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Habitat degradation increases interspecific trophic competition between three spiny lobsters in Seychelles

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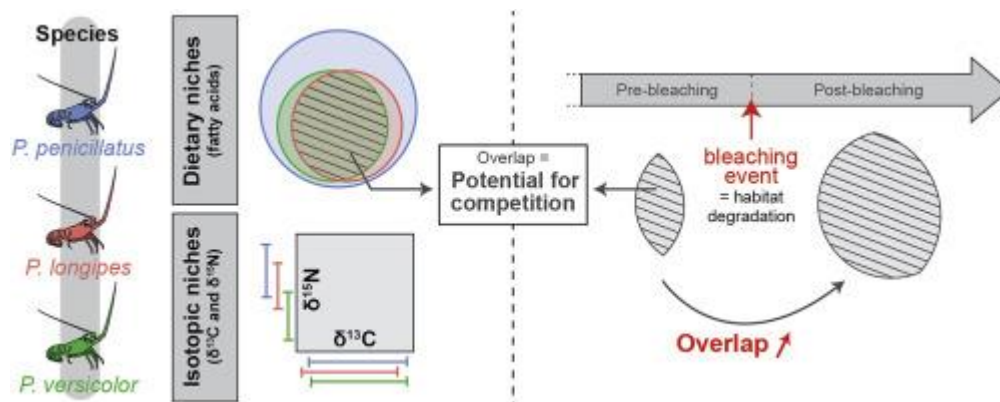
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Abstract :

Spiny lobsters (*P. penicillatus*, *P. longipes* and *P. versicolor*) are heavily dependent on habitats like coral reefs, known to be highly vulnerable to climate change-driven degradation. Yet, little is known about their trophic ecology and their adaptive capacity to a changing environment. In this study, we used fatty acids (FA) analysed in the hepatopancreas and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes analysed in tail muscle of three spiny lobster species from Seychelles coastal waters to (1) infer habitat usage, dietary patterns and potential for resource competition and (2) investigate the effects of reef type and coral bleaching on their trophic niche metrics. We found that there was a potential for interspecific competition between the three species, shown by their high dietary overlap (FA niche overlap ranging from 71.2% to 99.5% for *P. longipes* and *P. versicolor* in *P. penicillatus*) and similar habitat use ($\delta^{13}\text{C}$ value ranges). *P. penicillatus* was more a generalist than the two other species (i.e., had larger FA niche) and *P. versicolor* seemed to feed on smaller/earlier life stage prey than *P. longipes* (based on differences in $\delta^{15}\text{N}$ values), possibly allowing for their coexistence. The potential for resource competition of Seychelles spiny lobsters appeared higher in granite than carbonate reefs and in post-2016 coral bleaching reefs. Our results suggest that *P. penicillatus* could have a greater adaptive capacity to climate change due to its higher dietary plasticity and that competition between Seychelles spiny lobsters may increase in the future as the frequency and severity of bleaching events is predicted to increase with climate change.

Graphical abstract



Highlights

► We use trophic niche overlap to identify the potential for resource competition. ► There is a potential for resource competition between three spiny lobsters species. ► The largest species had the most diverse diet and the highest $\delta^{15}\text{N}$ values. ► Potential for competition was higher in the less vulnerable reef habitat type. ► Potential for competition seemed to increase following a coral bleaching event.

Keywords : Resource partitioning, Climate change, Coral bleaching, Decapod crustaceans, Benthic predators, Western Indian Ocean

43 1. Introduction

44 The stability, resilience and productivity of high-value marine invertebrate populations
45 are heavily dependent on prey and habitat quality (Österblom et al. 2008). Accurately
46 identifying the habitat use and trophic niche of such species is thus of great importance to
47 better understand stock dynamics. Sympatric species, sharing similar ecological needs such as
48 habitat and food preferences, are interesting case studies as their population dynamics may
49 also be influenced by interspecific interactions (Mason et al. 2011). Sympatric consumers are
50 thought to co-exist stably when resources are sufficient (Carvalho and Davoren 2020) while
51 possibly displaying high levels of interspecific competition when resource supply is limited
52 (Nie et al. 2019). Identifying and quantifying interspecific diet and habitat-niche relationships
53 are therefore key objectives to understand sympatric species' resource partitioning and
54 characterise their potential for competition (Costa-Pereira et al. 2019).

55 Spiny lobsters provide an important economic resource in different areas of the world
56 (Phillips 2013). In the Seychelles (Western Indian Ocean), catches mainly include *Panulirus*
57 *penicillatus* (pronghorn spiny lobster), *P. longipes* (longlegged spiny lobster) and *P.*
58 *versicolor* (painted spiny lobster) (Seychelles Fishing Authority 2016). Despite management
59 policies in place, stocks have remained unstable, with unpredictable catch variability from one
60 fishing season to another (e.g., 30.1 kg by fishing trip during the 1994/1995 fishing season vs
61 10.1 kg by fishing trip during the 2012/2013 fishing season) (Seychelles Fishing Authority
62 2016). In an attempt to sustainably manage the fishery, seasonal closures are implemented to
63 allow stocks to recover (e.g., 2017/2018 and 2018/2019 fishing seasons) (Seychelles Fishing
64 Authority 2018).

65 Habitat quality, including the type and complexity of coverage, is fundamentally
66 important for spiny lobsters in respects to their foraging and antipredation strategies (Holthuis
67 1991; MacArthur et al. 2011). Spiny lobsters are non-gregarious nocturnal species that are

68 found mainly in coastal environments, such as coral and rocky reefs, where they usually use
69 the crevices to hide from predators during the day, while they leave their den at dusk to feed
70 and mate during the night (Holthuis 1991). However, coastal reefs are under high human
71 pressure in the Seychelles due to increasing coastal development and global climate change
72 (Khan and Amelie 2015). In the last 25 years, coral reef habitats and granitic reefs supporting
73 encrusting corals have been degraded through multiple bleaching events, with the 2016
74 bleaching event affecting around 50% of hard corals in the Seychelles (Obura et al. 2017). As
75 spiny lobsters are generalist feeders, their diet composition is thought to be highly dependent
76 on prey availability, depending on their habitat characteristics (Blamey et al. 2019). A
77 modification of prey and habitat quality and availability through habitat degradation could
78 thus have altered spiny lobsters' diet and level of interspecific competition, further
79 influencing stock dynamics. Yet, there is a lack of knowledge on spiny lobsters' foraging
80 behaviour in the Western Indian Ocean, particularly in the Seychelles region, and on their
81 adaptive capacity to habitat change.

82 Trophic ecology of marine species can be studied through the use of ecological tracers
83 like stable isotopes (SI) of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) and fatty acid (FA) trophic
84 markers. $\delta^{13}\text{C}$ allows for the identification of primary production sources while $\delta^{15}\text{N}$ gives
85 information about the trophic position of an organism (Post 2002). The FA profiles observed
86 in the digestive tissues of a consumer reflect the FA composition of ingested prey and thus
87 can give insights into the consumer's diet (Iverson 2009). By studying spatial and temporal
88 changes in the biochemical composition of consumers, it is possible to examine intraspecific
89 and interspecific variations in their trophic ecology. For this, trophic niches inferred from SI
90 or FA data are particularly useful as their metrics (i.e., niche size and probability of niche
91 overlap) give both intra- and interspecific information. Typically, a species' niche size can be
92 used as a proxy for the diversity of biochemically distinct prey eaten by this species (i.e.,

93 intraspecific variability), while the probability of overlap between two species gives
94 indications on the degree of similarity of the biochemical composition of their prey (i.e.,
95 interspecific variability) (Costa-Pereira et al. 2019). Many studies successfully combined SI
96 and FA to study trophic overlap between co-occurring species (e.g., Connan et al. 2014;
97 Sardenne et al. 2016; Brewster et al. 2017).

98 Our study assessed the FA and SI composition of three species of spiny lobsters from the
99 Seychelles coastal waters with the main aim to examine interspecific differences and spatial-
100 temporal patterns in their habitat use, dietary inferences and trophic niche metrics. A
101 particular focus was to examine the effects of habitat type and habitat degradation through
102 coral bleaching on the potential for resource competition (i.e., dietary overlap) between the
103 three species.

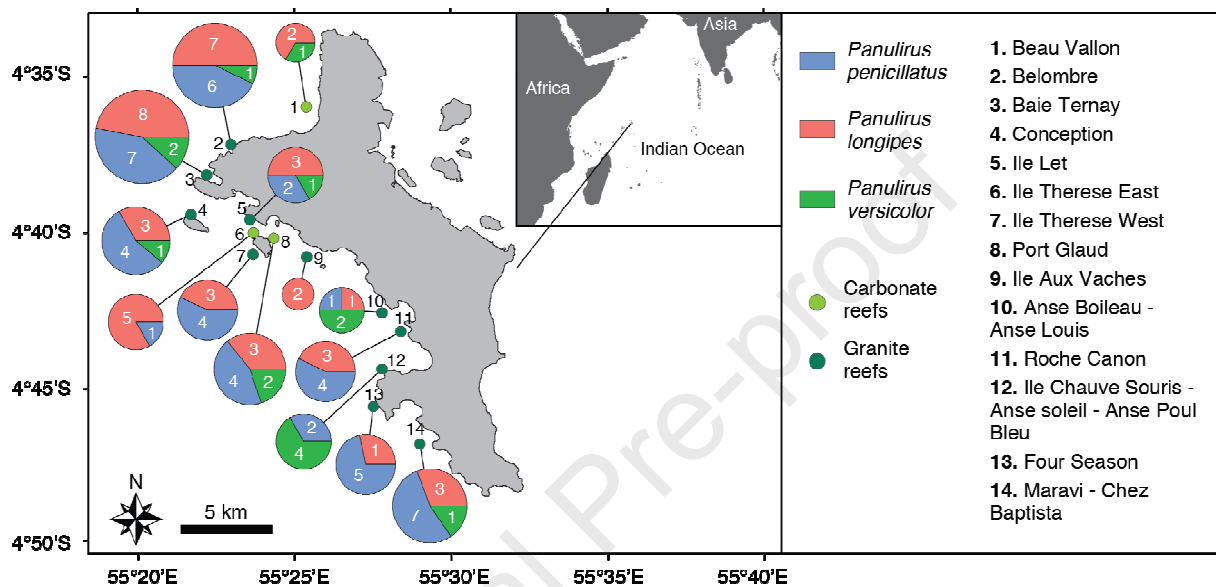
104

105 **2. Material and methods**

106 **2.1. Study area and sample collection**

107 *Panulirus penicillatus*, *P. longipes* and *P. versicolor* were sampled as part of the annual
108 Participatory Lobster Monitoring Program led by the Seychelles Fishing Authority (SFA) in
109 collaboration with local fishers (Seychelles Fishing Authority 2014). A total of 105 spiny
110 lobsters (47 *P. penicillatus*, 43 *P. longipes* and 15 *P. versicolor*), were caught in several
111 fishing areas on the west coast of the island of Mahé, Seychelles, during five sampling
112 campaigns in October/November from 2014 to 2018 (Fig. 1). The spiny lobsters were caught
113 at dusk, when they leave reef crevices and thus are the most catchable, using snorkel gear and
114 flashlights. The date, GPS location and carapace length (to the nearest 0.1 cm) were recorded
115 for each individual. Finally, a piece of tail muscle and the hepatopancreas were retrieved,
116 stored in amber glass at -20°C for a maximum of eight days before being transferred to -80 °C
117 in the SFA Research laboratory. Hepatopancreas tissue samples remained at -80°C for FA

118 analysis, and tail muscle tissues were freeze-dried over 72 hr and stored in a dry environment
 119 for SI analysis. Detailed numbers of the spiny lobsters' tissues sampled and analysed for FA
 120 and SI tracers across years and different habitat types (carbonate and granite reefs) are given
 121 in the supplementary material (Table S1).



122
 123 **Fig. 1** Locations of the three species of spiny lobster caught from the west coast of Mahé
 124 (Seychelles, Western Indian Ocean) during 2014-2018. The number of individuals caught per
 125 species is indicated in the corresponding chart; size of charts is proportional to the total
 126 number of spiny lobsters per site.

127

128 2.2. Fatty acid analyses

129 A total of 64 hepatopancreas samples were analysed for FA at the LIPIDOCEAN
 130 platform of the LEMAR (France). Lipids were extracted from around 200 mg of wet tissue
 131 using 6 mL of chloroform:methanol (2:1 v/v) in glass vials. Samples were then vortexed,
 132 sonicated in an ultrasonic bath for 15 min and stored at -20 °C (maximum 24h). Fatty acid
 133 methyl ester (FAME) were prepared using 1 mL of lipid extract in which 20 µL of an internal

134 standard (tricosanoic acid, C23:0, 0.115 $\mu\text{g}/\mu\text{L}$) was added to allow FA quantification.
135 Samples were then trans-esterified with 800 μL of methanolic sulphuric acid (3.4% v/v) at
136 100 $^{\circ}\text{C}$ for 10 min. After cooling, formed FAMES were retrieved by adding 800 μL of hexane
137 and washed with hexane-saturated distilled water (1.5 mL). Prepared FAMES were separated
138 using a gas chromatograph (Varian CP3800) with auto-sampler equipped with both polar and
139 non-polar capillary columns (ZB-WAX, 30 m length x 0.25 mm i.d. x 0.25 μm film thickness,
140 Phenomenex; and ZB-5 30 m length x 0.25 mm i.d. x 0.25 μm film thickness, Phenomenex), a
141 splitless injector and a flame ionization detector. Oven temperature was raised to 150 $^{\circ}\text{C}$ at 50
142 $^{\circ}\text{C}/\text{min}$, then to 170 $^{\circ}\text{C}$ at 3.5 $^{\circ}\text{C}/\text{min}$, to 185 $^{\circ}\text{C}$ at 1.5 $^{\circ}\text{C}/\text{min}$, to 225 $^{\circ}\text{C}$ at 2.4 $^{\circ}\text{C}/\text{min}$, and
143 finally to 250 $^{\circ}\text{C}$ at 5.5 $^{\circ}\text{C}/\text{min}$. The identification of FAME was carried out by comparison of
144 retention times with four commercially available standards (37-components, BAME, PUFA
145 no. 1, and PUFA no. 3 FAME mix; Supelco). The concentration for each FA was converted
146 from the area of chromatogram peaks by using the C23:0 peak area as reference. The
147 analytical variability (mean CV) was 8.1 %, calculated using Supelco 37-component FAME
148 mix.

149 FAs were labelled according to their traditional C:Xn-Y nomenclature where C is the
150 number of carbons, X is the number of double bonds, and Y is the position the first double
151 bond from the terminal methyl end of the molecule. In non-methyl interrupted (NMI) FA,
152 double bonds are not separated by only one methyl group, thus they are labelled as C:X NMI
153 (n), where C is the number of carbons, X the number of double bonds and n the position(s) of
154 the double bonds from the terminal methyl end of the molecule. FAs were expressed as
155 percentage of total FA (% TFA), and means are presented with their standard error (mean \pm
156 SE).

157

158 **2.3. Stable isotope analyses**

159 A total of 105 tail muscle samples were analysed for SI of carbon and nitrogen at the
160 LIENSs laboratory (France). As Seychelles spiny lobsters have low total fat content (mean of
161 $0.74 \pm 0.14\%$ wet weight, measured for five *P. penicillatus* and five *P. longipes* in this study),
162 no lipid removal before SI analysis or no lipid correction on isotopic data were applied.
163 Samples were ground to powder and aliquots of 0.3-0.5 mg were placed in tin capsules.
164 Carbon and nitrogen ratios were determined with a continuous-flow mass spectrometer
165 Thermo Scientific Delta V Advantage coupled to an elemental analyser Thermo Scientific
166 Flash 2000. Measurements of international isotopic standards of known $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were
167 conducted: USGS-61 and USGS-62. Results are expressed in the δ unit notation as deviations
168 from standards (Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$)
169 following the formula: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R is $^{13}\text{C}/^{12}\text{C}$ or
170 $^{15}\text{N}/^{14}\text{N}$, respectively. Measurement errors (SD) of SI, calculated on all measured values of
171 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in isotopic reference materials, were $< 0.10 \text{ ‰}$ for both the nitrogen and carbon
172 isotope measurements. For each sample, the C:N ratio never exceeded 3.5 confirming that
173 there was no need for lipid normalisation on spiny lobsters' carbon stable isotope values (Post
174 et al. 2007).

175

176 **2.4. Statistics**

177 All statistical tests and data analyses were performed using R 3.5.2 software (R Core
178 Team 2018).

179 Prior to any univariate analysis, data were tested for normality and homoscedasticity.
180 An analysis of variance (ANOVA) or a Kruskal-Wallis test was used to compare carapace
181 lengths and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between species. When a difference was significant ($P <$
182 0.05), a post-hoc test was performed (Tukey's HSD after ANOVA and Dunn test with

183 Benjamini-Hochberg adjustment after Kruskal-Wallis). ANOVA, Kruskal-Wallis and Tukey's
184 HSD were computed using the included *stats* package in R, while Dunn post-hoc test was
185 computed using the *FSA* R package.

186 To compare trophic niches between species, FA and SI niches were computed and their
187 sizes and overlaps were calculated using the *nicheROVER* R package (see Swanson et al.
188 2015 for details on the method). This package uses a model developed in a Bayesian
189 framework to calculate probabilistic niche metrics (i.e., niche size and probabilities of
190 overlap) as opposed to the more traditional geometric-based computations. This method is
191 insensitive to sample size and can account for statistical uncertainty. FA and SI niches were
192 computed separately, and niche metrics were calculated using 1000 iterations of ellipses.
193 More specifically, niche overlaps were expressed in percentage of the niche of each species
194 and represent the probability of species A being found in the niche of species B. As FA
195 profiles contained a high number of dimensions (i.e., 23 FAs above trace levels, > 0.8%
196 TFA), non-metric multidimensional scaling (nMDS) ordinations using a Bray-Curtis
197 dissimilarity matrix were first generated using the *metaMDS* function from the R *vegan*
198 package. Then, nMDS coordinates of dimensions 1 and 2 were used to compute FA niches.
199 For SI, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were used to calculate isotopic niches. For visual
200 representation, mean ellipses coordinates were calculated using the mean coordinates of the
201 1000 ellipses from the Bayesian model. For representation of statistical uncertainty,
202 coordinates of the ellipses for the confidence interval at 95% (CI95% ellipses) were also
203 calculated using the mean coordinates of the 2.5% smallest ellipses, and the 2.5% largest
204 ellipses.

205 To identify potential prey implicated in interspecific trophic overlap and in trophic
206 segregation, we used well known FA trophic markers, including trophic markers of bacteria
207 (iso-branched FA and 18:1n-7), microalgae (16:1n-7, 20:5n-3 and 22:6n-3), macroalgae

208 (18:1n-9, 18:2n-6, 20:4n-6, 20:5n-3 and 22:6n-3) and bivalve molluscs and carnivorous
209 gastropods (NMI FAs and dimethyl acetal – DMA) (Budge et al. 2006; Meyer et al. 2019). As
210 some given trophic markers can originate from different prey types (Meyer et al. 2019), we
211 used parametric (Pearson) and non-parametric (Kendall) correlation tests on SI and FA
212 trophic markers to discriminate between potential prey origins. Correlation plots for each
213 species were computed using the *corrplot* R package (Fig. S1).

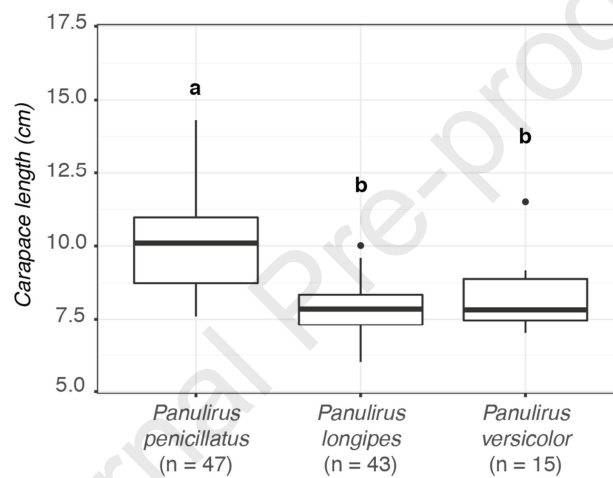
214 The effects of reef habitat type (carbonate *vs* granite) and habitat degradation (i.e.,
215 before and after coral bleaching event) on spiny lobsters' trophic ecology was investigated
216 using SI niche metrics. For this, isotopic niche sizes and overlaps were compared between
217 lobsters caught on carbonate and granite reefs for the three species, and between the pre- (i.e.,
218 2014-2015) and post-2016 bleaching event periods (i.e., 2016-2018) between *P. penicillatus*
219 and *P. longipes* only (due to low sample sizes for *P. versicolor*). Regarding FA niches, the
220 number of available data only allowed for the comparison of niche sizes and overlaps between
221 sampling years following the 2016 bleaching event (i.e., 2016, 2017 and 2018), for *P.*
222 *penicillatus* and *P. longipes* only.

223 Finally, we used associated probability to compare niche metrics between species or
224 among factors (i.e., reef habitat type, time period of reef degradation and sampling year
225 during the post-bleaching period). For each iteration of the model, we gave a value of 1 if one
226 niche metric value was greater than the other, 0 if not. The mean value calculated for the 1000
227 iterations represented the probability that one metric value was greater than the other. A
228 probability > 0.95 would be associated with a high certainty.

229

230 **3. Results**231 **3.1. Size of sampled spiny lobsters**

232 Over the sampling period, *P. penicillatus* was significantly larger than the two other
 233 species (Dunn test, $Z = -5.21$, $P < 0.001$ with *P. longipes*; $Z = 3.37$, $P = 0.001$ for *P.*
 234 *versicolor*) (Fig. 2). There was no significant difference in carapace length between *P.*
 235 *longipes* and *P. versicolor* ($P > 0.05$). For each species, there was no significant difference in
 236 carapace length over the sampling years ($P > 0.05$).



237 **Fig. 2** Carapace length (cm) of sampled spiny lobsters according to the species. A different
 238 letter indicates a significant difference ($P < 0.05$).

239

240 **3.2. Fatty acid niches**

241 For all three species, FA profiles in the hepatopancreas were characterized by
 242 dominance of the polyunsaturated FAs, followed by saturated FAs then monounsaturated FAs
 243 (Table 1). Among polyunsaturated FAs, 20:4n-6 was the dominant FA, with low proportions
 244 of 20:5n-3 and 22:6n-3. Monounsaturated FAs were dominated by 18:1n-9 and saturated FAs
 245 were dominated by 16:0 and 18:0.

246 *Panulirus penicillatus* had the lowest mean 20:4n-6 proportion (Tukey's HSD, $P <$
 247 0.001) but the highest mean proportion of 18:1n-9 (Dunn test, $P < 0.001$ with *P. versicolor*; P

248 = 0.03 with *P. longipes*) (Table 1). This species also had a higher mean 20:1n-7 proportion
 249 than *P. versicolor* (Dunn test, $P = 0.03$) and a higher mean 20:1n-9 proportion than *P.*
 250 *longipes* (Dunn test, $P < 0.001$). Concerning NMI FA, *P. penicillatus* had a higher 22:2 NMI
 251 (7,13) mean proportion than *P. longipes* (Tukey's HSD, $P = 0.02$) and the lowest 22:2 NMI
 252 (7,15) mean proportion (Dunn test, $P = 0.02$).

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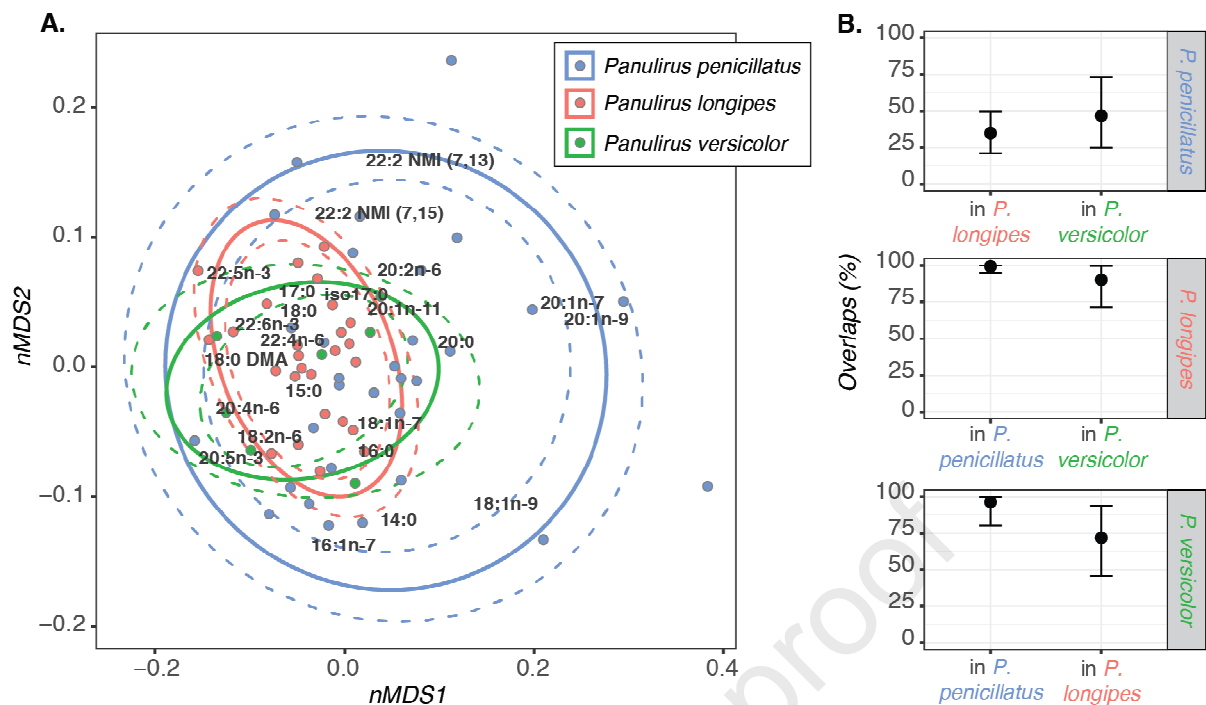
254 **Table 1** Fatty acid (FA) profiles analysed in the hepatopancreas of *Panulirus penicillatus*, *P.*
 255 *longipes* and *P. versicolor* across all sampling sites and time periods expressed as % of total
 256 FA and presented as mean \pm SE. The category "other" refers to the sum of FA compounds
 257 detected below trace level ($< 0.8\%$). Different letters indicate significant difference (Tukey's
 258 HSD or Dunn post-hoc tests). Σ SFA = sum of saturated FA, Σ MUFA = sum of
 259 monounsaturated FA, Σ PUFA = sum of polyunsaturated FA, NMI = non-methyl interrupted,
 260 DMA = dimethyl acetal.

Fatty acid	<i>P. penicillatus</i> (n = 31)	<i>P. longipes</i> (n = 27)	<i>P. versicolor</i> (n = 7)
<i>Saturated</i>			
14:0	2.5 \pm 0.3	2.2 \pm 0.1	1.8 \pm 0.2
15:0	1.1 \pm 0.1	1.16 \pm 0.04	1.2 \pm 0.1
16:0	17.4 \pm 0.4	17.0 \pm 0.4	17.6 \pm 0.8
17:0	1.6 \pm 0.1 ^b	2.0 \pm 0.1 ^a	1.4 \pm 0.1 ^b
18:0	9.9 \pm 0.2 ^{ab}	11.4 \pm 0.4 ^a	9.5 \pm 0.5 ^b
20:0	1.2 \pm 0.1 ^a	1.01 \pm 0.04 ^{ab}	0.8 \pm 0.1 ^b
Σ SFA	31.7 \pm 0.5	36.2 \pm 0.5	30.8 \pm 1.0
<i>Monounsaturated</i>			
16:1n-7	4.4 \pm 0.2	4.5 \pm 0.2	4.4 \pm 0.3
18:1n-7	3.6 \pm 0.1	3.5 \pm 0.1	3.7 \pm 0.1
18:1n-9	10.5 \pm 0.6 ^a	7.4 \pm 0.3 ^b	7.6 \pm 0.7 ^b
20:1n-7	1.0 \pm 0.1 ^a	0.69 \pm 0.03 ^{ab}	0.7 \pm 0.1 ^b
20:1n-9	1.3 \pm 0.1 ^a	0.66 \pm 0.02 ^b	1.0 \pm 0.1 ^a
20:1n-11	2.8 \pm 0.2	2.94 \pm 0.13	2.4 \pm 0.3
Σ MUFA	24.4 \pm 0.6 ^a	20.5 \pm 0.4 ^b	20.4 \pm 1.0 ^b
<i>Polyunsaturated</i>			
18:2n-6	1.29 \pm 0.04 ^b	1.5 \pm 0.1 ^a	1.5 \pm 0.1 ^{ab}
20:2n-6	1.3 \pm 0.1	1.18 \pm 0.03	1.24 \pm 0.03
20:4n-6	8.5 \pm 0.3 ^b	10.9 \pm 0.3 ^a	11.3 \pm 0.9 ^a
20:5n-3	7.1 \pm 0.4	7.6 \pm 0.3	7.8 \pm 0.5

22:4n-6	1.8 ± 0.1	1.8 ± 0.1	2.3 ± 0.3
22:5n-3	2.2 ± 0.1	2.5 ± 0.1	2.7 ± 0.1
22:6n-3	4.3 ± 0.4	4.0 ± 0.2	4.1 ± 0.4
Σ PUFA	38.2 ± 0.8 ^b	40.5 ± 0.8 ^{ab}	42.6 ± 1.5 ^a
<i>Branched FA, NMI FA and DMA</i>			
iso17:0	0.83 ± 0.04 ^b	1.01 ± 0.03 ^a	0.8 ± 0.1 ^{ab}
22:2 NMI (7,13)	1.5 ± 0.1 ^a	1.1 ± 0.1 ^b	1.2 ± 0.2 ^{ab}
22:2 NMI (7,15)	0.74 ± 0.05 ^b	0.86 ± 0.04 ^a	1.2 ± 0.2 ^a
18:0DMA	2.3 ± 0.1	2.4 ± 0.1	2.5 ± 0.3
Other ¹	11.0 ± 0.3	10.8 ± 0.2	11.3 ± 0.2

261 ¹ Includes the SFA 19:0, 21:0, 22:0, 24:0, the MUFA 16:1n-5, 16:1n-9, 17:1n-7, 18:1n-5, 18:1n-11, 22:1n-7,
 262 22:1n-9, 22:1n-11, 24:1n-9, the PUFA 16:2n-4, 16:3n-4, 16:3n-6, 16:4n-3, 18:3n-3, 18:3n-4, 18:3n-6, 18:4n-3,
 263 20:3n-3, 20:3n-6, 20:4n-3, 22:6n-3, the branched FA iso15:0, ante15:0, iso16:0, the NMI FA 20:2 NMI (5,11),
 264 20:2 NMI (5,13), 22:3 NMI (7,13,16) and the DMA 16:1n-7DMA, 16:0DMA.
 265

266 *Panulirus penicillatus* displayed the largest FA niche (niche size of 0.18 [CI95%: 0.13 –
 267 0.27]; associated probability of 1) with little-to-no overlap in CI with the other two species,
 268 while *P. longipes* and *P. versicolor* displayed similar niche sizes (0.04 [0.03 – 0.05] and 0.06
 269 [0.03 – 0.13] respectively) (Fig. 3A). *P. penicillatus* was separated from the two other species
 270 by monounsaturated FA such as 18:1n-9, 20:1n-7 and 20:1n-9, and by the NMI FA 22:2 NMI
 271 (7,13) and 22:2 NMI (7,15) (Fig. 3A). Both *P. longipes* and *P. versicolor* FA niches were
 272 included in *P. penicillatus* FA niche. There was a high overlap between *P. longipes* and *P.*
 273 *versicolor* niches (89.38% [72.40 – 99.70%] for *P. longipes* in *P. versicolor* niche and
 274 71.02% [45.29 – 93.80%] for *P. versicolor* in *P. longipes* niche) (Fig. 3B). By contrast, there
 275 was moderate niche overlap between *P. penicillatus* and the two other species (35.05% [21.30
 276 – 52.01%] in *P. longipes* niche and 46.64% [57.09 – 98.40%] in *P. versicolor* niche).
 277



278 **Fig. 3** Non-metric multidimensional scaling (nMDS) ordination of Bray-Curtis similarity
 279 matrix of hepatopancreas tissue fatty acid composition in the three spiny lobster species (A)
 280 and probabilities of niche overlap (%) between species (B). For each species, the mean ellipse
 281 is represented by a plain line and CI95% ellipses are represented by dashed lines (A).
 282 Overlaps (B) are presented as mean with their associated CI95%.

283

284 3.3. Isotopic niches

285 Among the three lobster species, *P. penicillatus* displayed the highest $\delta^{15}\text{N}$ values, *P.*
 286 *longipes* had intermediate values and *P. versicolor* showed the lowest $\delta^{15}\text{N}$ values (Tukey's
 287 HSD, $P = 0.002$ between *P. penicillatus* and *P. longipes*; $P < 0.001$ between *P. penicillatus*
 288 and *P. versicolor*; $P < 0.001$ between *P. longipes* and *P. versicolor*) (Table 2). Only *P.*
 289 *penicillatus* and *P. longipes* displayed a significant difference in $\delta^{13}\text{C}$ values (Tukey's HSD,
 290 $P = 0.03$), with *P. penicillatus* having higher values than *P. longipes* (Table 2).

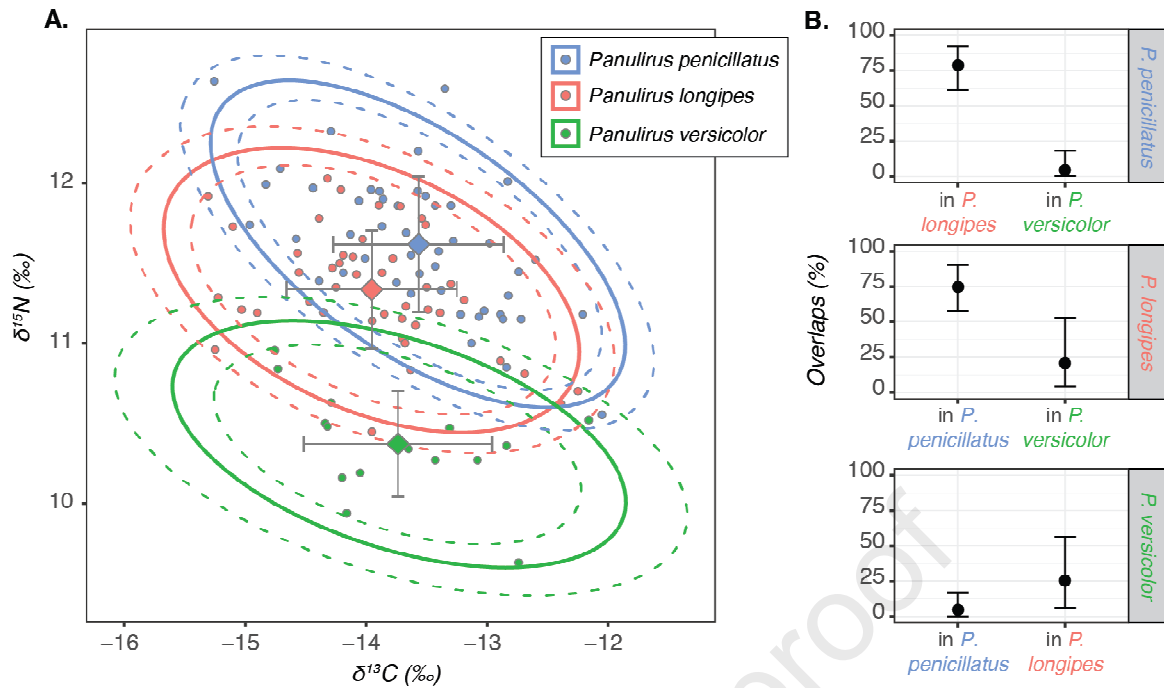
291

292 **Table 2** Mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) analysed in the white muscle of *Panulirus*
 293 *penicillatus*, *P. longipes* and *P. versicolor* across all sampling sites and time periods. Different
 294 letters indicate significant difference (Tukey's HSD or Dunn post-hoc tests).

Stable isotope ratio	<i>P. penicillatus</i> (n = 47)	<i>P. longipes</i> (n = 43)	<i>P. versicolor</i> (n = 15)
$\delta^{13}\text{C}$	$-13.6 \pm 0.1^{\text{a}}$	$-14.0 \pm 0.1^{\text{b}}$	$-13.7 \pm 0.2^{\text{ab}}$
$\delta^{15}\text{N}$	$11.6 \pm 0.1^{\text{a}}$	$11.3 \pm 0.1^{\text{b}}$	$10.4 \pm 0.1^{\text{c}}$

295
 296 All three species had similar SI niche sizes (4.33‰^2 [$3.30 - 5.73 \text{‰}^2$] for *P.*
 297 *penicillatus*, 4.32‰^2 [$3.21 - 5.82 \text{‰}^2$] for *P. longipes* and 4.05‰^2 [$2.45 - 6.38 \text{‰}^2$] for *P.*
 298 *versicolor*) (Fig. 4A). There was a high overlap between *P. penicillatus* and *P. longipes*
 299 isotopic niches (75.1% [$61.0 - 93.2\%$] for *P. penicillatus* in *P. longipes* and 78.1% [$58.7 -$
 300 90.2%] for *P. longipes* in *P. penicillatus*) (Fig. 4B). *P. versicolor* had moderate overlap with
 301 *P. longipes* (20.9% [$6.4 - 59.0\%$] for *P. versicolor* in *P. longipes* and 25.6% [$4.5 - 58.4\%$] for
 302 *P. longipes* in *P. versicolor*) and little overlap with *P. penicillatus* (4.6% [$0.1 - 18.8\%$] for *P.*
 303 *versicolor* in *P. penicillatus* and 4.8% [$0.2 - 21.4\%$] for *P. penicillatus* in *P. versicolor*).

304



305 **Fig. 4** $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) in the white muscle of the three spiny lobster species (A)
 306 and niche overlaps (%) between species (B). For each species, the mean \pm SD for stable
 307 isotope values is also given, and the mean ellipse and CI95% ellipses are represented by a
 308 plain line and dashed lines, respectively (A). Overlaps (B) are presented as mean with their
 309 associated CI95 %.

310

311 3.4. Effect of habitat type and habitat degradation due to coral bleaching on 312 spiny lobsters' trophic niche metrics

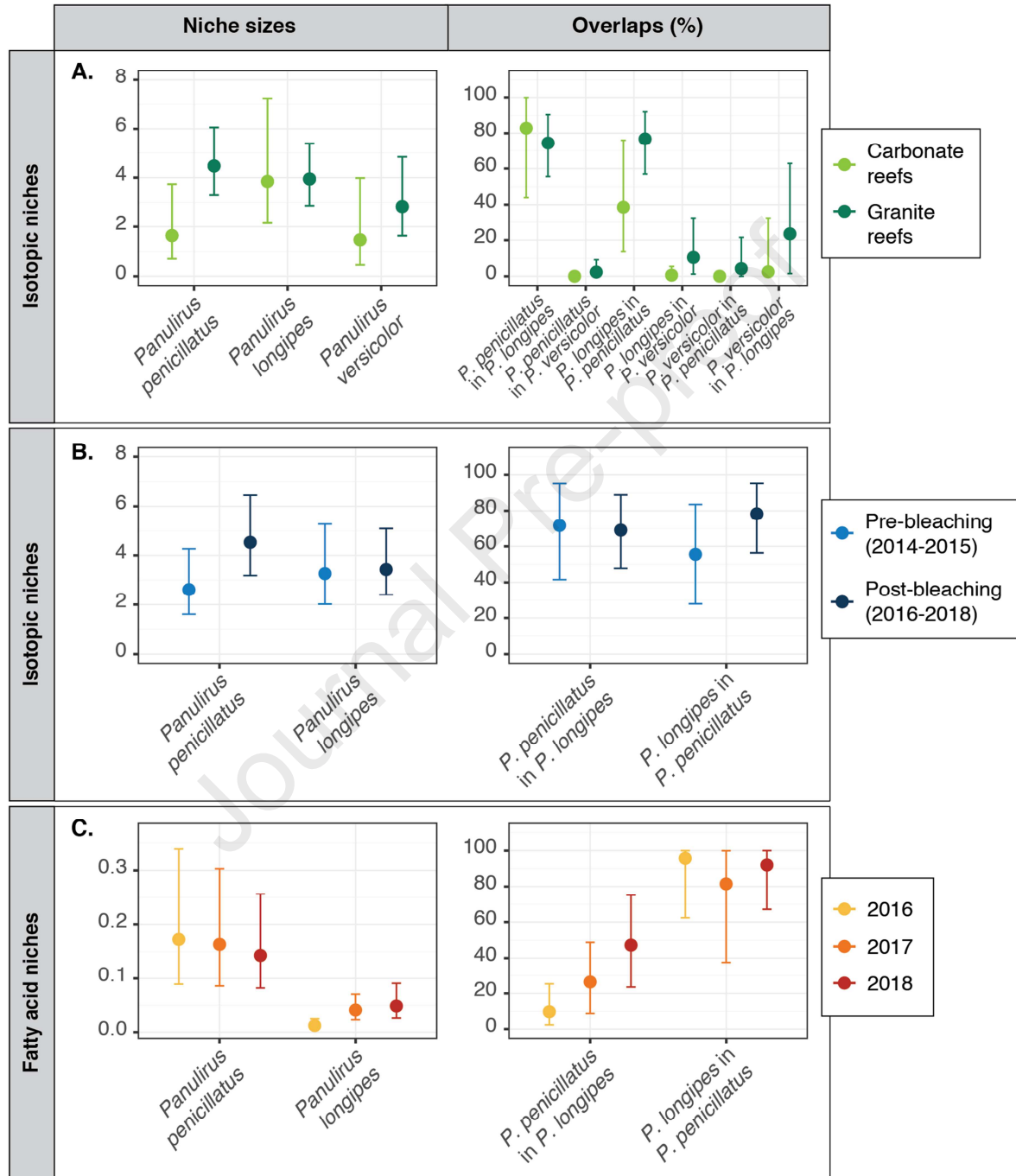
313 The isotopic niche size of *P. penicillatus* was larger in granite reefs than in carbonate
 314 reefs (4.4‰^2 [$3.2 - 5.8 \text{‰}^2$] and 1.6‰^2 [$0.7 - 3.6 \text{‰}^2$] respectively; associated probability of
 315 0.99) with little overlap in CI95% between the two habitat types (Fig. 5A). In spite of the
 316 uncertainty around the mean (i.e., high overlap in CI95%), it also appeared that the isotopic
 317 niche of *P. versicolor* was larger in granite reefs than in carbonate reefs (2.9‰^2 [$1.6 - 5.3 \text{‰}^2$]
 318 and 1.4‰^2 [$0.5 - 3.8 \text{‰}^2$] respectively; associated probability of 0.90). Except for the
 319 isotopic niche overlap of *P. penicillatus* in *P. longipes*, interspecific overlap of isotopic niches

320 seemed to be higher in granite reefs than in carbonate reefs (2.2% [0.1 – 9.8%] and 0.0%
 321 respectively for *P. penicillatus* in *P. versicolor*, associated probability of 0.97; 76.3% [58.3 –
 322 92.0%] and 37.8% [14.9 – 76.1%] respectively for *P. longipes* in *P. penicillatus*, associated
 323 probability of 0.96; 9.5% [1.4 – 26.5%] and 0.6% [0.0 – 5.2%] respectively for *P. longipes* in
 324 *P. versicolor*, associated probability of 0.97; 3.9% [0.0 – 19.8%] and 0.0% respectively for *P.*
 325 *versicolor* in *P. penicillatus*, associated probability of 0.90; 21.1% [1.7 – 59.9%] and 2.5%
 326 [0.0 – 31.7%] respectively for *P. versicolor* in *P. longipes*; associated probability of 0.95)
 327 (Fig. 5A).

328 The isotopic niche size of *P. penicillatus* appeared greater during the post-bleaching
 329 period (4.5 ‰² [3.2 – 6.4 ‰²]) than during the pre-bleaching period (2.6 ‰² [1.6 – 4.2 ‰²];
 330 associated probability of 0.97), with moderate overlap in CI95% (Fig. 5B). The isotopic niche
 331 overlap between *P. longipes* and *P. penicillatus* also seemed higher during the post-bleaching
 332 period (78.2% [56.0 – 94.4%]) than during the pre-bleaching period (55.5% [30.9 – 80.6%];
 333 associated probability of 0.91) with moderate overlap in CI95% (Fig. 5B). After the 2016
 334 bleaching event, the FA niche size of *P. longipes* was greater in 2017 (0.042 [0.023 – 0.077])
 335 and in 2018 (0.049 [0.026 – 0.090]) than in 2016 (0.012 [0.006 – 0.024]; associated
 336 probabilities of 0.99 between 2017 and 2016 and of 1 between 2018 and 2016), with little-to-
 337 no overlap in CI95% between 2016 and both other years (Fig. 5C). The FA niche overlap
 338 between *P. penicillatus* and *P. longipes* also seemed larger in 2017 (26.3% [8.2 – 50.6%] for
 339 *P. penicillatus* in *P. longipes*) and in 2018 (48.1% [22.8 – 77.5%] for *P. penicillatus* in *P.*
 340 *longipes*) than in 2016 (10.1% [2.3 – 24.7%] for *P. penicillatus* in *P. longipes*; associated
 341 probabilities of 0.92 between 2017 and 2016, of 1 between 2018 and 2016) (Fig. 5C).

342 For all calculated trophic niche metrics of Fig. 5, niche ellipses are presented in Fig. S2.
 343 Isotopic niches according to the sampling year (i.e., 2014 to 2018) for *P. penicillatus* and *P.*
 344 *longipes* only (due to low sample sizes for *P. versicolor*) and their associated metrics are

345 presented in Fig. S3. Spiny lobsters' FA niches in carbonate and granite reefs did not allow
 346 for any interpretation but are however presented in Fig. S4 for information purposes.
 347



348 **Fig. 5** Inter- and intraspecific differences in the trophic niche sizes and overlaps of spiny
 349 lobster species related to (A) different reef habitat types, (B) pre- and post-bleaching periods
 350 for isotopic niches, and (C) sampling years after 2016 coral bleaching event for FA niches.
 351 Niche sizes and overlaps are presented as mean with their associated CI95 %.

352

353 **4. Discussion**

354 The present study revealed novel insights into the trophic ecology and interspecific
355 competition between three sympatric spiny lobster species (*P. penicillatus*, *P. longipes* and *P.*
356 *versicolor*) in Seychelles coastal waters. We highlighted a substantial potential for dietary
357 overlap between the three species, as revealed by both interspecific FA and isotopic niche
358 overlaps. The use of FA trophic markers further assisted in inferring the dietary source of this
359 overlap. Use of SI in complement to FAs allowed for inference of habitat use and suggested
360 that resources may partially be segregated between the three spiny lobster species that could
361 allow for their coexistence. However, isotopic niche overlap was higher in the less vulnerable-
362 to-degradation reef type and coral bleaching increased FA and isotopic niche overlaps. We
363 thus suggest that climate change-driven coral reef degradation might increase the risk of
364 competition between these spiny lobster species through the reduction of coral reef structural
365 complexity and thus prey availability.

366

367 **4.1. Characterisation of trophic overlap and potential for competition**

368 As the biochemical composition of consumers largely reflects that of their prey (Iverson
369 2009), similar FA and SI niches characterise similar dietary patterns. Our study found high
370 habitat use and dietary similarities between the three Seychelles spiny lobster species,
371 consistently with previous reported findings (Sardenne et al. 2021). The $\delta^{13}\text{C}$ value ranges and
372 FA profiles of the three species were distinctive of benthic consumers (high in 20:4n-6 with
373 low-to-moderate levels of 20:5n-3 and 22:6n-3). The presence of iso-branched FA (i.e.,
374 iso17:0) along with high proportions of 18:1n-7 in the hepatopancreas also suggested a food
375 web partially based on bacteria, known to support benthic food webs, at least in part (Kelly
376 and Scheibling 2012).

377 Dietary similarities between Seychelles spiny lobsters were characterised by the
378 presence of several FA trophic markers in the hepatopancreas, allowing for the identification
379 of prey implicated in the dietary overlap. First, trophic markers of bacteria (i.e., iso17:0 and
380 18:1n-7) could indicate consumption of benthic detritivores, such as polychaetes, known to be
381 eaten in small proportions by spiny lobsters in some areas (e.g., the coast off Western
382 Australia, MacArthur et al. 2011). Fleshy algae FA trophic markers (i.e., 18:2n-6, 20:4n-6 and
383 22:5n-3, Meyer et al. 2019) suggest either direct consumption of fleshy algae, which can
384 support benthic food webs in shallow coastal waters (Kelly and Scheibling 2012) and has
385 been found in the gut contents of some spiny lobsters (Blamey et al. 2019), or consumption of
386 herbivorous prey, such as echinoderms, which are among the most common prey found in the
387 guts of spiny lobsters (Butler and Kintzing 2016). Here, the predominance of primary or
388 secondary consumption of fleshy algae in spiny lobsters' diet was difficult to determine. $\delta^{13}\text{C}$
389 values in macroalgae are highly variable (from -27 to -8 ‰, Fry and Sherr 1989) and, after
390 taking into account the trophic fractionation factor (1-2 ‰, Post 2002), both primary and
391 secondary consumption could occur according to our isotopic data. It is possible that it
392 depends on the conditions in sampling sites. Typically, secondary consumption of fleshy
393 algae would predominate on reefs where herbivores are abundant and macroalgae are limited,
394 while primary consumption, whether intentional or accidental through feeding on epiphyte
395 fauna found on the algae (Williams 2007), would predominate on reefs where macroalgae are
396 abundant.

397 The presence of a diverse number of FA trophic markers and variability in isotopic
398 values in this study suggest that Seychelles spiny lobsters are generalist feeders, which is in
399 accordance with previous studies on spiny lobsters' diet (Williams 2007). This could be an
400 advantage for these species' survival, as dietary plasticity would help them overcome
401 fluctuations in food availability (Korpimäki et al. 2020). However, we suggest that

402 competition between spiny lobsters could occur in this area or could emerge in the near
403 future, if shared resources (e.g., prey, habitat) become limited. Coexistence and avoidance of
404 competition would therefore be closely linked to ecosystem health and to resource segregation
405 mechanisms.

406

407 **4.2. Resource partitioning among spiny lobsters**

408 Partial resource segregation between the three spiny lobster species was also identified
409 in this study, as suggested by the difference in FA niche size between *P. penicillatus* and the
410 other two species and by differences in trophic position between the three species.

411 *Panulirus penicillatus* had a much larger FA niche in comparison with the two other
412 species, suggesting a difference in the ingested proportions of certain types of prey. Its FA
413 niche differed from FA niches of both other species largely due to positive anomalies of
414 several FA trophic markers like 18:1n-9, 20:1n-7, 20:1n-9, 22:2 NMI (7,13) and 22:2 NMI
415 (7,15). In coastal benthic systems, 18:1n-9 can originate from several dietary sources, such as
416 macroalgae, mangrove detritus or animal tissues (Meyer et al. 2019). Here, 18:1n-9 was
417 negatively correlated with trophic markers of macroalgae and mangrove materials (20:4n-6
418 and 22:5n-3, Fig. S1; Meyer et al. 2019), suggesting animal origin. This was also the case for
419 20:1n-7 and 20:1n-9, both negatively correlated with trophic markers of macroalgae,
420 mangrove material and seagrass (20:4n-6, 22:5n-3 and 18:2n-6, Fig. S1; Meyer et al. 2019).
421 The FA 20:1n-9 is known to indicate secondary consumption of zooplankton, for example
422 through consumption of carnivorous fish (Pethybridge et al. 2010). Moreover, NMI FA are
423 trophic markers of bivalve molluscs and carnivorous gastropods (Iverson 2009), suggesting
424 that *P. penicillatus* eats these prey in higher proportions than the two other spiny lobster
425 species. FA niche results were supported by isotopic niche results, as *P. penicillatus* had a
426 higher trophic position than the two other species that is consistent with higher proportions of

427 carnivorous gastropods and fish in its diet. We thus suggest that *P. penicillatus* may be more
428 of a generalist than *P. longipes* and *P. versicolor*, with a higher level of carnivory. Such a
429 difference in diet could be due to the size of *P. penicillatus* individuals, which tend to be
430 larger than individuals of the two other species. Previous studies showed that the size range of
431 prey that can be consumed by spiny lobster is function of their size, with larger individuals
432 being able to eat larger prey (e.g., Haley et al. 2011; Blamey and Branch 2012). Thus, the
433 larger size of *P. penicillatus* may allow it to have access to more resources, resulting in a
434 larger niche size.

435 Both *P. longipes* and *P. versicolor* had a low isotopic niche overlap, with *P. versicolor*
436 being characterised by significantly lower $\delta^{15}\text{N}$ values, while they had a very high FA niche
437 overlap that suggests high dietary similarities. Because all spiny lobsters were caught at the
438 same geographical locations, we suggest that variations in $\delta^{15}\text{N}$ values reflect differences in
439 trophic position rather than differences in biochemical processes at the base of food webs (i.e.,
440 isotopic baselines). This may be due to size-selective predation, with both species feeding on
441 different size fractions and/or different life stages of the same prey. Such resource partitioning
442 could allow and even promote the stable coexistence of two consumers (de Roos et al. 2008).
443 Moreover, body size is recognized as an important factor influencing trophic structure as it
444 determines interaction between potential prey and predators, with larger consumers being able
445 to eat larger prey. This has led to the theory that there is a positive relationship between a
446 consumer's trophic position and its body size (Jennings et al. 2002). Thus, if *P. versicolor* is
447 specializing on smaller prey (either juveniles or small adults), it would feed on prey with a
448 lower trophic position than those of *P. longipes* (as suggested by our results), while having the
449 same size and feeding on the same prey species than *P. longipes*. Such findings would be of
450 major importance in case of food scarcity, especially if *P. versicolor* feeds on earlier
451 development stages of prey than *P. longipes* and *P. penicillatus*, and not only smaller prey

452 species. Different prey life-history stages are linked by growth and reproduction, and
453 predation on one stage may decrease the abundance of other stages (Murdoch et al. 2003).
454 Thus, prey eaten by *P. versicolor* would not grow and be available for *P. longipes* and *P.*
455 *penicillatus* to feed on. Given its larger trophic niche, *P. penicillatus* may be able to better
456 overcome this compared to *P. longipes*. Thus, this could accentuate the effects of food
457 scarcity for *P. longipes*, which already has a high level of trophic niche overlap with *P.*
458 *penicillatus*.

459

460 **4.3. Effect of habitat type and coral bleaching**

461 The type of reef habitat had an effect on spiny lobsters' isotopic niche overlaps, with
462 higher overlap between lobsters from granite reefs than for those from carbonate reefs, for all
463 studied species. This was most obvious for *P. versicolor*, which had no isotopic niche overlap
464 with *P. penicillatus* from carbonate reefs while there was a possibility of overlap with *P.*
465 *penicillatus* from granite reefs, and had a higher overlap with *P. longipes* on granite reefs than
466 on carbonate reefs. Although FA niches could not be computed for this comparison, results
467 suggest a higher potential of competition for prey on granite reefs than on carbonate reefs,
468 especially for *P. versicolor*. This would be consistent with carbonate reefs being recognized
469 as very productive ecosystems, with a high species diversity and structural complexity
470 (Graham and Nash 2013) that would provide sufficient prey of good quality for spiny lobsters
471 to coexist.

472 Our results also showed a possible effect of habitat degradation on spiny lobsters' diet
473 and foraging dynamics, especially coral reef degradation following the 2016 bleaching event
474 (Obura et al. 2017). The isotopic niche size of *P. penicillatus* seemed to increase after the
475 coral bleaching event, due to higher variability in $\delta^{15}\text{N}$ values (Fig. S1), and although we did
476 not have FA data prior to the bleaching event, the FA niche of *P. longipes* has increased

477 during the post-bleaching period. This suggests a possible diversification of prey size class in
478 *P. penicillatus* diet between the pre- and post-bleaching periods and a diversification of *P.*
479 *longipes* diet after the habitat degradation. Given the large decline in coral cover and as such
480 the loss of reef complexity that provide habitat for a variety of potential prey species, we
481 suggest that such modifications in isotopic and FA niches may be the consequences of a
482 decrease in prey availability. In ecological theory, dietary diversity increases when prey
483 abundance decreases (Tinker et al. 2008) and, as generalist feeders, spiny lobsters are known
484 to adapt their diet according to several factors, such as prey species composition and/or prey
485 availability (Haley et al. 2011; Blamey et al. 2019). This would also be consistent with the
486 loss of species richness that has been reported after loss of coral cover in Seychelles
487 (Robinson et al. 2019). Such drastic changes in spiny lobsters' diet, closely similar at core
488 between the three species, may have important consequences on their foraging behaviour and
489 maintenance. By influencing prey availability and thus spiny lobsters' diet diversity, the 2016
490 bleaching event could also have increased the risk of competition between the three lobster
491 species. This hypothesis is supported by the increase of isotopic niche overlap between *P.*
492 *penicillatus* and *P. longipes* between the pre- and post-bleaching periods and by the increase
493 in their FA niche overlap between 2016 and 2018.

494 The effects of reef habitat type and habitat degradation through coral bleaching on spiny
495 lobsters' diet and foraging dynamics are of high interest for the prediction of fishing stock
496 evolution. Indeed, carbonate reefs are known to be more vulnerable to bleaching and reef
497 degradation than granite reefs (Obura et al. 2017). In addition, granite reefs are quicker to
498 recover than carbonate reefs after degradation, due in part to corals from carbonate reefs being
499 in competition with macroalgae (Obura et al. 2017). Due to climate change and its associated
500 rise in sea surface temperatures, bleaching events are predicted to increase in frequency,
501 thereby weakening corals ecosystems in the long-term (Hoegh-Guldberg 2011). As the

502 reduction of Seychelles spiny lobsters' potential of interspecific competition partly depends
503 on the health and complexity of carbonate reefs, it is likely that the predicted instability of
504 coral reefs could add further instability to the already unstable Seychelles spiny lobster stocks.

505

506 **5. Conclusion**

507 This study provides important baseline information on Seychelles spiny lobsters' trophic
508 ecology and on their potential for resource competition in the context of a changing climate
509 and associated habitat (i.e., coral reefs) degradation. All three species had biochemical
510 compositions that suggested diets consisting of polychaetes, echinoderms, and fleshy algae.
511 As the largest species, *P. penicillatus* had the highest trophic position and the largest trophic
512 niche, presumably feeding more on carnivorous gastropods and fish than the two other spiny
513 lobster species. Although having very similar trophic niche than the two other species, *P.*
514 *versicolor* may feed on smaller prey and/or early life stages. These segregation mechanisms
515 could potentially minimise the effects of competition among these spiny lobster species. Our
516 data also showed that the level of resource segregation was dependent on their habitat. Spiny
517 lobsters' trophic niche overlap was higher on granite reefs than on carbonate reefs, the latter
518 being more degraded following multiple bleaching events. As recent habitat degradation (i.e.,
519 following the 2016 coral bleaching event) also led to an increase in trophic niche overlap, this
520 raises questions about the future evolution of competition between these spiny lobster species
521 and, ultimately, their adaptive capacity and population stability.

522 Although our results provide key information to better understand Seychelles spiny
523 lobsters' trophic interactions and dynamics, further studies are still needed. Most of the
524 available samples were from *P. penicillatus* and *P. longipes*, which did not allow all the
525 analyses to be performed on *P. versicolor* data. Moreover, the FA and SI profiles of a
526 consumer only does not allow quantitative identification of its diet. Information about FA and

527 SI profiles from lobsters' prey collected at different sites and time periods would bring new
528 elements on the spatio-temporal variations in resource sharing and segregation among
529 Seychelles spiny lobster species, and thus help understand the variability in their interspecific
530 competition. In light of our findings, it is crucial to maintain monitoring of trophic ecology
531 and habitat use of spiny lobsters' around Seychelles islands if the fishery is to be successfully
532 managed under changing climate.

533

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542

543 **Author's contribution** Conceptualization: NB; Funding acquisition: NB, RG; Data
544 acquisition: NB, RG, MR, MAS, FS, FLG; Statistical analysis: MAS, HP, LB; Writing – 1st
545 draft: MAS; Review & editing: all co-authors.

546

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551

552 **Data availability** The dataset analysed in the current study is available from the
553 corresponding author on reasonable request. The R code used to compute FA and isotopic
554 niches and to represent niche ellipses is available on Github:
555 https://github.com/magalisabino/FattyAcid_Isotopic_niche_computing.

556 **Declaration of competing interest** The authors declare that they have no conflict of interest.

557

558 **Ethical approval** All applicable international, national, and institutional guidelines for the
559 care and use of animals were followed. All procedures performed in studies involving animals
560 were in accordance with the ethical standards of the Ministry of Environment, Energy, and
561 Climate Change, Seychelles.

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Highlights

- We use trophic niche overlap to identify the potential for resource competition
- There is a potential for resource competition between three spiny lobsters species
- The largest species had the most diverse diet and the highest $\delta^{15}\text{N}$ values
- Potential for competition was higher in the less vulnerable reef habitat type
- Potential for competition seemed to increase following a coral bleaching event

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Habitat degradation increases interspecific competition between three spiny lobsters in Seychelles

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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