Strategies for segregation during foraging in sympatric otariids of the Peruvian upwelling Humboldt Current System

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ABSTRACT: The competitive exclusion principle predicts that species exhibit segregation mechanisms to coexist. In the Humboldt Current System, South American sea lions *Otaria byronia* (SASL) coexist with South American fur seals *Arctocephalus australis* (SAFS); however, the existence of temporal and spatial partitioning in foraging strategies remains unknown. To compare foraging strategies, we analyzed locations of 35 adults (18 SASL, 17 SAFS; 4 and 8 females, 14 and 9 males, respectively) equipped with satellite tags in Punta San Juan, Peru (2013–2017). We evaluated (1) distance and duration of foraging trips, (2) utilization distributions (UDs), (3) foraging by hour and (4) association of foraging with environmental variables. Regular interval tracks (every 30 min) were modeled, and residence time was estimated to determine foraging events. Proportion overlap and analysis of similarity compared groups in core areas (50% UD) and home ranges (95% UD). Generalized additive mixed models were built to determine if hour of day and environmental conditions had an effect on foraging. Multiple mechanisms for foraging segregation that explain coexistence were found. Duration and distance between species–sex groups were significantly different, except for trip duration between SASL sexes. SAFS traveled longer distances and duration than SASL, and males traveled longer distances and duration than conspecific females. Female UDs overlapped, while male UDs did not. Core areas between sexes overlapped in SAFS and SASL, but home ranges were significantly different. Hour of day had a significant effect on foraging events in SAFS females and SASL males. Environmental conditions during foraging by SASL and SAFS females reflected coastal and offshore habitats, respectively. However, interspecific segregation was not evident between males.

KEY WORDS: Interspecific segregation · Pinnipeds · Coexistence · *Arctocephalus australis* · *Otaria byronia*

1. INTRODUCTION

The ways in which species partition available resources within ecological communities is a major determinant of the diversity of coexisting species. However, coexisting species that share similar mor-phological traits may compete for resources (Hutchinson & MacArthur 1959). Competition can compromise the fitness of the species involved and may ultimately lead to the competitive exclusion of one species, especially when resources are limited. The principle of competitive exclusion predicts that

coexisting species will exhibit resource partitioning (spatial, temporal or dietary segregation), occupying different ecological niches (Pianka 1974, Schoener 1974). Thus, coexisting species must differ in their ecological requirements by at least some minimal amount to avoid competitive exclusion (Pianka 1974).

The otariids (fur seals and sea lions) include sympatric marine mammal species with similar life-history traits and foraging habits. In general, in areas where fur seals and sea lions live in sympatry, fur seal populations are typically larger and appear to outcompete sea lions (Wickens & York 1997, Arnould & Costa 2006). Many studies in both northern and southern latitudes have examined potential competition between sympatric fur seals and sea lions, and their results are mixed. Some have found segregation with no trophic overlap (*Callorhinus ursinus* and *Zalophus californianus*, Antonelis et al. 1990; *Arctocephalus galapagoensis* and *Z. wollebaeki*, Dellinger & Trillmich 1999; *A. forsteri* and *A. pusillus doriferus*, Page et al. 2005; *Z. californianus* and *A. townsendi*, Aurioles-Gamboa & Camacho-Ríos 2007; *A. australis* and *Otaria byronia*, Franco-Trecu et al. 2012), whereas others have determined spatial segregation (*A. galapagoensis* and *Z. wollebaeki*, Jeglinski et al. 2013, Páez-Rosas et al. 2014; *A. australis* and *O. byronia*, Riverón et al. 2021), or both dietary and spatial overlap (*C. ursinus* and *Eumetopias jubatus*, Waite et al. 2012; *A. galapagoensis* and *Z. wollebaeki*, Villegas-Amtmann et al. 2013).

In the southern Pacific Ocean, South American fur seals *A. australis* (SAFS) and South American sea lions *O. byronia* (SASL) can be found in sympatry along the coastline of Peru. The present study is based on data collected at Punta San Juan (PSJ), Peru, a protected area which supports important breeding colonies of both species in sympatry year round, making it a suitable location to study coexistence (Cárdenas-Alayza et al. 2021). SAFS and SASL are sexually dimorphic otariids, with differential reproductive roles between both sexes. Reproductive roles can influence habitat selection and differential intraspecific foraging behavior in various ways. Foraging behavior of adult females (3–4+ yr old) is constrained by provisioning of offspring, limiting the duration of foraging trips to 2–4 d (Majluf 1987, Soto et al. 2004, Ganoza 2016). Adult males, in contrast, can extend their foraging trips in terms of duration and distance. Territorial males have restrictions during the breeding season, during which they fast for longer periods on shore to compete for access to females, which requires spending a significant portion of their time on land (Majluf 1987, Soto & Trites

2011). Therefore, in our study species, sexual segregation plays a major role in the way nutritional demands are satisfied.

The Humboldt Current System (HCS) in Peru is recognized as one of the most intense and productive of the Eastern Boundary Upwelling Systems (Bakun & Weeks 2008). Cold, nutrient-rich water rises to the euphotic layer through a combination of the South East trade winds and the Coriolis force that fuels Ekman transport, elevating primary productivity in the upper pelagic and nearshore areas (Echevin et al. 2008). In the HCS, it is hypothesized that the pumping of nutrient-rich waters towards the surface and the variability in the pronounced oxygen minimum zones are promoted by westward motions of mesoscale thermal fronts or eddies (Chaigneau & Pizarro 2005, Chaigneau et al. 2008). The HCS is also characterized by recurring El Niño–Southern Oscillation (ENSO) events, which can vary in intensity and duration. ENSO involves a cycle of warm El Niño and cold La Niña events, and is the most prominent climate signal on Earth (McPhaden et al. 2006). When the HCS is affected by warming events, such as El Niño or Kelvin waves, food web composition is altered (Tam et al. 2008). These changes impact the success of predator foraging events and, depending on their intensity and duration, can decrease reproductive output and survival rates in top predators (Majluf 1991, Trillmich & Dellinger 1991). Extraordinary El Niño events (e.g. 1982–83, 1997–98) have triggered significant changes in the food web composition, causing nutritional stress and mortality in top predators (Forcada et al. 2006, Oliveira 2011, Bond & Lavers 2014, Sprogis et al. 2018).

The southern coast of Peru is characterized by a narrow continental shelf, reaching depths of over 1000 m within less than 50 km offshore. The shallow productive upwelling waters and shallow thermocline are related to an upper minimum oxygen layer at similar depths of approximately 50–80 m on average, constraining expansion of vertical habitat (Echevin et al. 2008, Demarcq 2009, Bertrand et al. 2010). These features limit the potential habitat for otariid prey to be linked to the benthos. Composition of diet items consumed by otariids in PSJ reveal that demersal and benthic habitats are not targeted by SAFS or SASL. SAFS diet is mostly composed of prey items from pelagic (52.35%) and demersal–pelagic (47.25%) habitats, while SASL prey items are mostly of demersal–pelagic (69.44%) and pelagic (23.88%) origin (Cárdenas-Alayza et al. 2022). Both otariids share Peruvian anchovy *Engraulis ringens* as an important prey item and complement their diets with

2 other important items: cephalopods in SAFS and red squat lobsters *Pleuroncodes monodon* in SASL (Cárdenas-Alayza et al. 2022).

Previous studies have described SAFS in Peru as epipelagic nocturnal foragers that dive in the range of 11–30 m (Trillmich et al. 1986). However, at present, there are no published data on the spatial use patterns of SAFS in this ecosystem. In northern Chile, pelagic foraging was observed in juvenile male SASL, with average dive depths of 30 m (Hückstädt et al. 2014, 2016). Thus, in a highly pelagic environment such as the south Peruvian coast, where the combination of a narrow continental shelf (80 km from shore) and a shallow oxycline (50–80 m) compress the habitat for potential prey (Bertrand et al. 2010, 2011), we hypothesized that pelagic foraging strategies exist for both species combined with other forms of temporal and spatial segregation. In this study, we aimed to determine if temporal and spatial segregation among species and sex groups are influenced by morphological (body mass), behavioral or environmental conditions during foraging. Specific objectives included determination of interspecific and intraspecific differences in (1) distance and duration of foraging trips; (2) utilization distributions (area covered) for core areas and home ranges; (3) time of foraging by hour of day; and (4) environmental conditions associated with foraging events.

In otariids, body size is positively related to dive duration, enabling larger animals to dive deeper and forage more efficiently (Costa et al. 2004, Weise et al. 2010). Both study species have a strong sexual dimorphism, with males being 2–4 times larger than females (Ralls & Mesnick 2002). Since male otariids are not involved in parental care, they can maximize their fitness by traveling farther in search of more profitable foraging grounds or prey in comparison to females. We anticipated that males of both species would travel longer distances, forage for longer durations and cover larger areas in comparison to females. Due to time constraints linked to maternal attendance in both species, we expected females to have reduced ranges in terms of distance, duration and consequently, area covered compared to males. In terms of temporal segregation, based on nocturnal epipelagic foraging behavior previously reported in SAFS (Trillmich et al. 1986), we expected SAFS to forage mostly at night to capture prey in the scattering layer during diel vertical migration, whereas we expected SASL to forage throughout the day and night as reported in other sea lion species (Villegas-Amtmann et al. 2008, Riet-Sapriza et al. 2013, Schwarz et al. 2021). Also, based on previous studies

that compared fur seals and sea lions in other locations, we expected SAFS to make trips of longer distances and duration in offshore habitat in comparison to SASL that forage closer to shore (Franco-Trecu et al. 2012, Waite et al. 2012, Riverón et al. 2021).

To understand the relationship between otariid foraging events in the HCS marine environment, we selected a suite of variables to describe key oceanographic features. In the HCS, a general cross-shore gradient is produced by coastal upwelling, concentrating lower sea surface temperatures (SSTs) and higher concentrations of chlorophyll *a* (chl *a*) closer to shore (Echevin et al. 2008, Gutiérrez et al. 2011). Within this gradient, dynamic mesoscale eddies can occur, generating profitable foraging grounds for predators (Chaigneau & Pizarro 2005, Chaigneau et al. 2008). The proximity to fronts and the large-scale thermal gradient serve as indicators of their location and intensity. Due to the constraints of otariid female foraging behaviors to ensure offspring survival, we expected females of both species to reflect conditions of the inshore environment and males to reflect the offshore environmental conditions, as reported in other otariids (Page et al. 2006, Staniland & Robinson 2008). Finally, we hypothesized that males will target eddies since they have more time to explore less permanent oceanographic features.

2. MATERIALS AND METHODS

2.1. Data collection

Satellite transmitting tags were deployed on 17 SAFS (8 females and 9 males) and 18 SASL (4 females and 14 males) during austral spring and summer between 2013 and 2017 in PSJ (15° 22′ S, 75° 12′ W; Fig. 1). Adult females of both species were nursing newborn pups and were therefore estimated to be 4+ yr old. Adult male SAFS were selected from bulls holding tenure at territories, and therefore were an estimated age of 9+ yr old, and their feeding trips reflected post-tenure behavior. SASL males were categorized in the field as sub-adult males, which are reproductively mature individuals, but do not control female harems yet, and were estimated to be 5–8 yr old. Adult females were instrumented during the peak of pupping during their respective breeding season (SAFS: 19–20 November 2015; SASL: 24–25 February 2017). Males were all instrumented in November (SAFS: 15 November 2014, 13–14 November 2016; SASL: 15–19 November 2013, 13–14 November 2014, 13–18 November 2015; for tracking
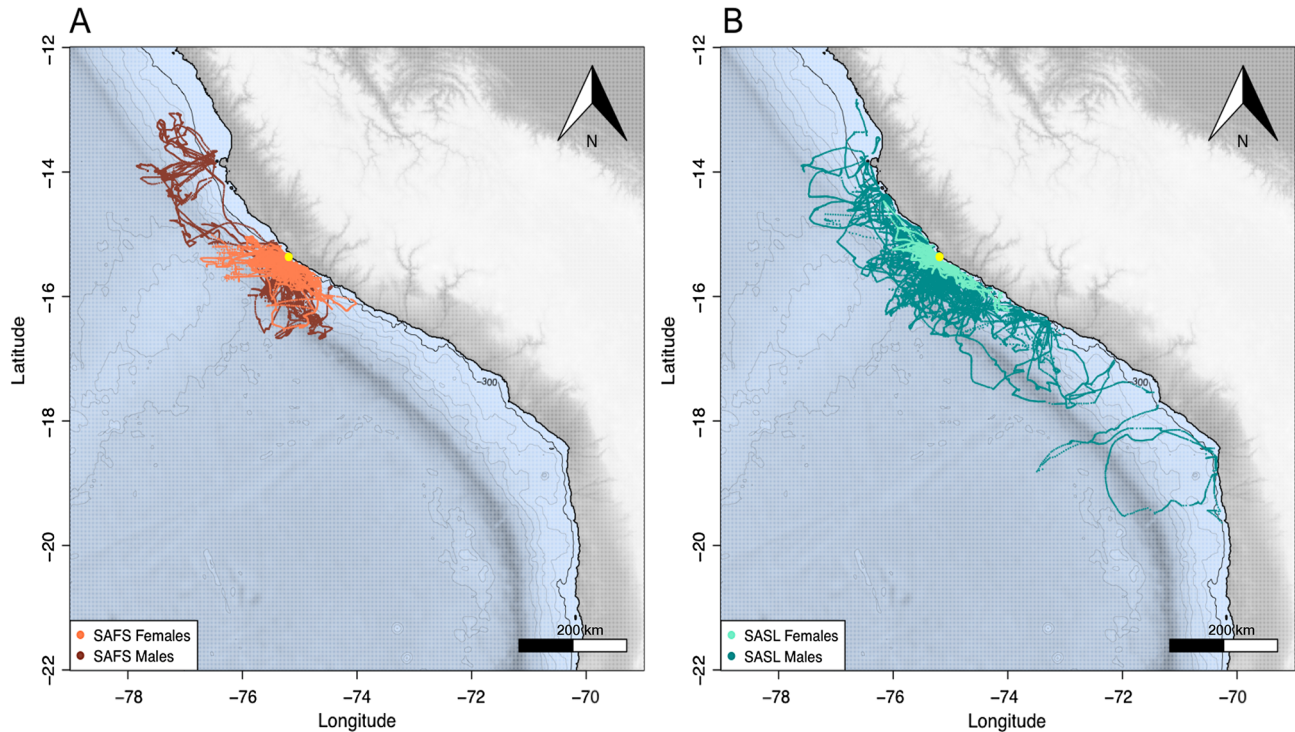
Fig. 1. Tracks for (A) South American fur seals (SAFS) and (B) South American sea lions (SASL) in the study area between 2013 and 2017. Yellow circle indicates the Punta San Juan, Peru breeding colony, the location of otariid instrumentation

durations according to ID see Table A1 in the Appendix).

All animals (except female SAFS) were anesthetized using a combination of midazolam, butorphanol and medetomidine administered via plastic dart (Adkesson et al. 2019a,b). Female SAFS were captured using a hoop net and then anesthetized with isoflurane gas (1–5%) mixed with oxygen (Jankowski et al. 2015). Body mass was obtained using a tripod and field scale to the nearest 100 g (Mini Crane Scale 300 kg, OCS-L). Standard body length was measured to the nearest 0.5 cm. All animals were determined to be in good health by a veterinarian based on physical examination and veterinary assessment of routine blood parameters. Antagonist drugs (flumazenil, naltrexone and atipamezole) were administered, and all animals returned safely back into the colony or immediate surroundings.

Sampling and methodology were approved by the Peruvian government under research permits Resolución Jefatural Nos. 09-2013-, 024-2014-, 008-2015- and 019-2016-SERNANP-RNSIIPG issued by the Peruvian National Service of Natural Protected Areas and the Peruvian Ministry of the Environment. Procedures were approved by the Ethics Committee of Universidad Peruana Cayetano Heredia (Constancia #005-02-18).

During restraint, each individual was instrumented with satellite transmitting tags (Spot 5, Spot 6 and Mk10 from Wildlife Computers) that communicate with the Argos satellite system. Tags were programmed to contact satellites every 4–6 h throughout a 24 h period, taking into account satellite passes available at the time and location of study. Animal locations and associated errors were estimated by calculating the distance between tags and the satellites present during the time of message transmission. Additionally, geographically referenced sightings of tagged individuals were added to the location records of each animal.

2.2. Track construction

A range of possible locations were modeled using a forward particle correlated random walk method following Tremblay et al. (2009). Fifty particles were projected every 30 min based on animal speed and Argos location class quality to inform the model using MATLAB (MATLAB 2018). For each individual, 1 average track and associated error distribution was

computed to describe the most likely track. Land locations were filtered out by using a combination of 5 km circular buffers around known pinniped colonies along the coast of Peru (including islands), a bathymetry gridded map (GEBCO v. 2020) and a limit for a minimum number of 15 h to consider a foraging trip at sea, based on previous findings (Hückstädt et al. 2014, Ganoza 2016) (Fig. 1). Individuals were tracked for 23–78 d. A summary of individual identification, deployment date, body mass, length, number of days and number of trips for each individual is included in Table A1. To determine study groups, we assessed if groups were independent based on body size (2-way ANOVA with Tukey post hoc test, $p < 0.01$).

2.3. Foraging trips and events

Total distance (km) and duration at sea (d) were estimated for each trip. Results are reported as mean ± SD for each species and sex group. We tested for inter- and intraspecific differences between mean distance and duration for each species and sex group (Kruskal-Wallis [K-W], $p < 0.05$). We estimated residence time (RT) as a foraging index to calculate the time spent (in hours) for area-restricted search by individuals in areas of radius 'r' (in km) and maximum time (in hours) during which they actively explored or foraged, following Barraquand & Benhamou (2008). Individuals were presumed to be in 'foraging' mode based on movements that include high tortuosity, slower speeds and repeated entries in/out of an area, whereas low tortuosity and high speeds were presumably associated with transiting or commuting between foraging areas and/or haulouts. Multiple size radii and time thresholds were tested for each individual. RT was tested within 10 different radii from 1 km; and then for every 5 km interval in the range of 5–45 km during a maximum time of 3, 6, 8 and 12 h. An RT series was constructed for each animal and all radii, resulting in 40 possible RT series per individual. The RT series with the highest contrast was selected, and segments were categorized as either high or low RT following the segmentation method of Lavielle (2005), using the 'adehabitatLT' package in R (Calenge 2006).

2.4. Utilization distributions

We used kernel density estimations to calculate the utilization distribution (UD); 50% and 95% UD kernels (grid size = 200) with the R package 'adehabi-tatHR' (Calenge 2006). Proportion of overlap of the home range (95% UD) and core areas (50% UD) were estimated using 'adehabitatHR' and are reported in ranges from 0 (no overlap) to 1 (complete overlap). Bhattacharyya's affinity (BA) was estimated to measure the distance between the distribution of all locations where presumed foraging activity took place. Analysis of similarity (ANOSIM) of BA values was performed based on 999 permutations, to test the similarity between groups for each probable UD (50 and 95%) using the R package 'vegan' v.2.5-7 (Oksanen et al. 2020). ANOSIM values range from −1 to 1, with 0 indicating a random grouping, and were tested for significant differences between groups (ANOSIM statistic, $p < 0.05$).

2.5. Foraging by hour of day

We first explored the density of foraging events by hour of day to assess if there was interspecific segregation between the occurrence of foraging by hour of day for each sex. To determine if hour of day (1 h blocks) had a significant effect on the foraging events for each species and sex group, we constructed a generalized additive mixed model (GAMM) using the R package 'mgcv' (Wood 2011). We used a binomial distribution, with a 1, 0 response variable for foraging and hour of day as the explanatory variable. Since the data were analyzed in 1 h cycles (n = 24), we chose a cyclic penalized cubic regression spline as a smoother. Because changes in time of sunrise (05:20–06:10 h) and sunset (17:50–18:20 h) were less than our sampling interval of 1 h blocks within our study area and period, we did not include day length in our analysis. Animal ID served to assign random effects. A continuous time index for each foraging trip was constructed and assigned to indicate a corAR1 temporal correlation structure.

2.6. Associated environmental conditions

Since species and sex groups were tracked in different sampling seasons, differences in environmental conditions between tracking seasons were compared (ANOVA, with Tukey post hoc test, $p < 0.01$) using SST anomaly (SSTA) records collected by the Dirección de Hidrografía y Navegación at San Juan de Marcona marine station located <5 km from PSJ, where pinnipeds were instrumented.

In this study, due to various logistical constraints, we tracked species and sex groups in different sea-

sons, making it complicated to compare all groups simultaneously. Therefore, we focused on evaluating preferences for marine features in species and sex groups while foraging at sea. To achieve this, we selected environmental variables that describe inshore versus offshore marine environments in relation to distance from the coast, as well as variables that represent the formation of thermal fronts. Environmental variables include: distance to the coast (DC; source: NOAA ETOPO1, 1 arc minute), SST (source: MODIS, 4 km), chl *a* concentration (source: MODIS-Aqua, 4.5 km), proximity to thermal fronts (km) and gradient of thermal fronts (°C km^{-1}) both in a 5 × 5 pixel range (4 km pixel^{-1}). We extracted daily SST and chl *a* for each location during feeding trips from remote sensor databases using the R package 'raster' v.3.4-5 (Hijmans 2020). Thermal fronts were constructed from daily composite SST maps (MODIS, 4.5 km) following Roa-Pascuali et al. (2015). Due to cloud coverage, some dates and locations do not have associated data. We extracted values during high RT locations (presumed foraging events) and compared mean values between species (Wilcoxon test, p < 0.001).

To determine which variables best explained environmental conditions during foraging, we conducted a forward selection process for each species and sex group, constructing a GAMM with binomial distribution (1, 0 response variable) and cubic-spline smoothers to model non-parametric relationships. Animal ID was set as a random effect, and a corAR1 error structure was used to account for temporal correlation. If more than 25% of locations lacked information, the covariate was not included in model selection. We then assessed for collinearity between remaining candidate explanatory variables and did not include covariates that had a Spearman rank correlation >0.8 (p < 0.05). Finally, we only kept locations that had information for all environmental covariates included in the global model. To avoid overfitting, knots were set to 5. Model selection was done through a forward selection process which consisted of evaluating if the addition of a new covariate produced a significant improvement in the model, evaluated with ANOVA tests (chi squared, p < 0.05). Analyses were done with the R statistical program v.3.6.3 (R Core Team 2020).

3. RESULTS

3.1. Body mass

Body mass and length were strongly correlated (Pearson = 0.95, p < 0.05), so we proceeded with group comparisons using body mass only. As expected, species and sex groups significantly differed from each other in terms of body mass (SAFS females: 45.5 ± 7.6 kg [SD]; SASL females: 75.9 ± 9.5 kg; SAFS males: 109.3 ± 9.9 kg; SASL males: 183.3 ± 33.4 kg), allowing us to make comparisons among the 4 groups (2-way ANOVA with Tukey post hoc test, p < 0.01; Fig. 2).

3.2. Trip distance and duration

SAFS traveled longer distances during trips at sea than SASL (Table 1), when comparing both females (K-W = 14.8, n = 149, p < 0.01) and males (K-W = 8.8, n = 276, p < 0.01). Also, intraspecific differences were found for trip distance between male and female SAFS (K-W = 4.1, n =
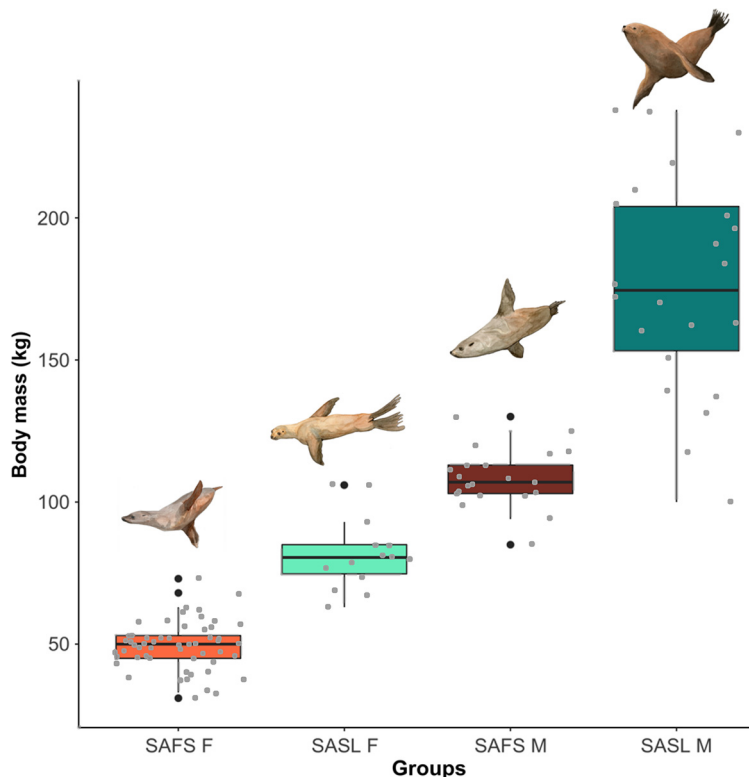

Fig. 2. Body mass (kg) according to species and sex groups (ANOVA, p < 0.01). SAFS: South American fur seal; SASL: South American sea lion; F: females; M: males. Grey dots: body mass of each individual; horizontal black line: median value (50th percentile); box: 25th to 75th percent-ile of dataset; whiskers: 5th and 95th percentiles; black dots: outliers

Table 1. Number of individuals (N ind), number of trips (N trips), trip duration, and trip distance for each species–sex group included in this study. Results are reported as mean ± SD. SAFS: South American fur seal; SASL: South American sea lion

Group	N ind	N trips	Trip duration (d)	Trip distance (km)
SAFS females	8	77	3.65±3.38	221.81±286.06
SASL females	4	72	2.16±2.02	81.76±64.08
SAFS males	9	57	8.32±11.44	298.03±277.97
SASL males	14	219	2.87±2.50	178.52±184.09

134, p < 0.05) and between male and female SASL (K-W = 19.5, n = 291, p < 0.01); males always traveled greater distances. Mean trip duration was longer in SAFS than SASL (Table 1), for both females (K-W = 8.5, n = 149, p < 0.01) and males (K-W = 14.6, n = 276, p < 0.01). Among SAFS, males had longer trip durations (K-W = 4.6, n = 134, p < 0.05), but we found no differences in trip duration between male and female SASL (K-W = 3.6, n = 291, p = 0.0592).

For males, due to tracking during multiple seasons, we were able to compare if there were differences in foraging trip duration and distance between years. We found a significant difference in trip duration in SAFS males between 2014–15 and 2016–17 (K-W = 4.1, n = 114, p < 0.05), but no significant differences in the distance traveled. In SASL males, we found significant differences between all seasons for both duration (K-W = 17.2, n = 219, p < 0.05) and distance (K-W = 70.2, n = 438, p < 0.05). However, post hoc tests were not possible due to small sample sizes per season.

3.3. UDs

Home ranges (95% UD) of females (SAFS: 9166.06 km², SASL: 14 450.21 km²) were smaller than those of males (SAFS: 55 537.99 km²; SASL: 106 615.05 km²). Core areas (50% UD) of females (SAFS: 1074.52 km²; SASL: 1645.23 km²) were also smaller than those of males (SAFS: 7806.89 km²; SASL: 10 894.50 km²). For both sexes, home range and core areas of SAFS were smaller than those of SASL.

Home ranges and core areas of SAFS females overlapped by 0.43–0.50 with those of SASL females, whereas the home ranges and core areas of SASL females overlapped by 0.70–0.83 with those of SAFS females in 95 and 50% UDs, respectively. Home ranges and core areas of SAFS males overlapped by

Table 2. Proportion of overlap for each group for core area (50% utilization distribution, UD) and home range (95% UD). Values represent the proportion of overlap for the group in the rows by the group in the column. Proportion of overlap >0.70 is highlighted in **bold**. SAFS: South American fur seal; SASL: South American sea lion; F: females; M: males

	SAFS F	SAFS M	SASL F	SASL M
50% UD				
SAFS F	–	**1.00**	0.50	**1.00**
SAFS M	0.18	–	0.11	**0.71**
SASL F	**0.83**	**1.00**	–	**1.00**
SASL M	0.11	0.43	0.07	–
95% UD				
SAFS F	–	**0.83**	0.43	**1.00**
SAFS M	0.20	–	0.13	**0.85**
SASL F	**0.70**	**0.82**	–	**1.00**
SASL M	0.12	0.41	0.07	–

0.85–0.71 with those of SASL males, whereas the home ranges and core areas of SASL males overlapped by 0.41–0.43 with those of SAFS males in 95 and 50% UDs, respectively (Table 2). In regards to intraspecific overlap, SAFS females overlapped by 0.83–1 with SAFS males, whereas SASL females completely overlapped with SASL males in 95 and 50% UDs, respectively (Table 2).

No significant differences were detected between the distribution of SAFS and SASL females for both 50 and 95% UDs, confirming that female foraging grounds overlap in space and are considered similar (Fig. 3A). Meanwhile, SAFS and SASL males were significantly different in both 50 and 95% UDs (Fig. 3B). In both species, between males and females, significant differences occurred at 95% UDs, suggesting sexual segregation between home ranges. However, 50% UD core areas were not significantly different between males and females (Fig. 3C,D).

3.4. Foraging by hour of day

Hour of day had a significant effect (p < 0.01) on the probability of foraging events in female SAFS and male SASL. Foraging events for female SAFS concentrated during dark hours (00:00–05:00, 18:00–23:00 h) and for SASL males in daylight hours (06:00–15:00 h), whereas in the other groups, the effect of hour of day was not identified as significant (Table 3, Fig. 4; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m702p153_supp.pdf).
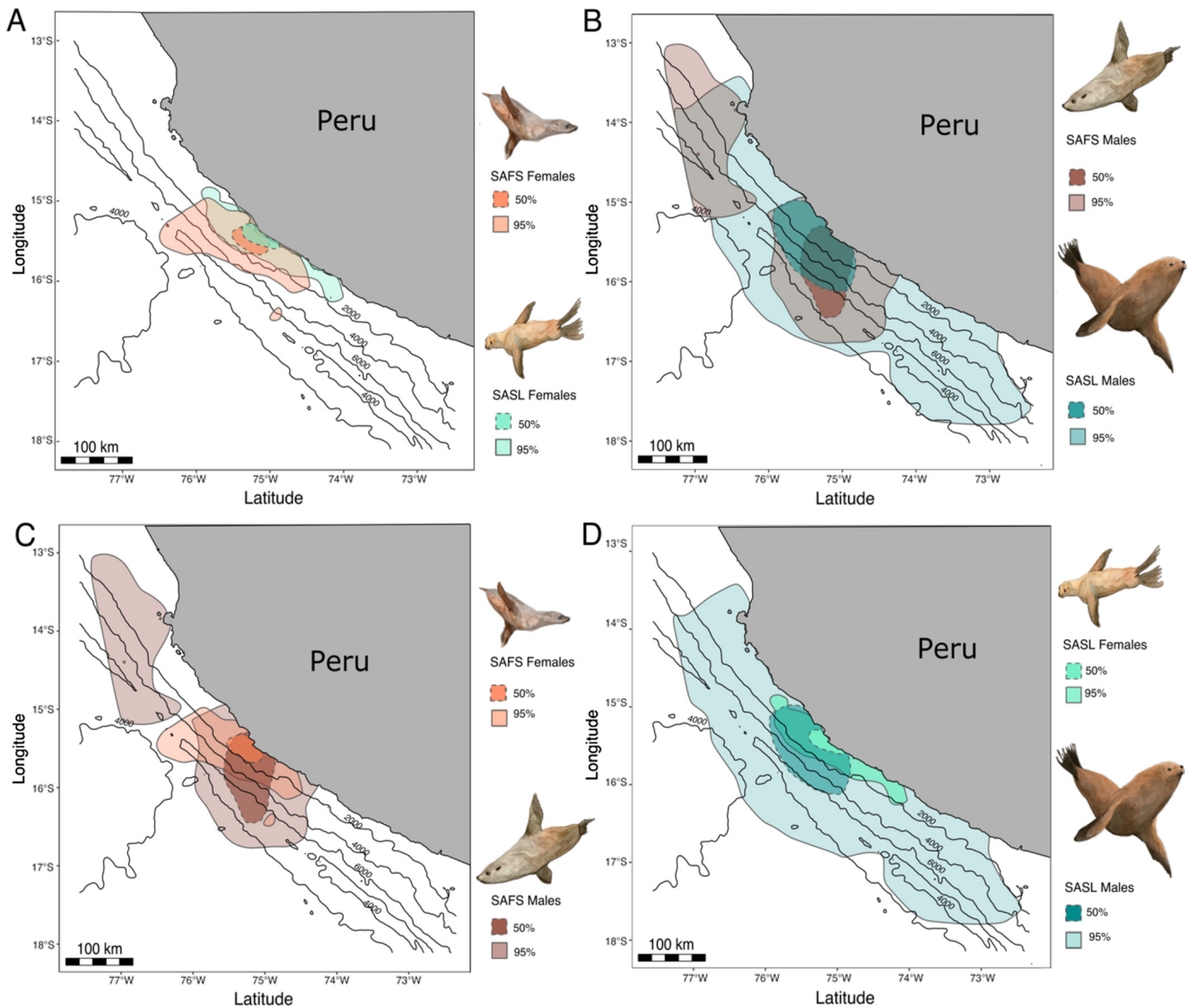
Fig. 3. Filled contours of utilization distributions (UDs) for 50% core foraging ranges (dotted lines) and 95% home ranges (continuous lines) for (A) South American fur seal (SAFS) females and South American sea lion (SASL) females; (B) SAFS males and SASL males; (C) SAFS females and SAFS males; and (D) SASL females and SASL males. Black lines represent coastline and isobaths for depths of 2000, 4000 and 6000 m

Table 3. Results from the generalized additive mixed models to test for effect of Hour in the probability of foraging events for each species–sex group included in this study. N represents the number of observations per group. SAFS: South American fur seal; SASL: South American sea lion

Group	N	Hour	p	Log-likelihood	df	Adj. R^2
SAFS females	24818	6.208	<0.01	−56037.49	3.12	0.0006
SASL females	22650	0.056	0.339	−53855.38	1.16	<0.0001
SAFS males	60927	0	0.908	−148151.6	1	<0.0001
SASL males	91209	5.532	<0.01	−216553.8	3.08	0.0003

3.5. Associated environmental conditions

SSTA served as a proxy to evaluate overall variability in environmental conditions in the study area during the months in which pinnipeds were tracked. SSTA values ranged from −0.70 ± 0.24 (SD) to +1.70 ± 0.23°C (2013−14: −0.70 ± 0.24°C; 2014−15:
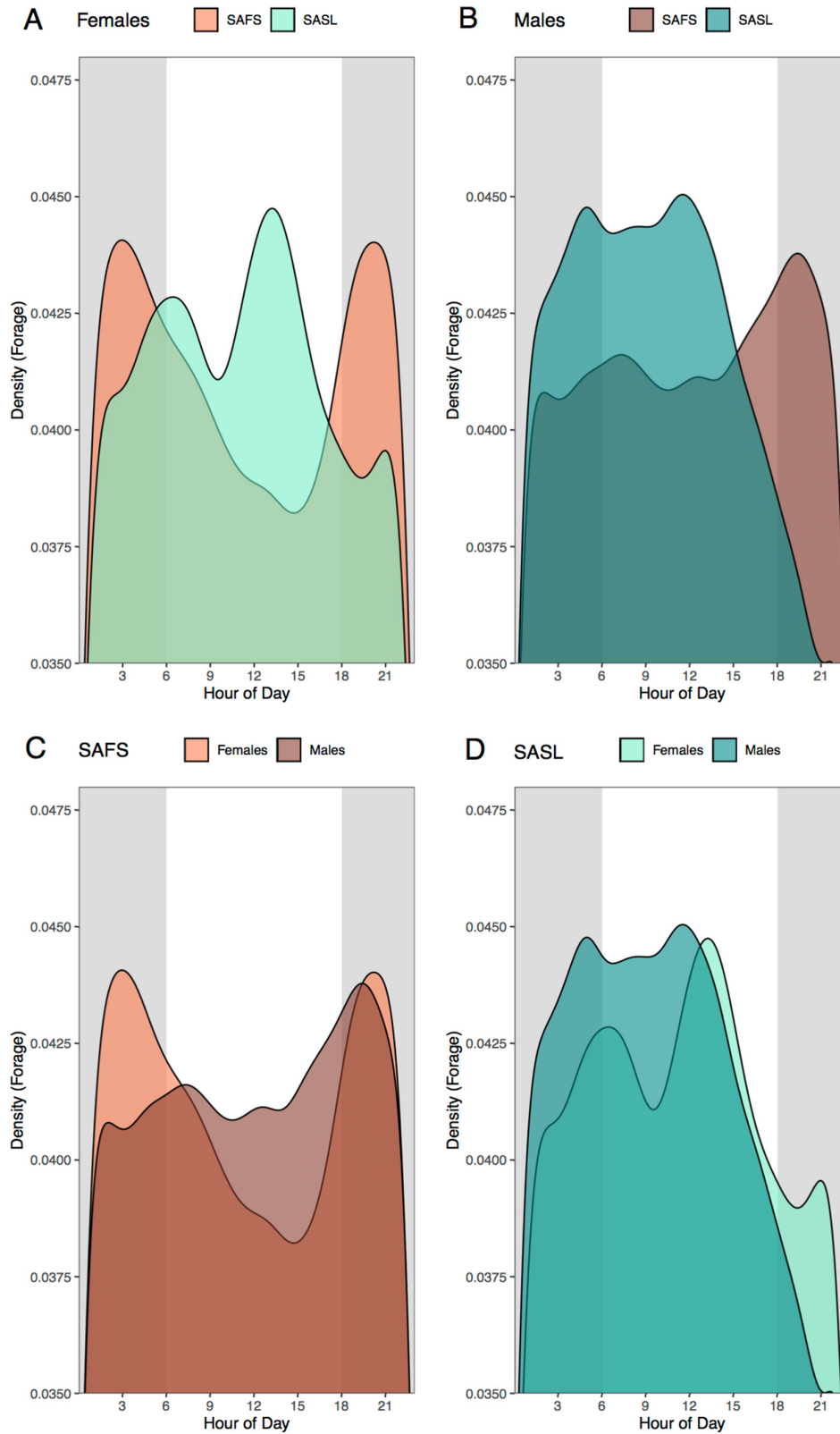
Fig. 4. Density plots of foraging events by hour of day for (A) South American fur seal (SAFS) females and South American sea lion (SASL) females; (B) SAFS males and SASL males; (C) SAFS females and SAFS males; and (D) SASL females and SASL males. Shaded areas indicate dark hours (00:00−05:00 h, 18:00−23:00 h) in the study area

−0.60 ± 0.31°C; 2015−16: +1.70 ± 0.23°C; 2016−17: −0.03 ± 0.53°C; 2017: +0.24 ± 0.83°C). Significant variation among environmental conditions between tracking seasons based on SSTA values were found ($F_{4,14}$ = 18.39, p < 0.01). The 2015−16 season, which took place between November 2015 and February 2016, during which SAFS females were tracked, was the only season that differed significantly from the rest (p < 0.05).

Mean values of environmental variables encountered while foraging were significantly different between species (Wilcoxon test, p < 0.001), except for SST between females (Fig. 5). Descriptive parameters of the environmental variables (minimum, maximum, median, mean and SD) for locations where animals were presumed to be foraging are reported in Table A2.

In the HCS, higher SST, lower chl *a*, increased proximity to thermal fronts and higher front gradient are characteristic of offshore waters, while the opposite describes coastal waters. SAFS females were associated with higher SST, lower chl *a*, increased front proximity and front gradient and higher DC, characterizing an offshore environment.

In contrast, SASL females were associated with lower SST, higher chl *a*, reduced front proximity and front gradient and lower DC. In females, distinct preferences were found for chl *a*, front proximity, front gradient and DC (Fig. 5, Table A2). Among males, differences were not as evident. SAFS and SASL were positively and similarly associated with the majority of variables. However, SAFS males showed a bimodal pattern, with higher values in DC in comparison to SASL males (Fig. 5, Table A2).

In the forward selection process, the only variable discarded was SST for the SAFS female model, due to 39% missing information. All other covariates remained after being checked for collinearity (Spearman rank, rho < 0.55; Fig. S2). Throughout the GAMM forward selection process, in general, adding terms improved model performance (ANOVA, p < 0.01; Table 4). The best-fitting models for SAFS females included chl *a*, front proximity, front gradient and DC. The best-fitting models for SASL females and SASL males included all covariates, and the best model for SAFS males included only SST, chl *a* and front proximity (Table 4).

Table 4. Results from the forward selection process of covariates that characterize the environment during foraging using a generalized additive mixed model. **Bold** indicates the best-fitting model, and N represents the number of observations per group. SAFS: South American fur seal; SASL: South American sea lion. All values in the table were significant at p < 0.01, except for chl *a* in SAFS males group model that included SST, Chl *a*, Proximity to thermal front and Gradient of front (not significant), and (line below that in the table) chl *a* in the group model that included the same plus DC (p < 0.05). Sea surface temperature (SST) was not included in the SAFS females models due to missing values in 39% of foraging locations. DC: distance to coast

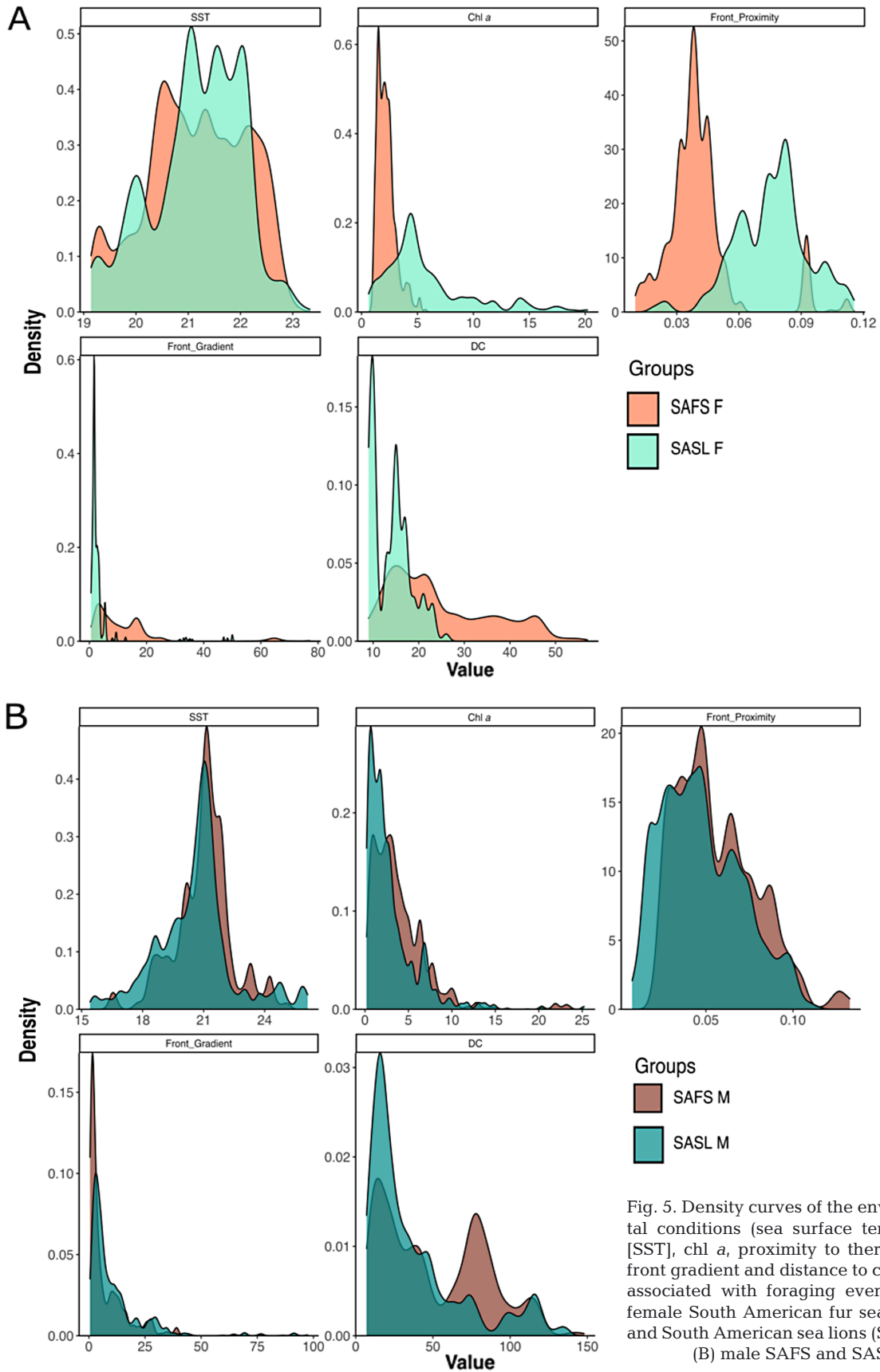| Group	SST	Chl *a*	Proximity to thermal front	Gradient of front	DC	Log-likelihood	df	Adj. R^2
SAFS females	−	432.8				−32203.29	3.99	0.0494
N = 14286	−	427.4	141.8			−32328.98	6.98	0.0629
	−	608.2	138.9	231.6		−33964.49	9.7	0.0932
	−	**580.1**	**174.3**	**282.8**	**608.1**	**−35384.95**	**12.7**	**0.165**
SASL females	217.7					−43395.54	3.98	0.0287
N = 18423	153.4	265.4				−44243.44	6.95	0.0815
	194.2	290.3	253.5			−45400.05	9.93	0.113
	167.5	124.8	72.23	325.30		−46215.19	12.77	0.154
	83.4	**111.3**	**22.6**	**497.9**	**7035.2**	**−56823.42**	**15.43**	**0.279**
SAFS males	221.0					−126784.5	3.96	0.0292
N = 51849	220.1	1.3				−126812.9	4.85	0.0291
	310.5	**2.5**	**1269.6**			**−133128.4**	**8.06**	**0.124**
	224.3	0.0	1051.0	298.9		−131095.6	9.96	0.104
	249.5	0.9	710.5	300.1	62.7	−133079.6	13.59	0.103
SASL males	71.35					−159739.4	3.58	−0.005
N = 65040	31.5	261.9				−161470.9	6.56	−0.001
	17.2	237.3	63.7			−161359.8	9.35	0.006
	26.8	219.7	63.2	150.7		−164919.2	12.17	0.009
	67.8	**161.8**	**245.4**	**597.0**	**2111.3**	**−168627.1**	**15.8**	**0.032**

Fig. 5. Density curves of the environmental conditions (sea surface temperature [SST], chl *a*, proximity to thermal front, front gradient and distance to coast [DC]) associated with foraging events by (A) female South American fur seals (SAFS) and South American sea lions (SASL) and (B) male SAFS and SASL

4. DISCUSSION

The results of our study reveal that sympatric otariids in the Humboldt Current System employ a suite of strategies to segregate while foraging in their environment according to species and sex groups. We found that for both species, sexual dimorphism and energetic constraints associated with reproductive roles are important drivers for segregation in space and time, showing differences in how males and females partition habitat use. As expected, female trip duration and distance were shorter, and females had smaller core and home range areas compared to males. When we compared between species according to sex, segregation was clearer between females than males. Female SAFS traveled longer distances and durations towards offshore habitats, while female SASL foraged in cooler coastal inshore habitats. In contrast, males had more complex foraging strategies that were more difficult to tease apart. Interestingly, we identified temporal patterns by hour of day in SAFS females and SASL males, evidencing partitioning mechanisms that are not necessarily linked to a specific sex or species, but may be a response to environmental cues (i.e. prey availability) that require further exploration.

4.1. Foraging trips and UDs

Although they are smaller in size, both female and male SAFS made trips of longer distance and duration in comparison to SASL females and males. This agrees with similar studies in other locations, where fur seals foraged farther offshore in comparison to sea lions (Franco-Trecu et al. 2012, Waite et al. 2012, Riverón et al. 2021). In terms of area, female and male SASL cover larger home ranges and core areas compared to SAFS. This reveals different use of the foraging grounds at an interspecific level. SASL have larger home ranges as a group, covering larger areas parallel to the coastline that envelop the SAFS home range. In contrast, SAFS travel farther offshore during feeding trips, and males to specific foraging grounds. The varying lengths in distance and duration of foraging trips across reduced areas can be indicative of specialized foraging grounds, suggesting potential foraging site fidelity (Staniland & Robinson 2008, Baylis et al. 2018).

As hypothesized, females of both species did show more constrained foraging trips in terms of distance traveled, home ranges and core areas compared to males, which agrees with findings that compared male and female otariids in other study locations (Page et al. 2006, Staniland & Robinson 2008). Interestingly, neither sex of SASL showed a substantial difference in the duration of their foraging trips when compared (marginal p-value), despite marked dimorphism. We acknowledge that the inclusion of subadult male SASL, in contrast to territorial bull SAFS males, represents a limitation in this study. Post-tenure foraging trips in reproductive bull otariids that lack parental duties can be expected to be longer or farther in distance to recover from periods of fasting onshore (Majluf 1987, Staniland & Robinson 2008). This contrasts with subadult males, which are expected to have lower energetic demands, which can partly explain shorter trips. Our finding agrees with male SASL reported to behave like central place foragers in the Falkland Islands, making short trips along the shelf, and returning to land to rest (Baylis et al. 2016). Also, among SASL males, body mass had the widest range since this age class included sub-adult males that were still growing at different rates with high interindividual variability, in contrast to the other study groups that were more homogeneous in mass and size. We therefore expected more variability in the foraging strategies between individuals within this group. This can also explain the differences found between distance and duration of foraging trips in SASL males across years in our study. We therefore recommend that foraging behaviors of SASL be further explored, coupling tracking with depth sensors to better understand their foraging strategies.

In terms of spatial segregation, female home ranges or core areas were not significantly different. This high overlap can be explained by the distribution of main prey items that are most readily available in the HCS. Peruvian anchovy and red squat lobster are the 2 main prey reported to be consumed by SASL and SAFS in HCS (Sielfeld et al. 2018, Sarmiento-Devia et al. 2020, Cárdenas-Alayza et al. 2022). Red squat lobsters are associated with cold coastal waters, and they are found within the first 30 km from the coast (Yuffra et al. 2018), explaining shorter trips within the coastal habitat covered by SASL. Red squat lobsters and anchovies have a high degree of spatial overlap in areas 50 km from the coastline. However, Peruvian anchovies, the preferred prey item of SAFS and second-most preferred by SASL, tend to expand further offshore (Gutiérrez et al. 2008). Anchovies aggregate densely in patches, which makes them profitable foraging grounds preferred by SAFS as already reported in other regions (Naya et al. 2002, Franco-Trecu et al. 2013, Baylis et al. 2014).

In this study, female fur seals and sea lions were not tracked in the same calendar months/seasons because we targeted females nursing recently newborn pups, and tracked these subsequent to pupping (SAFS breed during October–December and SASL breed during January–March). Thus, SAFS females were tracked from November to January and SASL females from February to March. This 2 mo difference in breeding seasons contributes yet another mechanism for segregation known as allochrony to partition resources during energetically critical times, which has been postulated as one of the founding drivers behind speciation (Taylor & Friesen 2017). However, during our study, an extraordinary El Niño developed during the 2015−16 season, generating differences in environmental conditions that were significantly different from other seasons, which can also contribute to some of the patterns in foraging ecology of SAFS females. Thus we recommend continuing tracking efforts to better understand the foraging behaviors of SAFS females and their response to environmental cues in the dynamic HCS.

In the spatial realm, home ranges and core areas between males were significantly different, suggesting different spatial use. Among SAFS males, the clustered number of foraging locations and the bimodal distribution of DC (Fig. 5) suggest a repetitive exploration of specific foraging grounds. In contrast, SASL males made shorter and faster trips within a wider and enveloping range parallel to the coast. Finally, when comparing sexes among SASL and SAFS, the ANOSIM suggested that core areas (50 % UD) proximate to the PSJ colony were similar, while home ranges (95 % UD) were significantly different. This result supports the hypothesis that both males and females actively utilize the marine area off PSJ and may also suggest that intraspecific competition (in core areas) can enhance coexistence by decreasing interspecific competition pressures, as postulated by the Lotka-Volterra model (Schoener 1974).

4.2. Foraging by hour of day

In this study, we found that the probability of foraging events increased in the night hours for SAFS females and in the first hours of the daytime for SASL males, partly validating our hypothesis of nocturnal foraging patterns in SAFS and daylight foraging in SASL. Nocturnal foraging by SAFS females may be a synergistic effect between the energetic constraints of provisioning their young and the vertical diel

migration of prey items such as Peruvian anchovies, squids and myctophids, making them more available at night (Ayón et al. 2008). Since we did not find a significant effect of hour of day in male SAFS, we reject our hypothesis that this pattern holds for all SAFS, reflecting different strategies between sexes in this species.

SASL males have a preference for foraging by hour of day, targeting the last hours of darkness and the first hours of dawn. Preferred foraging in the dawn hours by SASL males may be a strategy to reduce competition with other otariid age classes and/or predator species or a preference for a specific prey (Chilvers & Wilkinson 2009). In the HCS, anchovy schools and red squat lobsters have diel migration patterns within the first 20 m of the water column during nighttime, forming a profitable foraging ground (Gutierrez et al. 2005). Recent studies have found that the same age class in Galapagos sea lions *Zalophus wollebaeki* have different foraging modes (pelagic, benthic and nocturnal divers, Schwarz et al. 2021). Thus, it is possible that there are more categories or groups with their own distinct strategies in SASL as well. It is also possible that individuals can switch between strategies according to prey availability. Thus, we recommend further research on specialized foraging modes beyond species and sex groups in the HCS.

4.3. Associated environmental conditions

We acknowledge that a limitation in this study is the lack of overlap while tracking all groups under similar environmental conditions. The coastal El Niño Index, which is calculated as the 3 mo moving average SST in the El Niño 1+2 region (Takahashi et al. 2011) during the months when SAFS and SASL were tracked, shows conditions during the study period based on SSTAs that varied in range of −0.39 ± 0.16 to 1.88 ± 0.27°C (2013−14: −0.39 ± 016°C; 2014−15: +0.17 ± 0.34°C; 2015−16: +1.88 ± 0.27°C; 2016−17: +0.75 ± 0.49°C; 2017: +1.28 ± 0.18°C). These records mostly agree with the trend found for the local SSTA in the PSJ bay area (see Section 3.5). The tracking season with the warmest SSTA was 2015−16, when an extraordinary El Niño was reported (L'Heureux et al. 2017). However, in 2017, a coastal El Niño developed that had warming effects in northern Peru, but not in southern Peru where PSJ is located, explaining the differences in the SSTA values between regions and indices (Paulino Rojas et al. 2019).

Regardless, environmental variables associated with discrete foraging events show clear interspecific differences for females. When compared, environmental conditions targeted during SASL female foraging reflect the coastal habitat, characterized by lower DC, higher chl *a*, reduced proximity to thermal fronts and lower front gradient values, whereas SAFS females are associated with the offshore environment, characterized by higher DC, lower chl *a*, greater front proximity and higher front gradient values. It is important to note that SST measured at female locations had a wide range and was not significantly different between species. Thus, SST is not recommended as an explanatory environmental variable to compare these groups. Evidence from an analysis of hard parts in stomach contents indicated that SAFS in PSJ consume Peruvian anchovy and squids (Cárdenas-Alayza et al. 2022) that tend to be more available in offshore waters (Argüelles et al. 2012). In contrast, the more coastal red squat lobster (Gutiérrez et al. 2008, Yuffra et al. 2018) is the primary prey item of SASL (Sielfeld et al. 2018, Sarmiento-Devia et al. 2020, Cárdenas-Alayza et al. 2022), supporting environmental variables associated with female foraging patterns.

Among males, ranges in the environmental variables targeted by SAFS and SASL males highly overlapped. The best-fitting models for SAFS males included SST, chl *a* and proximity to thermal fronts, whereas models for SASL males included all environmental covariates. Because of their wider distribution, SASL males target areas of lower SST, lower chl *a*, lower front proximity and lower DC, which could be a result of individual or sub-group strategies within the group. Results should be interpreted with caution, and further studies exploring individual strategies should be conducted. We acknowledge that this study may have associated errors in the identification of foraging events based on locations and oceanographic information from bathymetric and remote sensing information alone. Thus, we recommend that future studies involve tags with depth recorders and coupled sensors to refine the validation of foraging events according to *in situ* oceanographic conditions.

Sympatric otariids in the HCS show a series of segregation mechanisms while foraging at sea, associated with reproductive roles and species. Whether these segregation mechanisms have changed or not in recent years is unknown. Answering this question is key to understanding the current state of decline reported for both SAFS and SASL populations in PSJ, which suggests a limitation in resources (Cárdenas-Alayza et al. 2021). The Peruvian HCS contains one

of the largest monospecific fisheries in the world based on Peruvian anchovy, along with large artisanal fishing fleets that target cephalopods and other small pelagic fish species (Fréon et al. 2008, De la Puente et al. 2020). Therefore, it is possible that other sources of competition may exist.

Segregation mechanisms only make sense if prey are partly limited and spatially partitioned. In the case of very high availability of prey, coexistence could occur without much need for segregation. However, in the case of food shortage, segregation mechanisms could sustain coexistence, by taking advantage of differential abilities to cope with such a situation. In the latter case, the differences observed in the foraging ecologies may depict a situation of one species outcompeting another, which could not be considered as a coexistence mechanism. If the segregation we observed is stable over time and if both populations continue to coexist, it might indeed be induced by their ability to segregate. This raises the question of the dynamics of segregation mechanisms with respect to food availability, and calls for maintenance of long-term monitoring and research programs to compare theses indices over time.

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Appendix. Metadata and summary information on individuals; and descriptive statistics on environmental covariates

Table A1. Species, sex, individual identification number (ID), deployment date, mass, length, number of days tracked and number of trips recorded for each individual. SAFS: South American fur seal; SASL: South American sea lion. Dates are d/mo/yr

No.	Species	Sex	ID	Deployment date	Mass (kg)	Length (cm)	Days	Trips
1	SAFS	F	A00_157689	19/11/2015	38.00	114.0	57.69	16
2	SAFS	F	A02_157694	19/11/2015	47.80	124.0	23.19	6
3	SAFS	F	A03_157695	19/11/2015	52.20	125.0	53.83	9
4	SAFS	F	A04_157696	19/11/2015	56.00	131.0	75.38	11
5	SAFS	F	A05_157697	19/11/2015	40.10	115.0	45.38	9
6	SAFS	F	A06_157698	20/11/2015	47.60	121.0	49.40	15
7	SAFS	F	A07right_8	20/11/2015	33.70	111.0	34.50	8
8	SAFS	F	44Y_157700	20/11/2015	48.80	127.0	26.44	4
9	SASL	F	F01_157689	24/02/2017	74.50	146.0	72.77	23
10	SASL	F	F02_157697	25/02/2017	63.30	135.0	78.02	29
11	SASL	F	F04_157699	25/02/2017	85.00	143.0	76.31	23
12	SASL	F	F05_157700	25/02/2017	86.00	148.5	48.85	19
13	SAFS	M	36Y_143666	15/11/2014	118.80	158.0	56.19	5
14	SAFS	M	39Y_143667	15/11/2014	117.30	151.0	43.68	12
15	SAFS	M	41Y_143663	15/11/2014	107.20	150.0	66.19	10
16	SAFS	M	C55_143664	13/11/2016	113.30	148.0	60.15	3
17	SAFS	M	C56_143665	13/11/2016	99.20	151.0	70.38	9
18	SAFS	M	C57_157694	13/11/2016	106.60	147.0	50.40	3
19	SAFS	M	C58_157695	14/11/2016	103.40	159.5	46.88	9
20	SAFS	M	C59_157697	14/11/2016	102.40	158.0	40.87	3
21	SAFS	M	C60_157699	14/11/2016	94.10	153.5	70.87	4
22	SASL	M	03V_134432	15/11/2013	151.40	174.5	73.75	22
23	SASL	M	04V_134430	15/11/2013	237.20	205.0	70.79	14
24	SASL	M	05V_134433	15/11/2013	219.40	198.0	72.29	18
25	SASL	M	06V_134429	16/11/2013	238.60	203.0	73.75	16
26	SASL	M	12V_134431	19/11/2013	184.10	183.0	67.40	14
27	SASL	M	13V_141850	13/11/2014	196.60	196.5	36.75	11
28	SASL	M	15V_141852	13/11/2014	201.60	200.0	70.58	7
29	SASL	M	17V_141853	14/11/2014	162.40	190.0	73.71	14
30	SASL	M	19V_157686	17/11/2015	160.60	196.0	61.90	12
31	SASL	M	20V_157685	17/11/2015	139.30	189.0	60.88	14
32	SASL	M	22V_157688	17/11/2015	191.90	191.0	67.42	25
33	SASL	M	23V_157693	17/11/2015	131.60	170.5	71.96	21
34	SASL	M	25V_157690	18/11/2015	137.80	185.0	72.92	13
35	SASL	M	27V_157692	18/11/2015	172.00	191.1	69.50	20

Table A2. Descriptive statistics for the environmental covariates extracted for foraging event locations for each species and sex group. SAFS: South American fur seal; SASL: South American sea lion; SST: sea surface temperature

Group	Environmental covariate	SST (°C)	Chl a (mg m^{-3})	Proximity to thermal front (km)	Gradient of front (°C km^{-1})	Distance to coast (km)
SAFS females	N obs	4408	6294	5852	5862	6348
	Min	19.28	0.71	0.01	1.28	4.00
	Max	23.03	5.92	0.11	93.50	57.00
	Median	21.29	2.15	0.04	9.88	19.00
	Mean	21.16	2.27	0.04	14.29	22.47
	SD	0.92	0.84	0.01	16.30	11.09
SASL females	N obs	4269	4392	4356	4356	4170
	Min	19.07	0.63	0.01	0.57	9.00
	Max	23.33	20.20	0.11	50.00	26.00
	Median	21.26	4.58	0.07	1.94	15.00
	Mean	21.12	5.85	0.07	3.69	13.93
	SD	0.84	3.88	0.01	7.00	4.16
SAFS males	N obs	12264	12474	13197	13197	12996
	Min	16.11	0.22	0.01	0.48	7.00
	Max	25.22	23.47	0.13	39.13	148.00
	Median	21.08	3.26	0.05	3.55	42.00
	Mean	20.97	3.95	0.05	7.48	51.20
	SD	1.39	3.38	0.02	8.30	34.27
SASL males	N obs	14223	17367	18036	18075	18345
	Min	15.41	0.18	0.00	0.64	4.00
	Max	26.11	25.23	0.11	98.57	147.00
	Median	20.71	2.05	0.03	8.92	23.00
	Mean	20.48	3.05	0.04	13.88	40.46
	SD	1.89	3.10	0.02	14.69	36.11