Investigating spatiotemporal variation in the diet of Westland Petrel through metabarcoding, a non-invasive technique

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Abstract

As top predators, seabirds are in one way or another impacted by any changes in marine communities, whether they are linked to climate change or caused by commercial fishing activities. However, their high mobility and foraging behaviour enables them to exploit prey distributed patchily in time and space. This capacity of adaptation comes to light through the study of their diet. Traditionally, the diet of seabirds is assessed through the morphological identification of prey remains in regurgitates. The sampling method is invasive for the bird and limited in terms of resolution. However, the recent optimization of

DNA-based approaches is now providing a non-invasive and more comprehensive and accurate characterization of animals' diet. Here, we used a non-invasive metabarcoding approach to characterize the diet of the Westland petrel (*Procellaria westlandica*), an endangered burrowing species, endemic to the South Island of New Zealand. We collected 99 fresh faecal samples at two different seasons and in two different sub-colonies. Besides from describing the diet of the Westland petrel, our aim was to account for seasonal and spatial variations in the diet of the petrel and assess potential impact with the fishery industry in New Zealand.

We found that amphipods were the most common prey, or secondary prey, followed by cephalopods and fish, suggesting a close link between the composition of prey items and New Zealand's commercial fishing activities but, also, some level of natural predation.

Our results show significant differences in diet between seasons (before hatching vs chick rearing season) and between sampling sites (two sub-colonies 1.5 km apart), which suggests variability and adaptability in the foraging strategy of the Westland petrel.

Due to its non-invasive nature, the method used here can be applied on a great number of samples to draw a comprehensive picture of the diet dynamic in seabirds and unravel their adaptability or ecological requirements. This work demonstrates how dietary DNA (dDNA) can inform the conservation of an endangered species with elusive foraging behaviour. In our example, dDNA provided valuable information regarding the diet preferences of an iconic species contributing to New Zealand's unique biodiversity.

Introduction

The study of animal diets is a critical component in many aspects of ecology, including community ecology (Corse et al., 2010), population dynamics (Morrison et al., 2014; Read and Bowen, 2001) and conservation biology (Lyngdoh et al., 2014; Xiang et al., 2012). In predators, spatial and seasonal variations in diet composition may reflect a certain degree of flexibility in foraging behaviour (Whelan et al., 2000), that could be relevant for understanding trophic interactions and, also, for conserving endangered species (Davies et al., 2001; Farias and Kittlein, 2008; Vander Zanden et al., 2000; Vinson and Angradi, 2011). Shedding light onto these patterns is essential in the case of seabirds, which are top predators within marine ecosystems.

Seabirds are known to modify their feeding habits depending on the time of the year (Harding et al., 2007; Kowalczyk et al., 2015) and their breeding site (McInnes et al., 2017a; Thompson et al., 1999). These birds spend most of their lives at sea but during the breeding season, some remain in coastal areas as their foraging trips are restricted in number and length to allow them to regularly feed their chicks in the nest. To achieve this, seabirds have adopted a variety of foraging strategies (McInnes et al., 2017a; Ydenberg et al., 1994), such as switching between short and long foraging trips to feed their chicks while maintaining their body condition during the breeding season (Baduini, 2003; Ropert-Coudert et al., 2004), or providing the chicks with highly nutritive processed stomach oil (Baduini, 2003). The majority of studies that aim at describing the diet of seabirds have been carried out during the chick rearing period only. Often, this is because data are collected based on the morphological analysis of regurgitates obtained from parents coming back to the nest to feed their chicks (Calixto-Albarrán and Osorno, 2000; Croxall et al., 1988; Klages and Cooper, 1992; Suryan et al., 2002). This approach however, allows considering prey communities as a fixed parameter across time, instead of treating it as a dynamic pattern (Barrett et al., 2007; Komura et al., 2018).

Consequently, many studies do not explore switches in diet, although it is known that the ability to switch to new prey may potentially represent a driver to escape from striking population declines and, even, from local extinctions of threatened populations (Marone et

al., 2017). Many seabird populations have been decreasing rapidly in recent years (Grémillet et al., 2018; Thibault et al., 2019) and detailed knowledge of their diet preferences through space and time is key to understand and better manage current and future threats, including commercial fishing activities or climate-driven changes to their ecosystem (Frainer et al., 2017).

Selecting the correct experimental design and the most efficient methodological approach for the accurate characterization of seabird diet is essential, but also challenging (Ocké, 2013), mainly because direct observations of elusive seabirds (e.g. nocturnal) are difficult and rare. For decades, the morphological identification of stomach contents or regurgitates has been widely used to identify prey items of predators (Carreon-Martinez and Heath, 2010; Egeter et al., 2015; Freeman, 1998; Imber, 1976; Krüger et al., 2014). However, this methodology usually requires that gut content is obtained by stimulating regurgitation after capturing individual birds through a technique that has been called “lavage” (Barrett et al., 2007; Ryan and Jackson, 1986; Wilson, 1984). Such an invasive sampling method (Lefort et al., 2019) is not only unethical, but also potentially dangerous for the birds. Furthermore, the efficiency of this method is usually limited because many individuals would have empty stomachs while sampled, and highly digested prey items may not be identifiable to genus or species level.

The ability to identify prey remains from stomach content also varies in relation to prey species, because some species (in particular soft-bodied prey) are digested faster than others, leading to potential biases in the characterization of the diet (Boyer et al., 2015; Deagle et al., 2007; Gales, 1988). Other standard approaches, such as fatty-acid or stable-isotope analyses, can be used to infer the trophic position of predators in the food web, as well as potential switches in feeding sites (Elsdon, 2010; Hobson and Clark, 1992; Logan et al., 2006; MacNeil et al., 2005; Phillips and Eldridge, 2006; Taipale et al., 2011). Although they provide valuable information about trophic interactions, these methods do not reach a fine-scale resolution, usually lacking genus or species-level identification, which may be critical for the planning of conservation management actions (Bocher et al., 2000; Cherel et al., 2000; Deagle et al., 2007; Guest et al., 2009; Guillerault et al., 2017). In the last decade, parallel to the development and optimization of genomic techniques, DNA metabarcoding

approaches (and specifically dDNA) (de Sousa et al., 2019) have allowed the accurate identification of prey species within the diet of a high variety of taxa including invertebrates (Kerley et al., 2018; Mollot et al., 2014; Pinol et al., 2014; Valentini et al., 2016) and vertebrates (Andriollo et al., 2019; Guillerault et al., 2017; Kamenova et al., 2018; Leray et al., 2015; Sullins et al., 2018).

The Westland petrel (*Procellaria westlandica*) is endemic to New Zealand and listed as an endangered species on the IUCN red list (BirdLife International, 2020). It is one of the few burrowing birds breeding on the main islands of New Zealand. This iconic species was once widespread in New Zealand (Waugh and Wilson, 2017; Wood and Otley, 2013), but its breeding distribution is now restricted to the West Coast of the South Island, within the Paparoa National Park and its surroundings (Jackson, 1958; Waugh and Wilson, 2017) . Between May and June, females lay a single egg, which is incubated by both parents during 69 days (Warham, 1990). Chick rearing is also carried out by both parents between September and November. After the breeding season, Westland petrels travel to South American waters (Baker and Coleman, 1977), where they remain until late March (March to November) (Landers et al., 2011). Regarding their foraging behaviour, Westland petrels are known to be nocturnal, but they occasionally feed during daytime (Waugh et al., 2018). Previous studies based on morphological analysis of regurgitates found that their most abundant prey items were fish, followed by cephalopods and crustaceans (Freeman, 1998; Imber, 1976). The diet of Westland petrels is therefore closely linked to fishing activity in New Zealand waters. However, it remains unclear whether fishing has a net positive or negative impact on *P. westlandica*. The overall population has increased significantly since the 70's (Wood and Davis, 2003; Wood and Otley, 2013), together with the rise of fishing activity, potentially because of increase feeding on bycatch and other fishing waste. However, being trapped and killed in fishing nets is one of the main threats of *P. westlandica*, together with mammal predation, degradation of habitat and erosion of their nesting grounds (Taylor, 2000; Waugh et al., 2008; Waugh and Wilson, 2017).

Although the diet of the Westland petrel has been assessed before (Freeman, 1998; Imber, 1976), the precise composition of their current diet is unknown, as is potential temporal variations in diet throughout the breeding season. In this work, we present the first attempt

147 to characterize the diet of this seabird through a DNA-based approach. To do this, we used a
148 non-invasive DNA sampling approach (Lefort et al., 2019) by collecting faecal samples, and
149 carried out a DNA metabarcoding analysis using the 16S gene to identify prey items within
150 the diet of the Westland petrel. This amplicon was chosen for the study as it has shown to
151 be effective for the characterization of seabirds' diet (Komura et al., 2018; McInnes et al.,
152 2017; Young et al., 2020). The birds' diet was compared between two breeding sub-colonies
153 (1.5 km apart), and two different times (10 weeks apart). We expected to find differences in
154 diet between early breeding season (before hatching) and late breeding season (after
155 hatching or chick rearing), which would be consistent with switches in feeding and foraging
156 behaviour. We expected to find no significant differences in the diet of the different sub-
157 colonies owing to their relatively close proximity. Moreover, this study also aims to better
158 understand the impact that fishing activities could have on Westland petrels.
159

160 **Material and Methods**

161 *Study area and sample collection*

162 A total of 99 faecal samples were collected from two different sampling sites located in the
163 West Coast of the South Island of New Zealand, the Paparoa National Park (NP) (-42.146317,
164 171.340293) (49 samples) and a private land (PL) (-42.164358, 171.337603) (50 samples)
165 (Table S1). The collected samples were very fresh and usually line-shaped, which could only
166 correspond to faeces produced by birds as they landed on the previous day. Hence, each
167 bird could only produce one of these faeces, and samples were considered independent.
168 Very few older faecal samples were observed on the sites, as these were probably rapidly
169 washed away in this extremely rainy location.
170 Forty-eight samples were collected before hatching (BH) on the 9th and 10th of July 2015,
171 and 51 samples were collected during chick rearing (CR) on the 22nd and 23rd of September
172 2015 (Table 1). To avoid cross-contamination, each fresh faecal sample was collected using
173 an individual sterile cotton swab and placed in a clean, single-use Ziplock bag. Samples were
174 then placed in a cooled icebox for transportation to the laboratory (within the following two
175 days), where they were stored at -80°C until DNA extraction. Leaf litter samples were also
176 collected to serve as negative controls.
177

178 *DNA extraction, PCR amplification and sequencing*

179 For each faecal sample, we performed a DNA extraction on one small subsample collected
180 with a cotton swab. We used the QIAamp DNA Stool Mini Kit (Trevelline et al., 2018, 2016)
181 for which we followed the manufacturer's protocol (Handbook from 03/2014, reference:
182 1081060_HB_LS) with few modifications. In brief, half volumes of all reagents were used
183 and the extraction was carried out in 1.5 ml tubes, instead of 2 ml tubes. Also, after adding
184 half an InhibitEx Tablet, we performed only one centrifugation, rather than 2 (Steps 6 and 7
185 in the protocol were joined). Later, on step 13, we mixed 200 µl of ethanol by pipetting and
186 600 µl of the mix were added to the column. From step 14, volumes recommended by the
187 manufacturer's protocol were used. Finally, samples were eluted in 100 µl of elution buffer
188 (AE) and DNA extracts stored at -20°C.

189

190 Later, two different PCR amplifications were performed from each DNA extract. First, we
191 used a pair of primers specific for Chordata (fish) (16S1F, 16S2R), which amplifies 155 bp of
192 the 16S gene (Deagle et al., 2009, 2005). Second, we used a pair of primers designed for
193 Malacostraca (crustaceans) (Chord_16S_F_TagA, Chord_16S_R_Short) (Deagle et al., 2009)
194 but also known to amplify cephalopods in an efficient manner (Olmos-Pérez et al., 2017),
195 which amplifies 205 bp of the 16S gene (Deagle et al., 2009). These two pairs of primers
196 were chosen to allow the detection of a wide range of potential prey, including the main
197 taxa identified morphologically in previous studies, namely fish, cephalopods and
198 crustaceans (Freeman, 1998; Imber, 1976). PCR conditions for both primer pairs were the
199 same as in Olmos-Perez et al. (2017), with the exception of the Taq polymerase. Here, the
200 FirePOLE® Taq polymerase was used for all amplifications, following manufacturer's
201 protocol (Solis BioDyne). Negative controls containing DNA-free water were added to each
202 PCR run. After checking the results in a 1.5% agarose gel, PCR products were purified using
203 AMPURE magnetic beads, following the manufacturer's standard protocol and, finally, for
204 each sample, both PCR products were pooled. Second stage PCR amplifications and
205 subsequent sequencing steps were carried out by New Zealand Genomics Limited (NZGL,
206 University of Otago) according to the Illumina "16S Metagenomic Sequencing Library
207 Preparation Manual" Rev B. The resulting amplicons indexed with Nextera adapters (Index
208 Set C) in unique combinations were arranged in two plates. Each plate also included a 16S
209 mock community sample using Index Set D.

210 Sequencing was performed by NZGL on Illumina MiSeq 2x300bp reads (Illumina MiSeq v3
211 8reagent kit).
212
213 *Bioinformatic library filtering*
214 Metabarcoding library filtering was performed using a toolbox of software (Creedy et al.,
215 2019). First, we trimmed the two pairs of primers separately using *cutadapt* (Martin, 2011),
216 leaving the maximum error rate as default (e=0.1). At this point, we had two sets of trimmed
217 sequences. The following filtering steps were done twice in each pair of primers. Pair reads
218 were merged using PEAR (Zhang et al., 2014), setting the minimum quality threshold (*Phred*
219 score) at 30 (-q 30). After merging, all sequences were merged into a single *fastq* file using
220 the *sed* command and all the subsequent steps were performed using *vsearch v2.8.1*
221 (Rognes et al., 2016). This step was followed by the quality rate filtering, which aims to
222 remove all sequences with sequencing errors, using the *fastx_filter* command
223 (*fastq_maxee*=1). The library was dereplicated using the *derep_fulllength* command and,
224 after, frequency errors were detected and deleted using again the *fastx_filter* command
225 (*minsize*=2) in order to delete the singletons, as such low frequency variants are likely to be
226 PCR errors. The following step was filtering sequences by length (indel filtering) with the
227 command *fastx_filter* (*fastq_minlen*=50, *fastq_maxlen*=325). At this stage, merged
228 sequences that were shorter than 50bp or longer that 400bp were discarded. This step was
229 followed by the filtering *de novo* of potential chimeras using the *uchime_denovo* command.
230 After this step, we obtain a *fasta* file, with Amplicon Single Variants (ASVs). Next, we
231 performed the Operational Taxonomic Unit (OTU) picking, applying the centroid-based
232 greedy clustering algorithm with a cut-off threshold of 97% (Xiong and Zhan, 2018) using the
233 *cluster_size* command (*id* 0.97), and obtained a *fasta* file with all the OTUs present in the
234 sampling. Finally, we mapped a by-sample reads to OTUs in order to obtain an OTU table,
235 using *usearch_global* command. Thus, at this point of the pipeline, we obtained two output
236 files, an OTU table and a *fasta* file with the subsequent sequence of all the clustered OTUs.
237
238 All OTUs were compared to the NCBI database using BLASTn (Johnson et al., 2008) and the
239 pertinent multiple-file JSON was downloaded from the web interface. We then used a
240 customized R script, based on the functions *fromJSON* and *classification* from R packages
241 *rjson* (Couture-Beil and Couture-Beil, 2018) and *taxize* (Chamberlain and Szöcs, 2013),

242 respectively, to assign a taxonomic classification to each clustered OTU. Moreover, we
243 performed SINTAX classification against the MIDORI database (Leray et al., 2018). For that
244 purpose, we used the *vsearch* commands *makeudb_search* and *sintax*, to convert the
245 database, which was downloaded from the MIDORI website in *fasta* file, into database
246 format and classify our OTUs, respectively.
247
248 Regarding taxonomic assignment, OTUs with BLAST query coverage under 60% or BLAST
249 identities lower than 75% were discarded. Reads present in the negative control were
250 substracted to each sample, as they were considered as potential contaminations. Also,
251 singletons among samples and OTUS were also considered as potential contamination and
252 removed from the dataset as were any OTUs matching to Westland Petrel. A manual filter
253 was also carried out in the taxonomic assignment table, discarding every OTU which could
254 not be a potential prey for biological reasons. Potential prey OTUs within the phyla
255 Arthropoda,Chordata and the Mollusca families Octopodidae and Histiotheutidae were
256 assigned using the following criteria to taxonomical categories: OTUs with identity higher
257 than 97% were determined at species level, OTUs between 93 and 97% were assigned to
258 genus level, and OTUs with identity below 93% were assigned to family level. In the case of
259 the Mollusca family Loliginidae, OTUs were aligned with 100 Loliginidae sequences retrieved
260 from Genbank (Benson et al., 2012). The 16S fragment was exactly the same for several
261 genus of this family, meaning that this amplicon fragment has not enough resolution to
262 resolve genus and species identity within this family. Thus, OTUs matching the Loliginidae
263 family were only assigned to family level, regardless of their percentage of identity retrieved
264 from the BLASTn taxonomic assignment.
265
266 *Biodiversity analyses*
267 In order to evaluate the impact of commercial marine species on the diet of *P. westlandica*,
268 we collected ecological information from Fishbase (Froese and Pauly, 2010) and Sealifebase
269 (Palomares and Pauly, 2010) to determine the distribution of each prey taxa. Considering
270 that *P. westlandica* is able to dive up to 15 m for fishing (Waugh et al., 2018), we specifically
271 looked for information about the depth at which the prey species is usually present (shallow
272 versus deep sea) and therefore naturally reachable for the Westland petrel. We also
273 checked whether those prey species had been detected in previous publications (Table 1).

To measure the completeness of our sampling, we evaluated the total richness of prey in the diet of *P. westlandica*, using a rarefaction curve and a bootstrap estimator using the function *specpool* in the R package *vegan* (Oksanen et al., 2013). Moreover, as a measure of the quality of our sequencing, we plotted the number of sequence reads per OTU detected and the cumulative frequency of sequence reads per OTU detected. The diet of Westland petrels was described using two different metrics. First, we calculated the Frequency of Occurrence (FOO), which gives the information about the number of samples in which an OTU is present. This was calculated by transforming the number of reads to presence/absence (1-0) and, subsequently, summing the counts of samples that contain a given prey item (OTU), expressed as a proportion of all samples (Deagle et al., 2019). Second, we calculated the Relative Read Abundance (RRA), which is the proportion of reads of each prey item (OTU) in each sample (Deagle et al., 2019), which was calculated using the OTU table of abundances. Both metrics were computed with customized scripts using the R package *dplyr* (Wickham et al., 2021). These two metrics are different proxies, FOO is a proxy for occurrence and RRA is a proxy for relative food biomass (Cavallo et al., 2018; Deagle et al., 2019). FOO and RRA were calculated overall to describe the diet of Westland petrels as a species, and also compared between seasons: before hatching (BH) versus chick rearing (CR); and between sub-colonies: natural park (NP) versus private land (PL).

To estimate the effects of seasonality and sub-colony location on diet diversity and composition, we computed a negative binomial Generalized Linear Model (GLM) (McCullagh and Nelder, 1989) with a log link function, applying the function *manyglm* from the R package *mvabund* (Wang et al., 2017). Two different GLM analyses were performed, one with abundance as the dependant variable (using the OTU table of abundances, as for computing RRA) and one with occurrences as the dependant variable (as for FOO calculations). For both GLM analyses, the predictor variables were season (two factor levels: BH and CR) and site (two factor levels: NP and PL) as well as the interaction between these variables. An analysis of Deviance (Dev) was performed to test the fitness of the model, with 999 bootstraps iterations as a resampling method (Davison and Hinkley, 1997), using the function *anova.manyglm* from the package *mvabund* (Wang et al., 2017). Moreover, an ordination to visualize the differences in community composition between the two seasons

305 (BH and CR) and the two sub-colonies or sites (NP and PL) was computed and plotted using
306 the *cord* function from the R package *ecoCopula* (Popovic et al, 2021).
307
308 Finally, we estimated and plotted the standard alpha diversity, as a proxy for prey species
309 richness, comparing the two factors studied, season and site. For that purpose, we used the
310 functions *diversity* and *plot_richness* from R packages *vegan* and *phyloseq* (McMurdie and
311 Holmes, 2012; Oksanen et al., 2013), respectively. In addition, we computed pairwise
312 comparisons between the alpha diversity values (Simpson) of the group levels through the
313 pairwise Wilcoxon rank sum test (Gehan, 1965), using the function *pairwise.wilcox.text* from
314 the R package *stats* (Team and others, 2013) .
315

316 **Results**

317 *Amplification success and library quality*

318 All 98 samples were successfully amplified with both pairs of primers and sequenced with
319 Illumina MiSeq. We obtained a total of 9,847,628 raw reads. After trimming with *cutadapt*
320 the Malacostraca pair of primers (Deagle et al., 2005), we obtained 7,085,188 reads and
321 3,010,097 merged reads (84,97% of the raw data was merged). In the next step, we
322 obtained 3,010,097 quality filtered reads, which resulted in 150,973 dereplicated unique
323 sequences. Finally, after indel and chimera filtering, we obtained 31,691 ASVs, which were
324 clustered in 1,147 OTUs (Fig.S1). In the case of the Chordata pair of primers, after trimming
325 we obtained 321,240 reads which resulted in 20 OTUs, in which only 1 OTU with 3 reads was
326 different from the OTU set obtained with the Malacostraca pair of primers. Thus, the
327 sequences from the Chordata primers were discarded, and only the reads obtained with the
328 Malacostraca pair of primers were retained for subsequent analyses. The 1,147 OTUs
329 comprised 2,567,254 reads, from which 127,088 were discarded manually as they were
330 considered as contaminants (not potential prey), 560,586 reads were considered as low-
331 quality assignment (query cover < 60% and percentage of identity < 75%), 1,371,994 reads
332 did not match against Genbank and, 507,231 were considered as the reads of potential prey
333 of the Westland petrels. These prey reads belonged to 79 OTUs (Table 1), and 17 samples
334 had only unassigned or undetermined OTUs and, hence, were not used in the subsequent

335 analyses. We were not able to recover any additionnal assignment from MIDORI compared
336 to those obtained from Genbank. Thus, this information was discarded.
337
338 *Characterization of the diet of* P. westlandica
339 Species richness estimation (using bootstrap) suggested that our sampling captured 89.2%
340 of the total diversity of prey items within the diet of *P. westlandica* (Fig.S2). The number of
341 sequence reads per OTUs detected (Fig.S3) and the cumulative frequency of the OTUs
342 detected (Fig.S4) are both measures of sequence depth, which was enough to characterize
343 the diet of the Westland petrel. Out of the 79 OTUs recovered by metabarcoding, 24.02%
344 (19 OTUs, 195,358 reads) were identified to species level, 29.11% (23 OTUs, 222,447 reads)
345 were identified to genus level and 100% (56 OTUs, 316,587 reads) were identified to family
346 level (Table 1).
347 Globally, arthropods (crustaceans in this case) were the most common potential prey in the
348 diet of Westland petrels. In total, they were present in 62.03% of the samples (FOO) and
349 represented 45.57% of the sequences (RRA) and 65.82% of the OTUs. Actinopterygii (bony
350 fish) were next, being present in 59.49% of the samples and comprising 42.13% of all
351 sequences and 24.05% of all OTUs. Finally, cephalopods were present in 53.16% of the
352 samples and made up 12.29% of the sequences and 10.12% of the OTUs (Fig.1). Within
353 arthropods, talitrids (landhoppers and sandhoppers) were by far the most abundant taxa.
354 They were present in 58.23% of the samples and made up 44.35% of the sequences. Other
355 minor arthropod taxa were identified, such as the families Pilumnidae (pilumnid crabs) and
356 Penaeidae (penaeid shrimps), among others (<1% total reads; Table 2). With the exception
357 of four OTUs, which were identified to species level, arthropods were identified to family
358 level.
359
360 Within Chordata (ray-finned fish in this case), Hoki (*Macruronus novaezelandiae*) was the
361 most common species as it was present in 26.58% of the samples and represented 10.5% of
362 all sequences. The Cocky gurnard (*Lepidotrigla modesta*) and the Southern hake (*Merluccius*
363 *australis*) were also important prey items, being present in 18.99% and 17.72 % of the
364 samples and comprising 9.69% and 10.01% of all sequences, respectively. Next were
365 cutlassfish, identified to family level (Trichiuridae), and the Thorntooth grenadier
366 (*Lepidorhynchus denticulatus*) both present in 11.39% of the samples and comprising 5.77%

and 3.8% of all sequences, respectively. As in the case of arthropods, we detected few other minor taxa, such as the Pink cusk-eel (*Genypterus blacodes*) or the Hawknose grenadier (*Coelorinchus oliverianus*), among others (around 1% reads: Table 2; Fig.2). Out of 19 OTUs of Actinopterygii, three OTUs were identified to genus level, two OTUs were identified to family and the remaining 13 OTUs were identified to species level (Table 1).

According to our results, within cephalopods, eight different OTUs were identified as prey items, six of them were assigned to family level, one to genus level and one to species level (Table 1). The most common cephalopod prey item was the Common Octopus (*Octopus vulgaris*), which was present in 32.91% of the samples, followed by the pencil squids (family Loliginidae), present in 31.65%. However, in terms of number of reads, pencil squids comprised 7.68% of all reads and octopodids 4.46% of them. Finally, Oegopsida squids (Family Histiotheutidae) were present in 2.53% of the samples but comprised less than 1% of the reads (Table 2; Fig. 2).

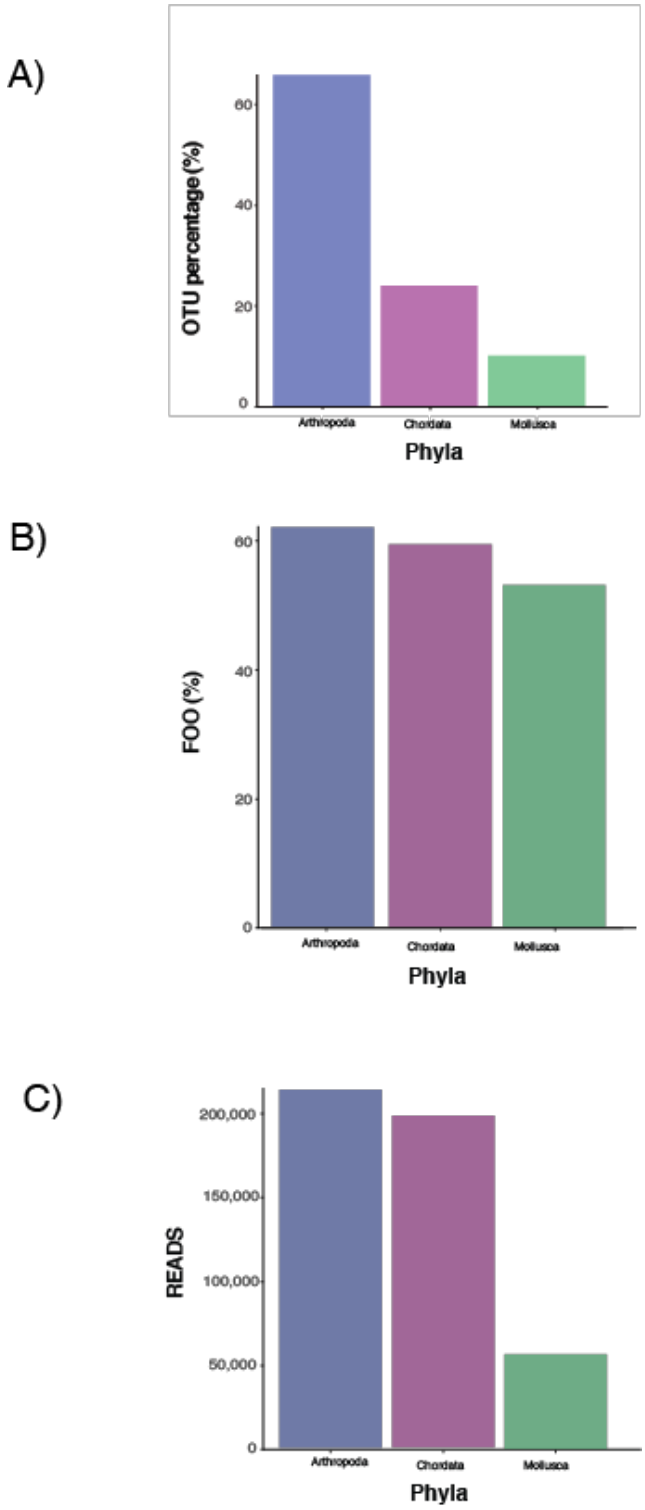
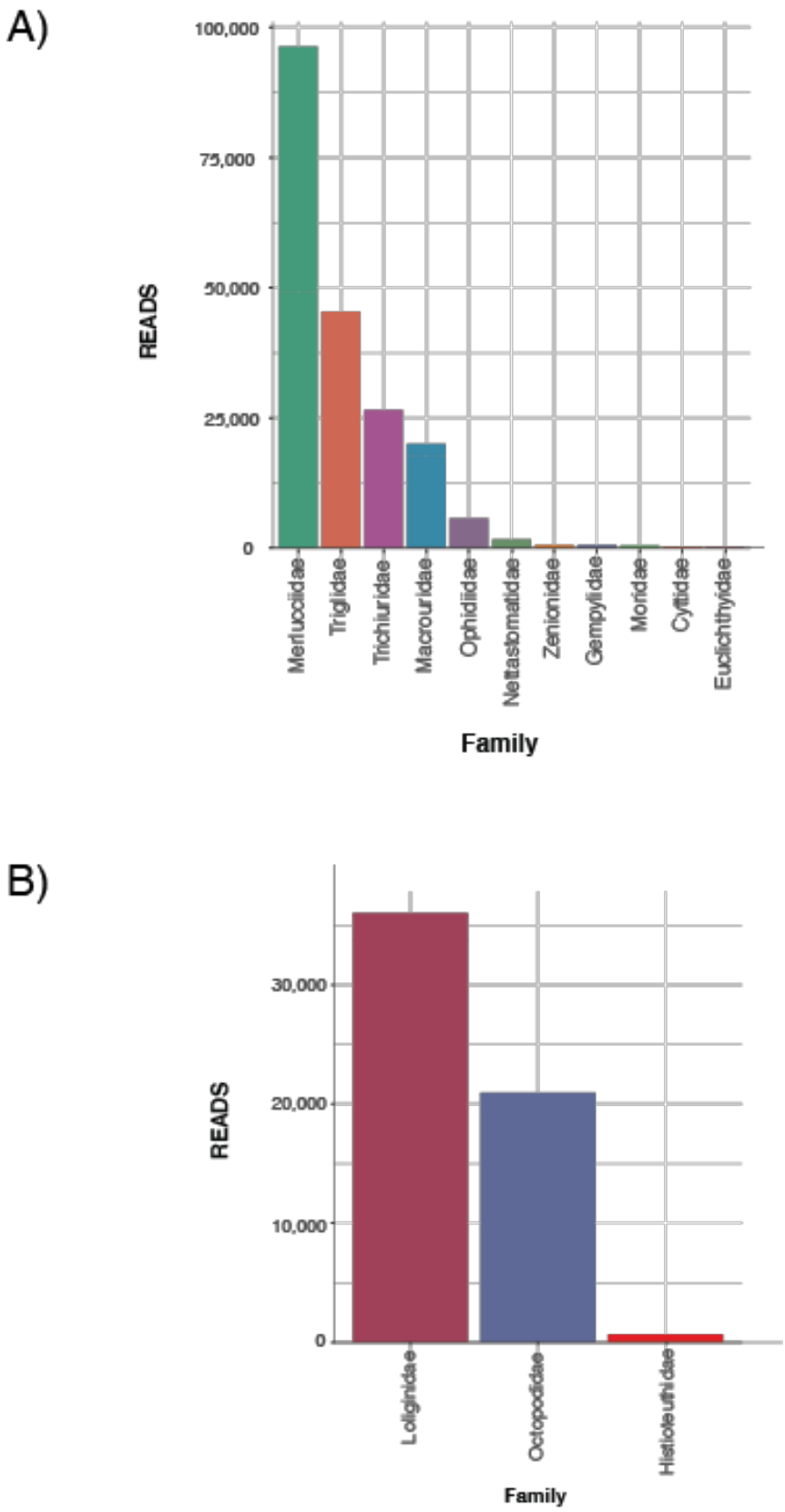


Figure 1. Prey phyla identified using three different biodiversity metrics: A) Number of OTUs as a proxy of diversity, B) Frequency of occurrence (FOO) refers to the percentage of samples in which the prey item is present and C) Read abundance .



387

388 **Figure 2**. Read abundance classified by family for A) Fish prey items B) Cephalopod prey items

389

390

Seasonal variation in the diet of P.westlandica

According to Frequency of Occurrence (FOO) and Relative Read Abundance (RRA), our results show important differences between seasons (Fig. 3) and between sampling sites (Fig.4).

Prey community composition varied significantly between the two different seasons both in terms of read abundance ($Dev_{1,79} = 232.5$, $p = 0.004$) and prey occurrence ($Dev_{1,79} = 189.2$, $p = 0.004$) (Fig. 3). These differences are also shown in the graphical ordination by the different colours of the samples belonging to both seasons (Fig. S5).

When looking at frequency of occurrence, during the early breading season (before hatching), merluccids were the most common prey, followed by talitrids and then by cephalopods (pencil squids and octopuses showing the same value of FOO). In contrast, during the late breading season (chick rearing), talitrids were the most common prey followed by octopodids and pencil squids (Table 2; Fig.3A). A similar pattern was observed for relative read abundance, although with greater differences in the metric values (Table 2; Fig.3B).

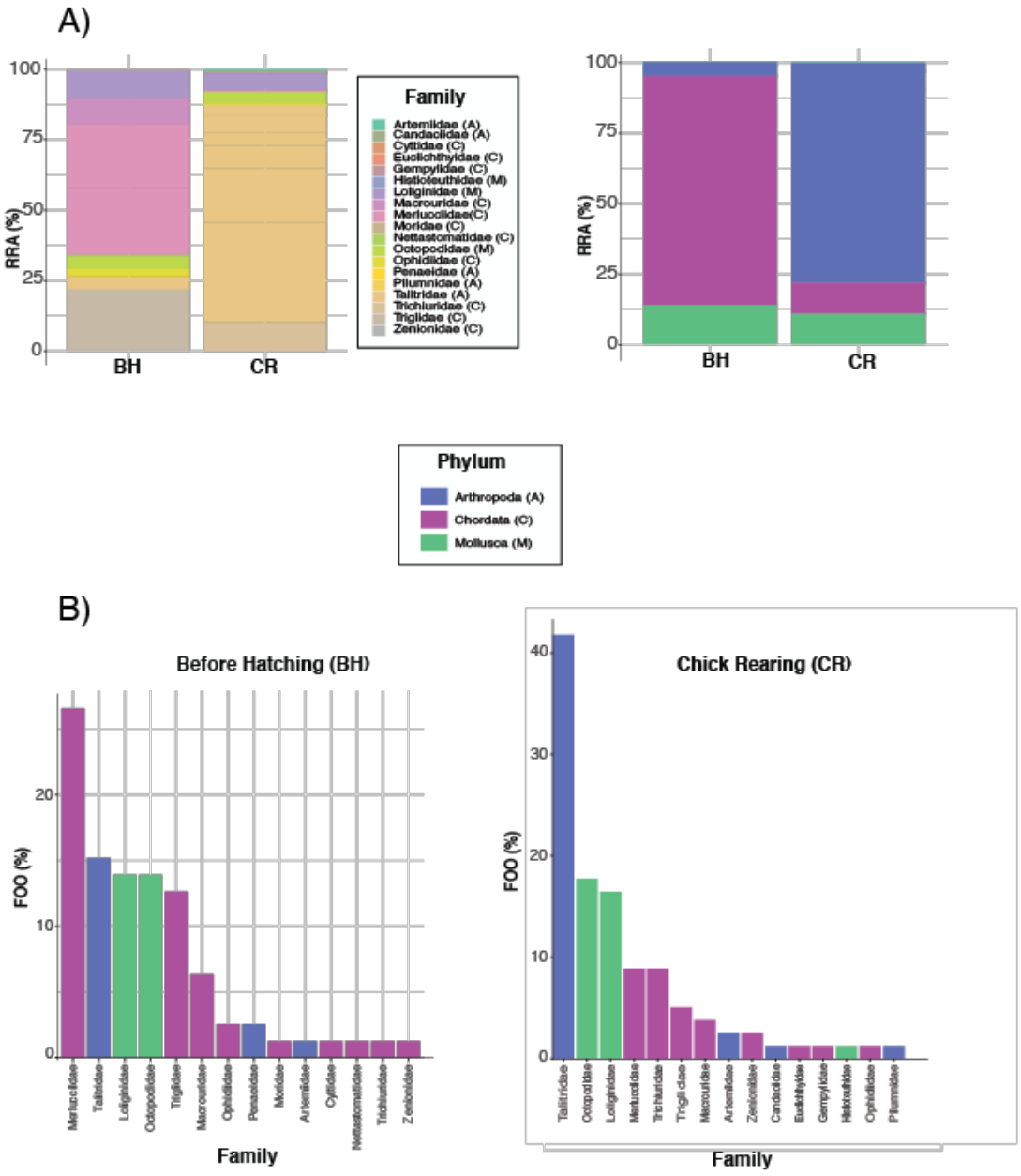


Figure 3. Seasonal variations at family level between the early breeding season or before hatching (BH) and the late breeding season or chick rearing (CR), according to two biodiversity metrics: A) Relative Read Abundance (RRA) and B) Frequency of Occurrence (FOO). Taxa with less than 1% of FOO or RRA were not included in the plots.

Talitrids were the most common prey group overall and during Chick Rearing (CR), representing more than 99% of all arthropods identified in this study. Although a minor prey, the Banana shrimp (*Penaeus merguiensis*), was present in 2.53% of samples before hatching but it was absent during the chick rearing season. In the same way, the Bristly crab

419 (*Pilumnus hirtellus*) and *Candacia armata* comprised both 1.27% of samples before hatching
420 and were absent during chick rearing (Table 2).
421 Fifteen OTUs of Actinopterygii fish were identified in the samples collected before hatching
422 (13 identified at species level and 2 at family level), compared to 9 OTUs (corresponding to 8
423 species) during the chick rearing season. Hoki was the most common fish species detected
424 before hatching, followed by Cocky gurnard and Southern hake. During the chick rearing
425 season, Trichiuridae fish were the most common followed by Southern hake and Cocky
426 gurnard (both showed the same FOO value).
427 With regards to cephalopods, Pencil squids (Loliginidae) and octopodids (Octopodidae) were
428 present in the same number of samples, while, during the chick rearing season, octopodids
429 were most common than pencil squids. Interestingly, an Oegopsida squid (Histioteuthidae)
430 was also detected during the chick rearing season while it was completely absent before
431 hatching (Table 2; Fig.3A and B).
432 Regarding species richness, the values of alpha diversity (Simpson) were not significantly
433 different between seasons, with lower diversity observed before hatching (α [mean ± SE] =
434 0.31 ± 0.05) compared to the chick rearing season (α [mean ± SE] = 0.28 ± 0.04) (Fig.5).
435
436 *Geographical variation in the diet of* P.westlandica
437 Significant differences in prey community were observed between the two sub-colonies,
438 both in terms of read abundance ($Dev_{1,79}$ = 203, p = 0.002) and occurrence of prey items
439 ($Dev_{1,79}$ = 172.6, p = 0.003) (Fig. 4). Differences in community composition between sub-
440 colonies are shown in the ordination biplot, represented by different shapes (Fig.S5).
441
442 Arthropods (talitrids) were found to be by far the most commonly detected prey group in
443 the sub-colony located within the Paparoa National Park (NP), followed by octopodids and
444 pencil squids. In contrast, in the Private Land (PL), merluccids were the most common group
445 of prey, followed by talitrids and pencil squids.
446 Eleven OTUs of Actinopteriigy were identified in samples collected in the PL (10 identified at
447 species level and 1 at family level), while 17 OTUs (15 identified at species level and 2 at
448 family level) were found in the NP. Cutlassfish (family Trichiuridae) were the most common
449 prey within NP, followed by Hoki, Southern hake and Cocky gurnard. In PL samples,

however, Hoki was the most common fish item taxa, followed, in this case, by Cocky gurnard and Southern hake (Table 2).

With regards to cephalopods, Common Octopuses were the most common group followed by pencil squids in NP, and both were present in the same number of samples in PL. In terms of read abundance, pencil squids were slightly more abundant than Common Octopuses in NP and the same pattern is shown in PL. (Table 2; Fig.4A and B).

In contrast to seasonal variation, no significant differences in species richness (alpha diversity) were observed in prey diversity when comparing the two sub-colonies NP (**α** [mean ± SE] = 0.31 ± 0.05) and PL (**α** [mean ± SE] = 0.28 ± 0.04) (Fig.5).

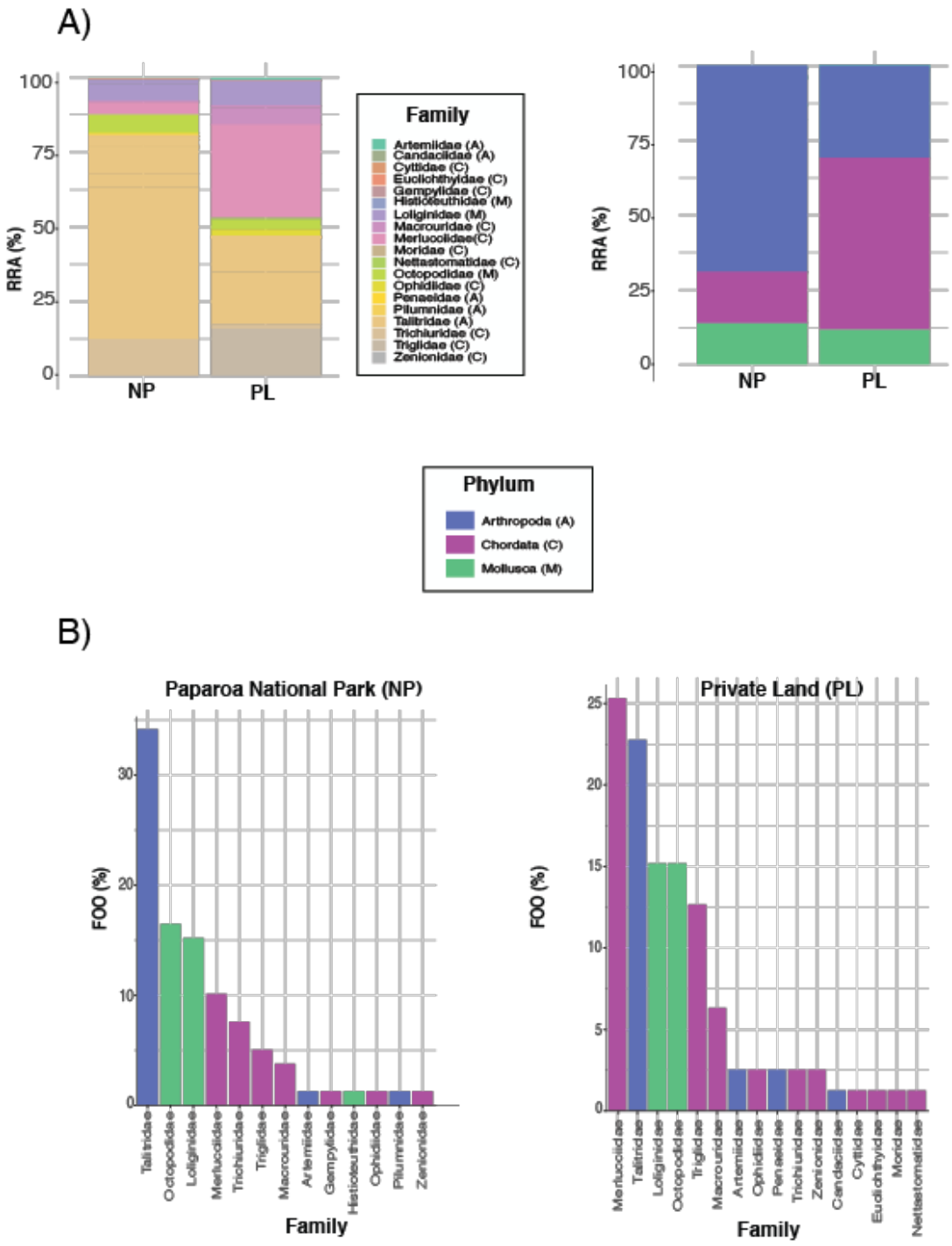


Figure 4. Geographical variations at family level between the two sub-colonies: the Paparoa National Park (NP) and the private land (PL), according to two biodiversity metrics: A) Relative Read Abundance (RRA) and B) Frequency of Occurrence (FOO). Taxa with less than 1% of FOO or RRA were not included in the plots.

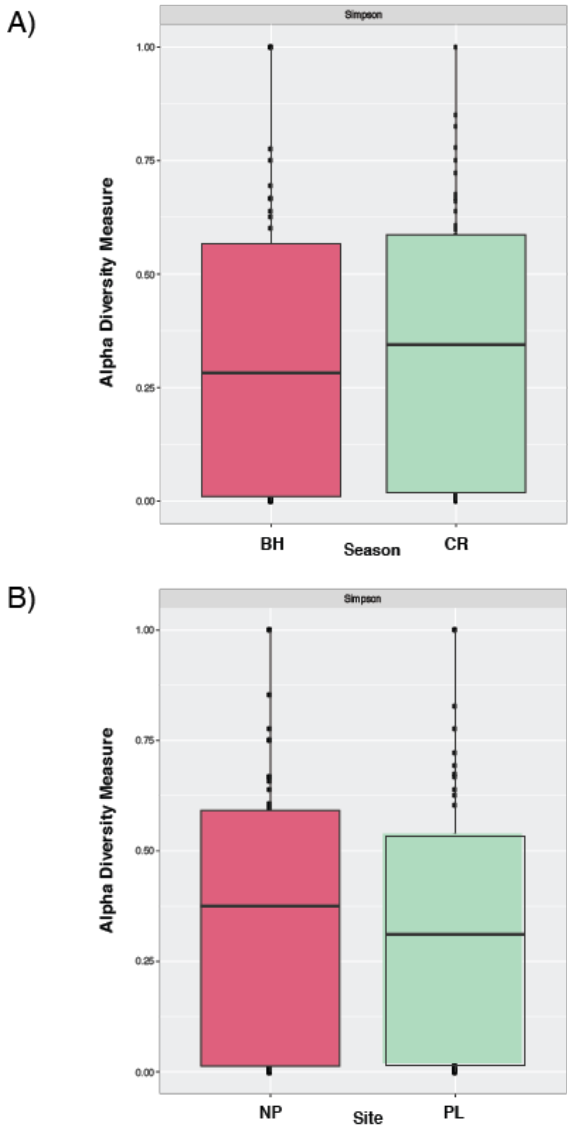


Figure 5. **A)** Seasonal and **B)** geographical differences in prey items according to alpha diversity measures.

Discussion

This is the first attempt to characterize the diet of the New Zealand endemic Westland petrel using a DNA metabarcoding approach. Aside from the molecular non-invasive approach, the novelty of this study lies in the analysis of samples from multiple seasons and sub-colonies. Although metabarcoding is a valuable tool in conservation genomics, it is still not a flawless approach. In our approach, we were able to infer almost 90% of the prey species within the diet of the Westland petrel, however, the resolution of the amplicon was insufficient for assigning amphipods to species level. This limitation may be due to the short size of the amplicon and/or the incompleteness of existing genetic databases (Pompanon et al., 2012). In addition, the two primer pairs approach proved unnecessary as the Chordata

primer pair was did not add any valuable information to the data set obtained with the Malacostraca primer pair. This underlines the need of further optimization of metabarcoding pipelines to minimize efforts and obtain the most realistic set of biological sequences that would represent the community or environment of interest.

The observed seasonal and geographical variations in the diet of *P. westlandica* provide a broad picture of the feeding requirements and foraging ecology of this species. Previous works on the diet of *P. westlandica* were based on morphological identification of prey remains and carried out exclusively during the breeding or chick rearing season (Freeman, 1998; Imber, 1976). Our study shows the presence of fish, cephalopods and amphipods (crustaceans) in the diet of *P. westlandica*, confirming the results of previous approaches (Freeman, 1998; Imber, 1976). However, the relative importance of each type of prey differs considerably between these studies and the current work, where we identified a number of taxa undetected before in such high proportions.

The phylum showing the highest percentage of prey reads was Arthropoda (45.57% of the reads, compared to 42.14% of reads for fish). These were mainly represented by talitrids (landhoppers or sandhoppers) (order Amphipoda). These animals can range from 1 mm to 34 cm in size. However, most species are microscopical benthic zooplankton and are known to be common prey of many cephalopods (Villanueva et al., 2017) and fish, including Hoki (Connell et al., 2010; Livingston and Rutherford, 1988) and Hake (Dunn et al., 2010). Therefore, Amphipods detected in this study could potentially be secondary prey. However, several seabirds such as penguins feed regularly on amphipods (Jarman et al., 2013; Knox, 2006), and large amphipods could potentially represent a fundamental food source for Antarctic seabirds (Centro de Investigacion Dinamica de Ecosistemas Marinos de Altas Latitudes, 2017), where they play a similar role as the krill (Euphausiacea) in the water column. Moreover, amphipods are found in the stomachs of other Procellariiformes, such as the Providence petrel (*Pterodroma solandri*) (Bester et al., 2011; Lock et al., 1992), the Blue petrel (*Halobaena caerulea*) (Croxall, 1987) and the Wilson's storm petrel (*Oceanites oceanicus*). These birds are known to feed on amphipods when krill is not available (Quillfeldt et al., 2019, 2005, 2001, 2000). Imber (1976) found no planktonic crustacean in the stomach of *P. westlandica* and Freeman (1998) only detected small percentage of taxa belonging to three different families: Euphausiidae or krill (*Nyctiphanes australis* and

Thysanoessa gregaria), Caridea or caridean shrimps (*Notostomus auriculatus* and an unidentified species) and Cymothoidae (unidentified species). Although it remains unclear whether Amphipods are primary prey, secondary prey (Sheppard et al., 2005) or both, we can confirm that these taxa play a major role in the flow of energy through the food web.

Fish are major prey items of Procellariiformes (Bester et al., 2011; Bocher et al., 2000; da Silva Fonseca and Petry, 2007; Freeman, 1998; Imber, 1976; Prince and Morgan, 1987; Spear et al., 2007; Stewart et al., 1999), and the Westland petrel is not an exception. According to our results, fish (all belonging to the order Actinopteriigy) represent 15.03% of the prey reads, and are the second most abundant phylum. In addition, fish DNA was detected in 37.93% of the samples. The fish species identified by our approach are consistent with previous studies (Freeman, 1998; Imber, 1976) but also include new species. In concordance with previous knowledge, the Hoki was identified as the most abundant fish prey item. However, we also found Hake, another Merlucciidae, and Cocky gurnard followed Hoki in abundance and occurrence, which were not identified by previous approaches.

Hoki and Hake live between 28 and 1,000 m below sea level (Table 1), which makes these fish rarely catchable naturally for Westland petrels, who only dive down to 15 m below the surface (Freeman, 1998). However, these species, especially Hoki, are some of the main fishery species caught in New Zealand waters (Livingston and Rutherford, 1988). The fishing season for Merlucciids spans mainly between June and September, thereby encompassing most of the Westland petrel's breeding season (Waugh et al., 2018; Waugh and Wilson, 2017), and including both sampling events of this study. Thus, the Westland petrels could scavenge these fish species from fishing vessels. In many cases, what is available for seabirds in the fishing boat decks are the leftovers from the fish, such as stomachs. These stomachs, may contain fish prey items, which could explain the high abundance of talitrids in our results.

The same conclusion could apply to a number of other fish species with deep depth ranges, that are naturally unreachable to the petrel, but are important fishery species (Freeman, 1998; Froese and Pauly, 2010). These include rattails (Macrouridae), such as the Thorntooth grenadier as well as two newly identified prey items, namely the Hacknose grenadier and the Banded whiptail, among other fish species living in deep sea waters (Table 1). In the case of Hoki, however, natural predation may be possible at night, as this fish species is

known to migrate to surface waters to feed during the night (McClatchie and Dunford, 2003; O'Driscoll et al., 2009), when *P. westlandica* forages more actively (Waugh et al., 2018).

Cocky gurnard, in contrast, which can sometimes be found in shallow waters (Froese and Pauly, 2010), could be caught naturally by the petrel. However, as stated before, it is also a known fishery species that could have been scavenged from the fishing waste. Also, many fish species belonging to the family Trichiuridae can live close to the surface. Myctophid fishes, which were reported to be natural prey of the Westland petrel (Freeman, 1998; Imber, 1976), were not identified in our sampling. It is possible that these species are no longer selected by the Westland petrel, as previous studies were conducted more than 20 years ago for Freeman (Freeman, 1998) and more than 45 years ago for (Imber, 1976).

In conclusion, our study confirms that Westland petrel extensively use fish waste from the Hoki fishery and other inshore small fisheries, at least in the winter season (Freeman, 1998), but they could also catch some fish species naturally in certain situations. It is common for opportunistic seabirds to feed on fishery waste, however, if the dependence on this food source is very high, changes and new regulations in fishing activity could modify the birds' behaviour and potentially impact their survival and population size (Abrams, 1983; Freeman, 1998; Oro et al., 1996, 1995).

According to our results, 12.29% of prey reads, belonged to cephalopods, and these taxa were detected in 53.16% of the samples. Six out of eight cephalopod OTUs could only be assigned to family level. Only the common Octopus (*Octopus vulgaris*) was assigned to genus level, a taxon already found in previous studies (Freeman, 1998; Imber, 1976). Our results are consistent with Freeman (1998), which states that fish prey items are followed by (Davies et al., 2009; Pierce et al., 2010) cephalopods within the Westland petrel's diet. In the case of *Histioteuthis sp.,* they are are deep-sea squid (Voss et al., 1998), but migrate to surface water at night by vertical migration (Roper and Young, 1975), thus they become catchable by Westland petrel. The other two families, Loliginidae and Octopodidae (Common octopus), which were also identified in previous studies, are present from surface waters down to 500 m deep, and thus naturally catchable for the Westland petrel. Nevertheless, these families also include several commercial species as well as species

commonly reported as bycatch (Davies et al., 2009; Pierce et al., 2010). Therefore, it is possible that petrels fed on some cephalopods through fishery waste.

A number of other Mollusca prey species were, listed in previous studies (Freeman, 1998; Imber, 1976), but not detected in our approach. These include cephalopods belonging to the orders Sepioidea or Vampyromorpha, among others. It is unclear whether their absence in our analysis is due to the lack of genetic sequences in the NCBI database or a change in the feeding habits of the birds in the past 20 years.

Marked dietary switches between breeding and non-breeding seasons have been documented for several seabirds (Howells et al., 2018), and are considered a sign of plasticity in behaviour (Quillfeldt et al., 2019). These switches may reflect variation in prey availability, a change of strategy between seasons, or a combination of both (Howells et al., 2018; Paleczny et al., 2015; Sydeman et al., 2015). Because these variations can severely affect marine top predator's populations (Cury et al., 2000; Reid and Croxall, 2001) it is essential to understand their drivers to ensure the conservation of the Westland petrel.

As hypothesized before, there is a clear seasonal variation in the diet of *P. westlandica*, both in terms of read abundance (food biomass) and the occurrence of prey species, meaning that the composition of the diet changes in a substantial way between incubation and chick-rearing season. This change is particularly visible for fish (specifically merluccids) and talitrids, with fish being the most abundant prey before hatching while talitrids are by far the most common prey during the chick rearing season. One explanation could be that adult petrels feed their chicks with highly nutritive fish and cephalopods, while they feed themselves mainly with crustaceans (and some cephalopods). This hypothesis is highly consistent with the significant loss of weight in adult seabirds during the breeding season, while their chicks experience rapid growth (Ainley, 1990; Barrett et al., 1985; Leal et al., 2017). In this case, the choice of prey items by adults may be influenced by the developmental stage and the needs of the chicks. Despite these seasonal differences in prey preferences, prey species richness remains similar between in seasons.

Our results suggest that seasonal variations may be more influenced by changes in foraging strategy, rather than changes in prey availability. Indeed, the peak of the Hoki fishery in

New Zealand encompasses both July (before hatching period) and September (chick rearing period), which means, fishery waste would be equally available during both seasons.

Contrary to our expectation, we found significant differences in prey composition between both sub-colonies. A possible explanation of these differences could be that seabirds from nearby sub-colonies forage in different locations, possibly to avoid or decrease inter-colony competition (Cecere et al., 2015; Grémillet et al., 2004; Wakefield et al., 2013). Another possible explanation, is that the birds' diet could change every day depending on resource availability, and prey resources may have been very different in the two consecutive days used for collecting samples in both sub-colonies. Finally, the sub-colonies might be different genetic haplotypes, occupying slightly different dietary niches. In order to clarify the origin of these differences in prey community composition between sub-colonies, further studies on the foraging ecology and population genetics of the Westland petrel should be conducted.

Sustainable management of worldwide fishery industry needs information regarding the overlap of marine organisms, such as seabirds, with fishing industry (Frederiksen et al., 2004; McInnes et al., 2017b; Okes et al., 2009). Seabirds scavenge food from fishery waste and results in a high number of incidental kills through bycatch, potentially disturbing on population dynamics (Brothers, 1999; McInnes et al., 2017b; Sullivan et al., 2006; Tuck et al., 2011; Watkins et al., 2008; Waugh et al., 2008; Waugh and Wilson, 2017). But, also, the diet of seabirds relies on this commercial activity, as fishery waste is a nutritious prey, naturally unreachable by seabirds. That is why understanding these interactions is essential for seabird conservation and efficient ecosystem-based fishing regulation (Becker and Beissinger, 2006; Freeman, 1998; Furness, 2003; Furness and Tasker, 2000; McInnes et al., 2017b; Phillips et al., 1999; Waugh et al., 2008). In this context, non-invasive dietary studies can provide knowledge to assess risks as well as the needs of these species that may rely heavily on commercial fishing activity (Gaglio et al., 2018; McInnes et al., 2017a, 2017b). This issue is particularly urgent in the case of endangered species, such as the Westland petrel, and, in this study, we show a link between fisheries in New Zealand and the diet of the petrel, that should be taken into account in management strategies.

Our results show the potential of non-invasive dietary studies in highlighting the reliance of endangered seabirds on commercial fishing activity (Gaglio et al., 2018; McInnes et al., 2017a, 2017b). Such study should draw attention to the complexity that lies in the implementation of fishing regulations and the associated risks for the conservation of endangered species. In the case of Westland petrel, these regulations should take into account, not only the close link between the commercial fishing and the diet preferences of the birds regarding fish and cephalopods, but also the high number of birds' deaths happening every year through bycatch, as the Westland petrel is the fourth seabird species in terms of bycatch risk in New Zealand (OpenSeas, 2019). Several mitigation solutions have been suggested by practitioners or already included in conservation reports, to limit the number of accidental kills in seabirds and find a sustainable equilibrium between fishery industry and threatened species. Thus, research on how seabirds in general, and Westland petrel in particular, interact with the fishing gear is essential to develop bycatch reduction techniques and using or developing gear less dangerous for the seabirds.

Author contribution

Designed the study: SB. Obtained funding: SB. Collected samples: SB. Performed laboratory analyses: MCL, SB. Analysed the data and prepared the figures: MQ. Wrote the first draft of the manuscript MQ, SB. All authors contributed to the writing of the final manuscript.

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Table 1. OTU list after filtering the contaminants, low quality sequences and the sequences that gave no hits. For each OTU, the taxonomical classification is given, together with the standard parameters provided by the BLAST search against the NCBI database. The penultimate column indicates whether the OTU was identified in previous studies or not. The last column gives the depth at which each OTU is naturally found, and coloured rows indicates OTUs whose depth range overlaps with the dive depth of the Westland petrel.

OTU_ID	Phylum	Class	Order	Family	Genus	Species	Size	E-value	% of identity	Alignment length	Query cover	Previously identified	Depth (m)
OTU_43	Arthropoda	Branchiopoda	Anostraca	Artemiidae	*Artemia*	*Artemia franciscana*	2482	2.36E-71	1	151	0.9934	NO	0.1-0.6
OTU_81	Arthropoda	Maxillopoda	Calanoida	Candaciidae	*Candacia*	*Candacia armata*	761	2.13E-50	1	113	0.9912	NO	-
OTU_66	Arthropoda	Malacostraca	Decapoda	Penaeidae	*Penaeus*	*Penaeus merguiensis*	1216	7.47E-82	1	170	0.9941	NO	10-45
OTU_65	Arthropoda	Malacostraca	Decapoda	Pilumnidae	*Pilumnus*	*Pilumnus hirtellus*	1269	2.57E-76	0.9939	163	0.9939	NO	10-80
OTU_7	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	92506	8.65E-16	0.8485	99	0.6528	NO	0-0.1
OTU_16	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	50055	1.92E-07	0.8000	95	0.6370	NO	0-0.1
OTU_17	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	28822	6.68E-17	0.8092	131	0.8819	NO	0-0.1
OTU_28	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	11687	3.99E-19	0.8014	146	0.9931	NO	0-0.1
OTU_212	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	75	1.92E-07	0.8061	98	0.6370	NO	0-0.1
OTU_229	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	14954	8.93E-06	0.7895	95	0.6370	NO	0-0.1
OTU_304	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	46	3.05E-10	0.7813	128	0.8936	NO	0-0.1
OTU_309	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	44	3.97E-24	0.8219	146	0.9931	NO	0-0.1
OTU_323	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	192	6.64E-22	0.8321	131	0.8819	NO	0-0.1
OTU_402	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	23	1.92E-07	0.8081	99	0.6370	NO	0-0.1
OTU_405	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	138	1.82E-27	0.8356	146	0.9930	NO	0-0.1
OTU_406	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	28	1.92E-07	0.8061	98	0.6370	NO	0-0.1
OTU_416	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	777	8.65E-16	0.8557	97	0.6389	NO	0-0.1
OTU_434	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	660	3.08E-15	0.8485	99	0.6503	NO	0-0.1
OTU_471	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	23	1.92E-07	0.8000	95	0.6370	NO	0-0.1
OTU_524	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	21	2.41E-21	0.8182	143	0.9724	NO	0-0.1
OTU_529	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	23	1.92E-07	0.8000	95	0.6370	NO	0-0.1
OTU_557	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	148	8.93E-06	0.7895	95	0.6370	NO	0-0.1

OTU_593	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	16	1.86E-17	0.8043	138	0.9306	NO	0-0.1
OTU_615	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	146	3.99E-19	0.8041	148	0.9931	NO	0-0.1
OTU_636	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	47	1.92E-07	0.8000	95	0.6370	NO	0-0.1
OTU_662	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	312	5.12E-18	0.8106	132	0.8951	NO	0-0.1
OTU_666	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	646	5.08E-23	0.8333	132	0.8951	NO	0-0.1
OTU_681	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	32	1.4337E-13	0.8404	94	0.6294	NO	0-0.1
OTU_684	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	13	3.14E-15	0.7970	133	0.9034	NO	0-0.1
OTU_691	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	64	1.11E-19	0.8095	147	0.9931	NO	0-0.1
OTU_724	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	3816	0.00011547	0.7849	93	0.6233	NO	0-0.1
OTU_785	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	67	8.51E-21	0.8095	147	0.9930	NO	0-0.1
OTU_786	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	237	5.16E-13	0.7879	132	0.8951	NO	0-0.1
OTU_788	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	25	4.93E-18	0.8071	140	0.9712	NO	0-0.1
OTU_802	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	15	1.86E-17	0.8586	99	0.6528	NO	0-0.1
OTU_811	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	8	1.84E-17	0.7959	147	0.9930	NO	0-0.1
OTU_828	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	10	3.99E-19	0.8027	147	0.9931	NO	0-0.1
OTU_869	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	67	2.40E-11	0.8333	90	0.6084	NO	0-0.1
OTU_894	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	8	1.92E-07	0.8081	99	0.6370	NO	0-0.1
OTU_908	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	1592	3.99E-19	0.8014	146	0.9931	NO	0-0.1
OTU_914	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	83	3.01E-05	0.7957	93	0.6187	NO	0-0.1
OTU_936	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	7	3.50E-15	0.8030	132	0.7975	NO	0-0.1
OTU_937	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	6	2.37E-10	0.8533	75	0.6239	NO	0-0.1
OTU_949	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	5	1.41E-23	0.8900	100	0.6713	NO	0-0.1
OTU_979	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	20	8.79E-11	0.7762	143	0.9517	NO	0-0.1
OTU_1000	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	8	2.38E-16	0.8485	99	0.6643	NO	0-0.1
OTU_1055	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	56	4.02E-14	0.8523	88	0.6042	NO	0-0.1
OTU_1057	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	5	2.77E-15	0.8049	123	0.9167	NO	0-0.1
OTU_1059	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	68	4.93E-18	0.8082	146	0.9928	NO	0-0.1

OTU_1065	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	206	1.48E-08	0.7963	108	0.7123	NO	0-0.1
OTU_1104	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	6	6.32E-17	0.8721	86	0.6159	NO	0-0.1
OTU_1144	Arthropoda	Malacostraca	Amphipoda	Talitridae	not identified	not identified	28	3.96E-19	0.8014	146	0.9930	NO	0-0.1
OTU_59	Chordata	Actinopterygii	Anguilliformes	Nettastomatidae	not identified	not identified	1636	6.92E-64	0.8595	242	0.9958	NO	Deep-sea
OTU_169	Chordata	Actinopterygii	Gadiformes	Euclichthyidae	*Euclichthys*	*Euclichthys polynemus*	148	2.04E-103	0.9953	212	0.9953	NO	250-920
OTU_22	Chordata	Actinopterygii	Gadiformes	Macrouridae	*Lepidorhynchus*	*Lepidorhynchus denticulatus*	17801	7.50E-108	1	217	0.9954	Freeman, 1998; Imber, 1976	270-450
OTU_54	Chordata	Actinopterygii	Gadiformes	Macrouridae	*Coelorinchus*	*Coelorinchus oliverianus*	2067	9.59E-107	1	215	0.9953	Freeman, 1998 (genus level)	400-600
OTU_216	Chordata	Actinopterygii	Gadiformes	Macrouridae	*Coelorinchus*	*Coelorinchus fasciatus*	107	2.08E-103	0.9907	215	0.9953	Freeman, 1998 (genus level); Imber, 1976 (genus level)	400-600
OTU_1075	Chordata	Actinopterygii	Gadiformes	Macrouridae	*Coelorinchus*	*Coelorinchus oliverianus*	12	1.27E-95	0.9721	215	0.9861	Freeman, 1998 (family level)	400-600
OTU_12	Chordata	Actinopterygii	Gadiformes	Merlucciidae	*Macruronus*	*Macruronus novaezelandiae*	49195	9.59E-107	1	215	0.9953	Freeman, 1998	200-700
OTU_14	Chordata	Actinopterygii	Gadiformes	Merlucciidae	*Merluccius*	*Merluccius australis*	46909	3.43E-106	1	214	0.9953	Freeman, 1998 (family level)	28-1000
OTU_808	Chordata	Actinopterygii	Gadiformes	Merlucciidae	*Macruronus*	Macruronus sp.	66	2.55E-77	0.9302	215	0.9950	Freeman, 1998	0-1000
OTU_1008	Chordata	Actinopterygii	Gadiformes	Merlucciidae	*Merluccius*	*Merluccius productus*	14	1.32E-27	0.9867	75	0.6549	NO	0-1000
OTU_1086	Chordata	Actinopterygii	Gadiformes	Merlucciidae	not identified	not identified	44	3.61E-66	0.8884	215	0.9953	Freeman, 1998 (family level)	28-1000
OTU_107	Chordata	Actinopterygii	Gadiformes	Moridae	*Mora*	*Mora moro*	466	3.43E-106	1	214	0.9953	Freeman, 1998 (family level)	450-2500
OTU_38	Chordata	Actinopterygii	Ophidiiformes	Ophidiidae	*Genypterus*	*Genypterus blacodes*	5711	2.68E-107	1	216	0.9954	NO	300-550
OTU_962	Chordata	Actinopterygii	Ophidiiformes	Ophidiidae	*Genypterus*	*Genypterus sp.*	10	4.55E-95	0.9676	216	0.9907	NO	22-1000
OTU_15	Chordata	Actinopterygii	Perciformes	Triglidae	*Lepidotrigla*	*Lepidotrigla modesta*	45382	4.46E-105	0.9953	215	0.9953	NO	10-300
OTU_96	Chordata	Actinopterygii	Scombriformes	Gempylidae	*Rexea*	*Rexea sp.*	565	2.15E-93	0.9589	219	0.9954	NO	100-800
OTU_18	Chordata	Actinopterygii	Scombriformes	Trichiuridae	*Trichiuridae environmental sample*	not identified	26490	1.74E-94	0.9515	227	0.9956	Imber, 1976 (family level)	0-1600
OTU_163	Chordata	Actinopterygii	Zeiformes	Cyttidae	*Cyttus*	*Cyttus traversi*	189	9.59E-107	1	215	0.9953	Freeman, 1998 (genus level)	200-978
OTU_86	Chordata	Actinopterygii	Zeiformes	Zenionidae	*Capromimus*	*Capromimus abbreviatus*	629	9.59E-107	1	215	0.9953	NO	87-500
OTU_19	Mollusca	Cephalopoda	Octopoda	Octopodidae	*Octopus*	*Octopus vulgaris*	20934	1.55E-78	1	164	0.9939	Freeman, 1998 (genus level)	0-100
OTU_1019	Mollusca	Cephalopoda	Octopoda	Octopodidae	*Octopus*	*Octopus sp.*	24	1.21E-64	0.9515	165	0.9939	Freeman, 1998 (genus level)	0-100
OTU_8	Mollusca	Cephalopoda	Teuthida	Loliginidae	not identified	not identified	104188	7.91E-87	1	179	0.9944	NO	0-400
OTU_60	Mollusca	Cephalopoda	Teuthida	Loliginidae	not identified	not identified	2092	2.82E-86	1	178	0.9944	NO	0-400
OTU_1003	Mollusca	Cephalopoda	Teuthida	Loliginidae	not identified	not identified	4	3.81E-60	0.9121	182	0.9944	NO	0-400

OTU_1040	Mollusca	Cephalopoda	Teuthida	Loliginidae	not identified	not identified	8	2.88E-66	0.9375	176	0.9831	NO	0-400
OTU_1125	Mollusca	Cephalopoda	Teuthida	Loliginidae	not identified	not identified	114	7.52E-77	1	161	0.9412	NO	0-400
OTU_80	Mollusca	Cephalopoda	Oegopsida	Histioteuthidae	not identified	not identified	660	6.68E-42	0.8919	148	0.9797	Freeman, 1998; Imber, 1976	300-400

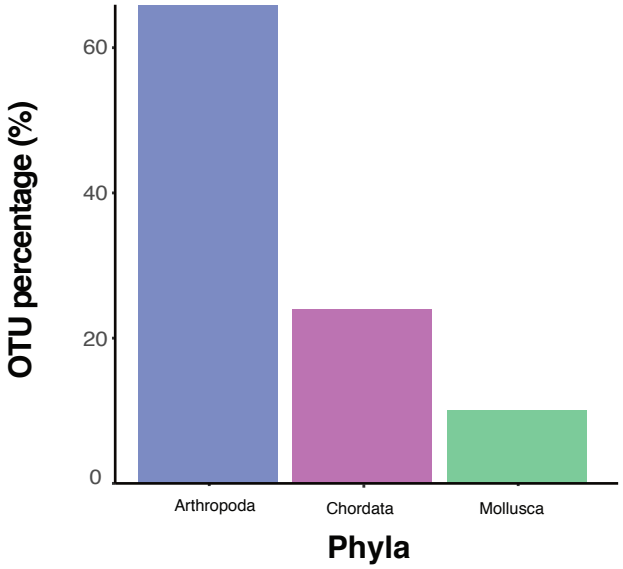
Table 2. Taxonomical classification of the prey items of *P. westlandica* until family level with its corresponding Relative Read Abundance (RRA) and Frequency Of Occurrence (FOO) values for the whole sampling and showing the differences among: A) the two different seasons, Before Hatching (BH) and Chick Rearing (CR) and B) the two different sites, the Paparoa Natural Park (NP) and the Privat Land (PL) in the surroundings.

Phylum	Class	Order	Family	Species	Common name	Total_FOO (%)	Total_RRA (%)	FOO_BH (%)	FOO_CR (%)	FOO_NP (%)	FOO_PL (%)	RRA_BH (%)	RRA_CR (%)	RRA_NP (%)	RRA_PL (%)
Arthropoda						62.0253	45.5703	17.7215	43.0380	35.4430	25.3165	4.7167	78.0671	68.8732	30.7305
	Branchiopoda					5.0633	0.5290	1.2658	2.5316	1.2658	2.5316	0.1240	0.8512	0.1418	0.7734
		Anostraca				5.0633	0.5290	1.2658	2.5316	1.2658	2.5316	0.1240	0.8512	0.1418	0.7734
			Artemiidae			5.0633	0.5290	1.2658	2.5316	1.2658	2.5316	0.1240	0.8512	0.1418	0.7734
				Artemia franciscana	Brine shrimp	5.0633	0.5290	1.2658	2.5316	1.2658	2.5316	0.1240	0.8512	0.1418	0.7734
	Malacostraca					59.4937	44.8790	16.4557	41.7722	34.1772	24.0506	4.5927	76.9264	68.7314	29.6940
		Amphipoda				58.2279	44.3492	15.1899	41.7722	34.1772	22.7848	4.0028	76.4422	68.0367	29.2665
			Talitridae		Landhoppers /sandhoppers	58.2279	44.3492	15.1899	41.7722	34.1772	22.7848	4.0028	76.4422	68.0367	29.2665
		Decapoda				5.0633	0.5298	2.5316	1.2658	1.2658	2.5316	0.5899	0.4842	0.6947	0.4275
			Penaeidae			3.7975	0.2596	2.5316	0	0	2.5316	0.5899	0	0	0.4275
				Penaeus merguiensis	Banana shrimp	3.7975	0.2596	2.5316	0	0	2.5316	0.5899	0	0	0.4275
			Pilumnidae			2.5316	0.2703	0	1.2658	1.2658	0	0	0.4842	0.6947	0
				Pilumnus hirtellus	Bristly crab	2.5316	0.2703	0	1.2658	1.2658	0	0	0.4842	0.6947	0
	Maxillopoda					2.5316	0.1622	0	1.2658	0	1.2658	0	0.2896	0	0.2631
		Calanoida				2.5316	0.1622	0	1.2658	0	1.2658	0	0.2896	0	0.2631
			Candaciidae			2.5316	0.1622	0	1.2658	0	1.2658	0	0.2896	0	0.2631
				Candacia armata		2.5316	0.1622	0	1.2658	0	1.2658	0	0.2896	0	0.2631

Chordata					59.4937	42.1361	32.9114	25.3165	22.7848	35.4430	81.0857	11.1206	17.3233	57.8982
	Actinopterygii				59.4937	42.1361	32.9114	25.3165	22.7848	35.4430	81.0857	11.1206	17.3233	57.8982
		Anguilliformes			2.5316	0.3492	1.2658	0	0	1.2658	0.7864	0	0	0.5699
			Nettastomatidae		2.5316	0.3492	1.2658	0	0	1.2658	0.7864	0	0	0.5699
				Duckbill eels	2.5316	0.3492	1.2658	0	0	1.2658	0.7864	0	0	0.5699
		Gadiformes			44.3038	24.9324	29.1139	13.9241	13.9241	29.1139	55.6787	0.4428	4.5750	37.8569
			Euclichthyidae		2.5316	0.0312	0	1.2658	0	1.2658	0	0.0559	0	0.0508
				Euclichthys polynemus	2.5316	0.0312	0	1.2658	0	1.2658	0	0.0559	0	0.0508
				Eucla cod	2.5316	0.0312	0	1.2658	0	1.2658	0	0.0559	0	0.0508
			Macrouridae		11.3924	4.2647	6.3291	3.7975	3.7975	6.3291	9.2668	0.2853	0.4093	6.7159
				Coelorinchus fasciatus	2.5316	0.0228	1.2658	0	0	1.2658	0.0514	0	0	0.0373
				Coelorinchus oliverianus	3.7975	0.4434	1.2658	1.2658	1.2658	1.2658	0.9191	0.0633	0.0908	0.6661
				Lepidorhynchus denticulatus	11.3924	3.7985	6.3291	3.7975	3.7975	6.3291	8.2962	0.2220	0.3185	6.0125
				Thorntooth grenadier	11.3924	3.7985	6.3291	3.7975	3.7975	6.3291	8.2962	0.2220	0.3185	6.0125
			Merlucciidae		36.7089	20.5373	26.5823	8.8608	10.1266	25.3165	46.1919	0.1016	4.1657	30.9308
				Macruronus novaezelandiae	26.5823	10.4990	21.5190	3.7975	6.3291	18.9873	23.5844	0.0797	4.1494	14.5369
				Hoki	26.5823	10.4990	21.5190	3.7975	6.3291	18.9873	23.5844	0.0797	4.1494	14.5369
				Macruronus sp.	6.3291	0.0139	6.3291	0	1.2658	5.0633	0.0318	0	0.0028	0.0213
				Southern merluccid Hakes	6.3291	0.0139	6.3291	0	1.2658	5.0633	0.0318	0	0.0028	0.0213
				Merluccius australis	17.7215	10.0129	11.3924	5.0633	5.0633	11.3924	22.5506	0.0219	0.0135	16.3545
				Southern hake	17.7215	10.0129	11.3924	5.0633	5.0633	11.3924	22.5506	0.0219	0.0135	16.3545
				Merluccius productus	1.2658	0.0026	1.2658	0	0	1.2658	0.0059	0	0	0.0043
				North Pacific hake	1.2658	0.0026	1.2658	0	0	1.2658	0.0059	0	0	0.0043
			Moridae		2.5316	0.0993	1.265823	0	0	1.2658	0.2200	0	0	0.1594
				Mora moro	2.5316	0.0993	1.2658	0	0	1.2658	0.2200	0	0	0.1594
				Common mora	2.5316	0.0993	1.2658	0	0	1.2658	0.2200	0	0	0.1594
		Ophidiiformes			5.0633	1.2202	2.5316	1.2658	1.2658	2.5316	2.4943	0.2060	0.0011	1.9941
			Ophidiidae		5.0633	1.2202	2.5316	1.2658	1.2658	2.5316	2.4943	0.2060	0.0011	1.9941
				Genypterus blacodes	5.0633	1.2181	2.5316	1.2658	1.2658	2.5316	2.4894	0.2060	0.0011	1.9906
				Pink cusk-eel	5.0633	1.2181	2.5316	1.2658	1.2658	2.5316	2.4894	0.2060	0.0011	1.9906
				Genypterus sp.	1.2658	0.0021	1.2658	0	0	1.2658	0.0049	0	0	0.0036
				Cusk-eels	1.2658	0.0021	1.2658	0	0	1.2658	0.0049	0	0	0.0036
		Perciformes			18.9873	9.6861	12.6582	5.0633	5.0633	12.6582	21.8574	0.0047	0.0067	15.8407
			Triglidae		18.9873	9.6861	12.6582	5.0633	5.0633	12.6582	21.8574	0.0047	0.0067	15.8407
				Lepidotrigla modesta	18.9873	9.6861	12.6582	5.0633	5.0633	12.6582	21.8574	0.0047	0.0067	15.8407
				Grooved gunard	18.9873	9.6861	12.6582	5.0633	5.0633	12.6582	21.8574	0.0047	0.0067	15.8407
		Scombriformes			11.3924	5.7736	1.2658	8.8608	7.5949	2.5316	0.0015	10.3660	12.6182	1.4281
			Gempylidae		2.5316	0.1204	0	1.2658	1.2658	0	0	0.2149	0.3084	0
				Rexea sp.	2.5316	0.1204	0	1.2658	1.2658	0	0	0.2149	0.3084	0
				Snake mackerels	2.5316	0.1204	0	1.2658	1.2658	0	0	0.2149	0.3084	0

			Trichiuridae		Cutlassfish	11.3924	5.6532	1.2658	8.8608	7.5949	2.5316	0.0015	10.1510	12.3099	1.4281
		Zeiformes				6.3291	0.1746	2.5316	2.5316	1.2658	3.7975	0.2675	0.1012	0.1222	0.2084
			Cyttidae			2.5316	0.0403	1.2658	0	0	1.2658	0.0916	0	0	0.0664
				Cyttus traversi	King dory	2.5316	0.0403	1.2658	0	0	1.2658	0.0916	0	0	0.0664
			Zenionidae			5.0633	0.1343	1.2658	2.5316	1.2658	2.5316	0.1759	0.1012	0.1222	0.1420
				Capromimus abbreviatus	Capro dory	5.0633	0.1343	1.2658	2.5316	1.2658	2.5316	0.1759	0.1012	0.1222	0.1420
Mollusca						53.1646	12.2936	22.7848	29.1139	27.8481	24.0506	14.1976	10.8123	13.8035	11.3713
	Cephalopoda					53.1646	12.2936	22.7848	29.1139	27.8481	24.0506	14.1976	10.8123	13.8035	11.3713
		Oegopsida				2.5316	0.1409	0	1.2658	1.2658	0	0	0.2552	0.3661	0
			Histioteuthidae		Oegopsida squids	2.5316	0.1409	0	1.2658	1.2658	0	0	0.2552	0.3661	0
		Octopoda				32.9114	4.4684	13.9241	17.7215	16.4557	15.1899	4.1876	4.6673	6.2895	3.2923
			Octopodidae		Octopodids	32.9114	4.4684	13.9241	17.7215	16.4557	15.1899	4.1876	4.6673	6.2895	3.2923
				Octopus vulgaris	Common octopus	32.9114	4.4639	13.9241	17.7215	16.4557	15.1899	4.1812	4.6642	6.2816	3.2898
				Octopus sp.		8.8608	0.0045	5.0633	3.7975	5.0633	3.7975	0.0064	0.0031	0.0078	0.0025
		Teuthida				31.6456	7.6843	13.9241	16.4557	15.1899	15.1899	10.0100	5.8898	7.1479	8.0791
			Loliginidae		Pencil squids	31.6456	7.6843	13.9241	16.4557	15.1899	15.1899	10.0100	5.8898	7.1479	8.0791

A)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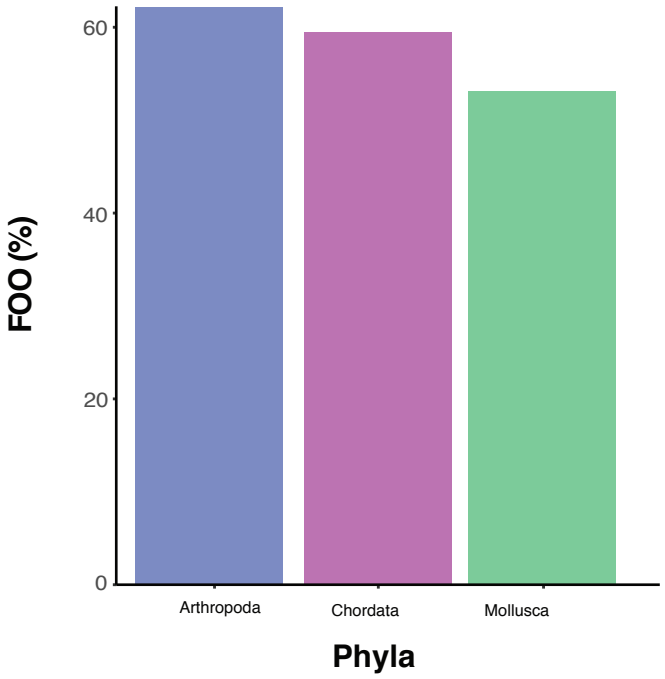
Chordata
Mollusca
Phyla

B)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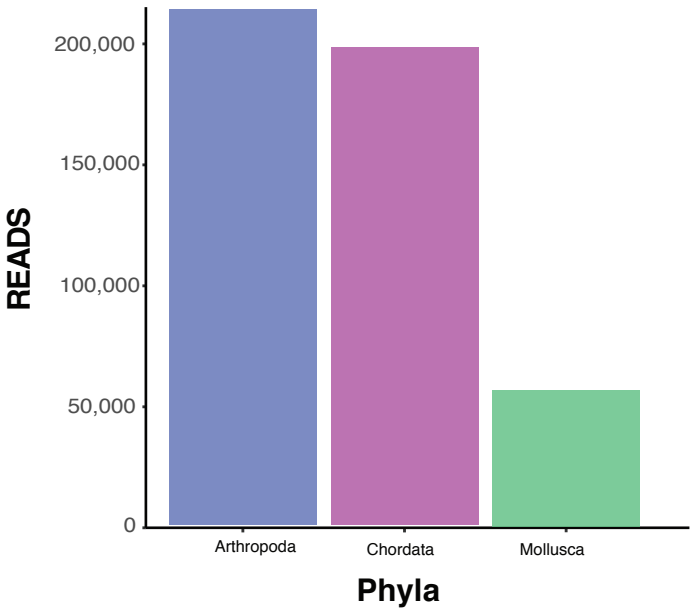
Arthropoda
Chordata
Mollusca
Phyla

C)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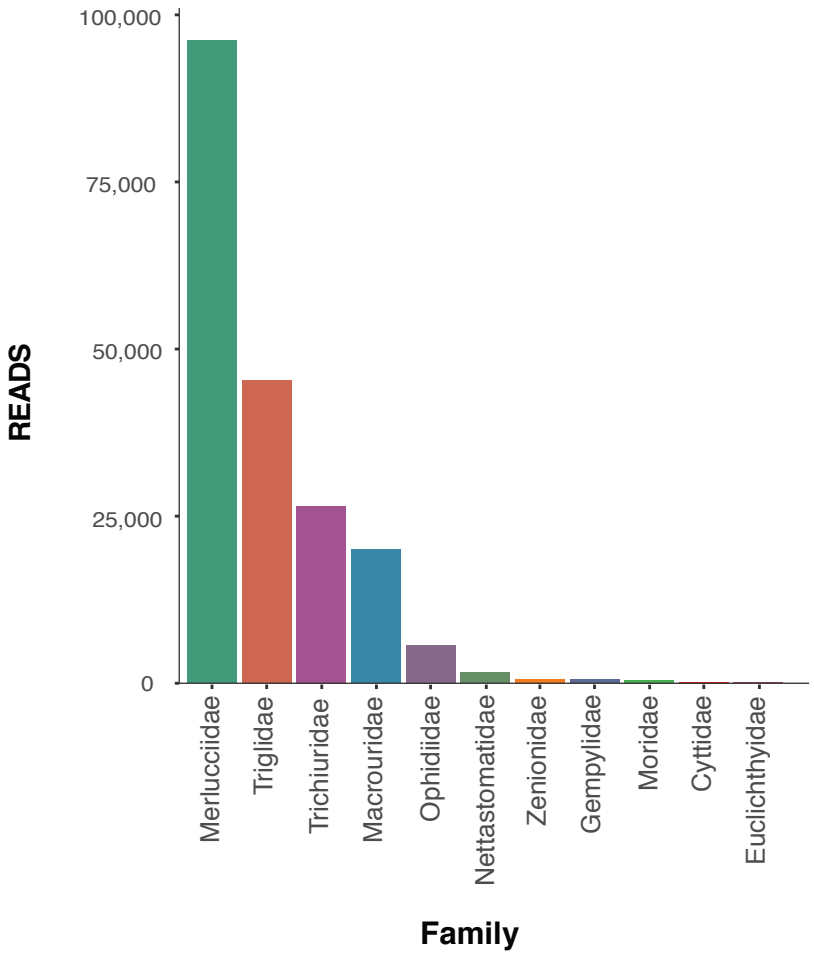
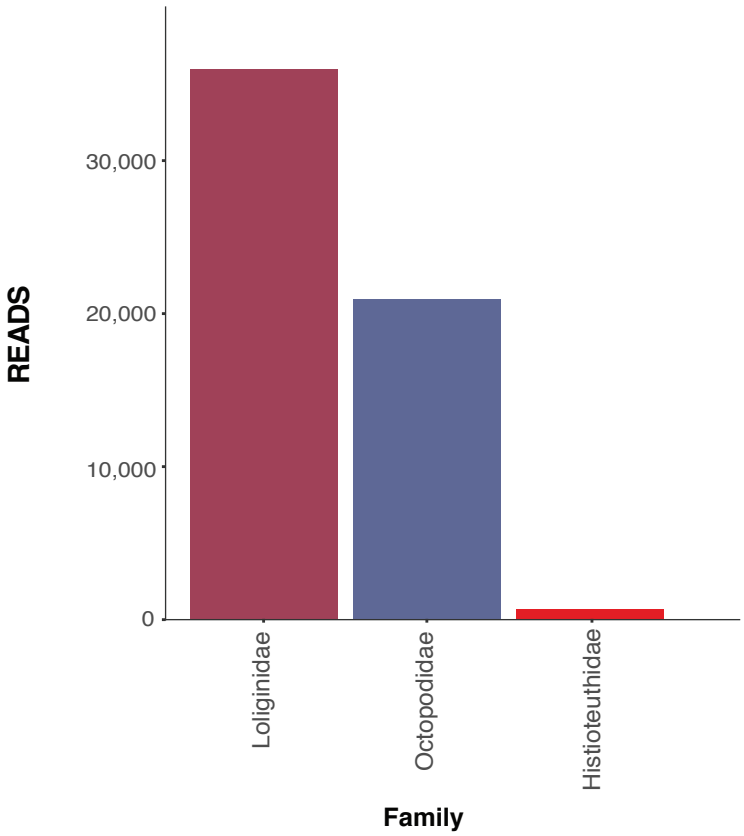
100,000
50,000
0
Arthropoda
Chordata
Mollusca
Phyla

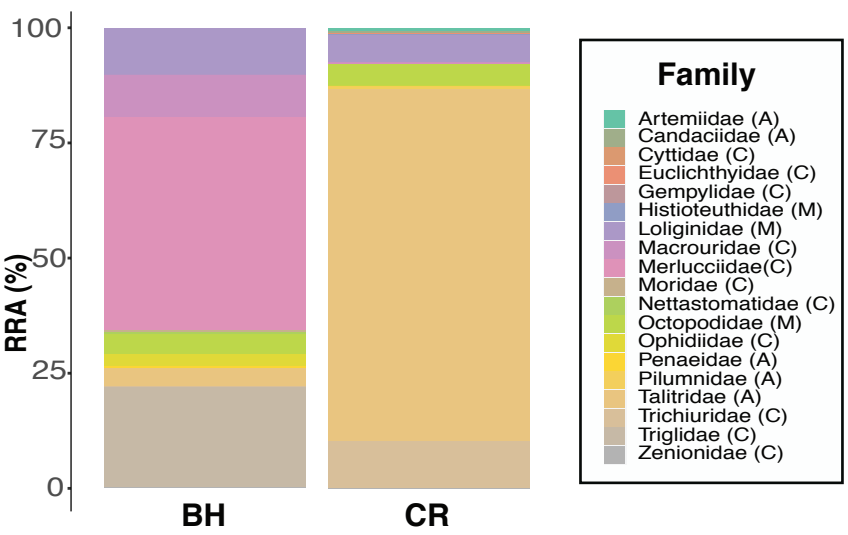
A)

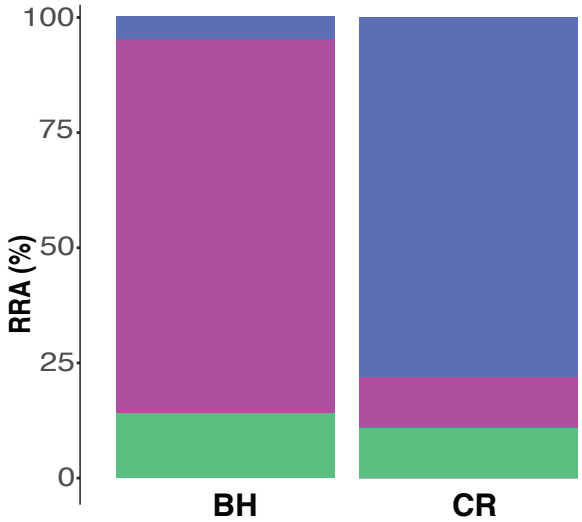

100,000
75,000
50,000
25,000
0
READS
Merlucciidae
Triglidae
Trichiuridae
Macrouridae
Ophidiidae
Nettastomatidae
Zenionidae
Gempylidae
Moridae
Cyttidae
Euclichthyidae
Family

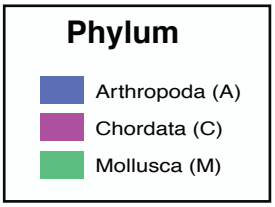
B)


30,000
20,000
10,000
0
READS
Loliginidae
Octopodidae
Histioteuthidae
Family

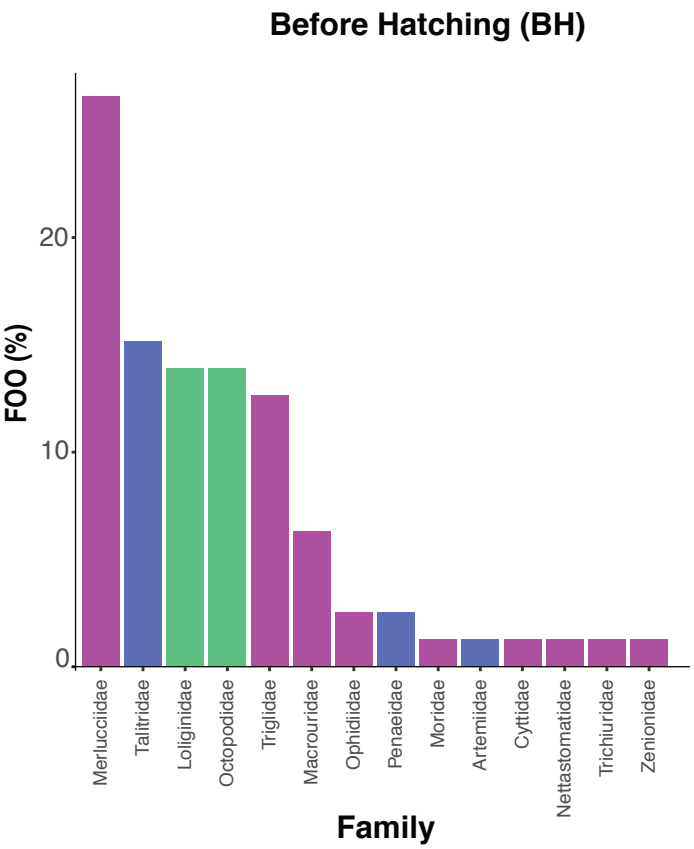
A)

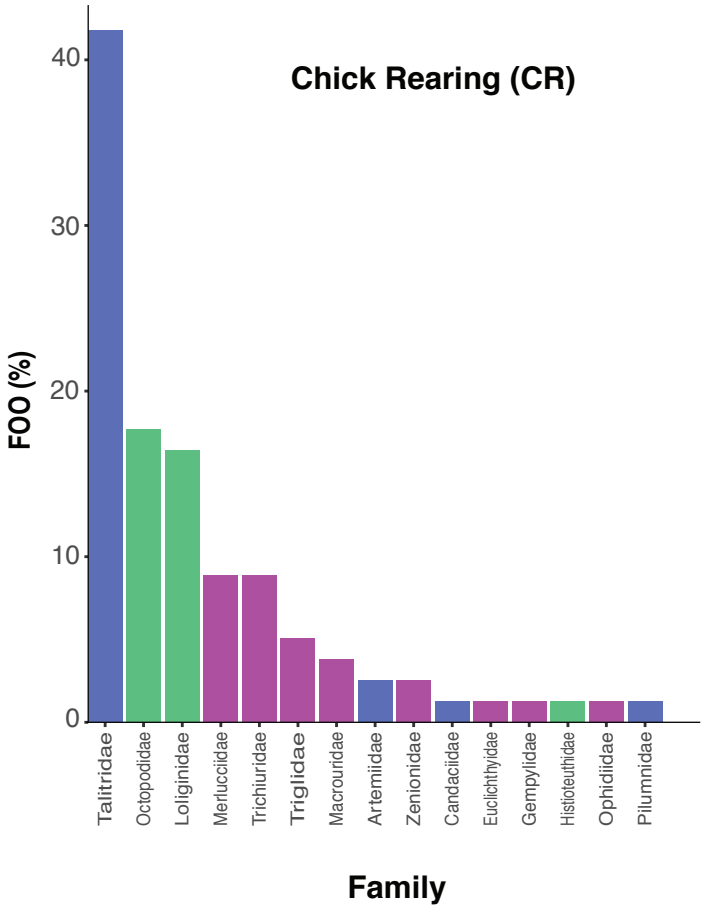

100
75
50
25
0
RRA (%)
BH
CR
Family
Artemiidae (A)
Candaciidae (A)
Cyttidae (C)
Euclichthyidae (C)
Gempylidae (C)
Histioteuthidae (M)
Loliginidae (M)
Macrouridae (C)
Merlucciidae(C)
Moridae (C)
Nettastomatidae (C)
Octopodidae (M)
Ophidiidae (C)
Penaeidae (A)
Pilumnidae (A)
Talitridae (A)
Trichiuridae (C)
Triglidae (C)
Zenionidae (C)


100
75
50
25
0
RRA (%)
BH
CR

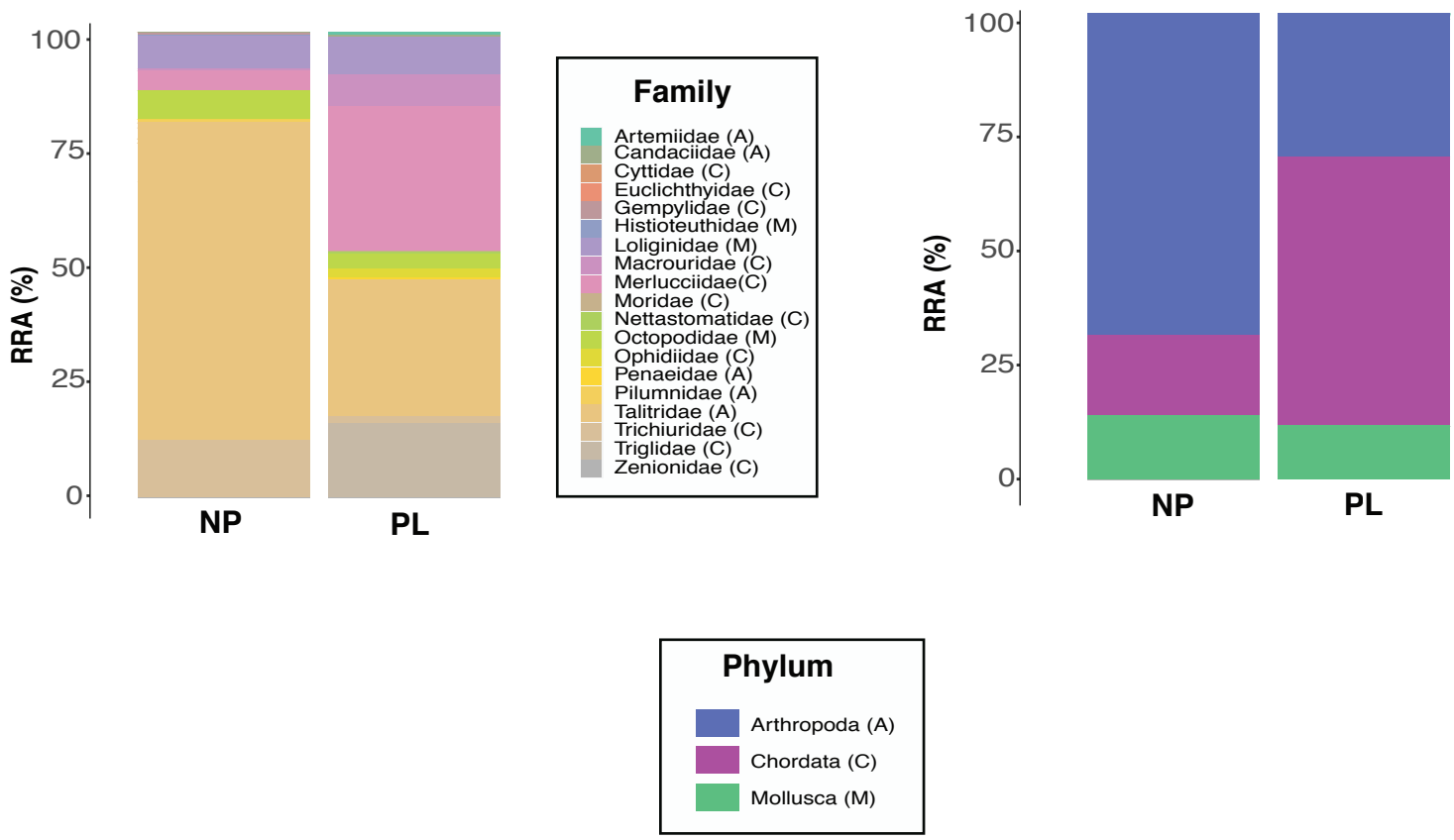

Phylum
Arthropoda (A)
Chordata (C)
Mollusca (M)

B)

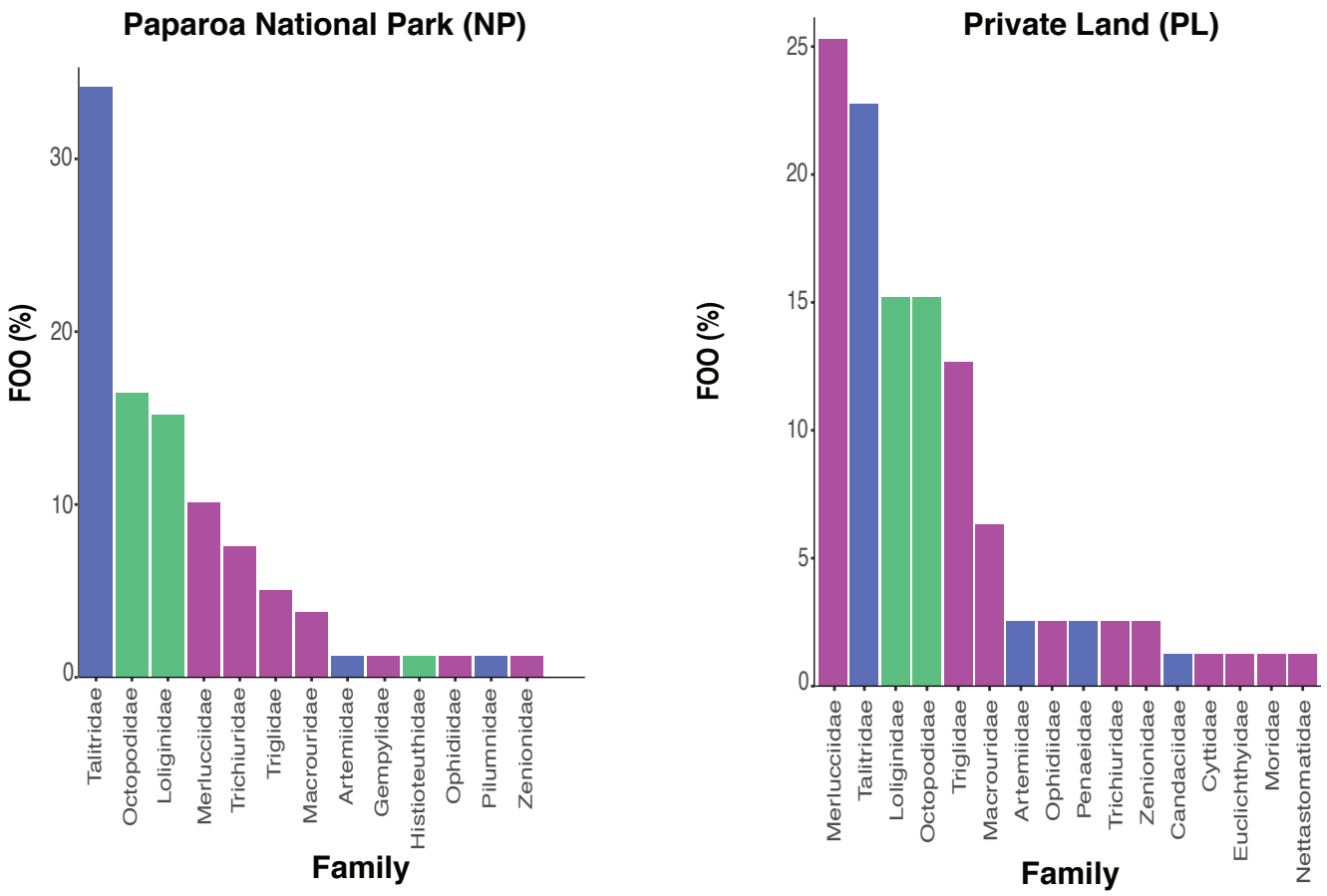

Before Hatching (BH)
20
10
0
FOO (%)
Merlucciidae
Talitridae
Loliginidae
Octopodidae
Triglidae
Macrouridae
Ophidiidae
Penaeidae
Moridae
Artemiidae
Cyttidae
Nettastomatidae
Trichiuridae
Zenionidae
Family


Chick Rearing (CR)
40
30
20
10
0
FOO (%)
Talitridae
Octopodidae
Loliginidae
Merlucciidae
Trichiuridae
Triglidae
Macrouridae
Artemiidae
Zenionidae
Candaciidae
Euclichthyidae
Gempylidae
Histioteuthidae
Ophidiidae
Pilumnidae
Family

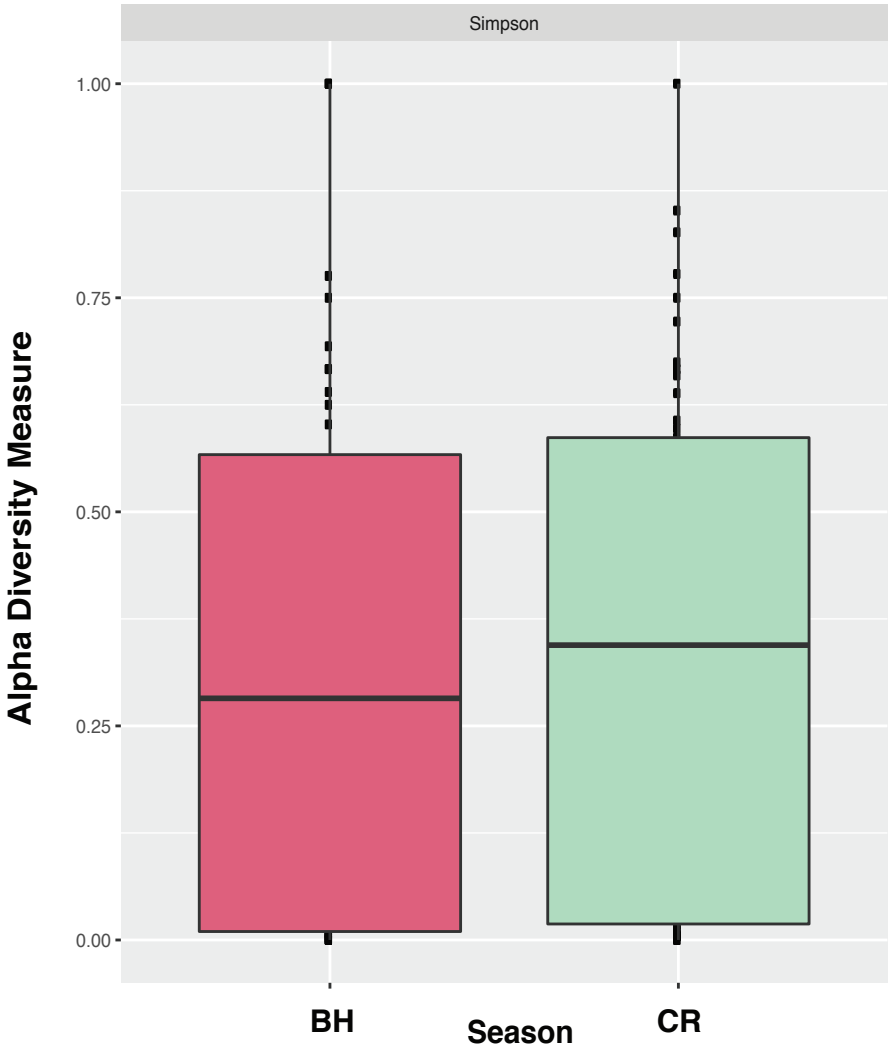
A)


100
75
50
25
0
RRA (%)
NP
PL
Family
Artemiidae (A)
Candaciidae (A)
Cyttidae (C)
Euclichthyidae (C)
Gempylidae (C)
Histioteuthidae (M)
Loliginidae (M)
Macrouridae (C)
Merlucciidae(C)
Moridae (C)
Nettastomatidae (C)
Octopodidae (M)
Ophidiidae (C)
Penaeidae (A)
Pilumnidae (A)
Talitridae (A)
Trichiuridae (C)
Triglidae (C)
Zenionidae (C)
Phylum
Arthropoda (A)
Chordata (C)
Mollusca (M)

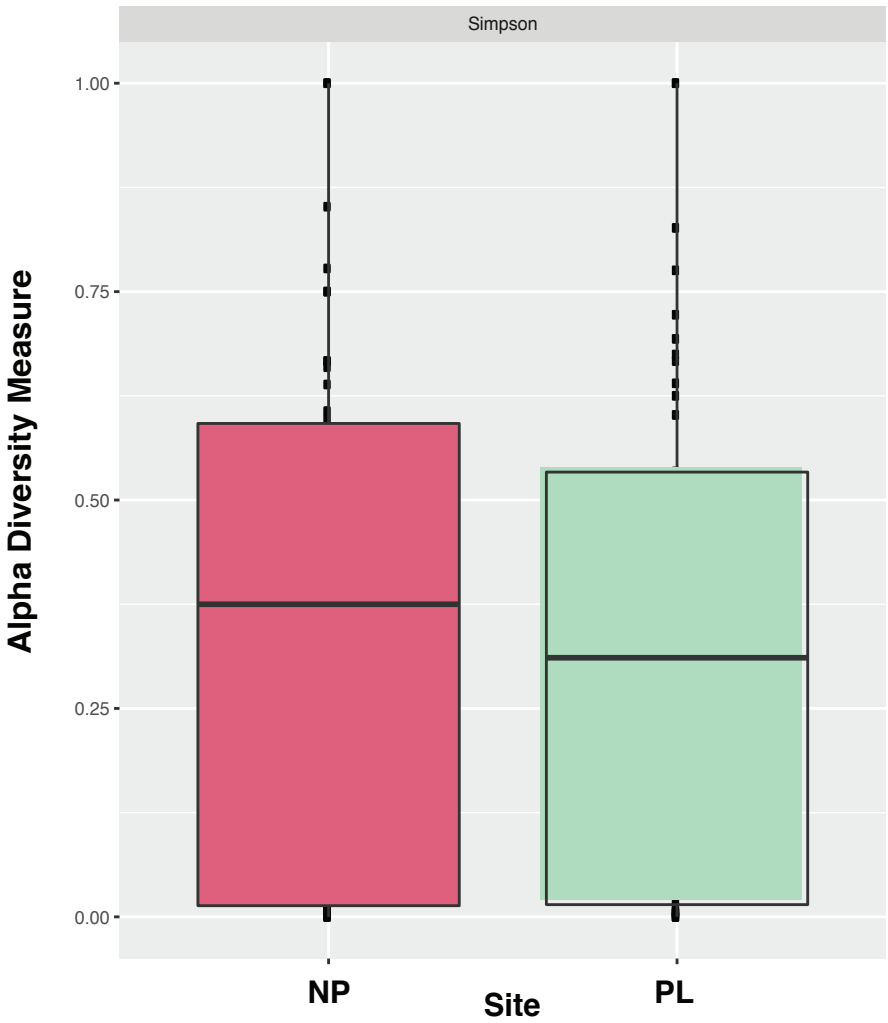
B)


Paparoa National Park (NP)
FOO (%)
30
20
10
0
Talitridae
Octopodidae
Loliginidae
Merlucciidae
Trichiuridae
Triglidae
Macrouridae
Artemiidae
Gempylidae
Histioteuthidae
Ophidiidae
Pilumnidae
Zenionidae
Family
Private Land (PL)
FOO (%)
25
20
15
10
5
0
Merlucciidae
Talitridae
Loliginidae
Octopodidae
Triglidae
Macrouridae
Artemiidae
Ophidiidae
Penaeidae
Trichiuridae
Zenionidae
Candaciidae
Cyttidae
Euclichthyidae
Moridae
Nettastomatidae
Family

A)


Simpson
1.00
0.75
0.50
0.25
0.00
Alpha Diversity Measure
BH
Season
CR

B)


Simpson
1.00
0.75
0.50
0.25
0.00
Alpha Diversity Measure
NP
Site
PL