



**HAL**  
open science

## Habitat degradation increases interspecific trophic competition between three spiny lobster species in Seychelles

Magali Sabino, Rodney Govinden, Heidi Pethybridge, Laura Blamey, Fabienne Le Grand, Fany Sardenne, Maria Rose, Paco Bustamante, Nathalie Bodin

► **To cite this version:**

Magali Sabino, Rodney Govinden, Heidi Pethybridge, Laura Blamey, Fabienne Le Grand, et al.. Habitat degradation increases interspecific trophic competition between three spiny lobster species in Seychelles. *Estuarine, Coastal and Shelf Science*, 2021, 256, pp.107368. 10.1016/j.ecss.2021.107368 . hal-03271774

**HAL Id: hal-03271774**

**<https://hal.science/hal-03271774v1>**

Submitted on 20 Jun 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

Sabino Magali A. <sup>1,2</sup>, Govinden Rodney <sup>1</sup>, Pethybridge Heidi <sup>3</sup>, Blamey Laura <sup>4</sup>, Le Grand Fabienne <sup>5</sup>, Sardenne Fany <sup>5</sup>, Rose Maria <sup>1</sup>, Bustamante Paco <sup>2,6</sup>, Bodin Nathalie <sup>1,7,8,\*</sup>

<sup>1</sup> Seychelles Fishing Authority (SFA), Fishing Port, Victoria, Mahé, Seychelles

<sup>2</sup> Littoral Environnement et Sociétés (LIENSs), UMR 7266 CNRS - La Rochelle Université, 2 rue Olympe de Gouges, 17000, La Rochelle, France

<sup>3</sup> CSIRO Oceans and Atmosphere, Hobart, Tasmania, Australia

<sup>4</sup> CSIRO Oceans and Atmosphere, Brisbane, Queensland, Australia

<sup>5</sup> Univ Brest, CNRS, IRD, Ifremer, LEMAR, IUEM, F-29280, Plouzané, France

<sup>6</sup> Institut Universitaire de France (IUF), 1 rue Descartes, 75005, Paris, France

<sup>7</sup> Institute for Research and Development (IRD), Fishing Port, Victoria, Mahé, Seychelles

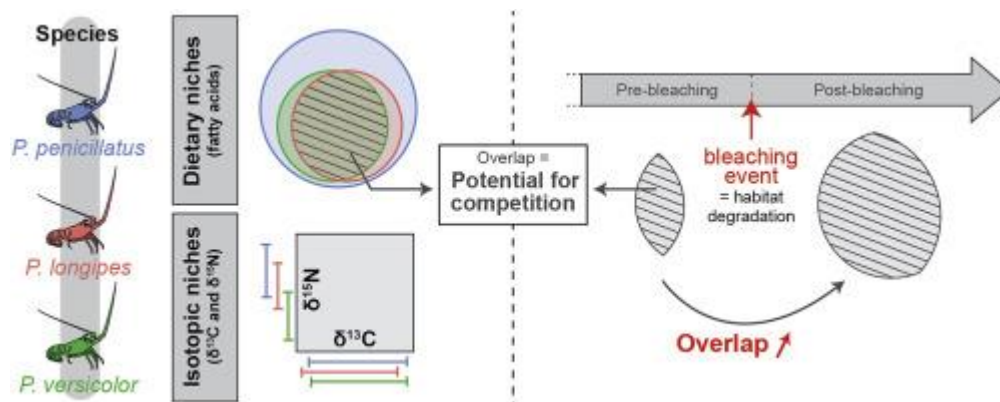
<sup>8</sup> Sustainable Ocean Seychelles (SOS), BeauBelle, Mahé, Seychelles

\* Corresponding author : Nathalie Bodin, email address : [natbod@gmail.com](mailto:natbod@gmail.com)

### 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.

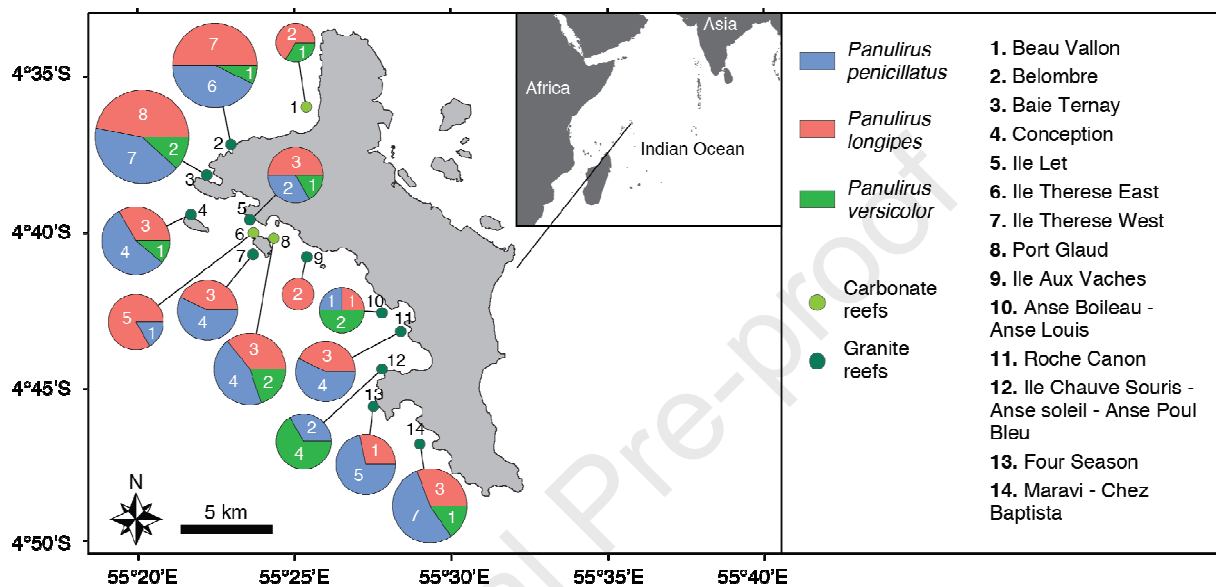
104

## 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  $\mu\text{L}$  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  $\mu\text{L}$  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  $\mu\text{m}$  film thickness,  
140 Phenomenex; and ZB-5 30 m length x 0.25 mm i.d. x 0.25  $\mu\text{m}$  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  $\delta$  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).

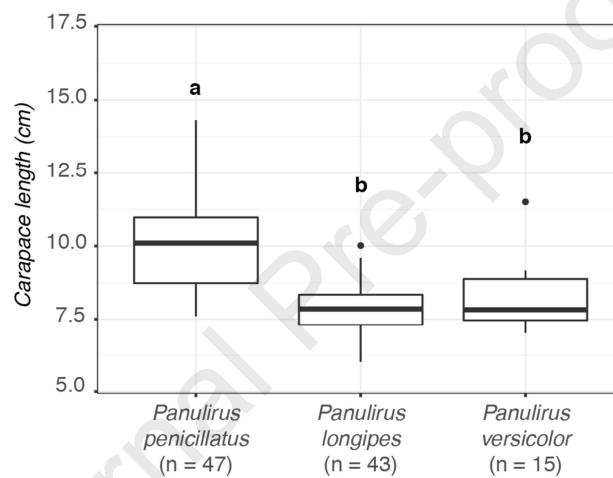
214 The effects of reef habitat type (carbonate *vs* granite) and habitat degradation (i.e.,  
215 before and after coral bleaching event) on spiny lobsters' trophic ecology was investigated  
216 using SI niche metrics. For this, isotopic niche sizes and overlaps were compared between  
217 lobsters 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,  $P = 0.02$ ).

253

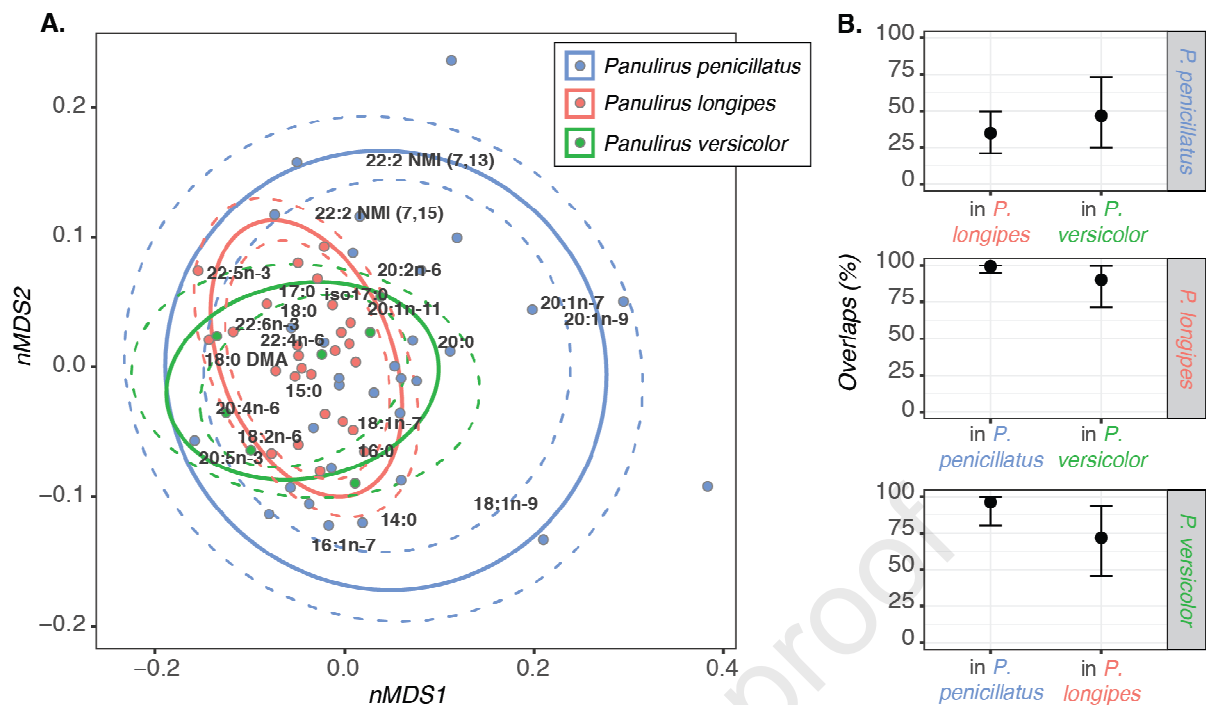
254 **Table 1** Fatty acid (FA) profiles analysed in the hepatopancreas of *Panulirus penicillatus*, *P.*  
 255 *longipes* and *P. versicolor* across all sampling sites and time periods expressed as % of total  
 256 FA and presented as mean  $\pm$  SE. The category "other" refers to the sum of FA compounds  
 257 detected below trace level ( $< 0.8\%$ ). Different letters indicate significant difference (Tukey's  
 258 HSD or Dunn post-hoc tests).  $\Sigma$ SFA = sum of saturated FA,  $\Sigma$ MUFA = sum of  
 259 monounsaturated FA,  $\Sigma$ 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 <sup>b</sup>	2.0 $\pm$ 0.1 <sup>a</sup>	1.4 $\pm$ 0.1 <sup>b</sup>
18:0	9.9 $\pm$ 0.2 <sup>ab</sup>	11.4 $\pm$ 0.4 <sup>a</sup>	9.5 $\pm$ 0.5 <sup>b</sup>
20:0	1.2 $\pm$ 0.1 <sup>a</sup>	1.01 $\pm$ 0.04 <sup>ab</sup>	0.8 $\pm$ 0.1 <sup>b</sup>
$\Sigma$ 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 <sup>a</sup>	7.4 $\pm$ 0.3 <sup>b</sup>	7.6 $\pm$ 0.7 <sup>b</sup>
20:1n-7	1.0 $\pm$ 0.1 <sup>a</sup>	0.69 $\pm$ 0.03 <sup>ab</sup>	0.7 $\pm$ 0.1 <sup>b</sup>
20:1n-9	1.3 $\pm$ 0.1 <sup>a</sup>	0.66 $\pm$ 0.02 <sup>b</sup>	1.0 $\pm$ 0.1 <sup>a</sup>
20:1n-11	2.8 $\pm$ 0.2	2.94 $\pm$ 0.13	2.4 $\pm$ 0.3
$\Sigma$ MUFA	24.4 $\pm$ 0.6 <sup>a</sup>	20.5 $\pm$ 0.4 <sup>b</sup>	20.4 $\pm$ 1.0 <sup>b</sup>
<i>Polyunsaturated</i>			
18:2n-6	1.29 $\pm$ 0.04 <sup>b</sup>	1.5 $\pm$ 0.1 <sup>a</sup>	1.5 $\pm$ 0.1 <sup>ab</sup>
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 <sup>b</sup>	10.9 $\pm$ 0.3 <sup>a</sup>	11.3 $\pm$ 0.9 <sup>a</sup>
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
$\Sigma$ PUFA	38.2 ± 0.8 <sup>b</sup>	40.5 ± 0.8 <sup>ab</sup>	42.6 ± 1.5 <sup>a</sup>
<i>Branched FA, NMI FA and DMA</i>			
iso17:0	0.83 ± 0.04 <sup>b</sup>	1.01 ± 0.03 <sup>a</sup>	0.8 ± 0.1 <sup>ab</sup>
22:2 NMI (7,13)	1.5 ± 0.1 <sup>a</sup>	1.1 ± 0.1 <sup>b</sup>	1.2 ± 0.2 <sup>ab</sup>
22:2 NMI (7,15)	0.74 ± 0.05 <sup>b</sup>	0.86 ± 0.04 <sup>a</sup>	1.2 ± 0.2 <sup>a</sup>
18:0DMA	2.3 ± 0.1	2.4 ± 0.1	2.5 ± 0.3
Other <sup>1</sup>	11.0 ± 0.3	10.8 ± 0.2	11.3 ± 0.2

261 <sup>1</sup> 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

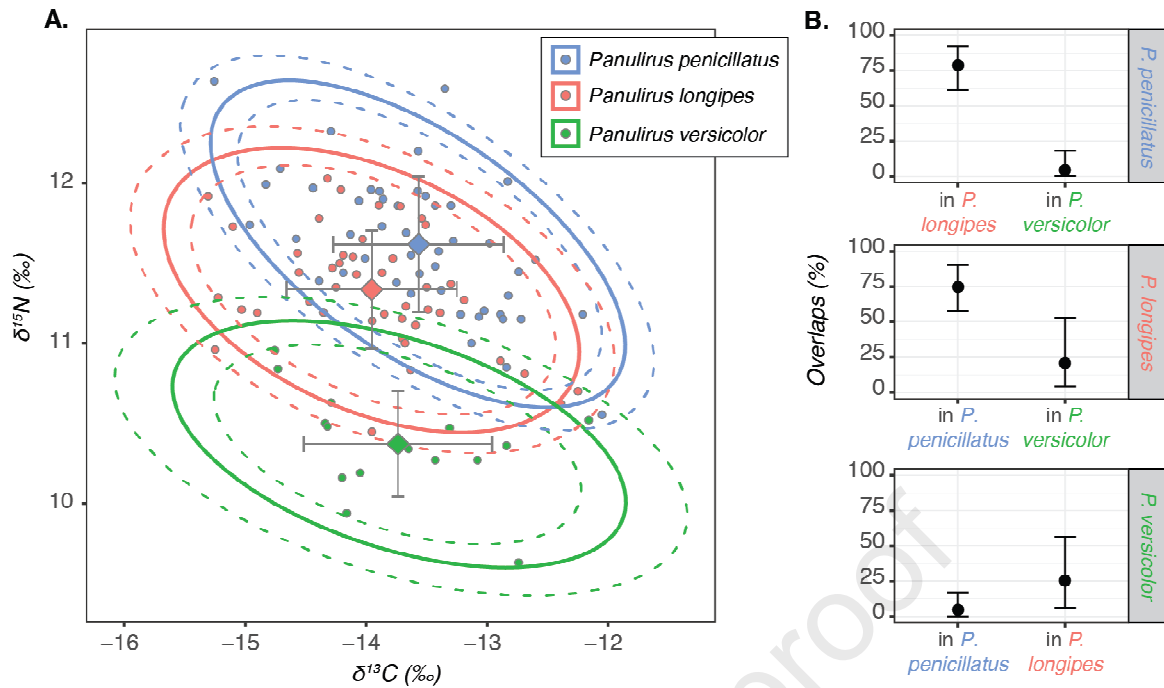
292 **Table 2** Mean ( $\pm$  SD)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (‰) analysed in the white muscle of *Panulirus*  
 293 *penicillatus*, *P. longipes* and *P. versicolor* across all sampling sites and time periods. Different  
 294 letters indicate significant difference (Tukey's 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 ( $4.33 \text{‰}^2$  [ $3.30 - 5.73 \text{‰}^2$ ] for *P.*  
 297 *penicillatus*,  $4.32 \text{‰}^2$  [ $3.21 - 5.82 \text{‰}^2$ ] for *P. longipes* and  $4.05 \text{‰}^2$  [ $2.45 - 6.38 \text{‰}^2$ ] 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

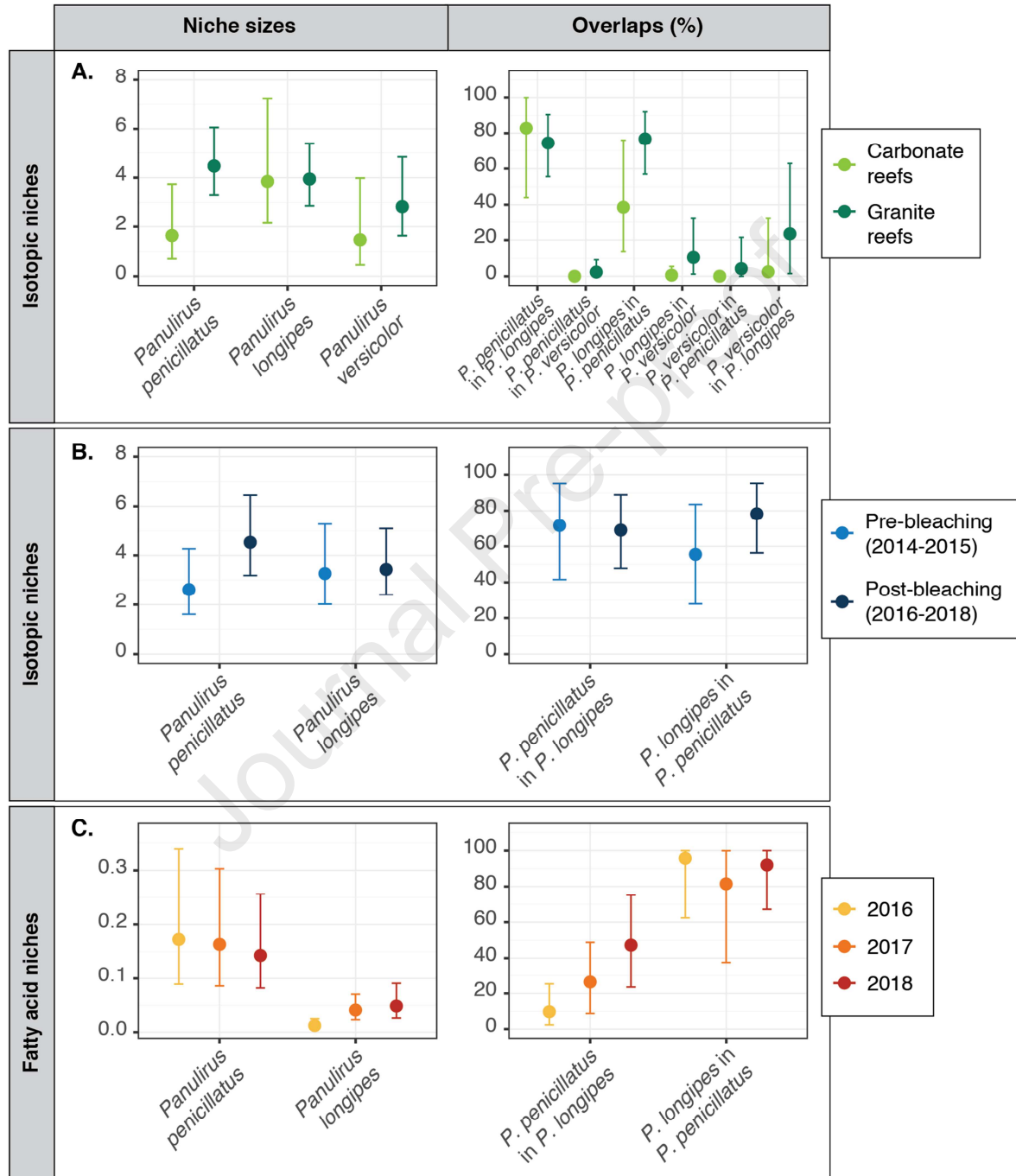
313 The isotopic niche size of *P. penicillatus* was larger in granite reefs than in carbonate  
 314 reefs ( $4.4 \text{‰}^2$  [ $3.2 - 5.8 \text{‰}^2$ ] and  $1.6 \text{‰}^2$  [ $0.7 - 3.6 \text{‰}^2$ ] respectively; associated probability of  
 315 0.99) with little overlap in CI95% between the two 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 ( $2.9 \text{‰}^2$  [ $1.6 - 5.3 \text{‰}^2$ ]  
 318 and  $1.4 \text{‰}^2$  [ $0.5 - 3.8 \text{‰}^2$ ] 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 ‰<sup>2</sup> [3.2 – 6.4 ‰<sup>2</sup>]) than during the pre-bleaching period (2.6 ‰<sup>2</sup> [1.6 – 4.2 ‰<sup>2</sup>];  
 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

534 **Acknowledgements** The authors would like to thank the lobster fishers who assisted with  
535 sampling. A special thank goes to the SFA Research staff (Kettyna Gabriel, Rodney Melanie,  
536 Stephanie Marie, Clara Belmont, and Marie-Corinne Balett), the R.V. L'Amitié crew and the  
537 Seychelles Maritime School Academy for the invaluable help in processing the samples. The  
538 authors are grateful to M. Brault-Favrou and G. Guillou for their support in the stable isotope  
539 analyses. Thanks are due to the CPER (Contrat de Projet Etat-Région) and the FEDER (Fonds  
540 Européen de Développement Régional) for funding the IRMS of LIENSs laboratory. The IUF  
541 (Institut Universitaire de France) is acknowledged for its support to PB as a Senior Member.

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

547 **Funding** The present work is a contribution to the Seychelles Participatory Lobster  
548 Monitoring Programme (PLMP) led by the Seychelles Fishing Authority (SFA), with the  
549 financial support of the Seychelles Government, the European Fisheries Partnership  
550 Agreement (EU-FPA), and the Institute for Research and Development (IRD).

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](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.

562 **References**

- 563 Blamey LK, Branch GM (2012) Regime shift of a kelp-forest benthic community induced by  
564 an “invasion” of the rock lobster *Jasus lalandii*. *J Exp Mar Bio Ecol* 420–421:33–47.  
565 doi: 10.1016/j.jembe.2012.03.022
- 566 Blamey LK, de Lecea AM, Jones LDS, Branch GM (2019) Diet of the spiny lobster *Jasus*  
567 *paulensis* from the Tristan da Cunha archipelago: Comparisons between islands, depths  
568 and lobster sizes. *Estuar Coast Shelf Sci* 219:262–272. doi: 10.1016/j.ecss.2019.02.021
- 569 Brewster JD, Giraldo C, Choy ES, MacPhee SA, Hoover C, Lynn B, McNicholl DG,  
570 Majewski A, Rosenberg B, Power M, Reist JD, Loseto LL (2017) A comparison of the  
571 trophic ecology of Beaufort Sea Gadidae using fatty acids and stable isotopes. *Polar Biol*  
572 41:149–162. doi: 10.1007/s00300-017-2178-0
- 573 Budge SM, Iverson SJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems  
574 using fatty acids: A primer on analysis and interpretation. *Mar Mammal Sci* 22:759–801.  
575 doi: 10.1111/j.1748-7692.2006.00079.x
- 576 Butler MJ, Kintzing MD (2016) An exception to the rule: Top-down control of a coral reef  
577 macroinvertebrate community by a tropical spiny lobster. *Bull Mar Sci* 92:137–152. doi:  
578 10.5343/bms.2015.1045
- 579 Carvalho PC, Davoren GK (2020) Niche dynamics of sympatric non-breeding shearwaters  
580 under varying prey availability. *Ibis* 162:701–712. doi: 10.1111/ibi.12783
- 581 Connan M, McQuaid CD, Bonnevie BT, Smale MJ, Cherel Y (2014) Combined stomach  
582 content, lipid and stable isotope analyses reveal spatial and trophic partitioning among  
583 three sympatric albatrosses from the Southern Ocean. *Mar Ecol Prog Ser* 497:259–272.  
584 doi: 10.3354/meps10606
- 585 Costa-Pereira R, Araújo MS, Souza FL, Ingram T (2019) Competition and resource breadth  
586 shape niche variation and overlap in multiple trophic dimensions. *Proc R Soc B Biol Sci*

- 587 286:1–9. doi: 10.1098/rspb.2019.0369
- 588 de Roos AM, Schellekens T, Van Kooten T, Persson L (2008) Stage-specific predator species  
589 help each other to persist while competing for a single prey. Proc Natl Acad Sci U S A  
590 105:13930–13935. doi: 10.1073/pnas.0803834105
- 591 Fry B, Sherr EB (1989)  $\delta^{13}\text{C}$  measurements as indicators of carbon flow in marine and  
592 freshwater ecosystems. In: Rundel PW, Ehleringer JR, Nagy KA (eds) Stable Isotopes in  
593 Ecological Research. Ecological Studies (Analysis and Synthesis). Springer, New-York,  
594 USA, pp 196–229. doi: 10.1007/978-1-4612-3498-2\_12
- 595 Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef  
596 ecosystems. Coral Reefs 32:315–326. doi: 10.1007/s00338-012-0984-y
- 597 Haley CN, Blamey LK, Atkinson LJ, Branch GM (2011) Dietary change of the rock lobster  
598 *Jasus lalandii* after an “invasive” geographic shift: Effects of size, density and food  
599 availability. Estuar Coast Shelf Sci 93:160–170. doi: 10.1016/j.ecss.2011.04.015
- 600 Hoegh-Guldberg O (2011) Coral reef ecosystems and anthropogenic climate change. Reg  
601 Environ Chang 11:215–227. doi: 10.1007/s10113-010-0189-2
- 602 Holthuis LB (1991) FAO species catalogue Vol. 13. Marine lobsters of the world An  
603 annotated and illustrated catalogue of species of interest to fisheries known to date. FAO  
604 Fish Synopsis 13:1–4. <http://www.fao.org/3/t0411e/t0411e00.htm>
- 605 Iverson SJ (2009) Tracing aquatic food webs using fatty acids: from qualitative indicators to  
606 quantitative determination. In: Kainz M, Brett MT, Arts MT (eds) Lipids in Aquatic  
607 Ecosystems. Springer New York, New-York, USA, pp 281–308. doi: 10.1007/978-0-  
608 387-89366-2\_12
- 609 Jennings S, Pinnegar JK, Polunin NVC, Warr KJ (2002) Linking size-based and trophic  
610 analyses of benthic community structure. Mar Ecol Prog Ser 226:77–85. doi:  
611 10.3354/meps226077

- 612 Kelly JR, Scheibling RE (2012) Fatty acids as dietary tracers in benthic food webs. *Mar Ecol*  
613 *Prog Ser* 446:1–22. doi: 10.3354/meps09559
- 614 Khan A, Amelie V (2015) Assessing climate change readiness in Seychelles: implications for  
615 ecosystem-based adaptation mainstreaming and marine spatial planning. *Reg Environ*  
616 *Chang* 15:721–733. doi: 10.1007/s10113-014-0662-4
- 617 Korpimäki E, Hongisto K, Masoero G, Laaksonen T (2020) The difference between generalist  
618 and specialist: the effects of wide fluctuations in main food abundance on numbers and  
619 reproduction of two co-existing predators. *J Avian Biol* 51:1–13. doi: 10.1111/jav.02508
- 620 MacArthur LD, Phillips DL, Hyndes GA, Hanson CE, Vanderklift MA (2011) Habitat  
621 surrounding patch reefs influences the diet and nutrition of the Western rock lobster. *Mar*  
622 *Ecol Prog Ser* 436:191–205. doi: 10.3354/meps09256
- 623 Mason NWH, De Bello F, Doležal J, Lepš J (2011) Niche overlap reveals the effects of  
624 competition, disturbance and contrasting assembly processes in experimental grassland  
625 communities. *J Ecol* 99:788–796. doi: 10.1111/j.1365-2745.2011.01801.x
- 626 Meyer L, Pethybridge H, Nichols PD, Beckmann C, Huveneers C (2019) Abiotic and biotic  
627 drivers of fatty acid tracers in ecology: A global analysis of chondrichthyan profiles.  
628 *Funct Ecol* 33:1243–1255. doi: 10.1111/1365-2435.13328
- 629 Murdoch WW, Briggs CJ, Nisbet RM (2003) *Consumer-resource dynamics*. Princeton  
630 University Press, Princeton, New Jersey. doi: 10.1515/9781400847259
- 631 Nie Y, Zhou W, Gao K, Swaisgood RR, Wei F (2019) Seasonal competition between  
632 sympatric species for a key resource: Implications for conservation management. *Biol*  
633 *Conserv* 234:1–6. doi: 10.1016/j.biocon.2019.03.013
- 634 Obura D, Gudka M, Rabi FA, Gian SB, Bijoux J, Freed S, Maharavo J, Mwaura J, Porter S,  
635 Sola E, Wickel J, Yahya S, Ahamada S (2017) Coral reef status report for the Western  
636 Indian Ocean. doi: 10.13140/RG.2.2.20642.07366

- 637 Österblom H, Olsson H, Blenckner T, Furness RW (2008) Junk food in marine ecosystems.  
638 *Oikos* 117:1075–1085. doi: 10.1111/j.0030-1299.2008.16501.x
- 639 Pethybridge H, Daley R, Virtue P, Nichols P (2010) Lipid composition and partitioning of  
640 deepwater chondrichthyans: Inferences of feeding ecology and distribution. *Mar Biol*  
641 157:1367–1384. doi: 10.1007/s00227-010-1416-6
- 642 Phillips BF (2013) *Lobsters: Biology, Management, Aquaculture and Fisheries*, 2nd editio.  
643 John Wiley & Sons. doi: 10.1002/9781118517444
- 644 Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and  
645 assumptions. *Ecology* 83:703–718. doi: 10.2307/3071875
- 646 Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting  
647 to the fat of the matter: Models, methods and assumptions for dealing with lipids in  
648 stable isotope analyses. *Oecologia* 152:179–189. doi: 10.1007/s00442-006-0630-x
- 649 R Core Team (2018) *R: A language and environment for statistical computing*.
- 650 Robinson JPW, Wilson SK, Jennings S, Graham NAJ (2019) Thermal stress induces  
651 persistently altered coral reef fish assemblages. *Glob Chang Biol* 25:2739–2750. doi:  
652 10.1111/gcb.14704
- 653 Sardenne F, Bodin N, Chassot E, Amiel A, Fouché E, Degroote M, Hollanda S, Pethybridge  
654 H, Lebreton B, Guillou G, Ménard F (2016) Trophic niches of sympatric tropical tuna in  
655 the Western Indian Ocean inferred by stable isotopes and neutral fatty acids. *Prog*  
656 *Oceanogr* 146:75–88. doi: 10.1016/j.pocean.2016.06.001
- 657 Sardenne F, Bodin N, Barret L, Blamey L, Govinden R, Gabriel K, Mangroo R, Munaron J-  
658 M, Le Loc'h F, Bideau A, Le Grand F, Sabino M, Bustamante P, Rowat D (2021) Diets  
659 of spiny lobsters from Mahé Island reefs, Seychelles reefs inferred by trophic tracers.  
660 *Reg Stud Mar Sci* 42:101640. doi: 10.1016/j.rsma.2021.101640
- 661 Seychelles Fishing Authority (2014) Fishery independent indices for the Seychelles lobster



- 662 resource. <https://www.oceandocs.org/bitstream/handle/1834/14833/Tech.074.pdf>
- 663 Seychelles Fishing Authority (2016) Report on the spiny lobster fishery - Summary of fishing  
664 activity for the 2015-2016 season.  
665 <https://www.oceandocs.org/bitstream/handle/1834/9895/Tech.079.pdf>
- 666 Seychelles Fishing Authority (2018) Lobster survey report 2018.  
667 <https://www.oceandocs.org/bitstream/handle/1834/15432/Tech.082.pdf>
- 668 Swanson HK, Lysy M, POwer M, Stasko AD, Johnson JD, Reist JD (2015) A new  
669 probabilistic method for quantifying n-dimensional ecological niches and niche overlap.  
670 Ecology 96:318–324. doi: 10.1890/14-0235.1
- 671 Tinker T, Bentall G, Estes JA (2008) Food limitation leads to behavioral diversification and  
672 dietary specialization in sea otters. PNAS 105:560–565. doi: 10.1073/pnas.0709263105
- 673 Williams KC (2007) Nutritional requirements and feeds development for post-larval spiny  
674 lobster: A review. Aquaculture 263:1–14. doi: 10.1016/j.aquaculture.2006.10.019
- 675

## 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

Journal Pre-proof

– Estuarine, Coastal and Shelf Science –

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

Magali A. Sabino<sup>1,2</sup>, Rodney Govinden<sup>1</sup>, Heidi Pethybridge<sup>3</sup>, Laura Blamey<sup>4</sup>, Fabienne Le Grand<sup>5</sup>, Fany Sardenne<sup>5</sup>, Maria Rose<sup>1</sup>, Paco Bustamante<sup>2,6</sup>, Nathalie Bodin<sup>1,7,8\*</sup>

<sup>1</sup> Seychelles Fishing Authority (SFA), Fishing Port, Victoria, Mahe, Republic of Seychelles

<sup>2</sup> Littoral Environnement et Sociétés (LIENSs), UMR 7266 CNRS - La Rochelle Université, 2 rue Olympe de Gouges, 17000 La Rochelle, France

<sup>3</sup> CSIRO Oceans and Atmosphere, Hobart, Tasmania, Australia

<sup>4</sup> CSIRO Oceans and Atmosphere, Brisbane, Australia

<sup>5</sup> Univ Brest, CNRS, IRD, Ifremer, LEMAR, IUEM, F-29280, Plouzané, France

<sup>6</sup> Institut Universitaire de France (IUF), 1 rue Descartes 75005 Paris, France

<sup>7</sup> Institute for Research and Development (IRD), Fishing Port, Victoria, Mahe, Seychelles

<sup>8</sup> Sustainable Ocean Seychelles (SOS), BeauBelle, Mahe, Republic of Seychelles

\*Email: [natbod@gmail.com](mailto:natbod@gmail.com)

**Author's contribution:**

Conceptualization: N Bodin;

Funding acquisition: N Bodin, R Govinden;

Data acquisition: N Bodin, R Govinden, M Rose, MA Sabino, F Sardenne, F Legrand;

Statistical analysis: MA Sabino, H Pethybridge, L Blamey;

Writing – 1st draft: MA Sabino;

Review & editing: all co-authors.

**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.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Journal Pre-proof