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

Susana Cardenas-Alayza, Dimitri Gutiérrez, Yann Tremblay

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1 **FULL TITLE:** Trends in sympatric otariid populations suggest resource limitations in the
2 Peruvian Humboldt Current System

3

4 **SHORT TITLE:** Resource limitation may influence recent trends in Peruvian otariids

5

6 **AUTHOR NAMES AND AFFILIATIONS:**

7 Cárdenas-Alayza, Susana ^{a,b,d}; Gutiérrez, Dimitri ^{b,c}; Tremblay, Yann ^d

8

9 a) Centro para la Sostenibilidad Ambiental, Universidad Peruana Cayetano Heredia, Lima
10 15074, Peru

11 b) Laboratorio de Ciencias del Mar, Universidad Peruana Cayetano Heredia, Lima 15102, Peru

12 c) Facultad de Ciencias y Filosofía, Programa Maestría en Ciencias del Mar, Universidad
13 Peruana Cayetano Heredia, Lima 15102, Peru

14 d) UMR 248 MARBEC : IRD – Univ. Montpellier – CNRS – Ifremer, Avenue Jean Monnet CS
15 30171, 34203, Sète cedex, France.

16

17 **CORRESPONDING AUTHOR:**

18 Susana Cárdenas-Alayza

19 **EMAIL:** susana.cardenas.a@upch.pe

20 **POSTAL ADDRESS:**

21 Centro para la Sostenibilidad Ambiental, Universidad Peruana Cayetano Heredia

22 Av. Armendáriz 445, Miraflores Lima 15074, Peru

23

24 **CO-AUTHORS:**

25 Dr. Dimitri Gutiérrez **EMAIL:** dimitri.gutierrez.a@upch.pe

26 Dr. Yann Tremblay **EMAIL:** yann.tremblay@ird.fr

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32 **HIGHLIGHTS**

- 33 • Limitations in population growth of Peruvian sympatric otariid populations
34 • Sea lions are the current ‘dominating’ otariid species in Peru
35 • Decrease in juveniles contributes towards population decline
36 • Resource partitioning between otariids needs to be further explored in Humboldt Current
37 System

38

39 **ABSTRACT**

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

52

53 **KEYWORDS**

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

56

57 **CREDIT AUTHOR STATEMENT**

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

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63 **1 INTRODUCTION**

64 Understanding how species coexist is an important theme in ecology. Coexistence theory is a
65 framework to understand how competitor traits can maintain species diversity and prevent
66 competitive exclusion, even among similar species in ecologically similar habitats (Chesson and
67 Kuang, 2008). Competition can compromise the fitness of one of the species involved, and may
68 ultimately lead to its exclusion (Pacala and Roughgarden, 1985). Under the resource-utilization
69 niche concept, two species cannot occupy the same ecological niche without exerting strong
70 competition on each other (Schoener, 1974). The Lotka–Volterra competition model states that
71 coexistence of two species is possible when the competitive effect that a species has on another
72 species (interspecific competition) is less than the competitive effect that it has on its own
73 species (intraspecific competition) (Chase et al., 2002; Chesson and Warner, 1981; Schoener,
74 1983). Furthermore, competitive interactions are known to be stronger between morphologically
75 and phylogenetically closely related sympatric species (Di Bitetti et al., 2009; Loveridge and
76 Macdonald, 2003; Schoener, 1983).

77

78 Otariids, composed of fur seals and sea lions, occur in sympatry in a number of upwelling
79 regions in the world and have many similar life-history traits and foraging habits (Bailleul et al.,
80 2005; Dellinger and Trillmich, 1999; Franco-Trecu et al., 2012; Jeglinski et al., 2013; Page et al.,
81 2005; Villegas-Amtmann et al., 2013; Waite et al., 2012). Coexisting species are expected to
82 develop strategies for niche differentiation when resources become scarce, to mitigate the
83 reduction in population attributes, such as growth, survival or fecundity (Begon et al., 2006). The
84 duration of coexistence in sympatric otariid seals is not known, and it is possible that sympatry
85 has resulted from recent population recoveries posterior to the period of commercial sealing
86 (Arnould and Costa, 2006). If sympatry is a result of recent events, it is possible that divergence
87 is not yet evident or that competitive exclusion is now occurring.

88

89 In sympatric fur seals and sea lions, past research have found mixed results with regards to
90 competition and segregation. Contrary to the situation in Peru, in many locations fur seal

91 populations are typically larger and they appear to outcompete sea lions (Wickens and York,
92 1997). Researchers studying sympatric otariids have found trophic segregation, differing
93 foraging strategies and contrasting population trends as mechanisms that explain coexistence
94 (Franco-Trecu et al., 2014; Pablo-Rodríguez et al., 2016; Páez-Rosas et al., 2012). More recent
95 studies demonstrate that intraspecific segregation, driven by interindividual specialization, takes
96 place in colonial species (such as otariids) that are constrained to limited foraging ranges that
97 overlap with conspecifics in similar niches (Jeglinski et al., 2013; Villegas-Amtmann et al.,
98 2013; Schwarz et al., 2021).

99

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

112

113 The Humboldt Current System (HCS) in Peru is recognized as the most productive of the Eastern
114 Boundary Upwelling Systems in the world (Bakun and Weeks, 2008). As other upwelling
115 ecosystems, cold nutrient rich water rises to the euphotic layer by a combination of the South
116 east trade winds and the Coriolis force that fuel Ekman transport, giving rise to primary
117 productivity in the upper pelagic and nearshore areas. Peru's coast is characterized by a narrow
118 continental shelf, shallow productive upwelling waters and a relatively shallow thermocline
119 related to an upper minimum oxygen layer at similar depths of approximately 50-80m, on
120 average (Bertrand et al., 2010; Demarcq, 2009; Echevin et al., 2008). These features limit the

121 potential habitat for otariid prey to be linked to the benthos. Thus, in this productive shallow
122 environment foraging on highly patchy, but dense prey resources near the surface, may preclude
123 the advantages of searching for more evenly distributed, but less dense, prey resources on the
124 benthos (Arnould and Costa, 2006), which are also constrained by bottom water hypoxia.

125

126 Furthermore, HCS is characterized by recurring El Niño Southern Oscillation (ENSO) events,
127 which can vary in intensity and duration. ENSO is known as a cycle of alternating warm El Niño
128 and cold La Niña events and is the most prominent climate signal on Earth (McPhaden et al.,
129 2006). When HCS is affected by an ENSO, increments of sea surface temperature and reduction
130 of primary productivity occur in the marine environment, altering distribution of habitats and
131 associated prey biomass. The ENSO events that occurred in 1982-83 and 1997-98, were
132 categorized as 'Extraordinary' and are well documented for dramatically altering species
133 composition and reducing marine biomass (Barber and Chavez, 1983; Tam et al., 2008). These
134 climatic signals were strong and felt worldwide, changing the availability of prey items and
135 causing declines in reproduction and survival of top marine predator populations around the
136 globe (Arias-Schreiber and Rivas, 1998; Bond and Lavers, 2014; Cárdenas-Alayza, 2012;
137 Forcada et al., 2006; Oliveira et al., 2006; Sprogis et al., 2018; Trathan et al., 2007).

138

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

151 both SAFS and SASL, respectively due to the 1997-98 ENSO (Oliveira et al., 2006, 2012).
152 Surveys post ENSO reflect population recoveries for both species but with a larger SASL
153 abundance. Similar fluctuations are observed until 2014, after which, there is a decline in SAFS.

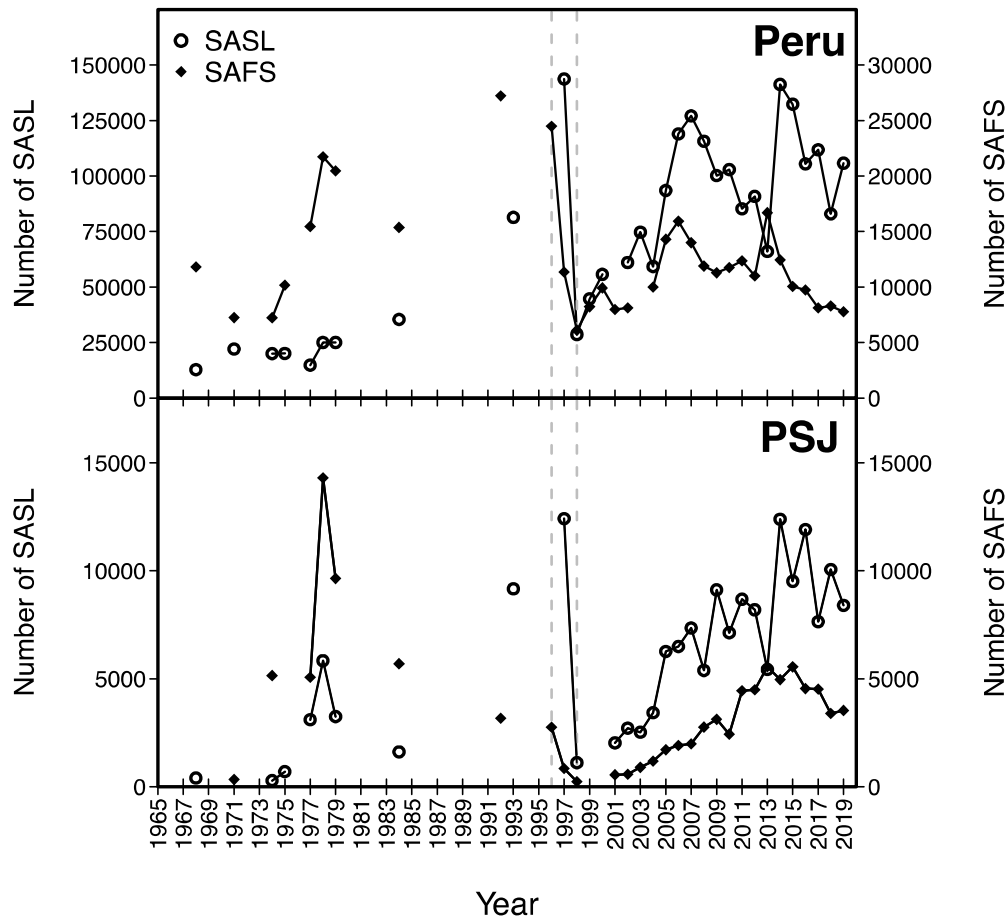
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155 Existence of sympatric colonies of SAFS and SASL implies that some mechanism currently
156 operates (or has in the past), to permit interspecific coexistence in the HCS ecosystem. Sympatry
157 of SAFS and SASL occur at only a few locations along the distribution ranges of our study
158 species in the HCS. Punta San Juan (PSJ), a peninsula on the south coast of Peru is a sympatric
159 site and is considered a historically important breeding center for otariids in Peru. The effects of
160 the 1997-98 ENSO also impacted this breeding site, with local reductions of ~87% in both
161 species. In PSJ, abundance declined from 2,751 to 345 in SAFS from November 1996 to
162 November 1999 and from 12,415 to 1,495 in February 1997 to February 1999 in SASL (Arias-
163 Schreiber and Rivas, 1998). Since the decline, weekly counts of otariids were conducted to
164 monitor population recovery. Although high resolution time series of marine megafauna
165 populations are scarce; at this location, weekly counts permit to study fluctuations in abundance,
166 which can help understand interspecific and intraspecific interactions in a common ecological
167 context. Thus, we consider that the long time series collected at PSJ (which accounts roughly for
168 10-50% of the total Peruvian populations in both species in this only site) provide an adequate
169 setting to study the coexistence of SAFS and SASL and is representative of their dynamics in
170 Peru.

171

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

181 resources, can offer a greater competitive advantage in comparison to a smaller species (SAFS)
 182 to sustain population abundance in a common environmental setting.



183
 184 **Figure 1.** Time series of the total number South American sea lions (SASL, open circles) and
 185 South American fur seals (SAFS, filled diamonds) counted on the coast of Peru (top) and Punta
 186 San Juan study site (bottom) between 1965-2019. Dashed grey vertical lines delimit the
 187 population decline caused by the 1997-98 ENSO. Time series were constructed with official
 188 counts from surveys obtained from various sources (Arias-Schreiber and Rivas, 1998; IMARPE,
 189 2018, 2017, 2016, 2015, 2014, 2013, 2012; Majluf and Trillmich, 1981; Muck and Fuentes,
 190 1987; SERNANP, 2016; Tovar and Fuentes, 1984).

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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 /m²).

224 2.2 Abundance time series

225

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

238

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

248

249 We identified the wavelength scale corresponding to one year using wavelet analysis in
250 WaveletComp R package v. 1.1 to extract the trend of abundance for both species. To test the
251 study hypothesis, the trend of abundance time series, density and ratios of abundance will be
252 compared between both species. Increasing or decreasing phase of trends, were determined with
253 first order derivatives. Turning points will permit to detect when the date of change in direction

254 of a species population trajectory occurred. Difference of first order derivatives was used to
255 understand which species was increasing over the other.

256

257 **2.3 Age-class proportions**

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

269

270 Age-class categories for this study includes: pups, juveniles, adult females, subadult males and
271 territorial males. These are based on the categories used in the field at PSJ for counting animals,
272 based on distinguishable anatomical features and behaviors (Vaz-Ferreira and Ponce de León,
273 1987). A 'juvenile' category was created in this study to group the 'yearling' (1 year old) and
274 'immature' (2-5 years old) categories used in the field. To estimate age-class proportions we
275 only used the dates that considered all the beforementioned categories. Median proportions and
276 interquartile range (IQR) were estimated .

277

278 Mean mass \pm SD of otariids according to age classes were estimated using PSJ Program
279 database. Mass was collected at PSJ between during otariid tagging and health assessment
280 fieldwork that involved weighing live animals during the study period. Mass of adult age classes
281 were collected during the breeding season while pupping was taking place. Meanwhile, pup mass
282 was collected during pup round-ups, approximately 2 months after the peak of pupping occurs in
283 each species (April for SASL and January for SAFS). Mass for the SAFS subadult male age-

284 class was obtained from the PSJ Program necropsy records of individuals that stranded dead in
285 PSJ due to interactions with longline fisheries, and is reported here. These animals were
286 confirmed to have died from interaction with fishing gear, carcasses were in good body condition
287 and therefore we consider their mass accurately represents their age-class. The only records of
288 mass for dead juveniles available in PSJ were in emaciated body condition, probably due to
289 nutritional stress, thus we do not consider they represent mass of healthy live individuals.

290

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

300

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

309

310 **2.4 Biomass times series**

311 Biomass time series were constructed for each species in tons (t) by calculating the product of
312 the abundance time series trend, the median age-class proportion and the mean mass per age-
313 class. A time series for total otariid biomass was created from the sum of the SASL and SAFS

314 biomass time series to determine the proportion of biomass that pertains to each species. To test
315 our hypothesis, the percentages of each of the species biomass over time are used to describe
316 interspecific competition and evaluate if SASL are dominating over SAFS. All analysis were
317 done using R software version 3.6.2.

318

319 **3 RESULTS**

320 **3.1 Abundance time series**

321 After removing high frequency signal from count data, annual trends of abundance were
322 extracted for each species. This revealed population trajectories in PSJ that vary between a range
323 of 829 - 4,550 individuals for SASL (Figure 2A) and 291 – 3,443 individuals for SAFS (Figure
324 2B) between 2001 to 2019. During this study period mean density of individuals during breeding
325 was 0.40 ± 0.23 ind /m² for SASL (January-March) and 0.12 ± 0.08 ind /m² for SAFS (October-
326 December).

327

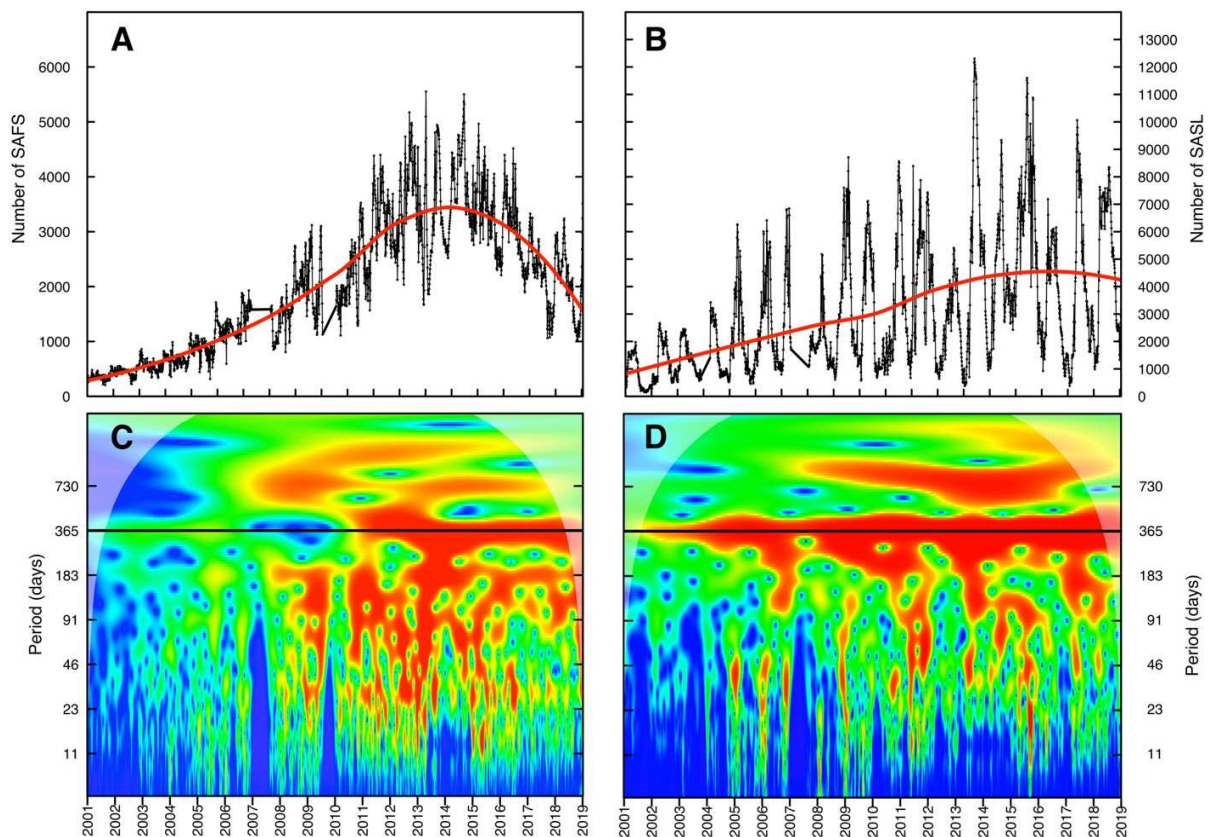
328 Throughout the abundance time series, there is always a higher abundance of SASL in
329 comparison to SAFS, with a median ratio of 1.65 SASL : 1 SAFS. The ratio of SASL to SAFS
330 starts at a maximum ratio of 2.84 SASL : 1 SAFS, followed by decreasing phase that hits a
331 minimum of 1.23 SASL :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

333

334 In general, both species started with a positive increasing phase and then both declined toward a
335 negative phase, with differing dates at each turning point. Turning points were detected as the
336 date when a change from positive to negative phases occurred. First, SAFS changed its phase
337 from positive to negative in November 2014. Then, 2.25 years after (in March 2017), SASL
338 changed its phase and started to decline. Linear regressions ($p < 0.05$) were adjusted to
339 standardized data of the (negative) declining phase for each species. Slopes were significantly
340 different from zero in both species ($R^2 = 0.99$, $p < 0.05$); being slope incline of SAFS ($B_0 = -$
341 $179.35 \pm SE 0.21$) steeper than SASL slope ($B_0 = -97.33 \pm SE 0.23$).

342

343 The difference between first orders derivatives describes which of the species had a higher
344 growth rate, at a given time, in comparison to the other. We used these values to organize the
345 time series into three different periods. Sea lions had a greater growth rate in comparison to
346 SAFS, during the first period (January 2001 - June 2007) and in the third period (March 2012 -
347 December 2019). SAFS had a stronger growth rate in comparison to SASL during the second
348 period (June 2007 - March 2012).
349



350
351 **Figure 2.** Top panel shows 3-day interpolated counts (black line) with trend of abundance (red
352 line) for A) SAFS and B) SASL collected in Punta San Juan, Peru. Bottom panel shows wavelet
353 spectrum with horizontal line indicating the annual signal at 365 days for C) SAFS and D) SASL
354 abundance time series.

355

356 3.2 Age-class proportions

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

364

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

370

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

379

380 **3.3 Biomass time series**

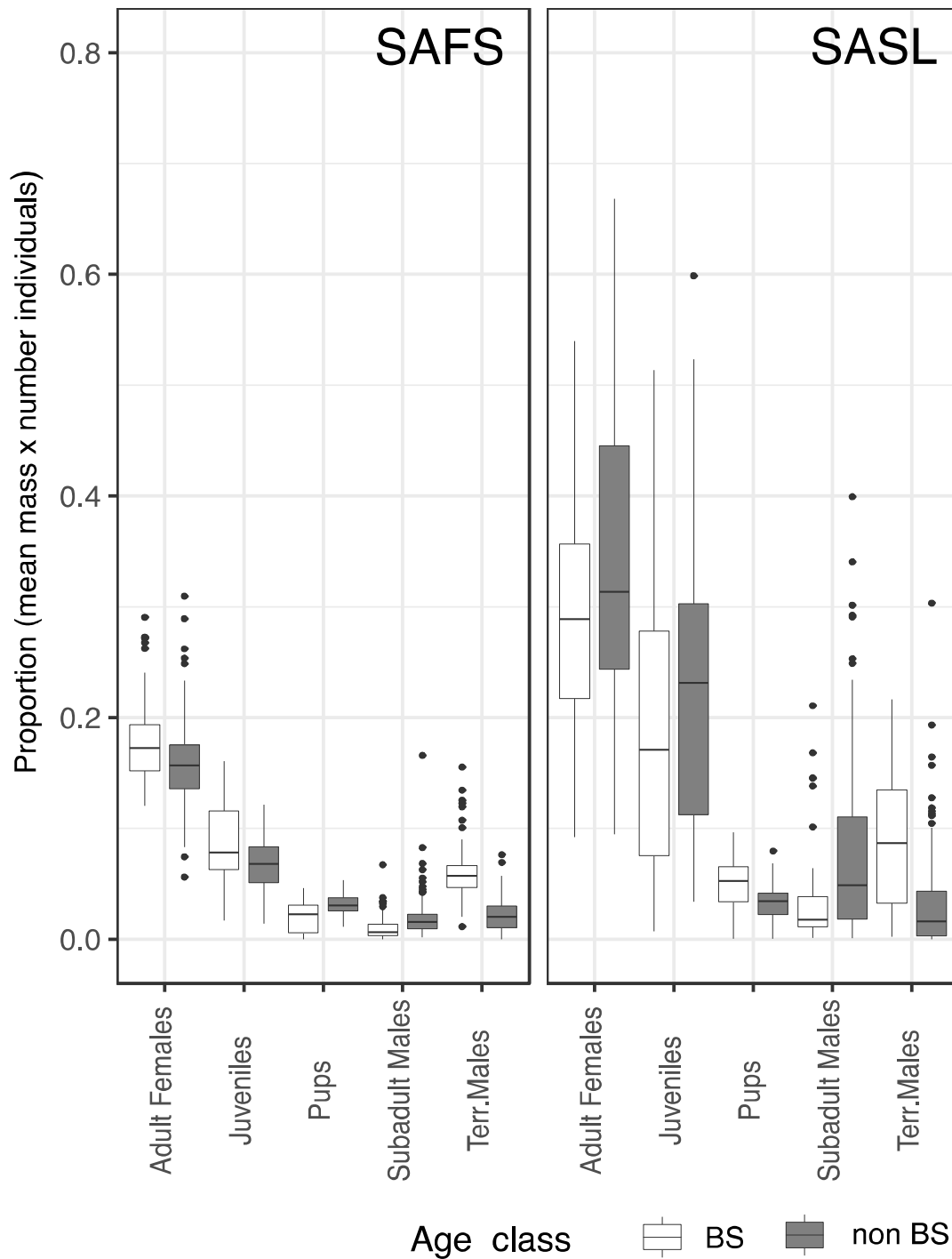
381 Total otariid biomass time series was in the range of 83.16 – 506.72 t with a mean of $335.26 \pm$
382 139.95 t and reached its maxima in March of 2016. Throughout the time series $82.61 \% \pm 3.75$ of
383 total biomass is composed on average by SASL (range: 77.72 - 88.97 %), and $17.39 \% \pm 3.75$ by
384 SAFS (range: 11.03 – 22.28 %). This trend continues until the end of the study period, with
385 88.63% of otariid biomass comprised by SASL and 11.36% by SAFS in the end of 2019. SASL
386 occupy a biomass in the range of 73.99 – 406.25 t with a mean 272.97 ± 108.61 t, reaching its

387 maxima in March 2017. Whereas SAFS occupy a biomass of 9.17 – 108.41 t with a mean of
388 62.30 ± 33.21 t, reaching its maxima in November 2014 (Figure 5).

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

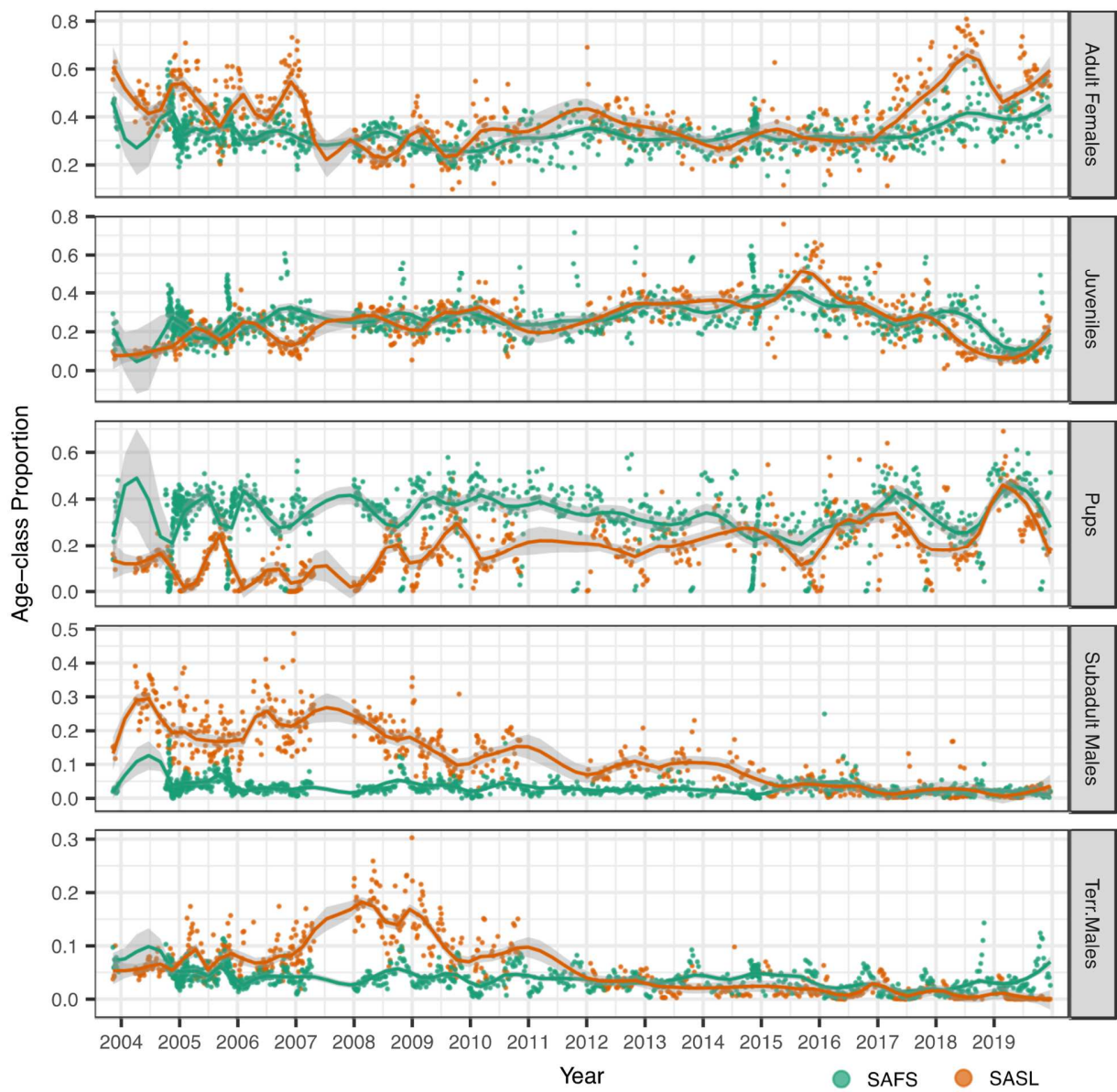
391

Species	Age-class	Proportion of age-class		Mass of age-class (kg)		
		<i>Median</i>	<i>IQR</i>	<i>Mean \pm SD</i>	<i>n</i>	<i>Source</i>
SASL	Pups	0.16	0.18	13.98 \pm 0.62	77	This study
	Juveniles	0.23	0.17	78.88 \pm 17.68	9	Hückstädt et al 2016
	Adult females	0.38	0.19	82.74 \pm 11.31	23	This study
	Subadult males	0.12	0.16	173.78 \pm 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 \pm 0.65	171	This study
	Juveniles	0.26	0.10	24.88 \pm 14.4	5606	Baker et al 1994
	Adult females	0.33	0.09	48.56 \pm 8.08	91	This study
	Subadult males	0.03	0.02	66.53 \pm 8.56	6	This study
	Territorial males	0.04	0.03	108.64 \pm 14.20	26	This study



392

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



396

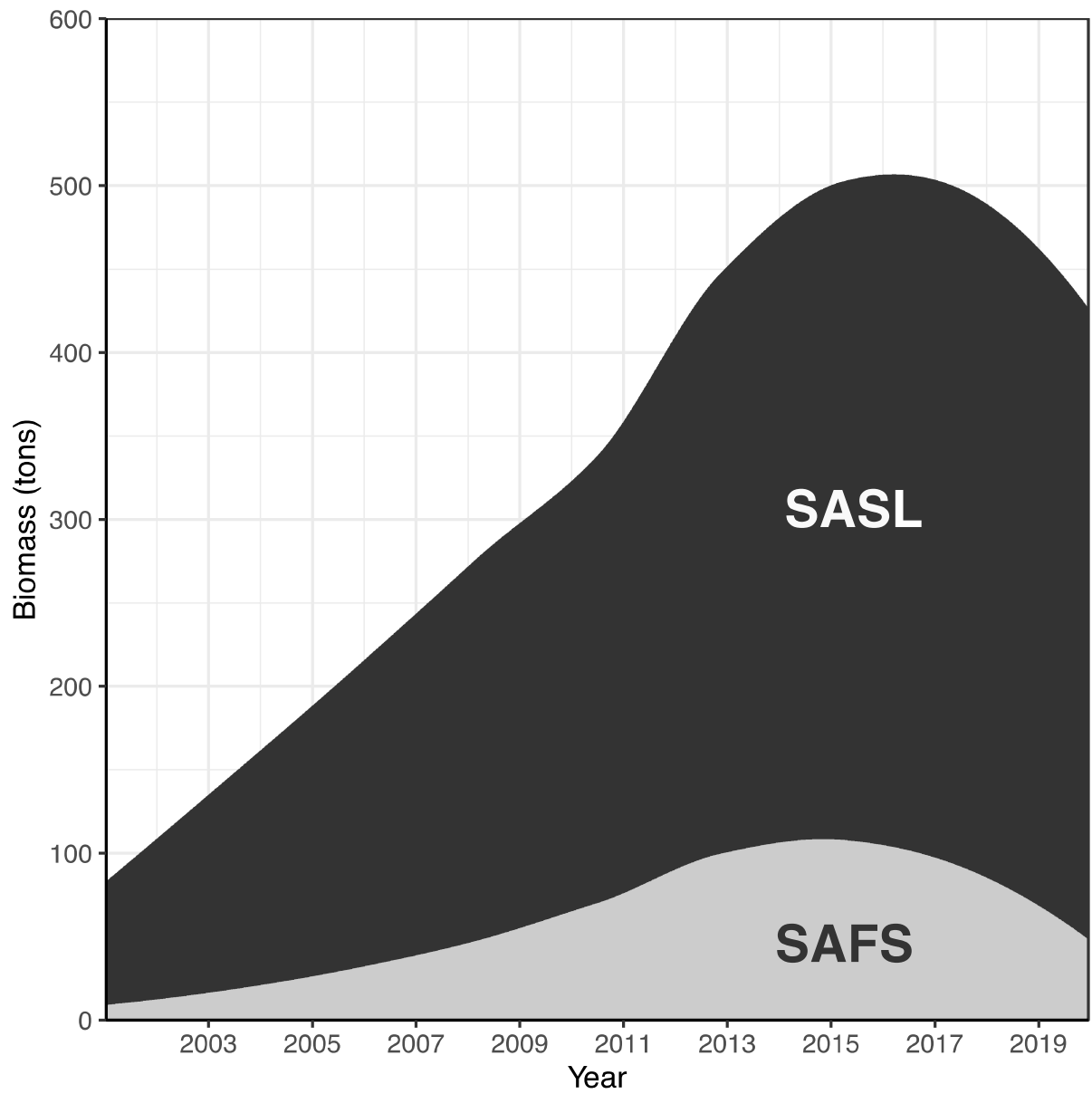
397 **Figure 4.** Time series of the proportion of age-classes for SAFS (green) and SASL (orange)
 398 constructed from weekly counts (circles) with smooth curve (line) with 95% CI (grey area). Age-
 399 class counts collected at Punta San Juan otariid breeding sites between November 2003 -
 400 December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

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405
 406 **Figure 5.** Stacked area chart of constructed biomass time series in tons (t) estimated from otariid
 407 abundance in Punta San Juan for SAFS (light gray) and SASL (dark grey) during years 2001-
 408 2019.

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414

415 **4 DISCUSSION**

416 **4.1 Changes in abundance, density and population trajectories**

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

433

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

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

450

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

468

469 Otariid breeding sites tend to show seasonal age-class proportions that reflect the roles of age-
470 classes and sexual segregation in their polygynous mating system (Bartholomew 1970). In this
471 study we found that PSJ breeding sites are occupied by different proportions of age-classes
472 during breeding and non-breeding season in both species, with females, pups and juveniles being
473 the most important age-classes throughout the year. Intra-annual dynamics show that from July

474 until December, the abundance of all SASL age-classes decrease to very low and can reach zero
475 abundance in PSJ. In contrast to SAFS, which is present year round, and has a slight decrease in
476 July-August (Appendix A). The wide variability in SASL in comparison to SAFS over the study
477 period is promoted by the arrival of larger number of animals in a given season and the higher
478 density at the breeding sites. Interestingly SAFS show a higher proportion of pups : female ratio
479 than SASL (Figure 4), which suggests that female condition may be better in SAFS. However,
480 this can be explained by the high site fidelity of breeding female SAFS at this site, where
481 experienced breeders return to pup (Majluf, 1989). Whereas in SASL, it is possible that a bulk of
482 the SASL females are young females.

483

484 In this study we found that SASL density (0.40 ± 0.23 ind / m²) at PSJ during breeding was 3-4
485 times SAFS density (0.12 ± 0.08 ind / m²). This can be explained by the difference in the social
486 tactics intrinsic to each species. Soto and Trites (2011) reported a lek-like mating system in
487 SASL with the highest female : male ratio recorded for this species in Ballestas Islands in Peru,
488 about 250km from our study site. Large abundances of females congregate to breed at what some
489 authors identify as population “hotspots”. These high density aggregations have been explained
490 as a means to enhance mate selection (Soto and Trites, 2011). Territorial males line up at the tide
491 line to display themselves to reproductive females. Females benefit from male competition and
492 avoid subadult male harassment while remaining in close proximity to foraging sites (Bradbury
493 and Gibson, 1983, Soto and Trites, 2011). Although there are no studies on the SASL mating
494 system at PSJ, we suppose that the social tactics described above also occurs and PSJ is an
495 important site for SASL breeding (S. Cárdenas-Alayza, personal observation).

496

497 We know from historical records that the SAFS population ranged between 9,644 - 14,303 and
498 SASL between 3,249 – 5,836 at the PSJ study site in 1978-79 (Figure 1). This shows that PSJ is
499 able to support larger abundances of these species on land and in the surrounding marine
500 environment. Interestingly, during the post 1997-98 ENSO recolonization process, SAFS
501 gathered in lower densities than SASL. Pre ENSO density of SAFS at PSJ was reported between
502 0.5 - 1 ind /m² (Majluf, 1989), considerably higher than average current density of 0.12 ± 0.08
503 ind / m² found in this study. In the 1980s and 1990s, 48% pup mortality was recorded in SAFS in

504 PSJ. This was caused by maladaptive aggression of females towards pups, attributed to the high
505 density aggregations (Harcourt, 1992a, 1992b; Majluf, 1992). Furthermore, SAFS currently
506 occupies many more beaches for breeding in PSJ in lower density, in comparison to the pre
507 1997-98 ENSO era (Cárdenas-Alayza, 2007). Other studies have demonstrated that habitat
508 selection for breeding sites by SAFS and SASL varies in Peru, and is driven by access to water
509 or shade for thermoregulation (Stevens and Boness, 2003). Therefore, availability of suitable
510 habitat features will also play a role in the occupation of breeding sites in a given area so that
511 each species can efficiently operate mating tactics characteristic of species social system.

512

513 **4.2 Contributing factors of population fluctuations in Peruvian otariids**

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

525

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

533 Finally, in 1976 commercial exploitation of both species was banned in Peru (Tovar and Fuentes,
534 1984).

535

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

557

558 Our results show that SAFS recently declined at a rate 1.5 faster than SASL. The steeper decline
559 in SAFS, is possibly linked to reduced recruitment in breeding adults at PSJ in recent years in
560 combination with juvenile dispersal and mortality from this site. In our study, the sympatric
561 otariids are exposed to the same environmental conditions, reason why the difference in this
562 response can also be linked to intrinsic species traits that respond differently to the changes in the

563 environment. A populations risk of extinction will depend both on the deterministic (harvest,
564 commercial exploitation, natural selection, etc.) and stochastic (environmental, genetic, etc.)
565 processes. The latter are more pronounced at small population sizes and can accelerate extinction
566 process started by deterministic factors (Palstra and Ruzzante, 2008). Previous studies have
567 shown that the effective population (N_e) is used as a tool to evaluate viable populations. High N_e
568 values retain high levels of genetic diversity and reduce probability of effects from inbreeding
569 depression (Oliveira et al., 2006, 2012; Wright, 1990). Whereas a population with a low N_e , is
570 susceptible to genetic drift and less apt to respond to selection (Oliveira, 2011).

571

572 After the 1997-98 ENSO, SAFS have a critical N_e value of 2,153 (Oliveira et al., 2006) while
573 SASL N_e is 7,715 (Oliveira et al., 2012). According to Oliveira et al (2009) population
574 reductions after the 1997-98 ENSO, may have caused a significant genetic bottleneck in the
575 Pacific population of SAFS and SASL, with loss of genetic diversity and presumably some loss
576 of evolutionary potential for the species (Oliveira et al., 2009; 2012). Furthermore, the rate of
577 loss of genetic diversity via genetic drift is greater in populations where N_e is small and
578 migration is limited, as is the case for SAFS. This can be evidenced in the information gathered
579 through Peru's nationwide surveys, where >90% of SAFS breeding population is mostly
580 restricted to latitude 15 -17° South, with PSJ supporting at least 40% of entire Peru SAFS
581 population. Meanwhile, SASL population is distributed continuously along the coast, with
582 important breeding sites in several latitudes (6, 13-14, 15 and 17° South) (IMARPE, 2018, 2017,
583 2016). Wider distribution of breeding sites with high density aggregations of SASL, suggest that
584 migration and dispersal rates in SASL are higher than SAFS, resulting in higher connectivity.
585 Therefore, even if there was genetic loss due to a bottleneck from a strong ENSO event, SASL
586 has mechanisms to counterbalance loss of genetic diversity with temporal gene flow through
587 migration. The difference in gene flow between these two species in HCS can be a key factor
588 explaining the limited response to achieve population growth under scenarios of environmental
589 change in SAFS in comparison to SASL suggested in this study, and should be further studied.

590

591 **4.3 Natural history traits that influence interspecific competition in otariids**

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

602

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

618

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

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

627

628 It is well documented that the HCS in Peru holds a world-leading monospecific forage fishery in
629 terms of landings of Peruvian anchovy, sustaining >5 million tons per year on average since
630 1960s (Bakun and Weeks, 2008; Chavez et al., 2008). In Peruvian otariids, the number of pups
631 born, mean birth dates and anchovy biomass were found to have direct relationships in SASL
632 and SAFS reproductive success, demonstrating that anchovy is a key resource in fulfilling the
633 energetic demands of both species (Cárdenas-Alayza, 2012; Soto et al., 2004). Other studies
634 have evaluated diet composition between these sympatric otariids in the decades of 1980s and
635 late 1990s in south Peru, but conclusions for resource partitioning are not clear. Vásquez (1995)
636 reported that otariid diets were both based on fish and cephalopods; with Peruvian anchovy
637 (*Engraulis ringens*) and Jack Mackerel (*Trachurus murphyi*) as the main consumed species.
638 Afterwards, Arias-Schreiber (2000) found that Peruvian anchovy, squids and a crustacean, the
639 Red squat lobster (*Pleuroncodes monodon*), were ranked as important prey items shared by the
640 sympatric species. Based on this, we understand that anchovy is an important prey shared by
641 both otariids during these study periods, but mechanisms for trophic segregation are not clearly
642 explained. Furthermore, prey availability may have changed in the last 20 years. Therefore,
643 resource partitioning research needs to be updated and further explored in these sympatric
644 species to disentangle current resource utilization in relation to population trajectories.

645

646 **4.4 Current and future trends**

647 In the final 5 years of our time series, both sympatric otariid populations were found to be in a
648 state of decline. SAFS were the first to decline in 2014, which coincides with a decrease in the
649 anchovy biomass estimated for the coast of Peru during this period. Anchovy biomass dropped
650 from 11,201 tons in 2013 to 3,799 tons in 2014 (Zavala et al., 2019). In 2014 anchovy landings
651 summed 1,302 tons, leaving an available biomass of 2,497 tons for all predators and other

652 fisheries to consume, which may have posed limitations for growth and maintenance of predator
653 populations. Warmer oceanographic conditions in HCS persisted and coincided with a reduced
654 anchovy biomass from 2014 to 2017 (Zavala et al., 2019). Changes in oceanographic conditions
655 can shrink and expand available habitat for prey items forcing new competition scenarios
656 between coexisting species. Thus, under a scenario of reduced anchovy biomass we consider it is
657 possible that prey availability is limiting population sizes at PSJ and can be responsible for the
658 declines observed in the juvenile and subadult age-class for both SAFS and SASL; as younger
659 individuals do not possess full diving capabilities.

660

661 Predictions for the future of HCS include scenarios with shoaling of the oxycline (Brochier et al.,
662 2013), compressing the pelagic habitat that sustains the abundant biomass of small pelagic fish
663 currently in the system (Bertrand et al., 2011). If this occurs, it will increase competition between
664 all the predators that depend on pelagic resources, unless they adapt foraging strategies under
665 new conditions. Under this hypothetical predicted scenario and our findings, we suspect SASL
666 will be the more resilient of the two sympatric otariid species that will thrive in HCS, given its
667 population recovery in the past 20 years. Therefore, to propose adequate management for the
668 future of these species, it is important to better understand current underlying foraging strategies
669 used by otariids of HCS and determine if trophic competition rules over space and time between
670 species. These studies are key to tease apart the underlying mechanisms behind the current
671 population trajectories revealed by the present study.

672

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687

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943

944 **Appendix A. Supplementary data.**

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

946

947 **Multimedia Component 1.**

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

953

954 **Multimedia Component 2.**

955 Multi-panel plot of South American sea lions counts by age-class according to day of year
956 collected at the main breeding site N7 in Punta San Juan, Peru. Classes include: Adult
957 Females, Juveniles, Pups, Subadult Males and Territorial Males. Total is the sum of all the
958 age-classes. Blue line is a fitted loess model to depict the trend in abundance throughout the
959 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

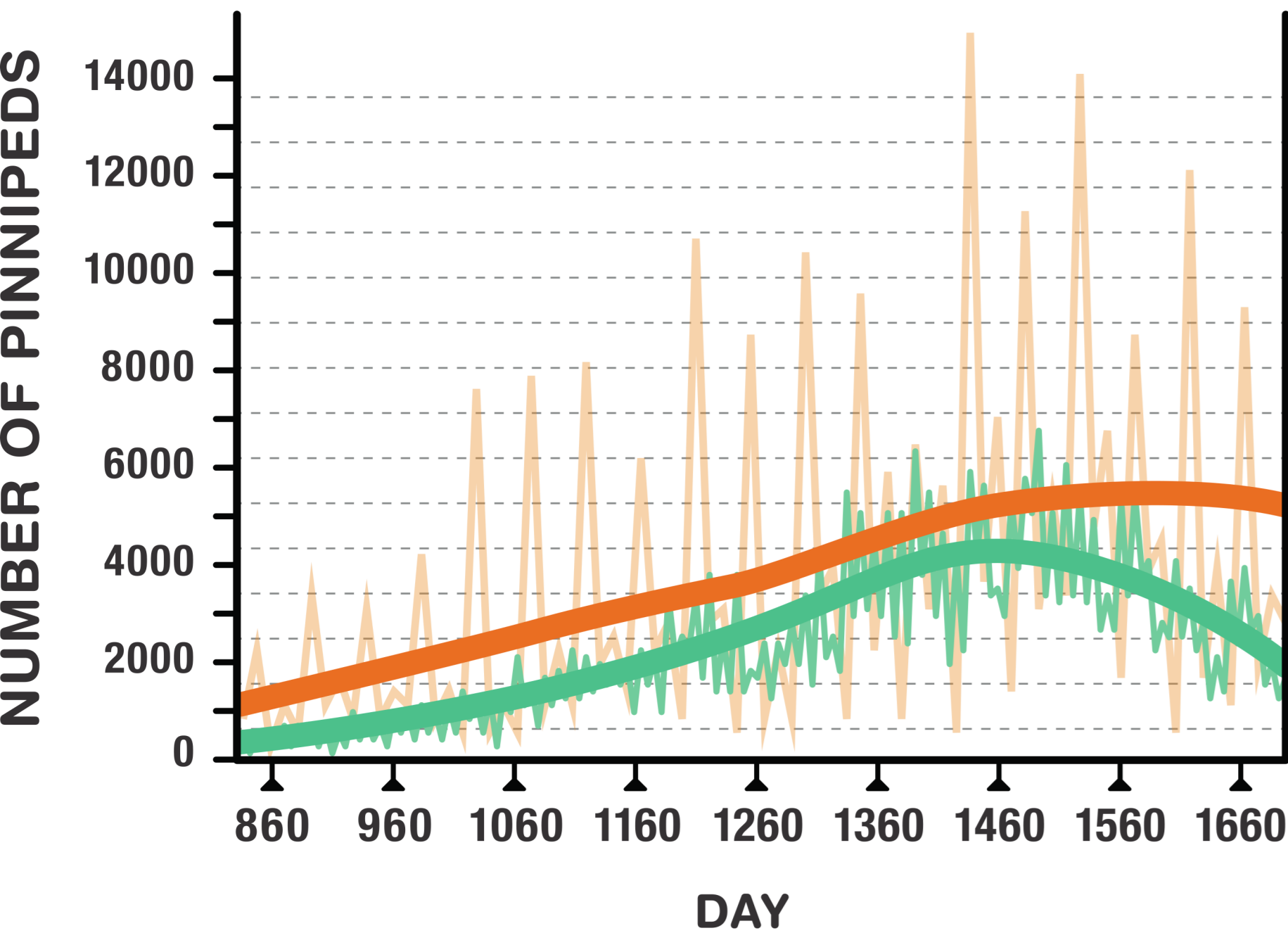


South American sea lions

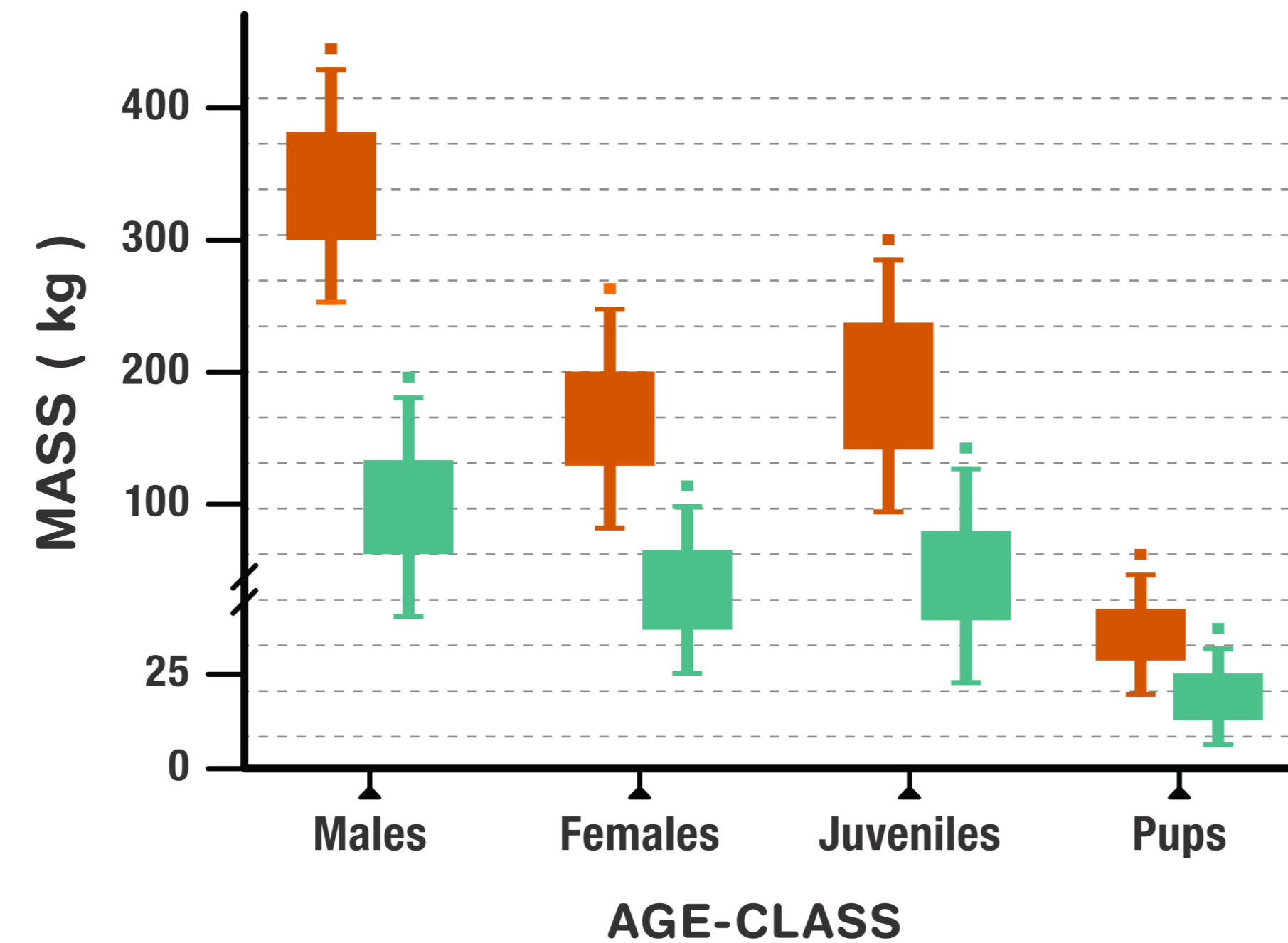


South American fur seals

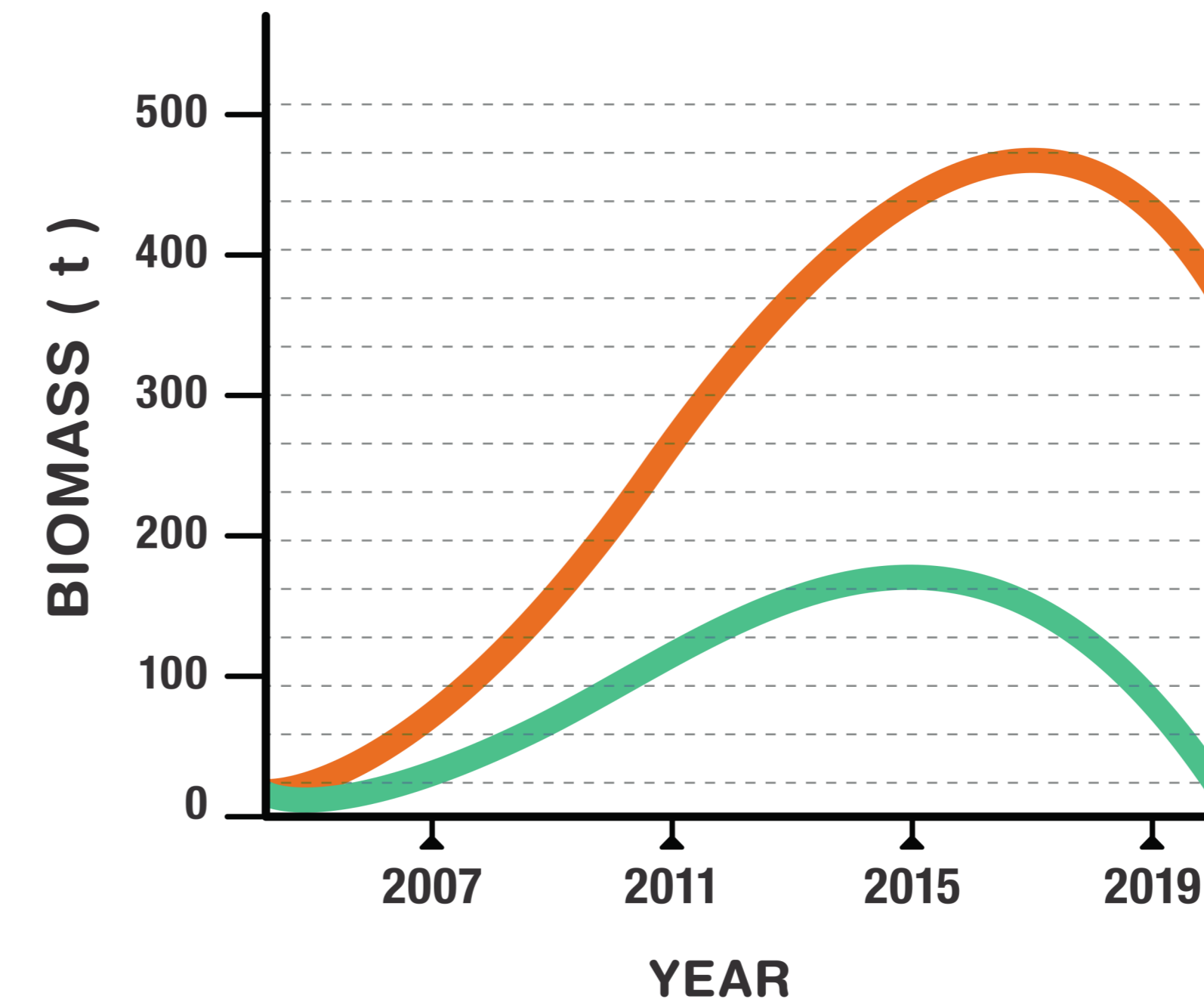
ABUNDANCE TIME SERIES (2001-2019)



MASS FOR EACH AGE-CLASS



BIOMASS TIME SERIES



Resource limitation may influence recent trends in Peruvian otariids

