

1 **Investigating spatiotemporal variation in the diet of Westland Petrel through** 2 **metabarcoding, a non-invasive technique**

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19 **Running head:** Spatiotemporal variation in diet of Westland Petrel

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22 *Procellaria westlandica*

23

24 **Abstract**

25 As top predators, seabirds are directly impacted by any changes in marine communities,
26 whether they are linked to climate change or caused by commercial fishing activities.

27 However, their high mobility allows them to adapt to changing conditions. For example,
28 seabirds can adapt their foraging behaviour according to the resources available at different
29 seasons. This capacity of adaptation comes to light through the study of their diet.

30 Traditionally, the diet of seabirds is assessed through the morphological identification of

31 prey remains in regurgitates, a method that is invasive for the bird and limited in terms of

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

40 We found that amphipods were the most common prey, or secondary prey, followed by
41 cephalopods and fish, suggesting a close link between the composition of prey items and
42 New Zealand's commercial fishing activities but, also, some level of natural predation.
43 Our results show significant differences in diet between seasons (before hatching vs chick
44 rearing season) and between sampling sites (two sub-colonies 1.5 km apart), which suggests
45 variability and adaptability in the foraging strategy of the Westland petrel.

46 Due to its non-invasive nature, the method used here can be applied on a great number of
47 samples to draw a comprehensive picture of the diet dynamic in seabirds and unravel their
48 adaptability or ecological requirements. This work demonstrates how environmental DNA
49 can inform the conservation of an endangered species with elusive foraging behaviour,
50 providing, in this case, valuable information regarding the diet preferences of an iconic
51 species within New Zealand's biodiversity.

52 **Introduction**

53 The study of animal diets is a critical component in many aspects of ecology, including
54 community ecology (Corse et al., 2010), population dynamics (Morrison et al., 2014; Read
55 and Bowen, 2001) and conservation biology (Lyngdoh et al., 2014; Xiang et al., 2012). In
56 predators in particular, spatial and seasonal variations in diet composition may reflect a
57 certain degree of flexibility in foraging behaviour (Whelan et al., 2000), that could be
58 relevant for understanding trophic interactions and, also, for conserving endangered species
59 (Davies et al., 2001; Farias and Kittlein, 2008; Vander Zanden et al., 2000; Vinson and
60 Angradi, 2011). Shedding light onto these patterns is essential in the case of seabirds, which
61 are top predators within marine ecosystems. Seabirds are known to modify their feeding
62 habits depending on the time of the year (Harding et al., 2007; Kowalczyk et al., 2015) and
63 their breeding site (McInnes et al., 2017a; Thompson et al., 1999). These birds spend most
64 of their lives at sea but during the breeding season, some remain in coastal areas as their
65 foraging trips are restricted in number and length to allow them to regularly feed their
66 chicks in the nest. To achieve this, seabirds have adopted a variety of foraging strategies
67 (McInnes et al., 2017a; Ydenberg et al., 1994), such as switching between short and long
68 foraging trips to feed their chicks while maintaining their body condition during the
69 breeding season (Baduini, 2003; Ropert-Coudert et al., 2004), or providing the chicks with
70 highly nutritive processed stomach oil (Baduini, 2003). The majority of studies that aim at
71 describing the diet of seabirds have been carried out during the chick rearing period only.
72 Often, this is because data are collected based on the morphological analysis of regurgitates
73 obtained from parents coming back to the nest to feed their chicks (Calixto-Albarrán and
74 Osorno, 2000; Croxall et al., 1988; Klages and Cooper, 1992; Suryan et al., 2002). This
75 approach however, leads to consider prey communities as a fixed parameter across time,
76 instead of treating it as a dynamic pattern (Barrett et al., 2007; Komura et al., 2018).
77 Consequently, many studies do not explore switches in diet, although it is known that the
78 ability to switch to new prey may potentially represent a driver to escape from striking
79 population declines and, even, from local extinctions of threatened populations (Marone et
80 al., 2017). Many seabird populations have been decreasing rapidly in recent years (Grémillet
81 et al., 2018; Thibault et al., 2019) and detailed knowledge of their diet preferences through
82 space and time is key to understand and better manage current and future threats,

83 including commercial fishing activities or climate-driven changes to their ecosystem (Frainer
84 et al., 2017).

85

86 Selecting the correct experimental design and the most efficient methodological approach
87 for the accurate characterization of seabird diet is essential, but also challenging (Ocké,
88 2013), mainly because direct observations of elusive seabirds (e.g. nocturnal) are difficult
89 and rare. For decades, the morphological identification of stomach contents or regurgitates
90 has been widely used to identify prey items of predators (Carreon-Martinez and Heath,
91 2010; Egeter et al., 2015; Freeman, 1998; Imber, 1976; Krüger et al., 2014). However, this
92 methodology usually requires that gut content is obtained by stimulating regurgitation after
93 capturing individual birds through a technique that has been called “lavage” (Barrett et al.,
94 2007; Ryan and Jackson, 1986; Wilson, 1984). Such an invasive sampling method (Lefort et
95 al., 2019) is not only unethical, but also potentially dangerous for the birds. Furthermore,
96 the efficiency of this method is usually limited because many individuals would have empty
97 stomachs at the moment of sampling, and highly digested prey items may not be
98 identifiable to genus or species level. The ability to identify prey remains from stomach
99 content also varies in relation to prey species, because some species (in particular soft-
100 bodied prey) are digested faster than others, leading to potential biases in the
101 characterization of the diet (Boyer et al., 2015; Deagle et al., 2007; Gales, 1988). More
102 recent approaches, such as fatty-acid or stable-isotope analyses, can be used to infer the
103 trophic position of predators in the food web, as well as potential switches in feeding sites.
104 Although they provide valuable information about trophic interactions, these methods do
105 not reach a fine-scale resolution, usually lacking genus or species-level identification, which
106 may be critical for the planning of conservation management actions (Bocher et al., 2000;
107 Chérel et al., 2000; Deagle et al., 2007; Guest et al., 2009; Guillerault et al., 2017). In the last
108 decade, parallel to the development and optimization of genomic techniques, DNA
109 metabarcoding approaches have allowed the accurate identification of prey species within
110 the diet of a high variety of taxa including invertebrates (Kerley et al., 2018; Mollot et al.,
111 2014; Pinol et al., 2014; Valentini et al., 2016) and vertebrates (Andriollo et al., 2019;
112 Guillerault et al., 2017; Kamenova et al., 2018; Leray et al., 2015; Sullins et al., 2018).

113

114 The Westland petrel (*Procellaria westlandica*) is endemic to New Zealand and listed as an
115 endangered species on the IUCN red list (BirdLife International, 2020). It is one of the few
116 burrowing birds breeding on the main islands. This iconic species was once widespread in
117 New Zealand (Waugh and Wilson, 2017; Wood and Otley, 2013), but its breeding
118 distribution is now restricted to the West Coast of the South Island, within the Paparoa
119 National Park and its surroundings (Jackson, 1958; Waugh and Wilson, 2017) (March to
120 November) (Landers et al., 2011). Between May and June, females lay a single egg, which is
121 incubated by both parents during 69 days (Warham, 1990). Chick rearing is also carried out
122 by both parents between September and November. After the breeding season, Westland
123 petrels travel to South American waters (Baker and Coleman, 1977) where they remain until
124 late March (Landers et al., 2011). Regarding their foraging behaviour, Westland petrels are
125 known to be nocturnal, but they occasionally feed during daytime (Waugh et al., 2018).
126 Previous studies based on morphological analysis of regurgitates found that their most
127 abundant prey items were fish, followed by cephalopods and crustaceans (Freeman, 1998;
128 Imber, 1976). The diet of Westland petrels is therefore closely linked to fishing activity in
129 New Zealand waters. However, it remains unclear whether fishing has a net positive or
130 negative impact on *P. westlandica*. The overall population has increased significantly since
131 the 70's (Wood and Davis, 2003; Wood and Otley, 2013), together with the rise of fishing
132 activity, potentially because of increase feeding on bycatch and other fishing waste.
133 However, being trapped and killed in fishing nets is one of the main threats of *P.*
134 *westlandica*, together with mammal predation, degradation of habitat and erosion of their
135 nesting grounds (Taylor, 2000; Waugh et al., 2008; Waugh and Wilson, 2017).
136 Although the diet of the Westland petrel has been assessed before (Freeman, 1998; Imber,
137 1976), the precise composition of their current diet is unknown, as is potential temporal
138 variations in diet throughout the breeding season. In this work, we present the first attempt
139 to characterize the diet of this seabird through a DNA-based approach. To do this, we used a
140 non-invasive DNA sampling approach (Lefort et al., 2019) by collecting faecal samples, and
141 carried out a DNA metabarcoding analysis using the 16S gene to identify prey items within
142 the diet of the Westland petrel. Prey identity was used to establish potential interactions
143 with the fishing activity in New Zealand. The birds' diet was compared between two
144 breeding sub-colonies (1.5 km apart), and two different times (10 weeks apart). We
145 expected to find differences in diet between early breeding season (before hatching) and

146 late breeding season (after hatching or chick rearing), which would be consistent with
147 switches in feeding and foraging behaviour. We expected to find no significant differences in
148 the diet of the different sub-colonies owing to their relatively close proximity. Moreover,
149 this study also aims to better understand the impact that fishing activities could have on
150 Westland petrels.

151

152 **Material and Methods**

153 *Study area and sample collection*

154 A total of 99 fresh faecal samples were collected from two different sampling sites located
155 in the West Coast of the South Island of New Zealand, the Paparoa National Park (NP) (-
156 42.146317, 171.340293) (49 samples) and a private land (PL) (-42.164358, 171.337603) (50
157 samples) (Table S1). Forty-eight samples were collected before hatching (BH) on the 9th and
158 10th of July 2015, and 51 samples were collected during chick rearing (CR) on the 22nd and
159 23rd of September 2015 (Table 1). To avoid cross-contamination, each fresh faecal sample
160 was collected using an individual sterile cotton swab and placed in a clean, single-use
161 Ziplock bag. Samples were then placed in a cooled icebox for transportation to the
162 laboratory (within the following two days), where they were stored at -80°C until DNA
163 extraction. Leaf litter samples were also collected to serve as negative controls.

164

165 *DNA extraction, PCR amplification and sequencing*

166 We performed a DNA extraction on one small subsample of each faecal sample, using the
167 QIAamp DNA Stool Mini Kit for which we followed the manufacturer's protocol with few
168 modifications. In brief, half volumes of all reagents were used and the extraction was
169 carried out in 1.5 ml tubes, instead of 2 ml tubes. Also, after adding half an InhibitEx Tablet,
170 we performed one centrifugation, rather than 2 (Steps 6 and 7 in the protocol were joined).
171 Later, on step 13, we mixed 200 µl of ethanol by pipetting and 600 µl of the mix were added
172 to the column. From step 14, volumes recommended by the manufacturer's protocol were
173 used. Finally, samples were eluted in 100 µl of elution buffer (AE) and DNA extracts stored
174 at -20°C.

175

176 Later, two different PCR amplifications were performed from each DNA extract. First, we
177 used a pair of primers specific for Chordata (16S1F, 16S2R), which amplifies 155 bp of the
178 16S gene (Deagle et al., 2009, 2005). Second, we used a pair of primers specific to
179 Malacostraca (Chord_16S_F_TagA, Chord_16S_R_Short), which amplifies 205 bp of the 16S
180 gene (Deagle et al., 2009). These two pairs of primers were chosen to allow the detection of
181 a wide range of potential prey, including the main taxa identified morphologically in
182 previous studies (Freeman, 1998; Imber, 1976). PCR conditions for both primer pairs were
183 the same as in (Olmos-Perez et al., 2017), with the exception of the Taq polymerase. Here,
184 the FirePOLE® Taq polymerase was used for all amplifications, following manufacturer's
185 protocol (Solis BioDyne). After checking the results in a 1.5% agarose gel, PCR products were
186 purified using magnetic beads, and for each sample, both PCR products were pooled.
187 Second stage PCR amplifications and subsequent sequencing steps were carried out by New
188 Zealand Genomics Limited (NZGL, University of Otago). The resulting amplicons were
189 arranged in two plates and indexed with Nextera adapters (Index Set C) in unique
190 combinations. Each plate included a 16S mock community sample using Index Set D.
191 Sequencing was performed by NZGL on Illumina MiSeq 2x300bp reads (600 cycles) (Illumina
192 MiSeq v3 reagent kit).

193

194 *Bioinformatic library filtering*

195 Demultiplexing and adapter trimming was carried out by NZGL. The metabarcoding library
196 filtering was performed using the software *vsearch v2.8.1* (Rognes et al., 2016). First, we
197 used the *fastq_mergepairs* command to align the forward and reverse read pairs, allowing a
198 maximum of 25 differences between both pairs. At this stage, merged sequences that were
199 shorter than 100bp or longer than 300bp were discarded. This step was followed by the
200 calculation of the quality statistics for each read pair retained, using the *fastq_eestats*.
201 Paired reads were then filtered by quality using the *fastq_filter* command
202 (*fastq_maxee=0.5*) and fastq files converted to fasta. The library was dereplicated at sample
203 level using the *derep_fulllength* command leading to unique sequences in each individual
204 sample, at this point one fasta file was produced per sample. All reads were then
205 aggregated in one single fasta file. Reads were then dereplicated across all samples, again
206 with *derep_fulllength* command, and singletons were removed (*minuniquesize = 2*). This
207 step was followed by a pre-clustering step before chimera detection at 98% using the

208 *cluster_size* command. After pre-clustering, we only retained unique sequences using *grep*
209 command and we detected chimeras *de novo* using the *uchime_denovo* command, again
210 only retaining the unique sequences after this step. All non-chimeric and non-singleton
211 sequences from each sample were then retained in a single fasta file, using a customized
212 Perl script, *map.pl*, from the *vsearch* pipeline available at this Github repository:
213 <https://github.com/torognes/vsearch> (last accessed on April 2020). Finally, we performed
214 the Operational Taxonomic Unit (OTU) picking, with a cut-off threshold of 97% (Xiong and
215 Zhan, 2018), using the *cluster_size* command, which produced an OTU table and fasta file
216 with all the sequences belonging to each OTU.

217

218 All OTUs were compared to the NCBI database using BLASTn (Johnson et al., 2008) and the
219 pertinent multiple-file JSON was downloaded from the web interface. We then used a
220 customized R script, based on the functions *fromJSON* and *classification* from R packages
221 *rjson* (Couture-Beil and Couture-Beil, 2018) and *taxize* (Chamberlain and Szöcs, 2013),
222 respectively, to assign a taxonomic classification to each clustered OTU. Regarding
223 taxonomic assignment, OTUs with BLAST query coverage under 60% or BLAST identities
224 lower than 74% were discarded. Read abundances equal to 1 (singletons among samples
225 and OTUS) were considered as potential contamination and removed from the dataset as
226 were any OTUs matching to Westland Petrel. Every other OTUs were retained for
227 subsequent statistical analyses. Potential prey (or secondary prey) OTUs within the phyla
228 Arthropoda and Chordata were assigned using the following criteria to taxonomical
229 categories: OTUs with identity higher than 97% were determined at species level, OTUs
230 between 93 and 97% were assigned to genus level, and OTUs with identity below 93% were
231 assigned to family level. In the case of the phylum Mollusca, we determined the assignment
232 threshold from the distance matrix of the alignment of the sequences. To do that, we first
233 computed a “raw” pairwise genetic distance matrix within the alignment of 411
234 Cephalopoda homologous retrieved from Genbank sequences using the function *dist.dna*
235 from R package *ape* (Paradis et al., 2005), we then calculated the threshold value applying
236 the function *localMinima* from R package *spider* (Brown et al., 2012). Based on this analysis,
237 we used a threshold of 98.6% to assign OTUs to species level within Mollusca.

238

239

240 *Biodiversity analyses*

241 In order to evaluate the impact of commercial marine species on the diet of *P. westlandica*,
242 we collected ecological information from Fishbase (Froese and Pauly, 2010) and Sealifebase
243 (Palomares and Pauly, 2010) to determine the distribution of each prey taxa. Considering
244 that *P. westlandica* is able to dive up to 15 m for fishing (Waugh et al., 2018), we specifically
245 looked for information about the depth at which the prey species is usually present (shallow
246 versus deep sea) and therefore naturally reachable for the Westland petrel. We also
247 checked whether those prey species had been detected in previous publications (Table 1).
248 To measure the completeness of our sampling, we evaluated the total richness of prey in
249 the diet of *P. westlandica*, using a rarefaction curve and a bootstrap estimator using the
250 function *specpool* in the R package *vegan* (Oksanen et al., 2013). The diet of Westland
251 petrels was described using two different metrics. First we calculated the Frequency of
252 Occurrence (FOO) by transforming the number of reads to presence/absence (1-0) and,
253 subsequently, summing the counts of samples that contain a given prey item (OTU),
254 expressed as a proportion of all samples (Deagle et al., 2019). Second, we calculated the
255 Relative Read Abundance (RRA), which is the proportion of reads of each prey item (OTU) in
256 a given sample (Deagle et al., 2019). These two metrics are different proxies, FOO is a proxy
257 for occurrence and RRA is a proxy for relative food biomass (Cavallo et al., 2018; Deagle et
258 al., 2019). FOO and RRA were calculated overall and also compared between seasons:
259 before hatching (BH) versus chick rearing (CR); and between sub-colonies: natural park (NP)
260 versus private land (PL).

261

262 To estimate the effects of seasonality and sub-colony location on diet diversity and
263 composition, we computed a negative binomial Generalized Linear Model (GLM) (McCullagh
264 and Nelder, 1989) with a log link function, applying the function *manyglm* from the R
265 package *mvabund* (Wang et al., 2017). Two different GLM analyses were performed, one
266 with abundance as the dependant variable and one with occurrences (presence/absence) as
267 the dependant variable. For both GLM analyses, the predictor variables were season (two
268 factor levels: BH and CR) and site (two factor levels: NP and PL) as well as the interaction
269 between these variables. An analysis of Deviance (Dev) was performed to test the fitness of
270 the model, with 999 bootstraps iterations as a resampling method (Davison and Hinkley,
271 1997), using the function *anova.manyglm* from the package *mvabund* (Wang et al., 2017).

272

273 Finally, we estimated and plotted the standard alpha diversity, as a proxy for prey species
274 richness, comparing the two factors studied, season and site. For that purpose, we used the
275 functions *estimate_richness* and *plot_richness* from R package *phyloseq* (McMurdie and
276 Holmes, 2012). In addition, we computed pairwise comparisons between the alpha diversity
277 values (Shannon) of the group levels through the pairwise Wilcoxon rank sum test (Gehan,
278 1965), using the function *pairwise.wilcox.test* from the R package *stats* (Team and others,
279 2013).

280

281 **Results**

282 *Amplification success and library quality*

283 All 99 samples were successfully amplified with both pairs of primers and sequenced with
284 Illumina MiSeq. We obtained a total of 9,847,628 raw reads, which resulted in 2,061,401
285 merged reads. After quality filtering, dereplication and removal of chimeras and singletons,
286 1,844,930 reads remained. These included only 494 (0.027%) singletons, which were
287 removed as they were considered as potential contaminants. The remaining reads clustered
288 into 395 OTUs. After assigning a taxonomy to each OTU, 532,228 reads had no hit against
289 the BLAST database, 147,134 reads could not be confidently identified (low percentage of
290 identity and/or low query coverage), 223,239 reads were considered as contaminants. The
291 remaining 942,329 reads were considered as prey or secondary prey and, hence, were
292 included in the subsequent analyses (Fig.S1). These prey reads belonged to 78 OTUs (Table
293 1), and were detected in 87 out of 99 samples.

294

295 *Characterization of the diet of P. westlandica*

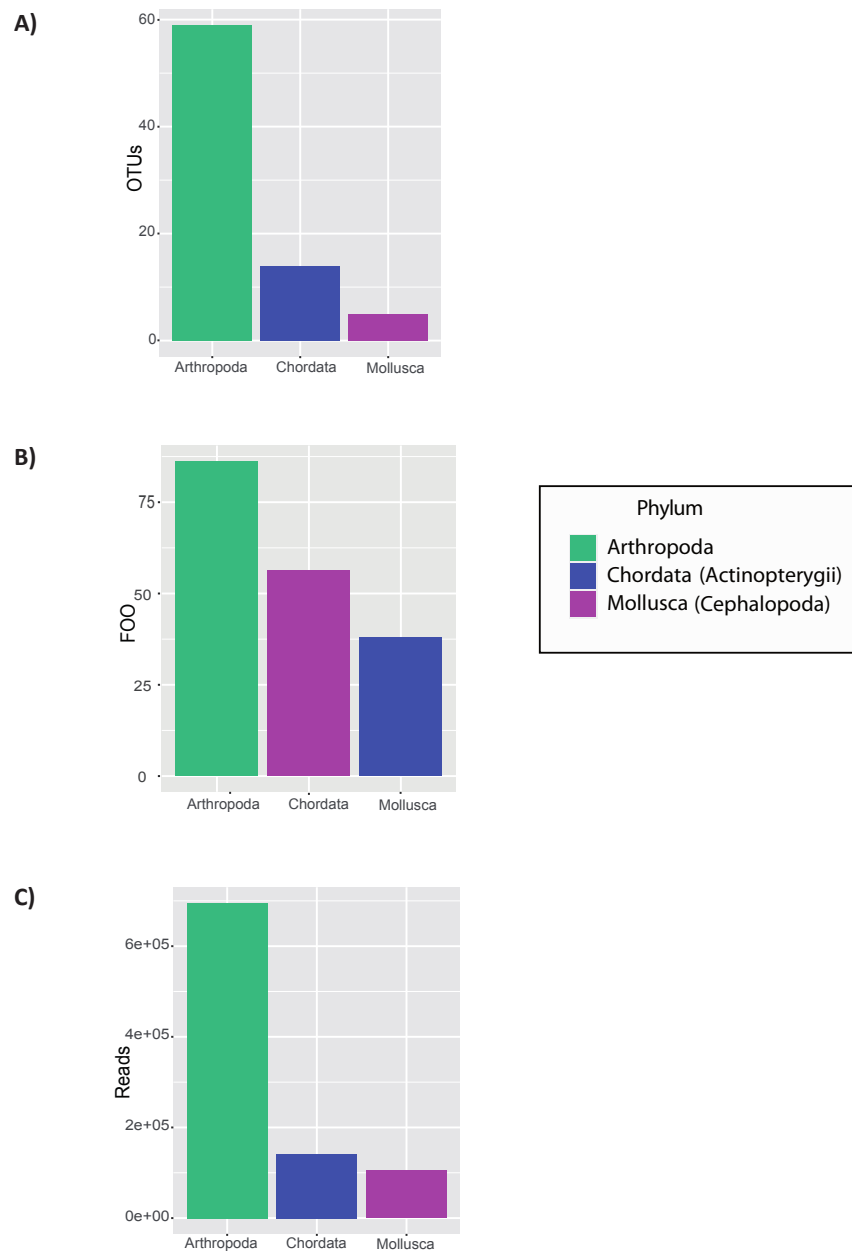
296 Species richness estimation (using bootstrap) suggested that our sampling captured 83.75%
297 of the total diversity of prey items within the diet of *P. westlandica* (Fig.S2). Out of the 78
298 OTUs recovered by metabarcoding, 13.69% (15 OTUs, 129,038 reads) were identified to
299 species level, 13.77% (17 OTUs, 129,802 reads) were identified to genus level and 86.22%
300 (61 OTUs, 812,527 reads) were identified to family level (Table 1).

301 Arthropods (crustaceans in this case) were the most common prey or secondary prey
302 phylum across both seasons and sites. In total, they were present in 86.21% of the samples

303 (FOO) and represented 73.79% of the sequences (RRA) and 71.8% of the OTUs.
304 Actinopterygii (bony fish) were next, being present in 37.93% of the samples and comprising
305 15.02% of all sequences and 17.95% of all OTUs. Finally, cephalopods were present in
306 56.32% of the samples and made up 11.17% of the sequences and 6.41% of the OTUs
307 (Fig.1). Within arthropods, talitrids (landhoppers and sandhoppers) were by far the most
308 abundant taxa. They were present in 85.1% of the samples and made up 73.34% of the
309 sequences. Other minor arthropod taxa were identified, such as the families Pilumnidae
310 (pilumnid crabs) and Penaeidae (penaeid shrimps), among others (<1% total reads; Fig.S3;
311 Table 2). With the exception of four OTUs, which were identified to species level,
312 arthropods were identified to family level.

313
314 Within Chordata (fish in this case), Hoki (*Macruronus novaezelandiae*) was the most
315 common species as it was present in 14.94% of the samples and represented 3.87% of all
316 sequences. The Southern hake (*Merluccius australis*) and the Cocky gunard (*Lepidotrigla*
317 *modesta*) were also important prey items, being present in 10.34% and 9. % of the samples
318 and comprising 3.6% and 3.53% of all sequences, respectively. Next were cutlassfish,
319 identified to family level (Trichiuridae), and present in 5.75% of the samples and comprising
320 1.67% of all sequences. Finally, the Thorntooth grenadier (*Lepidorhynchus denticulatus*) was
321 present in 6.9% of the samples and comprised 1.62% of all sequences. As in the case of
322 arthropods, we detected few other minor taxa, such as the Pink cusk-eel (*Genypterus*
323 *blacodes*) or the Hawknose grenadier (*Coelorinchus oliverianus*), among others (<1% reads:
324 Table 2; Fig.2). Out of 14 OTUs of Actinopterygii, one OTU was identified to genus level, two
325 OTUs were identified to family and the remaining 11 OTUs were identified to species level
326 (Table 1).

327
328 According to our results, within cephalopods, five different OTUs were identified as prey
329 items and were all assigned to family level (Table 1). The most common cephalopod prey
330 item were pencil squids (family Loliginidae), which were present in 31.03% of the samples
331 and comprised 9.39% of all sequences. Octopodids (family Octopodidae) were present in
332 28.74% of the samples and made up 1.73% of all sequences. Finally, Oegopsida squids
333 (Family Histioteuthidae) were present in 1.15% of the samples but comprised less than 1%
334 of the reads (Table 2; Fig. 2).



335

336 **Figure 1.** Phyla identified using three different biodiversity metrics: A) Number of OTUs as a proxy of diversity,

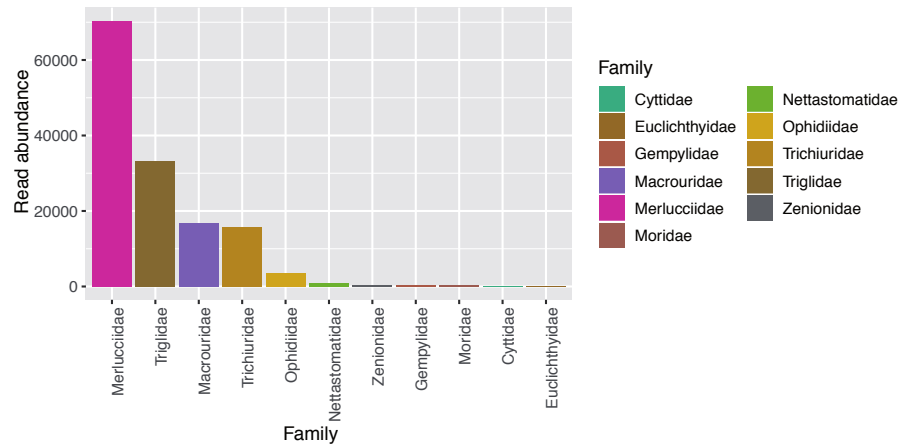
337 B) Frequency of occurrence (FOO) refers to the percentage of samples in which the prey item is present and C)

338 Read abundance as a proxy of relative food biomass.

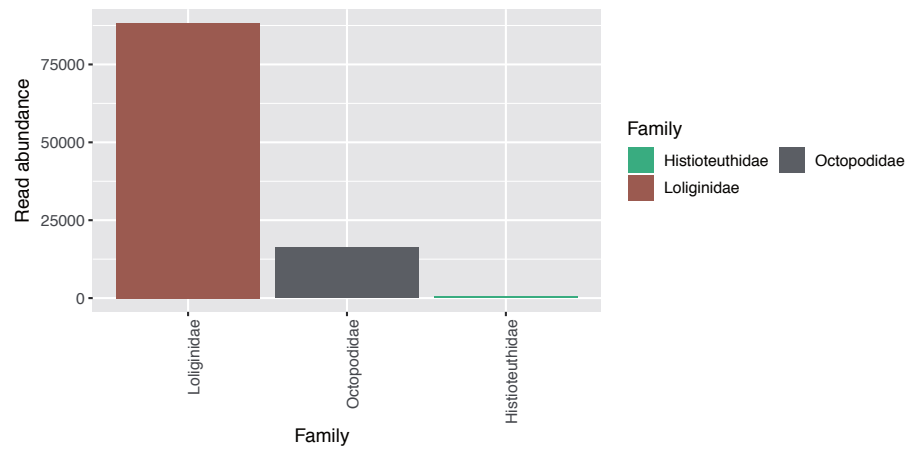
339

340

A)



B)



341

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

343

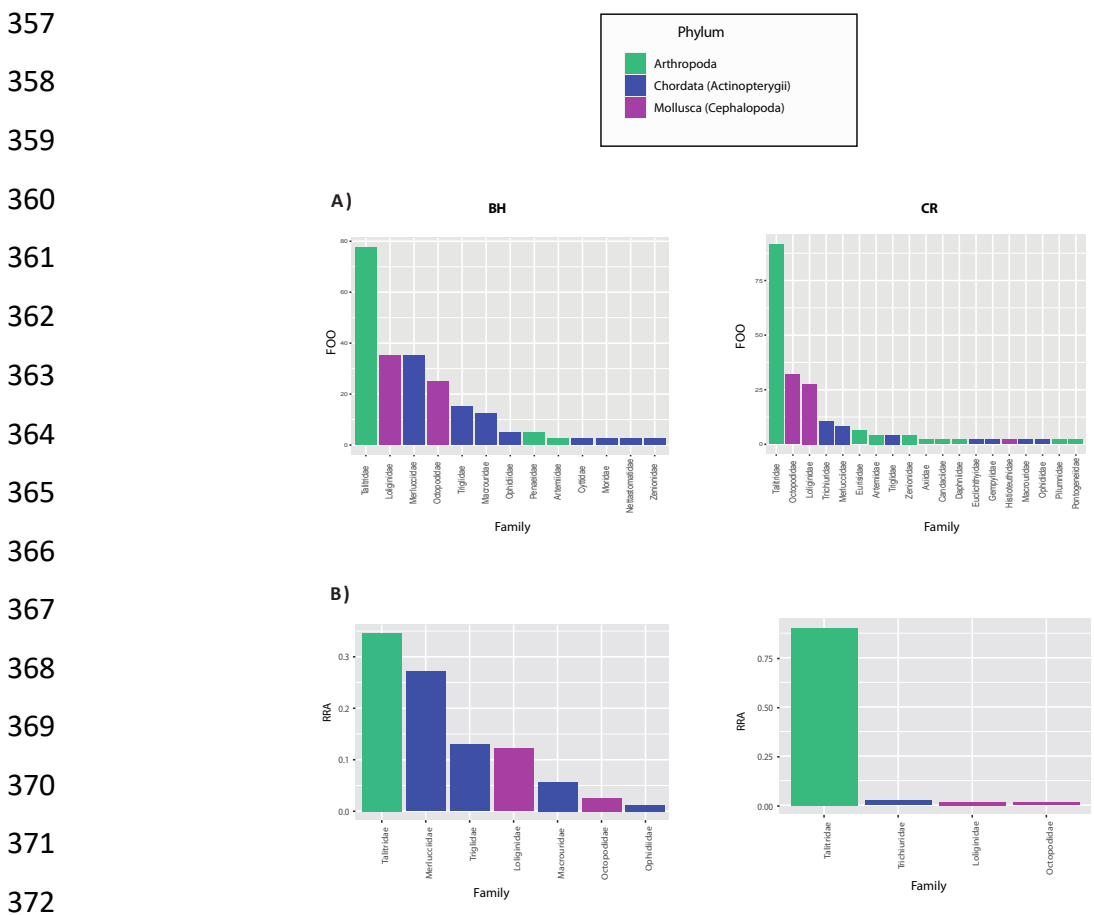
344

345 *Seasonal variation in the diet of P. westlandica*

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

349 Prey community composition varied significantly between the two different seasons both in
 350 terms of read abundance (Analysis of Deviance: $Dev_{1,87} = 205.3$, $p = 0.002$) and prey
 351 occurrence (Analysis of Deviance: $Dev_{1,87} = 181.1$, $p = 0.001$) (Fig. 3).

352 When looking at frequency of occurrence, in both seasons, crustaceans (mostly talitrids,
 353 amphipods) were the most common prey, followed by cephalopods and then by
 354 Actinopterygii fish (Table 2; Fig.). The same pattern was observed for relative read
 355 abundance, except that during the early breeding season (before hatching), fish reads were
 356 more important than those of cephalopods (Table 2; Fig.3B).



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

377 Talitrids were by far the most common prey group overall and represented more than 99%
378 of all arthropods identified in this study. Although a minor prey, the Banana shrimp
379 (*Penaeus merguensis*), was present in 5% of samples before hatching but it was absent
380 during the chick rearing season (Table 2).

381 Eleven species of Actinopterygii fish were identified in the samples collected before
382 hatching, compared to ten species during the chick rearing season. Hoki was the most
383 common fish species detected before hatching, followed by Southern Hake and Cocky
384 gunard. During the chick rearing season, Trichiuridae fish were the most common followed
385 by Southern hake and Cocky gunard.

386 With regards to cephalopods, Pencil squids (Loliginidae) were the most common taxa before
387 hatching followed by octopodids (Octopodidae), while it was the other way around, during
388 the chick rearing season. Interestingly, an Oegopsida squid (Histiotteuthidae) was also
389 detected during the chick rearing season while it was completely absent before hatching
390 (Table 2; Fig.3A and B).

391 Regarding species richness, the values of alpha diversity (Shannon) were significantly
392 different between seasons, with lower diversity observed before hatching (α [mean \pm SE] =
393 0.31 ± 0.06) compared to the chick rearing season (α [mean \pm SE] = 0.58 ± 0.07) (Fig.5).

394

395 *Geographical variation in the diet of P. westlandica*

396 Significant differences in prey community were observed between the two sub-colonies,
397 both in terms of read abundance (Analysis of Deviance: $Dev_{1,87} = 152.6$, $p = 0.015$) and
398 occurrence of prey items (Analysis of Deviance: $Dev_{1,87} = 139.5$, $p = 0.017$) (Fig. 4).

399

400 Arthropods were found to be by far the most commonly detected prey group in both sub-
401 colonies. However, in NP, cephalopods were more common and produced more reads than
402 Actinopterygii fish, while in PL, these two groups had the same occurrence and
403 Actinopterygii fish produced more reads than cephalopods.

404 Thirteen species of Actinopteriigy were identified in samples collected in the PL, while nine
405 were found in the NP. Hoki and fish from the Trichiuridae family were the most common
406 fish detected in NP samples, followed by Cocky gunard. In PL samples, Hoki was also the
407 most common fish item taxa, followed, in this case, by Southern hake and Cocky gunard
408 (Table 2).

409 With regards to cephalopods, pencil squids were the most common group followed by
410 octopodids. However, these values did not differ as much as in the case of seasonal
411 variation (Table 2; Fig.4A and B).

412

413 In contrast to seasonal variation, no significant differences in species richness (alpha
414 diversity) were observed in prey diversity when comparing the two sub-colonies NP (α
415 [mean \pm SE] = 0.48 \pm 0.07) and PL (α [mean \pm SE] = 0.58 \pm 0.07) (Fig.5).

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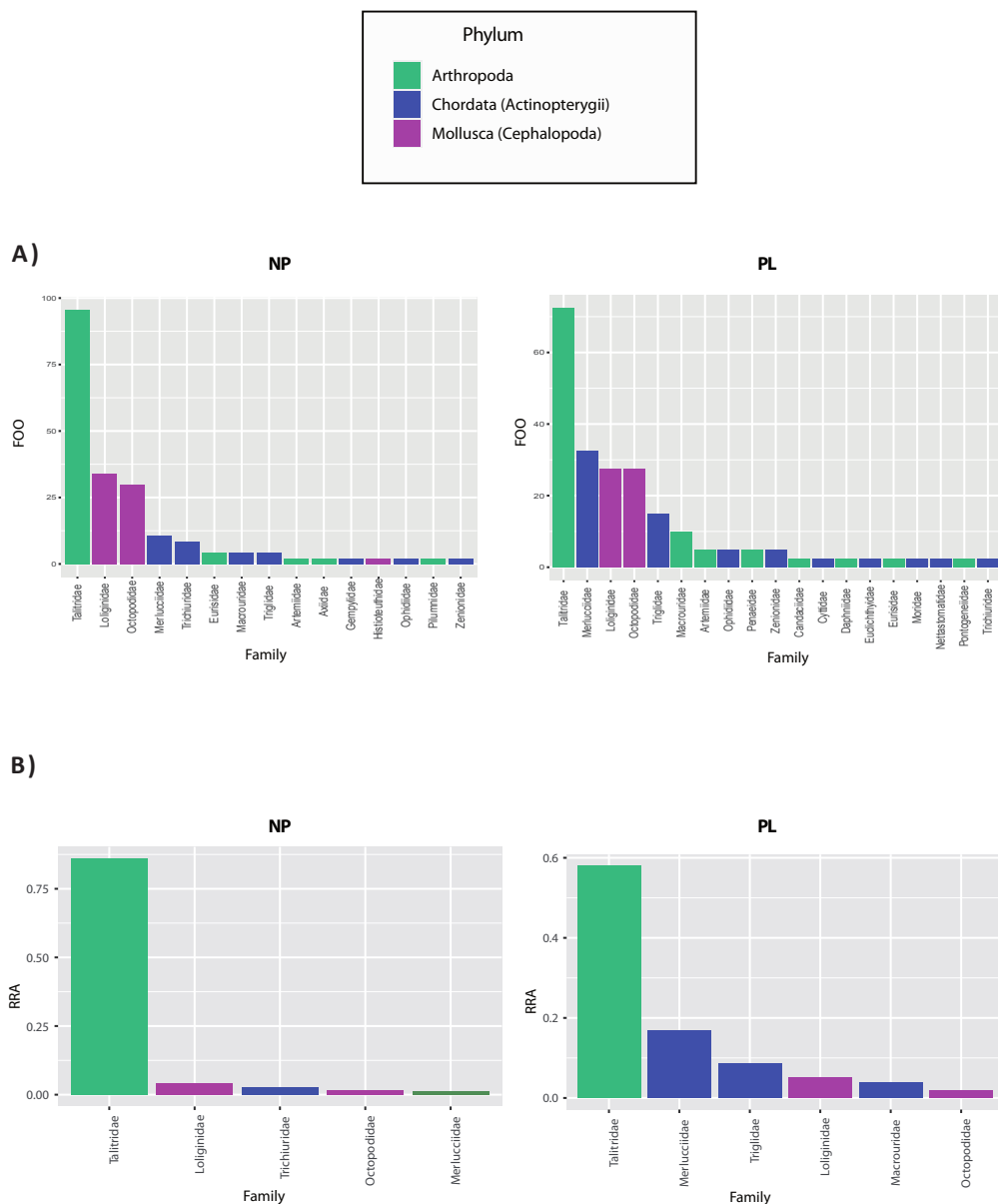
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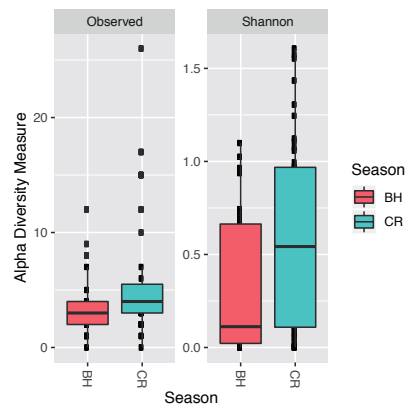
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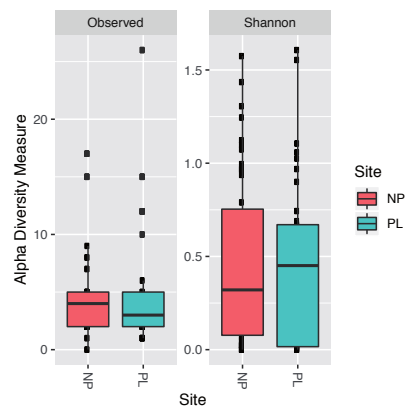


435 **Figure 4.** Geographical variations at family level among the two sub-colonies: the Paparoa National Park (NP)
436 and the private land (PL), according to two biodiversity metrics: A) Frequency of Occurrence (FOO) and B)
437 Relative Read Abundance (RRA). Taxa with less than 1% of FOO or RRA were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

A)



B)



438

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

440

441 Discussion

442 This is the first attempt to characterize the diet of the New Zealand endemic Westland

443 petrel using a DNA metabarcoding approach. Aside from the molecular non-invasive

444 approach, the novelty of this study lies in the analysis of samples from multiple seasons and

445 sub-colonies. The observed seasonal and geographical variations in the diet of *P.*

446 *westlandica* provide a broad picture of the feeding requirements and foraging ecology of

447 this species. Previous works on the diet of *P. westlandica* were based on morphological

448 identification of prey remains and carried out exclusively during the breeding or chick

449 rearing season (Freeman, 1998; Imber, 1976). Our study shows the presence of fish,
450 cephalopods and amphipods (crustaceans) in the diet of *P. westlandica*, confirming the
451 results of previous approaches (Freeman, 1998; Imber, 1976). However, the relative
452 importance of each type of prey differs considerably between these studies and the current
453 work, where we identified a number of taxa undetected before in such high percentage.

454

455 The phylum showing the highest percentage of prey items is Arthropoda (71.8% of the
456 OTUs), mainly represented by the order Amphipoda. These animals can range from 1 mm to
457 34 cm in size. However, most species are microscopical benthic zooplankton and are known
458 to be common prey of many cephalopods (Villanueva et al., 2017) and fish, including Hoki
459 (Connell et al., 2010; Livingston and Rutherford, 1988) and Hake (Dunn et al., 2010).
460 Therefore, Amphipods detected in this study could potentially be secondary prey. However,
461 several seabirds such as penguins feed regularly on amphipods (Jarman et al., 2013; Knox,
462 2006), and large amphipods could potentially represent a fundamental food source for
463 Antarctic seabirds (Centro de Investigacion Dinamica de Ecosistemas Marinos de Altas
464 Latitudes, 2017), where they play a similar role as the krill (Euphausiacea) in the water
465 column. Moreover, amphipods are found in the stomachs of other Procellariiformes, such as
466 the Providence petrel (*Pterodroma solandri*) (Bester et al., 2011; Lock et al., 1992), the Blue
467 petrel (*Halobaena caerulea*) (Croxall, 1987) and the Wilson's storm petrel (*Oceanites*
468 *oceanicus*). These birds are known to feed on amphipods when krill is not available
469 (Quillfeldt et al., 2019, 2005, 2001, 2000). Imber (1976) found no planktonic crustacean in
470 the stomach of *P. westlandica* and Freeman (1998) only detected small percentage of taxa
471 belonging to three different families: Euphausiidae or krill (*Nyctiphanes australis* and
472 *Thysanoessa gregaria*), Caridea or caridean shrimps (*Notostomus auriculatus* and an
473 unidentified species) and Cymothoidae (unidentified species). Although it remains unclear
474 whether Amphipods are primary or secondary prey (Sheppard et al., 2005), we can confirm
475 that these taxa play a major role in the flow of energy through the food web.

476

477 Fish are major prey items of Procellariiformes (Bester et al., 2011; Bocher et al., 2000; da
478 Silva Fonseca and Petry, 2007; Freeman, 1998; Imber, 1976; Prince and Morgan, 1987; Spear
479 et al., 2007; Stewart et al., 1999), and the Westland petrel is not an exception. According to
480 our results, fish (all belonging to the order Actinopteriigy) represent 15.03% of the prey

481 reads, and are the second most abundant phylum. In addition, fish DNA was detected in
482 37.93% of the samples. The fish species identified by our approach are consistent with
483 previous studies (Freeman, 1998; Imber, 1976) but also include new species. In coherence
484 with previous knowledge, the Hoki was identified as the most abundant fish prey item. We
485 also found that Hake, another Merlucciidae not previously identified in the diet of the
486 Westland petrel, is the second most predated fish species. Merlucciids, especially Hoki but
487 also Hake, are some of the main fishery species caught in New Zealand waters (Livingston
488 and Rutherford, 1988). The fishing season for Merlucciids spans mainly between June and
489 September, thereby encompassing most of the Westland petrel's breeding season (Waugh
490 et al., 2018; Waugh and Wilson, 2017), and including both sampling events of this study.

491
492 Hoki and Hake live between 28 and 1,000 m below sea level (Table 1), which makes these
493 fish not naturally catchable for Westland petrels, who only dive down to 15 m below the
494 surface (Freeman, 1998). Therefore, it is likely that these species are scavenged from fishing
495 vessels. The same conclusion could apply to a number of other fish species with deep depth
496 ranges, that are naturally unreachable to the petrel, but are important fishery species
497 (Freeman, 1998; Froese and Pauly, 2010). These include rattails (Macrouridae), such as the
498 Thorntooth grenadier as well as two newly identified prey items, namely the Hacknose
499 grenadier and the Banded whiptail, among other fish species living in deep sea waters
500 (Table 1). In the case of Hoki, however, natural predation may be possible at night, as this
501 fish species is known to migrate to surface waters to feed during the night (McClatchie and
502 Dunford, 2003; O'Driscoll et al., 2009), when *P. westlandica* forages more actively (Waugh et
503 al., 2018).

504
505 Another species that could potentially have been predated naturally by the Westland petrel
506 is the Cocky gurnard, a Perciforme belonging to the family Triglidae, which can be found
507 sometimes in shallow waters (Froese and Pauly, 2010). However, this gurnard is also a
508 known fishery species that could have been scavenged from the fishing waste. Also, many
509 fish species belonging to the family Trichiuridae can live close to the surface. Myctophid
510 fishes, which were reported to be natural prey of the Westland petrel (Freeman, 1998;
511 Imber, 1976), were not identified in our sampling. It is possible that these species are no

512 longer selected by the Westland petrel, as previous studies were conducted more than 20
513 years ago for Freeman (Freeman, 1998) and more than 40 years ago for (Imber, 1976).

514

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

522

523 According to our results, 11.18% of prey reads, belonged to cephalopods, and these taxa
524 were detected in 56.32% of the samples (compared to 37.93% for fish). Four out of five
525 cephalopod OTUs could only be assigned to family level. Only *Histioteuthis sp.* was assigned
526 to genus level, a taxon already found in previous studies (Freeman, 1998; Imber, 1976). Our
527 results are consistent with Freeman (1998), which states that fish prey items are followed
528 by (Davies et al., 2009; Pierce et al., 2010) cephalopods within the Westland petrel's diet.
529 *Histioteuthis sp.* are deep-sea squid (Voss et al., 1998), but migrate to surface water at night
530 by vertical migration (Roper and Young, 1975), thus they become catchable by Westland
531 petrel. The other two families, Loliginidae and Octopodidae, which were also identified in
532 previous studies, are present from surface waters down to 500 m deep, and thus naturally
533 catchable for the Westland petrel. Nevertheless, these families also include several
534 commercial species as well as species commonly reported as bycatch (Davies et al., 2009;
535 Pierce et al., 2010)- Therefore, it is possible that petrels fed on some cephalopods through
536 fishery waste.

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

542

543 Marked dietary switches between breeding and non-breeding seasons have been
544 documented for several seabirds (Howells et al., 2018), and are considered a sign of
545 plasticity in behaviour (Quillfeldt et al., 2019). These switches may reflect variation in prey
546 availability, a change of strategy between seasons, or a combination of both (Howells et al.,
547 2018; Paleczny et al., 2015; Sydeman et al., 2015). Because these variations can severely
548 affect marine top predator's populations (Cury et al., 2000; Reid and Croxall, 2001) it is
549 essential to understand their drivers to ensure the conservation of the Westland petrel.
550 As hypothesized before, there is a clear seasonal variation in the diet of *P. westlandica*, both
551 in terms of read abundance (food biomass) and the occurrence of prey species, meaning
552 that the composition of the diet changes in a substantial way between incubation and chick-
553 rearing season. This change is particularly visible for fish, but also for cephalopods, which
554 are both more abundant before hatching than during the chick rearing season. One
555 explanation could be that adult petrels feed their chicks with highly nutritive fish and
556 cephalopods, while they feed themselves mainly with crustaceans (and some cephalopods).
557 This hypothesis is highly consistent with the significant loss of weight in adult seabirds
558 during the breeding season, while their chicks experience rapid growth (Ainley, 1990;
559 Barrett et al., 1985; Leal et al., 2017). In this case, the choice of prey items by adults may be
560 influenced by the developmental stage and the needs of the chicks.

561

562 Our results suggest that these changes would be more influenced by a change of foraging
563 strategy, rather than a change in prey availability, as the peak of the Hoki fishery in New
564 Zealand encompasses both July (before hatching period) and September (chick rearing
565 period), which means, fishery waste would be equally available during both seasons.
566 Our results show significant higher alpha diversity or species richness (Observed and
567 Shannon) during the chick rearing period. The less diverse diet before hatching could be due
568 to a higher specialization, that would require a higher investment in time and energy for the
569 adult birds while they do not have to take care of the chicks. In contrast, one would expect a
570 more generalist diet during chick rearing, at a time when fishing trips must be limited in
571 time to take care of the chicks and energy management is crucial for the adults. Moreover,
572 it has been shown that a higher diversity and, consequently, a wider range of nutrients
573 (Hillebrand et al., 2009) increases chicks growth rate as well as their probability of fledging
574 (van Donk et al., 2017). Another potential explanation is the fact that petrel colonies

575 comprise more non-breeding adults towards the end of the breeding season i.e. during
576 chick rearing. These non-breeding individuals may cause a variation in the diet at the
577 population level.

578

579 Contrary to our expectation, we found significant differences between both sub-colonies. A
580 possible explanation of these differences is the fact that seabirds from nearby sub-colonies
581 forage in different locations, possibly to avoid or decrease inter-colony competition (Cecere
582 et al., 2015; Grémillet et al., 2004; Wakefield et al., 2013). Also, the diet could change every
583 day, depending on the resource availability or the foraging behaviour and habits could be
584 different depending on the sub-colonies. However, in order to clarify the origin of these
585 differences in prey community composition (not in diversity) between sub-colonies, further
586 studies on population dynamics and foraging ecology of the Westland petrel should be
587 conducted.

588

589 Sustainable management of worldwide fishery industry needs information regarding the
590 overlap of marine organisms, such as seabirds, with fishing industry (Frederiksen et al.,
591 2004; McInnes et al., 2017b; Okes et al., 2009). Seabirds scavenge food from fishery waste
592 and results in a high number of incidental kills through bycatch, potentially disturbing on
593 population dynamics (Brothers, 1999; McInnes et al., 2017b; Sullivan et al., 2006; Tuck et al.,
594 2011; Watkins et al., 2008; Waugh et al., 2008; Waugh and Wilson, 2017). But, also, the diet
595 of seabirds relies on this commercial activity, as fishery waste is a nutritious prey, naturally
596 unreachable by seabirds. That is why understanding these interactions is essential for
597 seabird conservation and efficient ecosystem-based fishing regulation (Becker and
598 Beissinger, 2006; Freeman, 1998; Furness, 2003; Furness and Tasker, 2000; McInnes et al.,
599 2017b; Phillips et al., 1999; Waugh et al., 2008). In this context, non-invasive dietary studies
600 can provide knowledge to assess risks as well as the needs of these species that may rely
601 heavily on commercial fishing activity (Gaglio et al., 2018; McInnes et al., 2017a, 2017b).
602 This issue is particularly urgent in the case of endangered species, such as the Westland
603 petrel, and, in this study, we show a link between fisheries in New Zealand and the diet of
604 the petrel, that could be taken into account in management strategies.

605

606 Our results should draw attention to the complexity that lies in the implementation of
607 fishing and conservation regulations. In the case of Westland petrel, these regulations
608 should take into account, not only the close link between the commercial fishing and the
609 diet preferences of the birds, but also the high number of birds' deaths happening every
610 year through bycatch, as the Westland petrel is the fourth seabird species in terms of
611 bycatch risk in New Zealand (OpenSeas, 2019). Several mitigation solutions have been
612 suggested by practitioners or already included in conservation reports, to limit the number
613 of accidental kills in seabirds and find a sustainable equilibrium between fishery industry
614 and threatened species. Thus, research on how seabirds in general, and Westland petrel in
615 particular, interact with the fishing gear would help to develop bycatch reduction
616 techniques and using or developing gear less dangerous for the seabirds.

617

618 **Author contribution**

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

622

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638

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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_40	Arthropoda	Branchiopoda	Anostraca	Artemiidae	<i>Artemia</i>	<i>Artemia franciscana</i>	1871	1.14E-88	0.994595	185	0.978723	NO	0.1-0.6
OTU_391	Arthropoda	Branchiopoda	Diplostraca	Daphniidae	Not identified	Not identified	2	2.08E-26	0.860656	122	0.636842	NO	-
OTU_1	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	346004	9.69E-25	0.802260	177	0.982857	NO	0-0.1
OTU_4	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	150978	3.49E-24	0.793296	179	0.988889	NO	0-0.1
OTU_7	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	74647	3.44E-34	0.831522	184	0.988950	NO	0-0.1
OTU_10	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	54540	3.51E-19	0.777174	184	0.983607	NO	0-0.1
OTU_16	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	22487	3.44E-34	0.828729	181	0.988950	NO	0-0.1
OTU_22	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	10161	5.71E-37	0.834254	181	0.983425	NO	0-0.1
OTU_23	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	9847	5.88E-17	0.773481	181	0.983333	NO	0-0.1
OTU_28	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	5507	9.69E-25	0.797753	178	0.983333	NO	0-0.1
OTU_35	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	3213	4.51E-23	0.796610	177	0.982857	NO	0-0.1
OTU_36	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	2757	1.61E-27	0.809783	184	0.988889	NO	0-0.1
OTU_37	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	2757	3.51E-19	0.777174	184	0.983607	NO	0-0.1
OTU_44	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	1624	4.48E-28	0.811111	180	0.983146	NO	0-0.1
OTU_48	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	1404	1.61E-27	0.807692	182	0.983051	NO	0-0.1
OTU_52	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	1303	5.88E-17	0.775956	183	0.982857	NO	0-0.1
OTU_53	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	1260	7.49E-26	0.803279	183	0.988889	NO	0-0.1
OTU_54	Arthropoda	Malacostraca	Decapoda	Pilumnidae	<i>Pilumnus</i>	<i>Pilumnus hirtellus</i>	986	1.89E-96	0.994975	199	0.990000	NO	10-80
OTU_56	Arthropoda	Malacostraca	Decapoda	Penaeidae	<i>Penaeus</i>	<i>Penaeus merguensis</i>	913	5.21E-102	1.000000	206	0.990338	NO	10-45
OTU_58	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	902	7.55E-21	0.786885	183	0.983425	NO	0-0.1
OTU_76	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	407	1.63E-17	0.771739	184	0.983607	NO	0-0.1
OTU_87	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not identified	Not identified	264	4.51E-23	0.794444	180	0.983333	NO	0-0.1

OTU_99	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	197	2.11E-16	0.798611	144	0.842424	NO	0-0.1
OTU_103	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	188	7.60E-16	0.767956	181	0.988889	NO	0-0.1
OTU_120	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	125	3.46E-29	0.807692	182	0.983516	NO	0-0.1
OTU_144	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	60	3.54E-14	0.763441	186	0.983607	NO	0-0.1
OTU_148	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	56	7.55E-21	0.786096	187	0.983607	NO	0-0.1
OTU_155	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	51	1.27E-13	0.762162	185	0.983333	NO	0-0.1
OTU_175	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	34	2.07E-31	0.817680	181	0.983146	NO	0-0.1
OTU_177	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	33	1.62E-22	0.791209	182	0.988889	NO	0-0.1
OTU_188	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	28	1.63E-17	0.774194	186	0.983607	NO	0-0.1
OTU_192	Arthropoda	Malacostraca	Amphipoda	Eusiridae	Not_identified	Not_identified	27	5.92E-12	0.809091	110	0.675159	NO	1-3
OTU_195	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	25	2.08E-26	0.806630	181	0.983051	NO	0-0.1
OTU_202	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	23	1.61E-27	0.804469	179	0.988889	NO	0-0.1
OTU_204	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	22	1.27E-13	0.760870	184	0.983516	NO	0-0.1
OTU_207	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	21	7.49E-26	0.802260	177	0.983146	NO	0-0.1
OTU_215	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	18	9.83E-15	0.768817	186	0.983240	NO	0-0.1
OTU_218	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	16	7.55E-21	0.782609	184	0.983607	NO	0-0.1
OTU_219	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	16	7.55E-21	0.785714	182	0.988889	NO	0-0.1
OTU_222	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	13	1.27E-13	0.759563	183	0.983516	NO	0-0.1
OTU_226	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	12	9.69E-25	0.801105	181	0.983051	NO	0-0.1
OTU_236	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	11	2.13E-11	0.761364	176	0.987805	NO	0-0.1
OTU_237	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	11	2.64E-40	0.846995	183	0.983425	NO	0-0.1
OTU_238	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	11	1.26E-18	0.775956	183	0.978142	NO	0-0.1
OTU_246	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	10	2.68E-30	0.821229	179	0.988439	NO	0-0.1
OTU_274	Arthropoda	Malacostraca	Decapoda	Axiidae	Not_identified	Not_identified	7	2.14E-06	0.737624	202	0.989418	NO	0-200
OTU_275	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	7	2.10E-21	0.788660	194	0.984293	NO	0-0.1
OTU_276	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	7	1.60E-32	0.827027	185	0.988889	NO	0-0.1
OTU_300	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	5	1.23E-38	0.840659	182	0.983425	NO	0-0.1

OTU_306	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	4	9.69E-25	0.828571	140	0.857143	NO	0-0.1
OTU_308	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	4	3.51E-19	0.778378	185	0.983607	NO	0-0.1
OTU_315	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	4	9.76E-20	0.849057	106	0.656250	NO	0-0.1
OTU_339	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	3	5.75E-32	0.817680	181	0.983333	NO	0-0.1
OTU_340	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	3	2.66E-35	0.829670	182	0.983333	NO	0-0.1
OTU_372	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	2	9.76E-20	0.784530	181	0.982659	NO	0-0.1
OTU_377	Arthropoda	Malacostraca	Amphipoda	Pontogeneiidae	Not_identified	Not_identified	2	9.83E-15	0.763441	186	0.988889	NO	5-90
OTU_381	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	2	1.25E-28	0.813187	182	0.988889	NO	0-0.1
OTU_384	Arthropoda	Malacostraca	Amphipoda	Talitridae	Not_identified	Not_identified	2	1.62E-22	0.792350	183	0.983051	NO	0-0.1
OTU_69	Arthropoda	Maxillopoda	Calanoida	Candaciidae	<i>Candacia</i>	<i>Candacia armata</i>	487	4.23E-68	0.993243	148	0.980000	NO	-
OTU_59	Chordata	Actinopterygii	Anguilliformes	Nettastomatidae	Not_identified	Not_identified	877	3.23E-79	0.866906	278	0.992754	NO	deep-sea
OTU_133	Chordata	Actinopterygii	Gadiformes	Euclithyidae	<i>Euclithys</i>	<i>Euclithys polynemus</i>	84	5.10E-117	0.979839	248	0.991968	NO	250-920
OTU_147	Chordata	Actinopterygii	Gadiformes	Macrouridae	<i>Coelorinchus</i>	<i>Coelorinchus fasciatus</i>	57	5.10E-117	0.976096	251	0.992063	Freeman, 1998 (genus level); Imber, 1976 (genus level)	400-800
OTU_47	Chordata	Actinopterygii	Gadiformes	Macrouridae	<i>Coelorinchus</i>	<i>Coelorinchus oliverianus</i>	1434	2.36E-120	0.984064	251	0.992063	Freeman, 1998 (genus level)	400-600
OTU_20	Chordata	Actinopterygii	Gadiformes	Macrouridae	<i>Lepidorhynchus</i>	<i>Lepidorhynchus denticulatus</i>	15234	1.82E-121	0.984190	253	0.992126	Freeman, 1998; Imber, 1976	270-450
OTU_12	Chordata	Actinopterygii	Gadiformes	Merlucciidae	<i>Macruronus</i>	<i>Macruronus novaezelandiae</i>	36442	2.36E-120	0.984064	251	0.992063	Freeman, 1998	200-700
OTU_14	Chordata	Actinopterygii	Gadiformes	Merlucciidae	<i>Merluccius</i>	<i>Merluccius australis</i>	33916	8.47E-120	0.984000	250	0.992032	Freeman, 1998 (family level)	28-1000
OTU_86	Chordata	Actinopterygii	Gadiformes	Moridae	<i>Mora</i>	<i>Mora moro</i>	277	8.54E-115	0.972112	251	0.992032	Freeman, 1998 (family level)	450-2500
OTU_32	Chordata	Actinopterygii	Ophidiiformes	Ophidiidae	<i>Genypterus</i>	<i>Genypterus blacodes</i>	3548	1.41E-122	0.988095	252	0.992095	NO	300-550
OTU_15	Chordata	Actinopterygii	Perciformes	Triglidae	<i>Lepidotrigla</i>	<i>Lepidotrigla modesta</i>	33305	2.36E-120	0.984064	251	0.992063	NO	10-300
OTU_18	Chordata	Actinopterygii	Scobriformes	Trichiuridae	Not_identified	Not_identified	15685	8.60E-110	0.946768	263	0.992424	Imber, 1976 (family level)	0-1600
OTU_84	Chordata	Actinopterygii	Scobriformes	Gempylidae	<i>Rexea</i>	Not_identified	285	1.11E-108	0.952941	255	0.992188	NO	100-800
OTU_77	Chordata	Actinopterygii	Zeiformes	Zenionidae	<i>Capromimus</i>	<i>Capromimus abbreviatus</i>	380	5.06E-122	0.988048	251	0.992063	NO	87-500
OTU_125	Chordata	Actinopterygii	Zeiformes	Cyttidae	<i>Cyttus</i>	<i>Cyttus traversi</i>	104	5.06E-122	0.988048	251	0.992063	Freeman, 1998 (genus level)	200-978
OTU_17	Mollusca	Cephalopoda	Octopoda	Octopodidae	Not_identified	Not_identified	16331	1.14E-93	0.985000	200	0.990050	Freeman, 1998; Imber, 1976 (genus level)	0-450
OTU_71	Mollusca	Cephalopoda	Oegopsida	Histioteuthidae	<i>Histioteuthis</i>	Not_identified	479	5.55E-57	0.896739	184	0.989189	Freeman, 1998; Imber, 1976	300-1400
OTU_6	Mollusca	Cephalopoda	Teuthida	Loiginidae	Not_identified	Not_identified	86867	5.21E-102	0.986047	215	0.990741	NO	0-400

OTU_46	Mollusca	Cephalopoda	Teuthida	Loliginidae	Not_identified	Not_identified	1559	1.87E-101	0.985981	214	0.990698	NO	0-400
OTU_134	Mollusca	Cephalopoda	Teuthida	Loliginidae	Not_identified	Not_identified	84	6.88E-86	0.989071	183	0.879227	NO	0-4

Table 2. Taxonomical classification of prey items in the diet of *P. westlandica* along with their Relative Read Abundance (RRA) and Frequency of Occurrence (FOO). Values are presented for the whole sampling and also detailed according to the two different seasons (Before Hatching: BH and Chick Rearing: CR) and according to the two different sites (Paparoa Natural Park: NP and the Private Land: PL).

Phylum	Class	Order	Family	Species	Common name	Total FOO (%)	Total RRA (%)	FOO BH (%)	FOO CR (%)	RRA BH (%)	RRA CR (%)	FOO NP (%)	FOO PL (%)	RRA NP (%)	RRA PL (%)
Arthropoda						86.2069	73.7939	80	91.4894	35.7822	94.1305	95.7447	75	89.7389	60.9839
	Branchiopoda					4.5977	0.1988	2.5	6.3830	0.0755	0.2621	2.1277	7.5	0.0380	0.4346
		Anostraca				3.4483	0.1986	2.5	4.2553	0.0755	0.2621	2.1277	5	0.0380	0.4341
			Artemiidae			3.4483	0.1986	2.5	4.2553	0.0755	0.2621	2.1277	5	0.0380	0.4341
				<i>Artemia franciscana</i>	Brine shrimp	3.4483	0.1986	2.5	4.2553	0.0755	0.2621	2.1277	5	0.0380	0.4341
		Cladocera				1.1494	0.0002	0	2.1277	0	0.0003	0	2.5	0	0.2409
			Daphniidae			1.1494	0.0002	0	2.1277	0	0.0003	0	2.5	0	0.2409
	Malacostraca					86.2069	73.5434	80	91.4894	35.7068	93.7934	95.7447	75	89.7009	60.4248
		Amphipoda				85.0575	73.3412	77.5	91.4894	35.3488	93.6387	95.7447	72.5	89.5089	60.1839
			Eurisiidae			3.4483	0.0002	0	6.3830	0	0.0003	4.2553	2.5	0	0.0005
			Pontogeneiidae			1.1494	0.0002	0	2.1277	0	0.0003	0	2.5	0	0.0005
			Talitridae		Landhoppers/sandhoppers	85.0575	73.3381	77.5	91.4894	35.3488	93.6352	95.7447	72.5	89.5065	60.1812
		Decapoda				3.4500	0.2023	5	2.1277	0.3579	0.1547	2.1277	5	0.1920	0.2409
			Axiidae		Thalassinidean crustaceans	1.15	0.0007	0	2.1277	0	0.0011	2.1277	0	0	0.0018
			Penaeidae			2.3	0.0969	5	0	0.3579	0	0	5	0	0.2391
				<i>Penaeus merguensis</i>	Banana shrimp	2.3	0.0969	5	0	0.3579	0	0	5	0	0.2391
			Pilumnidae			1.15	0.1046	0	2.1277	0	0.1536	2.1277	0	0.1920	0

		<i>Pilumnus hirtellus</i>	Bristly crab	1.15	0.1046	0	2.1277	0	0.1536	2.1277	0	0.1920	0	
Maxillopoda				1.1494	0.0517	0	2.1277	0	0.0751	0	2.5	0	0.1245	
	Calanoida			1.1494	0.0517	0	2.1277	0	0.0751	0	2	0	0.1245	
		Candaciidae		1.1494	0.0517	0	2.1277	0	0.0751	0	2.5	0	0.1245	
			<i>Candacia armata</i>	1.1494	0.0517	0	2.1277	0	0.0751	0	2.5	0	0.1245	
Chordata				37.9310	15.0296	45	31.9149	48.2577	2.7135	25.5319	52.5	3.9071	31.5495	
	Actinopterygii			37.9310	15.0296	45	31.9149	48.2577	2.7135	25.5319	52.5	3.9071	31.5495	
		Anguilliformes		1.1494	0.0931	2.5	0	0.3405	0	0	2.5	0	0.2275	
			Nettastomatidae	Duckbill eels	1.1494	0.0931	2.5	0	0.3405	0	0	2.5	0	0.2275
		Gadiformes		25.2874	9.2796	40	12.7660	33.6161	0.1368	14.8936	37.5	1.2149	21.0678	
			Euclichthyidae		1.1494	0.0089	0	2.1277	0	0.0130	0	2.5	0	0.0216
			<i>Euclichthys polynemus</i>	Eucla cod	1.1494	0.0089	0	2.1277	0	0.0130	0	2.5	0	0.0216
			Macrouridae		6.8966	1.7749	12.5	2.1277	6.2599	0.0947	4.2553	10	0.1188	0.1188
			<i>Coelorinchus fasciatus</i>	Banded whiptail	1.1494	0.0060	2.5	0	0.0221	0	0	2.5	0	0.0148
			<i>Coelorinchus oliverianus</i>	Hawknose grenadier	2.2989	0.1522	2.5	2.1277	0.5152	0.0173	2.1277	2.5	0.0217	0.3441
			<i>Lepidorhynchus denticulatus</i>	Thorntooth grenadier	6.8966	1.6166	12.5	2.1277	5.7226	0.0773	4.2553	10	0.0971	3.8216
			Merlucciidae		20.6897	7.4764	35	8.5106	27.2511	0.0291	10.6383	32.5	1.0962	16.7955
			<i>Macruronus novaezealandiae</i>	Hoki	14.9425	3.8672	30	2.1277	14.0981	0.0240	8.5106	22.5	1.0936	8.0057
			<i>Merluccius australis</i>	Southern hake	10.3448	3.5992	15	6.3830	13.1530	0.0051	4.2553	17.5	0.0026	8.7899
			Moridae		1.1494	0.0294	2.5	0	0.1051	0	0	2.5	0	0.0702
			<i>Mora moro</i>	Common mora	1.1494	0.0294	2.5	0	0.1051	0	0	2.5	0	0.0702
		Ophidiiformes		3.4483	0.3765	5	2.1277	1.2306	0.0592	2.1277	5	0.0004	0.9196	
			Ophidiidae		3.4483	0.3765	5	2.1277	1.2306	0.0592	2.1277	5	0.0004	0.9196
			<i>Genypterus blacodes</i>	Pink cusk-eel	3.4483	0.3765	5	2.1277	1.2306	0.0592	2.1277	5	0.0004	0.9196
		Perciformes		9.1954	3.5343	15	4.2553	12.9452	0.0008	4.2553	15	0.0010	8.6461	
			Triglidae		9.1954	3.5343	15	4.2553	12.9452	0.0008	4.2553	15	0.0010	8.6461
			<i>Lepidotrigla modesta</i>	Cocky gunard	9.1954	3.5343	15	4.2553	12.9452	0.0008	4.2553	15	0.0010	8.6461
		Scombriformes		5.7471	1.6947	0	10.6383	0	2.4916	8.5106	2.5	2.6629	0.6003	

	Gempylidae		1.1494	0.0302	0	2.1277	0	0.0438	2.1277	0	0.0547	0
		<i>Rexea sp.</i> Snake mackerels	1.1494	0.0302	0	2.1277	0	0.0438	2.1277	0	0.0547	0
	Trichiuridae		5.7471	1.6645	0	10.6383	0	2.4478	8.5106	2.5	2.6082	0.6003
Zeiformes			4.5977	0.0514	5	4.2553	0.1252	0.0251	2.1277	7.5	0.0279	0.0884
	Cyttidae		1.1494	0.0110	2.5	0	0.0407	0	0	0	0.0000	0.0272
		<i>Cyttus traversi</i> King dory	1.1494	0.0110	2.5	0	0.0407	0	0	2.5	0	0.0272
	Zenionidae		3.4483	0.0403	2.5	4.2553	0.0845	0.0251	2.1277	5	0.0279	0.0612
		<i>Capromimus abbreviatus</i> Capro dory	3.4483	0.0403	2.5	4.2553	0.0845	0.0251	2.1277	5	0.0279	0.0612
Mollusca			56.3218	11.1766	57.5	55.3191	15.3105	3.1556	59.5745	52.5	6.3537	7.0328
	Cephalopoda		56.3218	11.1766	57.5	55.3191	15.3105	3.1556	59.5745	52.5	6.3537	7.0328
	Oegopsida		1.1494	0.0508	0	2.1277	0	0.0754	2.1277	0	0.0943	0.0000
		Histioteuthidae Oegopsida squids	1.1494	0.0508	0	2.1277	0	0.0754	2.1277	0	0.0943	0.0000
	Octopoda		28.7356	1.7330	25	31.9149	2.5363	1.5208	29.7872	27.5	1.7319	1.9191
		Octopodidae Octopodids	28.7356	1.7330	25	31.9149	2.5363	1.5208	29.7872	27.5	0.0279	0.0612
	Teuthida		31.0345	9.3927	35	27.6596	12.7742	1.6348	34.0426	27.5	4.6218	5.1137
		Loliginidae Pencil squids	31.0345	9.3927	35	27.6596	12.7742	1.6348	34.0426	27.5	4.6218	5.1137