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DNA-metabarcoding confirms trophic flexibility and reveals new prey species in southeastern Galapagos sea lion rookeries

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DNA-metabarcoding confirms trophic flexibility and reveals new prey species in southeastern Galapagos sea lion rookeries

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DEDICATORIA

Para mi esposa Pakis y mi abuelita Violeta.

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RESUMEN

Los ecosistemas tropicales son un reto para los mamíferos marinos debido a su productividad baja y fluctuante. El lobo marino de Galápagos (*Zalophus wollebaeki*) ha adoptado flexibilidad trófica para hacer frente a tales condiciones. Sin embargo, las investigaciones previas sobre este tema se han centrado en unas pocas colonias, empleando métodos tradicionales como el análisis de excrementos. Contrariamente a los métodos tradicionales, el metabarcoding de ADN permite identificar cada presa consumida con una alta resolución taxonómica. Empleamos el metabarcoding para determinar los patrones tróficos del lobo marino de Galápagos en cinco colonias diferentes en la biorregión sureste de Galápagos, donde viven la mayoría de estos animales. Detectamos un total de 98 OTUs de presas, la mayoría asignadas a taxones de peces óseos. También encontramos nuevas presas, entre ellas un tiburón, rayas y varios peces de aguas profundas. Confirmamos la flexibilidad trófica en el lobo marino de Galápagos, ya que los individuos muestreados consumieron presas de diferentes hábitats y niveles tróficos. Se encontraron diferencias significativas en la dieta entre las colonias estudiadas, particularmente entre Santa Fe y Punta Pitt. La colonia de Punta Pitt, con una batimetría más pronunciada y menor productividad, se distinguía por presas de nivel trófico alto y de aguas profundas; mientras tanto, Santa Fe, situada en aguas más productivas y poco profundas sobre la plataforma, se caracterizaba más bien por peces pelágicos. La ubicación geográfica y la batimetría más heterogénea de las colonias de El Malecón, Española y Floreana permitirían a los animales acceder tanto a presas epipelágicas sobre la plataforma como a presas de aguas profundas fuera de la plataforma, en menor medida. La variación de la dieta intra-poblacional fue mayor en las colonias más pobladas con acceso a una gran diversidad de peces debido a su ubicación y a la influencia del afloramiento de la corriente de Cromwell. Gracias al metabarcoding, pudimos confirmar, con un inventario de presas más amplio, el comportamiento de flexibilidad trófica en el lobo marino de Galápagos a escala de biorregión. La cobertura de más colonias y el hallazgo de más y nuevas presas en nuestro estudio, han contribuido en nuestra comprensión de los patrones de alimentación de esta especie en peligro de extinción.

Palabras clave: Plasticidad trófica, lobo marino de Galápagos, ADN-metabarcoding, Islas Galápagos, batimetría.

ABSTRACT

Tropical ecosystems are challenging for marine mammals due to their fluctuating, low productivity. The Galapagos sea lion (*Zalophus wollebaeki*) has adopted trophic flexibility to face such conditions. However, previous research on this topic has focused in a few rookeries, employing traditional methods as the scat analysis. Contrary to traditional methods, the DNA-metabarcoding allows to identify every prey consumed with high taxonomic resolution. We employed the DNA-metabarcoding to determine the trophic patterns of the Galapagos sea lion in five different rookeries in the southeastern Galapagos bioregion, where most of these animals live. We detected a total of 98 prey OTUs, mostly assigned to bony-fish taxa. We also found newly reported prey, including a shark, rays, and several deep-sea fish. We confirmed trophic flexibility in the Galapagos sea lion, as individuals consumed prey from different habitats and trophic levels. Significant diet differentiations were found among rookeries, particularly between Santa Fe and Punta Pitt. The Punta Pitt rookery, with a more pronounced bathymetry and lower productivity, was distinguished by high-trophic level, deep-sea prey; meanwhile, Santa Fe, located in more productive, shallow waters over the shelf, was rather characterized by pelagic fish. The geographic location and more heterogenous bathymetry of El Malecon, Española, and Floreana rookeries would allow the animals there to access both, epipelagic prey over the shelf, and deep-sea prey out of the shelf in a lower extent. Intra-rookery diet variation was higher in more populated rookeries with access to a high fish diversity due to their location and the influence of the Cromwell current upwelling. Thanks to the DNA-metabarcoding we could confirm, with a broader prey inventory, the trophic flexibility behavior in the Galapagos sea lion at a bioregion scale. The coverage of more rookeries and the finding of more and new prey in our study, have contributed in our understanding of the foraging patterns of this endangered species.

Key words: Trophic plasticity, Galapagos sea lion, DNA-metabarcoding, Galapagos Islands, bathymetry.

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INTRODUCTION

Research on the trophic ecology of top predators is critical for understanding their behavior and for promoting their conservation (Sergio et al., 2008; Hazen et al., 2019). This is especially important for endangered species, living in a threatened, uncertain environment that affects their population dynamics. Under unfavorable ecological conditions, top predators may adopt trophic flexibility as a key strategy to survive. Trophic flexibility is the ability of a predator to take advantage of the most profitable prey under given circumstances (Tyus, 2011). Under strong competition and challenging conditions, and if a high diversity of prey is available, predator species may expand their diets, exploiting a wide range of prey coming from different habitats and trophic levels, decreasing intraspecific competition (Bolnick et al., 2003; Jaeger et al., 2009). This behavior usually implies different individuals to specialize in using different prey sources, yet with the population as a whole keeping a broad menu (Bolnick et al., 2003; Estes et al., 2003; Aráujo et al., 2011).

Thanks to the influence of oceanic currents, the waters surrounding the Galapagos Islands are usually rich and productive (Schaeffer et al., 2008). However, because of this reliance on changing oceanic currents and its tropical location, this ecosystem undergoes frequent periods of low productivity (*e.g.* El Niño–Southern Oscillation event ENSO), that result in constant food stress (Churchill et al., 2014; Páez-Rosas et al., 2012; 2020).

This makes this habitat challenging for marine mammals with high energetic requirements such as the endemic, endangered Galapagos sea lion (*Zalophus wollebaeki*) (Piedrahita et al., 2014; Trillmich, 2015).

Food scarcity and fluctuating productivity within the last four decades would explain a >60% decline in the population of Galapagos sea lions (Páez-Rosas et al., 2021). Thus, knowing what exactly these animals are eating, is a simple but paramount question to understand what foraging strategies are they following to face their uncertain habitat, and to conserve the species under such conditions. At the same time, as a top-predator, the Galapagos sea lion is regarded as a sentinel of the health archipelago's marine ecosystem (Drago et al., 2016; Páez-Rosas & Guevara 2017).

Previous research has shown evidence of trophic flexibility in the Galapagos sea lion as a strategy to survive in their demanding habitat and to avoid intraspecific competition (Páez-Rosas & Aurioles-Gamboa, 2010; Blakeway et al., 2021). Different individuals within a same rookery (*i.e.* population) are capable of exploding a high diversity of prey from different marine habitats (Páez-Rosas et al., 2017; Schwarz et al., 2021), and of adjusting their diet according to seasonal oceanographic events such as ENSO (Páez-Rosas et al., 2020; Schwarz et al., 2022). Additionally, every individual keeps its own dietary preferences while being constrained by their nutritional needs, physiological capacities or by a dependent pup in the case of females (Villegas-Amtmman et al., 2017; Urquía & Páez-Rosas, 2019). Therefore, different individuals specialize in exploiting different prey sources (Páez-Rosas and Aurioles-Gamboa, 2010; 2014); these individual preferences may still be flexible when there is intensified competition or resources fluctuation (Svanback & Persson, 2004; Páez-Rosas et al., 2017).

At a broader geographic-scale, in the inter-population level, the bathymetric profile, upwellings, and oceanic current dynamics would be the major variables in determining food availability and hence the diet of sea lions in different regions of the Galapagos archipelago (Wolf et al. 2008; Páez-Rosas et al., 2017).

Previous research has already tried to identify the prey and foraging strategies of Galapagos sea lions in some rookeries, through the morphological characterization of hard-remains in scats and the analysis of stable isotopes. The morphological identification of fish otoliths and cephalopod beaks is a simple and cheap method that allows directly identifying the prey, sometimes up to the species level (Casper et al., 2007). Nevertheless, the results obtained from this method can be heavily skewed because of the differential digestion of remains from different sources; for instance, cephalopod beaks tend to be regurgitated, some otoliths may be fully digested or degraded to become unrecognizable, while prey with soft bodies are undetected (Peters et al., 2005; Casper et al., 2007). Stable isotope analysis, on the other hand, allows for accurate long-term inferences about the trophic level and the foraging area (Newsome et al., 2007; Nielsen et al., 2018). However, stable isotope analysis does not provide the specific identity of prey unless an extensive sampling over all potential prey is done (Deagle et al., 2005; Lerner et al., 2018). Thus, due to the limitations of previously used methods, tens of potential Galapagos sea lion prey remain unknown for science, and our knowledge on the trophic ecology of these endemic marine mammals would still be incomplete (Nielsen et al., 2018; de-Sousa et al., 2019).

The sensitive DNA-metabarcoding method, on the other hand, makes it possible to detect in theory every prey item consumed within a 48h. time frame (Casper et al., 2007; Nielsen et al., 2018). This method consists on extracting the total DNA from predator scats to then target there an identifiable genetic sequence such as the 16S barcode; then, all the barcode sequences obtained from the sample are matched to a database so we can say what species or taxa were contained in the diet (Vences et al., 2016; de Sousa et al., 2019). DNA survives far better than macroscopic remains to animal digestion; moreover, the detection of prey through the DNA-metabarcoding doesn’t depend on whether it had solid structures that remained intact after the predator's digestion, and the results are not skewed by the differential survival of these (Jeanniard-du-Dot et al., 2017; Nielsen et al., 2018). The DNA-metabarcoding or other similar DNA-based approaches, have already been applied for trophic studies in other wild pinnipeds (Casper et al., 2007; Peters et al., 2015; Berry et al., 2017; Jeanniard-du-Dot et al., 2017; Brassea-Pérez et al., 2019; Nelms et al., 2019; Thomas et al. 2022); in all these studies, it was possible to detect more prey and even new prey species that were not reported with alternative methodologies in the same species.

Due the technological development of DNA sequencing and bioinformatics, hundreds of samples can be analyzed fast and cheap through the DNA-metabarcoding method (Nielsen et al., 2018); this in turn lets us to expand our study over several rookeries, so that we can compare their diets and assess whether they share the same trophic resources. Therefore, by employing correctly the DNA-metabarcoding, we may expect to identify every egested prey by predators even to the species level, giving us a broader idea of what animals in several rookeries are they feeding and what trophic strategies they follow (Nielsen et al., 2018; de-Sousa et al., 2019). Thus, we applied —for the first time ever— the DNA-metabarcoding technology to find out what Galapagos sea lions are eating in five different rookeries in the southeastern bioregion, where most of these animals are concentrated (Riofrío-Lazo et al., 2017; Páez-Rosas et al. 2021). With a more complete prey inventory in hand, we further asked 1) What kind of species prey are found and what are the most important for these populations? 2) Do the southeastern bioregion rookeries display a high degree of trophic flexibility, as seen in rookeries studied by previous research? 3) How diverse is the Galapagos sea lion diet in the southeastern bioregion, and what prey in particular are driving the diet differences among its main rookeries?

METHODS

Sample collection

Our sampling covered the southeastern bioregion of the Galapagos archipelago, from July to August 2021. We sampled five different rookeries, two in San Cristobal Island —El Malecón (0.90072˚ S; 89.610117˚ W) and Punta Pitt (0.705069˚ S; 89.254961˚ W)—, and one in Santa Fe (0.8044˚ S; 90.041073˚ W), Floreana (1.227624˚ S; 90.444702 ˚ W) and Española (1.369293˚ S; 89.745053˚ W) Islands (Fig. 1).

We collected at least 50 scats from adult sea lions per rookery; when possible, scats were immediately collected after the individual defecated; the rest of samples were collected opportunistically, identifying adult individual scats by its size and collecting fresh samples only. All samples were collected over a span of 2 sunrises and 2 sunsets at each rookery, thus ensuring that no more than one scat was collected per individual (so that a sampled scat is equivalent to one sampled individual). Each scat was collected in previously sterilized aluminum foil and placed in plastic bags that were immediately stored at -20˚C until DNA extraction.

Laboratory procedures

A total of 60 samples from El Malecón, 32 from Punta Pitt, and 30 samples from Santa Fe, Floreana and Española rookeries were selected for DNA extractions. From the selected samples, around 220 mg of fecal material was subsampled by putting together different parts of the frozen scats from each individual. From this, total DNA was extracted by following the "human DNA analysis protocol" of the QIAGEN QIAamp® Fast DNA Stool Mini Kit, following manufacturer instructions with some modifications including the decreasing of incubation temperature from 70 to 50˚C, and the final elution of extracted DNA in 100µl of

TAE buffer. DNA concentration was further quantified through spectrophotometry using the Nanodrop 2000®, and integrity was assessed by running the DNA in a 1% agarose gel electrophoresis. In each DNA extraction batch, we included a negative control where all the proceeding was carried out but without including a scat sample.

We employed PCR for targeting a ~250 pb hypervariable loop region of the 16S rRNA gene of every organism contained in the scat samples. The primers employed for PCR were those designed by Vences et al., (2016); although these were initially designed for targeting vertebrate sequences, we found these primers can also target invertebrates as tested both, *in silico* and by directly amplifying the expected 16S region in DNA extracted from tissue of a Galapagos octopus (*Octopus oculifer*). The primers employed were modified for applying a dual-index framework for Illumina platforms (Vences et al., 2016). This allowed us to do multiplex sequencing but without losing the identity of each individual sample by labelling them with a unique combination of a couple of 8-bp index sequences that never repeated among samples. Blocking primers (5'-TGGAGCTTCAATTAACTTACCCAATCAGAATTTATTC-3') were designed in order to decrease the amplification of sea lion DNA in our PCRs. However, we also decided to do a second trial of PCRs without including the blocking primers, as these may also prevent the amplification of some prey DNA (McIness et al., 2017); both, the PCR with and without blocking primers were performed in duplicate. GoTaq® DNA Polymerase (Thermo Fisher Scientific) was employed for PCRs, using 2µl of our DNA stocks for the reactions without blocking primers, and 4µl in the reactions with blocking primers (total of 25µl PCR reaction).

All the PCR products were loaded in an 1.5% agarose gel for roughly quantifying amplicon concentration, and according to this concentration 1-6µl of PCR product (1µl) was added to the pooled library (so that an approximately equimolar concentration was reached in the library). The pooled library was gel-purified through band extraction employing the Qiagen MinElute® kit, after which the entire library was concentrated in two columns containing 14µl of eluate. Library integrity was visualized in a 1.5% agarose-gel and concentration was read in a Qubit 2.0 fluorometer. Library sequencing was conducted on the Illumina MiSeq platform employing the MiSeq Reagent Kit v2 for 250 cycles in both directions, following the manufacturers' protocols.

Bioinformatics and data filtering

For demultiplexing, reorienting, primer/adapter removing, filtering and clustering the Illumina raw reads, we employed the OTU workflow (default settings) implemented in the Pipecraft software (Anslan et al., 2017). From this process, we got high quality, chimera-filtered reads, that were further clustered into OTUs with a 97% similarity threshold. To assign taxonomy to our OTUs, we compared them to the MIDORI 16S database (MIDORI_UNIQ_NUC_GB245_lrRNA_RAW.fasta; Leray et al., 2022.), employing the Blastn component implemented in Pipecraft as well. This process was executed for the blocking primer and no blocking primer dataset. As we found that both datasets contained potential prey OTUs (although the blocking primer dataset let us to recuperate more prey reads), we finally decided to pool both datasets in a single one for running it again in Pipecraft under the same parameters for getting the OTUs we filtered and analyzed further. This time, we added to the Midori database the newly obtained 16S sequences for two potential prey species: Galapagos octopus, *Octopus oculifer* (GenBank accession: OQ725638), and mottled scorpionfish, *Pontinus clemensi* (GenBank accession: OQ725637).

For correcting tag switching errors, removing reads from a sample that are not supposed to be in that sample (Carlsen et al., 2012), we calculated the relative abundance for every OTU in every scat sample and negative controls. The threshold for considering (or not) the occurrence of an OTU in a sample as a tag switching errors –of 0.000514– was determined by the maximum relative abundance of sea lion OTUs in any of our negative controls. Thus, the occurrence of an OTU in a sample was nullified if its relative abundance was <0.000514 in that sample. After this, artifacts (an OTU with no blast hits, and OTUs having <70% id% against the Midori entries) and obvious contaminants were removed. As the lab where we did PCRs and library preps never worked with marine species, it was easy to identify such contaminants (including some few reads from amphibians, land reptiles, acari, rotifers, and domestic animals); potential environmental contaminations (coprophage insects, human) and sea lion OTUs were removed as well. For furtherly removing potential marine environmental contaminants ("less obvious contaminants") and correcting for cross-contamination artifacts, we applied a method combining the removal of maximum taxon contamination and a sample-based threshold (this would be the optimum method for accurate artifact filtering according to Drake et al., 2022). For this purpose, we firstly nullified the occurrence of OTUs in every sample containing less or equal reads of the same OTU remaining in any of our negative controls.

Then, from the remaining reads, a double approach for sample-based threshold was employed. Firstly, a sample-specific threshold was set based on the percentage of reads coming from contamination sources (Human, mites, land arthropods, domestic animals, and the Sipunculid worm that appeared in the negative controls) within the sample; then, in every sample, all the OTUs occurring in a proportion less or equal than the contamination reads, were removed. A second step of sample-based threshold was done over the remaining read, where the OTUs representing <1% in each individual sample were removed as well. A couple of remaining singletons were also omitted in our read matrix. After all filtering steps, all the samples with <30 remaining prey reads, were removed from further analysis. From this we got our final prey reads occurrence matrix. Our final sample size was 124 scats, with 36 analyzed scats from El Malecón rookery, 23 from Punta Pitt, 22 from Santa Fe, 20 from Floreana, and 23 from Española.

The taxonomic assignment of the remaining prey OTUs after the filtering steps was manually verified in order to accurately link these OTUs with a species (or the lowest possible taxonomic category). Every OTU with an id% ≥96% (see Deagle et al., 2013; Brassea-Pérez et al., 2019; Thomas et al., 2022) with the best hit species from Blastn, was assigned to that species provided its record is confirmed in the Galapagos area; otherwise, that OTU was identified just at the genus level (again, confirming that genus is recorded in Galapagos). The prey species distributions and records were retrieved from the FishBase (Froese & Pauly, 2022), SeaLifeBase (Palomares & Pauly, 2022), and Charles Darwin Foundation Species Checklist (CDF, n.d.) databases. OTUs with an id% <96% with the best hit in our initial classification, were screened at the NCBI Blastn server (Madden, 2003); according to how the OTU sequences clustered with their best Blastn hits in a Fast Minimum Evolution tree, they were assigned either to a genus, subfamily, family, or order in particular.

Statistical analyses

For testing the sufficiency of our sequencing coverage to detect all the potential prey OTUs (Operational Taxonomic Unit) contained in our library, a OTU rarefaction curve was plotted for each rookery, employing the commands from the *phyloseq* (McMurdie & Holmes, 2013) and *MiscMetabar* (Taudière, 2022) R packages.

Although the use of the relative read abundance could let a prey quantitative analysis, this is still an undeveloped and questionable topic in trophic metabarcoding studies. The differential prey digestion rates, times and digestibility, the different sample qualities and specific concentration of mitochondria, as well as bias on the primers annealing into DNA from different species and bias in DNA extraction (DNA from some prey and tissues is more easily extracted than others), make the quantitative analysis of metabarcoding reads a highly speculative exercise that could lead to biased and erroneous conclusions about prey importance and biomass consumed (Thomas et al., 2014; Nielsen et al., 2017). For this reason, for further statistical analyses, our prey read matrix was transformed into a presence/absence (0, 1) matrix. The handling of dietary metabarcoding data as occurrences is a conservative and reliable option for avoiding the DNA recovery biases own of dietary metabarcoding studies, especially when lots of prey items are expected to be found (Deagle et al., 2019).

With our presence/absence data matrix, basic richness statistics (at a rookery and sea lion individual level) and rarified richness (assuming a N=20, which is the smallest sample size for any of the studied rookeries) were calculated at the OTU and genus/species level. This was done by employing the functions of the *phyloseq* and *vegan* (Dixon, 2003) R packages. To test for a significant relationship between the OTU and genus/species prey richness with the rookery population size (data from Páez-Rosas et al., 2021), a non-parametric Spearman correlation was carried out. Prey richness per individual was examined as well; for determining whether sea lions consumed a wider prey richness at the individual level in some rookeries than in others, a Kruskal-Wallis rank sum test was performed over the prey richness per individual values across different rookeries.

All the prey found across the different rookeries were summarized through the percent of occurrence (POO) of each item; the POO is the percentage of the frequency of occurrence of a prey item in a rookery rescaled so that the sum of the POOs of every prey item in a rookery sum 100% (Deagle et al., 2019). The prey found were also grouped according to their habitat into 5 categories: Epipelagic (0-200 mts deep), Mesopelagic (200-1,000 mts), Bathypelagic (1,000-3,000 mts), Rocky bottom (0-200 mts), and Rocky bottom-deep (>200 mts). Prey were also classified according to their trophic level in 5 categories: Planktivore between trophic levels 2.0 and 2.5, Planktivore 2.6-3, Carnivore 3.1-3.5, Carnivore 3.6-4, and Carnivore 4.1-4.5. The prey classified into their respective habitat and trophic level categories, were summarized through the POO as well. Information about each prey habitat, deepness range, and trophic level, was retrieved from FishBase and SeaLifeBase.

For testing the significance of diet composition differences among different rookeries, we employed a nonparametric (permutational) multivariate analysis of variance (ADONIS), implemented in the *vegan* R package. This ADONIS was run under 9999 permutations, and based on Jaccard distances among individuals grouped in their respective rookeries; Jaccard distances are the most appropriate for handing presence/absence data. To find out exactly in which rookeries we had significative differences in the ADONIS, we also caried out a pairwise ADONIS (*pairwiseAdonis* package; Martínez-Arbizu, 2022) employing a Holm correction for *p*-values (Holm, 1979). The dietary niche overlap among each pair of rookeries was also measured using the Schoener overlap index (Schoener, 1970), which ranges from 0 (meaning no shared prey items) to 1 (full diet overlap); this last analysis was performed with the functions of the R *FSAmisc* package (Ogle, 2022). For visualizing differences in diet composition among individuals and different rookeries, a nonmetric multidimensional scaling (NMDS) was performed, implementing the functions of the *phyloseq* package. This NMDS was also based in Jaccard distances among individuals, and set with a k=3 (3 dimensions), as this was the value in which the stress reached a value <0.05, showing the ecological distances (differences in diet composition) are well represented in the distances among data points displayed at the NMDS plot. For this analysis we had to discard two samples, ZP53 and ZF13, as these had prey not found in any other individual and hence were pulling heavily the scale of the ordination across the NMDS1 axis. The final results of the NMDS were plotted by using the *ggord* R function (Beck, 2017).

Diet differences within each rookery were examined as well. Firstly, we checked for the Sum of Squares (SS_A and SS_W) and pseudo-R^2 of the ADONIS, to determinate how much diet variance is explained by differences among rookeries, and how much is explained by differences within rookeries. For determining whether some rookeries had a broader intra-rookery diet variation (trophic breadth) than others, we examined the multivariate homogeneity in rookery diet dispersions through Anderson's PERMDISP2 procedure (Anderson, 2006) implemented in the *vegan* R package as well; for this analysis, we used the group centroid and run it under 9999 permutations. To find out which pair of rookeries are driving the significative differences in the PERMDISP, we carried out a PERMDISP-TukeyHSD (*vegan* package), employing a Holm correction for *p*-values as well. Finally, 95% confidence ellipses for each rookery were drawn in the NMDS to visualize how broad are the within-rookery diet differences in each case.

For finding out which prey items are exactly the ones driving the differences in the diet composition among rookeries, an indicator species analysis (ISA) was carried out, by employing the functions of the R *indicspecies* package (De Cáceres et al., 2022). The species-site group association function employed for this analysis was the “IndVal” function (9999 permutations), which delivers a statistic ranging from 0 to 1, being higher when a prey item tends to be more abundant and more exclusively found in a rookery (or group of rookeries) in particular (Dufrêne & Legendre, 1997). ISAs were also performed to test whether prey from a particular habitat or trophic level tended to be more abundant and exclusive for any rookery (or group of rookeries) in particular.

RESULTS

Metabarcoding overview and general trends

All our samples contained *Zalophus* genus 16S reads, confirming all of them became from Galapagos sea lion individuals. Both, the blocking and no-blocking primer assays gave us potential prey reads, yet the former essay let us to recuperate significatively more prey reads per sample than the later (Wilcoxon test, $p = 0.045$). Overall, and after all the filtering steps, we got a total of 244,189 prey 16S reads (Supplementary File S1). Our sequencing coverage would be enough to detect every prey OTUs (including rare prey) contained in our libraries, since the rarefaction curves of all the five rookeries reached an asymptote in ~9000 reads on average; we got the most reads for the El Malecón and Santa Fe rookeries, and the least reads for Floreana and Española (Fig. 2).

The vast majority (99.80 %) of the prey reads belonged to bony ray-finned fish (Actinopterygii), 3 reads (<0.01%) belonged to a Humboldt squid (*Dosidicus gigas*), while the remaining reads (0.20%) belonged to sharks and rays (Chondrichthyes). After filtering we got a total of 98 prey OTUs (Supplementary File S2), of which 58 could be identified up to the species level, 30 to the genus level, 5 to family, and 5 to the order level (Supplementary File S1). All the blast hits used for taxonomic assignment had an E-value <4.89E-41. Accordingly, the prey OTUs found were classified into 49 unique species (46 Actinopterygii, 2 Chondrichthyes, 1 squid), 70 genera (66 Actinopterygii, 3 Chondrichthyes, 1 squid), 48 families (44 Actinopterygii, 3 Chondrichthyes, 1 squid), and 31 orders (27 Actinopterygii, 3 Chondrichthyes, 1 squid). The 98 prey OTUs were finally classified into 85 unique taxonomic entities, either species, genus, family or order (some of them may overlap though).

The prey species Pacific sardine, *Sardinops sagax*, was strikingly the one that more sequencing reads generated (126,408 or the 51.76% of the total prey reads obtained), followed by greeneyes, *Chlorophthalmus* sp. (31,700 or 12.98% of the reads), razorback scabbardfish, *Assurger anzac* (24,037 or 9.84%), and Pacific creolefish, *Paranthias colonus* (7,842 or 3.21%). Other recurrent prey in all the five southeastern rookeries but with a lower importance included lizardfishes, *Aulopus sp.*, threadfin goosefish, *Lophiodes spirulus*; threadfin bass, *Pronotogrammus multifasciatus*; Chub mackerel, *Scomber japonicus*; and Serraninae family fish (Figure 3a and Supplementary File S1).

Prey richness and trophic flexibility

The southeastern rookeries where the highest prey richness was consumed were Floreana, Española, and El Malecón; meanwhile, Santa Fe and Punta Pitt displayed the lowest prey richness (Tables 1 and 2, Fig. 2). We didn't find a significative relationship between rookery population size (2014) and prey richness, both in terms of OTUs (Spearman correlation, p = 0.450, *rho* = 0.50; Table 1) and species/genus (p = 0.493, *rho* = 0.41; Table 2). The sea lions from all the five rookeries tended to consume around the same prey number (OTUs: Kruskal-Wallis test, $\chi^2_4 = 2.28$, $p = 0.683$; species/genera: $\chi^2_4 = 3.13$, $p = 0.537$; Table 2); even if a couple of samples showed >10 different prey, in average few prey OTUs (Table 1) and species/genera (Table 2) were detected per individual.

The sea lion prey at all the southeastern rookeries came from different habitats and trophic levels. At the five rookeries, we found prey coming from epipelagic, rocky bottom and rocky bottom-deep habitats. Prey from the rocky bottom habitat were relatively common across the five rookeries (Fig. 3b). Similarly, all the rookeries included prey from four different trophic levels, spanning from high trophic level Planktivores (2.6), to high trophic level Carnivores

(4.5). Carnivore prey were in general more frequent than Planktivores in all the rookeries, being those from trophic levels 3.1 to 4.0 the most recurrent (Fig. 3c).

3.3 Diet variations among and within rookeries

Diet composition was significantly different among rookeries (ADONIS, *Model*-$F_{4,119} = 3.198$ $p < 0.001$). Specifically, the diet composition in Punta Pitt differed from all the other rookeries; the diet in Santa Fe also differed from the one in Floreana and Española (Table 3). The El Malecón rookery was the one with the highest dietary niche overlap with the rest of the rookeries but Punta Pitt, as measured by the Schoener index. Punta Pitt was rather the rookery with the lowest niche overlap with the other ones, especially with Santa Fe (Table 4). The visualization at the NMDS plot (Fig. 4a; stress = 0.045), also agrees with this diet differentiation of Santa Fe and Punta Pitt. The diets in El Malecón, Floreana and Española showed an overlap. Some of the individuals from these three rookeries had diets similar to that in Santa Fe, and a few a similarity with Punta Pitt; however, the remaining individuals, in particular some coming from Floreana, had notably different prey from that seen in the rest of animals sampled in the southeastern rookeries (Fig. 4a).

There was evidence for important diet variation inside each rookery as well. While a 9.7% (ADONIS, $SS_A = 5.098$) of variance in diet was explained by the rookery grouping variable, the remaining 90.3% ($SS_W = 47.418$) was explained by within-group variation. Moreover, the diet multivariate dispersions of the different rookeries were not homogenous (PERMDISP, $F_{4,119} = 4.316$, $p = 0.003$); in particular the diet in Santa Fe had a significantly different dispersion compared to that seen in Floreana and Española (Table 3). Floreana displayed the highest within-rookery variation in diet composition when visualizing differences at the NMDS (Fig. 4a); thus, there were individuals within Floreana having highly divergent diets. Española and El Malecón, in that order, also showed high within-rookery variations, but not as evident as in Floreana. On the other hand, Punta Pitt and Santa Fe showed the smallest within-rookery diet variations, hence the individuals from these rookeries had the most restricted diets (Fig. 4a).

Prey driving diet differentiation among rookeries

The ISA (Table 4) showed that OTU_134, corresponding to the prey species *A. anzac,* is critical for driving the differentiation of the diet of the Punta Pitt sea lions from the rest of rookeries. Similarly, the absence in Punta Pitt of OTU_033, corresponding to the notorious prey *S. sagax* which was substantially present in the other four rookeries, would also contribute enormously to differentiating the diet profiles of this rookery. The OTU_118, assigned to *Anthias* sp., would also contribute to differentiate the diet Punta Pitt, together with the one in Española. The diet in Santa Fe, together with the one in Española, would be distinguished by the presence of OTU_028, corresponding to jack mackerel, *Trachurus symmetricus*. Although with a lower statistical significance compared to the already mentioned cases, the diet in Floreana showed the highest number of different prey OTUs which drove its differentiation from the rest of the rookeries, a total of 5 OTUs all assigned to different prey species. Besides OTU_118 and OTU_028, the Española rookery diet was also distinguished by OTU_087, assigned to the order Ophidiiformes.

The NMDS vectors (Fig. 4b) also indicated that OTU_118 and OTU_134 differentiated apart the diet at the Punta Pitt rookery, among others such as OTU_005 (*Ophichthus triserialis*), OTU_011 (*Chlorophthalmus sp.*), OTU_076 (*Myctophum nitidulum*), OTU_101 (*Epinephelus labriformis*), OTU_161 (*Aetobatus narinari*) and OTU_164 (*Dosidicus gigas*). The rookery that overlapped the least in diet with Punta Pitt, Santa Fe, was differentiated by OTU_028 again, OTU_025 (*Decapterus muroadsi*), OTU_131 (*Auxis thazard*), OTU_133 (*Thunnus sp.*), OTU_158 (*Carcharhinus sp.*), among others. The Floreana individuals that presented particularly different diets from the rest of rookeries, where differentiated by several OTUs, outstanding OTU_032 (*Opisthonema medirastre*), OTU_56 (*Bodianus diplotaenia*), OTU_059 (*Nicholsina denticulata*), OTU_067 (*Orthopristis cantharinus*), OTU_069 (*Xenocys jessiae*), OTU_092 (*Stegastes beebei*), and OTU_152 (*Fistularia commersoni*).

The results from the ISA and NMDS vectors are supported by the exclusivity and/or high POO of the regarding prey in the respective rookery/ies (Fig. 3a). No statistical support was obtained for other trends. However, when checking for trends in the prey POOs (Fig. 3a) we observed that Lutajniformes were only present in the diets of Floreana and Española, Pleuronectiformes and Syngnathiformes occurred more frequently in Floreana. *P. clemensi* and the recurrent prey *P. colonus* were absent in Santa Fe only, while lancer stargazer, *Kathetostoma* occurred more frequently in Santa Fe. Sharks (Carcharhiniformes) as prey occurred only in Santa Fe, Rajiformes rays only in El Malecón, Myliobatiformes were more frequent in Punta Pitt, while the Humboldt squid, *D. gigas*, occurred in the Punta Pitt diet only.

When grouping the prey according to their habitat, we found that epipelagic prey was significantly associated to all rookeries excepting Punta Pitt (ISA, IndVal = 0.748, $p < 0.001$); mesopelagic prey were also a significant driver of the differentiation of the diets of Punta Pitt, Santa Fe, and Española from the Floreana and El Malecón rookeries (IndVal = 0.445, $p = 0.027$). Additionally, rocky bottom-deep prey tended to have a higher POO in Punta Pitt than in the other rookeries; similarly, the few bathypelagic prey detected, were exclusives for Punta Pitt and Española (Fig. 3b). When prey were grouped according to their trophic level, Planktivores from trophic levels 2.6 to 3 were significantly associated to all rookeries excepting Punta Pitt again (ISA, IndVal = 0.731, $p < 0.001$); furthermore, Carnivore prey from the highest trophic levels, 4.1 to 4.5, were significantly associated to all rookeries excepting El Malecón

(IndVal = 0.641, p = 0.003). Finally, there were also sporadic records of lower trophic level Planktivores (2.0-2.5) in El Malecón, Punta Pitt and Floreana (Fig. 3c).

DISCUSSION

Completing the Galapagos sea lion prey inventory

The use of the DNA-metabarcoding for assessing the diet of the southeastern Galapagos sea lions let us find 85 prey from different, unique taxonomic entities. Thereby, the application of this method allowed us to discover tens of new prey species. Considering previous diet studies in the Galapagos sea lion (Dellinger & Trillmich, 1999; Salazar & Bustamante, 2003; Páez-Rosas & Aurioles-Gamboa, 2010; 2014; Páez-Rosas et al., 2017; 2020), 48 of the OTUs found in our study (56.5%) correspond to taxa that have never been reported before for this species. This included mainly prey of minor importance, but also important prey found in a high frequency, including the scombriform *Assurger anzac*, which was the most important prey for Punta Pitt rookery. The aulopiform *Chlorophthalmus sp.* was also an important prey reported for the first time in the southeastern bioregion, as it has only been reported before in the western rookeries (Dellinger & Trillmich, 1999). This is also the first study in reporting Chondrichthyes —one shark OTU and three ray OTUs— in the Galapagos sea lion diet. Other novel prey include 11 taxa of deep-sea fish species (bathypelagic and demersal/benthic living >200 mts deep).

The finding of tens of new prey in this study would be explained mainly by the advantages of the DNA-metabarcoding method. Many of the previously undetected fish prey could have otoliths that digest easily or that are not recorded in otolith guides (Peters et al., 2005; Casper et al., 2007); this last could be the case of deep-sea species, which are in general remote and hard to study. Likewise, the lack of otoliths in sharks and rays (Fowler et al., 2005) could have difficulted their detection in the Galapagos sea lion diet. However, the use of DNA in dietary studies overcome all these limitations around availability and digestion rate of otoliths, and lets the detection of prey that not necessarily leave hard remains in scats (Jeanniard-du-Dot et al., 2017; Nielsen et al., 2018). Thereby, in other trophic studies in pinnipeds, the application of the DNA-barcoding has thereby let the detection of sharks and rays as in our case, but also of soft-bodied animals including cnidarians, mollusks, and agnathans (*e.g.* Berry et al., 2017; Brassea-Pérez et al., 2019).

Other factors besides the method, however, could also explain why we found so many new prey. For example, the inclusion of the Punta Pitt rookery —whose diet has never been studied— led us to unveil several novel deep-sea prey species. Diet variations along time could also explain why we found novel prey, but also why some diet items, reported as important in previous studies, were not observed in our study (~42 taxa). For example, in the El Malecón rookery, we reported important prey that have never been identified for the southeastern region, such as *Chlorophthalmus sp.*, or *S. japonicus,* this last being reported as a minor prey only (Páez-Rosas et al., 2020). Meanwhile, prey reported as important in previous years in the same rookery such as *Opisthonema berlangai* (Páez-Rosas & Aurioles-Gamboa, 2014; Páez-Rosas et al., 2020) were absent in our records. Such temporal diet shifts in the Galapagos sea lions would be linked with environmental changes, like the strong ENSO event in 2015-2016, together with the trophic flexibility sea lions have to face those changes (Villegas-Amtmann et al., 2011; Páez-Rosas et al., 2020). Similar temporary changes have been observed in the diet of the California sea lion, *Zalophus californianus*, in the Northeast Pacific; this population went from being a *S. sagax* specialist in 1998, to having a fairly varied diet by 2016, this presumably in response to climatic variations in the region (Weise & Harvey, 2008; Robinson et al., 2018).

Seasonal environmental changes would also be linked with diet shifts in other Galapagos marine consumers, including the Blue-footed Boobies, *Sula nebouxii* (Anchundia et al., 2014), marine iguana, *Amblyrhynchus cristatus* (Anslan et al., 2021) and green sea turtles, *Chelonia mydas* (Carrión-Cortez et al., 2010).

Note some prey OTUs couldn’t be identified to the species or genus level. Such unidentified OTUs could be voids in the Midori database we employed for taxonomic assignment, which highlights the importance of keep increasing the barcoding efforts over the world (Adamowicz, 2015; Miya et al., 2015; Leray et al., 2018) in order to get more complete reference databases. For instance, the inclusion of understudied fish and invertebrates from the unexplored deep-sea, as well as Galapagos endemics lacking in barcode databases, is imperative for a more accurate study of the trophic ecology of Galapagos marine predators. Anyhow, our study joins to a body of literature supporting the usefulness of DNA-based studies in broadening our understanding of animal diet, revealing prey that were undetectable by traditional methods. We expect the usefulness of these methods keeps increasing, as global barcoding efforts increase as well.

Important prey in the southeastern bioregion

As found in previous research (Páez-Rosas & Aurioles-Gamboa, 2010; 2014; Páez-Rosas et al., 2017; 2020) we confirmed that bony fish make up the vast majority of the Galapagos sea lion’s diet. This fact corresponds with the high fish diversity found in the Galapagos Islands (Briggs et al., 2012), comprising a diverse food source for this predator. Although there is controversy about translating the number of reads into prey importance in dietary DNA-metabarcoding (Thomas et al., 2014), the strikingly high number of *S. sagax* reads we got suggest this was a remarkable prey for Galapagos sea lions in the southeastern bioregion. This prey was also the one with the highest POO in this bioregion. However, *Chlorophthalmus sp.*, *A. anzac*, and *P.*

colonus would also be important prey according to the number of reads and their high POO in one or more southeastern rookeries.

Considering the trophic flexibility of sea lions, diet variations along time, and marked inter-rookery differences, to limit the "list" of important prey to these four species, and to use this information for management purposes, could be overly simplistic. The Galapagos sea lion should be rather considered as a "plastic specialist" (Porras-Peters et al., 2008), that although its diet may focus mainly on a few of important prey, these may change seasonally. A long-term study across time and different rookeries (see Thomas et al., 2022), should be done then for taking dietary results to management. Thanks to the increasing development of sequencing and bioinformatics technologies, such long-term studies involving hundreds and even thousand and samples, are viable by applying the DNA-metabarcoding method (Nielsen et al., 2018). Our study indeed demonstrates the Galapagos sea lion diet across different rookeries can be studied thoroughly with this methodology, opening new possibilities for a comprehensive close monitoring of this species diet in the future.

Sea lion prey richness and trophic flexibility

The feeding patterns described for the Galapagos sea lion in previous research show trophic flexibility —use of prey from different habitats and trophic levels—, accompanied by individual specialization level (Páez-Rosas & Aurioles-Gamboa, 2010; Páez-Rosas et al., 2017); such conditions also observed in all the southeastern rookeries in our study.

Although no significant correlation was found between prey richness and rookery population size, we think a relationship could still exist between these two variables. We found that El Malecón and Floreana rookeries displayed the highest prey richness, while being the most populated in this bioregion (Riofrío-Lazo et al., 2017; Páez-Rosas et al., 2021); meanwhile, the less populated rookeries —Punta Pitt and Santa Fe— had a lower prey richness.

This would be an indication of trophic flexibility Galapagos sea lions adopted to face more intense competition levels in a resource-limited environment with high population densities (Páez-Rosas et al., 2017). Similar dietary differentiations have been reported in the California sea lion, *Zalophus californianus*, to prevent intraspecific competition in densely populated rookeries (Porras-Peters et al., 2008; Rosas-Hernández et al., 2019). However, the fact Española had a richer diet despite being less populated than Punta Pitt, and the statistical non-significance of the prey richness-population size relationship, could suggest an influence of other factors such as the different oceanographic contexts of each rookery.

Another indication of trophic flexibility in southeastern Galapagos sea lions was the finding of prey coming from different habitats and trophic levels. Our results agree with the three foraging strategies described for this species: epipelagic, mesopelagic and benthic (Villegas-Amtmann et al., 2008; Páez-Rosas & Aurioles-Gamboa, 2010; Schwarz et al., 2022). The use of different feeding habitats is a usual characteristic of high trophic level predators that face high intra-specific competition, but low inter-specific competition (Matich et al., 2010; Kernaleguen et al., 2015). This is exactly the case of the Galapagos sea lion in the southeastern bioregion, where in one hand, the most populated rookeries of this species exist, but in the other hand there is no other potential competitor, such as the Galapagos fur seal, *Arctocephalus galapagoensis*, which is only present in the northern and western bioregion of the archipelago (Páez-Rosas et al., 2021). The predation on prey from different trophic levels also agree with previous research in El Malecón rookery, where low trophic overlaps were found within this population (Páez-Rosas & Aurioles-Gamboa, 2010). A flexible diet and the exploitation of different prey sources make Galapagos sea lions able to live in a tropical habitat (Páez-Rosas et al., 2017). Tropics are marginal habitats for pinnipeds in general, due to its either low or uncertain productivity, relying on the dynamics of oceanic currents that may change and lead to extended and frequent starvation periods as seen during ENSO (Costa et al., 2006; Capotondi et al., 2015). Accordingly, not only the Galapagos sea lion, but other tropical pinnipeds such as the Hawaiian monk seal (*Neomonachus schauinslandi*) exhibit trophic flexibility and plasticity in foraging behaviors (Kienle et al., 2019).

Individual specialization had support in our DNA-metabarcoding results. Firstly, across all rookeries, the individuals' diet consisted of only a few items in average (2-3 OTUs or genus/species). Likewise, there was intra-rookery diet variation in different degrees, showing that individuals within the same rookeries were exploiting different prey sources. This individual specialization on certain prey items would help sea lions in avoiding intraspecific competition, as different individuals would specialize into distinct prey items accordingly their diving skills, and physiological and nutritional needs (Páez-Rosas et al., 2017; Urquía & Páez-Rosas, 2019). However, these individual preferences are also flexible, as they shift with increasing competition and resource fluctuations (Svanback & Persson, 2004). Accordingly, the Galapagos sea lion cannot be considered as an opportunistic, generalist predator as suggested in the past (Dellinger & Trillmich, 1999). Rather, this species presents a wide, varied diet at the rookery and bioregion level, but accompanied by a degree of specialization at the individual level. Sea otters (*Enhydra lutris*) also show individual diet specialization, but contrary to Galapagos sea lions, this specialization was no flexible (Estes et al., 2003).

The trophic flexibility and individual specialization strategies are important for the Galapagos sea lion to face a challenging environment (Páez-Rosas et al., 2017; Schwarz et al., 2022). Until now, such behaviors have only been described in a few, isolated rookeries with a limited prey inventory. With our DNA-metabarcoding results, we confirmed —with a more complete prey inventory— these foraging strategies apply for all the main rookeries at the southeastern Galapagos bioregion.

Diet variations among and within rookeries

The inclusion of five different rookeries in our study let us to do inter-population diet comparisons. For discussing these differences, we assumed the diet of the sea lions in each rookery are actually reflecting the local conditions around those rookeries. Such assumption is supported by the site fidelity shown by both, male and female Galapagos sea lions, for foraging and breeding activities (Meise et al., 2013; Piedrahita et al., 2014; Drago et al., 2016). Moreover, scats show short-term information only (Nielsen et al., 2014), hence the DNA-metabarcoding should show prey consumed in the surroundings of each rookery. The distance that Galapagos sea lion females travel in their foraging trips would be an average of 27-46 km. (Jeglinski et al., 2015; Páez-Rosas et al., 2017); therefore, although the foraging areas of some rookeries would unavoidably overlap, dietary information will still capture the local effects of factors such as the bathymetry and the oceanographic dynamics around each rookery so that large-scale comparisons can be made.

Significant diet differentiations were found among rookeries, particularly between Santa Fe and Punta Pitt. The contrasting diets of these two rookeries may be associated to their similarly contrasting bathymetry. Santa Fe is located in the central part of the Galapagos archipelago, placed just over the continental shelf, hence it is surrounded by shallow waters characterized by a 200m isobath. Conversely, Punta Pitt, located in the eastern extreme of the archipelago, has a more pronounced bathymetry, with isobaths exceeding the 1000 mts. deep (Páez-Rosas et al., 2017). This may explain why the diet in Punta Pitt was characterized by several deep-sea species including *A. anzac*, *Anthias sp.*, *Chlorophthalmus sp.*, and the myctophid *M. nitidulum* (Froese & Pauly, 2022); note Galapagos sea lions can indeed dive up to 600 mts. deep, hence these animals are actually capable to get those deep-sea prey (Villegas-Amtmann et al., 2013). These same prey were either absent or in a low POO in Santa Fe.

Overall productivity differences between Punta Pitt and Santa Fe may also explain the nonconcurrent diets of these two sites. The Cromwell current upwelling is the main supply of nutrient-rich, cool water in the Galapagos archipelago (Palacios et al., 2006; Schaeffer et al., 2008). While this upwelling's effect is the strongest in the western Galapagos bioregion, its effects keep extending eastward. This generates a gradient in the archipelago, where temperature and productivity decrease as one moves from west to east (Palacios, 2004; Drago et al., 2016). In consequence, the productivity in Santa Fe —the second westernmost island in the southeastern bioregion— is higher than in Punta Pitt —which is rather located in the eastern tip of San Cristobal Island, the easternmost island in the archipelago—, being also more exposed to nutrient-poor warm currents (Palacios, 2002; Schaeffer et al., 2008). This increased productivity around Santa Fe would lead to phytoplankton blooms, which in turn are attractive for epipelagic planktivorous fish such as *S. sagax* (Froese & Pauly, 2022), the most important prey in this rookery according to our study. Phytoplankton blooms also lead to an increase in zooplankton, which is the food source for other epipelagic and mesopelagic fish characteristic of the diet in the Santa Fe rookery, including *T. symmetricus*, *A. thazard*, and *D. muroadsi* (Froese & Pauly, 2022).

Conversely, in Punta Pitt, where primary productivity is low, epipelagic fish relying on plankton are practically absent in the sea lion diet. Instead, the vast majority of these animals' diet is made of high-trophic level carnivore fish from the sea bottom. This bottom, benthic foraging on carnivore fish could also be a response of Galapagos sea lions to low productivity in Punta Pitt (Schwarz et al., 2022), as these prey sources are not as impacted as pelagic fish by changes in surface productivity (Miller & Sydeman., 2004; Ñiquen & Bouchon, 2004). This lower pelagic fish abundance in Punta Pitt could also explain why sea lions got unconventional prey —rays and squid— in a higher frequency in this rookery than in any other, which could be an indicator of trophic flexibility (Páez-Rosas & Aurioles-Gamboa, 2014; Páez-Rosas et al., 2020).

The diets in El Malecón, Floreana and Española were far more diverse than in Punta Pitt and Santa Fe. At the same time, the three formers, especially El Malecón, showed an important overlap with the Santa Fe diet; however, an overlap of these rookeries with Punta Pitt was also observed, but just in few individuals. As discussed above, this higher intra-rookery variation in El Malecón and Floreana would be partially explained by the elevated population in these rookeries. However, the geographic situation of these rookeries may also contribute to the wide prey diversity observed, since the animals living there would have nearby access to both, epipelagic prey in the continental shelf (explaining the overlap with Santa Fe), and deep-sea prey out of the shelf (similarity with Punta Pitt).

Note the sea lions of El Malecón, Floreana and Española still present a skewed preference towards the "Santa Fe-style" diet, characterized by pelagic fish. Although epipelagic fish are more sensitive to productivity fluctuations, in productive years (*e.g.* 2021) these are the most energy-efficient food sources for Galapagos sea lions due to their higher lipid content and the lower energetic investment required for accessing them (Tiernet et al., 2002; Drago et al., 2010); this in turn leads to an increased fitness of animals having this diet when oceanographic conditions are not harsh (Schwarz et al., 2022). However, not every sea lion from these rookeries got a pelagic diet, as some individuals rather got prey from the sea bottom, including deep-sea prey. This pattern agrees with previous research in El Malecón, where a group of female sea lions fed on epipelagic prey over the continental shelf, and another group on carnivore fish from deeper waters, off the shelf (Páez-Rosas et al., 2017). This resources partitioning would rely on the different individuals' body size and diving performance (Villegas-Amtmann et al., 2008; 2017); moreover, in the case of females, the selection of either a pelagic or bottom diet would depend on whether they are pregnant and on their pups' age (Villegas-Amtmann et al., 2017; Urquía & Páez-Rosas, 2019). These results hence would be another indication of trophic flexibility by Galapagos sea lions to prevent intraspecific competition (Páez-Rosas et al., 2017) and to face demanding situations such as mating, and maternal care and nursing in the case of females (Trillmich & Wolf, 2007; Urquía & Páez-Rosas, 2019).

The effects of the Cromwell current may also explain the broad, prey-rich diets in Floreana, Española and El Malecón rookeries. Floreana and Española are highly influenced by a southern "branch" of the Cromwell current upwelling, that arises after it hits the western islands of the archipelago, extending towards the east (Palacios, 2004; Schaeffer et al., 2008; Tompkins & Wolff, 2016). Meanwhile, El Malecón rookery is located in the western tip of San Cristobal Island, hence it is influenced by the Cromwell upwelling contrary to Punta Pitt, located in the same island but in the eastern side (Palacios, 2004; Schaeffer et al., 2008). These conditions would increase productivity and potential prey diversity around Floreana, Española, and west San Cristobal, compared to that seen in Punta Pitt (Edgar et al., 2004; Moity et al., 2019). Indeed, the marked productivity differences between the western and eastern sides of San Cristobal, would also explain diet differences between the marine iguana subspecies living in the different sides of the island (Anslan et al., 2021).

Thanks the methodological assets of the DNA-metabarcoding, we were able to study five different Galapagos sea lion rookeries in the southeastern bioregion, providing the first inter-rookery diet comparison in this area. Surrounding bathymetry and the differential influence of the Cromwell upwelling over each rookery would contribute to the major diet patterns we found in this study, such as the contrasting diets from Santa Fe and Punta Pitt and the broad diets in Floreana, Española and El Malecón. We highlight the critical importance the

Cromwell current upwelling has for the Galapagos sea lion, even in bioregions as the southeastern that don't receive the strongest effects of it.

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Tables

Table 1. Prey richness statistics per rookery at the OTU level. The population size (2014) for each rookery is shown as well.

Rookery	**N**	**Prey richness**	**Prey Richness Rarefaction N=20 (95% CI)**	**Average. prey richness / individual [med.] (range)**	**Pop. Size 2014**[a]
Malecón	36	43	30 (29.2 - 30.8)	2.69 [2] (1-12)	872
Punta Pitt	23	25	23 (22.5 - 23.5)	2.70 [2] (1-6)	499
Santa Fe	22	23	22 (21.6 - 22.4)	2.64 [2] (1-7)	289
Floreana	20	41	41	3.40 [2] (1-11)	731
Española	23	39	36 (35.5 - 36.5)	2.78 [2] (1-8)	434

a. Páez-Rosas et al., 2021

Table 2. Prey richness statistics per rookery at the species/genus level. The population size (2014) for each rookery is shown as well.

Rookery	**N**	**Prey richness**	**Prey Richness Rarefaction N=20 (95% CI)**	**Average. prey richness / individual [med.] (range)**	**Pop. Size 2014**[a]
Malecón	36	33	24 (23.4 – 24.6)	2.42 [2] (1-10)	872
Punta Pitt	23	22	20 (19.5 – 20.5)	2.61 [2] (1-6)	499
Santa Fe	22	21	20 (19.6 – 20.4)	2.45 [2] (1-6)	289
Floreana	20	36	36	3.00 [2] (1-8)	731
Española	23	31	29 (28.5 – 29.5)	2.43 [2] (1-7)	434

a. Páez-Rosas et al., 2021

Table 3. *P*-values of the pairwise ADONIS (up) and PERMDISP TukeyHSD (down) tests for examining, for each pair of rookeries, the significance of differences in diet composition and of multivariate homogeneity in diet dispersions, respectively. The *p*-values shown are corrected through Holm's method.

	Malecón	**Punta Pitt**	**Santa Fe**	**Floreana**
Punta Pitt	**0.001** 0.991	-	-	-
Santa Fe	0.321 0.151	**0.001** 0.451	-	-
Floreana	0.321 0.450	**0.001** 0.306	**0.010** **0.005**	-
Española	0.276 0.519	**0.014** 0.357	**0.020** **0.006**	0.321 0.999

Table 4. Schoener's overlap index for each pair of rookeries depicting dietary niche overlap (0 = no prey items shared; 1 = full niche overlap).

	Malecón	**Punta Pitt**	**Santa Fe**	**Floreana**
Punta Pitt	0.275	-	-	-
Santa Fe	0.512	0.220	-	-
Floreana	0.444	0.226	0.343	-
Espanola	0.467	0.330	0.383	0.376

Table 5. Prey OTUs driving the diet differentiation for each rookery or group rookeries according to the indicator species analysis (ISA). The IndVal statistic (~1 = prey highly abundant and exclusive for one rookery or group of rookeries) and its significance *p*-value are shown as well.

Rookery/ies	**OTU**	**Assig. taxonomic rank**	**IndVal**	***p*-value**
Punta Pitt	OTU_134	*Assurger anzac*	0.522	<0.001
Floreana	OTU_055	*Apogon atradorsatus*	0.387	0.004
Floreana	OTU_020	*Synodus lacertinus*	0.316	0.025
Floreana	OTU_056	*Bodianus diplotaenia*	0.316	0.024
Floreana	OTU_067	*Orthopristis cantharinus*	0.316	0.028
Floreana	OTU_152	*Fistularia commersonii*	0.316	0.028
Española	OTU_087	Undef. Ophidiiformes	0.361	0.020
Punta Pitt and Española	OTU_118	*Anthias sp.*	0.361	0.017
Santa Fe and Española	OTU_028	*Trachurus symmetricus*	0.413	0.013
All except. Punta Pitt	OTU_033	*Sardinops sagax*	0.704	<0.001

Figures

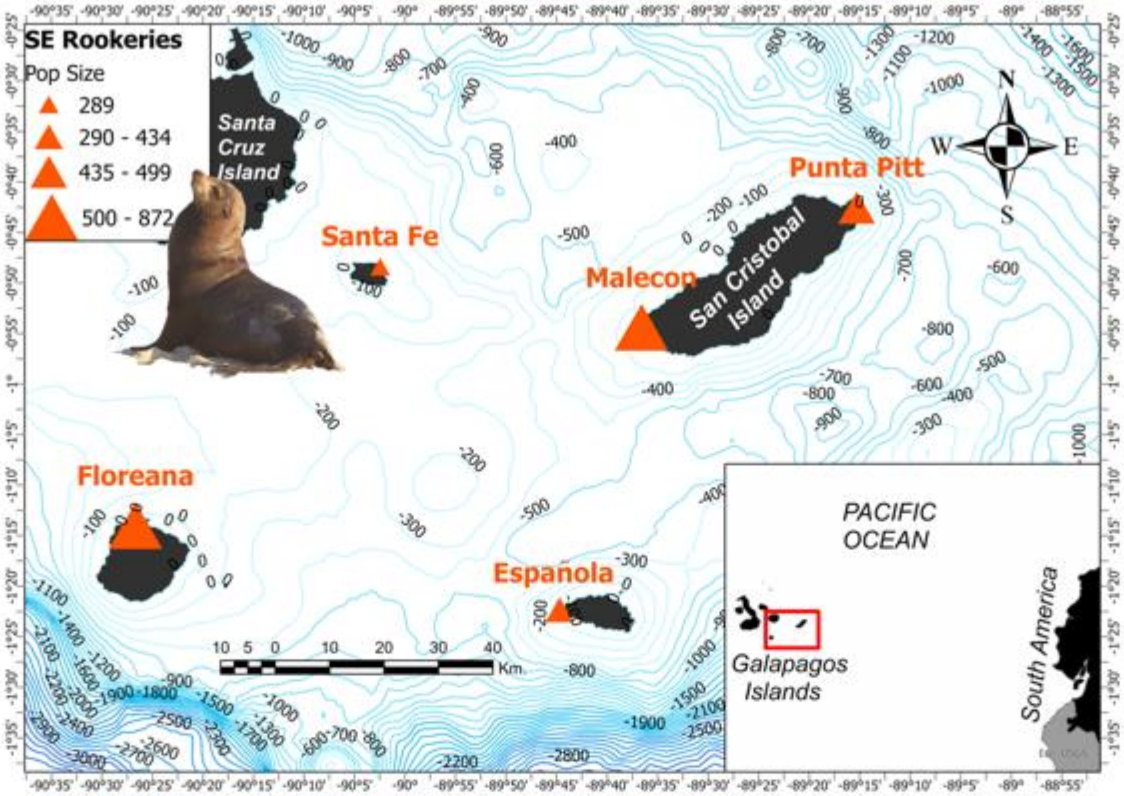

Figure 1. Map showing the location of the studied sea lion rookeries in Southeast Galapagos, and the bathymetry contour lines (-100 mts. intervals) of the study area. The size of the symbols representing each rookery (red triangles) is proportional to its population size according to Páez-Rosas et al. (2021).

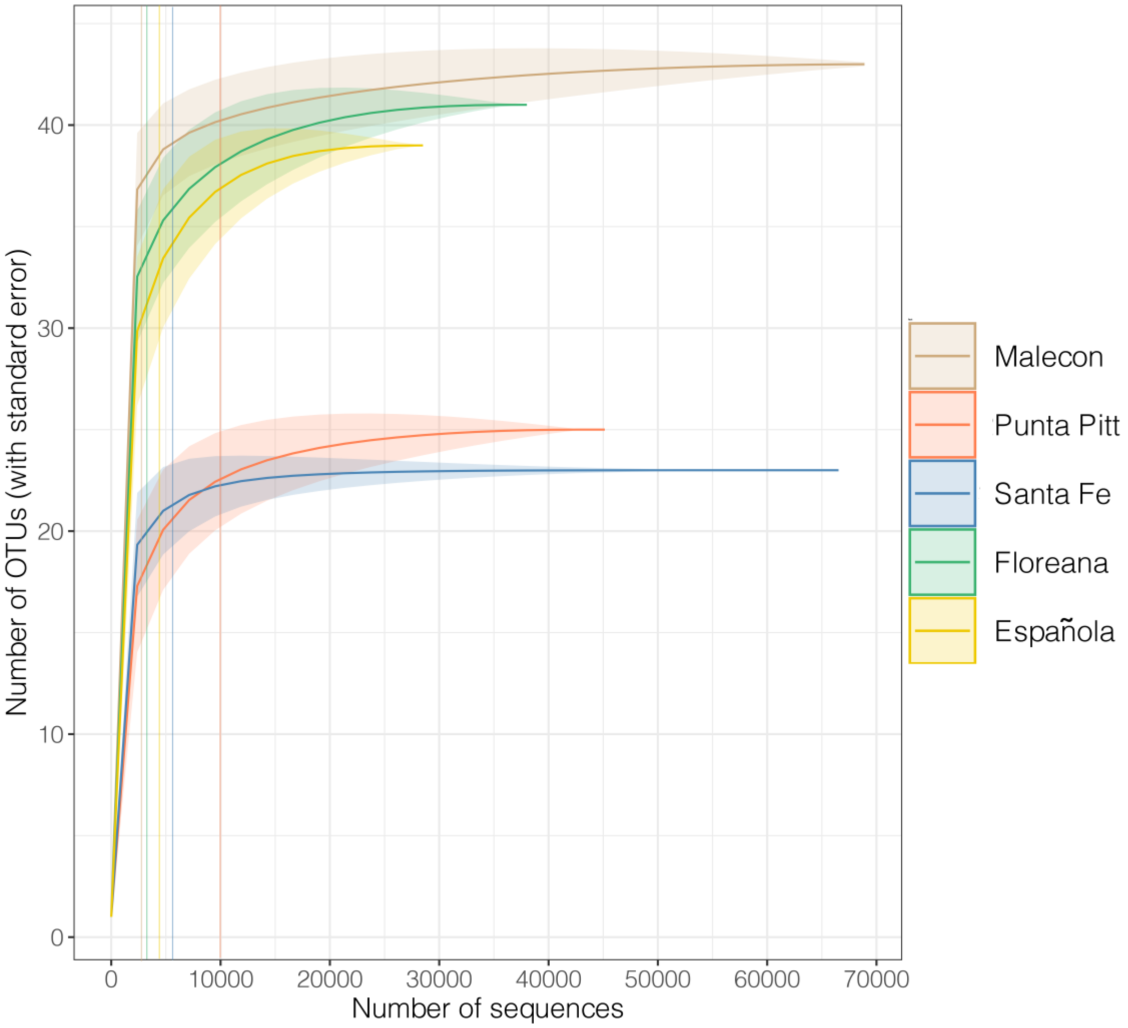

Figure 2. Rarefaction curves representing the number of OTUs found with an increasing number of reads sequenced, in each studied rookery in Southeast Galapagos. The vertical lines represent the number of reads, in each rookery, where the coefficient of variation of the rarefaction estimates drops to 0.05.

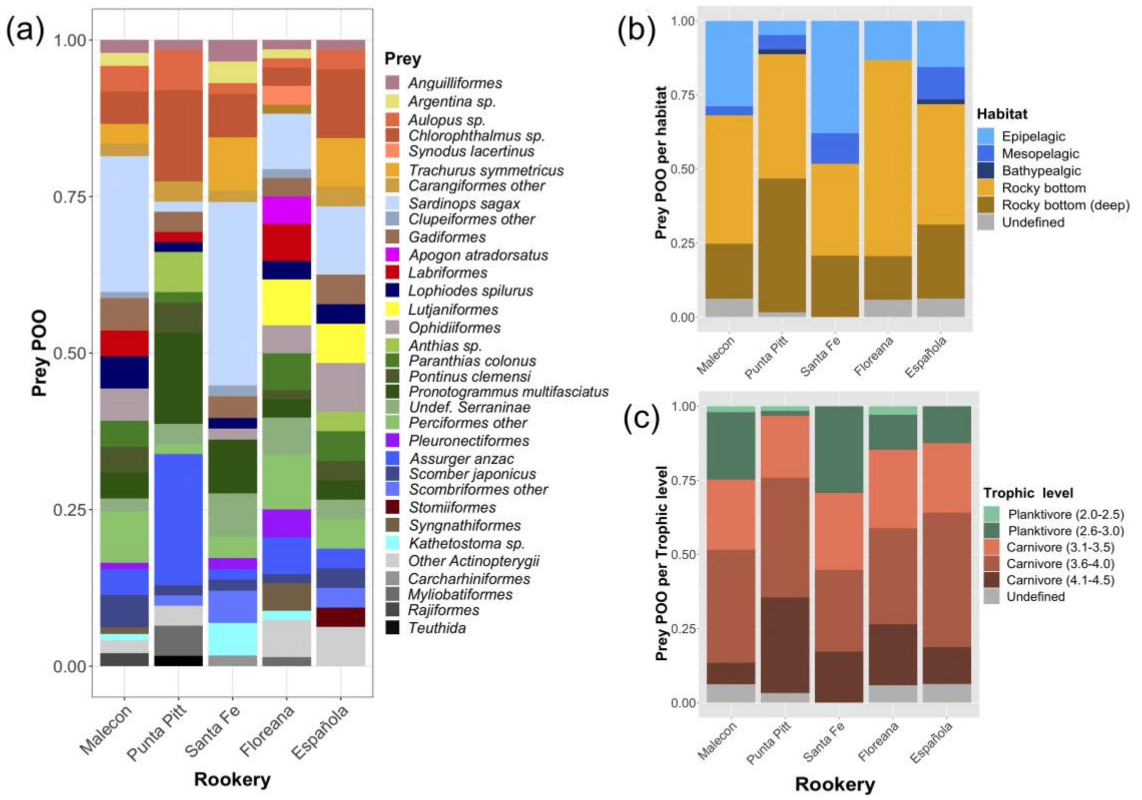

Figure 3. Percent of occurrence (POO) bar plots depicting the relative abundance of different prey across the studied rookeries in Southeast Galapagos. (a) Shows the most important (POO >5% in at least one rookery) prey species/genera, while minor prey is classified by order (if POO between 1 and 5%) or class (if POO <1%). (b) Shows prey classified according to the habitat where these are found: Epipelagic (0-200 mts deep), mesopelagic (200-1000 mts), bathypelagic (1000-3000 mts), rocky bottom (0-200 mts), rocky bottom-deep (>200 mts). (c) Shows prey classified according to the trophic level of these.

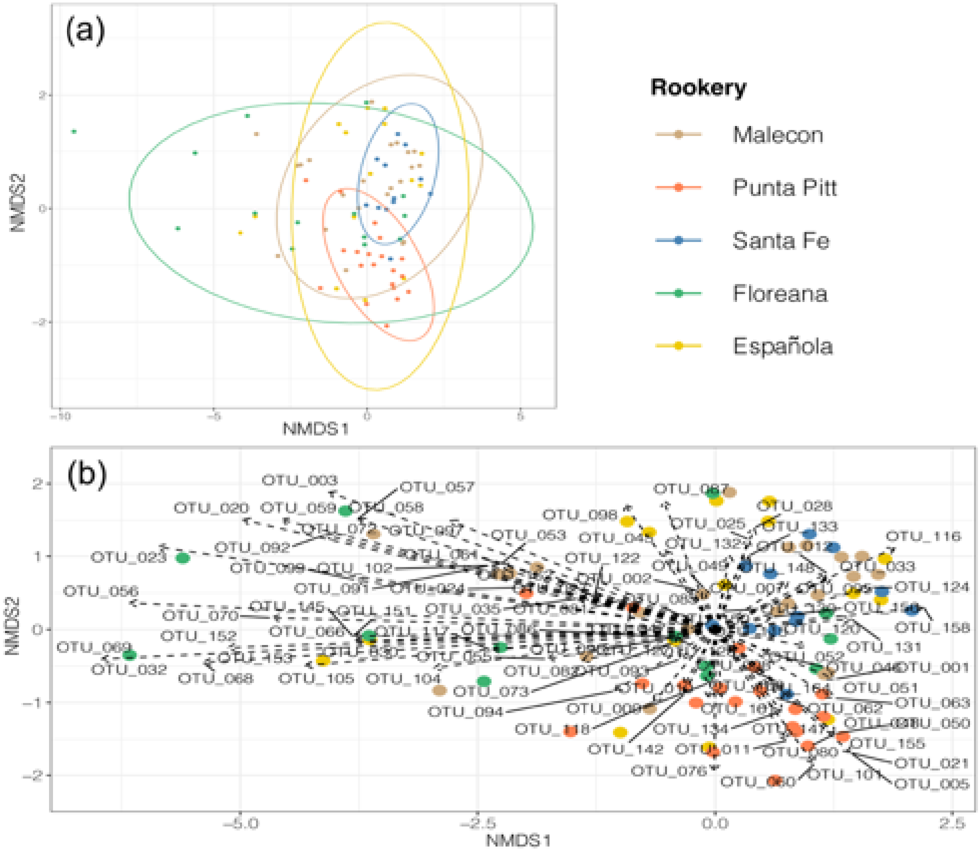

Figure 4. NMDS plot (Jaccard distances; k=3) showing the differences in diet composition among sea lion individuals from different rookeries. The distances plotted among data points reflect well the actual diet differences (stress=0.045). Samples ZP53 and ZF13 were omitted from this analysis as these were outliers stretching the scale of the ordination. (a) NMDS plot showing diet overlaps among rookeries, with 95% confidence ellipses drawn around the individuals belonging to a specific rookery. (b) NMDS plot showing vectors depicting the importance of every prey OTU when differentiating the diets of the studied sea lions (OTU_067 vector was omitted from the plot for a better visualization; this vector had the coordinates -7.95, 1.35).

Supplementary Information

Supplementary File S1. List of all prey OTUs found in this study, as well as the assigned taxonomic ranks, habitat, trophic level, and the total read counts for each of these. The OTUs and numbers shown in this file correspond to those obtained after carrying on all filtering steps

OTU_ID	max_assig_species_taxa	Order	Family	Habitat	Trophic_level	reads_sum
OTU_001	*Gnathophis sp.*	Anguilliformes	Congridae	Rocky bottom	Carnivore (4.1-4.5)	120
OTU_002	*Gnathophis sp.*	Anguilliformes	Congridae	Rocky bottom	Carnivore (4.1-4.5)	30
OTU_003	*Undef. Muraenidae*	Anguilliformes	Muraenidae	Undefined	Undefined	125
OTU_005	*Ophichthus triserialis*	Anguilliformes	Ophichthidae	Rocky bottom (deep)	Carnivore (3.6-4.0)	24
OTU_007	*Undef. Anguilliformes*	Anguilliformes		Undefined	Undefined	21
OTU_008	*Argentina sp.*	Argentiniformes	Argentinidae	Rocky bottom	Carnivore (3.1-3.5)	4416
OTU_009	*Guentherus altivela*	Ateleopodiformes	Ateleopodidae	Rocky bottom (deep)	Carnivore (3.1-3.5)	7
OTU_010	*Aulopus sp.*	Aulopiformes	Aulopidae	Rocky bottom	Carnivore (3.6-4.0)	886
OTU_011	*Chlorophthalmus sp.*	Aulopiformes	Chlorophthalmidae	Rocky bottom (deep)	Carnivore (3.6-4.0)	31693
OTU_012	*Chlorophthalmus sp.*	Aulopiformes	Chlorophthalmidae	Rocky bottom (deep)	Carnivore (3.6-4.0)	7
OTU_020	*Synodus lacertinus*	Aulopiformes	Synodontidae	Rocky bottom	Carnivore (4.1-4.5)	133
OTU_021	*Cheilopogon sp.*	Beloniformes	Exocoetidae	Epipelagic	Carnivore (3.6-4.0)	20
OTU_023	*Undef. Blenniiformes*	Blenniiformes		Undefined	Undefined	8
OTU_024	*Decapterus macarellus*	Carangiformes	Carangidae	Mesopelagic	Carnivore (3.6-4.0)	337
OTU_025	*Decapterus muroadsi*	Carangiformes	Carangidae	Epipelagic	Carnivore (3.1-3.5)	306
OTU_027	*Selar crumenophthalmus*	Carangiformes	Carangidae	Rocky bottom	Carnivore (3.6-4.0)	2833
OTU_028	*Trachurus symmetricus*	Carangiformes	Carangidae	Mesopelagic	Carnivore (3.6-4.0)	731
OTU_030	*Johnrandallia nigrirostris*	Chaetodontiformes	Chaetodontidae	Rocky bottom	Planktivore(2.6-3.0)	256
OTU_032	*Opisthonema medirastre*	Clupeiformes	Clupeidae	Epipelagic	Carnivore (3.1-3.5)	45
OTU_033	*Sardinops sagax*	Clupeiformes	Clupeidae	Epipelagic	Planktivore (2.6-3.0)	126404
OTU_035	*Sardinops sagax*	Clupeiformes	Clupeidae	Epipelagic	Planktivore(2.6-3.0)	4
OTU_045	*Etrumeus acuminatus*	Clupeiformes	Dussumieriidae	Epipelagic	Carnivore (3.1-3.5)	749
OTU_046	*Coelorinchus sp.*	Gadiformes	Macrouridae	Rocky bottom (deep)	Carnivore (3.1-3.5)	1650
OTU_047	*Coryphaenoides sp.*	Gadiformes	Macrouridae	Undefined	Undefined	17
OTU_048	*Gadella sp.*	Gadiformes	Moridae	Rocky bottom (deep)	Carnivore (3.1-3.5)	10
OTU_049	*Laemonema sp.*	Gadiformes	Moridae	Rocky bottom (deep)	Carnivore (3.1-3.5)	9
OTU_050	*Laemonema sp.*	Gadiformes	Moridae	Rocky bottom (deep)	Carnivore (3.1-3.5)	16
OTU_051	*Physiculus rastrelliger*	Gadiformes	Moridae	Rocky bottom	Carnivore (3.1-3.5)	177
OTU_052	*Physiculus rastrelliger*	Gadiformes	Moridae	Rocky bottom	Carnivore (3.1-3.5)	14
OTU_053	*Undef. Gerreidae*	Gerreiformes	Gerreidae	Undefined	Undefined	3555
OTU_055	*Apogon atradorsatus*	Kurtiformes	Apogonidae	Rocky bottom	Carnivore (3.1-3.5)	108
OTU_056	*Bodianus diplotaenia*	Labriformes	Labridae	Rocky bottom	Carnivore (3.1-3.5)	20
OTU_057	*Halichoeres dispilus*	Labriformes	Labridae	Rocky bottom	Carnivore (3.6-4.0)	1150

OTU_058	*Halichoeres nicholsi*	Labriformes	Labridae	Rocky bottom	Carnivore (3.6-4.0)	4155
OTU_059	*Nicholsina denticulata*	Labriformes	Labridae	Rocky bottom	Planktivore (2.0-2.5)	1108
OTU_060	*Scarus ghobban*	Labriformes	Labridae	Rocky bottom	Planktivore (2.0-2.5)	550
OTU_061	*Undef. Labridae*	Labriformes	Labridae	Undefined	Undefined	142
OTU_062	*Lophiodes spilurus*	Lophiiformes	Lophiidae	Rocky bottom	Carnivore (3.6-4.0)	3985
OTU_063	*Lophiodes spilurus*	Lophiiformes	Lophiidae	Rocky bottom	Carnivore (3.6-4.0)	201
OTU_066	*Anisotremus sp.*	Lutjaniformes	Haemulidae	Rocky bottom	Carnivore (3.1-3.5)	642
OTU_067	*Orthopristis cantharinus*	Lutjaniformes	Haemulidae	Rocky bottom	Carnivore (3.1-3.5)	69
OTU_068	*Xenichthys agassizii*	Lutjaniformes	Haemulidae	Rocky bottom	Carnivore (3.1-3.5)	594
OTU_069	*Xenocys jessiae*	Lutjaniformes	Haemulidae	Rocky bottom	Carnivore (3.1-3.5)	42
OTU_070	*Lutjanus sp.*	Lutjaniformes	Lutjanidae	Rocky bottom	Carnivore (4.1-4.5)	2475
OTU_072	*Mugil cephalus*	Mugiliformes	Mugilidae	Rocky bottom	Planktivore (2.0-2.5)	413
OTU_073	*Diaphus sp.*	Myctophiformes	Myctophidae	Undefined	Undefined	15
OTU_076	*Myctophum nitidulum*	Myctophiformes	Myctophidae	Bathypealgic	Carnivore (3.1-3.5)	6
OTU_080	*Diplacanthopoma sp.*	Ophidiiformes	Bythitidae	Rocky bottom (deep)	Carnivore (3.6-4.0)	21
OTU_081	*Brotula clarkae*	Ophidiiformes	Ophidiidae	Rocky bottom (deep)	Carnivore (3.6-4.0)	1869
OTU_082	*Brotula clarkae*	Ophidiiformes	Ophidiidae	Rocky bottom (deep)	Carnivore (3.6-4.0)	41
OTU_085	*Chilara taylori*	Ophidiiformes	Ophidiidae	Rocky bottom	Carnivore (4.1-4.5)	154
OTU_086	*Undef. Ophidiidae*	Ophidiiformes	Ophidiidae	Undefined	Undefined	25
OTU_087	*Undef. Ophidiiformes*	Ophidiiformes		Undefined	Undefined	67
OTU_088	*Caulolatilus princeps*	Perciformes	Malacanthidae	Rocky bottom	Carnivore (3.6-4.0)	4
OTU_089	*Peristedion sp.*	Perciformes	Peristediidae	Rocky bottom (deep)	Carnivore (3.1-3.5)	242
OTU_091	*Chromis alta*	Perciformes	Pomacentridae	Rocky bottom	Carnivore (3.1-3.5)	454
OTU_092	*Stegastes beebei*	Perciformes	Pomacentridae	Rocky bottom	Planktivore(2.6-3.0)	114
OTU_093	*Pontinus clemensi*	Perciformes	Scorpaenidae	Rocky bottom	Carnivore (3.6-4.0)	502
OTU_094	*Pontinus clemensi*	Perciformes	Scorpaenidae	Rocky bottom	Carnivore (3.6-4.0)	391
OTU_095	*Pontinus clemensi*	Perciformes	Scorpaenidae	Rocky bottom	Carnivore (3.6-4.0)	219
OTU_096	*Pontinus sp.*	Perciformes	Scorpaenidae	Rocky bottom	Carnivore (3.6-4.0)	72
OTU_097	*Scorpaena sp.*	Perciformes	Scorpaenidae	Rocky bottom	Carnivore (3.6-4.0)	1972
OTU_098	*Scorpaena sp.*	Perciformes	Scorpaenidae	Rocky bottom	Carnivore (3.6-4.0)	11
OTU_099	*Alphestes immaculatus*	Perciformes	Serranidae	Rocky bottom	Carnivore (3.1-3.5)	574
OTU_101	*Epinephelus labriformis*	Perciformes	Serranidae	Rocky bottom	Carnivore (3.6-4.0)	154
OTU_102	*Liopropoma fasciatum*	Perciformes	Serranidae	Rocky bottom	Carnivore (3.6-4.0)	221
OTU_104	*Paranthias colonus*	Perciformes	Serranidae	Rocky bottom	Carnivore (3.6-4.0)	7800
OTU_105	*Paranthias colonus*	Perciformes	Serranidae	Rocky bottom	Carnivore (3.6-4.0)	42
OTU_115	*Pronotogrammus multifasciatus*	Perciformes	Serranidae	Rocky bottom	Carnivore (3.1-3.5)	4494
OTU_116	*Pronotogrammus multifasciatus*	Perciformes	Serranidae	Rocky bottom	Carnivore (3.1-3.5)	3
OTU_117	*Rypticus sp.*	Perciformes	Serranidae	Rocky bottom	Carnivore (3.6-4.0)	6

OTU_118	*Anthias sp.*	Perciformes	Serranidae	Rocky bottom (deep)	Carnivore (4.1-4.5)	260
OTU_120	*Undef. Serraninae*	Perciformes	Serranidae	Rocky bottom	Carnivore (3.6-4.0)	4113
OTU_121	*Bellator sp.*	Perciformes	Triglidae	Rocky bottom	Carnivore (3.1-3.5)	129
OTU_122	*Prionotus stephanophrys*	Perciformes	Triglidae	Rocky bottom	Carnivore (3.1-3.5)	250
OTU_124	*Citharichthys sp.*	Pleuronectiformes	Cyclopsettidae	Rocky bottom	Carnivore (3.1-3.5)	1879
OTU_127	*Hippoglossina stomata*	Pleuronectiformes	Paralichthyidae	Rocky bottom	Carnivore (3.6-4.0)	46
OTU_128	*Undef. Pleuronectiformes*	Pleuronectiformes		Undefined	Undefined	117
OTU_130	*Seriolella punctata*	Scombriformes	Centrolophidae	Rocky bottom (deep)	Carnivore (3.1-3.5)	239
OTU_131	*Auxis thazard*	Scombriformes	Scombridae	Epipelagic	Carnivore (4.1-4.5)	486
OTU_132	*Scomber japonicus*	Scombriformes	Scombridae	Epipelagic	Carnivore (3.1-3.5)	601
OTU_133	*Thunnus sp.*	Scombriformes	Scombridae	Mesopelagic	Carnivore (4.1-4.5)	17
OTU_134	*Assurger anzac*	Scombriformes	Trichiuridae	Rocky bottom (deep)	Carnivore (4.1-4.5)	24035
OTU_142	*Assurger anzac*	Scombriformes	Trichiuridae	Rocky bottom (deep)	Carnivore (4.1-4.5)	2
OTU_145	*Calamus brachysomus*	Spariformes	Sparidae	Rocky bottom	Carnivore (3.6-4.0)	111
OTU_147	*Vinciguerria sp.*	Stomiiformes	Phosichthyidae	Bathypealgic	Carnivore (3.1-3.5)	5
OTU_148	*Maurolicus sp.*	Stomiiformes	Sternoptychidae	Mesopelagic	Carnivore (3.1-3.5)	9
OTU_150	*Callionymus sp.*	Syngnathiformes	Callionymidae	Undefined	Undefined	7
OTU_151	*Fistularia corneta*	Syngnathiformes	Fistulariidae	Epipelagic	Carnivore (4.1-4.5)	16
OTU_152	*Fistularia commersonii*	Syngnathiformes	Fistulariidae	Rocky bottom	Carnivore (4.1-4.5)	55
OTU_153	*Xanthichthys mento*	Tetraodontiformes	Balistidae	Rocky bottom	Carnivore (3.6-4.0)	257
OTU_155	*Hoplostethus atlanticus*	Trachichthyiformes	Trachichthyidae	Mesopelagic	Carnivore (3.6-4.0)	6
OTU_156	*Kathetostoma sp.*	Uranoscopiformes	Uranoscopidae	Rocky bottom (deep)	Carnivore (4.1-4.5)	1330
OTU_158	*Carcharhinus sp.*	Carcharhiniformes	Carcharhinidae	Rocky bottom	Carnivore (4.1-4.5)	278
OTU_160	*Hypanus dipterurus*	Myliobatiformes	Dasyatidae	Rocky bottom	Carnivore (4.1-4.5)	11
OTU_161	*Aetobatus narinari*	Myliobatiformes	Myliobatidae	Rocky bottom	Carnivore (4.1-4.5)	40
OTU_162	*Undef. Rajiformes*	Rajiformes		Undefined	Undefined	157
OTU_164	*Dosidicus gigas*	Teuthida	Ommastrephidae	Mesopelagic	Undefined	3
					TOTAL	244189

Supplementary File S2. Fasta file containing the sequences of all prey OTUs found in this study

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>OTU_001

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>OTU_115

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