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A stable foraging polymorphism buffers Galápagos sea lions against environmental change

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SUMMARY

Understanding the ability of animals to cope with a changing environment is critical in a world affected by anthropogenic disturbance.[1] Individual foraging strategies may influence the coping ability of entire populations, as these strategies can be adapted to contrasting conditions, allowing populations with foraging polymorphisms to be more resilient toward environmental change.[2,3] However, environmentally dependent fitness consequences of individual foraging strategies and their effects on population dynamics have not been conclusively documented.[4,5] Here, we use biologging data from endangered Galápagos sea lion females (*Zalophus wollebaeki*) to show that benthically foraging individuals dig after sand-dwelling prey species while pelagic foragers hunt in more open waters. These specialized foraging behaviors result in distinct and temporally stable patterns of vibrissae abrasion. Using vibrissae length as a visual marker for the benthic versus pelagic foraging strategies, we furthermore uncovered an environment-dependent fitness trade-off between benthic and pelagic foragers, suggesting that the foraging polymorphism could help to buffer the population against the negative effects of climate change. However, demographic projections suggest that this buffering effect is unlikely to be sufficient to reverse the ongoing population decline of the past four decades.[6] Our study shows how crucial a deeper understanding of behavioral polymorphisms can be for predicting how populations cope within a rapidly changing world.

RESULTS

We investigated the fitness consequences of individual foraging strategies and the population-level responses to environmental changes in an intensively studied island population of the endangered Galápagos sea lions. In this population, a recent study uncovered evidence for three discrete foraging strategies corresponding to benthic, nocturnal-pelagic, and diurnal-pelagic foragers that differ significantly in the way that individuals used both space (horizontal and vertical) and time (Figures 1A and 1B).[3] Here, we used detailed data from 34 adult female individuals fitted with biologgers to characterize this foraging polymorphism in detail, allowing us to describe a distinct and temporally stable phenotypic marker for the foraging polymorphism. We then used this marker to investigate a long-term dataset of 77 females breeding over 15 years to uncover links between foraging behavior and individual fitness components including pupping success and offspring survival across a range of sea surface temperature (SST) conditions. Finally, we used strategy-dependent survival and reproductive rate estimates to parameterize demographic models aimed at predicting changes in the population growth rate for different foraging strategies across a range of projected environmental scenarios.

Characterizing foraging strategies

In order to characterize these strategies in greater detail, we looked for ways to describe and analyze the behavior of the females during foraging. Using acceleration data from 34 females equipped with biologgers, we calculated the horizontal body orientation (pitch) during putative foraging episodes within dives (see STAR Methods for details). The pitch proved to be an insightful measure of foraging behavior, as the direction of the head in a three-dimensional environment is highly informative about hunting preferences. Benthic foragers exhibited significantly greater average pitches during foraging episodes (Figure 2A; benthic/diurnal, est. 0.13, $p = 0.003$; benthic/nocturnal, est. 0.21, $p < 0.001$; $n = 47{,}396$ dives of 34 individuals), indicating that their bodies were more often oriented toward the sea floor (see also Table S1). Frequent negative spikes in pitch (Figure 2B) furthermore suggested that benthic foragers dive headfirst into

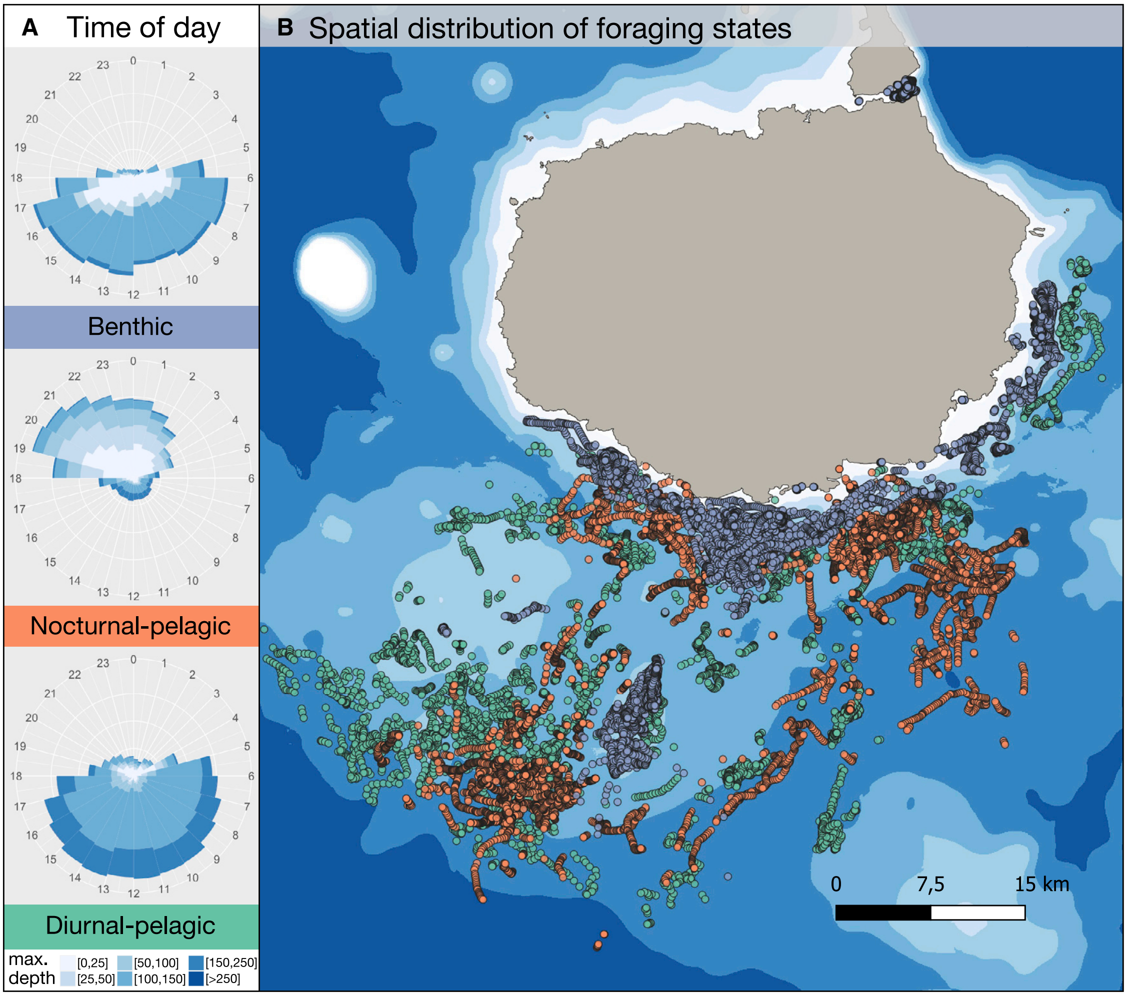

Figure 1. Spatial and temporal variation among three foraging strategies in Galápagos sea lions

Time depth recorder and GPS loggers were deployed on 34 animals to reveal three distinct foraging strategies: benthic (blue), nocturnal-pelagic (orange), and diurnal-pelagic (green).

(A) Temporal and vertical distribution of dives.

(B) Spatial distribution of foraging dives. Redrawn from Schwarz et al.[3]

the benthos, where they can prey on benthic species such as cusk-eels (*Chilara taylori* and *Otophidium indefatigable*[7]), which spend the day buried in sandy substrates.[8] By contrast, pelagic foragers showed as many negative as positive spikes in pitch, reflecting the expected pattern of individuals hunting fish in open water (Figure 2B).

As the vibrissae of otariids grow continuously at a constant rate (0.08–0.16 mm day^{-1})[9,10] and are not shed by adults,[11] we hypothesized that the distinct foraging behavior of benthic females would result in greater levels of vibrissae abrasion. We therefore quantified the relative vibrissae length (quotient of the distance from the snout to the tip of longest vibrissa and the distance from the snout to the eye) from photographs (Figure 2C; see STAR Methods for details). We found a strong association between vibrissae length and foraging strategy, with benthic foragers having significantly shorter vibrissae than females that foraged pelagically (Figure 2D; $F_{3,23} = 8.388$, $p < 0.001$, $n = 27$; see also Table S2). Furthermore, repeated measurements derived from multiple photographs of the same individuals taken both within seasons and 18 months after the first photograph revealed high levels of within-individual consistency and temporal stability of vibrissae length (within-season repeatability, Pearson's $r = 0.96$; between season repeatability, Pearson's $r = 0.94$). Consequently, the measurements of vibrissae length provide a reliable and temporally stable proxy for the female foraging strategy, allowing us to scale up to a larger dataset of photographed females ($n = 77$) for which detailed life-history data are available.

Fitness consequences of foraging strategies

To investigate the adaptive significance of the foraging polymorphism across a range of SST values, we classified all 77 adult females into short- versus long-vibrissae individuals based on their relative vibrissae length (defined from here on as benthic and pelagic foragers, respectively; STAR Methods). Using 15 years of individual-based life-history data, we compared pupping rates

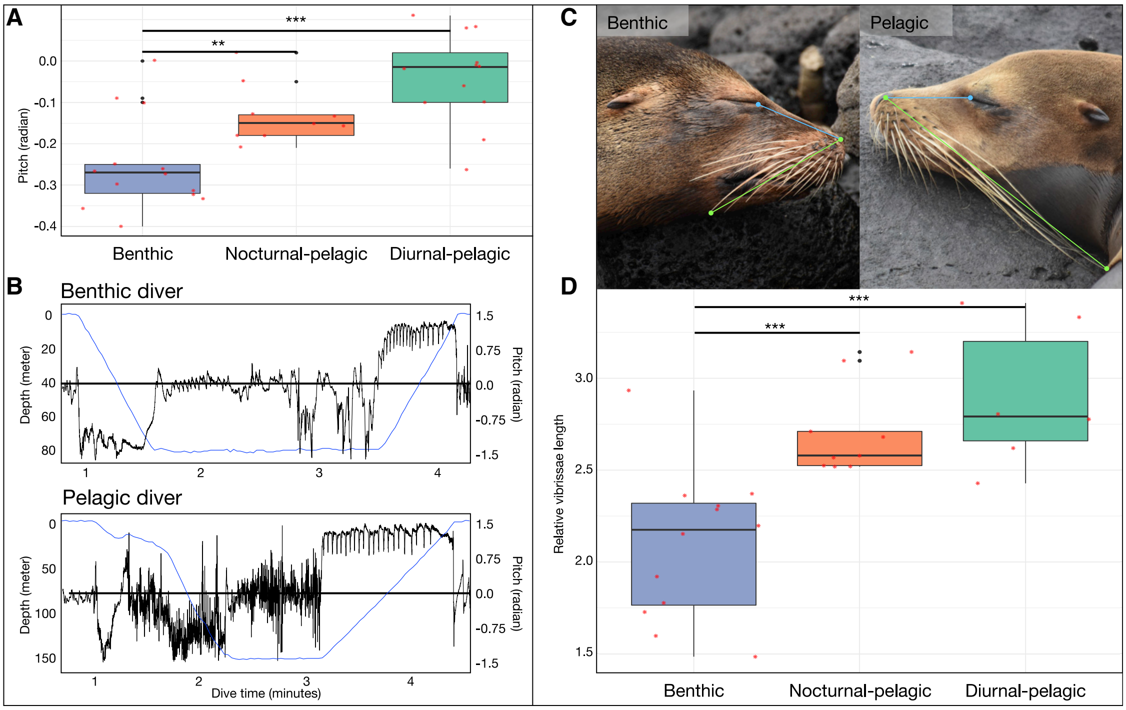

Figure 2. Detailed characterization of foraging strategies

(A) The pitch (in radians) during foraging episodes of the three foraging groups (SD, upper/lower quartile, median, and individual data points are shown as red asterisks; n = 34; see also Table S1).

(B) The pitch (black) during a dive (blue) of a benthic (upper panel) and a pelagic diver (lower panel).

(C) Example photographs of animals with short (left) and long (right) vibrissae, together with the distances measured to estimate relative vibrissae length (distance snout to tip of longest vibrissa [green]/distance snout to eye [blue]).

(D) The greatly reduced relative vibrissae length of benthic foragers relative to pelagic foragers (SD, upper/lower quartile, median, and individual data points are shown as red asterisks; n = 27; ***$p < 0.001$; see also Table S2).

(590 observations with 168 pups born to 77 females), offspring body condition (using the scaled mass index;[12] 159 pups born to 71 females), and offspring survival (160 pups born to 71 females) of benthic and pelagic foragers across a range of annual mean SST values from 22.2°C to 25.4°C with a median of 23.3°C (2003–2018; meteorological station, Charles Darwin Research Station, Puerto Ayora, Santa Cruz Island). We identified significant interactions between the foraging strategy and SST for both pupping probability ($p = 0.027$) and pup body condition ($p = 0.049$). Specifically, pupping probability and offspring body condition both declined with increasing SST in pelagic foragers but remained stable in benthic foragers (Figures 3A and 3B). First-year pup survival showed a similar pattern (Figure 3C), although the interaction was not statistically significant ($p = 0.23$; see also Table S3).

Demographic modeling

Based on parameter estimates from these models, we estimated the pupping (R) and first-year offspring survival (Φ_P) rates of benthic and pelagic foragers with respect to SST. We used these estimates together with population vital rate data from juveniles and adults (Φ_J and Φ_A) obtained over the last 16 years to estimate the median population growth rate (λ) of benthic and pelagic foragers over a range of SST values (22°C–25°C), based on a fully age-structured matrix model[13] (Figure 3D). We found that λ decreased strongly for pelagic foragers with increasing SST (median $\lambda = 0.95$ at 22°C versus 0.87 at 25°C) but did not vary appreciably with respect to SST in the benthic foragers (median $\lambda = 0.92$ at 22°C versus 0.94 at 25°C). Furthermore, median λ failed to reach equilibrium ($\lambda = 1.0$) under any of the SST scenarios, with median estimates predicting declines of between 5% and 15% per annum (Figure 3E).

DISCUSSION

We have shown that distinct foraging strategies of female Galápagos sea lions result in readily distinguishable patterns of vibrissae abrasion, allowing the reliable visual identification of pelagic and benthic foragers as well as confirming the stability of these strategies over time spans of at least 18 months. Temporal stability of individual foraging strategies over extended timescales has also been demonstrated in other pinniped species[14,15] and has been predicted to have far-reaching consequences for a population's ecological and evolutionary dynamics via foraging-specific life-history traits.[2]

We have furthermore demonstrated that these foraging strategies have SST-dependent fitness consequences, supporting the idea of a trade-off between different fitness components in benthic and pelagic foragers. Across most marine ecosystems including the Galápagos Islands, SST is a key indicator of

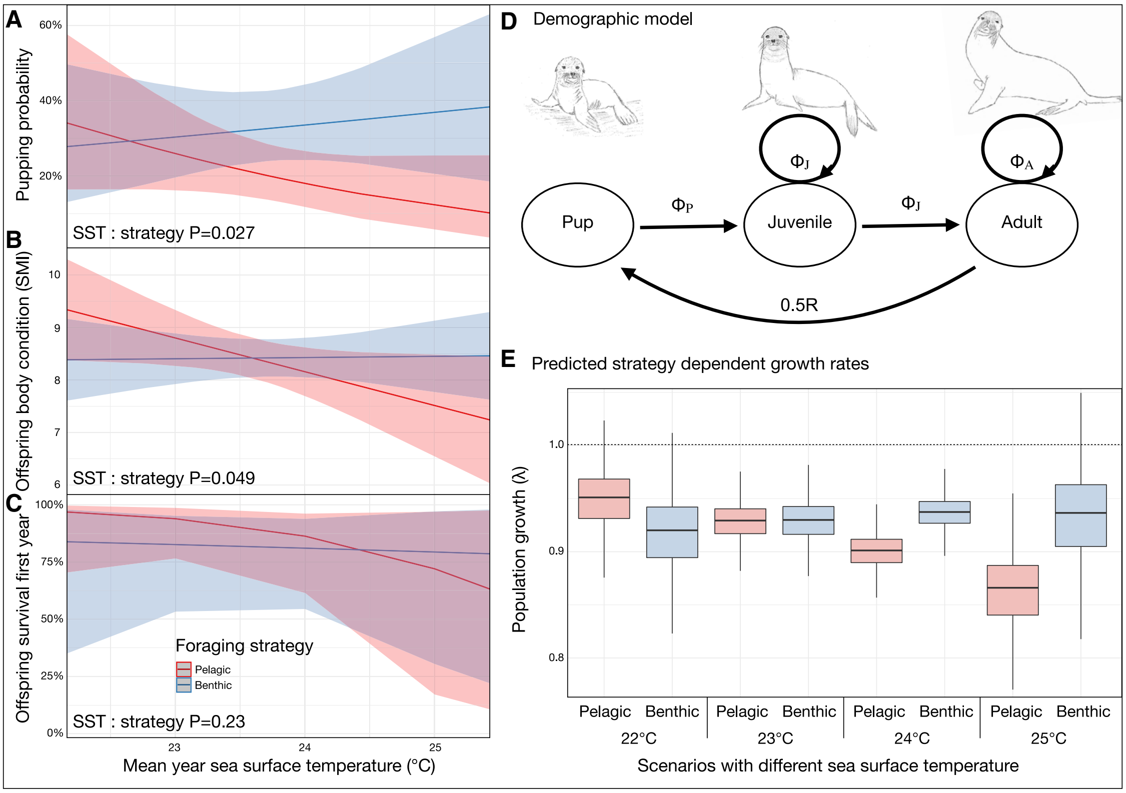

Figure 3. Consequences of pelagic and benthic foraging strategies for individual fitness parameters and population growth

(A) Pupping probability (over 15 years, n = 77 females, 590 observations, and 168 pups).

(B and C) Offspring body condition (over 14 years, n = 71 females and 159 pups) (B) and offspring first-year survival (over 14 years, n = 71 females and 160 pups) (C) mean with SD of benthic and pelagic foragers as a function of sea surface temperature (SST) (see also Table S3).

(D) Visual representation of the demographic model (survival rate, Φ and pupping rate, R).

(E) Predicted population growth rates (λ) for both strategies under different SST conditions (SD, upper/lower quartiles, median).

oceanic productivity as it reflects the intensity of influx of cold, nutrient-rich waters,[16,17] which in turn affects the distribution and abundance of prey species.[18] Pelagic prey fish species are especially affected by increasing SST[19] compared with benthic prey,[20] explaining the negative effect of rising SST on the reproductive success of pelagic foragers. Benthic foragers, in contrast, appear to have a more energetically expensive strategy[21–23] as well as preying on fish species that tend to have a lower lipid content (energy density) than pelagic species.[24,25] Hence, benthically foraging Galápagos sea lions appear to follow an energetically less profitable but more reliable foraging strategy, whereas pelagically foraging sea lions profit energetically under stable conditions but are strongly negatively affected by increasing SST.

This trade-off appears to have important repercussions for predicting future population trends for this endangered predator, which has been steadily declining both at our study site[6] and across the entire archipelago over the last 40 years.[26] The Galápagos Islands are strongly impacted by climate change through long-term increases in sea surface temperature (SST) and increasingly frequent occurrences of extreme weather events such as the El Niño Southern Oscillation.[27,28] As benthic foragers appear to be less sensitive to increasing SST, they should help to buffer the population against ongoing environmental warming. However, this buffering effect appears unlikely to be sufficient to reverse the ongoing decline, as the median growth rate remained below equilibrium in all of our simulations. Projected reductions in the numbers of both pelagic and benthic foragers, even under conditions of low SST, suggest that the ongoing population decline cannot be solely attributed to increasing SST. Thus, additional contributing factors such as overfishing or entanglement of sea lions in fishing gear[29] need to be considered as well.

Differences in female reproductive performance, and thus, fitness between foraging strategies have been previously documented in pinnipeds.[25,30,31] However, in these studies, one strategy always outperformed the others, thereby likely not describing the whole picture as the co-existence of multiple foraging strategies suggests equal benefits.[32,33] Furthermore, when comparing the fitness outcome of different foraging strategies across species, pelagic foraging species generally outperform benthic foraging species in terms of their reproductive performance.[34] In our study, an intra-specific perspective suggests that the fitness of benthic foragers is moderate but stable (but see Spekman et al.[35]), while pelagic foragers appear more sensitive to changes in surface productivity and are therefore more likely to experience booms and busts in a fluctuating environment. Our study therefore highlights the importance of a long-term approach, which allows quantification of the fitness payoffs of different strategies under variable environmental conditions (see also Abrahms et al.[36]).

In conclusion, we discovered a previously overlooked visual marker for a foraging polymorphism, which allowed us to document an SST-dependent trade-off between benthic and pelagic diving strategies in Galápagos sea lions. This trade-off could help to explain the maintenance of this foraging polymorphism and enable multiple foraging strategies to coexist.[32,33] We could also show that benthic and pelagic foragers differ in their contributions to population growth depending on SST, thereby demonstrating the potential of behavioral polymorphisms to (at least partially) buffer natural populations against environmental change. As in Darwin's finches, mockingbirds,[37,38] and marine iguanas,[39,40] the sea lions of the Galápagos Islands provide another vivid natural example of how variation is of key relevance in a changing environment.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.02.007.

A video abstract is available at https://doi.org/10.1016/j.cub.2022.02.007#mmc3.

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AUTHOR CONTRIBUTIONS

Conceptualization, J.F.L.S. and O.K.; methodology, J.F.L.S. and F.Z.; formal analysis, J.F.L.S. and F.Z., with the help of S.K., S.M., and A.T.; investigation, J.F.L.S., F.Z., E.J.D., P.P., and F.T.; writing – original draft, J.F.L.S.; writing – review & editing, J.F.L.S., J.I.H., O.K., F.Z., E.J.D., S.M., P.P., F.T., A.T., and D.P.-R.; funding acquisition, O.K. and F.T.; supervision, O.K. and J.F.L.S.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Analyzed and raw data	This paper	https://doi.org/10.5061/dryad.f4qrfj6wn
Experimental models: Organisms/strains		
Galápagos sea lion (*Zalophus wollebaeki*), wild	Galápagos Islands, colony of Caamaño, (0° 45’ S, 90° 16’ W)	N/A
Software and algorithms		
R version 4.0.4	The R Foundation	https://www.r-project.org
MATLAB version 6.5	MathWorks	https://www.mathworks.com
Automated broken stick algorithm	See Heerah et al.[41]	https://doi.org/10.1371/journal.pone.0099329.s002
Tagtools	See DeRuiter[42]	http://www.animaltags.org/doku.php?id=tagwiki:tools:stats
GIMP version 2.10.14	The GIMP team, 1995-2019	https://www.gimp.org
Ggeffects	See Lüdecke[43]	https://cran.r-project.org/web/packages/ggeffects/index.html
DHARMa	See Hartig[44]	https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html
Other		
Biologger MK10	Wildlife Computers, Redmond, WA, USA	https://wildlifecomputers.com/our-tags/tdr/tdr10/

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to, and will be fulfilled by, the Lead Contact, Jonas Schwarz (jonas.fl.schwarz@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Pictures of vibrissae, analyzed vibrissae length data and reproductive data have been deposited at Dryad and are publicly available as of the date of publication. Accession numbers are listed in the key resources table. The raw datasets of the dive and acceleration data have not been deposited in a public repository because the files are exceedingly large, but are available from the corresponding authors on request.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Galápagos sea lion

This study took place on the islet of Caamaño, a sea lion colony located in the centre of the Galápagos archipelago near Santa Cruz Island (0° 45’ S, 90° 16’ W). The resident population of Galápagos sea lions (*Zalophus wollebaeki*) has been monitored since 2003, including annual birth and growth assessments of pups, the tagging of individuals, and census rounds (see Trillmich et al.[6]). Sea lion pups from the Caamaño population were captured by hand when they were 3 to 10 days old to acquire their body condition. They were released immediately after measurements were taken, always within 10 minutes at the same spot of the capture. For photographing of vibrissae, all suitable adult females (age between 4 and 17 years) were included. Females for biologger deployment were suckling either a new-born pup or a one-year-old immature. They were captured and restrained with hoop-nets without anaesthesia and were released at the spot of capture ca. 15 minutes after the capture. All procedures were in accordance with the ethics committee standards of Bielefeld University and approved by the Galápagos National Park (research permits PC-74-18, and PC-94-19). We followed all applicable national guidelines for the care and use of wild animals.

METHOD DETAILS

Dive data

A total of 34 lactating females were caught and equipped with biologgers (MK10, Wildlife Computers, Redmond, WA, USA) on the dorsum behind the shoulder blades (see Jeglinski et al.[45] for more details). Over a period of two weeks (median 15 days, range 3–22) between October and December of 2018 and 2019, depth (every 2 seconds), GPS positions (every 4 minutes) and acceleration data (32 hertz) were collected. Putative foraging episodes of dives were identified though high vertical sinuosity of segments using an automated broken stick algorithm[41] as performed in Schwarz et al.[3] Body orientation during putative foraging episodes was calculated as pitch from the acceleration data using the R package *tagtools*.[42]

Vibrissae measurement

In 2019, 27 of the 34 individuals fitted with biologgers had a photograph of their head taken (distance 15 to 5 meters; CANON EOS 2000) to analyse the length of their longest vibrissa. Only photographs capturing the head in profile and allowing the clear identification of the tip of the longest vibrissa were used. Relative vibrissa length was calculated by dividing the relative distance (in pixels) between the upper end of the nostril opening and the tip of the longest vibrissa by the relative distance from the *Caruncula lacrimalis* of the eye to the upper end of the nostril opening (see Figure 2C). This was performed by a blinded observer (Friederike Zenth) using the image editing program *GIMP* (The GIMP team, GIMP 2.10.14, 1995-2019). The females' age was known to the nearest year (mean = 10, min. = 4, max. = 17 years). Another 55 adult females were photographed and their relative vibrissae length calculated, resulting in 82 individuals with known vibrissae length. For 42 of those individuals, a second picture was taken on another day within the same field season (mean time interval = 5 days) to investigate the repeatability of this approach. To further explore the stability of vibrissae length over longer timescales, we additionally photographed 28 animals' vibrissae 18 months after their initial photograph.

QUANTIFICATION AND STATISTICAL ANALYSIS

Pitch and vibrissae length differences

Mean pitch during discrete foraging episodes of each dive were used to compare foraging pitches among the three strategies (as identified by Schwarz et al.[3]) with a linear mixed model, which included subject identity as a random effect (see Table S1). Relative vibrissae length was analysed using a linear model, including foraging strategy and the females' age as explanatory variables (see Table S2). The significance threshold was set to a p = 0.05.

Fitness consequences

Of the 82 individuals with known vibrissae length, no reproductive information was available for five individuals, which were excluded from further analysis. The distributions of vibrissae length among the benthic and pelagic foraging foragers were used to train a Gaussian Bayes' rule classifier, i.e. a probabilistic model that derives a threshold for dividing females into two groups based on their relative vibrissae length. The vibrissae length threshold was calculated to be ~1.4, yielding a total of 36 individuals with short vibrissae (benthic foragers) and 41 individuals with long vibrissae (pelagic foragers). The posterior class probability obtained from the classifier exceeded 0.8 for 52 of the 77 individuals.

We used the long-term dataset covering the years 2003 to 2018 to compare the fitness of benthic versus pelagic foraging strategies in relation to the annual mean SST. In particular, we investigated the effects of SST (centred min. to 22°C), foraging strategy, as well as their interaction, and maternal age at offspring birth (centred min. to 4 years) on pupping rate, pup body condition and offspring first-year survival. Pupping rate was based on all birth records of females beginning in the year of tagging or at an age of at least four years, while pup body condition was quantified using the scaled mass index (SMI),[12] utilizing mass and length data of pups gathered between four and 90 days after birth. To calculate first-year survival of the offspring, survival to one year was recorded if an individual was observed during a census round one year after it was born; otherwise, that individual was assumed to have died.

We used a linear mixed model to analyse pup body condition, while pupping rate and first-year offspring survival were analysed using a mixed logistic regression model. Included in all three models were the aforementioned covariate effects as well as the *i*-th year and the *j*-th mother ID as random effects to correct for annual and individual influences. In the model on pupping rates, we additionally accounted for the fact that females are less likely to give birth in a given year if they reared a pup the year before (dummy variable; 0 = no pup born in prior year; 1 = pup born in prior year; see Table S3). The resulting model specifications are given in the following:

$$\mathrm{logit}\left(\Pr\left(\mathit{pupping}\ \mathrm{rate}_{\mathrm{ij}} = 1|\gamma_{\mathrm{i}},\gamma_{\mathrm{j}}\right)\right)$$

$$= \beta_0 + \beta_1 \mathrm{SST}_{\mathrm{ij}} + \beta_2 \mathrm{Strategy}_{\mathrm{ij}} + \beta_3 \mathrm{SST}_{\mathrm{ij}}\ \mathrm{x}\ \mathrm{Strategy}_{\mathrm{ij}} + \beta_4 \mathrm{Age}_{\mathrm{ij}} + \beta_5 \mathrm{PervYear}_{\mathrm{ij}} + \gamma_{\mathrm{i}} + \gamma_{\mathrm{j}}$$

$$\textit{body condition}|\gamma_i, \gamma_j$$

$$= \beta_0 + \beta_1 \mathrm{SST}_{ij} + \beta_2 \mathrm{Strategy}_{ij} + \beta_3 \mathrm{SST}_{ij} \text{ x } \mathrm{Strategy}_{ij} + \beta_4 \mathrm{Age}_{ij} + \gamma_i + \gamma_j$$

$$\mathrm{logit}\left(\Pr\left(\textit{first year } \mathrm{survival}_{ij} = 1|\gamma_i, \gamma_j\right)\right)$$

$$= \beta_0 + \beta_1 \mathrm{SST}_{ij} + \beta_2 \mathrm{Strategy}_{ij} + \beta_3 \mathrm{SST}_{ij} \text{ x } \mathrm{Strategy}_{ij} + \beta_4 \mathrm{Age}_{ij} + \gamma_i + \gamma_j$$

For all models, we performed residual checks using a simulation-based approach implemented in the DHARMa package.[44]

Population matrix model

Reproduction rates and first-year survival were computed for each foraging strategy (benthic and pelagic) and for SSTs ranging from 22°C to 25°C with the *ggeffects* R package[46,43] from the models described above. Survival rates of the other age classes were derived from census data spanning the years 2003 to 2016 inclusive.[6] Both juvenile and adult survival rates were pooled into a single age class each.

The resulting survival and pupping rate estimates were used to populate a projection matrix model[13]: n(t + 1) = A*n(t) with t being an annual time step, n the female population vector and A the Leslie matrix[47] expressed as:

$$A = \begin{bmatrix} 0 & 0 & 0.5R \\ \Phi_P & 0 & 0 \\ 0 & \Phi_J & 0 \\ 0 & 0 & \Phi_A \end{bmatrix}$$

with the transition probabilities between life stages being survival of pups (Φ_P), juveniles (Φ_J) and adults (Φ_A), and R being the reproductive rates of adults starting from the age of 4 years. We then calculated the dominant eigenvalues to predict population growth rate over the next 50 years,[13] for each strategy and across a range of SST values. Since we only followed females and their female offspring,[13] we multiplied reproductive rates by 0.5 in all matrix models.[48] All models assumed a birth-pulse post-breeding approach; hence, pup survival was a separate matrix entry and was not incorporated into fertility entries.[13]

To account for potential uncertainties in the estimation of Φ_P, Φ_J, Φ_A, and R and to control for any associated errors in the matrix model, we used a Monte Carlo approach to evaluate an array of possible outcomes to achieve better reliability. With the *ggeffects* package, Gaussian distributions were derived for survival and reproduction rate based on the *ggeffects* estimates. We then sampled 50,000 transition and reproduction rates randomly from their respective densities to produce 50,000 dissimilar Leslie matrices for each SST and foraging strategy in order to perform a stochastic estimation of the annual population growth, λ, and its uncertainty. We conducted all analyses in the statistical environment R version 4.0.4, except for the population matrix model, which was analysed in MATLAB version 6.5.

Data availability

All vibrissae photographs, measured relative vibrissae length and raw data of the reproductive history of females used in this study are available through the Dryad Digital Repository https://doi.org/10.5061/dryad.f4qrfj6wn.