

Diets of spiny lobsters from Mahé Island reefs, Seychelles reefs inferred by trophic tracers

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Abstract :

Spiny lobsters (*Panulirus longipes*, *P. penicillatus* and *P. versicolor*) are an important resource in Seychelles, where they inhabit coastal carbonate and granite reefs that have been impacted by multiple coral bleaching events over the past two decades. Little is known about their biology and ecology in this region. Interspecific competition for food resources was previously suggested, but no quantitative data on the diets of spiny lobsters were available. Using carbon and nitrogen stable isotope compositions and fatty acid profiles of three spiny lobster species and their potential prey, a Bayesian mixing model for diet estimation was applied to compare the diet proportions of spiny lobsters among species and between reef types (carbonate and granite reefs). Model outputs suggested the three lobster species consume mainly crustaceans (*Anomoura* hermit crabs; half of the diet), then Echinoidea (sea urchins), algae and molluscs. *P. versicolor* was found to consume slightly more molluscs and algae than the two other studied species, which was consistent with its lower trophic level (2.4 vs 2.8 for the two other species). Trophic level did not increase with carapace length of spiny lobsters, but large individuals had higher carbon isotopic values suggesting that they might feed closer to the coast or more on detritus feeders than their smaller congeners. Diets of spiny lobsters were fairly similar between carbonate and granite reefs, except that lobster inhabiting granite reefs consumed more sea urchins. While our overall findings were consistent with gut contents of *Panulirus* spp. from other world regions, they should be confirmed, as the discrimination of several prey based on trophic tracers was low, which increased mixing model uncertainty.

Keywords : Fatty acids, Stable isotopes, Bayesian mixing model, *Panulirus* sp, tropical reef habitats, Western Indian Ocean.

42 1. Introduction

44 To maintain ecosystems in a healthy, productive, and resilient condition, several elements
affecting species populations should be considered, such as interactions with other species or
environmental changes (Pikitch et al., 2004). To reach this goal, ecosystem-based fisheries
46 management requires fisheries research to account for relationships between target species and
their habitats, including trophic interactions (Bellchambers et al., 2010; Tam et al., 2017).

48 Spiny lobsters *Panulirus longipes*, *P. penicillatus* and *P. versicolor* are important
ecological, social and economic resources in the Seychelles Archipelago, a small island state in the
50 Western Indian Ocean (Fig. 1). They are found on shallow coral and granite reefs and in recent
years, recurrent coral bleaching events have resulted in the loss of coral cover and structural
52 complexity on these reefs and an increase in macroalgae cover (Graham et al., 2006; Harris et al.,
2014). Although variable depending on the year, approximately three metric tons of spiny lobster
54 (*P. longipes*, *P. penicillatus* and *P. versicolor*) are landed each year by the artisanal fishery (Barret,
2019), most of it being sold to local hotels and restaurants. Declines in catch per unit effort (CPUE)
56 (24%) in the 2016-2017 season, and continued suppressed CPUE from independent fishery surveys
have resulted in a temporary closure of the fishery (SFA Fisheries Research Section, 2019), and
58 highlighted the need for an ecosystem-based approach to fishery management, particularly given
the new ecological conditions, i.e. recurrent coral bleaching events and likely habitat modification.

60 Despite the importance of spiny lobsters for the Seychelles, little is known about their
biology and ecology in the region (Barret, 2019). As part of a precautionary approach to fisheries
62 management, a number of management measures are in place, including the prohibition of traps to
catch lobsters (they may only be caught using snorkelling) (Payet and Isidore, 2002). This avoids
64 a possible modification of the diet toward bait, as has been observed in Western Australia
(MacArthur et al., 2011). However, the diet of spiny lobsters in the region remains unknown. A
66 recent study based on trophic tracers, i.e. carbon and nitrogen stable isotope compositions (SI; $\delta^{13}\text{C}$

and $\delta^{15}\text{N}$) and fatty acids (FAs) profiles, compared trophic niches of three spiny lobster species and found a high probability of dietary competition among these species (Sabino et al., 2020). While this study did not analyse the potential prey of spiny lobsters, results were consistent with the content analysis of *Panulirus* spp. in other world regions: *Panulirus* spp. are opportunists, mainly feeding on crustaceans and molluscs, and to a lesser extent on red algae (Briones-Fourzán et al., 2019; Castañeda-Fernández-de-Lara et al., 2005; Joll and Phillips, 1984; Mashai et al., 2001). However, the proportion of algae might be underestimated due to a rapid gastric evacuation (< 12 h ; Waddington, 2008). Additionally, the predominant benthic habitat surrounding a reef can be an important source of variation for the diet of spiny lobsters (Blamey et al., 2019; Goñi et al., 2001; MacArthur et al., 2011). Similar variability in diet probably occurs for spiny lobsters from Seychelles, as their potential for dietary competition was higher in granite reefs than in carbonate reefs (Sabino et al., 2020), probably in relation to the higher prey diversity in carbonate reefs (Robinson et al., 2019). However, quantitative diet studies are needed to better describe their trophic ecology while considering their different types of reef habitat in Seychelles.

SI and FAs are intrinsic ecological tracers commonly used to infer assimilated diet in consumers (Ramos and González-Solís, 2012), including in spiny lobsters (e.g. Blamey et al., 2019; Guest et al., 2009; Sabino et al., 2020; Waddington et al., 2008). $\delta^{13}\text{C}$ values allow for the discrimination of habitat types (e.g. coastal vs offshore, the latter being characterised by more negative $\delta^{13}\text{C}$ values; France, 1995) and $\delta^{15}\text{N}$ values inform on the species' trophic level due to a ^{15}N enrichment with increasing trophic levels (Vander Zanden et al., 1997). SI reflect the diet of spiny lobsters in the last three months (Waddington and MacArthur, 2008). FAs makeup lipids, and FAs of fat depots such as the hepatopancreas in crustaceans, reflect the FA profiles of prey assimilated by consumers in the last few days to weeks, depending on species (Antonio and Richoux, 2016; Shu-Chien et al., 2017). Both SI and FA data can be used for the quantitative diet

reconstruction through mixing models (e.g. Jankowska et al., 2018; Neubauer and Jensen, 2015; Young et al., 2018).

The objective of this study was to compare the trophic ecology of the three tropical spiny lobsters commonly caught in the Seychelles (*P. longipes*, *P. penicillatus* and *P. versicolor*) using SI and FA data from spiny lobsters and their potential prey. Specifically, we were interested in (1) what are the main preys of spiny lobster in Seychelles, (2) do diet and trophic level differ between spiny lobster species, and (3) does spiny lobster diet differ between reef types (carbonate vs granite reefs)?

2. Material and methods

2.1. Organism collection

Spiny lobsters and their potential prey were collected from the shallow coastal waters from reefs around the coast of Mahé, the main island of the Seychelles Archipelago, home to around 90% of the country's population, and supporting 60% of the licensed lobster fishermen. Based on literature (Table S1), potential lobster prey (n=74 individuals from 13 species and 7 phylogenetic classes) were collected by scuba-divers at four sites (maximum 10 meters depth) (Fig. 1) in April 2018 and October 2019. Spiny lobsters (26 *P. longipes*, 31 *P. penicillatus* and 7 *P. versicolor*) were collected by divers on snorkel from 15 sites (12 granite and 3 carbonate reefs) in October 2018 and May 2019 (Table 1). Granite reefs are granitic rocky reefs with coral growth on the granite substrate, and carbonate reefs are continuous carbonate fringing reefs (Harris et al., 2014). Note that many carbonate reefs have deteriorated or collapsed following multiple coral bleaching events (Obura et al., 2017) and therefore most lobsters in our study were found on granitic reefs. All organisms were frozen at -80°C immediately after collection until further processing (less than seven days after collection) at the Seychelles Fishing Authority Research Laboratory. For spiny lobsters, a sample of hepatopancreas (for FA analysis) and a sample of tail muscle (for SI analysis) were carefully

116 dissected from the organism. Potential prey were identified to species level whenever possible and
their tissues were sampled for both FA and SI analysis. For echinoderms, a sample of muscle was
118 carefully dissected from the Aristotle's lantern; for bivalves, gastropods and anomurans (decapod
malacostracans - hermit crabs), the whole body tissue was collected after removing the shells;
120 finally, polyps of *Palythoa* (anthozoan) were kept whole and algae (green algae of the Chlorophyta
phylum; brown algae of the Ochrophyta phylum; and red algae or Rhodophyta) were kept with
122 their small epiphytes (< 1 mm).

All prey and spiny lobster samples were then kept at -80°C for a maximum of five months, freeze-
124 dried for 72 hours, then ground to a homogeneous powder with a ball mill, and stored again at -
80°C prior to subsequent analysis.

126

2.2. Stable isotope analysis

128 For potential prey items, carbon isotope composition was analysed on a subsample acidified with
HCl at 0.5 to 2 N (according to the effervescence) to remove carbonate, then rinsed three times
130 with distilled water, and freeze-dried for 48 hours. Nitrogen isotope composition was analysed on
a subsample of the bulk powder. For lobster muscle, the bulk powder was analysed for both carbon
132 and nitrogen isotope composition, as the muscle did not contain carbonate neither high lipid content
(fat content is 0.7% wet weight and C:N ratio remains < 3.5). Acidified and bulk powders were
134 weighted into tin capsules and analysed by continuous flow on a Flash EA2000 elemental analyser
coupled to a Delta V Plus isotope ratio mass spectrometer (Thermo Fisher scientific) at the Pôle
136 Spectrométrie Océan, University of Brest, France, or on a Flash EA1112 elemental analyser
coupled to a Delta V Advantage isotope ratio mass spectrometer (Thermo Fisher scientific) at the
138 LIENSs stable isotope facility, University of La Rochelle, France. Calibrations were based on
reference materials (IAEA-600, IAEA-CH-6 and IAEA-N-2). Results were reported in the δ unit
140 notation and expressed as parts per thousand (‰) relative to the international standards

(atmospheric N₂ for nitrogen and Vienna-Pee Dee Belemnite for carbon). Analytical precision based on replicate measurements of acetanilide was < 0.15 ‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at both laboratories. Inter-laboratory replicate measurements on reference materials (n=9), acetanilide (n=3), urea (n=3), casein (n=3), and lobster samples (n=3) found no significant differences in results between laboratories, with all differences below the analytical precision (< 0.15 ‰). C:N ratios were determined from % element weights.

2.2. Fatty acid analysis

Subsamples of dry powders (n=141) were treated as described in Sardenne *et al.* (2019). Lipids were extracted from 50-100 mg of dry tissue with 6 mL of CHCl₃:MeOH (2:1, v/v) mixture directly added into glass vials. Extracts were flushed with nitrogen, vortexed, sonicated for 15-20 minutes, and stored for 24 hours at -20°C. Tricosanoic acid (23:0) was added as an internal standard to 2 mL of lipid extract. Total lipids were transesterified with 800 μL of H₂SO₄ (3.8 % in MeOH) at 100°C for 10 min then washed with hexane-saturated distilled water. Fatty acid methyl esters (FAME) and dimethyl acetals (DMA; from vinyl ether lipids) were separated and quantified on a Varian CP8400 gas chromatography equipped with a Zebron ZB-WAX column (30 m length, 0.25 mm internal diameter, 0.25 μm film thickness; Phenomenex) and a flame ionisation detector at the Lipidocean facility, University of Brest, France. Samples were injected in splitless mode at 280°C and carried by hydrogen gas. The oven temperature was raised from 60°C to 150 °C at 50 °C.min⁻¹, to 170 °C at 3.5 °C.min⁻¹, to 185 °C at 1.5 °C.min⁻¹, to 225 °C at 2.4 °C.min⁻¹ and then to 250°C at 5.5 °C.min⁻¹. FAMES were identified by comparing sample retention times to those of four external standard mixtures (37-components, BAME, PUFA no. 1, and PUFA no. 3 FAME mix; Supelco) using Galaxie 1.9.3.2 software (Varian). The mean analytical variability of the method was 8.1%, based on Supelco 37-component FAME mix routinely checked. Individual FA results were expressed as a percentage of the total identified FAs, for 44 FAs accounting for > 1.5% in at

166 least two samples. Total fat content was calculated as the sum of individual fatty acids (based on
23:0 concentration) and expressed in $\mu\text{g}\cdot\text{mg}^{-1}$ of dry tissue.

168

2.3. Data analysis

170 2.3.1. Fractionation factors (FFs) and trophic level calculation

Calculations of trophic levels and Bayesian mixing model include FFs (also called ‘trophic
172 enrichment factors’ or ‘trophic discriminant factors’) to take into account for isotopic enrichment
in heavier isotopes (^{13}C and ^{15}N) between successive trophic levels, i.e. between consumers and
174 their prey. Although FFs are commonly set to 0.5‰ and 3.5‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in marine systems,
respectively, FFs are influenced by biological factors (e.g., species, tissue, age, food nutrients)
176 (McCutchan et al., 2003; Vander Zanden et al., 2001) and a large range of FF values have been
used to compute the trophic level of spiny lobsters based on $\delta^{15}\text{N}$ values: e.g. 3.5‰ for *Jasus*
178 *edwardsii* (Guest et al., 2009), 2.6‰ for *P. cygnus* (Waddington et al., 2008). To better take into
account FFs variability in the Seychelles marine food web, FFs were estimated for each potential
180 prey of spiny lobster with simple linear regressions, as FFs tend to decrease with increasing isotopic
ratios of prey (Caut et al., 2009). FFs estimation was thus based on the isotopic values of potential
182 prey, and a diet experiment on *P. cygnus* (Waddington and MacArthur, 2008) ([Fig. S1b](#)). The
obtained FFs were used to compute the trophic levels of spiny lobsters (see below) and included in
184 the Bayesian mixing model (see section 2.3.2).

Trophic levels were calculated relative to the $\delta^{15}\text{N}$ values of macroalgae (red, green and brown
186 algae, average $\delta^{15}\text{N} = 6.5 \pm 0.5$ ‰, n=18), according to the following equation:

$$\text{Trophic level} = \frac{\delta^{15}\text{N}_{\text{spiny lobster}} - \delta^{15}\text{N}_{\text{macroalgae}}}{FF_{15\text{N}}} + 1$$

188 with FF_{15N} the average FF for ^{15}N between lobster tail muscle and macroalgae previously computed
from [Fig. S1b](#): $FF_{15N} = 2.9 \pm 0.4\%$. This calculation assumes the isotopic baseline to be the same
190 for the three spiny lobster species.

192 2.3.2. Diet estimation using mixing modelling method

A Bayesian mixing model was run to estimate the proportional contribution of sampled prey to the
194 diet of spiny lobsters, based on SI values and FA profiles summarized through PCA. Because the
discriminatory power of mixing models starts to decline above six or seven potential prey items
196 (Phillips et al., 2014), the prey species (n=13) were grouped as much as possible while respecting
the phylogeny (n=9 classes) ([Table 2](#)). The model was run with two different groupings to compare
198 (i) the diet among the three spiny lobster species, and (ii) the diet of spiny lobsters between reef
types (granite vs carbonate reefs, regardless of the species because of low sample size and
200 unbalanced design). The Bayesian mixing model included three types of parameters that were set
as follow:

202 (i) *Fractionation factors*. For SI, FFs were obtained as described in section 2.3.1. For FA
profiles, FFs were set to 0 as the bioconversion of FA was assumed to be negligible in the
204 hepatopancreas of spiny lobster due to its high proportion of dietary lipids (Shu-Chien et
al., 2017).

206 (ii) *Concentration dependencies*. Disparities among prey in the concentrations of trophic
tracers induce different contributions of each prey to consumers' values (Phillips and
208 Koch, 2002). Percent of carbon and nitrogen elements and total fat content were thus
included for each potential prey.

210 (iii) *Priors*. Model priors on diet source proportions should be included when potential sources
have similar values of trophic tracers (Franco-Trecu et al., 2013). Priors on the nine prey

212 class proportions were thus included, based on the literature on stomach content for
213 *Panulirus* species ([Table S1](#)).

214 Samples for the posterior distributions were drawn by Markov Chain Monte Carlo (MCMC)
simulation methods (10,000 iterations, 4 parallel MCMC chains, and 1,000 burn-in rate). Model
216 convergence diagnostics are presented in [Fig. S2](#). Strong negative correlations between prey
proportions may impair model estimations. To avoid this and to obtain a comprehensive overview
218 of lobsters' diet, proportions of prey classes were grouped *a posteriori* (Phillips et al., 2014) on a
phylogenetic basis (i.e. Mollusc for Bivalvia and Gastropoda classes; Algae for Chlorophyta,
220 Ochrophyta and Rhodophyta phylum).

222 2.3.3. Variability in trophic tracers and diet estimations

Factors explaining variability in trophic tracers were assessed using ANOVA for univariate data
224 (trophic level, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values), and PERMANOVA for multivariate FA profiles (non-
transformed data). SIMPER analysis was used to detect FAs that contribute the most to differences
226 among groups. For potential prey, the influence of the two fixed factors 'Class' (nine phylogenetic
classes) and 'Reef type' (granite vs carbonate reefs) was assessed. For spiny lobsters, the influence
228 of 'Species' (*P. longipes*, *P. penicillatus*, and *P. versicolor*), 'Reef type' (granite vs carbonate
reefs), 'Carapace length' and the interaction 'Species*Carapace length' were considered as fixed
230 factors. Homogeneity of residuals was tested with Levene's test. Since homogeneity was found for
all groups, parametric post hoc Tukey HSD tests were used to refine differences among groups.
232 Diet estimations, i.e. outputs from the Bayesian mixing model, were compared among spiny lobster
species and between reef types in the Bayesian framework (no test value, only probabilities were
234 reported).

Data analyses were performed using R software 3.5.0 (R Development Core Team et al., 2018),
236 the JAGS program, and the “simmr” package (Parnell et al., 2013). All results are reported as
means \pm SD.

238

3. Results

240 3.1. Variability in trophic tracers among potential lobster prey

Among the potential prey of spiny lobsters, the phylogenetic species class (i.e. ‘Class’) explained
242 most of the variability in trophic tracers, while reef type explained no difference. $\delta^{13}\text{C}$ values varied
between species’ class ($F=39.6$, $df=8$, $p<0.001$; 83.4% of explained variability), with values
244 ranging from $-23.8 \pm 0.7\text{‰}$ for green algae of the Ulvophyceae class (*Chlorodesmis* spp.) to -10.8
 $\pm 1.6\text{‰}$ for brown algae of the Phaeophyceae class (*Turbinaria decurrens*) (Fig. 2a). Reef type
246 explained 0.5% of the variability in $\delta^{13}\text{C}$ values ($F=2.0$, $df=1$, $p=0.16$). Similarly, $\delta^{15}\text{N}$ values
varied between species’ class ($F=59.2$, $df=8$, $p<0.001$; 88.2% of explained variability), with values
248 ranging from $6.0 \pm 0.4\text{‰}$ for *Turbinaria decurrens* to $12.4 \pm 0.1\text{‰}$ for the Echinoidea class (sea
urchin *Echinothrix diadema*) (Fig. 2a). The reef type explained only 0.1% of the variability in $\delta^{15}\text{N}$
250 values ($F=0.3$, $df=1$, $p=0.59$). Regarding FA profiles, species’ class and reef type explained 85.1%
($\chi^2=645.9$, $df=8$, $p < 0.001$) and 0.3% ($\chi^2=1.9$, $df=1$, $p = 0.17$) of the variability, respectively. PCA
252 projection captured 39.5% the variability in FA profiles with 16:0, 18:0 DMA, 18:4n-1, 20:1n-11,
20:5n-3, and 22:5n-6 the six main discriminant FAs (Fig. 2b). PCA highlighted differences in FA
254 profiles according to the phylogenetic groups: (i) the algae group (including Chlorophyta,
Phaeophyceae, and Rhodophyta phylums; PCA’ bottom left panel) with the highest levels in 14:0,
256 16:0, 16:1n-7, and 18:3n-6; (ii) the Arthropod phylum (Malacostraca class; PCA’ top left panel), with
the highest levels in 18:1n-7, 20:4n-6 and 20:5n-3; (iii) the Mollusc phylum (Bivalvia and
258 Gastropoda classes; PCA’ right panels), with the highest levels in three nonmethylated interrupted

(NMI) FAs (22:2 NMI (7,13), 22:2 NMI (7,15), and 22:3 NMI), 16:1n-7 DMA, 22:1n-11, 22:5n-
260 3, and 22:4n-6; (iv) the Echinoderm phylum (Echinoidea class; PCA' top right panel), with the
highest levels in 18:0; and (v) the Cnidaria phylum (Anthozoa class), rich in 18:4n-1 ([Fig. 2b](#);
262 [Table 2](#)).

264 3.2. Variability in trophic tracers among spiny lobsters

Regarding carapace length, individuals ranged from 60.2–143.2 mm CL with *P. penicillatus*
266 significantly larger than *P. longipes* and *P. versicolor* ($F=17.2$, $df=2$, $p < 0.001$; [Fig. 3a](#)). Regardless
of species and due to unbalanced sampling design, individuals from both reef types were of similar
268 carapace length (101.3 ± 27.1 and 88.8 ± 16.7 mm CL for carbonate and granite reefs, respectively;
 $F=3.6$, $df=1$, $p = 0.06$). *P. penicillatus* tended however to be larger in carbonate than in granite reefs
270 (Table 1). Regarding $\delta^{13}\text{C}$ values, studied individuals ranged from -15.3 to -12.2‰ with no
difference observed among species, reef type, or interaction between species and carapace length
272 ($F=2.2$, $df=2$, $p = 0.13$; $F=0.3$, $df=1$, $p = 0.58$; and $F=2.3$, $df=2$, $p = 0.11$, respectively). However,
 $\delta^{13}\text{C}$ values increased with carapace length (slope = 0.02 ; $R^2 = 0.25$; $F=12.6$, $df=1$, $p < 0.001$;
274 16.0% of explained variability), from -14.3 ± 0.6 ‰ below 80 mm CL to -13.0 ± 0.3 ‰ above 120
mm CL, especially for *P. penicillatus* (slope = 0.02, $R^2=0.20$; $F=8.6$, $df=1$, $p < 0.01$; [Fig. 4](#)).
276 Regarding trophic level, studied individuals ranged from 2.3 to 3.1, and only an inter-specific
difference was detected ($F=32.1$, $df=2$, $p < 0.001$; 51.9% of explained variability), *P. versicolor*
278 having a significantly lower trophic level than the two other species (mean trophic level of 2.4 vs.
2.8; [Fig. 3b](#)). No influence of carapace length, reef type, or interaction between species and
280 carapace length on the trophic level was detected ($F=0.1$, $df=1$, $p = 0.94$; $F=2.0$, $df=1$, $p = 0.17$; and
 $F=0.3$, $df=2$, $p = 0.75$, respectively). Regarding FA profiles, only the carapace length was found to
282 be an influencing factor ($\chi^2=17.8$, $df=1$, $p < 0.001$; 7.2% of explained variability). No influence of

species, reef type, or interaction between species and carapace length on FA profiles was detected
284 ($\chi^2=4.1$, $df=2$, $p = 0.13$; $\chi^2=0.4$, $df=1$, $p = 0.55$; and $\chi^2=3.3$, $df=2$, $p = 0.19$, respectively).

286 3.3. Mixing model outputs

3.3.1. Model diagnostics

288 MCMC chains of the mixing model did converge to 1. However, *a posteriori* groupings were
required due to negative correlations between Malacostraca and Phaeophyceae (Pearson's
290 correlation coefficient r ranged from -0.57 to -0.92 according to lobster species and reef type), and
to a lesser extent between Echinoidea and Malacostraca or Gastropoda. Despite the grouping of
292 Chlorophyta, Ochrophyta, and Rhodophyta (under the 'Algae' group) and of Gastropoda and
Bivalvia (under the 'Mollusc' group), a strong negative correlation remained for some groups (r of
294 -0.87 between Malacostraca and Alga and of -0.69 between Echinoidea and Mollusc; [Fig. S2](#)),
indicating the low discrimination of these groups in lobster diets and the possible overestimation
296 of Malacostraca and Echinoidea proportions over Algae and Mollusc proportions in the spiny
lobsters' diet.

298

3.3.2. Model outputs

300 *Inter-specific comparisons.* Similar trends were observed for the three spiny lobster species, with
Malacostraca identified as their main prey (average proportion: 47-63% of the diet), followed by
302 Echinoidea (16-32% of the diet), Algae (8-18% of the diet), Mollusc (5-17% of the diet), and
Anthozoa (1-2% of the diet) ([Fig. 5a](#)). Due to large distributions in model outputs, dietary
304 proportions of most potential prey were similar among spiny lobsters (at $\alpha=0.05$). For instance,
dietary proportions for Malacostraca were as follows: *P. penicillatus* 63±14%, *P. longipes*

306 48±10%, and *P. versicolor* 47±12%, with 81.7% and 90.7% probability that *P. penicillatus*
consumed more Malacostraca than *P. longipes* and *P. versicolor*, respectively. Noticeable
308 differences mainly concerned *P. versicolor*: (i) 94.8% and 88.3% probability that *P. versicolor*
consumed less Echinoidea than *P. longipes* and *P. penicillatus*, respectively; (ii) 78.6% and 83.6%
310 probability that *P. versicolor* consumed more Mollusc than *P. longipes* and *P. penicillatus*,
respectively, and (iii) 50.2% and 66.2% probability that *P. versicolor* consumed more Algae than
312 *P. longipes* and *P. penicillatus*, respectively ([Fig. 5a](#)).

314 *Reef habitats comparison.* Spiny lobsters caught from both carbonate reefs (n=7) and granite reefs
(n=57) were found to mainly feed on Malacostraca (half of their diets; [Fig. 5b](#)). However, spiny
316 lobsters from granite reefs had 83.9% and 92.4% probability of feeding more on Echinoidea and
less on Molluscs than their congeners from carbonate reefs, respectively ([Fig. 5b](#)).

318

4. Discussion

320 The diet of three spiny lobsters (*Panulirus* spp.) from Mahé Island, Seychelles was investigated
based on SI compositions and FA profiles of muscle and hepatopancreas, respectively, and their
322 potential prey, using a Bayesian mixing model. Based on model outputs, half of the diet for all
three lobster species consisted of Malacostraca. Increasing $\delta^{13}\text{C}$ values with increasing carapace
324 length suggested that spiny lobsters might feed closer to the coast or more on detritus feeders with
increasing size length, and individuals from carbonate reefs fed more on Molluscs than those from
326 granite reefs. The main inter-specific difference observed was the lower trophic level of
P. versicolor, related to its higher consumption of algae and molluscs than the two other species.

328

4.1. Diet of spiny lobsters from reefs of Mahé Island

330 Diet estimations from the mixing model were based on trophic tracers, and thus correspond to a diet assimilation over several days to months, based on turnover rates of SI and FA muscle and
332 hepatopancreas (Antonio and Richoux, 2016; Waddington and MacArthur, 2008). According to the mixing model, diet profiles of the three spiny lobster species were similar, with
334 Malacostraca: Anomura (hermit crabs) found to be their main prey. A similar finding has been observed from a reef lagoon of Puerto Morelos, Mexico, where hermit crabs and brachyurans were
336 the main prey in the gut contents of *P. argus* juveniles (Briones-Fourzán et al., 2003). Preponderance of crustaceans in the diet of spiny lobsters has been observed in several *Panulirus*
338 spp., usually in similar proportions to those of molluscs, depending on environmental factors such as reef type, season etc. (Table S1). In our study, molluscs (gastropods + bivalves) ranked third to
340 fourth in main prey items of spiny lobsters, which was lower than expected based on data from the literature (first to third main prey; Table S1). Around Mahé Island, bivalves do not form dense
342 settlements (Selin et al., 1992; Taylor, 1968) and represent less than 14% of molluscs, which are dominated by gastropods (Barnes et al., 2009). It may explain why few bivalves were found by
344 divers at the sampled sites (only the oyster *Pinctada margaritifera*). Consequently, bivalves contributed to a low proportion of the Seychelles spiny lobster' diets (< 10% of the diets whatever
346 the species), while they can be an important food source of *Panulirus* spp. in other regions of the world (e.g. Gulf of Mexico, Baja California; Table S1) and of other spiny lobsters e.g. *Jasus* spp.
348 (Mayfield et al., 2000; Pollock, 1979). Echinoidea (sea urchins) were found to be an important diet component for the three species (16–32% of the diet). Our results are in accordance with
350 observations from other regions, although Seychelles spiny lobsters seemed to rely more on Echinoidea compared to the 4–28% and 4–8% gut volume for *P. guttatus* and *P. argus* from
352 Yucatan peninsula, Mexico, respectively (Briones-Fourzán et al., 2019). This relatively high consumption of sea urchin could be related to the high abundance of sea urchins in shallow areas

354 around Mahé Island (Pittman, 1996) and has already been suggested based on the high 20:4n-6
levels of both sea urchins and spiny lobsters in Seychelles (Sabino et al., 2020; Sardenne et al.,
356 2017). However, spiny lobsters from granite reefs seemed to feed more on Echinoidea and less on
molluscs than individuals from carbonate reefs, while sea urchins are mainly found in patchy reefs
358 of Mahé Island, i.e. reefs with a sand, rock or rubble base (Jan-Claas, 2020). This suggests spiny
lobsters might move between reef types, despite narrow home ranges being suspected for these
360 species and similar to results from related species (650 m² per week based on 50% utilisation
distribution of *P. interruptus* from California, USA; Withy-Allen and Hovel, 2013).

362 Interspecific differences in diet proportions were small, but *P. versicolor* consumed slightly more
algae than the two other species, which is consistent with its lower trophic level (2.4 vs. 2.8). This
364 dietary difference could help to reduce interspecific competition, as even a small difference in
trophic level favoured co-occurrence between *Panulirus* species on Caribbean reefs (Segura-García
366 et al., 2016). Overall, the trophic levels of Seychelles spiny lobsters (ranging from 2.3 to 3.1, n=64)
were similar to those derived from $\delta^{15}\text{N}$ values for *P. cygnus* from Western Australia (1.9–2.2)
368 (Waddington et al., 2008) and *Jasus edwardsii* from New Zealand (2.5–4.0) (Jack and Wing, 2011).
Such large ranges highlight the lobster's diet plasticity and their opportunistic feeding behaviour
370 ([Table S1](#)). Regardless of the species, no ontogenetic change in trophic level was observed (i.e. no
correlation between $\delta^{15}\text{N}$ derived trophic level and carapace length). In contrast, $\delta^{13}\text{C}$ values
372 increased with spiny lobster size, indicating that large individuals may feed closer to the coast or
more on prey with a strong benthic affinity (e.g. prey feeding on benthic organic matter with high
374 $\delta^{13}\text{C}$ values) than their smaller/younger congeners. While limited information is available on
lobster size distribution with bathymetry in shallow areas, ontogenetic changes in dietary
376 preferences are known for other spiny lobster species: e.g. it was observed for *Jasus paulensis*, *J.*
lalandii and *P. cygnus* (Blamey et al., 2019; Dumas et al., 2013; Haley et al., 2011; Mayfield et
378 al., 2000). However, size related changes either in spatial distribution or in diet remain to be

detangled. The size ranges of the three species were too narrow in the present study to define size classes to be included in the mixing model, but it would be interesting to explore this aspect further by including juveniles in the dataset.

4.2. Study caveats

Caveats regarding mixing model outputs should be highlighted, since uncertainties in the estimated dietary proportions of algae, Malacostraca, and Echinoidea remain strong despite *a posteriori* aggregations of specific prey classes, which could thus bias the results. These uncertainties have two main origins: (i) a low discrimination of some potential prey based on their SI compositions and FA profiles. Using additional trophic tracers such as sulphur or mercury stable isotopes might improve this discrimination (e.g. Higgs et al., 2016; Jack et al., 2009); and (ii) the influence of FF parameters, which were estimated from linear regressions based on one diet experiment only. Additional diet experiments would be required to accurately estimate FFs (for both SI and FAs) and thus increase robustness of the model setup as previously highlighted (Brett et al., 2016; Phillips et al., 2014).

Apart from the model parameters, more samples of spiny lobsters from carbonate reefs and of juveniles/small adults is needed. Due to loss of carbonate reefs in the region, samples of lobsters from this habitat was small and could prevent detection of any differences between reef types and ontogenetic stages. Some potential prey were also probably missing, especially bivalve and decapod species, which have reduced contributions to lobster's diets.

4.3. Future directions

Several integrated trophic indicators are particularly suitable for the implementation of an ecosystem-based fisheries management, including the monitoring of trophic levels of catches and the mean number of trophic links per species (Tam et al., 2017). The present study will provide a

404 baseline for trophic level of spiny lobsters from Seychelles and might initiate monitoring. For
instance, the seasonal monitoring of trophic level would help to detect diet shifts in the past few
406 months (e.g. following coral bleaching or after the fishing season). For the sampling to be non-
lethal, muscle tissue can be sampled from the last segment of the fourth walking leg (ca. 0.5 g of
408 wet tissue is required), which will start to grow again at the next molt, as after natural autotomy.
Monitoring may also allow trophic links per spiny lobsters species to be identified, especially
410 regarding (i) potential shift in the diets of spiny lobsters before and after coral bleaching on
carbonate reefs, as the dietary competition among spiny lobsters has increased after the coral
412 bleaching event of 2016 (Sabino et al., 2020); and (ii) the influence of predator abundance, by
comparing diets in heavily fished and protected regions throughout the ontogeny of spiny lobsters.
414 Spiny lobsters have several predators especially at juvenile stage, such as octopus, small sharks,
groupers, and snappers, which influence their sheltering and foraging behaviours (Ellis, 2018;
416 Smith and Herrkind, 1992).

418 **Conclusion**

Spiny lobsters from Seychelles are generalist feeders that appear to mainly feed on crustaceans,
420 sea urchins and algae. Dietary differences related to species, reef type and ontogeny were weak,
but *P. versicolor* had a lower trophic level than the two other species. Lobsters from carbonate
422 reefs fed more on Molluscs than those from granite reefs, and large lobsters probably fed closer to
the coast or more on detritus feeders than the small ones. These results should however be refined
424 by including more individuals (including size ranges) and prey types, trophic tracers, and
parameters from diet experiments.

426

428 Acknowledgments

430 This work is a contribution to the project SEYCCAT-BGF1/L/N6 “*Science based restoration of*
431 *commercially important spiny lobster habitats to help develop a sustainable fishery*” led by the
Marine Conservation Society Seychelles (MCSS); and to the Seychelles Participatory Lobster
432 Monitoring Programme (PLMP) led by the Seychelles Fishing Authority (SFA). The project
benefited from the financial support of the Seychelles' Conservation and Climate Adaptation Trust
434 (SEYCCAT), the Seychelles Gouvernement, the European Fisheries Partnership Agreement (EU-
FPA), and the Institute for Research and Development (IRD). The authors would like to thank the
436 lobster fishermen and the R.V. L’Amitie crew who assisted with sampling, and are grateful to G.
Guillou from the Plateforme Analyses Isotopiques of LIENSs (University of La Rochelle, France)
438 for his support in the lobster stable isotope analysis.

440 Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

442

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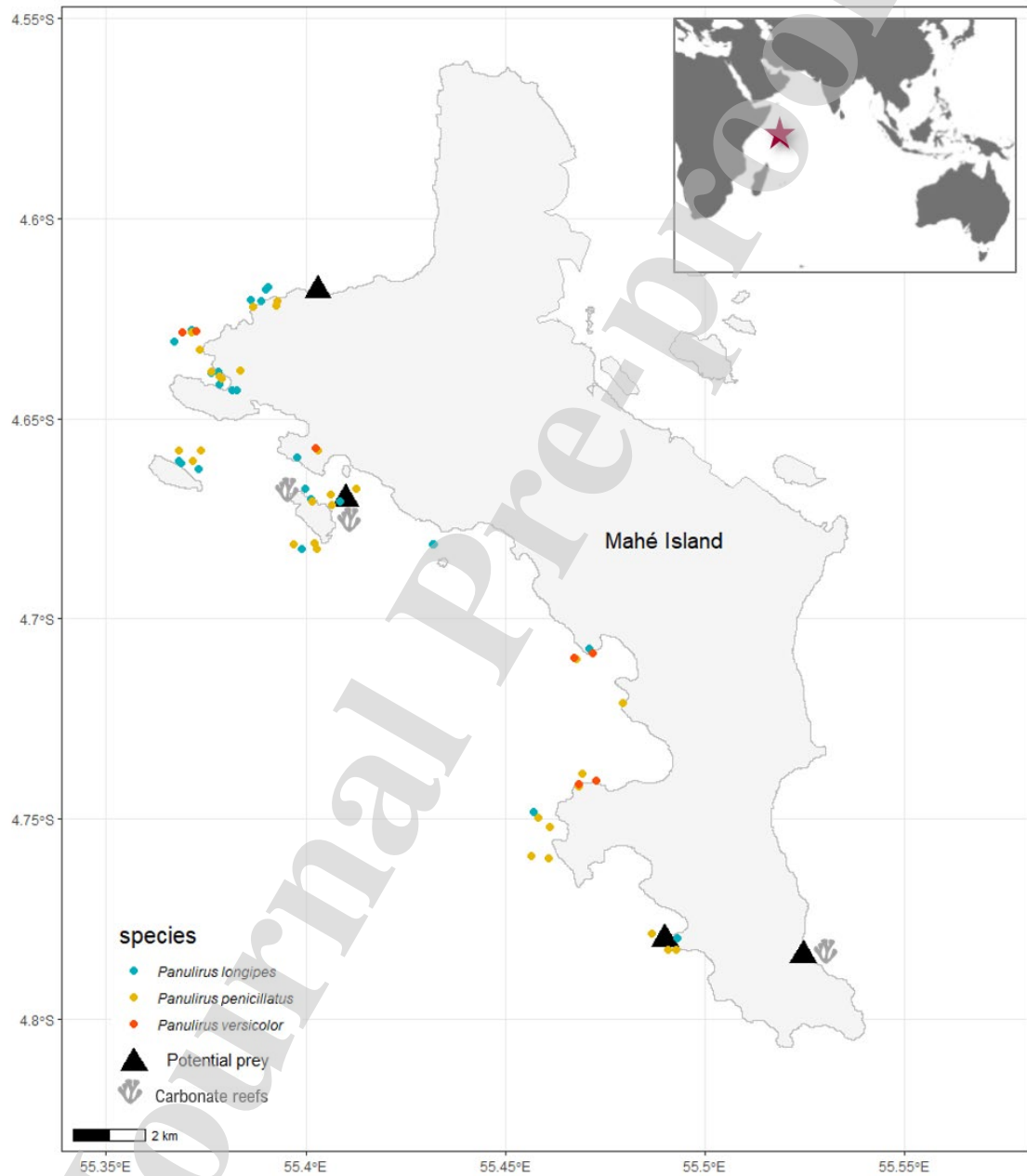
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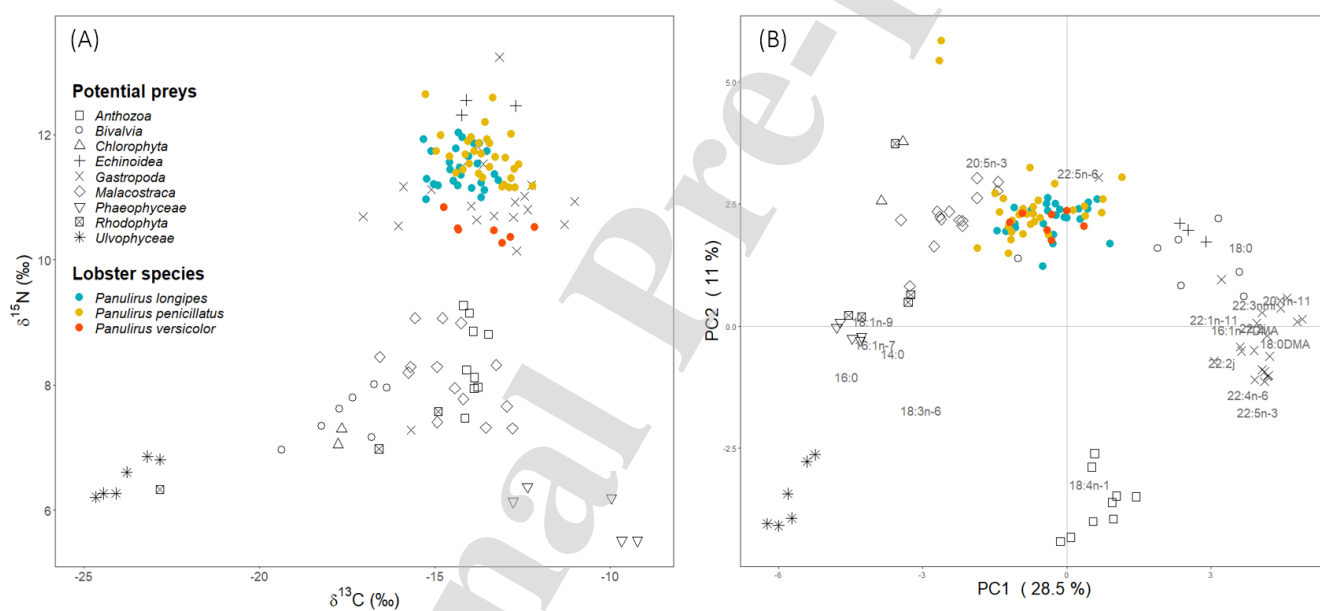
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628 **Figure 1.** Sampling sites of spiny lobsters *Panulirus longipes*, *P. penicillatus* and *P. versicolor*
 and their potential prey collected from the coastal shallow waters of the west coast of Mahé
 630 Island, Seychelles, located in the Western Indian Ocean (red star on the top right panel). Sites
 correspond to granite reefs unless specified (three carbonate reefs).



632

634 **Figure 2.** Trophic tracers of spiny lobsters and their potential prey presented with (A) a biplot of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotopic values,
 636 and (B) a principal component analysis based on 44 fatty acids with spiny lobsters' observations superimposed (only FA contributing the most to the discrimination are indicated in grey).



638

Figure 3. Boxplots of (A) carapace length, and (B) trophic level, for three spiny lobster species of Mahé Island, Seychelles. Trophic level was estimated based on $\delta^{15}\text{N}$ values of the lobster tail muscle relative to the $\delta^{15}\text{N}$ values of macroalgae (red, green and brown macroalgae) (see material and methods for details). Stars denotes significant differences between species (Tukey HSD test; NS = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$).

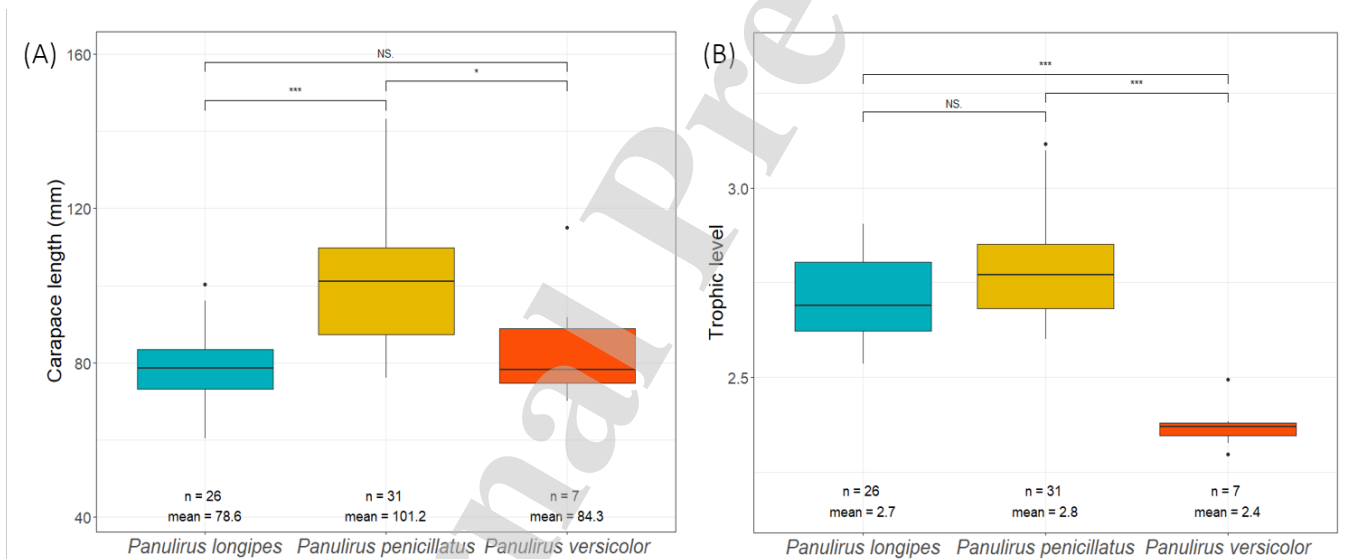


Figure 4. Relationships between $\delta^{13}\text{C}$ values (‰) of tail muscle and carapace length (mm) of three spiny lobsters ($n = 64$) caught from Mahé Island, Seychelles (simple linear regressions). Black line is linear regression for the three species together (slope = 0.02, $R^2 = 0.25$).

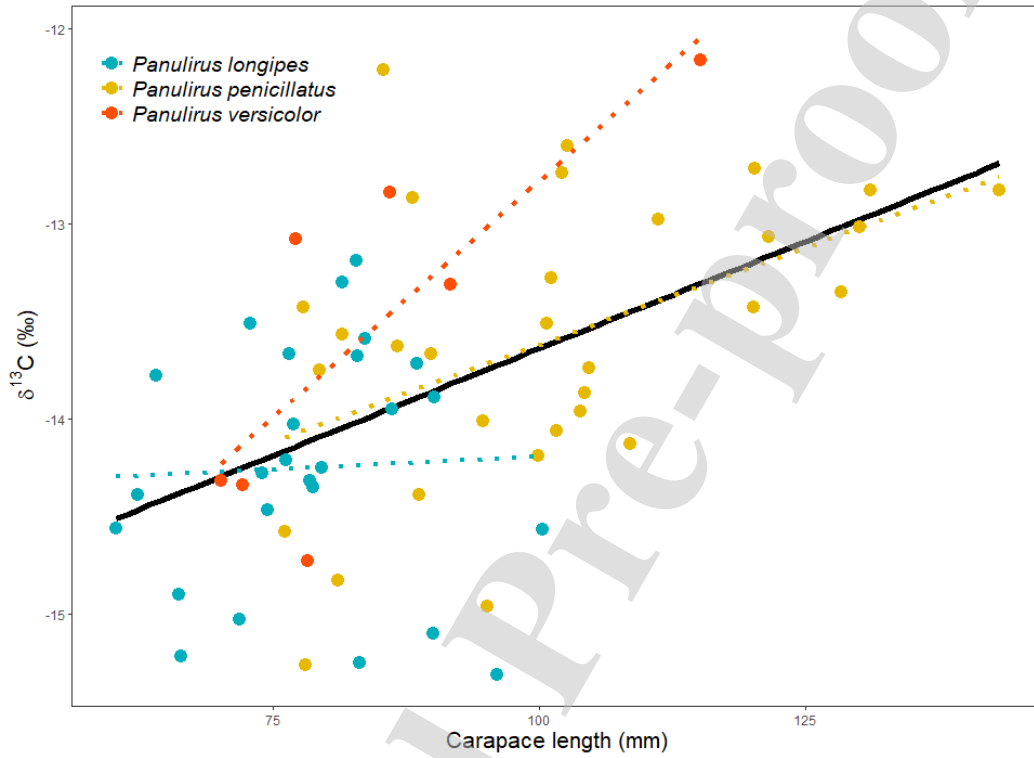


Figure 5. Outputs of the Bayesian mixing model estimating the prey proportions in the diet of spiny lobsters (A) among species, and (B) between reef types, based on isotopic values and fatty acid profiles. To improve model diagnostics, bivalves and gastropods were grouped *a posteriori* under the ‘Mollusc’ group, and brown, green and red algae were grouped under the ‘Algae’ group. Proportions’ summary (Mean \pm SD) is indicated for each group.

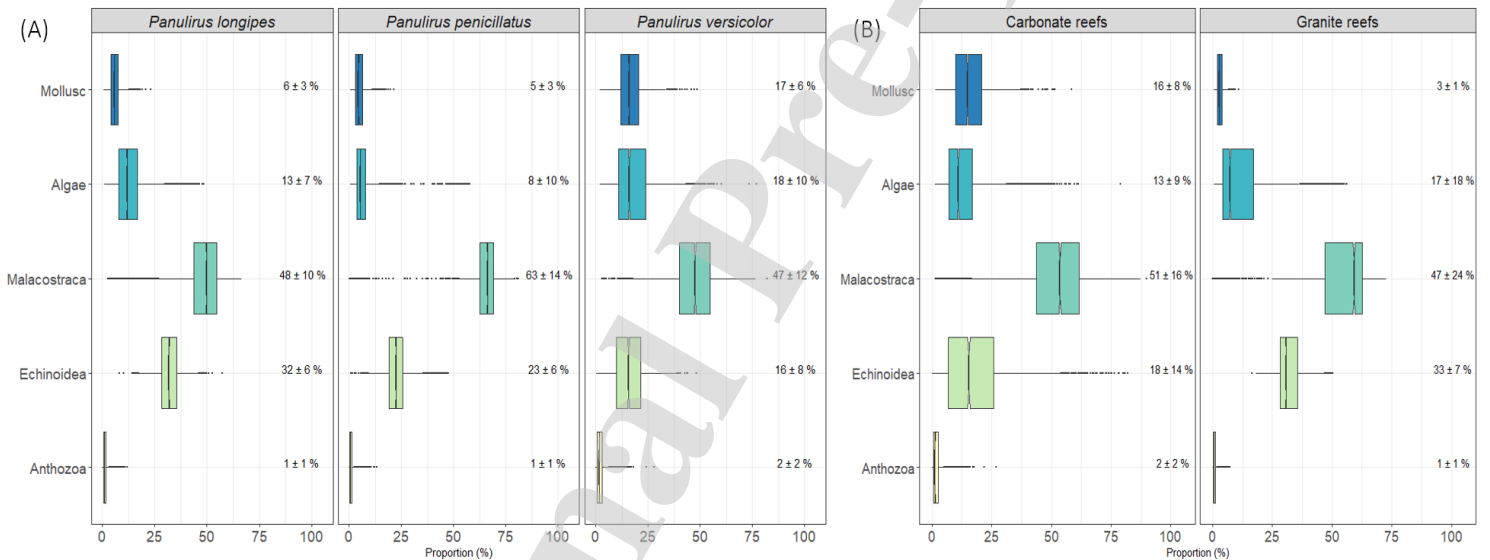


Table 1. Details on the sampling design of spiny lobsters from reefs of Mahé Island, Seychelles.

Species	Habitat type	N	Carapace length (mm)
<i>Panulirus longipes</i>	Carbonate reefs	3	77.6 ± 5.1
<i>Panulirus longipes</i>	Granite reefs	23	78.7 ± 10.6
<i>Panulirus penicillatus</i>	Carbonate reefs	4	119.1 ± 21.7
<i>Panulirus penicillatus</i>	Granite reefs	27	98.5 ± 16.0
<i>Panulirus versicolor</i>	Granite reefs	7	84.3 ± 15.5

Table 2. Mean \pm standard deviation for isotopic values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, in ‰), total lipid content (TLC, in $\mu\text{g}\cdot\text{mg}^{-1}$ in dry weight), and proportions of fatty acids contributing the most to species discrimination (in % of total fatty acids) for 13 potential prey species and three spiny lobster species caught from reefs around Mahé Island, Seychelles. See material and methods for details on analysis. When $n = 2$, only mean values are provided.

Phylum	Class	Species	N	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	TLC ($\mu\text{g}\cdot\text{mg}^{-1}$)	16:0 (%)	18:0DMA (%)	18:1n-9 (%)	18:4n-1 (%)	20:1n-11 (%)	20:4n-6 (%)	20:5n-3 (%)	22:5n-6 (%)	22:6n-3 (%)	
Potential prey	Chlorophyta	Chlorophyta	<i>Chlorophyta spp</i>	2	-17.7	7.2	0.7	23.0	0.0	5.1	0.0	3.3	4.1	5.5	0.8	8.0
		Ulvophyceae	<i>Chlorodesmis spp</i>	6	-23.8 \pm 0.7	6.5 \pm 0.3	3.2 \pm 0.6	41.6 \pm 2.6	0.0 \pm 0.0	9.1 \pm 0.8	0.0 \pm 0.0	0.0 \pm 0.0	1.6 \pm 0.3	1.9 \pm 0.3	0.1 \pm 0.0	0.4 \pm 0.1
	Ochrophyta	Phaeophyceae	<i>Turbinaria decurrens</i>	5	-10.8 \pm 1.6	6.0 \pm 0.4	2.5 \pm 0.4	35.6 \pm 3.4	0.0 \pm 0.0	13.8 \pm 0.9	0.0 \pm 0.0	0.0 \pm 0.1	13.5 \pm 0.8	1.7 \pm 0.4	0.1 \pm 0.0	0.0 \pm 0.1
	Rhodophyta	Rhodophyta	<i>Rhodophyta sp1</i>	2	-22.8	6.3	0.3	51.3	0.0	11.9	0.0	0.0	8.6	5.0	0.0	0.0
		Rhodophyta	<i>Rhodophyta sp2</i>	3	-16.0 \pm 1.0	7.2 \pm 0.3	0.3 \pm 0.1	45.0 \pm 4.7	0.0 \pm 0.0	5.5 \pm 1.9	0.1 \pm 0.1	0.4 \pm 0.2	12.2 \pm 7.1	1.8 \pm 0.2	1.3 \pm 1.7	1.0 \pm 0.2
	Arthropod	Malacostraca	<i>Calcinus laevimanus</i>	10	-14.3 \pm 1.3	7.8 \pm 0.4	2.9 \pm 0.8	22.6 \pm 5.6	3.1 \pm 1.0	5.8 \pm 0.7	0.0 \pm 0.0	0.3 \pm 0.1	14.3 \pm 2.6	11.1 \pm 1.7	0.9 \pm 0.2	3.7 \pm 1.3
		Malacostraca	<i>Dardanus lagopodes</i>	5	-15.0 \pm 0.6	8.7 \pm 0.4	2.0 \pm 0.4	20.9 \pm 5.6	3.3 \pm 2.3	6.3 \pm 1.0	0.0 \pm 0.0	0.3 \pm 0.1	11.8 \pm 2.5	11.5 \pm 2.8	1.1 \pm 0.2	5.5 \pm 2.5
	Cnidaria	Anthozoa	<i>Palythoa natalensis</i>	9	-13.9 \pm 0.2	8.4 \pm 0.6	0.7 \pm 0.2	24.3 \pm 2.3	5.4 \pm 1.2	2.3 \pm 0.2	4.5 \pm 2.3	0.7 \pm 0.3	7.8 \pm 1.4	2.4 \pm 0.6	0.3 \pm 0.1	3.9 \pm 0.6
	Echinoderm	Echinoidea	<i>Echinothrix diadema</i>	3	-13.7 \pm 0.9	12.4 \pm 0.1	3.5 \pm 0.1	10.7 \pm 0.1	6.7 \pm 0.9	0.4 \pm 0.1	0.1 \pm 0.0	8.7 \pm 0.6	26.7 \pm 0.4	7.4 \pm 1.7	1.0 \pm 0.1	0.7 \pm 0.1
	Mollusc	Bivalvia	<i>Pinctada margaritifera</i>	7	-17.5 \pm 1.0	7.6 \pm 0.4	5.1 \pm 2.4	12.5 \pm 5.1	7.4 \pm 4.1	4.0 \pm 0.8	0.1 \pm 0.1	5.4 \pm 1.7	6.1 \pm 1.4	4.1 \pm 2.4	1.8 \pm 0.5	12.6 \pm 3.4
		Gastropoda	<i>Conus spp</i>	7	-13.7 \pm 2.0	10.8 \pm 1.8	3.8 \pm 1.4	12.0 \pm 7.5	8.5 \pm 2.4	2.7 \pm 0.7	0.0 \pm 0.0	5.5 \pm 1.2	11.3 \pm 3.2	3.0 \pm 1.8	0.5 \pm 0.6	0.8 \pm 0.7
		Gastropoda	<i>Latirolagena smaragdulus</i>	8	-13.6 \pm 1.5	10.7 \pm 0.3	3.1 \pm 0.2	5.9 \pm 0.3	8.5 \pm 1.7	2.5 \pm 0.2	0.2 \pm 0.1	8.1 \pm 0.5	14.3 \pm 0.5	1.3 \pm 0.2	0.1 \pm 0.0	0.2 \pm 0.0
		Gastropoda	<i>Vasum turbinellus</i>	7	-13.7 \pm 1.5	11.2 \pm 0.2	3.0 \pm 1.0	5.7 \pm 1.4	7.7 \pm 3.4	1.6 \pm 0.4	0.1 \pm 0.0	6.6 \pm 1.1	15.3 \pm 1.5	1.9 \pm 0.2	0.5 \pm 0.2	1.5 \pm 1.9
Lobsters	Arthropod	Malacostraca	<i>Panulirus longipes</i>	26	-14.3 \pm 0.6	11.5 \pm 0.3	52.7 \pm 16.4	17.1 \pm 2.1	2.4 \pm 0.6	7.4 \pm 1.4	0.0 \pm 0.0	2.9 \pm 0.6	10.8 \pm 1.3	7.7 \pm 1.3	0.7 \pm 0.1	4.0 \pm 1.0
		Malacostraca	<i>Panulirus penicillatus</i>	31	-13.6 \pm 0.7	11.7 \pm 0.4	52.7 \pm 20.1	17.4 \pm 2.0	2.3 \pm 0.8	10.5 \pm 3.6	0.0 \pm 0.0	2.8 \pm 0.9	8.5 \pm 1.9	7.1 \pm 2.0	0.5 \pm 0.2	4.3 \pm 2.2
		Malacostraca	<i>Panulirus versicolor</i>	7	-13.5 \pm 0.9	10.5 \pm 0.2	43.6 \pm 22.5	17.6 \pm 2.1	2.5 \pm 0.7	7.6 \pm 2.0	0.0 \pm 0.0	2.4 \pm 0.7	11.3 \pm 2.3	7.8 \pm 1.3	0.7 \pm 0.2	4.1 \pm 1.2

Authors' contribution

Conceptualization: NB, LBa, LBl, DR; Funding acquisition: DR, NB, RG; Sampling: NB, LBa, LBl, KC, RM; Laboratory analyses: FS, SB, AB, JMM, FLL, FLG; Statistical analysis: FS; Writing – 1st draft: FS; 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:

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