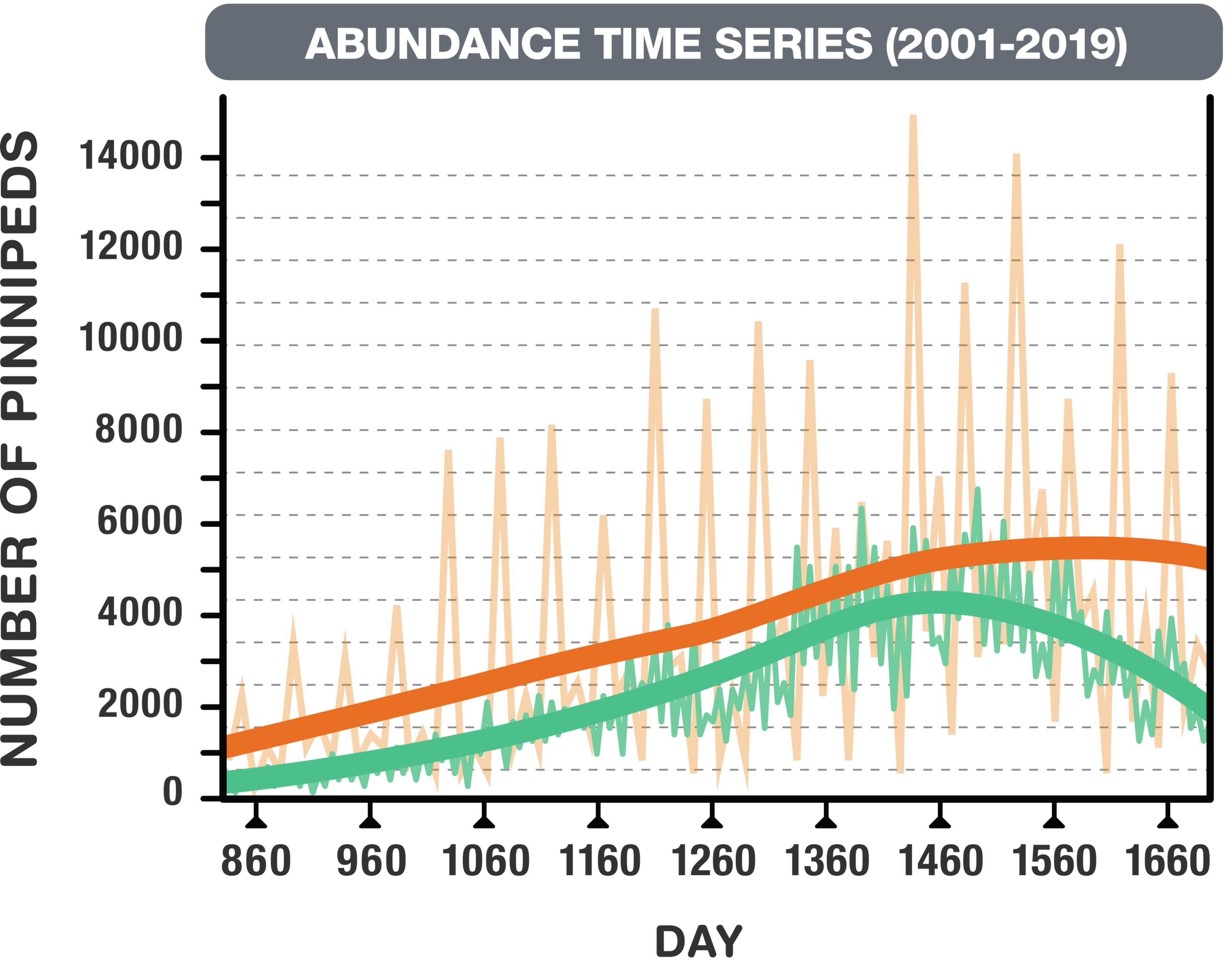
STUDY SPECIES



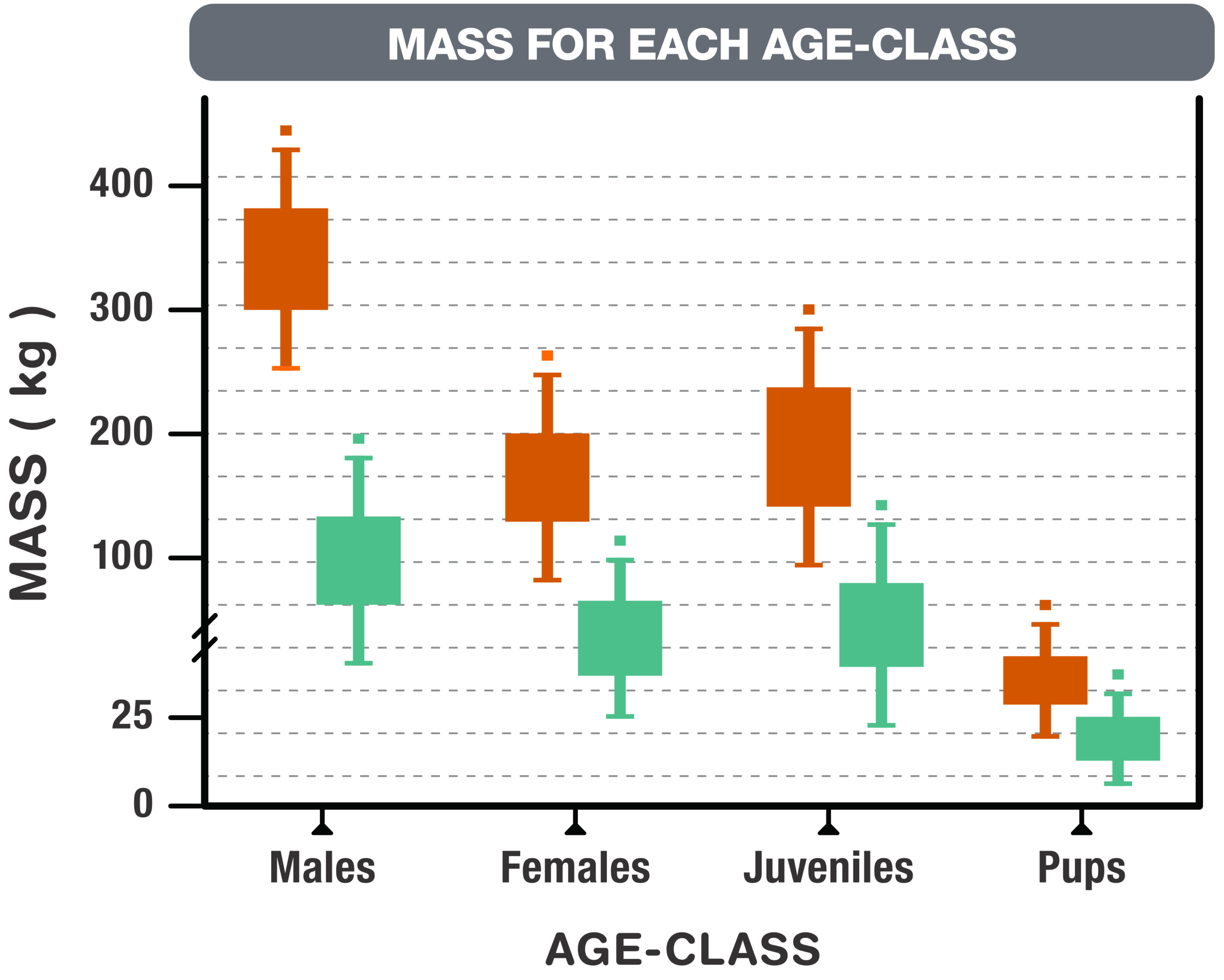
South American sea lions



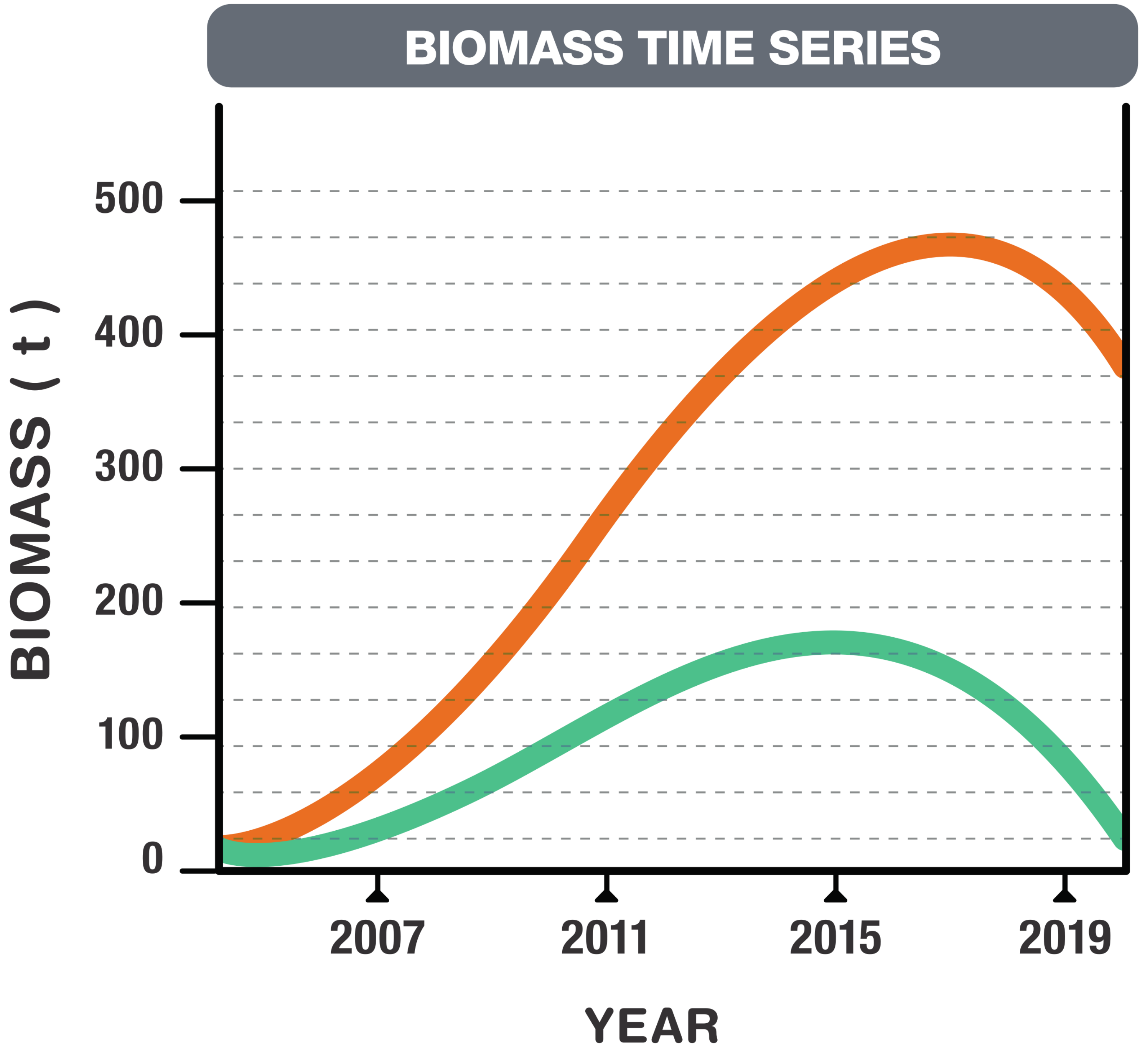
South American fur seals



ABUNDANCE TIME SERIES (2001-2019)



MASS FOR EACH AGE-CLASS



BIOMASS TIME SERIES

✓ **Resource limitation may influence recent trends in Peruvian otariids**