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

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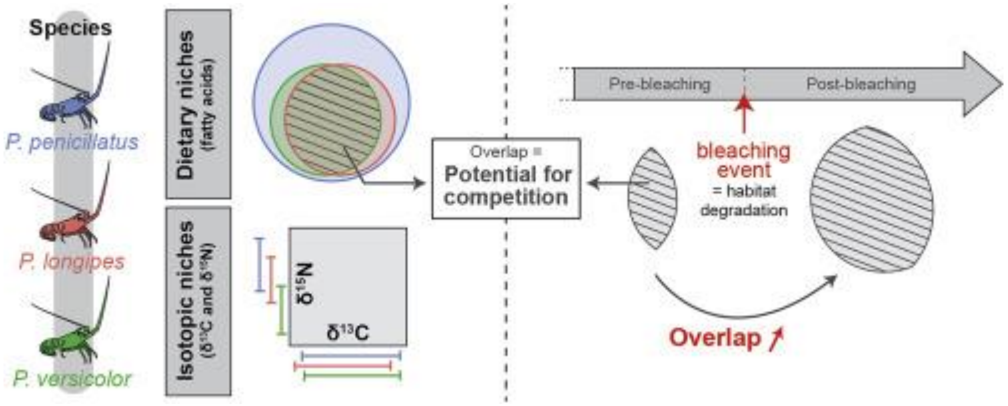
Abstract :

Spiny lobsters (P. penicillatus, P. longipes and P. versicolor) are heavily dependent on habitats like coral reefs, known to be highly vulnerable to climate change-driven degradation. Yet, little is known about their trophic ecology and their adaptive capacity to a changing environment. In this study, we used fatty acids (FA) analysed in the hepatopancreas and δ13C and δ15N 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 (δ13C 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 δ15N 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 $\delta^{15}N$ 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

1. Introduction

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

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

Habitat quality, including the type and complexity of coverage, is fundamentally important for spiny lobsters in respects to their foraging and antipredation strategies (Holthuis 1991; MacArthur et al. 2011). Spiny lobsters are non-gregarious nocturnal species that are found mainly in coastal environments, such as coral and rocky reefs, where they usually use the crevices to hide from predators during the day, while they leave their den at dusk to feed and mate during the night (Holthuis 1991). However, coastal reefs are under high human pressure in the Seychelles due to increasing coastal development and global climate change (Khan and Amelie 2015). In the last 25 years, coral reef habitats and granitic reefs supporting encrusting corals have been degraded through multiple bleaching events, with the 2016 bleaching event affecting around 50% of hard corals in the Seychelles (Obura et al. 2017). As spiny lobsters are generalist feeders, their diet composition is thought to be highly dependent on prey availability, depending on their habitat characteristics (Blamey et al. 2019). A modification of prey and habitat quality and availability through habitat degradation could thus have altered spiny lobsters' diet and level of interspecific competition, further influencing stock dynamics. Yet, there is a lack of knowledge on spiny lobsters' foraging behaviour in the Western Indian Ocean, particularly in the Seychelles region, and on their adaptive capacity to habitat change.

Trophic ecology of marine species can be studied through the use of ecological tracers like stable isotopes (SI) of carbon (δ^{13}C) and nitrogen (δ^{15}N) and fatty acid (FA) trophic markers. δ^{13}C allows for the identification of primary production sources while δ^{15}N gives information about the trophic position of an organism (Post 2002). The FA profiles observed in the digestive tissues of a consumer reflect the FA composition of ingested prey and thus can give insights into the consumer's diet (Iverson 2009). By studying spatial and temporal changes in the biochemical composition of consumers, it is possible to examine intraspecific and interspecific variations in their trophic ecology. For this, trophic niches inferred from SI or FA data are particularly useful as their metrics (i.e., niche size and probability of niche overlap) give both intra- and interspecific information. Typically, a species' niche size can be used as a proxy for the diversity of biochemically distinct prey eaten by this species (i.e., intraspecific variability), while the probability of overlap between two species gives indications on the degree of similarity of the biochemical composition of their prey (i.e., interspecific variability) (Costa-Pereira et al. 2019). Many studies successfully combined SI and FA to study trophic overlap between co-occurring species (e.g., Connan et al. 2014; Sardenne et al. 2016; Brewster et al. 2017).

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

2. Material and methods

2.1. Study area and sample collection

Panulirus penicillatus, P. longipes and *P. versicolor* were sampled as part of the annual Participatory Lobster Monitoring Program led by the Seychelles Fishing Authority (SFA) in collaboration with local fishers (Seychelles Fishing Authority 2014). A total of 105 spiny lobsters (47 *P. penicillatus*, 43 *P. longipes* and 15 *P. versicolor*), were caught in several fishing areas on the west coast of the island of Mahé, Seychelles, during five sampling campaigns in October/November from 2014 to 2018 (Fig. 1). The spiny lobsters were caught at dusk, when they leave reef crevices and thus are the most catchable, using snorkel gear and flashlights. The date, GPS location and carapace length (to the nearest 0.1 cm) were recorded for each individual. Finally, a piece of tail muscle and the hepatopancreas were retrieved, stored in amber glass at -20°C for a maximum of eight days before being transferred to -80 °C in the SFA Research laboratory. Hepatopancreas tissue samples remained at -80°C for FA analysis, and tail muscle tissues were freeze-dried over 72 hr and stored in a dry environment for SI analysis. Detailed numbers of the spiny lobsters' tissues sampled and analysed for FA and SI tracers across years and different habitat types (carbonate and granite reefs) are given in the supplementary material (Table S1).

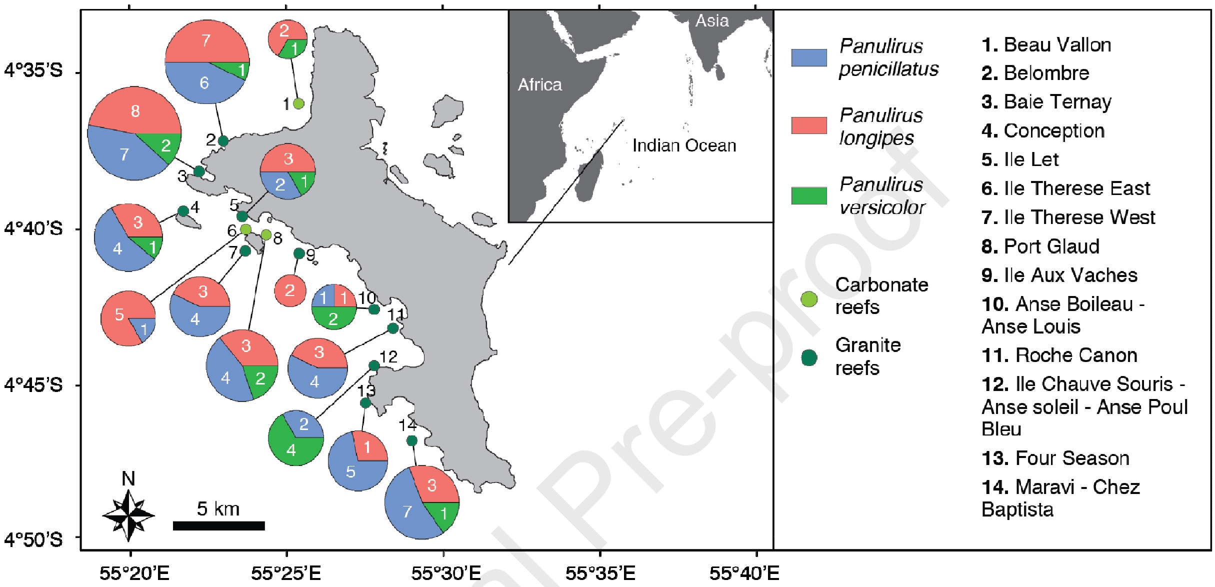


Fig. 1 Locations of the three species of spiny lobster caught from the west coast of Mahé (Seychelles, Western Indian Ocean) during 2014-2018. The number of individuals caught per species is indicated in the corresponding chart; size of charts is proportional to the total number of spiny lobsters per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

2.2. Fatty acid analyses

A total of 64 hepatopancreas samples were analysed for FA at the LIPIDOCEAN platform of the LEMAR (France). Lipids were extracted from around 200 mg of wet tissue using 6 mL of chloroform:methanol (2:1 v/v) in glass vials. Samples were then vortexed, sonicated in an ultrasonic bath for 15 min and stored at -20 °C (maximum 24h). Fatty acid methyl ester (FAME) were prepared using 1 mL of lipid extract in which 20 µL of an internal standard (tricosanoic acid, C23:0, 0.115 µg/µL) was added to allow FA quantification. Samples were then trans-esterified with 800 µL of methanolic sulphuric acid (3.4% v/v) at 100 °C for 10 min. After cooling, formed FAMEs were retrieved by adding 800 µL of hexane and washed with hexane-saturated distilled water (1.5 mL). Prepared FAMEs were separated using a gas chromatograph (Varian CP3800) with auto-sampler equipped with both polar and non-polar capillary columns (ZB-WAX, 30 m length x 0.25 mm i.d. x 0.25 µm film thickness, Phenomenex; and ZB-5 30 m length x 0.25 mm i.d. x 0.25 µm film thickness, Phenomenex), a splitless injector and a flame ionization detector. Oven temperature was raised to 150 °C at 50 °C/min, then to 170 °C at 3.5 °C/min, to 185 °C at 1.5 °C/min, to 225 °C at 2.4 °C/min, and finally to 250 °C at 5.5 °C/min. The identification of FAME was carried out by comparison of retention times with four commercially available standards (37-components, BAME, PUFA no. 1, and PUFA no. 3 FAME mix; Supelco). The concentration for each FA was converted from the area of chromatogram peaks by using the C23:0 peak area as reference. The analytical variability (mean CV) was 8.1 %, calculated using Supelco 37-component FAME mix.

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

2.3. Stable isotope analyses

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

2.4. Statistics

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

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

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

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

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

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

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

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

3. Results

3.1. Size of sampled spiny lobsters

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

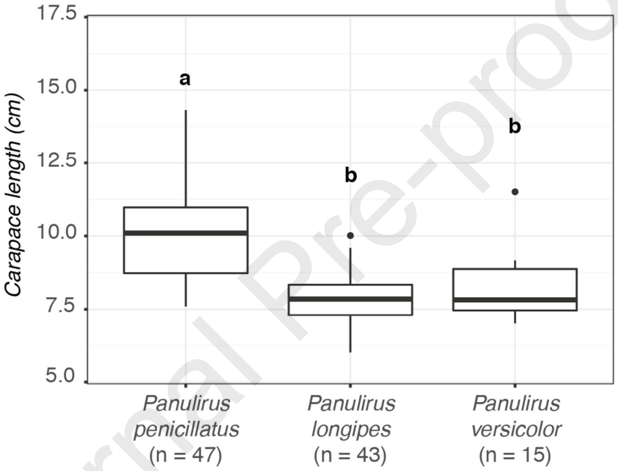


Fig. 2 Carapace length (cm) of sampled spiny lobsters according to the species. A different letter indicates a significant difference ($P < 0.05$).

3.2. Fatty acid niches

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

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

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

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

Fatty acid	***P. penicillatus*** **(n = 31)**	***P. longipes*** **(n = 27)**	***P. versicolor*** **(n = 7)**
Saturated			
14:0	2.5 ± 0.3	2.2 ± 0.1	1.8 ± 0.2
15:0	1.1 ± 0.1	1.16 ± 0.04	1.2 ± 0.1
16:0	17.4 ± 0.4	17.0 ± 0.4	17.6 ± 0.8
17:0	1.6 ± 0.1$^{\mathbf{b}}$	2.0 ± 0.1$^{\mathbf{a}}$	1.4 ± 0.1$^{\mathbf{b}}$
18:0	9.9 ± 0.2$^{\mathbf{ab}}$	11.4 ± 0.4$^{\mathbf{a}}$	9.5 ± 0.5$^{\mathbf{b}}$
20:0	1.2 ± 0.1$^{\mathbf{a}}$	1.01 ± 0.04$^{\mathbf{ab}}$	0.8 ± 0.1$^{\mathbf{b}}$
∑SFA	31.7 ± 0.5	36.2 ± 0.5	30.8 ± 1.0
Monounsaturated			
16:1n-7	4.4 ± 0.2	4.5 ± 0.2	4.4 ± 0.3
18:1n-7	3.6 ± 0.1	3.5 ± 0.1	3.7 ± 0.1
18:1n-9	10.5 ± 0.6$^{\mathbf{a}}$	7.4 ± 0.3$^{\mathbf{b}}$	7.6 ± 0.7$^{\mathbf{b}}$
20:1n-7	1.0 ± 0.1$^{\mathbf{a}}$	0.69 ± 0.03$^{\mathbf{ab}}$	0.7 ± 0.1$^{\mathbf{b}}$
20:1n-9	1.3 ± 0.1$^{\mathbf{a}}$	0.66 ± 0.02$^{\mathbf{b}}$	1.0 ± 0.1$^{\mathbf{a}}$
20:1n-11	2.8 ± 0.2	2.94 ± 0.13	2.4 ± 0.3
∑MUFA	24.4 ± 0.6$^{\mathbf{a}}$	20.5 ± 0.4$^{\mathbf{b}}$	20.4 ± 1.0$^{\mathbf{b}}$
Polyunsaturated			
18:2n-6	1.29 ± 0.04$^{\mathbf{b}}$	1.5 ± 0.1$^{\mathbf{a}}$	1.5 ± 0.1$^{\mathbf{ab}}$
20:2n-6	1.3 ± 0.1	1.18 ± 0.03	1.24 ± 0.03
20:4n-6	8.5 ± 0.3$^{\mathbf{b}}$	10.9 ± 0.3$^{\mathbf{a}}$	11.3 ± 0.9$^{\mathbf{a}}$
20:5n-3	7.1 ± 0.4	7.6 ± 0.3	7.8 ± 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
∑PUFA	38.2 ± 0.8$^{\mathbf{b}}$	40.5 ± 0.8$^{\mathbf{ab}}$	42.6 ± 1.5$^{\mathbf{a}}$
Branched FA, NMI FA and DMA			
iso17:0	0.83 ± 0.04$^{\mathbf{b}}$	1.01 ± 0.03$^{\mathbf{a}}$	0.8 ± 0.1$^{\mathbf{ab}}$
22:2 NMI (7,13)	1.5 ± 0.1$^{\mathbf{a}}$	1.1 ± 0.1$^{\mathbf{b}}$	1.2 ± 0.2$^{\mathbf{ab}}$
22:2 NMI (7,15)	0.74 ± 0.05$^{\mathbf{b}}$	0.86 ± 0.04$^{\mathbf{a}}$	1.2 ± 0.2$^{\mathbf{a}}$
18:0DMA	2.3 ± 0.1	2.4 ± 0.1	2.5 ± 0.3
Other[1]	11.0 ± 0.3	10.8 ± 0.2	11.3 ± 0.2

[1] Includes the SFA 19:0, 21:0, 22:0, 24:0, the MUFA 16:1n-5, 16:1n-9, 17:1n-7, 18:1n-5, 18:1n-11, 22:1n-7, 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, 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), 20:2 NMI (5,13), 22:3 NMI (7,13,16) and the DMA 16:1n-7DMA, 16:0DMA.

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

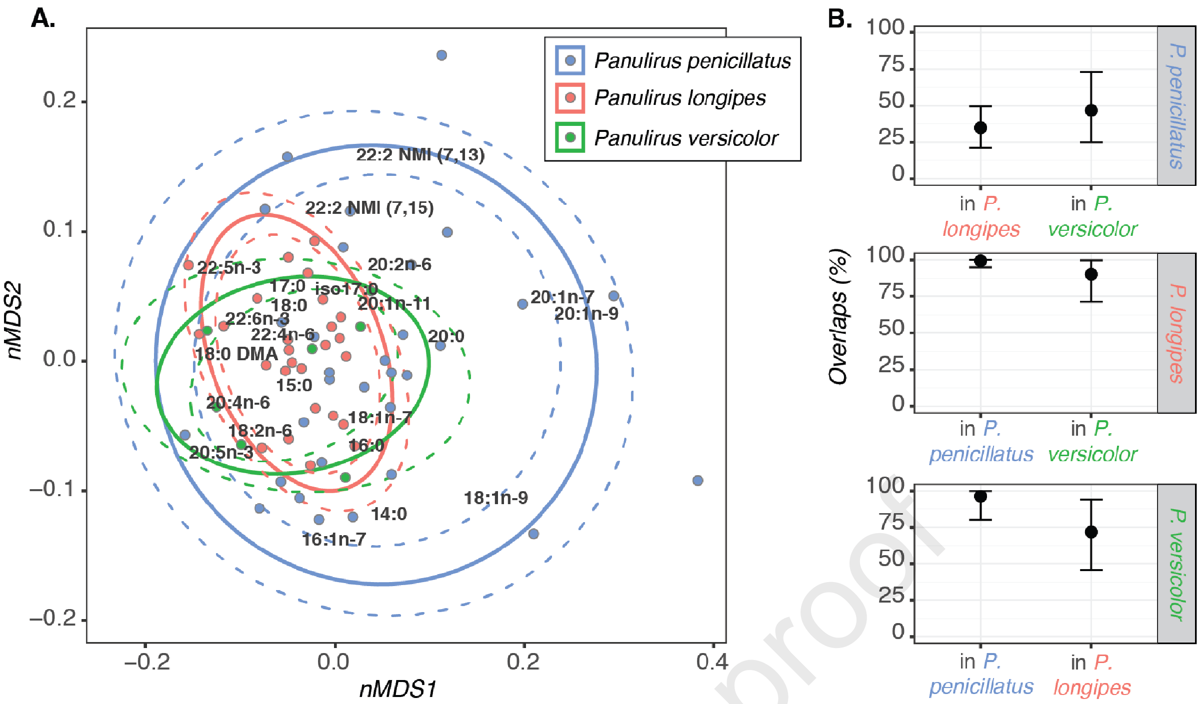


Fig. 3 Non-metric multidimensional scaling (nMDS) ordination of Bray-Curtis similarity matrix of hepatopancreas tissue fatty acid composition in the three spiny lobster species (A) and probabilities of niche overlap (%) between species (B). For each species, the mean ellipse is represented by a plain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

3.3. Isotopic niches

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

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

Stable isotope ratio	***P. penicillatus*** **(n = 47)**	***P. longipes*** **(n = 43)**	***P. versicolor*** **(n = 15)**
δ^{13}C	-13.6 ± 0.1$^{\mathbf{a}}$	-14.0 ± 0.1$^{\mathbf{b}}$	-13.7 ± 0.2$^{\mathbf{ab}}$
δ^{15}N	11.6 ± 0.1$^{\mathbf{a}}$	11.3 ± 0.1$^{\mathbf{b}}$	10.4 ± 0.1$^{\mathbf{c}}$

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

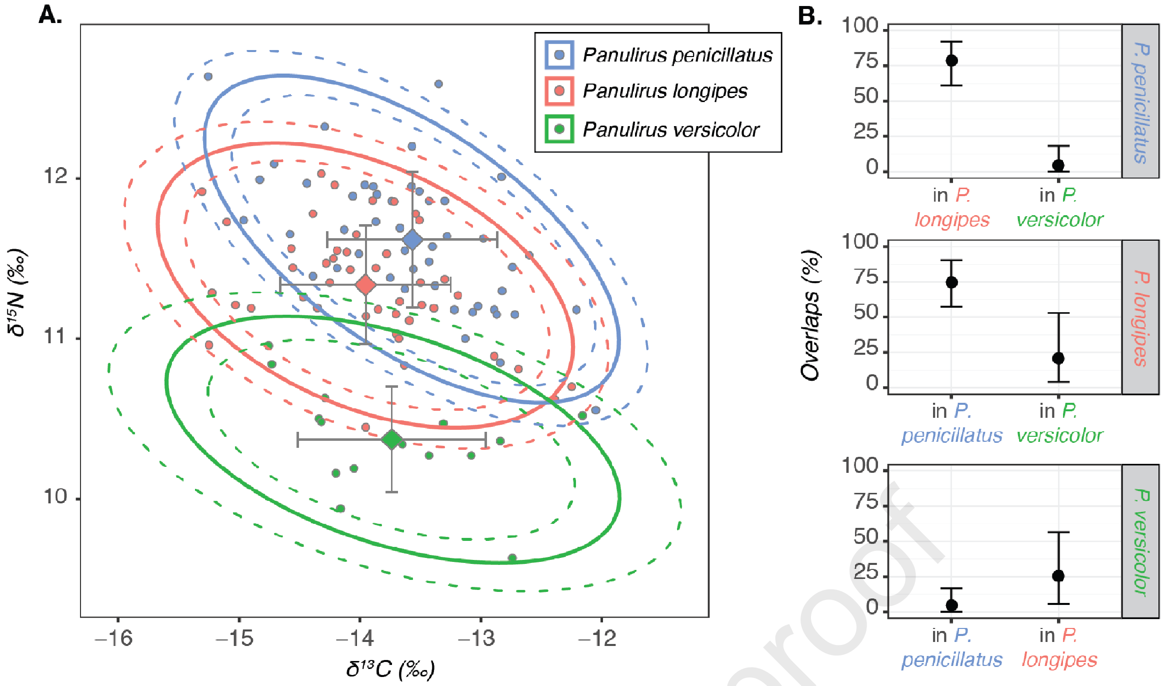


Fig. 4 □^{13}C and □^{15}N values (‰) in the white muscle of the three spiny lobster species (A) and niche overlaps (%) between species (B). For each species, the mean ± SD for stable isotope values is also given, and the mean ellipse and CI95% ellipses are represented by a plain line and dashed lines,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

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

The isotopic niche size of *P. penicillatus* was larger in granite reefs than in carbonate reefs (4.4 ‰^{2} [3.2 – 5.8 ‰^{2}] and 1.6 ‰^{2} [0.7 – 3.6 ‰^{2}] respectively; associated probability of 0.99) with little overlap in CI95% between the two habitat types (Fig. 5A). In spite of the uncertainty around the mean (i.e., high overlap in CI95%), it also appeared that the isotopic niche of *P. versicolor* was larger in granite reefs than in carbonate reefs (2.9 ‰^{2} [1.6 – 5.3‰^{2}] and 1.4 ‰^{2} [0.5 – 3.8 ‰^{2}] respectively; associated probability of 0.90). Except for the isotopic niche overlap of *P. penicillatus* in *P. longipes*, interspecific overlap of isotopic niches seemed to be higher in granite reefs than in carbonate reefs (2.2% [0.1 – 9.8%] and 0.0% respectively for *P. penicillatus* in *P. versicolor*, associated probability of 0.97; 76.3% [58.3 – 92.0%] and 37.8% [14.9 – 76.1%] respectively for *P. longipes* in *P. penicillatus*, associated probability of 0.96; 9.5% [1.4 – 26.5%] and 0.6% [0.0 – 5.2%] respectively for *P. longipes* in *P. versicolor*, associated probability of 0.97; 3.9% [0.0 – 19.8%] and 0.0% respectively for *P. versicolor* in *P. penicillatus*, associated probability of 0.90; 21.1% [1.7 – 59.9%] and 2.5% [0.0 – 31.7%] respectively for *P. versicolor* in *P. longipes*; associated probability of 0.95) (Fig. 5A).

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

For all calculated trophic niche metrics of Fig. 5, niche ellipses are presented in Fig. S2. Isotopic niches according to the sampling year (i.e., 2014 to 2018) for *P. penicillatus* and *P. longipes* only (due to low sample sizes for *P. versicolor*) and their associated metrics are presented in Fig. S3. Spiny lobsters' FA niches in carbonate and granite reefs did not allow for any interpretation but are however presented in Fig. S4 for information purposes.

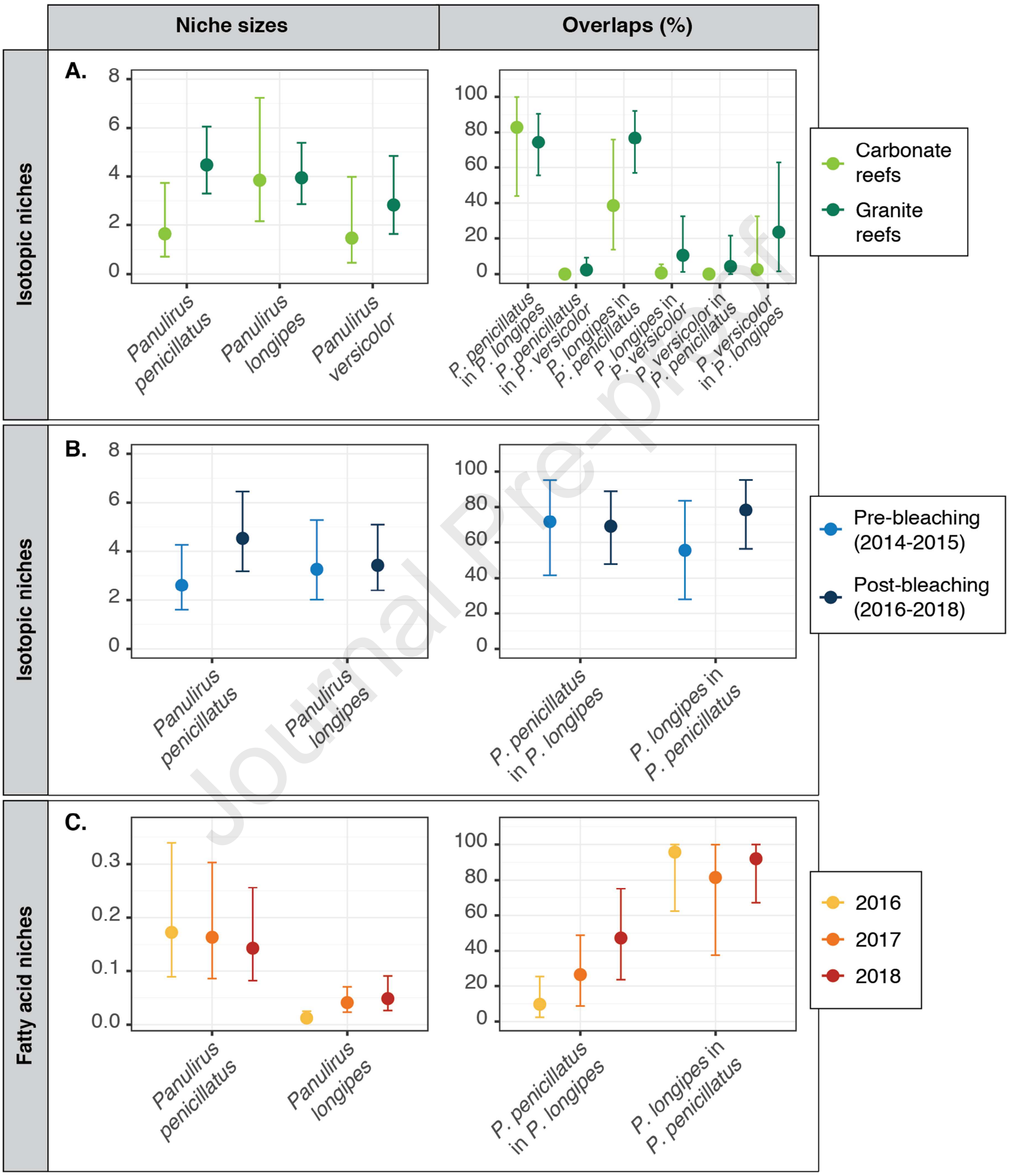


Fig. 5 Inter- and intraspecific differences in the trophic niche sizes and overlaps of spiny lobster species related to (A) different reef habitat types, (B) pre- and post-bleaching periods for isotopic niches, and (C) sampling years after 2016 coral bleaching event for FA niches. Niche sizes and overlaps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

4. Discussion

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

4.1. Characterisation of trophic overlap and potential for competition

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

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

The presence of a diverse number of FA trophic markers and variability in isotopic values in this study suggest that Seychelles spiny lobsters are generalist feeders, which is in accordance with previous studies on spiny lobsters' diet (Williams 2007). This could be an advantage for these species' survival, as dietary plasticity would help them overcome fluctuations in food availability (Korpimäki et al. 2020). However, we suggest that competition between spiny lobsters could occur in this area or could emerge in the near future, if shared resources (e.g., prey, habitat) become limited. Coexistence and avoidance of competition would therefore be closely linked to ecosystem health and to resource segregation mechanisms.

4.2. Resource partitioning among spiny lobsters

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

Panulirus penicillatus had a much larger FA niche in comparison with the two other species, suggesting a difference in the ingested proportions of certain types of prey. Its FA niche differed from FA niches of both other species largely due to positive anomalies of several FA trophic markers like 18:1n-9, 20:1n-7, 20:1n-9, 22:2 NMI (7,13) and 22:2 NMI (7,15). In coastal benthic systems, 18:1n-9 can originate from several dietary sources, such as macroalgae, mangrove detritus or animal tissues (Meyer et al. 2019). Here, 18:1n-9 was negatively correlated with trophic markers of macroalgae and mangrove materials (20:4n-6 and 22:5n-3, Fig. S1; Meyer et al. 2019), suggesting animal origin. This was also the case for 20:1n-7 and 20:1n-9, both negatively correlated with trophic markers of macroalgae, mangrove material and seagrass (20:4n-6, 22:5n-3 and 18:2n-6, Fig. S1; Meyer et al. 2019). The FA 20:1n-9 is known to indicate secondary consumption of zooplankton, for example through consumption of carnivorous fish (Pethybridge et al. 2010). Moreover, NMI FA are trophic markers of bivalve molluscs and carnivorous gastropods (Iverson 2009), suggesting that *P. penicillatus* eats these prey in higher proportions than the two other spiny lobster species. FA niche results were supported by isotopic niche results, as *P. penicillatus* had a higher trophic position than the two other species that is consistent with higher proportions of carnivorous gastropods and fish in its diet. We thus suggest that *P. penicillatus* may be more of a generalist than *P. longipes* and *P. versicolor*, with a higher level of carnivory. Such a difference in diet could be due to the size of *P. penicillatus* individuals, which tend to be larger than individuals of the two other species. Previous studies showed that the size range of prey that can be consumed by spiny lobster is function of their size, with larger individuals being able to eat larger prey (e.g., Haley et al. 2011; Blamey and Branch 2012). Thus, the larger size of *P. penicillatus* may allow it to have access to more resources, resulting in a larger niche size.

Both *P. longipes* and *P. versicolor* had a low isotopic niche overlap, with *P. versicolor* being characterised by significantly lower □^{15}N values, while they had a very high FA niche overlap that suggests high dietary similarities. Because all spiny lobsters were caught at the same geographical locations, we suggest that variations in □^{15}N values reflect differences in trophic position rather than differences in biochemical processes at the base of food webs (i.e., isotopic baselines). This may be due to size-selective predation, with both species feeding on different size fractions and/or different life stages of the same prey. Such resource partitioning could allow and even promote the stable coexistence of two consumers (de Roos et al. 2008). Moreover, body size is recognized as an important factor influencing trophic structure as it determines interaction between potential prey and predators, with larger consumers being able to eat larger prey. This has led to the theory that there is a positive relationship between a consumer’s trophic position and its body size (Jennings et al. 2002). Thus, if *P. versicolor* is specializing on smaller prey (either juveniles or small adults), it would feed on prey with a lower trophic position than those of *P. longipes* (as suggested by our results), while having the same size and feeding on the same prey species than *P. longipes*. Such findings would be of major importance in case of food scarcity, especially if *P. versicolor* feeds on earlier development stages of prey than *P. longipes* and *P. penicillatus*, and not only smaller prey species. Different prey life-history stages are linked by growth and reproduction, and predation on one stage may decrease the abundance of other stages (Murdoch et al. 2003). Thus, prey eaten by *P. versicolor* would not grow and be available for *P. longipes* and *P. penicillatus* to feed on. Given its larger trophic niche, *P. penicillatus* may be able to better overcome this compared to *P. longipes*. Thus, this could accentuate the effects of food scarcity for *P. longipes*, which already has a high level of trophic niche overlap with *P. penicillatus*.

4.3. Effect of habitat type and coral bleaching

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

Our results also showed a possible effect of habitat degradation on spiny lobsters' diet and foraging dynamics, especially coral reef degradation following the 2016 bleaching event (Obura et al. 2017). The isotopic niche size of *P. penicillatus* seemed to increase after the coral bleaching event, due to higher variability in δ^{15}N values (Fig. S1), and although we did not have FA data prior to the bleaching event, the FA niche of *P. longipes* has increased during the post-bleaching period. This suggests a possible diversification of prey size class in *P. penicillatus* diet between the pre- and post-bleaching periods and a diversification of *P. longipes* diet after the habitat degradation. Given the large decline in coral cover and as such the loss of reef complexity that provide habitat for a variety of potential prey species, we suggest that such modifications in isotopic and FA niches may be the consequences of a decrease in prey availability. In ecological theory, dietary diversity increases when prey abundance decreases (Tinker et al. 2008) and, as generalist feeders, spiny lobsters are known to adapt their diet according to several factors, such as prey species composition and/or prey availability (Haley et al. 2011; Blamey et al. 2019). This would also be consistent with the loss of species richness that has been reported after loss of coral cover in Seychelles (Robinson et al. 2019). Such drastic changes in spiny lobsters' diet, closely similar at core between the three species, may have important consequences on their foraging behaviour and maintenance. By influencing prey availability and thus spiny lobsters' diet diversity, the 2016 bleaching event could also have increased the risk of competition between the three lobster species. This hypothesis is supported by the increase of isotopic niche overlap between *P. penicillatus* and *P. longipes* between the pre- and post-bleaching periods and by the increase in their FA niche overlap between 2016 and 2018.

The effects of reef habitat type and habitat degradation through coral bleaching on spiny lobsters' diet and foraging dynamics are of high interest for the prediction of fishing stock evolution. Indeed, carbonate reefs are known to be more vulnerable to bleaching and reef degradation than granite reefs (Obura et al. 2017). In addition, granite reefs are quicker to recover than carbonate reefs after degradation, due in part to corals from carbonate reefs being in competition with macroalgae (Obura et al. 2017). Due to climate change and its associated rise in sea surface temperatures, bleaching events are predicted to increase in frequency, thereby weakening corals ecosystems in the long-term (Hoegh-Guldberg 2011). As the reduction of Seychelles spiny lobsters' potential of interspecific competition partly depends on the health and complexity of carbonate reefs, it is likely that the predicted instability of coral reefs could add further instability to the already unstable Seychelles spiny lobster stocks.

5. Conclusion

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

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

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

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

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

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

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

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Highlights

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

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Habitat degradation increases interspecific competition between three spiny lobsters in Seychelles

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Declaration of interests

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

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