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Trapezia Crabs That Dwell in Distinctive Day/Night Canopy Compartments of a Marine Animal Forest, Forage on Demersal Plankton

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Abstract: Canopies of branching corals harbor a wide range of sessile- and mobile-dwelling species that benefit from the physical compartments and the micro-environments created by the complex three-dimensional structures. Although different compartments within canopies are differentially used by inhabitant species, the distribution of mobile animals between coral canopy compartments are not fully explored. Here, we study *Stylophora pistillata*, a common branching coral in the Gulf of Eilat that harbors obligatory crabs from the family *Trapezia*. Two in situ surveys elucidated diel dynamics in compartmental distributions of *Trapezia* species within *S. pistillata* canopies compartments, associated with the crab's body size and day/night activities. Whereas all crabs were found within sheltered spaces in the coral canopy understory or in the base during day hours, laboratory experiments revealed that nighttime distributions of small and large crabs (in middle and up compartments, respectively) are not intraspecific competition-borne, but rather, the outcome of preferred crab-size location for a novel feeding type, predation on demersal plankton. This study, thus, disclosed the importance of studying the coral's three-dimensional structures and within canopies' compartments for understanding the biology of dwelling species in the animal forests' canopies.

Keywords: *Trapezia*; *Stylophora*; habitat complexity; coral canopy; diurnal; zooplankton; Eilat; marine animal forest; branching coral

1. Introduction

Scleractinian branching corals are the major habitat constructors and assemblers for the marine animal forests (MAFs, the living three-dimensional communities dominated by megabenthic suspension feeders) of coral reefs, providing a wide range of ecosystem services [1–3]. The complex three-dimensional (3D) structures of their canopies (the above-ground portion of the coral colony, formed by the collection of individual branches and spaces that have important ecological functions [4]) create ecological spaces within the canopies' compartments (structurally separated spaces) and provide food and shelter [1,5,6] to numerous taxa of sessile and mobile dwelling organisms (organisms that live most or all of their lives in close proximity to a host coral colony [7]). The high biodiversity allied with MAFs in general, and with branching corals in particular [6,8,9], is further associated with the diverse environmental conditions created within the compartmental heterogeneity of the 3D structures [1,2,10,11] and entitle many of the branching coral species as ecosystem engineering species [12,13].

The corals MAFs structurally and functionally resemble terrestrial forests (trees), all made by assembling hierarchical basic units, such as the corals' polyps and branches, as

compared to the trees' leaves and branches [5,14,15]. Yet, while canopies in terrestrial forests have been intensively studied as the functional structural framework that shape the assemblages and the behaviors of forest-dwelling species [16–21], studies on the distributions of the dwelling species within branching coral canopies are lacking [5,22]. Tree canopies may create numerous microclimate conditions, thus, providing unalike resource availabilities, microclimate preferences, various types of refuges, and a wide range of biological and environmental goods and services to the dwelling species [10,19,23,24]. Similarly, a branching coral canopy shapes several micro-environments, defined as compartments, that are different by their location upon the coral canopy from bottom to top. These compartments differ by being subjected to unalike current intensity, light regime, and properties, such as inclusive volume and access to food, altogether creating distinct compartmental distribution for dwelling species, that may also vary from day to night [5]. The distributions of dwelling species within and among canopy compartments and between day/night hours are not fully explored.

One of the widely distributed MAFs species in the northern Gulf of Eilat, Red Sea, is the branching coral *Stylophora pistillata* (Esper, 1792) (family: Pocilloporidae; Figure 1a). The canopy's architecture of *S. pistillata* is designed on iterative processes of polyps and branches [25–27], with growing branches typically added via dichotomous bifurcation at the branch tips, while side-growing branches are formed by the budding of lateral up-growing branches. Following colonial astogeny, *S. pistillata* develops shrub-like and nearly sphere-shaped canopies, inclusive of various compartments, all equipped with a wide range of inter- and intra-compartmental spaces between the structural mesh of up-growing and side-growing branches, spaces that are used by the coral's dwelling species [15].

Among the common and widely distributed dweller species within *S. pistillata* canopies are decapods of the genus *Trapezia*. These crabs are obligatory symbionts within pocilloporid corals [28–32] and are considered to have mutualistic relationships with the host corals, imposing positive impacts on coral growth [33] and health [34] while defending coral from predators [35,36]. The *Trapezia* species are further considered to be dependent on their coral hosts' tissues, since earlier findings on feeding behavior and follow-up of photosynthetically labeled carbon indicated that they feed on coral mucus, polyps, and detritus settled on the coral tissues [29,30,37–39], further retreating from senescing coral colonies [40]. The demographic structures of *Trapezia* species and specimens within the coral canopies are determined by the sizes of ecological volumes within canopies and the crabs' inter- and intraspecific interactions with other dwelling organisms [41,42], all leading to the existence of a single mating pair and several juveniles inhabiting a single coral canopy [22,29,41,43]. Tsuchiya and Taira [22], further suggested that intraspecific competition between adults and young crabs led to microhabitat segregation within canopy. The literature reveals that small corals host only one individual and that there is an association between the coexistence of more than a single *Trapezia* species per coral, as heterosexual pairs, and as individuals, based on the canopy size [5,22,41,44].

Trapezia crabs were further documented to move during night hours, when most predatory fish species are dormant, from their host canopies to larger canopies, in search of improved territorial sites or mates [37,41], and the larger crabs evict smaller crabs from selected colonies [42,45].

While most studies examined the *Trapezia*—host relationship primarily during day time, our field surveys on *S. pistillata* colonies at nighttime in Eilat's reefs (northern Red Sea) further documented an unnoticed before-feeding strategy for the *Trapezia* specimen that forage on free-swimming demersal plankton [46], addressing queries for the links between this feeding strategy and the crabs' positions within coral compartments at day and night hours [5]. To further elucidate the intimate site selection position, we tested the null hypothesis that *trapezia* activities do not differ between day and night, nor among *Trapezia* species and different crab sizes. Thus, the spatial and temporal partitioning within and between *Trapezia* species distributions among canopy compartments were investigated

by conducting field surveys and laboratory experiments while studying their feeding behaviors.
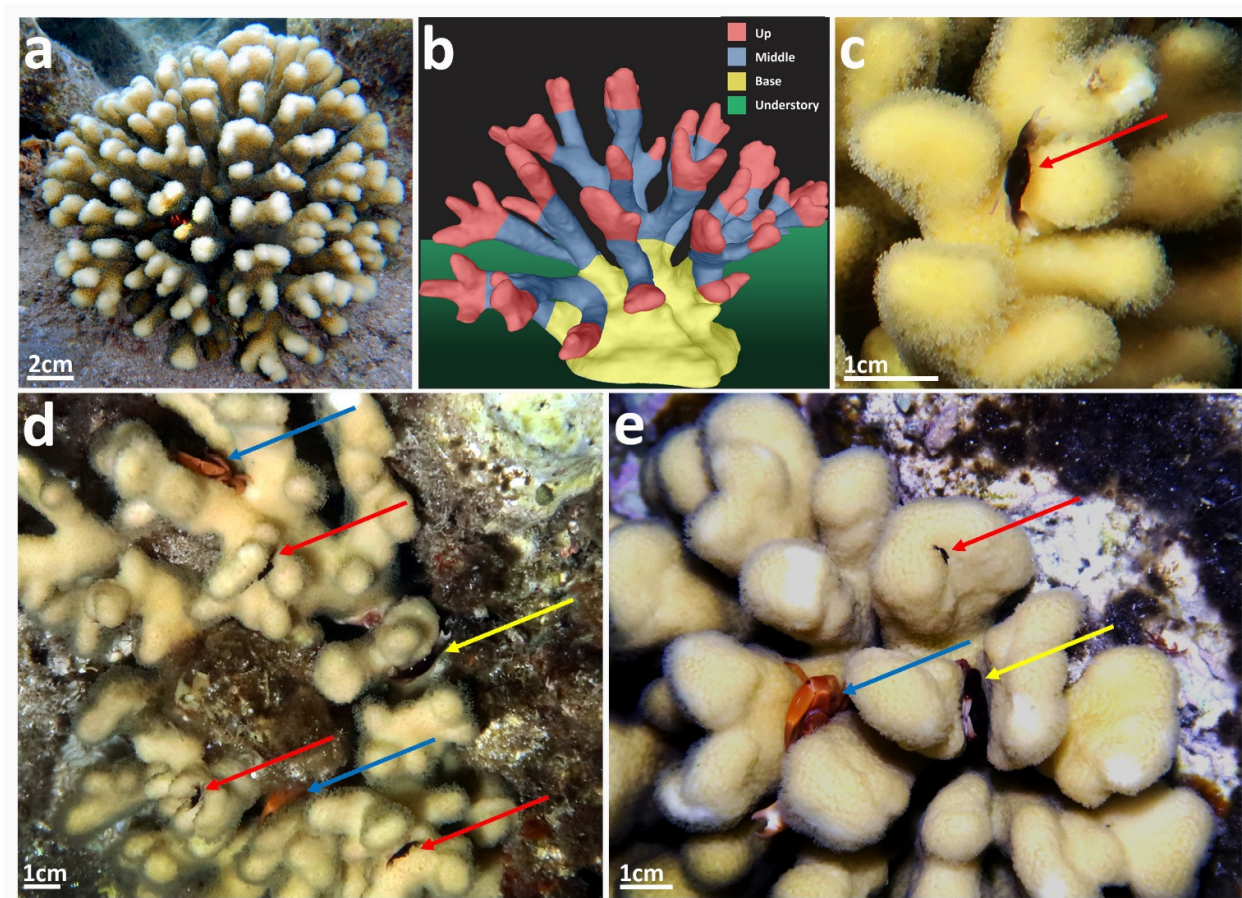

Figure 1. (**a**) *Stylophora pistillata* from Eilat's reef at day time (3 m depth); (**b**) Schematic illustration of *S. pistillata* sagittal section for the canopy compartments. Up: the upper most parts of the canopy, that border the 'outer-colonial' environment. This compartment outlines the canopy's internal volume and encloses the first Strahler order branches; Base: the coral most inner part composed by the canopy's two highest Strahler numbers for each individual coral colony; Middle: inner branches area, a space enclosed between the branches above the base and below branches of the first Strahler order; Understory: the 3D volume exists at the edge of the coral canopy's base and occupies the spaces between the coral's substrate plain to the parallel first canopy branches that shade on it; (**c**) *Trapezia digitalis* small body size at the up compartment, night time; (**d,e**) *Trapezia cymodoce* and *T. digitalis* distribution among *S. pistillata* canopy compartments at night, respectively. Arrows: Red—small *T. digitalis* at 'Up' compartment; Yellow—medium *T. digitalis* at 'middle' compartment; Blue—large *T. cymodoce* at 'Base' compartment.

2. Materials and Methods

2.1. Canopy Compartment Usage by Trapezia Crabs-Day and Night Field Surveys

Compartments composition of *Trapezia* species and individual crabs in the *Stylophora pistillata* canopy [5] were followed in two field surveys using SCUBA and snorkel (June to September of 2020–2021) at the Japanese Gardens, a narrow and shallow (>7 m depth) fringing reef on the west Israeli shoreline of the Gulf of Eilat, Red Sea (29°30′ N, 34°56′ E). In order to avoid repetition of the surveyed corals belt transects (50 × 2 m, >5 m apart, 1–7 m depth) were placed perpendicular to the coastline from the lagoon to the fore-reef (we considered belts containing >10 *S. pistillata* colonies). Each canopy was visually surveyed twice for 1–3 min (according to the coral complexity and size), first during the day (3:00–5:00 p.m.), and then during nighttime (8:30–11:30 p.m.) for the presence and compart-

ment allocation of the canopy's dwelling *Trapezia* species. Daytime surveys also included measurements of canopy attributes (height, diameter, Strahler numbers). The canopies Strahler numbers provided us the tool to sperate the canopy to different compartments [5]. Strahler numbering is a numerical measure of branching complexity, originally introduced in hydrology to define river stream based on a hierarchy of tributaries [47]. In the coral system, ordering initiates at the terminal branches and increases when two branches of equal order meet.

Trapezia individuals were categorized to three size groups (*Trapezia cymodoce* [Herbst, 1801] carapace width >2 cm = large, 1–2 cm = medium, <1 cm = small; *Trapezia digitalis* [Latreille, 1828] carapace width large >1.5 cm = large, 1–1.5 cm = medium, and <1 cm = small), and to the canopy compartment they were resident (up, middle, base, understory [5]; Figure 1b). Individual crabs traveling between the coral compartments during the surveys were assigned to all crossed compartments. To reduce artifacts caused by interference with the observer, observations began from a distance of one meter away from the coral colony, and then the observations were confirmed while slowly approaching the coral colony, using a flashlight for meticulous examinations [44]. Each colony was photographed underwater (using a Canon G7X, Tokyo, Japan and Nikon Coolpix W300, Tokyo, Japan) to verify doubtful results or to respond to emerging queries. All observations were made without manipulations or hand contacts to avoid biasing the organisms' behavior. Rare *Trapezia* species were considered as species appearing with a total of <10 specimens in all censuses, and they were omitted from further analyses.

2.2. Canopy Compartment Usage by Crabs-Laboratory Experiments

To test the distribution among coral compartments and the dynamics for the different group sizes of *T. cymodoce* and *T. digitalis* crabs at day and night and to assess the influence of the large size crabs on the compartmental distribution of smaller crabs (small and medium) within and between species, we conducted five experimental sets (August 2021 to April 2022). Each of these experiments was conducted for two days, on the first day with the presence and then, on the second day, with the absence of large body size *T. cymodoce* pairs. In each experiment, we documented the compartment locations of *Trapezia* specimen assigned within the coral canopy at day (12:00–4:00 p.m.) and at night (8:00 p.m.–12:00 a.m.). Prior to each experiment (the night before the experiment startup), crabs (according to each experiment design) were placed in the examined corals, and after the first day and night observations, large crabs were removed from the experiment for the day and night 'large size absence' observations.

Each one of the *Trapezia* individuals was involved only once in the experiments, totaling 237 *T. cymodoce* (30, 46, 161; small, medium, large, respectively), and 25 *T. digitalis* individuals (14, 11; small and medium, respectively). All crabs were collected from *S. pistillata* colonies provided by the Israeli Nature and Parks Authority (INPA) and from *S. pistillata* colonies (n = 21, sizes 118–2102 cm³; Supplementary Table S1) that were haphazardly sampled by SCUBA. All corals together with their dweller's *Trapezia* crabs were sample along the Gulf of Eilat, Red Sea (29°30′ N, 34°56′ E; 3–10 m depths) and were kept in a running seawater tables facility at the Interuniversity Institute for Marine Science in Eilat (IUI).

In all five experiments, we repeatedly used the same sampled *S. pistillata* colonies (n = 21, sizes 118–2102 cm³) that were first cleared of all other dwelling movable species (e.g., sea urchin, brittle stare, fishes, crabs, etc.), in order to prevent possible influences of interactions between *Trapezia* crabs and other species. Then, each coral was placed in an isolated closed container supplied by a running open seawater system. The crabs and all other dwelling species were removed from their original coral hosts prior to each experiment by placing the coral above an empty tank filled with seawater and then by pushing the animals out while carefully inserting a plastic Pasteur pipette or a metal stick between coral branches.

In the first experiment, we examined the distribution among the canopy compartments of combined three *T. cymodoce* body sizes (small, medium, and large), thus, we used the original *T. cymodoce* populations found on each of the 21 sampled *S. pistillata* canopies (Large 39, medium 25, and small 15; Figure 2; Supplementary Table S1). In the second and the third experiments, we added to each *S. pistillata* canopy one large pair of *T. cymodoce*, together with only one different *Trapezia* individual, as follows: in the second experiment, one medium-size *T. cymodoce* individuals/canopy (n = 21.), and in the third experiment, one small-size *T. cymodoce* individual (n = 15). In the next two experiments, we tested the outcomes of interspecific interactions, by introducing one *T. digitalis* individual together with *T. cymodoce* large pairs on each canopy. In these experiments, we used only two size classes of *T. digitalis*，small (n = 14; 4th exp.) and medium (n = 11; 5th exp.) (Figure 2).

2.3. Feeding on Planktonic Organisms-Laboratory Experiments

A total of 114 *T. cymodoce* individuals (66 large, 48 medium) were placed in pairs in closed system water tanks (29 × 29 × 29 cm) filled with fresh ambient seawater (23–24 °C, with room light [led illumination]). *Trapezia* pairs were assigned to one of three treatments designed by the host status: live coral, coral skeleton, and no coral (total 38 individuals per treatment, 11 large and 8 medium-size pairs, respectively). After one hour of acclimatization, each tank received 2–5 mL of live *Artemia* (1 mL = 5 individuals, 7–16 days old) to test the feeding behaviors of *Trapezia* crabs. We defined 'success' and 'failure' outcomes for two feeding behaviors: 1. Reaction—crab's response, observed by (I) continually flicking their antennas, (II) consistent movements of the maxillipeds (also accompanied with body cleaning behaviors), and both reactions could be accompanied by movements of the second pereiopods along the tomentum on the chela or toward the mouthparts, a behavior that has been described in relation to mucus collection [30]; 2. Predation: The crabs use the chelipeds to catch and eat the prey. Each individual *Trapezia* was observed for up to 15 min or less (once both behaviors were determined as 'success'). All experiments were conducted repeatedly from 9:00 a.m. to 2:00 a.m. of the following day. All *Trapezia* were provided by the INPA and, upon receiving, were kept for 1–3 days with their original coral host in the running sea water facility at the IUI before experimental assignment.

2.4. Statistical Analyses

We used Bray–Curtis dissimilarities matrix with zero adjustments of +1 (dummy variable) to compare the compartmental distribution between and within *Trapezia* species, between the coral canopies between *Trapezia* size groups and between the years. For the analyses of field observations, we used a 1.4 power transformation followed by a two-way PERMANOVA and a pairwise permutation MANOVA with false discovery rate adjustment (FDR). First, we used the crab's body size group with the interaction of time (day, night) as the fixed effects, and canopy sample ID as a random effect. As the outcome was significantly different between the size groups, we grouped each body sizes for each species by the observation time (day/night) and tested the compartmental distributions between years (2020, 2021), which were used as the fixed effects while canopy sample ID was considered as a random effect (R packages: [48–51]). The same analyses were employed in the laboratory experiments using a power transformation on the dissimilarity matrix data with time and size as the fixed effect, and coral ID as the random effect. For pairwise analyses, we grouped crabs by their body size with the presence or absence of large individuals in addition to the time. For the feeding experiments, we used Pearson's Chi-square followed by post hoc pairwise tests of independence for nominal data with the Fisher exact adjusted by FDR (R package: [52]). All analyses were performed using RStudio version 1.3.1093, and plots were made with Office software (Excel and PowerPoint).

Figure 2. A pictograph presentation for lab experiments (1–5) design on the canopy compartmental usage by *Trapezia* crabs, managed by two basic scenarios: with the 'presence' or 'absence' of large pairs of *Trapezia cymodoce*.

3. Results

3.1. Day and Night Surveys

A total of 114 and 79 coral canopies were day and night surveyed during the years 2020 and 2021, respectively (Figure 3; Supplementary Table S2 In both years, the most common *Trapezia* species was *T. cymodoce* (165/274 [day/night] individuals, in 2020 and 111/187 [day/night] individuals in 2021), followed by *T. digitalis* (30/126 [day/night] individuals in 2020, and 22/82 [day/night] in 2021). Two other *Trapezia* species, *Trapezia guttata* (Rüppell, 1830) (7/4 individual, 2020/2021, respectively), and *Trapezia rufopunctata* (Herbst, 1799) (6/0 individual, 2020/2021, respectively) were considered rare species and were omitted from our analyses. The compartmental distributions for *T. cymodoce* and *T. digitalis* were not different between years (*T. cymodoce*, $p > 0.05$, F = 2.45, $r^2 = 0.004$, df= 1; *T. digitalis*, $p > 0.05$, F = 2.46, $r^2 = 0.01$, df = 1, two-way PERMANOVA; Supplementary Tables S3 and S4).
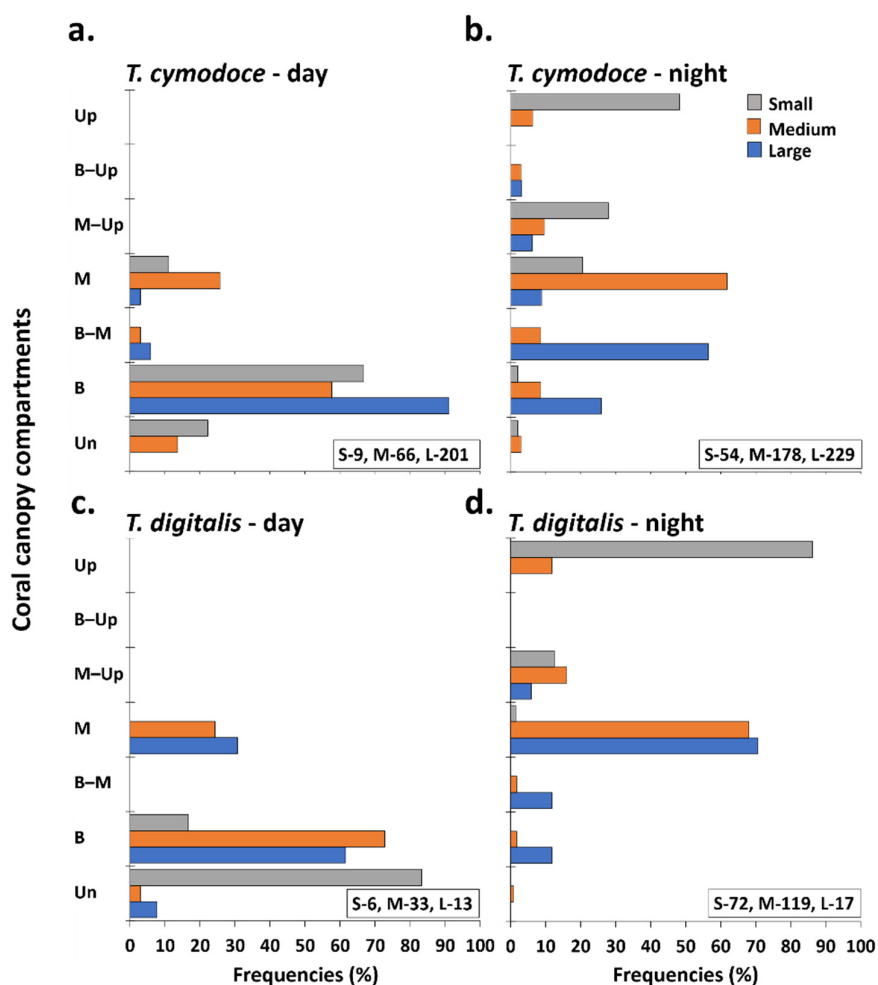

Figure 3. *Trapezia's* different body sizes (small, medium, large) diel distributions among *Stylophora pistillata* (n = 193) canopy compartments recorded over two years under in situ surveys (2020–2021). *Trapezia cymodoce* (**a**) day and (**b**) night frequencies (%); and *Trapezia digitalis* (**c**) day and (**d**) night frequencies (%). Total observations by body size (L= large, M= medium, S= small) are marked for each plot. Frequencies were calculated according to the total abundance of each species group size for each day time census. (Un) understory; (B) base; (M) middle; (B-Up) base, middle, and up; (M-Up) middle and up compartments.

The two years cumulative day and night differences for individuals documented in the same coral canopies were close to two-fold for *T. cymodoce* (276/461 individuals, day/night, respectively) and four-fold for *T. digitalis* (52/208 individuals, day/night, respectively). Out of the total surveyed canopies (n = 193), *T. cymodoce* and *T. digitalis* were found

in 75%/92.7%, and 17.6%/48.7% (day/night) observations, respectively. Both species were found together in the same canopy on 9.8%/43.5% (day/night) observations, where *T. digitalis* individuals were usually of medium and small sizes (8.3%/40.1%, day/night). *T. digitalis* large individuals were scarce in this survey, found only in 4.1%/4.7% (day/night) observations, coexisting with large *T. cymodoce* only on 1.6%/2.6% (day/night) observations.

Significant differences in daytime activities were recorded between the two species ($p < 0.001$, F model = 30.9, r^2 = 0.37, df = 11, two-ways PERMANOVA; Supplementary Table S5) and within species size groups (*T. cymodoce*, $p < 0.001$, F model = 9.87, r^2 = 0.03, df = 2; *T. digitalis*, $p < 0.001$ F model 5.17, r^2 = 0.04, df = 2, two-ways PERMANOVA; Supplementary Tables S6 and S7). Further, during the night hours, the common distribution design of either size group in both species was associated with the more exposed compartments (middle and up), as compared to the more protected compartmental spaces during day hours (understory and base; Figure 3). Differences were also recorded for compartmental distributions in day and night hours between the large-size groups of *T. digitalis* and *T. cymodoce* ($p > 0.05$, pairwise permutation MANOVA; Supplementary Table S8). Large *T. digitalis* individuals shared the same canopy compartments with *T. cymodoce* medium and small individuals at day (understory, base and middle; $p > 0.05$, pairwise permutation MANOVA; Supplementary Table S8) and night hours only with *T. cymodoce* medium-size individuals (base, middle, and middle to up; $p > 0.05$, pairwise permutation MANOVA; Supplementary Table S8). Large *T. cymodoce* crabs were significantly different from *T. digitalis* medium and small individuals for day/night compartmental distributions ($p < 0.05$, pairwise permutation MANOVA; Supplementary Table S8), as at day hours they were found at the lower compartments, while at night they migrated upward to the middle compartments (base 91%/25.86%, base to middle 6%/56.3%, and middle 3%/8.7% individual frequency, day/night, respectively). During day hours, compartmental distributions for medium and small-size *T. digitalis* were not significantly different from those of medium and small *T. cymodoce* individuals ($p > 0.05$, pairwise permutation MANOVA; Supplementary Table S8), indicating the same compartments preference at day hours, which includes the middle, and down to the understory, with higher frequencies at the lower and more sheltered compartments (understory and base; Figure 3). At night hours, the medium-size groups of the two crab species shared the same distribution pattern ($p > 0.05$, pairwise permutation MANOVA; Supplementary Table S8) and were more prevalent in the middle compartment (61.8% and 68.1% *T. cymodoce* and *T. digitalis*, respectively), while small crabs showed different distribution patterns ($p < 0.05$, pairwise permutation MANOVA; Supplementary Table S8), with *T. digitalis* individuals more common in the up compartments (86.1% up, 12.5% middle to up) and *T. cymodoce* individuals more common in the middle compartments (20.4% middle, 27.8% middle to up).

Comparison between day and night distribution shows that all size groups within species were different ($p < 0.05$, pairwise permutation MANOVA; Supplementary Tables S9 and S10), with the exception of large *T. digitalis* ($p > 0.05$, pairwise permutation MANOVA; Supplementary Table S10).

3.2. Canopy's Compartment Usage by Crabs-Laboratory Experiments

The laboratory observations revealed significant day/night changes in the canopy's compartmental distributions of both species in all different experimental settings (Figure 4a–e; Supplementary Tables S11–S15) and reflected changes between the different body sizes ($p < 0.05$, two-ways PERMANOVA; Supplementary Tables S16–S25). Interestingly, in each of the five experiments, the presence or the absence of large-sized *T. cymodoce* individuals did not change the temporal and the spatial compartmental distributions of the small- and medium-size groups ($p > 0.05$, pairwise permutation MANOVA; Supplementary Tables S26–S30), except for *T. digitalis* medium-size group yet, only for day hours. In the presence of large *T. cymodoce* individuals at day hours, medium *T. digitalis* were distributed in all coral compartments (understory, base, middle, and up), a distribution that was changed in the absence of large-size *T. cymodoce* individuals ($p < 0.05$, pairwise permutation MANOVA;

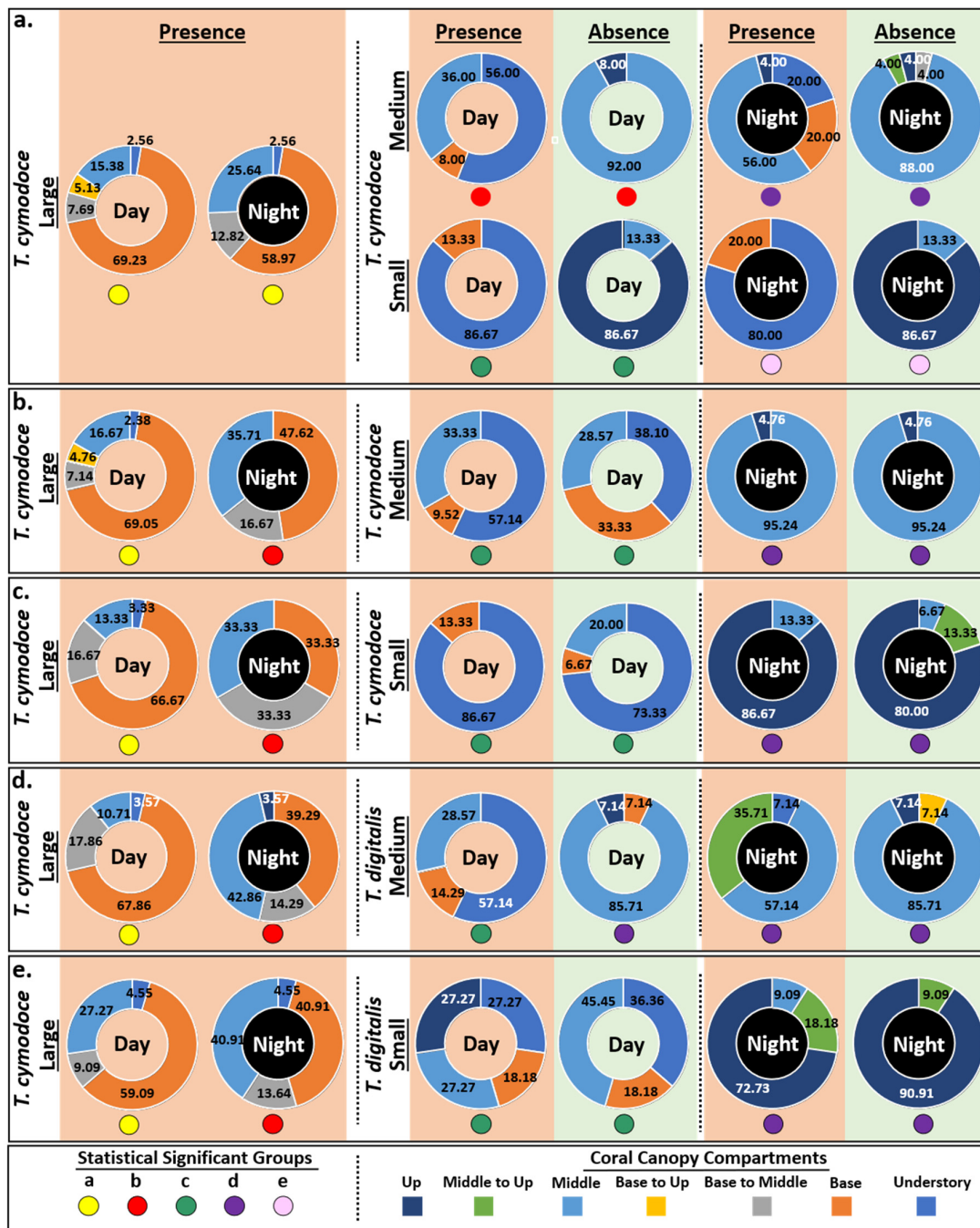Supplementary Table S29), indicating interference of large *T. cymodoce* for the day hours (Figure 4).

Figure 4. Day and night distribution patterns among *Stylophora pistillata* canopy compartments of different *Trapezia* body sizes with the presence or the absence of large *Trapezia cymodoce*. (**a**) *T. cymodoce* medium and small; (**b**) *T. cymodoce* medium; (**c**) *T. cymodoce* small; (**d**) *Trapezia digitalis* medium; (**e**) *T. digitalis* small. Color dots indicate significantly different groups (pairwise permutation MANOVA; Supplementary Tables S11–S30).

The distribution patterns along the two days treatments (with and without the presence of large *T. cymodoce*), and throughout all five experiments, showed that at daytime the canopy "up" compartment was rarely occupied by all size groups (*T. digitalis*: 13.6% small, and 3.6% medium; *T. cymodoce*: 1.1% medium, and 2.5% ["base to up"] large size), and

most crabs were recorded in the lower compartments (understory, base, and middle). Compartmental distribution changed at night hours, where the "up" compartment was commonly occupied by the small-size groups (*T. digitalis* 81.8%, and *T. cymodoce* 85%) and the middle compartment by the medium-size groups (*T. digitalis* 71.4%, and *T. cymodoce* 92.4%). The up and middle compartments enabled sheltering of the small-body-size crabs between the small branches (Strahler order 1 and 2) or within the small bifurcation points, and yet to be found at the edge of the canopy (Figure 1c–e).

T. cymodoce large individuals across all treatments (n = 161) were mostly found in the base compartment (67%, 45% day and night, respectively), though, at night, they were also prevalent in the middle compartments (middle: 16%, 35%; base to middle 7%, 18%, day and night, respectively).

3.3. Plankton Foraging-Laboratory Experiments

With the presence of *Artemia* prey, a reaction behavior was observed in all *Trapezia* crabs in the 'live coral' treatment, and, in all, except a single large individual, in the 'coral skeleton' experiment (Supplementary Table S31). *Artemia* presence in the 'non-coral' treatment triggered crabs' reaction behavior only for 33% of the large body size individuals (12/36).

Most *Trapezia* crabs in the 'live coral' and 'coral skeleton' treatments caught and ate *Artemia* (35/38 in both treatments), with just a single large-size and two medium-sized crabs that failed to catch prey within 15 min from *Artemia* introduction. When *Artemia* were introduced to the tanks, the crabs migrated to the more open spaces within the corals' canopies (middle to up compartments) as part of their food acquisition. In 'non-coral' treatments, the crabs did not show any sign of predation behavior (0/38 predation success). Furthermore, the *Trapezia* crabs ignored the *Artemia* prey even in cases where the *Artemia* individuals were swimming towards them or physically contacted their bodies.

For both behaviors, no significant differences were found between crabs in 'live coral' and 'coral skeleton' treatments, and these two treatments were significantly different from crabs in the 'non-coral' treatment (Pearson chi-squared test: $p < 0.05$, df = 2, $\chi^2 = 63.2$, and $p < 0.05$, df = 2, $\chi^2 = 90.7$, 'reaction' and 'predation' behaviors, respectfully). Differences between the medium- and large-size crabs' behaviors, were significant only for the reaction behavior in the 'non-coral' treatment (Pearson chi-squared test: $p < 0.05$, df = 1, $\chi^2 = 10.36$; Table 1).

Table 1. Feeding on planktonic organisms by large and medium size *Trapezia cymodoce* crabs — summary results for laboratory experiments. Pearson's chi-square followed by Fisher exact pairwise tests of independence for nominal data analyses of predation and reaction behaviors (failure/success) of individuals examined on different substrates: live corals ('live'); coral skeletons ('dead'); and without corals ('none'), following the introduction of live *Artemia*. Asterisk indicates statistical significance.

| | | Treatment Type | | | | | | Between Treatments | |
| | | Live | | Dead | | None | | | |
Type of behavior	Failure/Success	Medium	Large	Medium	Large	Medium	Large	χ^2	p
Predation	Failure	2	1	2	1	16	22	90.7	<0.001 *
	Success	14	21	14	21	0	0		
Reaction	Failure	0	0	0	1	16	10	63.2	<0.001 *
	Success	16	22	16	21	0	12		
Within treatments—between body sizes		χ^2	p	χ^2	p	χ^2	p		
Predation		0.08	>0.05	0.08	>0.05	0.95	>0.05		
Reaction		0.95	>0.05	0	1	10.36	<0.001 *		

4. Discussion

Branching coral colonies, such as other MAFs, are known to harbor a wide range of coral-dwelling invertebrates and fishes whose communities' structures vary over space and time [9,53–56], reminiscent of the documentations for terrestrial forests [10,19,57,58] and marine algal forests [59,60]. The structures, sizes (that are developed through specific astogenic pathways [15]), and the inclusive special compartments [5] of MAFs canopies are subject to temporal and spatial changes in associated epifauna [7,44,61]. In these coral species that behave like ecosystem engineers, the more structured the living 3D shapes, the increased heterogeneity of interactions are foreseen in the interplay of living communities and space utilization [62–64]. Yet, knowledge gaps hinder our abilities to evaluate the ecological properties, as well as the ecological services provided by branching corals' canopies.

This study focuses on the *Stylophora pistillata* canopy's diel compartmental utilization by two *Trapezia* crab species (specific dwellers in pocilloporid corals [31,32]), in association with the *Trapezia* crab's abilities to prey on demersal plankton [46]. Results revealed that the crabs did dwell in different canopy compartments in relation to day/night hours and crabs' body sizes. During the day hours, crabs reside in the lower and more protected compartments (the understory and base; [5]), while during the night hours, when demersal plankton become available [65–67], crabs exploit the more exposed compartments (middle and up; Figure 1). Thus, the coral canopy's 3D structure and primarily its major compartments (as constructed by the Strahler order number of branches [5]) reveal a phenomenon of compartmental preference by *Trapezia* crabs that further show temporal variation in diel compartmental allocation and in size distributions. Moreover, this diel compartmental distribution, where *Trapezia* individuals hide during the day and are more visible during the night might, indicate for a nocturnal activity nature in the crabs' life history strategies [68].

Throughout the two-year study, *Trapezia* compartmental distribution patterns in the coral canopy were consistent for the variables crab sizes and daytime. Both *Trapezia* species use the coral's 3D structural features that are probably most optimal for vital functions (e.g., protection and feeding). During the day, crabs adopted a cryptic status within the coral's canopy to minimize the foraging efficiency of predators [68,69] where small and medium-size carbs further benefited from the smaller crevices found at the coral base and understory, and larger crabs were hidden between the lower parts of branches emerging from the coral base (Figure 1). These results are consistent with previous studies on other *Trapezia* species, revealing that adult crabs reside in the coral central parts, while juveniles dwell in tunnels or crevices in the coral base [22,37,42,43]. Yet, former studies did not examine the nocturnal distributions when daytime predation pressure is reduced [68–70]. Comparably with the upward nocturnal movement of most *Acropora*-dwelling species [71], this study reveals that at nighttime (when predation pressure is low), *Trapezia* crabs migrate towards the coral-exposed compartments. Small-size crabs are located at the upper compartment (up), medium-size carbs at the middle to up compartments, and large crabs at the base to middle compartments.

As in other crabs [72–74], the *Trapezia* literature indicates a domination related to crabs' body sizes, where larger crabs expel a smaller one [42]. Yet, only few studies have examined the hierarchy-related class sizes distributions between adults and young on a colony [22,29,42]. The main driver for spatial and temporal distribution patterns of species is the availability of resources [75,76]. With regard to the availability of spatial resources, the *Trapezia's* compartmental allocation suggests subordination dynamics between the crab's different body sizes, where the animal occupies the most desirable portion of its biological niche [77]. During the day hours, large *Trapezia* individuals are found mostly at the canopy base, the canopy part with the highest Strahler order branches, which is enclosed from above by the structure complexity (e.g., length, shape, width, etc.) of the other lower-order branches. Altogether, these branches construct the deeper spaces inside the canopy, where hosted organisms are less vulnerable to predation [68,78,79], since *Trapezia* crabs outside the coral host are easily eaten by a wide range of fish species [37]. During the night, large

individuals are found within the upper, yet deeper spaces (base and middle compartments), while smaller crabs are relegated to the more external and exposed parts (up and middle compartments) of the canopy [80], thus, circumventing the exhaustive daytime predation pressures [68,69], yet becoming more vulnerable to the less intensive nocturnal predation impacts, by predators, such as the hawkfish *Itycirrhitus wilhelmi* [69,81].

The fact that smaller size crabs do not switch compartmentation sites in the absence of larger size crabs at night time may further support the view that the different chosen compartments extend beyond the provision of the shelter alone. Further, plankton predation by the *Trapezia* crabs is probably of prime importance to the crabs' diet. The common idea is that *Trapezia* crabs rely primarily on coral tissue and mucus as a food source [30,37–39], hence, we may expect that in the absence of the large crab size, the smaller crabs would be evenly distributed on the coral tissues without any distinct compartmental allocation. The current outcome for daytime-specific site distributions highlights the possibility that the different body sizes' locations are associated with predation efficiencies (or "optimal foraging partitioning"), attesting for the importance of predation on demersal plankton to the biology of the *Trapezia* crabs. Hence, the large and the small animals at night occupy the most desirable biological niche for demersal foraging, and during the day, the most suitable hiding spaces as predation refuges.

In tropical forests, variable foraging parameters, such as perch sizes, attack types (different strategies for piking or catching food), and foraging height along the vertical axis of the canopy, are important in delineating niches separating between species and within-species body size groups, allowing the coexistence of a wider range of organisms within the same canopy spaces [82,83]. Similarly, the corals' canopy compartmental systems may create more biological niches, providing additional foraging grounds and features that are exploited differently by different crab sizes. These may further facilitate different food (detritus or demersal plankton) acquisition, and reduce intra- and inter-specific competition by channeling size classes into separate compartments within the canopy [84].

Branching corals, like other MAF organisms, are autogenic ecosystem engineers that are capable of modifying their intimate environments by their own structural complexity. Considering the *S. pistillata* canopies, these structures may change current flow velocity, modify the mean and turbulent flow structures, and impact sediment resuspension, as suggested for other marine forests [85]. This, in turn, may prolong the residence time of food particles (including demersal plankton) within various canopy compartments [86] and most likely leads to the creation of variable microenvironments characterized by different water dynamics. Therefore, fine analyses of coral canopies using more than a single method (here, we used the Strahler order as an analyzing tool of the coral canopy structure [5]) may shed more light on the biological features of the 3D spaces within a single coral canopy.

5. Conclusions

The coral dwelling *Trapezia* crabs use different compartments within the coral complex architecture differently between day and night and between different body size. During day hours crabs use the coral compartments primarily as a shelter, while at night shift compartments for predation activity. Lab experiments also showed that the partitioning distribution among the coral compartments of each carbs size groups is associated with the crabs' body size preference rather than with competition. Lab experiments also documented the relationship of *Trapezia* crabs with their host status (live, dead skeleton, and without coral), and reveled that crabs do catch and eat free-living plankton.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/jmse10101522/s1. Table S1: *Stylophora pistillata* attributes (n = 21) with their *Trapezia cymodoce* population for compartment usage in laboratory experiments. Table S2: Day and night survey results (2020–2021) for *T. cymodoce* and *Trapezia digitalis* crabs, Tables S3–S7: Two-ways PERMANOVA summary results for *T. cymodoce* and *T. digitalis* in day and night survey, Tables S8–S10: Pairwise permutation MANOVA with false discovery rate adjustment (FDR) summary results for *T. cymodoce* and T. *digitalis* in day and night survey. Tables S11–15: Summary results for laboratory experiments

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