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RESEARCH ARTICLE

# Trophic plasticity of mixotrophic corals under contrasting environments

Nicolas Sturaro[1] | Yunli Eric Hsieh[1] | Qi Chen[1] | Pei-Ling Wang[1,2] | Vianney Denis[1]

[1]Institute of Oceanography, National Taiwan University, Taipei, Taiwan

[2]Research Center for Future Earth, National Taiwan University, Taipei, Taiwan

**Correspondence**
Vianney Denis
Email: vianney.denis@gmail.com

**Present address**
Nicolas Sturaro, Biology of Marine Organisms and Biomimetics, University of Mons, Mons, Belgium

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## Abstract

1. Mixotrophic organisms can derive nutrition from both auto- and heterotrophy, which allows them to use a variety of trophic pathways to sustain their metabolic demands under variable conditions. Therefore, when facing environmental change, these organisms are expected to demonstrate an intrinsic ability to acclimatize through trophic plasticity.
2. Scleractinian corals are ecologically important mixotrophs, but understanding their trophic plasticity has been impaired by an oversimplification towards inconsistent proxies of coral diet and overlooking intraspecific variability.
3. Here, we applied a Bayesian analysis of carbon and nitrogen stable isotope data to determine the trophic niches of six common species of scleractinian corals and their associated endosymbionts, and combined it with an unsupervised machine learning algorithm to identify trophic behaviours and strategies.
4. We found a variable amount of nutritional plasticity identified by different trophic behaviours within and between mixotrophic corals living under the same environmental conditions. Furthermore, we observed changes in trophic plasticity across environmental conditions. Corals from variable environments had larger host and endosymbiont niches than corals from stable environments. In addition, deeper corals had niches indicating a greater degree of heterotrophy than shallow corals. Collectively, corals exhibited distinct trophic strategies by promoting trophic niche differentiation along the mixotrophic continuum and conspecific individual colonies displayed high trophic variation.
5. Our results provide a foundation to understand how mixotrophic organisms may adjust their nutrition in response to ongoing global environmental change and the consequential modification of benthic assemblages.

KEYWORDS

coral reefs, food web, global change, high latitude, mesophotic, scleractinia, stable isotopes, trophic niche

Nicolas Sturaro and Yunli Eric Hsieh co-first author.

  

## 1 | INTRODUCTION

Mixotrophic organisms can use different sources of energy by merging autotrophy and heterotrophy to acquire organic carbon and other elements such as nitrogen, phosphorous or sulphur. This trophic flexibility depends on spatiotemporal variations in resource availability and allows mixotrophs to adapt and/or acclimate with a range of terrestrial and aquatic ecosystems (Selosse et al., 2017). In marine environments, they are widely distributed and provide essential linkages for the flow of energy (Stoecker et al., 2017). Mixotrophic scleractinian corals form the foundation of one of the most diverse ecosystems on Earth (Reaka-Kudla, 1997). Despite the integral role they play in ecosystem functioning, our understanding of how corals adjust their nutritional modes in response to differing environmental conditions is limited (Fox et al., 2018; Nahon et al., 2013; Radice et al., 2019). Investigating coral trophic ecology represents an opportunity to evaluate how these organisms are likely to respond to environmental change at the individual (colony) and population (species) levels.

Scleractinian corals derive energy and nutrients from both autotrophy, via symbiosis with dinoflagellates of the family Symbiodiniaceae, and heterotrophy via the capture of allochthonous particles and/or the assimilation of dissolved inorganic and organic compounds (Houlbrèque & Ferrier-Pagès, 2009). In tropical oligotrophic waters, their ecological success has been related to their symbiotic associations (Frankowiak et al., 2016). Endosymbionts significantly contribute to the nutrition of their hosts with photosynthetically fixed carbon covering up to 140% of coral's daily energetic needs (Grottoli et al., 2006; Muscatine, 1990). Heterotrophy, oppositely, can supply up to 60% of the daily metabolic carbon demands of healthy corals and 100% of the demands of bleached individuals (Grottoli et al., 2006; Palardy et al., 2008). This provides corals with vital nutrients (e.g. nitrogen and phosphorus) that directly support growth and reproduction (Cox, 2007; Ferrier-Pagès et al., 2003). Light availability, seawater temperature, nutrient status and suspended particulate organic matter (SPOM) concentration all influence coral nutrition (Alamaru et al., 2009; Anthony & Fabricius, 2000; Houlbrèque & Ferrier-Pagès, 2009; Palardy et al., 2008). For instance, a slight increase in temperature can cause the breakdown of the mutualistic relationship and leads to coral bleaching (Apprill, 2020; Brown, 1997), which deprives corals of one of their main nutritional sources.

Coral trophic plasticity is undoubtedly an important driver of coral population dynamics and may underlie corals' responses to environmental change (Grottoli et al., 2017). A high degree of trophic plasticity may confer a considerable evolutionary advantage to some coral species that could better survive and recover from bleaching events (Grottoli et al., 2006). This ability is species specific and only a few species have been scrutinized to date (Conti-Jerpe et al., 2020; Grottoli et al., 2017; Radice et al., 2019). Indeed, trophic variability exists among coral species (Conti-Jerpe et al., 2020; Teece et al., 2011). There is also compelling evidence of high intraspecific trophic variability, notably among individual colonies that live only meters apart within a single reef system (Fox et al., 2019; Teece et al., 2011). So far, individual-level variation in nutritional strategy has been largely ignored in coral trophic ecology and population dynamics (Fox et al., 2019). More importantly, the coral diet has often been oversimplified in trophic strategy or functional diversity studies by taking into account corallite or polyp size as proxies of what corals eat; however, these variables exhibit inconsistencies regarding the relationships with nutrient acquisition and trophic plasticity (Alamaru et al., 2009; Conti-Jerpe et al., 2020; Houlbrèque & Ferrier-Pagès, 2009; Palardy et al., 2005). Furthermore, this approach overlooks dietary changes in response to environmental conditions (Fox et al., 2018). A better method of evaluating coral trophic plasticity is to ascertain their position in the food web and their role in energy flow through the ecosystem; that is, their ecological functions (sensu Bellwood et al., 2019). Accordingly, stable isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) has proven to be a useful tool to estimate consumers' trophic positions (Post, 2002) and assess nutritional fluxes acquired by coral hosts and endosymbionts (Ferrier-Pagès & Leal, 2018).

Delineating trophic niches is crucial for understanding the ecology of species (Hutchinson, 1957). In contrast to conventional techniques (e.g. gut content analysis), stable isotopes have the advantage of recording time-integrated assimilated diets and have been widely used to investigate trophic niche differences at the community and population levels (Jackson et al., 2011; Layman et al., 2007; Newsome et al., 2007). Because an organism's isotopic niche is linked to resource availability and feeding strategy, it can be used as a proxy for trophic niches (Newsome et al., 2007). The degree of trophic plasticity can be represented as the trophic niche size: larger is the isotopic niche wider is the use of resources (more mixotrophic, so a high degree of trophic plasticity) while a small isotopic niche indicates a more restricted use of resources (Conti-Jerpe et al., 2020; Radice et al., 2019). Such tools have revealed different trophic strategies for scleractinian corals in the Maldives (Radice et al., 2019) and at Hong Kong (Conti-Jerpe et al., 2020). Additionally, research showed nutritional plasticity of the widespread species *Palythoa tuberculosa* across the Indo-Pacific Ocean (Santos et al., 2021). Yet, to our knowledge, they have not been applied to study the trophic plasticity of different coral species under contrasting environments and/or account for temporal variation, which may undermine our ability to accurately predict how corals will respond to ongoing environmental change.

This study aims to evaluate trophic plasticity in scleractinian corals under different environmental conditions. We investigated shallow (~10 m) and deep (~40 m) waters at two environmentally contrasting areas of Taiwan, during both cold and warm seasons. We predicted that individuals of different species would exhibit different trophic strategies by promoting niche differentiation along the mixotrophic continuum as a way of avoiding interspecific resource competition, and predicted that individuals of the same species would exhibit a high degree of trophic variation. More specifically, we hypothesized that (a) corals from variable environments have larger host and endosymbiont niches than corals from stable environments; (b) corals living in deep

waters have niches that rely more on heterotrophic resources than shallow reef corals; and (c) corals in the warm season have niches with lower reliance on carbon from endosymbiont photosynthesis than in the cold season due to high precipitation resulting in relatively turbid waters and a reduction in light availability. To test these hypotheses, we investigated interspecific and intraspecific variability in coral trophic status, and combined Bayesian isotopic niche and unsupervised machine learning clustering algorithm approaches for six common species of scleractinian coral hosts and their associated algal endosymbionts.

## 2 | MATERIALS AND METHODS

### 2.1 | Study areas

Taiwan is located to the north of the East Indies Triangle; the region hosting the highest marine diversity in the world (Briggs, 2005). The main island spans tropical and subtropical latitudes from 21.90°N to 25.30°N and is located at the confluence of three marine ecoregions (Spalding et al., 2007), which create a unique environmental context where diverging habitats coexist at a relatively limited spatial scale. The study was conducted at two environmentally contrasting areas in Taiwan 2.5° of latitude apart located north and south of the main island (Figure S1). The north coast is characterized by the presence of non-reefal communities where the frequent influx of waters <18°C in winter prevents reef formation (Denis et al., 2019). Marginal coral communities are dominated by crustose coralline algae in shallow waters, which is typical of high-latitude benthic assemblages in Taiwan (Lin & Denis, 2019). To the north, limited light reaches deeper depths, and most photosynthetic organisms are absent below 40 m (Denis et al., 2019), where benthic communities are dominated by filter-feeding organisms (Lin & Denis, 2019). The south is typified by reefs at Green Island (Ludao), where well-developed and diversified fringing reefs benefit from the warm waters of the Kuroshio Current that flow along the East coast of Taiwan. Diversified mesophotic coral communities are present at depths below 40 m (De Palmas et al., 2021; Lin & Denis, 2019). Climate in Taiwan is strongly influenced by the monsoon, with northeasterly and southwesterly winds producing two distinctive seasons: a cold dry season from September to April and a warm wet season from May to August. The monthly average sea surface temperature typically ranges between 18.7 and 27.9°C in the north and 22.7 and 27.8°C in the south (Central Weather Bureau, Taiwan, https://www.cwb.gov.tw/eng). Precipitation is important during the warm wet season when thunderstorms and typhoons affect the island (Denis et al., 2019). On average, over the year, the north is typically characterized by two to three times more rainfall relative to the south (Central Weather Bureau, Taiwan, https://www.cwb.gov.tw/eng).

### 2.2 | Study species

Six common scleractinian coral species were investigated in this study: *Acropora muricata*, *Isopora palifera*, *Porites lutea*, *Psammocora profundacella*, *Stylophora pistillata* and *Tubastraea coccinea* (Figure 1). The first five species are zooxanthellate corals, while the last is azooxanthellate and represents a species with a purely heterotrophic diet. These species have different life-history strategies (Darling et al., 2012, 2019), morphologies, corallite widths, water clarity and exposure preferences (Coral Trait Database, https://coraltraits.org), and distributions around Taiwan (Dai & Horng, 2009; Figure 1). These species are found in shallow waters off the north and south Taiwanese coasts, with the exception of *I. palifera* which is absent in the north (Dai & Horng, 2009). They are all found in deep waters off the south Taiwanese coasts, with the exception of *A. muricata* (Dai & Horng, 2009; De Palmas et al., 2021; Denis et al., 2019).

### 2.3 | Sample collection

Fragments of the six coral species were sampled by technical divers in the cold and warm seasons of 2017 from shallow waters (~10 m) off north Taiwan (Bitou and Longdong) and shallow (~10 m) and deep (~40 m) waters off south Taiwan (Guiwan and Dabaisha; Figure S1; Tables S1 and S2). We haphazardly collected colony fragments (10–25 $cm^2$) using a hammer and chisel, with a minimum distance of 5 m between individuals to avoid sampling clones. Unfortunately, *A. muricata* could not be collected during the warm season in the north nor in the deep waters because of its extreme rarity or absence (Dai & Horng, 2009). Although this species is widely distributed throughout the Indo-Pacific, it is rarely found in the mesophotic zone (Muir & Pichon, 2019). *Isopora palifera* could not be collected during either season in the north (Table S2) because of its absence in the marginal coral assemblages of northern Taiwan (Dai & Horng, 2009). Immediately after collection, all samples were snap-frozen in liquid nitrogen, transported to the laboratory and kept frozen at −20°C.

To investigate whether particulate organic matter is a possible source of coral nutrition, seawater and sediment were collected from both areas, depths and seasons. SPOM was sampled using 4-L tanks for each factor ($n \geq 3$ per area; $n \geq 2$ per depth; $n \geq 3$ per season). Seawater was filtered through pre-combusted (450°C; 4 hr) Whatman glass-fibre filters (Grade GF/F, ∅ 47 mm and pore size 0.7 μm) at low pressure using a vacuum pump. The filters with captured SPOM were acidified by adding 1 N HCl (drop by drop) and then oven-dried at 50°C. Benthic particulate organic matter (BPOM) was sampled by collecting sediment between corals at a 1 cm depth using a plastic container ($n = 12$ per area; $n \geq 6$ per depth; $n \geq 9$ per season). The sediment was then sieved to remove coarse debris (>0.25 mm). BPOM required the direct addition of 1 N HCl because of its high carbonate content, and was then oven-dried at 50°C prior to isotopic analysis.

### 2.4 | Coral sample preparation

Coral samples were prepared following Sturaro et al. (2020). In brief, coral tissues were airbrushed from the skeletons of thawed

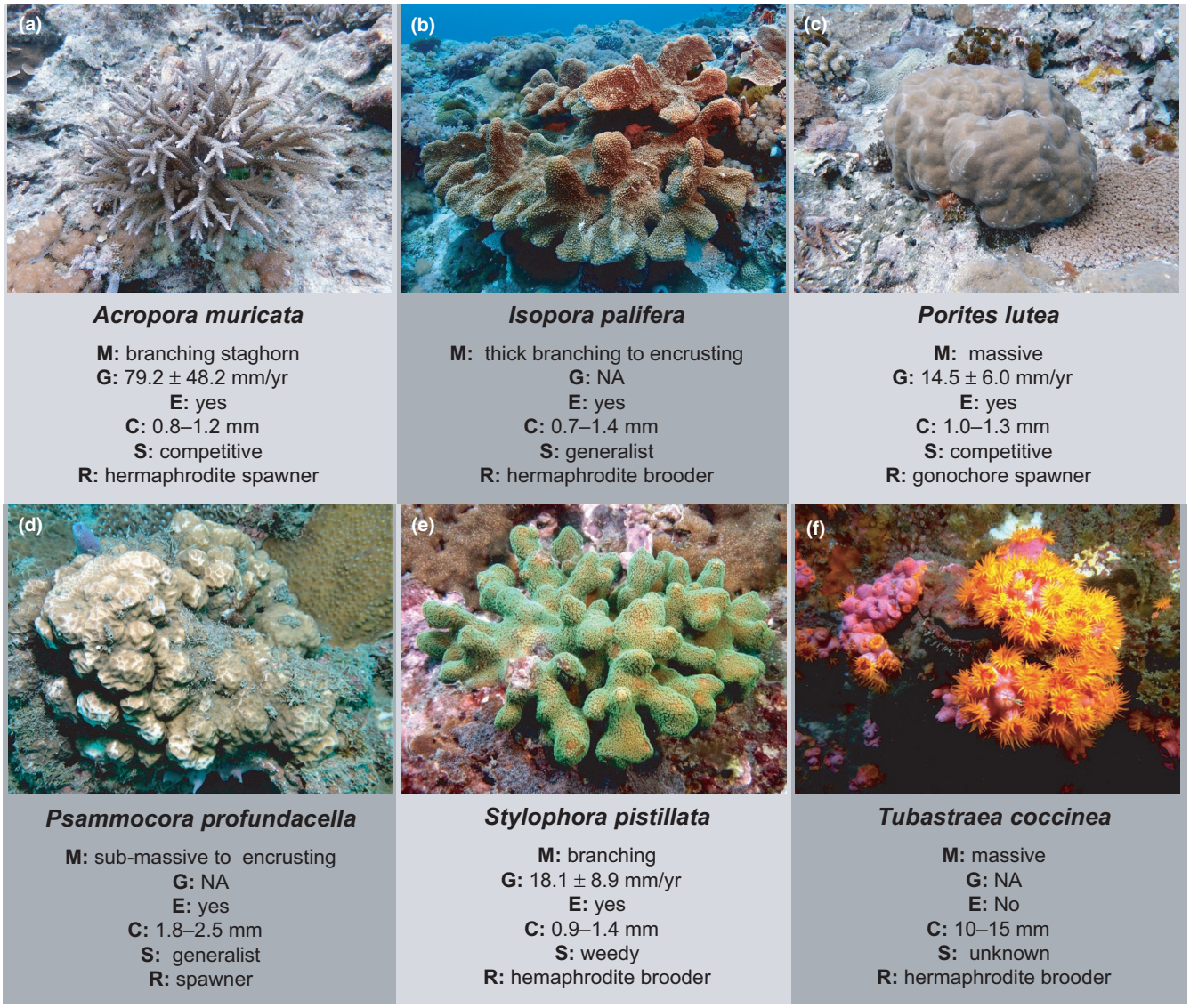


**FIGURE 1** The six scleractinian corals. (a) *Acropora muricata* (−5 m, south); (b) *Isopora palifera* (−8 m, south); (c) *Porites lutea* (−5 m, south); (d) *Psammocora profundacella* (−6 m, north); (e) *Stylophora pistillata* (−5 m, north) and (f) *Tubastraea coccinea* (−5 m, north). Photo credits: Chang-Feng Dai (d); Ming-Jay Ho (b) and Yoko Nozawa (a, c). M: Colony morphological structure; G: Growth rate (mm/yr); E: Presence of endosymbionts; C: Corallite width (mm); S: Ecological strategy; R: Reproduction; NA: Data not available. Trait data from the Coral Trait Database: https://coraltraits.org (last access 2021/02/09). Ecological strategies from Darling et al. (2012)

individual coral samples with artificial seawater. The resulting slurry was homogenized using an Ultra-Turrax® and then centrifuged for 10 min at 2,000*g* at 4°C to separate the homogenate into animal and endosymbiont fractions. Endosymbiont pellets were washed, re-suspended in Milli-Q® water, centrifuged for 2 min at 90*g* at 4°C and the supernatants discarded. This was repeated 10–12 times until no contamination by animal constituents (e.g. nematocysts) or mucus was visible under a microscope. For the animal tissue, the supernatant was filtered through pre-combusted Whatman glass-fibre filters. The filters and endosymbiont pellets were both acidified with 1 N HCl to remove carbonates. All of the prepared samples were then oven-dried at 50°C and ground into a homogeneous fine powder prior to isotopic analysis. For filters, the surface layer containing portions of the filter and the animal fraction was scraped. Around 0.7 mg of powder of Symbiodiniaceae and around 5 mg of powder of animal tissues and filters were weighed into tin capsules for each sample. Fewer endosymbiont ($n$ = 143) than animal samples ($n$ = 178) were analysed due to the presence of one azooxanthellate coral *T. coccinea* and to the insufficient dry weights of 7 and 5 endosymbiont samples for *P. lutea* and *P. profundacella*, respectively.

## 2.5 | Stable isotope analysis

Stable isotope ratios of carbon and nitrogen in particulate organic matter, coral hosts and endosymbiont tissues were measured at the Institute of Oceanography, National Taiwan University, using an isotope ratio mass spectrometer (DELTA V Advantage, Thermo

Fisher Scientific) coupled in continuous flow to an elemental analyser (FLASH 2000, Thermo Fisher Scientific). Stable isotope ratios are reported using the widespread δ notation: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1{,}000$, where $R$ is the ratio of the heavy to light isotopes in per mil (‰; Coplen, 2011). The $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios are expressed relative to the levels of $^{13}C$ in Vienna-Pee Dee Belemnite and $^{15}N$ in atmospheric $N_2$. Certified reference material USGS40 (L-glutamic acid: $\delta^{13}C = -26.4 \pm 0.1‰$; carbon weight composition wtC% = 40.8%; $\delta^{15}N = -4.5 \pm 0.1‰$; nitrogen weight composition wtN% = 9.5%) obtained from the International Atomic Energy Agency (Vienna, Austria) was inserted into all runs at regular intervals (once every six analyses) for data calibration. To assess drift over time, repetitive measurements of an internal standard (protein: $\delta^{13}C = -27.3 \pm 0.1‰$; $\delta^{15}N = 6.0 \pm 0.1‰$) were also taken. Standard deviations of the multi-batch replicate measurements of the standards analysed, interspersed among the samples, were ≤0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. Animal tissue and Symbiodiniaceae elemental data are expressed as the ratio between carbon and nitrogen concentrations (C:N mass ratios) relative to % dry mass.

## 2.6 | Data analysis

Species-specific coral host and endosymbiont standard ellipse areas ($‰^2$) that represent individual core isotopic niches were estimated using Stable Isotope Bayesian Ellipses in R (SIBER version 2.1.4; Jackson et al., 2011). To account for sample size differences, areas of the ellipses associated with each species or group (Standard Ellipse Area B; $SEA_B$) were computed using Bayesian inference (Markov chain Monte Carlo parameters: 2 chains, 200,000 iterations, 10,000 burn-ins and thins = 50). Model solutions were presented using credibility intervals of probability density distribution plots. A unique standard ellipse area corrected for sample size ($SEA_c$) was also calculated for each species for all environmental conditions combined (total) and for subgroups under different conditions. The $SEA_c$ contains *c*. 40% of the variation of a group and has been demonstrated to be a robust metric for comparing groups with different sample sizes (Jackson et al., 2011). The Bayesian estimate, $SEA_B$, captures all the same properties as $SEA_c$, being unbiased with respect to sample size and exhibiting more uncertainty with a smaller sample size (Jackson et al., 2011). To characterize the interaction between the coral hosts and their associated endosymbionts, the amount of isotopic niche overlap between the two groups $SEA_c$ was calculated as a proportion of the host niche area using SIBER (Conti-Jerpe et al., 2020).

Permutational multivariate analysis of variance (PERMANOVA; Anderson, 2017; Anderson et al., 2008) was used to examine the $\delta^{13}C$ and $\delta^{15}N$ values of the coral hosts and endosymbionts, as well as the C:N ratios and the relative differences between coral host and endosymbiont $\delta^{13}C$ ($\Delta^{13}C$) and $\delta^{15}N$ ($\Delta^{15}N$) values in regard to the following factors: species (*A. muricata*, *I. palifera*, *P. lutea*, *P. profundacella*, *S. pistillata* and *T. coccinea*), area (north and south), depth (shallow and deep), and season (warm and cold). PERMANOVA was also used to examine the $\delta^{13}C$ and $\delta^{15}N$ values of the particulate organic matter in regard to the factors area (north and south), depth (shallow and deep) and season (warm and cold). This method analyses variances in univariate or multivariate data caused by a set of explanatory factors that are based on Euclidean distances so that effects linked to each factor, and interactions between factors, can be tested. PERMANOVA can analyse unbalanced design with no limit on the number of factors that can be used (Anderson et al., 2008). When PERMANOVA is used with univariate data, *p*-values are obtained by permutation, thus avoiding the assumption of normality (Anderson, 2017). Here, all factors (species, area, depth and season) were treated as fixed, and 9,999 residual random permutations were run in a reduced model. Post-hoc tests (pairwise comparisons) were conducted to investigate significant interactions and/or significant main effects. Statistical significance was determined with an alpha value of 0.05.

An unsupervised *k*-means clustering algorithm (Macqueen, 1967) was adopted to identify the most appropriate number of clusters in the dataset. The first analysis was conducted for all conditions combined using all the data (total), while three other analyses were done using data from subgroups according to area and depth. This approach is a centroid-based partitional clustering method in which centroids are the arithmetically calculated centres of the clusters where *k* represents the number of clusters. The initial centroid for each cluster was randomly selected. Each of the remaining data points was iteratively assigned to the cluster to minimize the sum of the squared error of each centroid. We used R package NbClust (Charrad et al., 2014) to determine an optimum number of clusters (*k*) among individuals to minimize the total error sum of squares among the groups based on stable isotope values,. This package provides 30 indices that determine the number of clusters in a dataset, and offers the best clustering consensus scheme from a variety of results. The significance of *k* clusters was tested with 9,999 permutations. This approach allowed individuals (genotypes or colonies) of the same species to be ascribed to different clusters, and the proportion of individuals in each cluster was calculated for each species. A trophic behaviour is represented by a cluster of individuals (i.e. colonies) sharing similar isotopic values (possibly including individuals from various species). The combination of several trophic behaviours in one species could indicate different trophic strategies. The strategies may vary between two extremes: generalist and specialist, which can be defined for each species according to the number of trophic behaviours they exhibit.

Correlation analyses were performed on the coral host and endosymbiont stable isotope data using Pearson's correlation coefficient. All coral host and endosymbiont $\delta^{15}N$ and $\delta^{13}C$ values are shown as means ± *SE*. $\delta^{15}N$ range (NR) and $\delta^{13}C$ range (CR) were also calculated according to Layman et al. (2007). A large NR among individuals suggests more trophic levels and thus a greater degree of trophic plasticity, while a large CR indicates multiple resources along the mixotrophic continuum. To disentangle the effects of photosynthetic fractionation and heterotrophic carbon and nitrogen incorporation, we calculated differences between host and endosymbiont $\delta^{13}C$ and $\delta^{15}N$ values ($\Delta^{13}C = \delta^{13}C_{host} - \delta^{13}C_{endosymbiont}$ and $\Delta^{15}N = \delta^{15}N_{host} - \delta^{15}N_{endosymbiont}$, respectively). Although

not a quantitative estimate of the heterotrophic contribution to a coral's metabolic demands, the isotopic proxy ($\Delta^{13}C$) indicates deviations from a fully autotrophic diet (Fox et al., 2018; Muscatine et al., 1989; Williams et al., 2018). $\Delta^{15}N$ also indicates dietary contributions via heterotrophy (Conti-Jerpe et al., 2020). All statistical analyses were conducted using PRIMER 6 & PERMANOVA+ and R (version 3.5.1).

## 3 | RESULTS

### 3.1 | Stable isotope values of coral hosts, endosymbionts and particulate organic matter

#### 3.1.1 | $\delta^{13}C$ and $\delta^{15}N$ values and C:N ratios of coral hosts

The $\delta^{13}C$ values of coral hosts ranged from −13.4 ± 0.4‰ (*I. palifera* in shallow waters off the south coast) to −21.6 ± 0.1‰ (*T. coccinea* in shallow waters off the south coast), and from 3.0 ± 0.1‰ (*A. muricata* in shallow waters off the south coast) to 8.9 ± 0.2‰ (*T. coccinea* in shallow waters off the north coast) for $\delta^{15}N$ values (Table S3). Coral host $\delta^{13}C$ and $\delta^{15}N$ values significantly differed among species ($p < 0.001$; Table 1; Table S4). Pairwise tests revealed that species significantly differed ($p < 0.05$), except *P. profundacella* and *A. muricata*. Coral host $\delta^{13}C$ and $\delta^{15}N$ values did not significantly differ between seasons (Figure 2; Table 1; Table S4).

Mean coral host $\delta^{13}C$ values significantly differed between shallow and deep reefs (Figure 2), with values being more negative in deep individuals (Table S3), while no significant differences were found in $\delta^{15}N$ values (Table S4). A significant interaction between species and depth ($p < 0.001$) indicated that the effect of depth on $\delta^{13}C$ values depended upon the species considered. Those for *Isopora palifera*, *P. lutea* and *P. profundacella* were significantly more negative in deep individuals than shallow ones ($p \leq 0.002$), but not *S. pistillata* ($p = 0.080$; Table S5).

Mean coral host $\delta^{15}N$ values significantly differed between north and south, with higher values in northern individuals, while no difference was observed in $\delta^{13}C$ values (Figure 2; Table S3; Table S4). There was a significant interaction between species and area in coral

**TABLE 1** Four-way PERMANOVA testing the effects of species, area, depth, season and their interactions on coral host and endosymbiont carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios

| Source | *df* | SS | MS | Pseudo-*F* | *p* |
|---|---|---|---|---|---|
| Coral host | | | | | |
| Species | 5 | 464.38 | 92.88 | 83.48 | **<0.001** |
| Area | 1 | 93.87 | 93.87 | 84.38 | **<0.001** |
| Depth | 1 | 27.88 | 27.88 | 25.06 | **<0.001** |
| Season | 1 | 1.98 | 1.98 | 1.78 | 0.171 |
| Species × Area | 4 | 15.66 | 3.92 | 3.52 | **0.005** |
| Species × Depth | 4 | 24.75 | 6.19 | 5.56 | **<0.001** |
| Species × Season | 5 | 15.17 | 3.03 | 2.73 | **0.012** |
| Area × Season | 1 | 12.18 | 12.18 | 10.95 | **<0.001** |
| Depth × Season | 1 | 0.20 | 0.20 | 0.18 | 0.798 |
| Species × Area × Season | 3 | 6.71 | 2.24 | 2.01 | 0.089 |
| Species × Depth × Season | 4 | 2.03 | 0.51 | 0.46 | 0.836 |
| Residuals | 147 | 163.54 | 1.11 | | |
| Endosymbiont | | | | | |
| Species | 4 | 187.80 | 46.95 | 33.49 | **<0.001** |
| Area | 1 | 36.44 | 36.44 | 25.99 | **<0.001** |
| Depth | 1 | 39.95 | 39.95 | 28.49 | **<0.001** |
| Season | 1 | 2.43 | 2.43 | 1.74 | 0.179 |
| Species × Area | 3 | 1.58 | 0.53 | 0.38 | 0.822 |
| Species × Depth | 3 | 17.10 | 5.70 | 4.06 | **0.005** |
| Species × Season | 4 | 13.55 | 3.39 | 2.42 | **0.042** |
| Area × Season | 1 | 22.83 | 22.83 | 16.29 | **<0.001** |
| Depth × Season | 1 | 4.83 | 4.83 | 3.44 | 0.051 |
| Species × Area × Season | 2 | 5.92 | 2.96 | 2.11 | 0.108 |
| Species × Depth × Season | 3 | 2.10 | 0.70 | 0.50 | 0.739 |
| Residuals | 118 | 165.42 | 1.40 | | |

*Note: df* = degrees of freedom, SS = sum of squares, MS = mean sum of squares, Pseudo-*F* = *F* value by permutation. Bold face indicates statistical significance ($p < 0.05$).

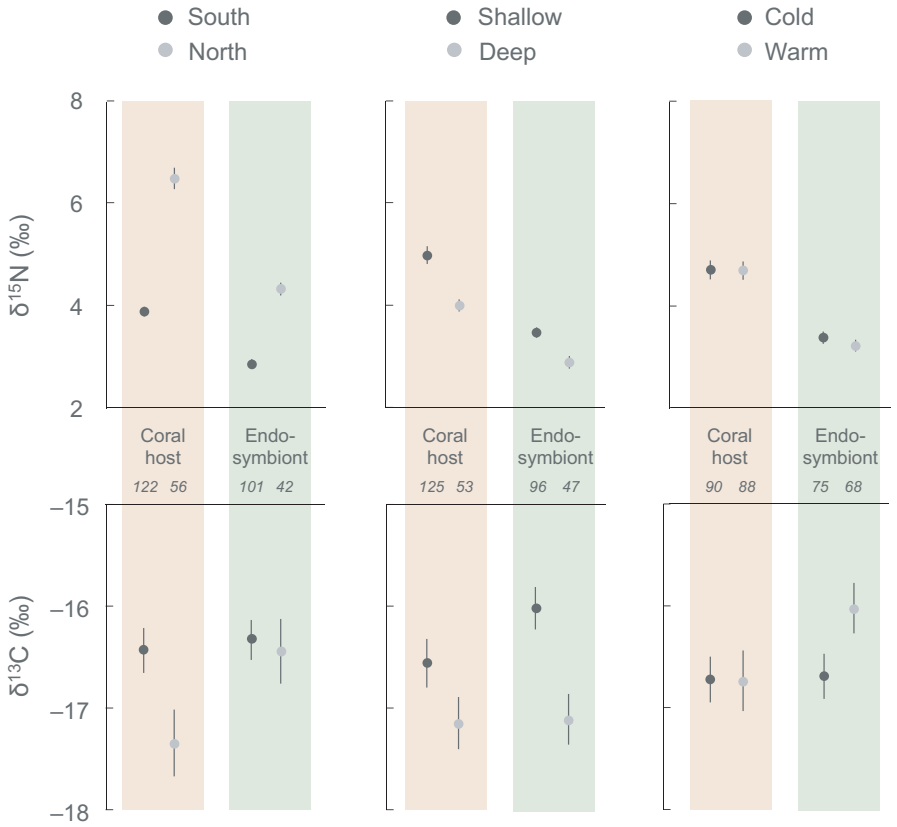


**FIGURE 2** Coral host and endosymbiont carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios by area, reef depth and season. Isotope values of the six species of scleractinian corals (Mean ± *SE*) are grouped by area (north and south areas), reef depth (shallow and deep waters) and season (warm and cold seasons). Among the six species, *Isopora palifera* was not present in the north area, while *Acropora muricata* was sampled during a single season in the north and was not found in deep waters off the south coast. *X*-axis labels give the number of coral host and endosymbiont samples (*n*) in each group

host $\delta^{15}N$ values ($p = 0.012$), as pairwise tests revealed that individuals of each species from the north were significantly different to those from the south ($p < 0.001$).

Coral host CR ranged from 0.8‰ (*T. coccinea*) to 5.4‰ (*I. palifera*) in shallow waters off the south coast, while NR ranged from 0.4‰ (*S. pistillata* in deep waters off the south coast) to 2.7‰ (*P. profundacella* in shallow waters off the north coast; Table S3). Coral host C:N ratios ranged from 5.8 ± 0.1 (*S. pistillata* in deep waters off the south coast) to 8.9 ± 0.6 (*I. palifera* in shallow waters off the south coast; Table S3). C:N ratios significantly differed among species ($p < 0.001$) and between depths ($p = 0.019$; Table S6), and were lower in deep waters than in shallow. Pairwise tests revealed that most species differed significantly ($p < 0.05$), except for *S. pistillata*–*P. lutea*, *S. pistillata*–*T. coccinea* and *A. muricata*–*P. profundacella*. C:N values did not significantly differ between areas or seasons (Table S6).

### 3.1.2 | Relationships between coral hosts and their associated endosymbionts

The isotopic compositions of the endosymbionts ranged from −14.0 ± 0.5‰ (*I. palifera* in shallow waters off the south coast) to −18.6 ± 0.4‰ (*S. pistillata* in shallow waters off the north coast) for $\delta^{13}C$ values, and from 1.9 ± 0.1‰ (*S. pistillata* in shallow and deep waters off the south coast) to 5.0 ± 0.2‰ (*P. lutea* in shallow waters off the north coast) for $\delta^{15}N$ (Table S7). Endosymbiont $\delta^{13}C$ and $\delta^{15}N$ values correlated with those of coral hosts (Pearson correlations: $R^2 = 0.89$, $p < 0.001$; $R^2 = 0.53$, $p < 0.001$; Figure S2). Therefore, variations in stable isotope compositions of endosymbionts mimicked the patterns in coral hosts (Table 1; Table S4).

Despite these significant correlations, $\Delta^{13}C$ and $\Delta^{15}N$ values were significantly different among coral species (Table S8). $\Delta^{13}C$ values ranged from −0.3 ± 0.1‰ (for *P. profundacella* in shallow waters off the north coast) to 0.7 ± 0.3‰ and 0.7 ± 0.2‰ (for *A. muricata* in shallow waters off the north coast and *I. palifera* in deep waters off the south coast, respectively), and $\Delta^{15}N$ values ranged from 0.1 ± 0.2‰ (for *P. lutea* in shallow waters off the south coast) to 1.6 ± 0.3‰ and 1.6 ± 0.1‰ (for *P. profundacella* in shallow waters off the north coast and *S. pistillata* in shallow waters off the south coast, respectively; Table 2). When accounting for area, depth and season, $\Delta^{13}C$ values in *I. palifera* were significantly higher than those in *A. muricata*, *P. lutea*, *P. profundacella* and *S. pistillata* (pairwise tests, $p < 0.05$). *Stylophora pistillata* had the highest $\Delta^{15}N$ values ($p < 0.05$), while *P. profundacella* had higher $\Delta^{15}N$ values than *A. muricata* ($p < 0.001$). $\Delta^{13}C$ values did not vary with area or season, but did with depth ($p = 0.018$; mean deep $\Delta^{13}C$ value = 0.2 ± 0.1‰, and mean shallow $\Delta^{13}C$ value = 0.4 ± 0.1‰ for the south). $\Delta^{15}N$ values varied with area, and there was significant interaction between species and area ($p = 0.001$), indicating that the area effect was species specific.

### 3.1.3 | Stable isotope values of particulate organic matter

SPOM $\delta^{13}C$ values did not differ significantly by reef area, depth or season (Table S9), although there was a change in $\delta^{13}C$ values

**TABLE 2** Mean $\Delta^{13}C$ ($\delta^{13}C_{coral\ host} - \delta^{13}C_{endosymbiont}$) and $\Delta^{15}N$ ($\delta^{15}N_{coral\ host} - \delta^{15}N_{endosymbiont}$) by environmental condition. Each environmental condition is represented by a code (SD: South Deep; SS: South Shallow and NS: North Shallow). See Table S2 for the number of samples (*n*) of each species and environmental condition

| | | $\Delta^{13}C$ (‰) | | $\Delta^{15}N$ (‰) | |
|---|---|---|---|---|---|
| **Species name** | **Env.** | **Mean** | ***SE*** | **Mean** | ***SE*** |
| *Acropora muricata* | SS | 0.1 | 0.1 | 0.2 | 0.1 |
| | NS | 0.7 | 0.3 | 0.6 | 0.2 |
| *Isopora palifera* | SD | 0.7 | 0.2 | 0.6 | 0.2 |
| | SS | 0.6 | 0.1 | 0.3 | 0.2 |
| *Porites lutea* | SD | 0.1 | 0.3 | 0.8 | 0.2 |
| | SS | 0.4 | 0.2 | 0.1 | 0.2 |
| | NS | −0.2 | 0.2 | 1.3 | 0.2 |
| *Psammocora profundacella* | SD | 0.1 | 0.2 | 0.7 | 0.2 |
| | SS | 0.6 | 0.2 | 0.9 | 0.2 |
| | NS | −0.3 | 0.1 | 1.6 | 0.3 |
| *Stylophora pistillata* | SD | −0.2 | 0.1 | 1.5 | 0.1 |
| | SS | 0.2 | 0.1 | 1.6 | 0.1 |
| | NS | 0.5 | 0.1 | 1.5 | 0.1 |

between the south (−22.6 ± 0.4‰) and the north (−25.3 ± 0.5‰). SPOM $\delta^{15}N$ values could not be measured due to insufficient material. BPOM $\delta^{13}C$ values significantly shifted from −19.6 ± 0.3‰ in the south to −21.9 ± 0.1‰ in the north ($p < 0.001$), while BPOM $\delta^{15}N$ values significantly differed between the south (5.1 ± 0.4‰) and the north (0.5 ± 0.4‰; $p < 0.001$; Table S9).

## 3.2 | Characterization of coral isotopic niches

We found distinct patterns in the isotopic niches of the six species of coral hosts and their endosymbionts (Figure 3; Figure S3). The isotopic niches of coral hosts *A. muricata*, *P. lutea* and *P. profundacella* were over twice the size of those of *S. pistillata* and *T. coccinea*. The isotopic niche of host *I. palifera* was of intermediate size, and overlapped those of *A. muricata*, *P. lutea* and *P. profundacella*. The isotopic niche of *S. pistillata* only overlapped the niche of *P. lutea*, while the niche of *T. coccinea* was the most distinct because of its lower $\delta^{13}C$ and higher $\delta^{15}N$ values (Figure 3).

Endosymbiont isotopic niche sizes were similar to or smaller than those of their coral hosts, and their niche positions had similar $\delta^{13}C$ values but lower $\delta^{15}N$ values (Figure 3; Figure S3). The niche overlap between host and endosymbiont $SEA_c$ ranged from 71% (high degree of resource sharing) to 7% (low degree of resource sharing), indicating a gradient ranging from autotrophy to heterotrophy (Table S10). There was a high overlap of host and endosymbiont niche areas in *A. muricata* (71%). The three species *P. lutea*, *I. palifera* and *P. profundacella* displayed partial niche overlap (50%, 45% and 33%, respectively), indicating that these species are mixotrophic. Last, *S. pistillata* had only a slight overlap (7%) between host and endosymbiont isotopic niches and occupied distinct isotopic niche spaces (Table S10).

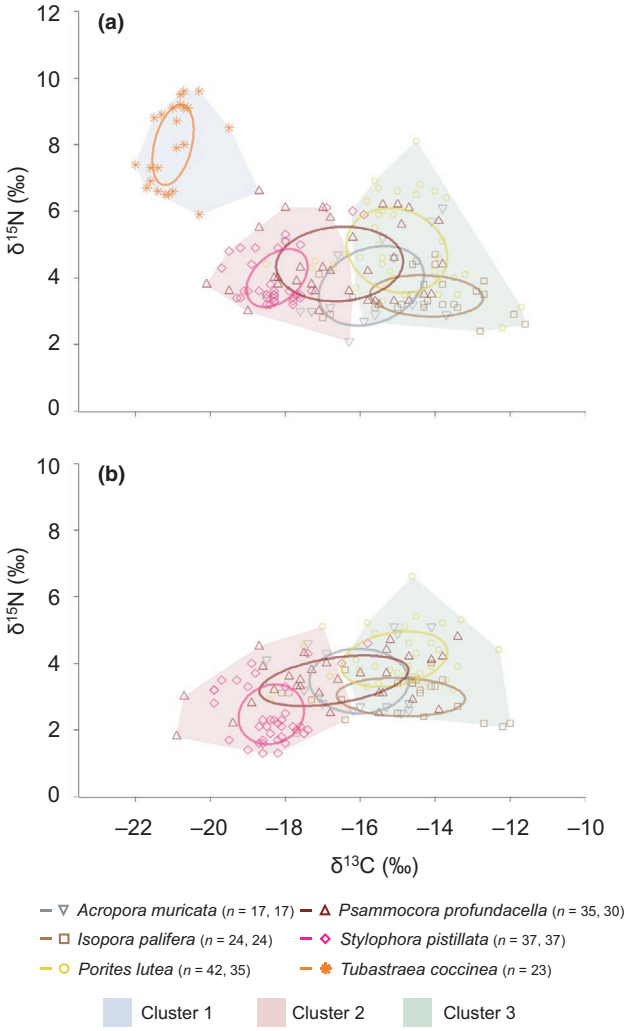


**FIGURE 3** The isotopic niches of scleractinian corals and the clusters identified by *k*-means analyses. Thick colour lines represent the isotopic niches and colour polygons the clusters on individual composition in stable isotopes of carbon and nitrogen for (a) coral hosts and (b) their endosymbionts. Each symbol represents an individual colony and the different symbols and colours represent the different species. Solid lines enclose the standard ellipse areas corrected for the sample size ($SEA_c$) of each species. Among the six species, *Isopora palifera* was not present in the north area, while *Acropora muricata* was sampled during a single season in the north and was not found in deep waters off the south coast. The number of coral individuals (for coral hosts and endosymbionts, respectively) appears between brackets after the names of each species

The isotopic niches of the coral hosts and their associated endosymbionts were generally larger in the north than in the south, except for *P. lutea* coral hosts. There were no size differences in the isotopic niches of coral hosts from shallow and deep reefs, whereas endosymbiont isotopic niches were larger in deep waters than in shallow, except for *I. palifera* (Figure 4; Table S3; Table S7). The niche overlap between host and endosymbiont $SEA_c$ varied across environmental conditions and ranged from 42% to 0% in

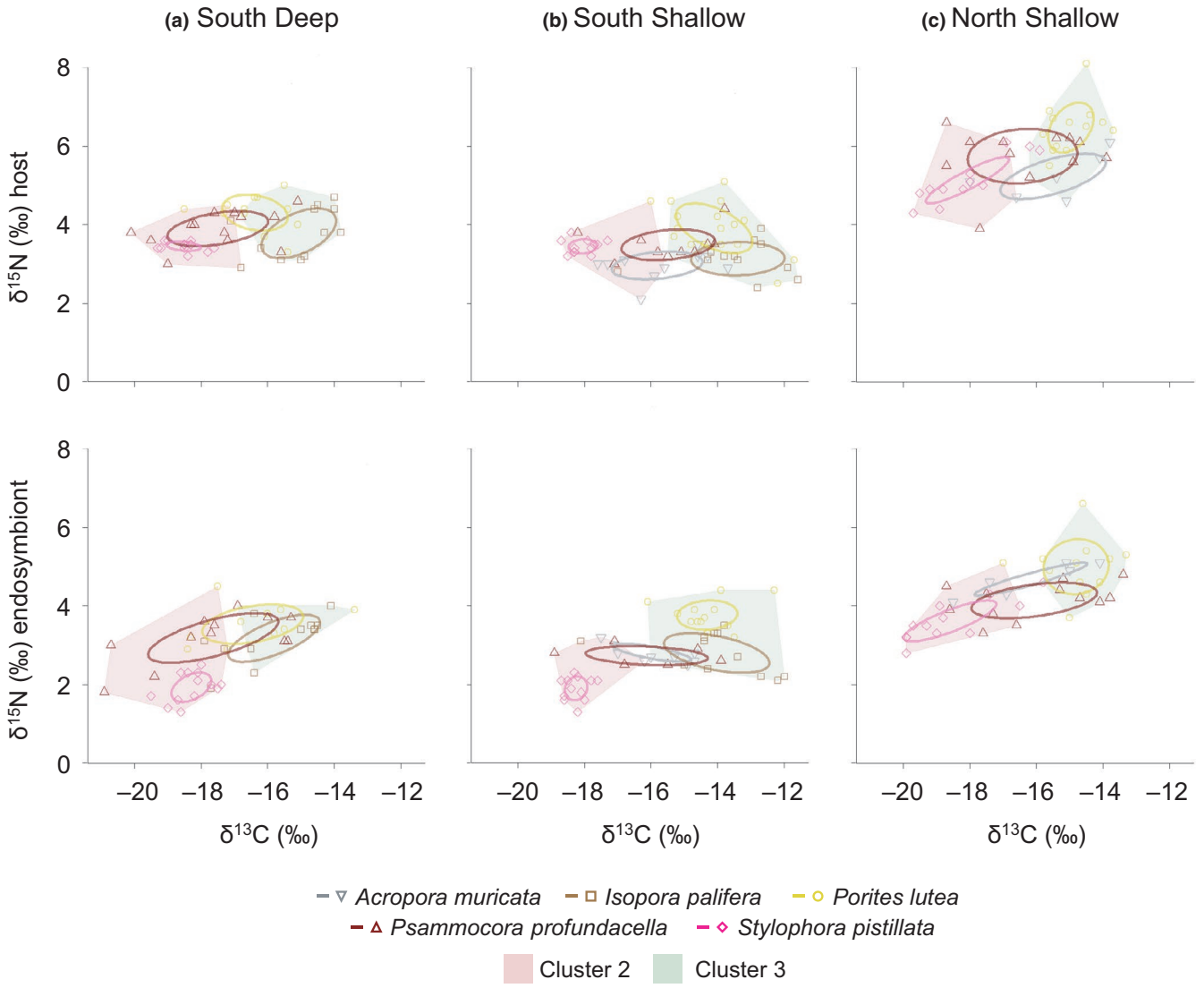


**FIGURE 4** The isotopic niches of scleractinian corals and the clusters identified by *k*-means analyses under different environmental conditions: (a) South Deep, (b) South Shallow and (c) North Shallow. Thick colour lines represent the isotopic niches and colour polygons the clusters on individual composition in stable isotopes of carbon and nitrogen for coral hosts (top) and their endosymbionts (below). Each small symbol represents an individual colony and the different symbols and colours represent the species. Solid lines enclose the standard ellipse areas corrected for the sample size ($SEA_c$) of each species. See Table S2 for the number of samples (*n*) of each species and environmental condition. Data are not shown for *Tubastraea coccinea* to avoid compressed data for symbiotic corals

deep waters of the south, 45% to 0% in shallow waters of the south, and 20% to 0% in shallow waters of the north (Figure S4; Table S10). In the north, there was no overlap of host and endosymbiont niche areas in *P. lutea*, *P. profundacella* and *S. pistillata*, while *A. muricata* displayed only a slight overlap (20%; Figure S4; Table S10).

### 3.3 | Coral individual partitioning

When all conditions are combined together, the *k*-means cluster analysis partitioned coral host and endosymbiont samples into three and two well-supported clusters (Figure 3; Table S11). For the coral hosts, cluster 1 was clearly distinctive in both $\delta^{13}C$ and $\delta^{15}N$ values, and was entirely composed of *T. coccinea* individuals excepting one individual of *P. profundacella*. The other clusters (2 and 3) included individuals from all species other than *T. coccinea*. Cluster 2 was composed of *S. pistillata* individuals, and to a lesser extent *P. profundacella* individuals. *Porites lutea* and *I. palifera* dominated cluster 3, which also included *P. profundacella*, *A. muricata* individuals and a few *S. pistillata* individuals. The most parsimonious representation of groupings for associated endosymbionts included two clusters and followed the same patterns of individual partitioning as the coral hosts (Figure 3; Table S11).

For each environmental condition, results of the *k*-means cluster analysis followed the same general patterns as the total output (all conditions combined). The analysis partitioned coral host and endosymbiont samples into three and two well-supported clusters,

respectively, except in the deep waters of south Taiwan where data were not analysed for *T. coccinea* due to small sample size (Table S11).

## 4 | DISCUSSION

We found varying degrees of trophic plasticity among and within scleractinian coral species living under the same environmental conditions. Furthermore, we observed changes in trophic plasticity across environmental conditions. The main outcomes were that (i) corals from variable environments in the north of Taiwan have larger host and endosymbiont niches than corals from stable environments in the south of Taiwan; (ii) deep coral populations had niches indicating a greater degree of heterotrophy than shallow corals; and (iii) corals did not exhibit seasonal differences in diet. Collectively, by promoting trophic niche differentiation along the mixotrophic continuum, individuals of targeted corals exhibited distinct trophic strategies.

### 4.1 | Trophic niche differentiation along the mixotrophic continuum

The six coral species exhibited distinct isotopic niche positions and sizes. Furthermore, the relationships between the $\delta^{13}C$ and $\delta^{15}N$ values of the coral hosts and their endosymbionts highlight, from an energetic perspective, the close link between host and endosymbiont nutrient sources. $\delta^{13}C$ values in corals and their endosymbionts are generally similar because of frequent nutrient exchange between them (Einbinder et al., 2009; Muscatine et al., 1989). Together with trophic niche differentiations, it suggests that corals do not always use the same nutrient sources and physiological pathways for nutrition.

The isotopic niche of the azooxanthellate *T. coccinea* had the lowest $\delta^{13}C$ values (mean −21.0‰) and highest $\delta^{15}N$ values (mean 8.0‰). These host values represent coral acquiring carbon and nitrogen solely from dissolved organic matter (Muscatine et al., 1989) and/or heterotrophic feeding on components of the SPOM (Ferrier-Pagès et al., 2011), which had $\delta^{13}C$ values of −22.6‰ in the south and −25.3‰ in the north. The fact that *T. coccinea* has a unique and narrow trophic niche, not overlapping with the other coral species, clearly characterizes its exclusive heterotrophic feeding compared to symbiotic corals that have access to additional resources.

The isotopic niches of the other species were less distinctive, but were separated (totally or partially) from each other. Among zooxanthellate corals, *S. pistillata* had the smallest isotopic niche, indicating a more restricted use of resources which was also confirmed by small CR ($\delta^{13}C$ range) among individuals. Its low $\delta^{13}C$ values and its proximity to *T. coccinea* suggest that this species is less dependent on autotrophy. The high $\Delta^{15}N$ values in *S. pistillata* (mean = +1.5‰) suggest a high capacity for heterotrophy. Furthermore, this species had only a slight or no overlap between host and endosymbiont isotopic niches (7% for all conditions combined and 0% for each area/depth condition) and occupied distinct isotopic niche spaces, indicating a decoupling of host and endosymbiont nutrition driven by host heterotrophy (Conti-Jerpe et al., 2020). For both study areas and depths, lower $\delta^{15}N$ values were obtained in the *S. pistillata* endosymbionts than in the other species (mean = 1.9‰ for both shallow and deep waters of the south; mean = 3.6‰ for shallow waters of the north), probably because some nitrogen is obtained from nitrogen-fixing bacteria (Lesser et al., 2018). Accordingly, *S. pistillata* performs well in regulating internal energy acquisition and allocation according to environmental conditions (Einbinder et al., 2009; Grottoli et al., 2017) which may explain why this species exhibited the lowest trophic plasticity. The fact that this species can compensate over 100% of its energy expenditures by means of predation (Sorokin, 1995) further allows this species to easily colonize new environments (Darling et al., 2012) to the detriment of its sensitivity to stress and resistance to bleaching (Swain et al., 2016).

*Isopora palifera* had the highest $\delta^{13}C$ values and an intermediate niche size, indicating that endosymbiont photosynthates are its main energy source. The low contribution of heterotrophy to this species' diet is reflected by its partial niche overlap between host and endosymbiont, low $\Delta^{15}N$ values (+0.3 to 0.6‰ according to environmental conditions), and positive $\Delta^{13}C$ values, which may be attributed to its ability to shuffle endosymbionts to maintain photosynthesis regardless of environmental conditions (Hsu et al., 2012). Previous findings demonstrated the susceptibility of autotrophic corals and the robustness of heterotrophic corals during elevated temperatures (Conti-Jerpe et al., 2020). As oceans warm and because of its reliance on autotrophy, this species may lose its competitive advantage in bright conditions and thus be highly affected by climate change through bleaching.

The isotopic niches of *A. muricata*, *P. lutea* and *P. profundacella* were in intermediate position between those of *S. pistillata* and *T. coccinea*. Their niches were also over twice as large; a variability among individuals (also reflected by large NR and CR) suggesting that these species can use a wide variety of resources (Radice et al., 2019). They are able to blend autotrophic and heterotrophic nutrition, a pattern consistent with the partial overlap observed between host and endosymbiont niches. This ability to feed through both pathways may explain why these species are representative of taxa more tolerant to stressful or variable environments (e.g. increasing depth, turbid waters and bleaching events; Anthony & Fabricius, 2000; Grottoli et al., 2006) and are less susceptible to bleaching than *S. pistillata* (Swain et al., 2016).

Several trophic pathways were identified under the same environmental condition (Figure 4). The different species had distinct isotopic niche positions and sizes with small overlaps, indicating that there may be intrinsic factors (e.g. coral morphology or host and endosymbiont physiology) as well as competition and extrinsic factors such as locally available resource breadth (e.g. prey diversity; Costa-Pereira et al., 2019) influencing their diet. *Tubastraea coccinea* and *S. pistillata* had the smallest niches under the same environmental condition. The niche positions of the other species, with larger isotopic niches, could easily be distinguished from one another (though partly overlapping), suggesting that they were using different trophic pathways.

## 4.2 | Coral trophic niches in contrasting environments

Our stable isotope data provide compelling evidence that acquisition of nutrients is specific to each coral colony. These findings support evidence of high inter-individual variation in heterotrophic nutrition of coral species in the Florida Keys (Teece et al., 2011) and on Palmyra Atoll (Fox et al., 2019) obtained through compound-specific isotope analyses of fatty acids and amino acids, respectively. This variation plays an important role in the dynamics of trophic niche expansion, and may be attributed to intrinsic and extrinsic (environmental) factors. Some species may adjust their diets to acclimatize to different environmental conditions (Ferrier-Pagès et al., 2011), which is one of the main causes of intraspecific variability. Host and endosymbiont isotopic niches were generally larger in the north than in the south, except for *P. lutea*. Resource availability across environmental gradients plays an important role in shaping trophic (physiological) coral niches (Fox et al., 2018; Radice et al., 2019). The north of Taiwan is turbid, sedimentary and phytoplankton rich, and its environmental conditions are more variable than those in the south (Denis et al., 2019), which may be reflected in the isotopic niches. Corals depend on heterotrophy in regions of high primary productivity (Fox et al., 2018), so the large isotopic niches observed in the north indicate that corals may use SPOM to obtain their nutritional and metabolic requirements (Anthony & Fabricius, 2000). Other factors could have influenced this pattern, including season (yet not significant here) and/or light-mediated fractionation (Muscatine et al., 1989). This fractionation occurs because photosynthetic rates are lower when light irradiance is reduced, which allows the preferential assimilation of $^{12}C$ and a depletion in $\delta^{13}C$ values (Muscatine et al., 1989). In the north, light may become limiting at a certain period of the year or in some microhabitats, affecting $\delta^{13}C$ values and expanding endosymbiont and coral host niches.

Corals from the north were more $^{15}N$-enriched than southern corals during both seasons, as found in coral host tissues at turbid sites around Moorea Island (Nahon et al., 2013). Such differences in $\delta^{15}N$ values among both coral host tissues and endosymbionts may have been caused by changes in the isotopic composition of the dissolved inorganic nutrients (DIN) that were assimilated by the endosymbionts, and/or during the fractionation process (Nahon et al., 2013). Because of the slow nitrogen turnover rate in coral tissue (>300 days; Tanaka et al., 2018), the distinction in $\delta^{15}N$ values of corals between the south and the north reflects spatial difference in nitrogen sources. This difference in $\delta^{15}N$ values between the two areas indicates the existence of two water masses with different DIN sources, which is consistent with current patterns off the coast of Taiwan (e.g. the south being affected by the Kuroshio Current pushing tropical water mass northeastward and the relative isolation of the north of Taiwan from the influence of this current [Chang et al., 2013; Liu et al., 2000]). Moreover, ground water or biotic processes can lead to large variations in the stable isotopic composition of the DIN pool in marine ecosystems (Swart et al., 2005). DIN $\delta^{15}N$ values can be up to 5‰ higher at eutrophic areas such as in the north of Taiwan, which is reflected in primary producers and higher trophic levels (Risk et al., 2009). Unexpectedly, the pattern in BPOM was the opposite of what was found in corals and endosymbionts. The BPOM $\delta^{15}N$ value is mainly determined by the primary producer responding to the euphotic zone's nutrient status. Therefore, the lower BPOM $\delta^{15}N$ in the north ($0.5 \pm 0.4$‰) compared to the south ($5.1 \pm 0.4$‰) may be attributed to $^{15}N$-depleted DIN assimilation or nitrogen fixation, having $\delta^{15}N$ values around −2 to +2‰ (Fry, 2006). The similar $\delta^{15}N$ values among the BPOM, coral host tissues and endosymbionts in the south may suggest a concurrent DIN source for them. However, the coral host tissues and endosymbionts having significantly higher $\delta^{15}N$ values than the BPOM in the north may imply an uncoupling of nitrogen nutrients for primary producers and corals. The $\delta^{15}N$ discrepancy among them in the north may infer particular microbial processes that occur in the sediments or symbiotic prokaryotes in corals (Cardini et al., 2014). Further research is needed to understand the processes involved in producing variable $\delta^{15}N$ values that characterize organic matter in the sediments from northern and southern areas of Taiwan.

The isotopic niches of *I. palifera*, *P. lutea* and *P. profundacella* had more negative $\delta^{13}C$ values in deep water than in shallow water, which may be due to low photosynthetic rates and/or high heterotrophic feeding (Muscatine et al., 1989). This was also reflected in their similar or higher $\Delta^{15}N$ values in deep than in shallow waters. These species may be able to expand their niches and shift from autotrophy to heterotrophy as depth increases. The lower niche overlap for *I. palifera* and *P. lutea* observed in deeper water, as well as their lower C:N ratios, further indicate that the heterotrophic acquisition of carbon can compensate for a reduction in photosynthetic carbon in some species (Alamaru et al., 2009; Conti-Jerpe et al., 2020). These lower C:N values may reflect a reduction in the amount of lipids stored in coral tissue (Post et al., 2007) and/or the fact that corals have greater access to nitrogen with depth (Radice et al., 2019). However, not all species change their diet with increasing depth (Crandall et al., 2016); for example, *S. pistillata*'s $\delta^{13}C$ and $\delta^{15}N$ values indicate that this species has low individual trophic variation and maintains the same trophic strategy independent of depth, such as observed in another Pocilloporidae species (Radice et al., 2019). The depth influence on coral carbon isotope ratios may be species context and context specific (Fox et al., 2018; Radice et al., 2019; Santos et al., 2021). For instance, in some regions, heterotrophic resources may be homogeneously distributed through the water column due to unique oceanographic regimes (Fox et al., 2018; Williams et al., 2018).

## 4.3 | Mixotrophic corals demonstrate diverse trophic strategies and behaviours

Coral host and endosymbiont individuals were partitioned into three and two clusters, respectively. Each coral species occupied two to three clusters revealing a variety of trophic behaviours within a species, except for *T. coccinea*. The same pattern was observed for

all conditions combined and for subgroups according to area and depth. Individual distribution among the different trophic behaviours indicated whether the corals were generalist or specialist species. *Psammocora profundacella* was the only species that exhibited three behaviours. Generalists survive many environments (Crandall et al., 2016; Darling et al., 2012), which may be why *P. profundacella* has a widespread distribution and is frequently observed in mesophotic and high-latitude habitats (Sugihara et al., 2014). Without extending across the three clusters, *A. muricata* exhibited similar patterns to *P. profundacella*. *Tubastraea coccinea* individuals only exhibited one behaviour, as did *S. pistillata* individuals with a few exceptions. Specialists have low environmental tolerance (Büchi & Vuilleumier, 2014), but perform well in a narrow range of environmental conditions. *Tubastraea coccinea* and *S. pistillata* thrive in specific habitats, and are common opportunistic species (Creed et al., 2017; Loya, 1976). The strategies of *I. palifera* and *P. lutea* reside between these extremes, indicating that trophic characterization should be combined with a wide range of other physiological features (e.g. reproduction) to facilitate the identification of 'performance niches'.

## 5 | CONCLUSIONS

Mixotrophic corals exhibited high trophic plasticity and used a variety of trophic pathways. Along the mixotrophic continuum, individuals of the focal corals displayed distinct trophic niches under the same environmental conditions. Furthermore, we observed changes in trophic plasticity across environmental conditions. The combined Bayesian isotopic niche and unsupervised machine learning approaches allowed us to identify behaviours and typify them in different trophic strategies. There were some common features with the adaptive strategies defined by Darling et al. (2012), with two extreme strategies identified: generalist and specialist, the latter being possibly translated into various behaviours (e.g. weedy, competitive or stress tolerant). In addition, we found high interindividual trophic variation within each species that favoured isotopic niche expansion and consequently different trophic behaviours. So, taking intraspecific variability into account is fundamental in defining a coral's trophic strategy. Overall, the Bayesian analysis combined with the unsupervised machine learning approach applied here offers a novel framework for quantifying trophic plasticity and identifying trophic strategies within scleractinian corals. Further work should be conducted to investigate the processes that underlie the origins of within- and between-individual variation to improve predictions of the responses of corals and other mixotrophic organisms to global environmental change.

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### CONFLICT OF INTEREST

We declare that none of the authors have a conflict of interest.

### AUTHORS' CONTRIBUTIONS

N.S. and V.D. conceived the study and designed the methodology; V.D., N.S., Q.C. and Y.E.H. conducted the sample collection; Y.E.H., N.S. and P.-L.W. prepared the samples and conducted the laboratory analyses; N.S., Y.E.H. and V.D. analysed the data; N.S., V.D. and Y.E.H. led the writing of the manuscript. All authors reviewed, approved and contributed to the final version of the manuscript.

### DATA AVAILABILITY STATEMENT

Isotope data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.2ngf1vhnt (Sturaro et al., 2021).

### ORCID

*Nicolas Sturaro* https://orcid.org/0000-0002-7225-0880
*Yunli Eric Hsieh* https://orcid.org/0000-0002-8745-8342
*Qi Chen* https://orcid.org/0000-0002-7575-550X
*Pei-Ling Wang* https://orcid.org/0000-0002-4392-3935
*Vianney Denis* https://orcid.org/0000-0002-0914-5586

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