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1 Feeding ecology of two deep-sea skates bycaught on demersal longlines off Kerguelen
2 Islands, Southern Indian Ocean.

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26 **Abstract**

27 Elasmobranchs, and particularly skates (Rajiforms), are commonly caught in fisheries worldwide as
28 targeted catch or bycatch. Their life history traits make them particularly sensitive to elevated fishing
29 mortality, especially in slow-growing deep-sea species. Knowledge of their ecology is key to ensure
30 effective conservation and mitigation measures, especially dietary references to understand trophic
31 relationships within the ecosystem. This study presents the first comprehensive description of diet
32 composition and trophic position of two skate species (*Bathyraja eatonii* and *B. irrasa*) caught as
33 bycatch in the French Patagonian toothfish (*Dissostichus eleginoides*) fishery in the Indian sector of
34 the Southern Ocean (Kerguelen waters). Stomach content and stable isotopic analyses were
35 performed on both species according to sex and maturity stage. DNA barcoding analysis was
36 performed on prey tissue samples to identify or confirm identification of prey items found in
37 stomachs. Overall, both skate species were generalist feeders with high $\delta^{15}\text{N}$ values. The higher $\delta^{15}\text{N}$
38 values of *B. irrasa* result in a higher estimated trophic position than *B. eatonii*. The diet of *B. eatonii*
39 mainly consisted of fish, pelagic crustaceans and squids, while *B. irrasa* preyed more on benthic
40 crustaceans, fish and annelids. While sex had no effect on diet and trophic position for both species,
41 maturity stage influenced the prey composition of *B. irrasa*. Annelids and isopods were prevalent in
42 the stomachs of immature individuals of *B. irrasa*, while mature individuals fed more on decapods
43 and fish. Our results revealed a wide range of prey items for these two generalist predators (> 57
44 species). Understanding the diet, trophic position and trophic relationships of *B. eatonii* and *B. irrasa*
45 is critical to a better comprehension of the impact of the exploitation of top predators on the
46 subantarctic demersal ecosystem.

47

48 **Keywords:** Trophic niche, Top predators, *Bathyraja*, Stable isotopes, DNA barcoding, stomach
49 contents

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51

52 **1. Introduction**

53 For the last decades, elasmobranch populations have experienced strong declines in large part due to
54 overfishing (Barbini et al., 2020; Oliver et al., 2015; Worm et al., 2013). Elasmobranchs and
55 especially skates (Rajiforms) are commonly caught in fisheries as targeted but also as non-targeted
56 catch (termed “bycatch”) and discarded (Oliver et al., 2015; Stevens et al., 2000). Furthermore, their
57 specific life-history traits – long life span, slow growth and late age at maturity – make them
58 intrinsically sensitive to elevated fishing mortality (Brander, 1981; Davidson et al., 2016; Dulvy et
59 al., 2014; Dulvy and Reynolds, 2002; Field et al., 2009). Bycatch has become an issue for global
60 fisheries management and conservation due to increasing awareness of anthropogenic impacts on the
61 environment (Soykan et al., 2008). Following the holistic approach of ecosystem-based fisheries
62 management, there is increasing pressure on the fishing industry to address the unintended
63 consequences of fishing (Pikitch et al., 2004; European Union, 2013). Managing environmental
64 impacts of fishing is therefore a priority, including improving baseline knowledge on species
65 affected by fisheries (Stobutzki et al., 2001; Tschopp et al., 2020).

66 An important step in the conservation and management of skate populations is to understand
67 their feeding ecology, which can be done by studying their feeding habits and trophic interactions.
68 Although skates are commonly considered as top predators alongside pinnipeds, seabirds and large
69 teleost fish, important differences in their feeding strategies exist between species, with some skates
70 being considered as generalists and other species as specialist consumers (Cortés, 1999; Barría et al.,
71 2018). Generalist species are likely to be less vulnerable to anthropogenic pressures, such as fishing,
72 because of their wide trophic niche (Barbini et al., 2020; Gallagher et al., 2015; Matich et al., 2011).
73 On the contrary, diet specialization is associated with narrow trophic niche and thus specialist
74 species are likely to be more vulnerable to environmental changes in marine ecosystems, especially
75 if their main prey becomes less abundant in the environment (Barbini et al., 2020). Stomach content

76 analysis is widely used in feeding ecology studies and provides information about the prey species
77 consumed; however, different rates of prey digestion and rare prey items may bias diet determination
78 (Brown et al., 2012). For this reason, stable isotope analysis (SIA) have been used as a
79 complementary method for a more integrative diet study (Matich et al., 2011). In most cases, SIA
80 does not allow prey determination at the species level, but it provides information about trophic
81 pathways through food webs and patterns in resource use (Blanco-Parra et al., 2012; Crook et al.,
82 2019). In marine ecological studies, carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic values of predator
83 tissues are frequently used. $\delta^{13}\text{C}$ varies little along the food chain and therefore provides an
84 indication of the primary production source responsible for the energy flow in a food web. In
85 contrast, consumers are enriched in $\delta^{15}\text{N}$ relative to their food and thus $\delta^{15}\text{N}$ indicates their relative
86 trophic position within the food web (Cherel and Hobson, 2007; Hussey et al., 2012).

87 Three species of skates are caught as bycatch in the demersal longline fisheries targeting
88 Patagonian toothfish (*Dissostichus eleginoides*) within the area of the Southern Indian Ocean under
89 regulation of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR;
90 CCAMLR Secretariat, 2014). Two of them, the Eaton's skate (*Bathyraja eatonii*) and the Kerguelen
91 sandpaper skate (*B. irrasa*), are frequently caught on the slopes of the Kerguelen Plateau (49°S,
92 69°E), where a French fishery operates between 500 and 2,000 m deep (Nowara et al., 2017; Ziegler
93 et al., 2021). They are large deep-sea skates (up to 115 cm total length (TL) for *B. eatonii* and 130
94 cm (TL) for *B. irrasa*) with partially overlapping bathymetric ranges (100 – 1,200 m for *B. eatonii*
95 and 800 – 1,800 m for *B. irrasa*) and constitute a major component of benthic fish biomass on the
96 Kerguelen Plateau (Duhamel et al., 2019, 2005; Nowara et al., 2017). *B. eatonii* is found on
97 continental shelves and slopes of all subantarctic islands and the Antarctic continent while *B. irrasa*
98 is endemic to the Kerguelen Plateau (Stehmann and Bürkel, 1990). In the highly regulated Kerguelen
99 fishery, measures have been implemented to reduce skate bycatch such as move-on rules, allocation
100 of individual fishing quotas based on the amount of skate bycatch, as well as the provision of support

101 tools for spatial avoidance of high-density areas (TAAF, 2019). Despite these mitigation measures,
102 skate bycatch still represents about 250 tons (5% of total catch) in the Kerguelen longline fishery, of
103 which 90% are released at sea with potentially high survival chance (CCAMLR Secretariat, 2022).
104 Given that their post-released survival is unknown, our ability to assess the impact of the fishery on
105 skate populations and demersal ecosystems remains limited (Valls et al., 2011; Wetherbee and
106 Cortés, 2004).

107 Studying food habits of these two species is one of the prerequisites to understand their
108 ecological role in the ecosystem and subsequently the impact of their exploitation on demersal
109 communities (Blanco-Parra et al., 2012; Brown-Vuillemin et al., 2020; Cailliet et al., 2005; Matich et
110 al., 2011; Navia et al., 2007). Deep-sea skates are often generalists, with diets composed of annelids,
111 crustaceans, cephalopods and fish; but prey group contribution varies with skate size. Many skate
112 species show ontogenetic changes in diet, with small individuals often feeding on crustaceans and
113 large individuals on fish (Barbini et al., 2018; Belleggia et al., 2008; Brown et al., 2012; Koen
114 Alonso, 2001; Main and Collins, 2011). Furthermore, ecological niche partitioning can arise among
115 species sharing similar morphology and habitat when they are competing for limited resources, as
116 described in *Bathyraja* species found over the Patagonian shelf, which specialize either on fish,
117 annelids or crustaceans (Tschopp et al., 2020). Understanding the trophic relationship of coexisting
118 species can indicate whether they share similar ecological niches, and whether they should be
119 considered as a functional unit, or should be managed separately (Barría et al., 2018).

120 Unraveling feeding ecology of *B. eatonii* and *B. irrasa* on the Kerguelen Plateau is therefore
121 crucial to assess their vulnerability and the potential ecosystem impact of skate biomass reduction
122 (Bizzarro et al., 2007; Ebert and Bizzarro, 2007). As a leader in ecosystem-based fishery
123 management, CCAMLR emphasizes the need to ensure efficient ecosystem fishery management and
124 biodiversity conservation of skate bycatch species (CCAMLR Secretariat, 2014). Thus, in this study
125 we undertook the first comprehensive study of feeding ecology of *B. eatonii* and *B. irrasa* off the

126 Kerguelen Plateau through stomach content and SIA analyses. The identification of prey species was
127 confirmed using DNA barcoding when muscle tissues were available. Our main objectives were to i)
128 describe diet of *B. eatonii* and *B. irrasa*; ii) test for potential differences in their feeding ecology
129 related to sex and maturity stage, and iii) provide information on their role in the marine food web.
130 Finally, we discuss our results in the context of ecosystem-based management and bycatch
131 mitigation.

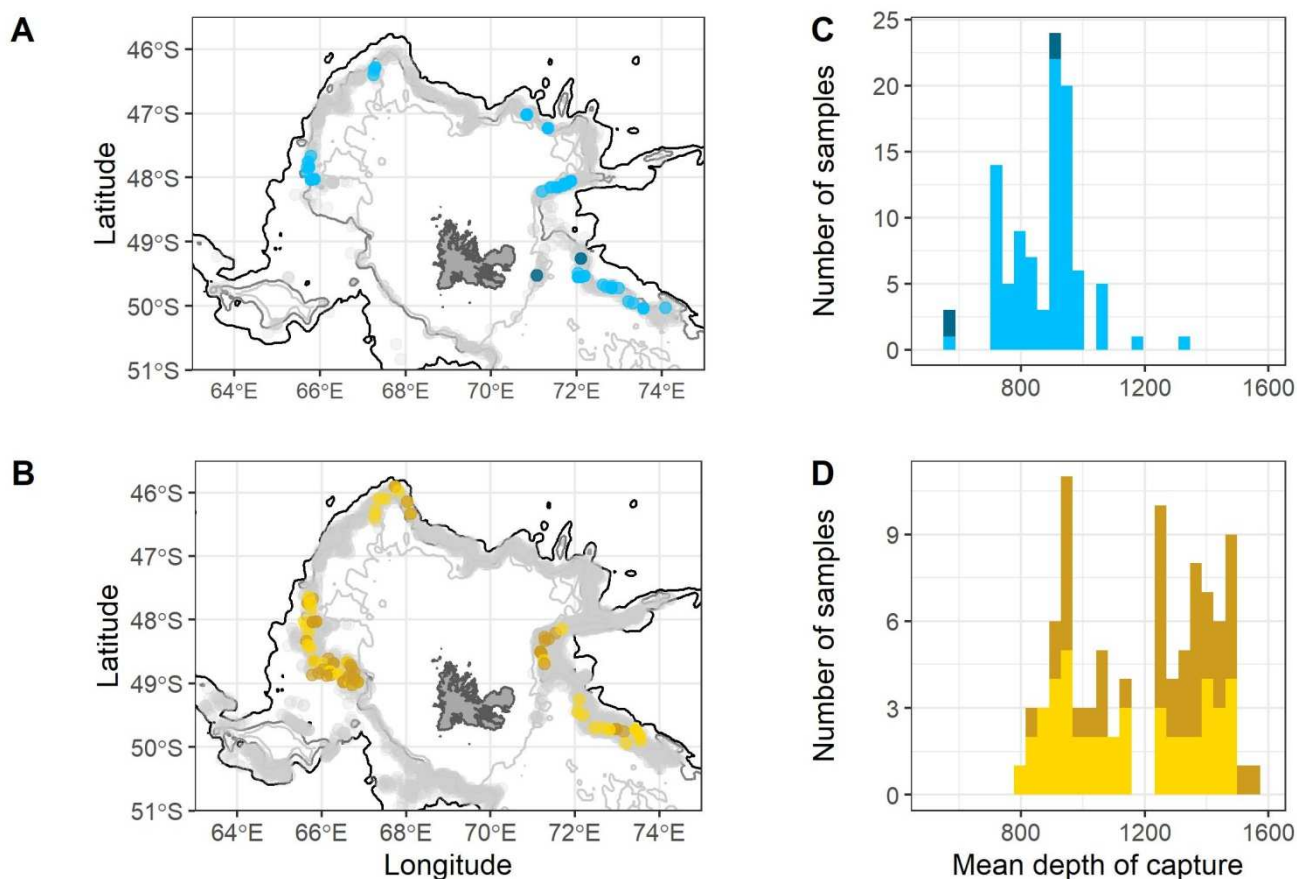
132

133 **2. Materials and Methods**

134 *2.1. Data collection*

135 Sampling was carried out onboard the French commercial longliners *Ile de la Réunion II* (March to
136 June 2020, and March to May 2021) and *Cap Kersaint* (March to June 2021) within the Kerguelen
137 Exclusive Economic Zone (EEZ) in the Indian sector of the Southern Ocean (Figures 1.A and 1.B) at
138 depths ranging from 500 to 1600 m (Figures 1.C and 1.D). Stomachs and tissues were collected from
139 dead individuals. All individuals were identified, sexed, weighed and measured (total and pelvic
140 lengths) following guidelines provided by the French Southern Ocean Fishery Observer Program
141 (Gasco, 2011). Following these guidelines, maturity stage was also determined using the internal
142 development of the reproductive system for females: immatures have small and undeveloped ovaries
143 with no visible ovarian follicles, while maturing females present developing follicles, typically small
144 and white, and mature females show big, fully developed ovaries with the presence of large and
145 yellow yolk-filled follicles. Immature males, have undeveloped testes, and claspers smaller than
146 pelvic fins, while maturing males present developing testes associated with noncalcified claspers
147 longer than pelvic fins, and matures show big and fully developed testes with the presence of large
148 lobules with long and fully calcified claspers. Whole stomachs were collected after palpation to
149 minimize the risk of collecting empty stomachs. When a stomach contained food items, strings were
150 tied around the esophagus and the gut before removing it. A total of 101 and 98 stomachs were

151 collected from *B. eatonii* and *B. irrasa*, respectively. Tissue samples from the dorsal-anterior muscle
 152 of the body were collected for stable isotope analysis from individuals from which stomachs had also
 153 been collected. A total of 69 and 73 muscle samples were collected from *B. eatonii* and *B. irrasa*,
 154 respectively. Stomachs were stored deep-frozen (-20°C) and tissue samples were kept in ethanol
 155 (90%). Location and depth were reported for each capture event.



156
 157 **Figure 1. (Two-column fitting image)** Location of skate bycatch (grey) and samples collected for
 158 A) *Bathyraja eatonii* (in blue) and C) *B. irrasa* (in yellow). Isobaths 500, 1,000 and 2,000 m
 159 are indicated on the map. Distribution of mean depth of hauls where samples of B) *B. eatonii*
 160 and D) *B. irrasa* were collected. Dark and light shading indicate immature and mature
 161 individuals, respectively.

162
 163 *2.2. Stomach content analysis*

164 A few empty stomachs were discarded from the analysis (n = 5 for *B. irrasa*). Whole stomachs were
 165 thawed and their content was weighed to the nearest 0.01 g using an electronic scale. Accumulated
 166 prey items (mainly cephalopod beaks without flesh attached, fish eye lenses and worn otoliths) were
 167 subsequently sorted and analyzed separately from fresh prey items (Cherel et al., 2000). Fresh

168 remains were sorted into four prey classes (fish, cephalopods, crustaceans and others) that were
169 weighed to the nearest 0.01 g. If present, the bait (the Atlantic mackerel *Scomber scombrus* that does
170 not occur in the fishing area) was also weighed and counted, but it was not included in further
171 analyses. Identification of prey was based on the examination of the remaining hard structures,
172 including sclerotized beaks for cephalopods, otoliths, jaws and caudal bones for fishes, and
173 exoskeletal remains for crustaceans. Prey items were counted and identified to the lowest taxonomic
174 level using reference materials held in the Centre d'Etudes Biologiques de Chizé (CEBC-CNRS,
175 France) and by reference to the available literature including Williams and McEldowney (1990) and
176 Duhamel et al. (2005) for fish, Boltovskoy (1999) for crustaceans, and Xavier and Cherel (2021) for
177 cephalopods. Species names of cephalopods followed a recent review on Southern Ocean squids that
178 includes taxonomic revisions conducted over the last decades (Cherel, 2020).

179

180 2.3. DNA barcoding and prey identification

181 Tissue samples (dorsal muscle in fish and mantle muscle in cephalopods) were collected either from
182 nearly intact and well identified prey items to build up a reference collection, or from digested and
183 undetermined prey items to help identification. Muscle samples (10 mg) were stored in ethanol
184 (90%) and DNA barcoding was conducted on 47 prey items. DNA was extracted using Qiagen DNA
185 extraction kit (QIAamp DNA Micro Kit). The COI region was amplified using the following primer
186 sets: (a) FishF1 and FishR1; (b) TelF1 and TelR1, (c) LCO1490, HCO2198, mlCOIintF,
187 dgHCO2198 (Table A.1). PCR amplifications were performed in a final volume of 20 μ L with 0.625
188 U of Qiagen Taq DNA polymerase containing 3 ng DNA, 1 \times reaction buffer, 2.5 mM MgCl₂,
189 0.26 mM dNTP, 0.3 mM of each primer, 5% DMSO. The PCR thermal regime consisted of an initial
190 denaturation step of 5 min at 94°C followed by 40 cycles of denaturing (40 s, 94°C), annealing (30 s,
191 52°C), and elongation (30 s at 72°C) with a final extension step of 5 min at 72°C. PCR products
192 were purified and Sanger sequenced in both directions by Eurofins sequencing (Germany). The

193 obtained sequences were visualized, assembled and edited using Geneious 11.1.5. (Genes Code
194 Corporation - Kearse et al., 2012). A BLASTn search was performed to identify sequences with the
195 best hits from the genomic sequence databases, NCBI and BOLD systems (Altschul et al., 1990;
196 Benson et al., 2005; Ratnasingham and Hebert, 2007). Species identification was confirmed when
197 the degree of similarity between the obtained sequences and reference sequences was higher than
198 99%.

199

200 2.4. Diet comparisons

201 Diet comparisons were conducted using fresh items, meaning that the few stomachs containing
202 accumulated prey items only (n = 3 for *B. eatonii*) were considered empty. In the same way,
203 stomachs containing only the bait were discarded (n = 3 for *B. eatonii*, and n = 1 for *B. irrasa*) and
204 not included in further analyses. Euphausiacea, Mysida and small amphipods such as Gammaridea
205 spp. and *Themisto gaudichaudii* were considered as secondary prey that were incidentally ingested
206 with primary prey, because they are known to be major food items of bathypelagic fish and
207 cephalopods in the Southern Ocean (Cherel and Hobson, 2005; Gaskett et al., 2001). These species
208 were often associated with damaged visceral cavity of their likely predators but this information was
209 not reported. They were consequently not considered as skate prey and excluded from statistical
210 analysis; this was also the case for parasites (Table A.2). Some stomachs containing only incidentally
211 ingested prey or parasites were therefore excluded (n = 4 for *B. eatonii*, and n = 1 for *B. irrasa*).
212 Thus, a total of 91 stomach contents were statistically analyzed for both *B. eatonii* and *B. irrasa*.

213 Prey items were grouped into one of the following seven ecological dietary categories:
214 pelagic fish, benthic and demersal fish, pelagic crustaceans, benthic crustaceans, squids, octopus and
215 worms (including Polychaeta and Priapulida). Cumulative prey curves were constructed using the
216 prey species and prey categories for each skate species against the randomly pooled number of
217 analyzed stomachs to check if a sufficient number of stomach contents had been collected to

218 accurately describe the diet of each predator (Cortés, 1997). Curves were generated after 100
219 randomizations of the original data using the Vegan Community Ecology package (Oksanen et al.,
220 2020) in R-Studio, version 4.1 (R Core Team 2021). When curves approached an asymptote, it was
221 considered that sufficient stomach samples had been processed to describe the diet. To statistically
222 assess the adequacy of sample size, a linear regression was performed on the final five points of the
223 curve. The levelling off of the prey curve was considered acceptable when the slope was $b < 0.05$
224 (Brown et al., 2012). To test dietary differences, males and females of each species were separated
225 into maturity classes, with immature individuals separated from maturing and mature individuals
226 (hereafter ‘mature individuals’).

227 Percent frequencies of occurrence and number of each prey group were calculated for each
228 skate species by sex and maturity stage. Comparisons of diet composition (frequency of occurrence
229 of each prey category) between species, maturity stages and sexes were assessed using nonmetric
230 multidimensional scaling (nMDS) ordination based on Bray-Curtis dissimilarities using species
231 presence/absence data (Brown-Vuillemin et al., 2020). Ordination mean plots were constructed
232 though bootstrap averages ($n = 100$). We also tested the correlation of environmental variables
233 (longitude, latitude and depth of sampling) with the ordination configuration to investigate
234 environmental drivers for the composition of dietary samples and test for sensibility to sampling. The
235 significance of fitted vectors was assessed using a permutation of environmental variables ($n = 999$).
236 Analyses of similarities (ANOSIM) also based on Bray-Curtis dissimilarities were used to test the
237 significance of the observed patterns in the NMDS (Somerfield et al., 2021). When a difference was
238 established by ANOSIM, a similarity percentage analysis (SIMPER) was performed to investigate
239 which prey category was mainly responsible for diet differentiation within groups. nMDS, ANOSIM
240 and SIMPER were performed using R-Studio and the Vegan Community Ecology package (Oksanen
241 et al., 2020).

242

243 2.5. *Stable isotope analysis*

244 Muscle samples were dried and powdered before extracting lipids using cyclohexane (C₆H₁₂). Since
245 lipids are depleted in ¹³C compared to proteins, lipid content can significantly affect the relative
246 abundance of ¹³C in consumer tissues (Bodin et al., 2007; Hussey et al., 2012; Post et al., 2007).
247 Relative abundance of ¹³C and ¹⁵N were obtained from ~0.5 mg of delipidated samples packed in tin
248 capsules, that were then measured by continuous flow on a Flash EA 2000 elemental analyzer
249 (Thermo Scientific, Milan, Italy) coupled to a Delta V Plus, isotope ratio mass spectrometer (Thermo
250 Scientific, Bremen, Germany) at the Pôle Spectrométrie Océan (Plouzané, France). For reference
251 standards, an in house standard Thermo-Acetanilide, USGS-61 (certified values : $\delta^{15}\text{N} = -2.87 \pm 0.04$
252 $\text{‰} / \delta^{13}\text{C} = -35.05 \pm 0.04 \text{‰}$ and measured values : $\delta^{15}\text{N} = -2.94 \pm 0.07 \text{‰} / \delta^{13}\text{C} = -35.07 \pm 0.06 \text{‰}$),
253 USGS-62 (certified values : $\delta^{15}\text{N} = +20.17 \pm 0.06 \text{‰} / \delta^{13}\text{C} = -14.79 \pm 0.04 \text{‰}$ and measured values :
254 $\delta^{15}\text{N} = -20.13 \pm 0.12 \text{‰} / \delta^{13}\text{C} = -14.77 \pm 0.09 \text{‰}$) and USGS-63 (certified values : $\delta^{15}\text{N} = +37.83 \pm$
255 $0.06 \text{‰} / \delta^{13}\text{C} = -1.17 \pm 0.04 \text{‰}$ and measured values : $\delta^{15}\text{N} = +37.84 \pm 0.15 \text{‰} / \delta^{13}\text{C} = -1.15 \pm 0.0$
256 9‰) were used for isotopic corrections and to assign the data to the appropriate isotopic scale.
257 Results were reported in δ unit notation and expressed as parts per thousand relative to international
258 standards (atmospheric N₂ for nitrogen and Vienna-Pee Dee Belemnite for carbon). Analytical
259 precision based on replicate measurements after every six samples using the in house standard
260 Thermo-Acetanilide was $< 0.17 \text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. C:N mass ratios were determined
261 from percentage element weights.
262 Values are mean \pm SD. Statistical tests were conducted using R-Studio and the Pipe-Friendly
263 Framework for Basic Statistical Tests package (Kassambara, 2021). Normality was assessed using a
264 Shapiro-Wilk test. We evaluated possible differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between sexes and
265 maturity classes within species and between species using Student's t-test when data were normally
266 distributed; otherwise Mann-Whitney test was used. Assuming a level of significance of 0.05, the
267 null hypothesis was rejected if the p value was < 0.05 .

268

269 **3. Results**

270 *3.1. Prey identification*

271 One thousand and fifteen fresh prey items were found in the pooled stomach contents. Most were
272 identified to species level based on morphological identification: 61% for fish (n = 74 prey items),
273 63% for cephalopods (n = 25 prey items) and 71% for crustaceans (n = 473 prey items). Among
274 these specimens, 47 identifications were checked by DNA barcoding. The method failed in nine
275 samples, but it worked on the 38 remaining samples, thus confirming the species identification of 25
276 fish and five cephalopods. Among morphologically unidentifiable prey items, four fish
277 (*Gymnoscopelus piabilis*, *Luciosudis normani*, *Macrourus whitsoni* and *Paraliparis*
278 *thalassobathyalis*) and four cephalopods (three *Muusoctopus thielei* and one *Filipovia knipovitchi*)
279 were identified through barcoding analysis. At the family level 8.4% (n = 85) of prey items remained
280 undetermined and only one prey item remained unidentified at all taxonomic levels. This remaining
281 unidentified prey item was the only occurrence in the stomach in which it was found; the sample was
282 therefore not included in further analysis (n = 1 for *B. eatonii*).

283

284 *3.2. Diet composition and intraspecific comparison*

285 While stomach contents were rarely empty when analyzed in the laboratory, more than half of the
286 skates sampled onboard were considered to have empty stomachs (based on palpation), and thus
287 were not sampled. Cumulative prey curves indicated sample sizes did not reach asymptote ($b < 0.05$)
288 at the species level but did using prey categories (Fig. A.1 and Fig. A.2). Sample sizes were thus
289 sufficient to describe the overall diet composition of *B. eatonii* and to investigate differences
290 between sex groups, but not sufficient for maturity groups with only four samples within the group
291 of immature individuals (Fig. A.3 and Fig. A.4). For *B. irrasa*, sample sizes were sufficient to
292 describe the overall diet composition at the prey category level, as well as to investigate differences

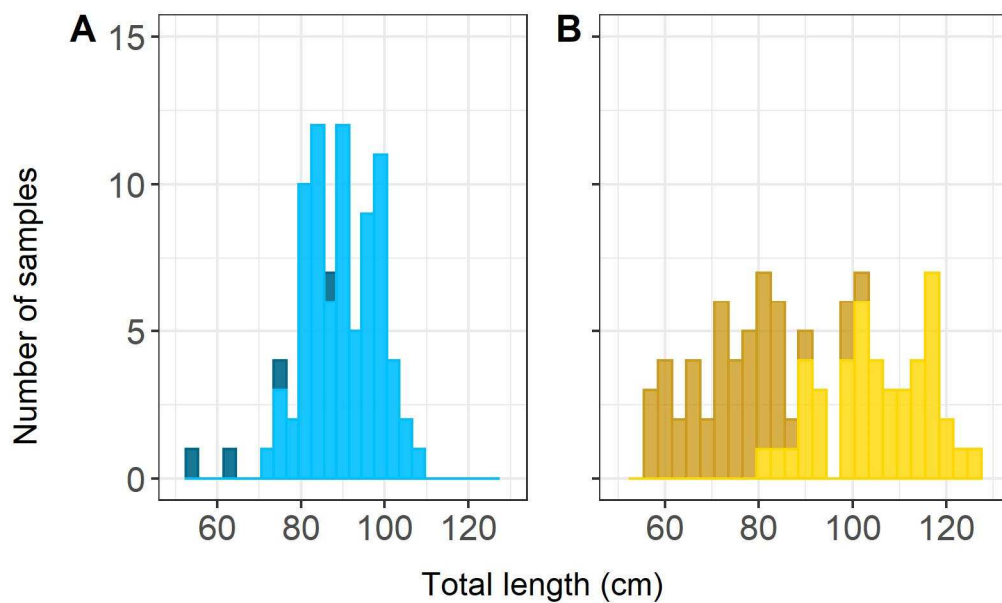
293 between both sex and maturity groups. Thus, only mature individual diet composition was analyzed
294 for intraspecific differences between sexes for *B. eatonii*, while interspecific differences were
295 explored for mature individuals only.

296

297 3.2.1. *Bathyraja eatonii*

298 A total of 90 individuals (64 females and 26 males) of *B. eatonii* were used for diet composition and
299 intraspecific comparison. *B. eatonii* ranged from 54 to 108 cm TL with only four stomachs collected
300 from immature individuals (Figure 2.A).

301



302

303 Figure 2. **(1.5-column fitting image)** Length distribution of individuals of A) *Bathyraja eatonii*
304 (in blue) and B) *B. irrasa* (in yellow). Dark and light shading indicate immature and mature
305 individuals in stacked bars, respectively.

306

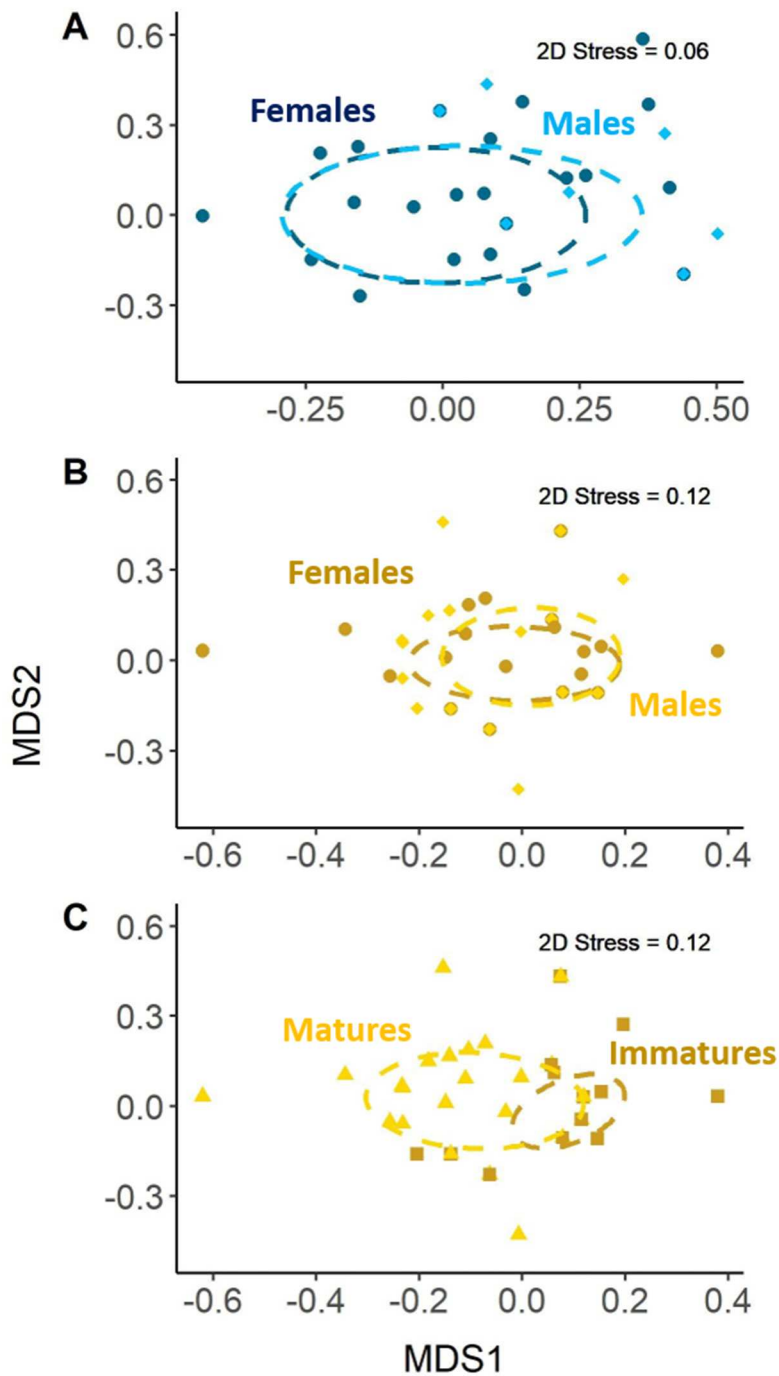
307 Stomach content analysis indicated that the diet of *B. eatonii* was dominated by fish, which
308 accounted for 68% of the diet by fresh mass (Table 1). Other significant food sources were
309 crustaceans (18%) and cephalopods (13%), while worms, mostly polychaetas, were negligible (<1%
310 by mass). On average, stomach samples contained 2.4 prey items. For mature individuals only (n =
311 86), a total of 210 fresh prey items from at least 44 species were found. Crustaceans were
312 predominant, occurring in 55 food samples (64%) and the most prevalent by number (54% - Table

313 2). Fish and cephalopods occurred in 54 and 14 dietary samples (63% and 16% respectively) and
314 ranked second and third by number (35% and 9%, respectively).

315 *Bathyraja eatonii* mature individuals fed on a large diversity of crustaceans (11 species), with
316 the isopod *Ceratoserolis trilobitoides* being the most important crustacean prey (30% by number).
317 Other crustacean prey items were the decapod *Campylonotus capensis* (7%) and specimens from the
318 genus *Pasiphaea* (5%). The second most important group by number was fish, with 25 species. Two
319 families dominated the fish diet. Myctophids ranked first (7% by number, at least 6 different
320 species), with *Gymnoscopelus piabilis* being the most abundant species (2%). Paralepidids were also
321 common prey (7%), but their high level of digestion precluded identifying them to the species level,
322 except for two individuals of *Magnisudis prionosa*. Nonmetric multidimensional scaling (nMDS)
323 ordinations and statistical analyses were unable to identify differences in dietary composition
324 between females and males for *B. eatonii* (ANOSIM, global *R* statistic 0.03, *p* = 0.151 – Figure 3.A).

325 Analysis of accumulated beaks increased the number of cephalopod prey, with the
326 onychoteuthid *Filipovia knipovitchi* being predominant (*n* = 5). Accumulated beaks added two taxa
327 to the skates' diets, namely the ommastrephid *Todarodes* sp. (*n* = 2) and the histioteuthid
328 *Histioteuthis eltaninae* (*n* = 3). Fish accumulated items included five individuals from counting eye
329 lenses, and seven individuals from analyzing worn otoliths, four of which were morid fish.

330



331
 332 **Figure 3. (Two-column fitting image)** Nonmetric multidimensional scaling (nMDS)
 333 ordinations of the occurrence of different prey categories in dietary samples of: A) *Bathyraja*
 334 *eatonii* with S.E. ellipses based on sex and B) *B. irrasa* with S.E. ellipses based on sex and C) *B. irrasa*
 335 *B. irrasa* with S.E. ellipses based on maturity. Females are in dark shades (plain circles) and males in light shades
 336 (diamonds). Immature individuals are in dark shades (square) and matures in light shades
 337 (triangles).
 338

339

340

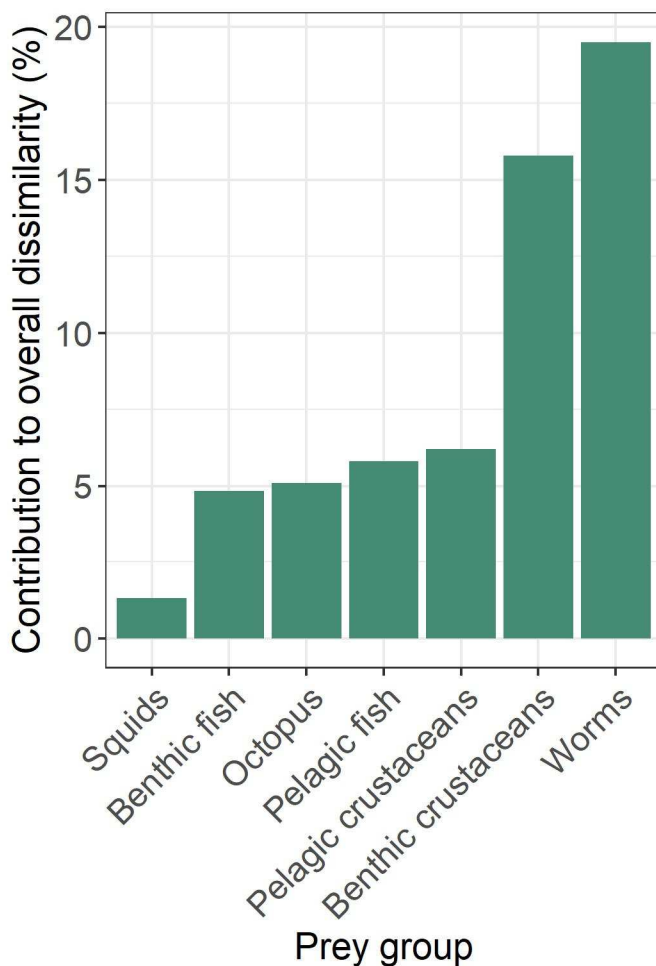
341 3.2.2. *Bathyraja irrasa*

342 A total of 91 individuals (49 females and 42 males) of *B. irrasa* were used for diet composition and
343 intraspecific comparison. *B. irrasa* ranged from 56 to 125 cm TL (Figure 2.B).

344 According to stomach content analysis, the diet of *B. irrasa* was dominated by crustaceans
345 and cephalopods, which accounted for 45% and 33% by fresh mass of the diet, respectively (Table
346 1). Other significant food sources were fish (19%), while worms were only minor prey items (3%).
347 In average, stomach samples contained 8.8 prey items. A total of 797 fresh prey items from at least
348 39 prey species were found. Prey items were dominated by crustaceans (548 prey items) occurring in
349 81 food samples (89%) and ranked first by number (69%). Worms ranked second by occurrence and
350 number (63% by occurrence and 23% by number) and fish ranked third (37% by occurrence and 6%
351 by number).

352 *Bathyraja irrasa* fed on a large diversity of crustaceans (13 species), of which isopods were
353 the main prey taxon. Statistical analyses were unable to identify differences in the dietary
354 composition between females and males (ANOSIM, global R statistic -0.005, $p < 0.571$ – Figure
355 3.B). However, nMDS ordinations indicated dietary segregation between immature and mature
356 individuals ($n = 46$ and $n = 45$) (ANOSIM, global R statistic 0.134, $p < 0.001$ – Figure 3.C). The
357 most important prey species was the isopod *Brucerolis bromleyana*, although they were found in
358 greater occurrence and abundance in immature (70% and 35%, respectively) than mature skates
359 (33% and 26%). Other isopods were recorded almost exclusively in the diet of immature individuals,
360 namely *Sursumura* sp. (57% and 21%) and *Ceratoserolis trilobitoides* (15% and 8%). In contrast, the
361 decapod *Thymopides grobovi* was less frequently found in the diet of immature (17%) than mature
362 individuals (58%). This is also highlighted by the SIMPER test showing that benthic crustaceans
363 (including Isopoda) had a substantial contribution to the dietary difference between maturity groups
364 (SIMPER, 16% among immature/mature – Figure 4). The second highest group in abundance was
365 Polychaeta, of which two families were particularly abundant in the overall diet, Polynoidae and

366 Nephtyidae. Polychaeta were more frequently encountered in the diet of immature individuals (72%
 367 and 48% respectively) than mature individuals (29% and 20%). This difference in stomach contents
 368 composition between immature and mature individuals is also supported by the SIMPER test
 369 showing that worms were responsible for the major difference in diet composition between maturity
 370 groups (SIMPER, 19% among immature/mature). *B. irrasa* mature individuals also fed on a large
 371 diversity of fish (n = 19 species) along with the octopuses *Muusoctopus thielei* and *Graneledone*
 372 *gonzalezi* (7% by number), in contrast with immature individuals. *Depth* was a significant vector
 373 ($r^2=0.15$, $p < 0.005$) explaining the ordination of samples as a function of the axis MDS2.



374
 375 Figure 4. **(Single-column fitting image)** Average contribution of prey groups to overall
 376 dissimilarity (%) between mature and immature individuals of *Bathyraja irrasa*.
 377

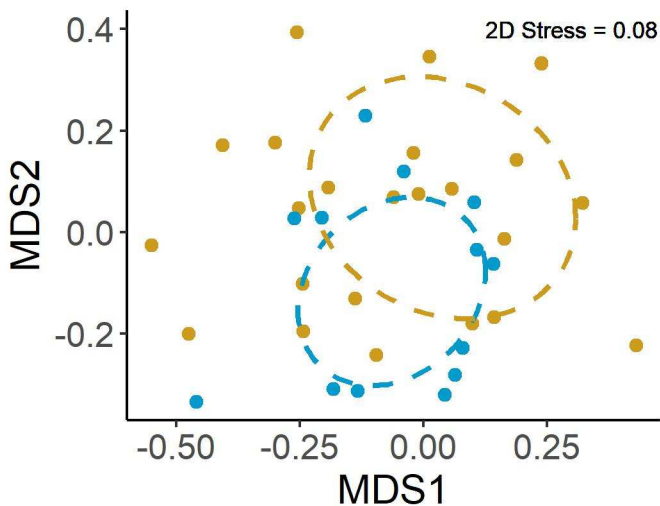
378 The analysis of accumulated prey items increased the number of cephalopod prey, with three
 379 additional squid species (*Todarodes* sp., *Gonatus antarcticus* and *Galiteuthis glacialis*), which

380 totaled 10 of the 13 accumulated beaks. Analysis of accumulated fish items included nine prey
381 found by counting pairs of eye lenses and vertebral remains, and 15 prey identified by heavily worn
382 otoliths that include those of an additional myctophid species, *Gymnoscopelus microlampas* (n = 1).
383 Samples also contained a small gastropod and a foraminifera, as well as pebbles and mud that were
384 considered incidentally ingested.

385

386 3.3. Interspecific diet comparison

387 Although analysis of mass composition showed *B. eatonii* fed primarily on fish (68%), while *B.*
388 *irrasa* preyed primarily on crustaceans and cephalopods (45% and 33% respectively – Table 1), both
389 nMDS ordinations and statistical analyses were unable to identify any differences in dietary
390 composition between the two skate species (ANOSIM, global *R* statistic 0.062, $p < 0.009$ – Figure
391 5). Environmental variables were fitted to the nMDS ordination and *Depth* appeared to be a
392 significant vector ($r^2=0.13$, $p < 0.01$) explaining the ordination of samples as a function of the axis
393 MDS2 while *Longitude* explained the ordination of samples as a function of the axis MDS1 ($r^2=0.09$,
394 $p < 0.01$).



395

396 Figure 5. **(Single-column fitting image)** Nonmetric multidimensional scaling (nMDS)
397 ordinations of the occurrence of different prey categories with S.E. ellipse for *Bathyraja eatonii*
398 (blue) and *B. irrasa* (yellow).
399

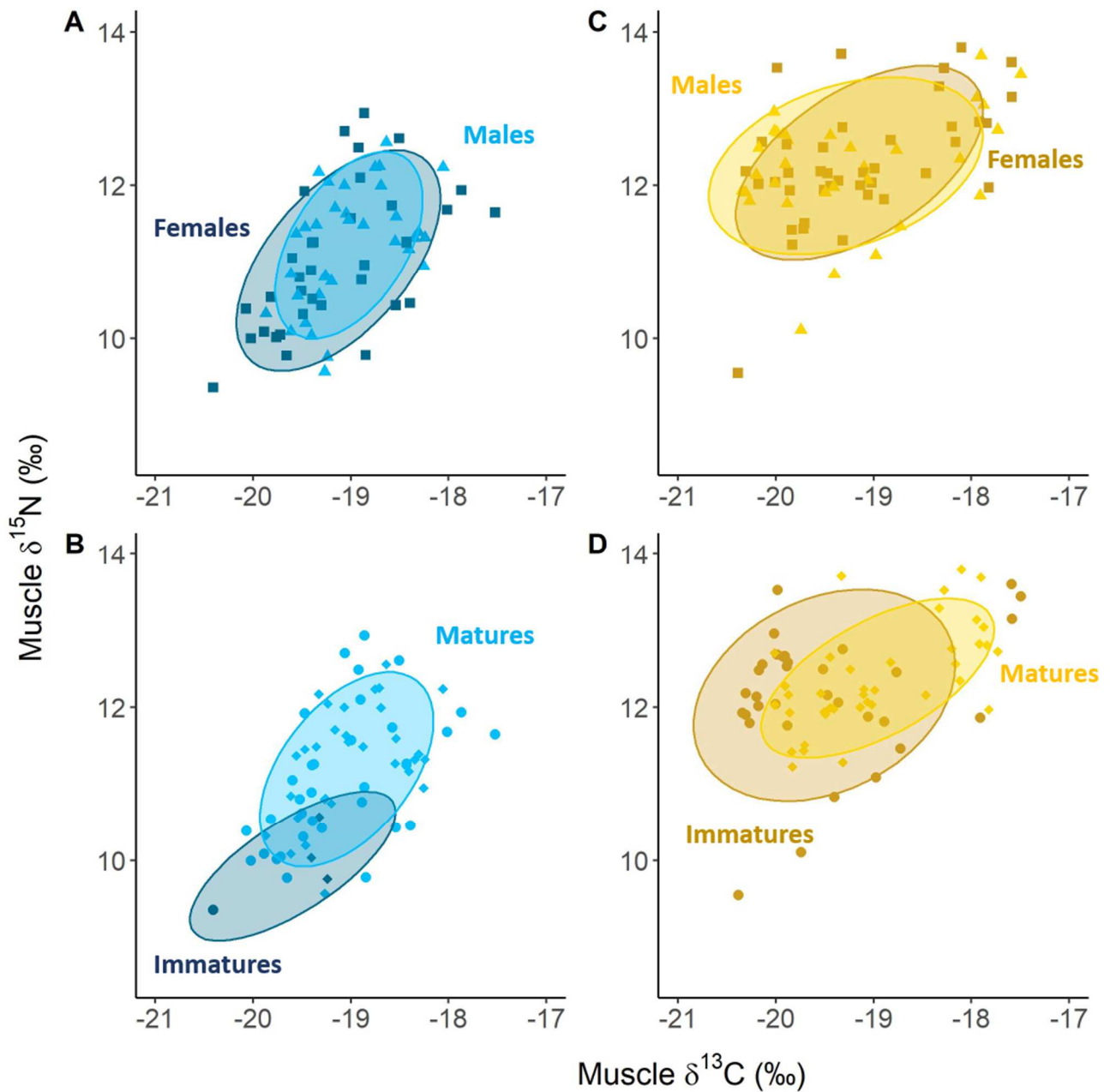
400 3.4. Stable isotopes

401 *Bathyraja eatonii* isotopic values ranged from -20.4 to -17.5 ‰ (mean = -19.1 ± 0.6 ‰) for
402 $\delta^{13}\text{C}$, and from 9.4 to 12.9 ‰ (mean = 11.1 ± 0.8 ‰) for $\delta^{15}\text{N}$ (Table 3). Muscle isotopic values
403 showed no differences between sex classes for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Figure 6.A), but $\delta^{15}\text{N}$ values
404 differed between maturity classes (t-test₆₇ = -3.1, $p < 0.004$; Table 4). Immature individuals had
405 lower mean $\delta^{15}\text{N}$ values than mature individuals (Figure 6.B).

406 *Bathyraja irrasa* isotopic values ranged from -20.4 to -17.5 ‰ (mean = -19.2 ± 0.8 ‰ for
407 $\delta^{13}\text{C}$) and from 9.6 to 13.8 ‰ (mean = 12.3 ± 0.8 ‰) for $\delta^{15}\text{N}$ (Table 3). One muscle sample was an
408 outlier ($\delta^{13}\text{C} = -23.13$ ‰ and $\delta^{15}\text{N} = 7.01$ ‰), which was therefore removed from the analysis.
409 Muscle isotopic composition between males and females showed no differences for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
410 values (Figure 6.C). However, $\delta^{13}\text{C}$ values differed between maturity classes (U-test = 365, $p <$
411 0.002 ; Table 4). Immature individuals had lower mean $\delta^{13}\text{C}$ values than mature individuals (Figure
412 6.D).

413
414 Muscle $\delta^{15}\text{N}$ values, but not $\delta^{13}\text{C}$ values, differed between species (U-test = 764, $p < 0.005$; Table 4)
415 with *B. eatonii* having lower $\delta^{15}\text{N}$ values than *B. irrasa* (Figure 7).

416



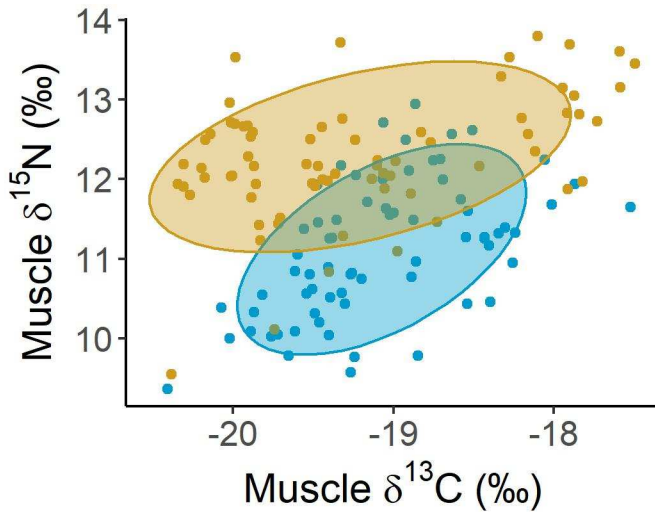
417

418 Figure 6. **(Two-column fitting image)** Muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and ellipse areas (70% of
 419 the data) of *Bathyraja eatonii* based on A) sex and B) maturity and *B. irrasa* based on C) sex and
 420 D) maturity. Females are in dark shades (square) and males in light shades (triangles).
 421 Immature individuals are in dark shades (plain circles) and matures in light shades
 422 (diamonds).
 423

424

425

426



426
 427 Figure 7. **(Single-column fitting image)** Muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and ellipse areas (70% of
 428 the data) of *Bathyraja eatonii* (blue) and *B. irrasa* (yellow).
 429

430 **4. Discussion**

431 The present study is the first to investigate the feeding ecology of two skate species commonly
 432 caught as bycatch in the French toothfish fishery occurring at the Kerguelen Islands. The majority of
 433 prey (73%) were identified to the species level, thus allowing a precise description of the diet of
 434 *Bathyraja eatonii* and *B. irrasa*. The use of barcoding analysis on prey tissues confirmed the
 435 morphological identification and allowed identifying well-digested prey items. We acknowledge that
 436 demersal longlines engender the risk of stomach washout during hauling, and thus may result in a
 437 potential underestimation of prey biomass, as well as introducing bias into the prey composition
 438 results (Barnett et al., 2013; Boyle et al., 2012). Nevertheless, the combination of stomach content
 439 and stable isotope analyses revealed interspecific differences in the trophic niches of the two skate
 440 species, and ontogenetic differences in the main feeding strategies used by different life stages of *B.*
 441 *irrasa*.

442
 443 *4.1. Interspecific diet comparison*

444 The wide variety of prey found in stomach contents (> 58 species) indicated that both *B. eatonii* and
 445 *B. irrasa* can be considered as generalist feeders (Tschopp et al., 2020). Diets were mainly composed

446 of crustaceans, fish and annelids, which is consistent with previous studies on the feeding ecology of
447 other skate species in subantarctic areas (Brickle et al., 2003; Main and Collins, 2011). Although
448 diets of both species were composed of the same prey groups, the proportions of mass, number and
449 occurrence of each prey group varied among skate species, as well as their specific composition. By
450 mass, fish dominated *B. eatonii* diet whereas crustaceans and cephalopods were most prevalent in the
451 diet of *B. irrasa*. Crustaceans were the main prey group by number. Interestingly, crustacean species
452 composition varied amongst skate species: *B. eatonii* diet was dominated in number by one benthic
453 isopod (*Ceratoserolis trilobitoides*) and two pelagic shrimps (*Campylonotus capensis* and *Pasiphaea*
454 sp.), while *B. irrasa* diet was dominated by different species of benthic isopods (*Brucerolis*
455 *bromleyana* and *Sursumura* sp.) and one species of benthic decapod (*Thymopides grobovi*). These
456 results showed that *B. eatonii* fed on both benthic and pelagic prey, whereas *B. irrasa* fed almost
457 exclusively on benthic prey. This difference was also supported by the importance of other pelagic
458 prey such as myctophid and paralepidid fishes as well as squids in *B. eatonii* diet, whereas other
459 major components of *B. irrasa* diet were benthic and demersal prey such as polychaetas and
460 octopuses. In addition, the occurrence of mud and small pebbles was observed in some *B. irrasa*
461 stomach contents, while none were observed in *B. eatonii* samples, which could be explained by
462 differences in feeding habitat (mud vs rocky bottom substratum). Inter-specific variations in prey
463 composition and prey habitat (pelagic vs benthic) have indeed been well documented in previous
464 studies on feeding habits of co-occurring skate species (Brickle et al., 2003; Tschopp et al., 2020).
465 Unexpectedly statistical analysis of diet composition did not provide evidence for different feeding
466 strategies between *B. irrasa* and *B. eatonii*. However, given the broad prey categories used and that
467 this analysis is based on prey species presence/absence data, variability observed in the abundance of
468 prey species consumed may be masked. Furthermore, the benthic feeding strategy of *B. irrasa* was
469 not supported by muscle $\delta^{13}\text{C}$ values integrating diet over several months, which showed similar
470 values to *B. eatonii*. In contrast, $\delta^{15}\text{N}$ value of *B. irrasa* were higher in comparison to *B. eatonii*,

471 which typically reflects a higher trophic position and/or stronger affinity to benthic food webs found
472 to be more enriched in ^{15}N than pelagic food web, especially in the deep-sea (Boyle et al., 2012).
473 Differences in ^{15}N values between the two species therefore confirm different feeding strategies.

474 Depth was found to explain a small proportion of the dissimilarities observed between the
475 two skate species. While their distribution overlaps, *B. eatonii* favors the continental shelf and upper
476 slope areas, whereas *B. irrassa* mainly inhabits slopes at greater depths (Duhamel et al., 2005).
477 Hence, variation in diet compositions may be related to the abundance of prey species among the
478 depth ranges. For example, myctophids are pelagic fish known to make important diel vertical
479 migrations; they could be trapped at the bottom during the day, thus vertically connecting the pelagic
480 and benthic food webs in slope areas (Cotté et al., 2022; Drazen and Sutton, 2016; Hunt and
481 Swadling, 2021). Videos made using cameras attached to longlines set on slopes deeper than 1000 m
482 showed myctophids sitting on the sea floor (Pers. Com.) revealing their accessibility to benthic
483 feeders such as skates. Hence partitioning food or habitat resources may be a strategy to avoid direct
484 competition between these two congeneric skate species (Barbini and Lucifora, 2012; Barría et al.,
485 2018).

486 Finally, we observed inter-specific variations in the number of ingested prey, the extent of
487 prey digestion, and the texture of gastric fluids during stomach content analysis, which suggest
488 differences in digestive systems and thus foraging habits (Cyrino et al., 2008). The high number of
489 both accumulated fish and prey items in each stomach of *B. irrassa* (8.8 in average) compared to *B.*
490 *eatonii* (2.4 in average) supported the hypothesis of greater digestion capability in *B. irrassa* due to its
491 benthic feeding strategy. Crustaceans are indeed harder to digest compared to cephalopods, which
492 are in turn harder to digest than fish (Cyrino et al., 2008). This variation in digestion rates among
493 species would also lead to a potential underestimation of easily digested prey species such as fishes
494 in *B. irrassa*, and an overestimation of prey more resistant to digestion such as crustaceans in *B.*
495 *eatonii* (Barnett et al., 2013; Boyle et al., 2012).

496

497 *4.2. Intraspecific diet comparisons*

498 Several studies conducted in different species of skates found no significant differences between
499 male and female diets (Blanco-Parra et al., 2012; Brown-Vuillemin et al., 2020). Similarly, *B. eatonii*
500 and *B. irrasa* did not display diet differentiation related to sex, and both sexes occupy similar trophic
501 niches on the Kerguelen Plateau according to SIA analyses, although the arrangement of teeth in the
502 jaw is different between males and females (Pers. Com.).

503 Nevertheless, many authors have documented variability in skate diet composition according to
504 maturity stages, indicating ontogenetic shifts in their feeding habits (Barbini and Lucifora, 2012;
505 Belleggia et al., 2008; Brown-Vuillemin et al., 2020). In this study, we found an effect of maturity
506 stage on *B. irrasa* diet: immature individuals fed mostly on small benthic crustaceans and annelid
507 worms, while mature individuals preyed more upon large crustaceans, teleost fish and cephalopods.
508 This result was consistent with other studies carried out on subantarctic skate diets such as *B.*
509 *albomaculata*, *B. brachyurops* and *B. griseocauda* (Brickle et al., 2003). This ontogenetic variation
510 could be explained by an improved ability to capture larger-sized prey with increased size of the jaw
511 and swimming speed, or changes in habitat and prey availability (Belleggia et al., 2008; Blanco-
512 Parra et al., 2012; Munroe et al., 2022; Orlov, 2003). The latter explanation is unlikely, since
513 immature and mature *B. irrasa* were found in similar habitats. Apart from the predator size, another
514 explanation could be changes in energetic and physiological needs associated to the cost of sexual
515 maturity, with fishes having a higher energy density than crustaceans and annelids (Munroe et al.,
516 2022; Schaafsma et al., 2018). Such variation in diet composition is typically associated with
517 variation in trophic position, with small individuals preying on crustaceans considered as secondary
518 consumers, whereas larger individuals preying on fish and cephalopods being tertiary consumers
519 (Belleggia et al., 2008). Immature and mature *B. irrasa* showed different $\delta^{13}\text{C}$ values, thus indicating
520 varying sources of primary production such as benthic/pelagic trophic chains. They would therefore

521 be part of two different trophic chains. In contrast, SIA showed no difference in $\delta^{13}\text{C}$ values for *B.*
522 *eatonii*, thus allowing a direct comparison of the $\delta^{15}\text{N}$ values of immature and mature skates that
523 suggested an ontogenetic shift with a higher position of mature individuals. However, the small
524 number of immature *B. eatonii* highlights the need to collect additional immature specimens,
525 especially outside the fishing area (particularly on the Plateau < 500 m) where they live.

526

527 4.3. Skates in the Kerguelen marine food web

528 Our results supported the hypothesis that skates should be considered as top predators (Barbini et al.,
529 2018; Brown-Vuillemin et al., 2020; Ebert and Bizzarro, 2007). Adult individuals of *Bathyraja*
530 species found on the slopes of the Kerguelen Plateau have similar diets to other benthic predators
531 such as the Patagonian toothfish. They also share some prey items with seabirds around Kerguelen
532 Islands, such as fish (Nototheniidae, Myctophidae), cephalopods (*Moroteuthopsis longimana*, *G.*
533 *antarcticus*, *Slosarczykovia circumantarctica*), shrimps, isopods and annelids (Delord et al., 2010;
534 Lescroëil et al., 2004). Despite the lack of detailed studies on the diet of Patagonian toothfish over the
535 Kerguelen Plateau, studies from elsewhere in the Southern Ocean indicated the species fed on high
536 proportions of meso- and bathy-pelagic fish such as myctophids (including *Gymnoscopelus* spp.),
537 and morids and macrourids, cephalopods (including *G. antarcticus*), crustaceans and polychaetes
538 (Duhamel, 1987; Goldsworthy et al., 2001; Troccoli et al., 2020). When comparing their stable
539 isotopic values, skates showed lower mean trophic position ($\delta^{15}\text{N}_{B. eatonii} = 11.1\text{‰}$ and $\delta^{15}\text{N}_{B. irrasa} =$
540 12.3‰) than toothfish ($\delta^{15}\text{N}_{D. eleginoides} > 14.0\text{‰}$) (Cherel et al., 2017). However, comparing isotopic
541 niches requires caution, because retention of urea in the body tissue of elasmobranchs may
542 complicate interpretations of stable isotope values. Since urea is enriched in ^{14}N compared to
543 proteins, $\delta^{15}\text{N}$ values of skates and sharks tend to be lower than those of bony fishes, which can
544 result in an underestimation of their trophic position (Carlisle et al., 2017; Kim and Koch, 2012).
545 Some skates were found in Patagonian toothfish diet, suggesting that skates and toothfish could have

546 predator-prey interactions within an exploited ecosystem (Duhamel, 1987). Thus, a decline in the
547 abundance of one of these predator species through overfishing could trigger an increase in the
548 abundance of the other species through the related release of competition (Barbini and Lucifora,
549 2012; Brown et al., 2012). Because little is known about trophic interactions resulting from the
550 effects of fishing on skates, dietary composition and trophic information of these bycatch species are
551 essential to understand their role in the ecosystem in order to forecast the possible ecosystem-level
552 effects of fisheries on species composition and diversity (Bizzarro et al., 2007; Brown et al., 2012;
553 Stevens et al., 2000; Subramaniam et al., 2022, 2020). The results of this study support the growing
554 body of knowledge that indicates that crustaceans, cephalopods and myctophids are important prey
555 items for marine predators in the Southern Ocean, particularly over the Kerguelen Plateau that
556 sustains a high diversity of predators in a wide range of habitats (Cherel, 2020; Doubleday et al.,
557 2016; Hulley and Duhamel, 2011; Jackson et al., 1998; Yang et al., 2022).

558

559 *4.4. Catchability and implications for skate bycatch reduction*

560 Relative vulnerability to fishing can be assessed through various parameters related to diet (e.g.
561 feeding strategy), as well as the extent to which skates may be attracted to fishing gear, all of which
562 impact catchability. Because no evidence of bites on prey were found in the diet composition
563 analysis, we assumed that both skate species used suction to capture their prey whole. In addition,
564 both species were found to display partially or fully benthic feeding strategies making them
565 susceptible to longline gear. Our results are thus useful in informing technical improvements to
566 fishing gear, such as on longlines, which would reduce skate catchability (Afonso et al., 2011).
567 Floating snoods enable the hook to float above the sea floor instead of being laid on it, and
568 consequently can allow skates to avoid longlines while foraging on the substrate, as the fully-benthic
569 *B. irrasa*.

570 In addition, we sometimes found more than one bait in stomach contents, suggesting that skates
571 could forage on baits without being captured systematically. Furthermore, *Antimora rostrata* and
572 *Macrourus* sp., which are the most common teleost fish bycatch in the toothfish fishery, also
573 occurred in the diet of skates, suggesting that they could feed on bycaught fish during the soaking
574 time of the line (Barnett et al., 2013; Duhamel et al., 2005). Although *Dissostichus eleginoides* was
575 absent from the diet of both skate species, such interactions with fishing lines would increase skate
576 catchability in the fishery (Georgeson et al., 2020; Stobutzki et al., 2001).

577

578 **5. Conclusion**

579 This study provides a comprehensive analysis of the feeding habits of *Bathyraja eatonii* and
580 *B. irrasa* over the Kerguelen Plateau. As top predators and among the 10 most abundant demersal
581 fish species there (Duhamel et al., 2019), significant changes in skate population dynamics due to
582 fishing mortality could influence the structure of the food web. Our results will contribute to
583 ecosystem models being developed in the region by increasing our understanding of deep-sea food
584 webs and predator-prey interactions over the Kerguelen Plateau (Clavareau et al., 2020;
585 Subramaniam et al., 2022). Interspecific differences in diet may be the consequence of competition
586 between these generalist species, but may also reflect differences in the abundance of prey by depth.
587 These disparities in feeding ecology emphasize the importance of considering species separately for
588 conservation programs when designing solutions to reduce catch rates or catchability. Possible
589 competition and niche overlap between skates and toothfish also stress the importance of fully
590 describing toothfish diets over the Kerguelen Plateau, and quantifying skate bycatch mortality to be
591 able to predict its ecosystem impacts.

592

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606

607 **References**

- 608 Afonso, A.S., Hazin, F.H.V., Carvalho, F., Pacheco, J.C., Hazin, H., Kerstetter, D.W., Murie, D.,
609 Burgess, G.H., 2011. Fishing gear modifications to reduce elasmobranch mortality in pelagic
610 and bottom longline fisheries off Northeast Brazil. *Fish. Res.* 108, 336–343.
611 <https://doi.org/10.1016/j.fishres.2011.01.007>
- 612 Altschul, S.F., Gish, W., Miller, W., Myers, E.W., Lipman, D.J., 1990. Basic Local Alignment
613 Search Tool. *J. Mol. Biol.* 403–410.
- 614 Barbini, S.A., Lucifora, L.O., 2012. Ontogenetic diet shifts and food partitioning between two small
615 sympatric skates (Chondrichthyes, Rajidae) in the Southwestern Atlantic. *Mar. Freshw. Res.*
616 63, 905. <https://doi.org/10.1071/MF12131>
- 617 Barbini, S.A., Lucifora, L.O., Sabadin, D.E., Figueroa, D.E., 2020. Ecological specialization is
618 associated with high conservation concern in skates (Chondrichthyes, Rajiformes). *Anim.*
619 *Conserv.* 23, 222–228. <https://doi.org/10.1111/acv.12531>
- 620 Barbini, S.A., Sabadin, D.E., Lucifora, L.O., 2018. Comparative analysis of feeding habits and
621 dietary niche breadth in skates: the importance of body size, snout length, and depth. *Rev.*
622 *Fish Biol. Fish.* 28, 625–636. <https://doi.org/10.1007/s11160-018-9522-5>
- 623 Barnett, L.A.K., Winton, M.V., Ainsley, S.M., Cailliet, G.M., Ebert, D.A., 2013. Comparative
624 Demography of Skates: Life-History Correlates of Productivity and Implications for
625 Management. *PLOS ONE* 8, e65000. <https://doi.org/10.1371/journal.pone.0065000>

- 626 Barría, C., Navarro, J., Coll, M., 2018a. Feeding habits of four sympatric sharks in two deep-water
627 fishery areas of the western Mediterranean Sea. Deep Sea Res. Part Oceanogr. Res. Pap. 142,
628 34–43. <https://doi.org/10.1016/j.dsr.2018.09.010>
- 629 Barría, C., Navarro, J., Coll, M., 2018b. Feeding habits of four sympatric sharks in two deep-water
630 fishery areas of the western Mediterranean Sea. Deep Sea Res. Part Oceanogr. Res. Pap. 142,
631 34–43. <https://doi.org/10.1016/j.dsr.2018.09.010>
- 632 Belleggia, M., Mabragaña, E., Figueroa, D.E., Scenna, L.B., Barbini, S.A., Astarloa, J.M.D. de,
633 2008. Food habits of the broad nose skate, *Bathyraja brachyurops* (Chondrichthyes, Rajidae),
634 in the south-west Atlantic. Sci. Mar. 72, 701–710.
635 <https://doi.org/10.3989/scimar.2008.72n4701>
- 636 Benson, D.A., Karsch-Mizrachi, I., Lipman, D.J., Ostell, J., Wheeler, D.L., 2005. GenBank. Nucleic
637 Acids Res. 33, D34–D38. <https://doi.org/10.1093/nar/gki063>
- 638 Bizzarro, J., Robinson, H., Rinewalt, C., Ebert, D., 2007. Comparative feeding ecology of four
639 sympatric skate species (*Bathyraja* and *Raja* spp.) off central California, U.S.A. Environ.
640 Biol. Fishes 80, 197–220.
- 641 Blanco-Parra, M.-P., Galván-Magaña, F., Márquez-Farías, J.F., Niño-Torres, C.A., 2012. Feeding
642 ecology and trophic level of the banded guitarfish, *Zapteryx exasperata*, inferred from stable
643 isotopes and stomach contents analysis. Environ. Biol. Fishes 95, 65–77.
644 <https://doi.org/10.1007/s10641-011-9862-7>
- 645 Bodin, N., Le Loc'h, F., Hily, C., 2007. Effect of lipid removal on carbon and nitrogen stable isotope
646 ratios in crustacean tissues. J. Exp. Mar. Biol. Ecol. 341, 168–175.
647 <https://doi.org/10.1016/j.jembe.2006.09.008>
- 648 Boltovskoy, D., 1999. South Atlantic Zooplankton.
- 649 Boyle, M.D., Ebert, D.A., Cailliet, G.M., 2012. Stable-isotope analysis of a deep-sea benthic-fish
650 assemblage: evidence of an enriched benthic food web. J. Fish Biol. 80, 1485–1507.
651 <https://doi.org/10.1111/j.1095-8649.2012.03243.x>
- 652 Brander, K., 1981. Disappearance of common skate *Raja batis* from Irish Sea. Nature 290, 48–49.
653 <https://doi.org/10.1038/290048a0>
- 654 Brickle, P., Laptikhovskiy, V., Pompert, J., Bishop, A., 2003. Ontogenetic changes in the feeding
655 habits and dietary overlap between three abundant rajid species on the Falkland Islands'
656 shelf. J. Mar. Biol. Assoc. U. K. 83, 1119–1125.
657 <https://doi.org/10.1017/S0025315403008373h>
- 658 Brown, S.C., Bizzarro, J.J., Cailliet, G.M., Ebert, D.A., 2012. Breaking with tradition: redefining
659 measures for diet description with a case study of the Aleutian skate *Bathyraja aleutica*
660 (Gilbert 1896). Environ. Biol. Fishes 95, 3–20. <https://doi.org/10.1007/s10641-011-9959-z>
- 661 Brown-Vuillemin, S., Barreau, T., Caraguel, J.-M., Iglésias, S.P., 2020. Trophic ecology and
662 ontogenetic diet shift of the blue skate (*Dipturus cf. flossada*). J. Fish Biol. 97, 515–526.
663 <https://doi.org/10.1111/jfb.14407>
- 664 Cailliet, G.M., Musick, J.A., Simpfendorfer, C.A., Stevens, J.D., 2005. Ecology and Life History
665 Characteristics of Chondrichthyan Fish, in: Fowler, S.L., Cavanagh, R.D., Camhi, M.,
666 Burgess, G.H., Cailliet, G.M., Fordham, S.V., Simpfendorfer, C.A., Musick, J.A. (Eds.),
667 Sharks, Rays and Chimaeras: The Status of the Condriichthyan Fishes.

668 Carlisle, A.B., Litvin, S.Y., Madigan, D.J., Lyons, K., Bigman, J.S., Ibarra, M., Bizzarro, J.J., 2017.
669 Interactive effects of urea and lipid content confound stable isotope analysis in elasmobranch
670 fishes. *Can. J. Fish. Aquat. Sci.* 74, 419–428. <https://doi.org/10.1139/cjfas-2015-0584>
671 CCAMLR Secretariat, 2022. Fishery Report 2021: *Dissostichus eleginoides* at Kerguelen Islands
672 French EEZ (Division 58.5.1) 11.
673 CCAMLR Secretariat, 2014. Review of skate (Rajiformes) by-catch in CCAMLR toothfish fisheries
674 (WG-FSA-14/12). CCAMLR, Hobart, Australia.
675 Cherel, Y., 2020. A review of Southern Ocean squids using nets and beaks. *Mar. Biodivers.* 50, 98.
676 <https://doi.org/10.1007/s12526-020-01113-4>
677 Cherel, Y., Hobson, K., 2007. Geographical variation in carbon stable isotope signatures of marine
678 predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar. Ecol. Prog.
679 Ser.* 329, 281–287. <https://doi.org/10.3354/meps329281>
680 Cherel, Y., Hobson, K.A., 2005. Stable isotopes, beaks and predators: a new tool to study the trophic
681 ecology of cephalopods, including giant and colossal squids. *Proc. R. Soc. B Biol. Sci.* 272,
682 1601–1607. <https://doi.org/10.1098/rspb.2005.3115>
683 Cherel, Y., Weimerskirch, H., Trouvé, C., Bost, C., 2000. Food and feeding ecology of the neritic-
684 slope forager black-browed albatross and its relationships with commercial fisheries in
685 Kerguelen waters. *Mar. Ecol. Prog. Ser.* 207, 183–199. <https://doi.org/10.3354/meps207183>
686 Cherel, Y., Xavier, J., de Grissac, S., Trouvé, C., Weimerskirch, H., 2017. Feeding ecology, isotopic
687 niche, and ingestion of fishery-related items of the wandering albatross *Diomedea exulans* at
688 Kerguelen and Crozet Islands. *Mar. Ecol. Prog. Ser.* 565, 197–215.
689 <https://doi.org/10.3354/meps11994>
690 Clavareau, L., Marzloff, M.P., Trenkel, V.M., Bulman, C.M., Gourguet, S., Le Gallic, B., Hervann,
691 P.-Y., Péron, C., Gasco, N., Faure, J., Tixier, P., 2020. Comparison of approaches for
692 incorporating depredation on fisheries catches into Ecopath. *ICES J. Mar. Sci.* 77, 3153–
693 3167. <https://doi.org/10.1093/icesjms/fsaa219>
694 Cortés, E., 1999. Standardized diet compositions and trophic levels of sharks. *ICES J. Mar. Sci.* 56,
695 707–717. <https://doi.org/10.1006/jmsc.1999.0489>
696 Cortés, E., 1997. A critical review of methods of studying fish feeding based on analysis of stomach
697 contents: application to elasmobranch fishes 54, 13.
698 Cotté, C., Ariza, A., Berne, A., Habasque, J., Lebourges-Dhaussy, A., Roudaut, G., Espinasse, B.,
699 Hunt, B.P.V., Pakhomov, E.A., Henschke, N., Péron, C., Conchon, A., Koedooder, C., Iazard,
700 L., Cherel, Y., 2022. Macrozooplankton and micronekton diversity and associated carbon
701 vertical patterns and fluxes under distinct productive conditions around the Kerguelen
702 Islands. *J. Mar. Syst.* 226, 103650. <https://doi.org/10.1016/j.jmarsys.2021.103650>
703 Crook, K.A., Barnett, A., Sheaves, M., Abrantes, K., 2019. Effects of lipid and urea extraction on
704 stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of two batoids: A call for more species-specific
705 investigations. *Limnol. Oceanogr. Methods* 17, 565–574. <https://doi.org/10.1002/lom3.10333>
706 Cyrino, J.E.P., Bureau, D.P., Kapoor, B.G., 2008. *Feeding and Digestive Functions in Fishes*. CRC
707 Press.
708 Davidson, L.N.K., Krawchuk, M.A., Dulvy, N.K., 2016. Why have global shark and ray landings
709 declined: improved management or overfishing? *Fish Fish.* 17, 438–458.
710 <https://doi.org/10.1111/faf.12119>

711 Delord, K., Cotté, C., Péron, C., Marteau, C., Pruvost, P., Gasco, N., Duhamel, G., Cherel, Y.,
712 Weimerskirch, H., 2010. At-sea distribution and diet of an endangered top predator:
713 relationship between white-chinned petrels and commercial longline fisheries. *Endanger.*
714 *Species Res.* 13, 1–16. <https://doi.org/10.3354/esr00309>

715 Dettai, A., Lautredou, A.-C., Bonillo, C., Goimbault, E., Busson, F., Causse, R., Couloux, A.,
716 Cruaud, C., Duhamel, G., Denys, G., Hauteceur, M., Iglesias, S., Koubbi, P., Lecointre, G.,
717 Moteki, M., Pruvost, P., Tercerie, S., Ozouf, C., 2011. The actinopterygian diversity of the
718 CEAMARC cruises: Barcoding and molecular taxonomy as a multi-level tool for new
719 findings. *Deep Sea Res. Part II Top. Stud. Oceanogr., Census of Antarctic Marine Life:*
720 *Diversity and Change in the Southern Ocean Ecosystems* 58, 250–263.
721 <https://doi.org/10.1016/j.dsr2.2010.05.021>

722 Doubleday, Z.A., Prowse, T.A.A., Arkhipkin, A., Pierce, G.J., Semmens, J., Steer, M., Leporati,
723 S.C., Lourenço, S., Quetglas, A., Sauer, W., Gillanders, B.M., 2016. Global proliferation of
724 cephalopods. *Curr. Biol.* 26, R406–R407. <https://doi.org/10.1016/j.cub.2016.04.002>

725 Drazen, J., Sutton, T., 2016. Dining in the Deep: The Feeding Ecology of Deep-Sea Fishes. *Annu.*
726 *Rev. Mar. Sci.* 9. <https://doi.org/10.1146/annurev-marine-010816-060543>

727 Duhamel, G., 1987. Ichtyofaune des secteurs indien occidental et atlantique oriental de l’océan
728 Austral : biogéographie, cycles biologiques et dynamique des populations. Université Pierre
729 et Marie Curie - Paris 6.

730 Duhamel, G., Gasco, N., Davaine, P., 2005. Poisson des Iles Kerguelen et Crozet. Guide régional de
731 l’océan Austral, Muséum national d’Histoire naturelle. ed, Patrimoines Naturels. Paris.

732 Duhamel, G., Péron, C., Sinègre, R., Chazeau, C., Gasco, N., Hauteceur, M., Martin, A., Durand, I.,
733 Causse, R., 2019. Important readjustments in the biomass and distribution of groundfish
734 species in the northern part of the Kerguelen Plateau and Skiff Bank. *CCAMLR Sci. Proc.*
735 *Second Symp. Kerguelen Plateau* 50.

736 Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K.,
737 Davidson, L.N., Fordham, S.V., Francis, M.P., Pollock, C.M., Simpfendorfer, C.A., Burgess,
738 G.H., Carpenter, K.E., Compagno, L.J., Ebert, D.A., Gibson, C., Heupel, M.R., Livingstone,
739 S.R., Sanciangco, J.C., Stevens, J.D., Valenti, S., White, W.T., 2014. Extinction risk and
740 conservation of the world’s sharks and rays. *eLife* 3, e00590.
741 <https://doi.org/10.7554/eLife.00590>

742 Dulvy, N.K., Reynolds, J.D., 2002. Predicting Extinction Vulnerability in Skates. *Conserv. Biol.* 16,
743 440–450. <https://doi.org/10.1046/j.1523-1739.2002.00416.x>

744 Ebert, D., Bizzarro, J., 2007. Standardized diet compositions and trophic levels of skates
745 (Chondrichthyes: Rajiformes: Rajoidei). *Environ. Biol. Fishes* 80, 221–237.
746 <https://doi.org/10.1007/s10641-007-9227-4>

747 Field, I.C., Meekan, M.G., Buckworth, R.C., Bradshaw, C.J.A., 2009. Chapter 4 Susceptibility of
748 Sharks, Rays and Chimaeras to Global Extinction, in: *Advances in Marine Biology*. Elsevier,
749 pp. 275–363. [https://doi.org/10.1016/S0065-2881\(09\)56004-X](https://doi.org/10.1016/S0065-2881(09)56004-X)

750 Gallagher, A.J., Hammerschlag, N., Cooke, S.J., Costa, D.P., Irschick, D.J., 2015. Evolutionary
751 theory as a tool for predicting extinction risk. *Trends Ecol. Evol.* 30, 61–65.
752 <https://doi.org/10.1016/j.tree.2014.12.001>

753 Gasco, N., 2011. Contributions to marine science by fishery observers in the French EEZ of
754 Kerguelen., in: Duhamel, G., Welsford, D. (Eds.), The Kerguelen Plateau: Marine Ecosystem
755 and Fisheries. Paris, pp. 93–98.

756 Gaskett, A.C., Bulman, C., He, X., Goldsworthy, S.D., 2001. Diet composition and guild structure of
757 mesopelagic and bathypelagic fishes near Macquarie Island, Australia. *N. Z. J. Mar. Freshw.*
758 *Res.* 35, 469–476. <https://doi.org/10.1080/00288330.2001.9517016>

759 Georgeson, L., Rigby, C.L., Emery, T.J., Fuller, M., Hartog, J., Williams, A.J., Hobday, A.J., Duffy,
760 C.A.J., Simpfendorfer, C.A., Okuda, T., Stobutzki, I.C., Nicol, S.J., 2020. Ecological risks of
761 demersal fishing on deepwater chondrichthyan populations in the Southern Indian and South
762 Pacific Oceans. *ICES J. Mar. Sci.* 77, 1711–1727. <https://doi.org/10.1093/icesjms/fsaa019>

763 Goldsworthy, S., He, X., Tuck, G., Lewis, M., Williams, R., 2001. Trophic interactions between the
764 Patagonian toothfish, its fishery, and seals and seabirds around Macquarie Island. *Mar. Ecol.*
765 *Prog. Ser.* 218, 283–302. <https://doi.org/10.3354/meps218283>

766 Hulley, P.A., Duhamel, G., 2011. Aspects of lanternfish distribution in the Kerguelen Plateau region.
767 Kerguelen Plateau *Mar. Ecosyst. Fish.* 183–195.

768 Hunt, B.P.V., Swadling, K.M., 2021. Macrozooplankton and micronekton community structure and
769 diel vertical migration in the Heard Island Region, Central Kerguelen Plateau. *J. Mar. Syst.*
770 221, 103575. <https://doi.org/10.1016/j.jmarsys.2021.103575>

771 Hussey, N.E., Olin, J.A., Kinney, M.J., McMeans, B.C., Fisk, A.T., 2012. Lipid extraction effects on
772 stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of elasmobranch muscle tissue. *J. Exp. Mar. Biol.*
773 *Ecol.* 434–435, 7–15. <https://doi.org/10.1016/j.jembe.2012.07.012>

774 Jackson, G., Mckinnon, J., Lalas, C., Ardern, R., Buxton, N., 1998. Food spectrum of the deepwater
775 squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in New Zealand waters. *Polar*
776 *Biol.* 20, 56–65. <https://doi.org/10.1007/s003000050276>

777 Kassambara, A., 2021. rstatix: Pipe-Friendly Framework for Basic Statistical Tests.

778 Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper,
779 A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P., Drummond, A., 2012.
780 Geneious Basic: An integrated and extendable desktop software platform for the organization
781 and analysis of sequence data. *Bioinformatics* 28, 1647–1649.
782 <https://doi.org/10.1093/bioinformatics/bts199>

783 Kim, S.L., Koch, P.L., 2012. Methods to collect, preserve, and prepare elasmobranch tissues for
784 stable isotope analysis. *Environ. Biol. Fishes* 95, 53–63. <https://doi.org/10.1007/s10641-011-9860-9>

785

786 Koen Alonso, M., 2001. Food habits of *Dipturus chilensis* (Pisces: Rajidae) off Patagonia,
787 Argentina. *ICES J. Mar. Sci.* 58, 288–297. <https://doi.org/10.1006/jmsc.2000.1010>

788 Leray, M., Yang, J.Y., Meyer, C.P., Mills, S.C., Agudelo, N., Ranwez, V., Boehm, J.T., Machida,
789 R.J., 2013. A new versatile primer set targeting a short fragment of the mitochondrial COI
790 region for metabarcoding metazoan diversity: application for characterizing coral reef fish
791 gut contents. *Front. Zool.* 10, 34. <https://doi.org/10.1186/1742-9994-10-34>

792 Lescroëll, A., Ridoux, V., Bost, C.A., 2004. Spatial and temporal variation in the diet of the gentoo
793 penguin (*Pygoscelis papua*) at Kerguelen Islands. *Polar Biol.* 27, 206–216.
794 <https://doi.org/10.1007/s00300-003-0571-3>

795 Main, C.E., Collins, M.A., 2011. Diet of the Antarctic starry skate *Amblyraja georgiana* (Rajidae,
796 Chondrichthyes) at South Georgia (Southern Ocean). *Polar Biol.* 34, 389–396.
797 <https://doi.org/10.1007/s00300-010-0894-9>

798 Matich, P., Heithaus, M.R., Layman, C.A., 2011. Contrasting patterns of individual specialization
799 and trophic coupling in two marine apex predators. *J. Anim. Ecol.* 80, 294–305.
800 <https://doi.org/10.1111/j.1365-2656.2010.01753.x>

801 Munroe, S., Meyer, L., Heithaus, M.R., 2022. Elasmobranch Foraging Strategies and Tactics, in:
802 Carrier, J.C., Simpfendorfer, C.A., Heithaus, M.R., Yopak, K.E. (Eds.), *Biology of Sharks*
803 *and Their Relatives*. p. 822.

804 Navia, A.F., Mejía-Falla, P.A., Giraldo, A., 2007. Feeding ecology of elasmobranch fishes in coastal
805 waters of the Colombian Eastern Tropical Pacific. *BMC Ecol.* 7, 8.
806 <https://doi.org/10.1186/1472-6785-7-8>

807 Nowara, G.B., Burch, P., Gasco, N., Welsford, D.C., Lamb, T.D., Chazeau, C., Duhamel, G.,
808 Pruvost, P., Wotherspoon, S., Candy, S.G., 2017. Distribution and abundance of skates
809 (*Bathyraja* spp.) on the Kerguelen Plateau through the lens of the toothfish fisheries. *Fish.*
810 *Res.* 186, 65–81. <https://doi.org/10.1016/j.fishres.2016.07.022>

811 Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin,
812 P.R., O’Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner,
813 H., 2020. *vegan: Community Ecology Package*.

814 Oliver, S., Braccini, M., Newman, S.J., Harvey, E.S., 2015. Global patterns in the bycatch of sharks
815 and rays. *Mar. Policy* 54, 86–97. <https://doi.org/10.1016/j.marpol.2014.12.017>

816 Orlov, A.M., 2003. Diets, feeding habits, and trophic relations of six deep-benthic skates (Rajidae) in
817 the western Bering Sea 7, 16.

818 Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P.,
819 Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel,
820 M., McAllister, M.K., Pope, J., Sainsbury, K.J., 2004. Ecosystem-Based Fishery
821 Management. *Science* 305, 346–347. <https://doi.org/10.1126/science.1098222>

822 Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., Montaña, C.G., 2007.
823 Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in
824 stable isotope analyses. *Oecologia* 152, 179–189. <https://doi.org/10.1007/s00442-006-0630-x>

825 R Core Team, 2021. *R: A language and environment for statistical computing*. R Foundation for
826 Statistical Computing, Vienna, Austria.

827 Ratnasingham, S., Hebert, P.D.N., 2007. *bold: The Barcode of Life Data System*
828 (<http://www.barcodinglife.org>). *Mol. Ecol. Notes* 7, 355–364. [https://doi.org/10.1111/j.1471-](https://doi.org/10.1111/j.1471-8286.2007.01678.x)
829 [8286.2007.01678.x](https://doi.org/10.1111/j.1471-8286.2007.01678.x)

830 Schaafsma, F.L., Cherel, Y., Flores, H., van Franeker, J.A., Lea, M.-A., Raymond, B., van de Putte,
831 A.P., 2018. Review: the energetic value of zooplankton and nekton species of the Southern
832 Ocean. *Mar. Biol.* 165, 129. <https://doi.org/10.1007/s00227-018-3386-z>

833 Somerfield, P.J., Clarke, K.R., Gorley, R.N., 2021. Analysis of similarities (ANOSIM) for 2-way
834 layouts using a generalised ANOSIM statistic, with comparative notes on Permutational
835 Multivariate Analysis of Variance (PERMANOVA). *Austral Ecol.* 46, 911–926.
836 <https://doi.org/10.1111/aec.13059>

837 Soykan, C., Moore, J., Zydalis, R., Crowder, L., Safina, C., Lewison, R., 2008. Why study bycatch?
838 An introduction to the Theme Section on fisheries bycatch. *Endanger. Species Res.* 5, 91–
839 102. <https://doi.org/10.3354/esr00175>

840 Stehmann, M., Bürkel, D., 1990. Rajidae, in: Gon, O., Heemstra, P.C. (Eds.), *Fishes of the Southern*
841 *Ocean*. Grahamstown, South Africa, pp. 86–97.

842 Stevens, J., Bonfil, R., Dulvy, N.K., Walker, P.A., 2000. The effects of fishing on sharks, rays, and
843 chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES J. Mar. Sci.*
844 57, 476–494. <https://doi.org/10.1006/jmsc.2000.0724>

845 Stobutzki, I., Miller, M., Brewer, D., 2001. Sustainability of fishery bycatch: a process for assessing
846 highly diverse and numerous bycatch. *Environ. Conserv.* 28, 167–181.
847 <https://doi.org/10.1017/S0376892901000170>

848 Subramaniam, R.C., Corney, S.P., Melbourne-Thomas, J., Péron, C., Ziegler, P., Swadling, K.M.,
849 2022. Spatially explicit food web modelling to consider fisheries impacts and ecosystem
850 representation within Marine Protected Areas on the Kerguelen Plateau. *ICES J. Mar. Sci.* 79,
851 1327–1339. <https://doi.org/10.1093/icesjms/fsac056>

852 Subramaniam, R.C., Melbourne-Thomas, J., Corney, S.P., Alexander, K., Péron, C., Ziegler, P.,
853 Swadling, K.M., 2020. Time-Dynamic Food Web Modeling to Explore Environmental
854 Drivers of Ecosystem Change on the Kerguelen Plateau. *Front. Mar. Sci.* 7.

855 TAAF (2019) Arrêté n°2019-59 du 2 juillet 2019 sur le Plan de gestion 2019-2025 de la pêche de
856 la légine Australe *Dissostichus eleginoides* dans les zones économiques exclusives des îles
857 Kerguelen et de l’archipel de Crozet, in: *Journal officiel des Terres australes et antarctiques*
858 *françaises*. 83 : 9.

859 Troccoli, G.H., Aguilar, E., Martínez, P.A., Belleggia, M., 2020. The diet of the Patagonian toothfish
860 *Dissostichus eleginoides*, a deep-sea top predator off Southwest Atlantic Ocean. *Polar Biol.*
861 43, 1595–1604. <https://doi.org/10.1007/s00300-020-02730-2>

862 Tschopp, A., Cristiani, F., García, N.A., Crespo, E.A., Coscarella, M.A., 2020. Trophic niche
863 partitioning of five skate species of genus *Bathyraja* in northern and central Patagonia,
864 Argentina. *J. Fish Biol.* 97, 656–667. <https://doi.org/10.1111/jfb.14416>

865 Valls, M., Quetglas, A., Ordines, F., Moranta, J., 2011. Feeding ecology of demersal elasmobranchs
866 from the shelf and slope off the Balearic Sea (western Mediterranean). *Sci. Mar.* 75, 633–
867 639.

868 Ward, R.D., Zemplak, T.S., Innes, B.H., Last, P.R., Hebert, P.D.N., 2005. DNA barcoding Australia’s
869 fish species. *Philos. Trans. R. Soc. B Biol. Sci.* 360, 1847–1857.
870 <https://doi.org/10.1098/rstb.2005.1716>

871 Wetherbee, B.M., Cortés, E., 2004. Food consumption and feeding habits, in: Carrier, J.C., Musick,
872 J.A., Heithaus, M. (Eds.), *Biology of Sharks and Their Relatives*. Boca Raton, Fla, pp. 225–
873 246.

874 Williams, R., McEldowney, A., 1990. A guide to the fish otoliths from waters off the Australian
875 Antarctic Territory. Kingston (Australia) Antarctic Div.

876 Worm, B., Davis, B., Kettner, L., Ward-Paige, C.A., Chapman, D., Heithaus, M.R., Kessel, S.T.,
877 Gruber, S.H., 2013. Global catches, exploitation rates, and rebuilding options for sharks. *Mar.*
878 *Policy* 40, 194–204. <https://doi.org/10.1016/j.marpol.2012.12.034>

879 Xavier, J., Cherel, Y., 2021. *Cephalopod Beak Guide For The Southern Ocean: an update on*
880 *taxonomy*, British Antarctic Survey. ed. Cambridge.

881 Yang, G., Atkinson, A., Pakhomov, E.A., Hill, S.L., Racault, M.-F., 2022. Massive circumpolar
 882 biomass of Southern Ocean zooplankton: Implications for food web structure, carbon export,
 883 and marine spatial planning. *Limnol. Oceanogr.* n/a. <https://doi.org/10.1002/lno.12219>
 884 Ziegler, P.E., Burch, P., Peron, C., Welsford, D.C., Farmer, B.M., Yates, P.M., Potts, J.M.,
 885 Woodcock, E.J., Barnes, T.C., Duhamel, G., Gardner, C., 2021. Development of robust
 886 assessment methods and harvest strategies for spatially complex, multi-jurisdictional
 887 Toothfish fisheries in the Southern Ocean - Final Report.

888
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 905 Tables

906 Table 1. Mass (mean [min – max]) and composition of the food in stomach contents of
 907 *Bathyraja eatonii* and *B. irrasa* in Kerguelen waters.

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	<i>Bathyraja eatonii</i> (n = 90)	<i>Bathyraja irrasa</i> (n = 91)
Mass (g)	28.0 [0.3 – 330.2]	36.6 [1.1 -213.3]
Fresh prey items (g)	27.9 [0.2 – 330.2]	36.5 [0.1 -213.3]
Fish (g)	14.1 [0 – 330.2]	6.0 [0 – 87.9]
Cephalopods (g)	2.6 [0 – 179.1]	10.2 [0 – 213.3]
Crustaceans (g)	3.7 [0 – 26.4]	14.0 [0 – 89.6]
Worms (g)	0.03 [0 – 1.3]	0.9 [0 – 13.5]
Bait (g)	7.2 [0 – 71.9]	5.4 [0 – 53.5]
Accumulated cephalopods (n)	19	13

Accumulated fishes (n)	12	24
Overall composition by mass (all samples pooled):		
Fish (%)	68.1	19.4
Cephalopods (%)	12.8	32.7
Crustaceans (%)	18.1	44.9
Other organisms (%)	0.1	3.0

910
911
912
913
914

Table 2. Frequency of occurrence and numbers of prey items identified in stomach contents from all 90 samples of *Bathyraja eatonii* pooled and 91 samples of *B. irrasa* pooled, excluding secondary prey.

Species	<i>Bathyraja eatonii</i>								<i>Bathyraja irrasa</i>							
	Immature (M=1, F=3)				Mature (M=25, F=61)				Immature (M=24, F=22)				Mature (M=18, F=27)			
	Occurrence		Number		Occurrence		Number		Occurrence		Number		Occurrence		Number	
	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)
FISH	3	75.0	4	57.2	54	62.8	73	34.8	14	30.4	17	2.8	20	44.4	28	14.0
Pelagic fish																
Centrolophidae																
<i>Icichthys australis</i>	-	-	-	-	1	1.2	1	0.5	-	-	-	-	-	-	-	-
Gempylidae																
<i>Paradiplospinus gracilis</i>	-	-	-	-	2	2.3	2	1.0	1	2.2	1	0.2	2	4.4	2	1.0
Melamphidae																
<i>Poromitra atlantica</i>	-	-	-	-	1	1.2	1	0.5	1	2.2	1	0.2	1	2.2	1	0.5
Microstomatidae																
<i>Nansenia antarctica</i>	-	-	-	-	1	1.2	1	0.5	-	-	-	-	-	-	-	-
Myctophidae																
<i>Electrona carlsbergi</i>	-	-	-	-	2	2.3	2	1.0	3	6.5	3	0.5	2	4.4	3	1.5
<i>Gymnoscopelus bolini</i>	-	-	-	-	2	2.3	2	1.0	1	2.2	1	0.2	-	-	-	-
<i>Gymnoscopelus braueri</i>	-	-	-	-	-	-	-	-	1	2.2	1	0.2	-	-	-	-
<i>Gymnoscopelus hintonoides</i>	-	-	-	-	2	2.3	2	1.0	-	-	-	-	-	-	-	-
<i>Gymnoscopelus microlampas</i>	-	-	-	-	1	1.2	1	0.5	-	-	-	-	-	-	-	-
<i>Gymnoscopelus nicholsi</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	2.2	1	0.5
<i>Gymnoscopelus piabilis</i>	1	25.0	1	14.3	5	5.8	5	2.4	-	-	-	-	2	4.4	2	1.0
<i>Protomyctophum bolini</i>	-	-	-	-	1	1.2	1	0.5	-	-	-	-	1	2.2	1	0.5
Unidentified Myctophidae	-	-	-	-	1	1.2	1	0.5	-	-	-	-	-	-	-	-
Notosudidae																
<i>Luciosudis normani</i>	-	-	-	-	1	1.2	1	0.5	-	-	-	-	-	-	-	-
Paralepididae																
<i>Magnisudis prionosa</i>	1	25.0	1	14.3	1	1.2	2	1.0	1	2.2	1	0.2	3	6.67	3	1.5
Unidentified Paralepididae	-	-	-	-	10	11.6	12	5.7	1	2.2	1	0.2	-	-	-	-
Stomiidae																
<i>Borostomias antarcticus</i>	-	-	-	-	1	1.2	1	0.5	-	-	-	-	-	-	-	-
Unidentified Stomiidae	-	-	-	-	1	1.2	1	0.5	-	-	-	-	1	2.2	1	0.5

Benthic and demersal fish																				
Achiropsettidae																				
	Unidentified Achiropsettidae				-	-	-	-	1	1.2	1	0.5	-	-	-	-	-			
Bathyracidae																				
	<i>Bathyraco antarcticus</i>				-	-	-	-	2	2.3	3	1.4	-	-	-	-	-			
Liparidae																				
	<i>Paraliparis thalassobathyalis</i>				-	-	-	-	1	1.2	1	0.5	-	-	-	-	-			
	<i>Paraliparis</i> sp.				-	-	-	-	2	2.3	2	1.0	2	4.4	3	0.5	1	2.2	1	0.5
Moridae																				
	<i>Antimora rostrata</i>				-	-	-	-	2	2.3	2	1.0	1	2.2	1	0.2	1	2.2	1	0.5
	<i>Guttigadus kongi</i>				-	-	-	-	1	1.2	2	1.0	-	-	-	-	-	-	-	-
	Unidentified Moridae				-	-	-	-	1	1.2	1	0.5	-	-	-	-	-	-	-	-
Macrouridae																				
	<i>Coryphaenoides armatus</i>				-	-	-	-	-	-	-	-	-	-	-	-	1	2.2	1	0.5
	<i>Coryphaenoides ferrieri</i>				-	-	-	-	-	-	-	-	-	-	-	-	1	2.2	1	0.5
	<i>Macrourus carinatus</i>				-	-	-	-	1	1.2	1	0.5	-	-	-	-	3	6.7	3	1.5
	<i>Macrourus whitsoni</i>				-	-	-	-	1	1.2	1	0.5	-	-	-	-	-	-	-	-
Muraenolepididae																				
	<i>Muraenolepis marmoratus</i>				2	50.0	2	28.6	3	3.5	3	1.4	-	-	-	-	-	-	-	-
Nototheniidae																				
	<i>Lepidonotothen squamifrons</i>				-	-	-	-	-	-	-	-	-	-	-	-	1	2.2	1	0.5
Zoarcidae																				
	<i>Lycenchelys hureaui</i>				-	-	-	-	1	1.2	1	0.5	3	6.5	4	0.7	-	-	-	-
	<i>Lycodapus antarcticus</i>				-	-	-	-	3	3.5	3	1.4	-	-	-	-	-	-	-	-
	<i>Melanostigma gelatinosum</i>				-	-	-	-	1	1.2	1	0.5	-	-	-	-	1	2.2	1	0.5
	Unidentified fish				-	-	-	-	14	16.3	15	7.1	-	-	-	-	4	8.9	5	2.5
CEPHALOPODS																				
Squids																				
Brachioteuthidae																				
	<i>Slosarczykovia circumantarctica</i>				-	-	-	-	3	3.5	3	1.4	-	-	-	-	-	-	-	-
Cranchiidae																				
	<i>Taonius notalia</i>				-	-	-	-	-	-	-	-	1	2.2	1	0.2	-	-	-	-
Gonatidae																				
	<i>Gonatus antarcticus</i>				-	-	-	-	1	1.2	1	0.5	-	-	-	-	1	2.2	1	0.5

Onychoteuthidae																
<i>Filippovia knipovitchi</i>	-	-	-	-	2	2.3	2	1.0	1	2.2	1	0.2	1	2.2	1	0.5
<i>Moroteuthopsis longimana</i>	1	25.0	1	14.3	3	3.5	3	1.4	-	-	-	-	-	-	-	-
<i>Moroteuthopsis</i> sp. B (Imber)	-	-	-	-	1	1.2	1	0.5	-	-	-	-	-	-	-	-
Mastigoteuthidae																
<i>Mastigoteuthis psychrophila</i>	-	-	-	-	1	1.2	1	0.5	-	-	-	-	-	-	-	-
Octopus																
Octopodidae																
<i>Graneledone gonzalezi</i>	-	-	-	-	-	-	-	-	-	-	-	-	2	4.4	3	1.5
<i>Muusoctopus thielei</i>	-	-	-	-	1	1.2	1	0.5	-	-	-	-	5	11.1	5	2.5
<i>G. gonzalezi</i> / <i>M. thielei</i>	-	-	-	-	4	4.7	6	2.9	-	-	-	-	4	8.9	5	2.5
Opisthoteuthidae																
<i>Opisthoteuthis</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	1	2.2	1	0.5
Unidentified cephalopods	-	-	-	-	1	1.2	1	0.5	1	2.2	1	0.2	1	2.2	1	0.5
CRUSTACEANS	1	25.0	2	28.6	55	64.0	113	53.8	43	93.5	425	71.2	38	84.4	123	61.5
Pelagic crustaceans																
Amphipoda																
<i>Pegohyperia princeps</i>	-	-	-	-	1	1.2	1	0.5	-	-	-	-	-	-	-	-
Caridea																
<i>Campylonotus capensis</i>	-	-	-	-	9	10.5	14	6.7	1	2.2	1	0.2	1	2.2	2	1.0
<i>Chorismus antarcticus</i>	-	-	-	-	1	1.2	1	0.5	-	-	-	-	-	-	-	-
<i>Chorismus tuberculatus</i>	-	-	-	-	1	1.2	1	0.5	-	-	-	-	-	-	-	-
<i>Nematocarcinus romenskyi</i>	-	-	-	-	2	2.3	2	1.0	2	4.4	2	0.3	4	8.9	4	2.0
<i>Nematocarcinus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	1	2.2	1	0.5
<i>Pasiphaea ledoyeri</i>	-	-	-	-	4	4.7	5	2.4	1	2.2	1	0.2	3	6.7	3	1.5
<i>Pasiphaea rathbunae</i>	-	-	-	-	3	3.5	3	1.4	1	2.2	1	0.2	2	4.4	2	1.0
<i>Pasiphaea scotiae</i>	-	-	-	-	-	-	-	-	-	-	-	-	2	4.4	2	1.0
<i>Pasiphaea</i> sp.	-	-	-	-	3	3.5	3	1.4	-	-	-	-	1	2.2	1	0.5
Unidentified Natantia	-	-	-	-	1	1.2	1	0.5	-	-	-	-	1	2.2	1	0.5
Lophogastrida																
<i>Neognathophausia gigas</i>	-	-	-	-	-	-	-	-	1	2.2	1	0.2	1	2.2	1	0.5
Benthic crustaceans																
Anomura																
<i>Paralomis</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	1	2.2	1	0.5

Isopoda																	
	<i>Brucerolis bromleyana</i>	-	-	-	-	2	2.4	2	1.0	32	69.6	210	35.2	15	33.3	51	25.5
	<i>Ceratoserolis trilobitoides</i>	1	25.0	2	28.6	25	29.1	63	30.0	7	15.2	46	7.7	2	4.4	2	1.0
	<i>Sursumura</i> sp.	-	-	-	-	-	-	-	-	26	56.5	125	20.9	3	6.7	3	1.5
	Unidentified Isopoda	-	-	-	-	1	1.2	1	0.5	2	4.4	14	2.4	3	6.7	4	2.0
Reptantia																	
	<i>Thymopides grobovi</i>	-	-	-	-	2	2.3	2	1.0	8	17.4	12	2.0	26	57.8	38	19.0
	Unidentified crustaceans	-	-	-	-	13	15.1	14	6.7	9	19.6	12	2.0	7	15.6	7	3.5
WORMS		-	-	-	-	3	3.5	5	2.4	39	84.8	152	25.5	18	40.0	32	16.0
Polychaeta																	
	Unidentified Nephtyidae	-	-	-	-	-	-	-	-	22	47.8	52	8.7	9	20.0	11	5.5
	Unidentified Nereidae	-	-	-	-	-	-	-	-	2	4.4	2	0.3	-	-	-	-
	Unidentified Polynoidae	-	-	-	-	3	3.5	5	2.4	33	71.7	81	13.6	13	28.9	18	9.0
	Unidentified Polychaeta	-	-	-	-	-	-	-	-	4	8.7	9	1.5	1	2.2	1	0.5
Priapulida																	
	<i>Priapulus tuberculaspinosus</i>	-	-	-	-	-	-	-	-	6	13.0	8	1.3	1	2.2	2	1.0
TOTAL		-	-	7	100	-	-	210	100	-	-	597	100	-	-	200	100

Table 3. Sample size (n) and mean (\pm standard deviation) of muscle isotopic values of *Bathyrāja eatonii* and *B. irrasa* for immature, mature and all individuals sampled.

Species	Groups	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C : N
<i>Bathyrāja eatonii</i>	males	34	-19.02 \pm 0.48	11.22 \pm 0.77	3.18 \pm 0.04
	females	35	-19.13 \pm 0.66	11.01 \pm 0.91	3.17 \pm 0.04
	immature	4	-19.60 \pm 0.55	9.93 \pm 0.50	3.15 \pm 0.02
	mature	65	-19.04 \pm 0.57	11.19 \pm 0.81	3.18 \pm 0.05
	all	69	-19.07 \pm 0.58	11.12 \pm 0.85	3.18 \pm 0.04
<i>Bathyrāja irrasa</i>	males	32	-19.29 \pm 0.89	12.26 \pm 0.73	3.19 \pm 0.06
	females	40	-19.15 \pm 0.80	12.30 \pm 0.80	3.20 \pm 0.07
	immature	33	-19.50 \pm 0.85	12.16 \pm 0.87	3.19 \pm 0.07
	mature	39	-18.96 \pm 0.76	12.38 \pm 0.66	3.20 \pm 0.06
	all	72	-19.21 \pm 0.84	12.28 \pm 0.77	3.20 \pm 0.06

Table 4. Statistical results for isotopic differences between species and within species depending on sex and maturity for *Bathyrāja eatonii* and *B. irrasa*. Student's t-test (t-test_{df}) was used when test assumptions were met; otherwise Mann-Whitney (U-test) was used. Significant results are indicated in bold, $p < 0.05$.

	Groups	Statistic		p-value
		$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	
	Species	$\delta^{13}\text{C}$	U-test = 2899	$p > 0.08$
		$\delta^{15}\text{N}$	U-test = 764	$p < 0.005$
<i>Bathyrāja eatonii</i>	Sex	$\delta^{13}\text{C}$	t-test ₆₇ = -0.78	$p > 0.4$
		$\delta^{15}\text{N}$	t-test ₆₇ = -0.99	$p > 0.3$
	Maturity	$\delta^{13}\text{C}$	U-test = 74	$p > 0.15$
		$\delta^{15}\text{N}$	t-test₆₇ = -3.07	$p < 0.004$
<i>Bathyrāja irrasa</i>	Sex	$\delta^{13}\text{C}$	U-test = 732	$p > 0.3$
		$\delta^{15}\text{N}$	U-test = 651	$p > 0.9$
	Maturity	$\delta^{13}\text{C}$	U-test = 365	$p < 0.002$
		$\delta^{15}\text{N}$	U-test = 557	$p > 0.3$

Table A.1. Primers used for the amplification and sequencing of the COI gene.

Primers	Sequences (5'-3')	References
TelF1	TCGACT AATCAYAAAGAYATYGGCAC	Dettai et al., 2011
TelR1	ACTTCTGGGTGNCC AAARAATCARAA	Dettai et al., 2011
FishF1	TCAACCAACCACAAAGACATTGGCAC	Ward et al., 2005
FishR1	TAGACTTCTGGGTGGCCAAAGAATCA	Ward et al., 2005
mICOLintF1	GGWACWGGWTGAACWGTWTAYCCYCC	Leray et al., 2013
DgHCO2198	TAAACTTCAGGGTGACCAAARAYCA	Leray et al., 2013

Table A.2. Frequency of occurrence and numbers of incidentally ingested prey items (including secondary prey items, indicated by an asterisk (*)) identified from stomach contents for all 90 samples of *Bathyrāja eatonii* pooled and 91 samples of *B. irrása* pooled.

	<i>Bathyrāja eatonii</i>								<i>Bathyrāja irrása</i>							
	Immature (M=1, F=3)				Mature (M=25, F=61)				Immature (M=24, F=22)				Mature (M=18, F=27)			
	Occurrence		Number		Occurrence		Number		Occurrence		Number		Occurrence		Number	
	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)
CRUSTACEANS																
Amphipoda																
<i>Gammaridea</i> spp.*	-	-	-	-	1	1,14	1	0,39	12	26,09	29	4,49	2	4,44	2	0,96
<i>Themisto gaudichaudii</i> *	-	-	-	-	4	4,55	6	2,36	-	-	-	-	-	-	-	-
Unidentified Amphipoda*	-	-	-	-	1	1,14	1	0,39	2	4,35	5	0,77	-	-	-	-
Copepoda																
<i>Paraeuchaeta</i> sp.*	-	-	-	-	-	-	-	-	2	4,35	2	0,31	-	-	-	-
Unidentified Pennellidae	-	-	-	-	-	-	-	-	-	-	-	-	1	2,22	1	0,48
Euphausiacea																
<i>Euphausia triacantha</i> *	-	-	-	-	9	10,23	13	5,12	2	4,35	3	0,46	3	6,67	3	1,44
<i>Euphausia vallentini</i> *	-	-	-	-	-	-	-	-	1	2,17	1	0,15	-	-	-	-
<i>Euphausia</i> sp.*	-	-	-	-	6	2,82	6	2,36	-	-	-	-	-	-	-	-
Isopoda																
Unidentified Flabellifera	-	-	-	-	2	2,27	2	0,79	4	8,70	4	0,62	1	2,22	1	0,48
Unidentified Gnathiidae	-	-	-	-	-	-	-	-	-	-	-	-	1	2,22	1	0,48
Mysida																
Unidentified Mysidacea *	-	-	-	-	10	11,36	16	6,30	5	10,87	5	0,77	1	2,22	1	0,48