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ORIGINAL PAPER

Collective exploitation of large prey by group foraging shapes aggregation and fitness of cnidarian polyps

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Abstract

Group living is widespread and beneficial to metazoans. It improves protection and survival opportunities, reinforcing interspecific competitiveness. Benthic cnidarians often colonize large surfaces. Evidence of collective capture and exploitation of large prey by small, clumped polyps suggests that aggregation is functional to access food resources hardly achievable by isolated individuals. In turn, the chance to catch large prey may represents a driver of aggregation in polyps, whether beneficial to their fitness. Here, the effects of group foraging on aggregation, asexual reproduction, and growth rates of *Aurelia coerulea* von Lendenfeld 1884 polyps were experimentally tested by providing them with either small or large prey, or a mix of both to simulate the co-occurrence of preys at sea. As expected, some polyps were not able to reach the large prey. Hence, the population was *a posteriori* divided into group-foragers and solitary-feeders. In general, the large prey diet resulted in higher population fitness and when simultaneously supplied with the small prey represented an energetic booster resulting beneficial for all group-members. The decrease of interindividual distances was reported among group-foragers, that converged towards each other. Cnidarians are basal in metazoan evolution, and the comprehension of their collective foraging behavior, as well as the processes leading to the selective feature driving them to forage in group or not, may be essential to better understand the evolution and spread of social foraging in animals. Moreover, the access to large prey by sessile polyps of *Aurelia coerulea* could be pivotal in determining the increase in abundance of adult bloom-forming medusae.

Keywords Cnidaria · Asexual reproduction · Somatic growth · Protocooperation · Gregariousness · Invertebrate behaviour

Introduction

Group living refers to individuals of the same species closely interacting for a period or their whole life (Wilson 1975). Proximity results in aggregations ranging from few to swarms of individuals (Wilson 1975; Brown 1982). The number of group members may be limited by resource availability, constantly balancing between intra-specific competition and cooperation (Brown 1982; Sheppard et al. 2021). Group living positively reflects on the survival rate of adults and juveniles because of enhanced protection, mating opportunities, and reinforced interspecific competitiveness (Ritz 1997; Krause and Ruxton 2002; Nowak 2006; Fitzgerald and Ives 2017), often allowing to overcome competition among group-members (Krause and Ruxton 2002). Group foraging, also referred to as social foraging (Giraldeau and Pyke 2019), is a further advantage

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of living closely to conspecifics. It is widespread in mammals (Silk 2007), fish (Schmitt and Strand 1982; Polyakov et al. 2022), birds (Hutto 1988; Fernández-Juricic et al. 2004), amphibians (Hoff et al. 1999), social insects (Quijano and Passino 2010; Frank and Linsenmair 2017) and spiders (Uetz 1992), flatworms (Cash et al. 1995), bacteria (Liu and Passino 2002), and marine invertebrates including gastropods (Brown and Alexander 1994) and hermit crabs (Kurta 1982; Laidre 2013). Group foraging reduces predation risk, improves information sharing (e.g., location of food patches) (Ritz 1997), and allows predation upon large prey hardly accessible to solitary individuals by sharing the capture efforts (Clark and Mangel 1986; Ritz 1997; De Waal 2005; Nowak 2006). Furthermore, the presence of multiple close individuals results in a network that reduces the chances of the prey to escape (Nowak 2006), increasing the individual predation success (Uetz 1988; Sutton et al. 2015). Individuals may differ in foraging abilities due to morphological (phenotypic) or physical constraints (e.g., position, energy reserves) limiting them to take part in the capture (Lendvai et al. 2004; Phillips et al. 2018).

Group-living is frequent in benthic Cnidaria that can create vast aggregations (Bo et al. 2015; Montseny et al. 2020), also contributing to the three-dimensional structures of marine animal forests (Rossi et al. 2017; Di Camillo et al. 2017). Benthic cnidarians encompass all Anthozoa species and sessile stages of Medusozoa. Generally, medusozoan's life cycle is determined by a sessile phase (the polyp) that develops from the settlement and metamorphosis of a free-swimming larva born by the sexual reproduction of adult medusae once it finds a suitable substrate. In scyphozoans, polyps (or scyphistomae) experience several asexually reproductive pathways (Schiariti et al. 2014) and can form juvenile gonochoric medusae (ephyrae) through strobilation (Ruppert et al. 2004). The class Scyphozoa encompasses the most common and numerous bloom-forming species of jellyfish with a worldwide distribution (Syazwan et al. 2020; Marambio et al. 2021; Riyas et al. 2021). Polyps often create dense aggregates (Miyake et al. 2002; Di Camillo et al. 2010) due to the contiguous settlement of planula larvae (Boero 1984; Gröndahl 1989), the production of clones through asexual reproduction (Ishii and Katsukoshi 2010), especially in food-rich sites (Duineveld et al. 2007; Houlbrèque and Ferrier-Pagès 2009). Warm seawater temperatures and the food abundance positively reflect on the survival rate of the ephyrae and increase their chances to reach the medusa stage (Lucas et al. 2012; Goldstein et al. 2017; Purcell 2019). In favourable conditions, one polyp can produce up to 20–30 ephyrae per strobilation cycle (Arai 1997). When food is abundant, the polyp population increases by asexual reproduction, thus multiplying the number of potentially strobilating individuals (2007). The dynamics of adult medusae are strongly influenced by their sessile phase, and the control of polyp population assumes a pivotal role in the management of jellyfish mass-occurrences (Boero et al. 2008; Schiariti et al. 2014; Marques et al. 2021). The synergistic effects of anthropic disturbances (eutrophication, overfishing, increase in seawater temperature, construction of submersed structures, etc.) has led to an increase in density and frequency of jellyfish blooms (Licandro et al. 2010; Lucas et al. 2012). During these events, the jellyfish density could reach from ten to hundreds of individuals per cubic meter (Licandro et al. 2010). Especially in coastal areas, the gelatinous mass has deleterious effects on several human sea-based activities, e.g., on tourism, fishing, and electricity industries (Purcell et al. 2007). Species of the genus *Aurelia* (Scyphozoa, Semaeostomeae) are among the most responsible for blooms worldwide (Schiariti et al. 2015; Dong 2019), and produce small polyps (ca. 0.5–1 mm in diameter) with a strong gregarious habit (up to 88 individuals per square centimetre; Miyake et al. 2002).

Collective feeding was observed in the wild when polyps display high degree of proximity. It occurs when small-sized polyps act simultaneously to capture and ingest prey much larger than any individual polyp, thus not catchable trough solitary actions (Musco et al. 2018; Gregorin et al. 2022, 2024a). Musco et al. (2018) reported multiple polyps of the coral *Astroides calycularis* (Pallas 1766) (Hexacorallia, Scleractinia) capturing the mauve stinger *Pelagia noctiluca* (Forskål 1775). The same behaviour was later documented by Ter Horst and Hoeksema (2021) and Gregorin et al. (2022) in other colonial corals while feeding on large gelatinous zooplankton specimens. Similarly, multiple hydrants of the hydroid species *Perarella schenideri* (Motz-Kossowska 1905) fed collectively on large polychaetes, sharing the capture effort and gains (Bavestrello et al. 2000; Cerrano et al. 2000). This collective action has been referred to as protocooperation (*sensu* Skelton 1979), namely a non-cognitive process allowing individuals to obtain reciprocal benefit from proximity. When applied to food provision and feeding behaviour (e.g., Herbert-Read et al. 2016; Musco et al. 2018; Gregorin et al. 2022), protocooperation may represent an additional advantage of group living for benthic cnidarians. Furthermore, similarly to group foraging, it could further promote polyps' gregariousness by reducing their intra-specific competition.

To the best of our knowledge, the above mentioned protocooperation in prey capture and feeding has never been referred to as group foraging in benthic Cnidarians. It is worth mentioning that the benefits deriving from collective feeding on large prey could influence the population dynamics of sessile species, since handling large prey requires considerable energetic costs, but it may also provide important energetic gains. Among scyphozoans with benthic stages, this feeding behaviour may reflect on the populations of their planktonic stages, influencing the dynamics of jellyfish blooms.

The present work aims at describing the effects of group foraging upon large prey on the fitness of *Aurelia coerulea* von Lendenfeld 1884 (Scyphozoa, Semaeostomeae) polyps and its influence on their aggregation level. Polyps were fed with a prey much larger than the individual polyp size and their interindividual distances, growth, and asexual reproduction rates were measured as response variables of the whole population, i.e., as the average response of the experimental groups. Moreover, the size of the large prey and the density of polyps were intentionally selected to prevent some individuals of the experimental group to capture of the large prey. Therefore, the capture of the large prey determined an *a posteriori* subdivision of the original population in two sub-groups: the polyps that captured the large prey and those excluded from the capture. All polyps exposed to the large-prey diet were assigned to one of these two sub-groups. This subdivision allowed to perform the second type of analyses, dealing with the "individual" level, i.e., the analysis polyps response based on the food item that they ingested. The interindividual distances, growth, and asexual reproduction were thus measured both within the original population (i.e., the population level, a priori hypothesis) and within the two sub-groups defined *a posteriori* (i.e., the individual level). We hypothesized that: (1) the chance to catch large prey promotes the overall aggregation of the population; (2) the collective capture of large prey enhances the average fitness of the experimental population; (3) polyps of the sub-group capturing the large prey show greater fitness and aggregation level.

Materials and methods

Polyps of *Aurelia coerula* were obtained from the Cattolica Aquarium (Italy), transferred to the laboratory in a thermostatic container and maintained in Filtered Sea Water (FSW; 0.22 µm Millipore filter membrane), renewed three times per week. Rearing stable conditions were set at 18.0 ± 0.5 °C, 16 h–8 h light-dark photoperiod, 38.0 ± 1.5 salinity. Two specimens of *A. coerula* were analysed through molecular analysis for the correct identification of the species and the haplotype characterization; the molecular analysis was performed at the Zoology Laboratory of the University of Salento (see Supplementary material "S1" for molecular identification methods and results). *Aurelia coerula* was selected as a suitable model species since it reproduces rapidly through asexual reproduction, leading to new clones surrounding the parent polyp (Sukhoputova et al. 2019). Polyps were fed twice a week with newly hatched nauplii of the brine shrimp *Artemia salina* (Linnaeus, 1758).

Experimental design

Differences in the aggregation level of polyps fed with either large or small prey, were tested considering the experimental factor "Prey type" (P), fixed, with three levels representing the experimental groups: Large Prey (LP), Small Prey (SP), and a mixture of both (MIX), this last simulating the co-occurrence of both small and large prey at sea. The SP experimental group served as control. Per each level of the factor P, three independent experimental units were considered, for a total of nine. The experimental unit consisted in a 200-mL glass bowl filled with 140 mL of FSW and including a Petri dish (6 cm diameter) as horizontal substrate for the settlement of polyps. Each experimental unit contained eight *A. coerulea* polyps randomly selected among fully developed individuals, without swelling tissue or budding indicating ongoing asexual reproduction. The polyps were left to settle inside a square area (4 cm^2) drawn on a Petri dish (Fig. 1a, b). The large prey supplied to the LP experimental group was the polychaete *Syllis prolifer*a Krohn 1852 (Annelida, Syllidae), presenting the size ratio of ca. 1:10 with respect to oral diameters of polyps, and palatable for cnidarian polyps (Bavestrello et al. 2000; Maggioni et al. 2017). Polychaetes were gathered from shallow rocky bottoms by scraping-off macroalgae, sorted and reared following Massa-Gallucci and Gambi (2014). The polychaetes were administrated randomly to polyps by dropping them ca. 20 cm above the experimental unit, to simulate the casual dislodging of the benthic vagile fauna from the substrate that may cause the prey to get in contact with polyps (Sebens 1981; Sun et al. 2022; Gregorin et al. 2024b). As soon as it touched the water surface, the polychaete started to move and swim, further randomizing its provision to the polyps. The SP experimental group was fed with 2-day-old *A. salina* nauplii, similar in size range and morphology to marine copepods, which dominate mesozooplankton assemblages in several ecosystems (Siokou-Frangou et al. 2010; Kiørboe 2011).

The amount of food provided was standardized based on the dry weights (d.w.) of the preys. Six polychaetes measuring [mean ± Standard error, SE] = 10.55 ± 1.10 mm long were selected to calculate the average d.w. After drying for 72 h at 60 °C, the mean d.w. was 0.22 ± 0.03 mg. Similarly, 5 different aliquots of an overcrowded culture (OC) of *A. salina* 2-days-old nauplii were haphazardly selected and dried. The OC was obtained by hydrating and hatching 0.31 mg dry cysts in 600 mL of FSW. Nauplii were collected 48 h later using a spot-light source for five minutes to concentrate them. The mean d.w. of the average polychaete

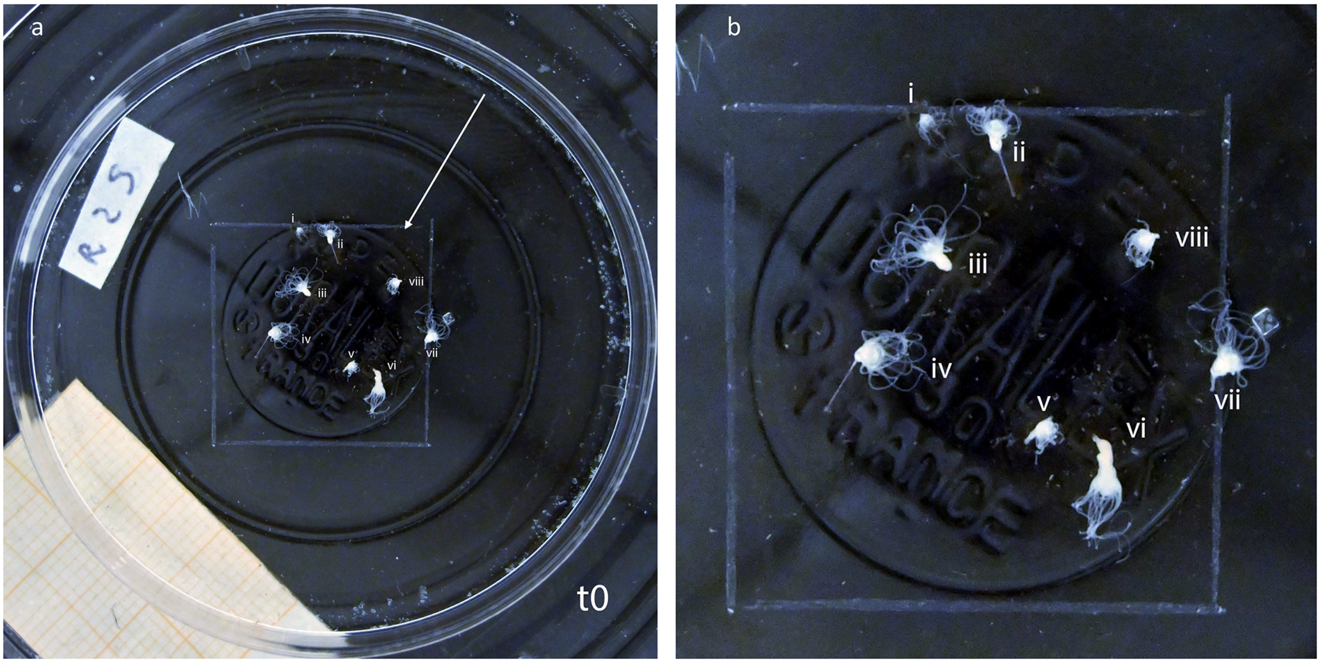

Fig. 1 Experimental units: Square area of the 4 cm^2 (white arrow) on the Petri dish, in which polyps settled at the beginning of the experiment (t_0); b) the 8 polyps were tagged with roman numbers and tracked throughout the experiment

corresponded to 35 µL of OC of *A. salina* 2-days-old nauplii. The three experimental groups were fed as follows: LP, two polychaetes of 10.55 ± 1.1 mm in length; SP, 70 µL of OC culture of nauplii; and MIX, one polychaete 10.55 ± 1.1 mm long plus 35 µL of OC culture of nauplii. The presence of unfed nauplii guaranteed that polyps were fed *ad libitum*. Unfed nauplii were removed at the following water renewal. Polyps were starved for 72 h before the start of the experiment.

Data collection and analyses

The experiment lasted for 36 days. Preliminary tests allowed for each prey to evaluate the digestion times required by polyps to return in a fasting condition (i.e., with empty gastric cavity) after the feeding event. Polyps of the three experimental groups were fed once per week with the respective diets, for a total of 6 feeding events. Photographs were taken from a fixed position twice per week, for a total of 11 sampling times (from t_0 at the start to t_{10}). After the feeding event, it was possible to know which food was ingested by each polyp thanks to the whitish-transparent colour of the column, which allows to see the gastric content. Photographs were processed with Adobe Photoshop CC 2019 to label polyps with Roman numbers from i to viii, allowing to follow each polyp individually throughout the trial (Fig. 1b). Given the long digestion times, one feeding event per week was considered enough to stimulate the growth and reproduction of polyps, and two sampling times per week were conceived to better check the fluctuations of response variables.

A priori analyses Effects of prey type on the aggregation and fitness of polyps at population level

The interindividual distances among polyps, their growth and asexual reproduction rates were considered as response variables. Polyp interindividual distances were measured from the photos by using the software ImageJ (Rasband 2012), following the Nearest Neighbour method (Clark and Evans 1954). Due to the spatial arrangement of polyps in such scarce population, the method was modified starting from a random polyp at t_0 (i) and measuring the distance between its nearest neighbour (i-ii, ii-iii, iii-iv, …) to avoid the repetition of already measured distances. In this case, the distance between the last and the first polyp (viii-i) was not considered, thus resulting in seven distances (d) in each experimental unit ($d = n - 1$). Distances were measured between the polyps belonging to the original population, not considering the position of the clones eventually produced during the experiment.

Growth of polyps was estimated by measuring the mouth disc diameter (MDD) (Gambill and Jarms 2014) by the software ImageJ (Rasband 2012). Differences in polyps' MDD across groups were checked at the beginning of the experiment, to avoid any size bias.

Asexual reproduction rate (population RR) was measured as the total number of clones produced at t_{10} and was assessed by using the formula 1a.

$$Population\ RR\ (\%) = \frac{Clones\ (t_{10})}{Population\ (n=8)} * 100 \tag{1a}$$

A posteriori analyses: Effects of prey type on aggregation and fitness at individual level

Since the polychaete prey was not accessible to all the polyps, after the feeding event (i.e., *a posteriori*) it was possible to discern the polyps that fed upon the polychaete and those that were excluded. This discrimination was possible thanks to their gastric content visible through the column. On this base, polyps in each experimental unit were divided into the sub-groups named "Eat" and "Excluded" and referred to as LP-Eat / LP-Excluded and MIX-Eat / MIX-Excluded based on their original experimental group (Fig. 2). Polyps recorded to have fed upon the large prey for most of the sampling times (≥ 6) were considered "Eat" polyps, while those eating the large prey occasionally (≤ 5) or never, were considered "Excluded". SP polyps did not receive the large prey and did not split in two sub-groups, thus remained referred to as SP.

The response variables were measured as described in the previous paragraph on the "Eat" sub-groups and compared with the SP group, to test the hypothesis that the sub-group capturing the large prey show greater fitness and aggregation level. The distances (d_{eat} and $d_{excluded}$) between individuals were measured as previously described ($d_{eat} = n_{eat} - 1$; $d_{excluded} = n_{excluded} - 1$) through the modified Nearest Neighbour method.

The individual RR referring to the sub-groups was calculated using formula 1b. This calculation considers only

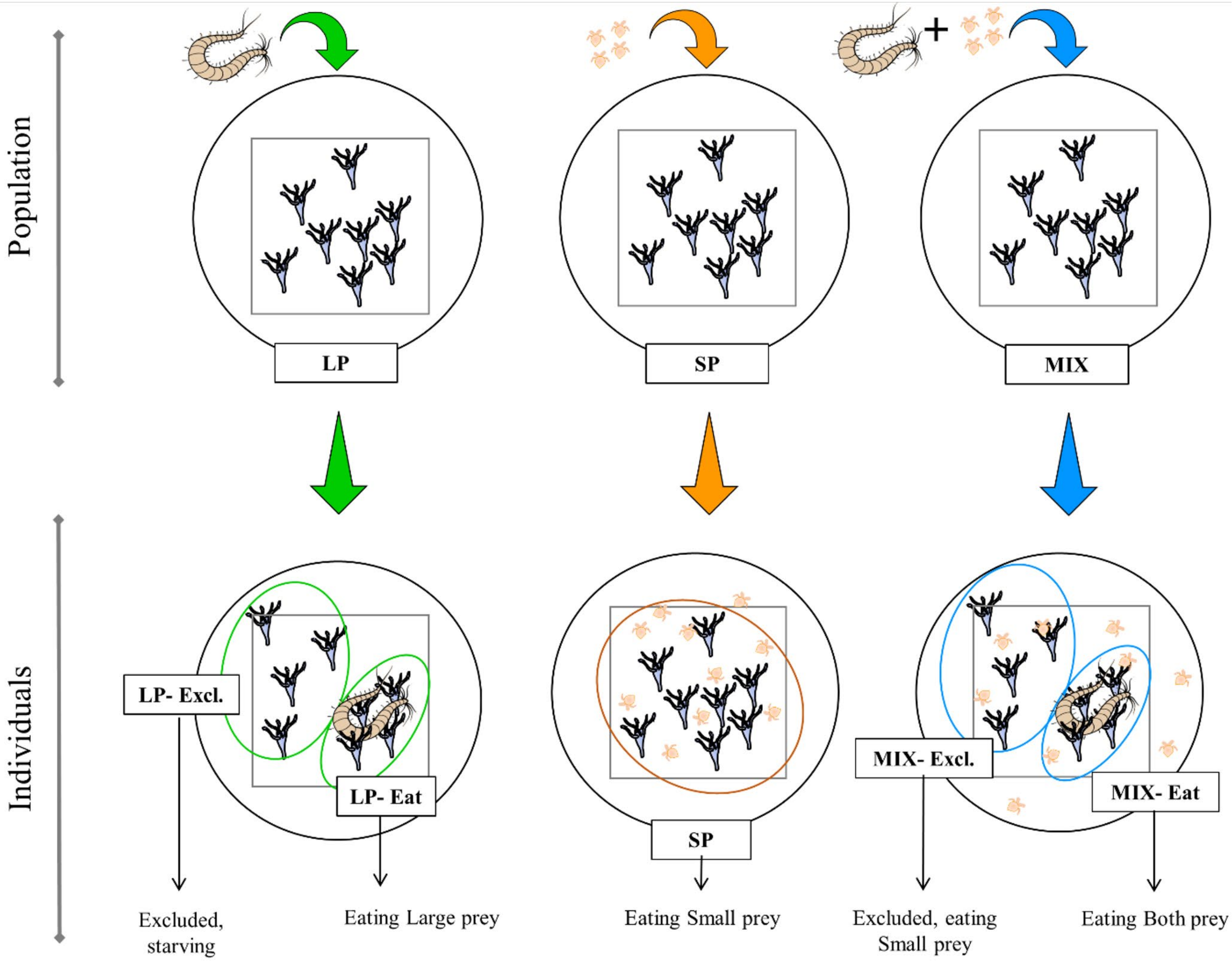

Fig. 2 Scheme of the experimental groups at population level (SP, LP, MIX) and sub-groups at individual level (LP-Eat, LP-Excl., MIX-Eat, MIX-Excl.). The black circles including polyps represent the experimental units. SP = Small Prey; LP = Large Prey; MIX = Both preys; Excl. = Excluded from the capture of the large prey; Eat = Involved in the capture of the large prey

the polyps that reproduced and the number of their clones. It is worth mentioning that the "LP-Excluded" polyps were starving for the whole experimental period while the "MIX-Excluded" ones fed upon the small prey.

$$Individual\ RR\ (\%) = \frac{Clones\ (t_{10})}{Effective\ parents} * 100 \tag{1b}$$

Statistical analysis

The experimental a priori hypotheses were tested through one-way Analysis of Variance (ANOVA) and Repeated Measures (RM) ANOVAs after checking compliance with the underlying assumptions. The Shapiro-Wilk's test (Shapiro and Wilk 1965) was used to check for normality of distribution, while the Cochran's C test (Cochran 1941) was applied to verify the homogeneity of variances. In the context of RM-ANOVA, tests of between-subject effects were corrected for departures from the assumption of symmetry of the variance-covariance matrix, as measured by the epsilon statistics. The Huynd-Feldt (Huynh and Feldt 1970, 1976) correction was applied for $\varepsilon \geq 0.75$ or above, while the Greenhouse–Geisser (Greenhouse and Geisser 1959) was preferred for $\varepsilon < 0.75$. The multivariate Pillai-Barlett trace (Pillai 1965) was also used to test for between-subject effects because particularly robust to deviations from sphericity, checked through Mauchly's test (Mauchly 1940). Specific comparisons among experimental groups were performed via *t*-test. As a result of the *a posteriori* reallocation of polyps into the two sub-groups based on their ingested food (See Fig. 2 "Individuals"), the sample sizes were different, hence group variances were suspected to be heterogeneous. In this case, the conservative Welch's test was then used instead of the usual *t*-test, to maintain the probability of Type I error (alpha) at the nominal 5% level (Welch 1938, 1947). The selected response variables (growth, reproduction, and aggregation level) changed slowly during the experimental period. For this reason, in some cases specific comparisons referring to different sub-set of times were analysed. Analysis of dispersions (Anderson 2006) was run when the profile analysis indicated high variance around the centroids of the response variables, followed by pairwise Tukey's Honestly Significant Difference tests.

Statistical analyses were made using the software Statistica and the R software environment 4.2.2. Ink (R Core Team 2022) with the packages *car* (Fox and Weisberg 2019) and *ggpubr* (Kassambara 2023). PERMDISP was carried out with the package *vegan* (Oksanen 2012) with the functions adonis2 and betadisper (Anderson 2006).

Results

Effects of prey type on the aggregation and fitness of polyps at population level

Polyps within all the experimental units ($n=8$) eventually moved on the substratum changing their position. The inter-individual distances among polyps increased from t_0 to t_{10} by [mean ± standard error, SE, d = n – 1 = 7 / experimental unit]: 3.17 ± 0.86 mm in SP, and 2.87 ± 1.5 mm in LP and 3.26 ± 4.19 mm in MIX, respectively (Fig. 3a; Table 1). In MIX groups, 30% of the cumulative number of measured distances showed a decreasing trend, as well as the 42.9% in the LP group and 19% in the SP group. The Pillai's test did not highlight any significant effect of time (Pillai, H = 0.268, $P=0.073$), neither a combined effect of Time × Group (Pillai, H = 0.108, $P=0.998$). Interindividual distance error around the mean increased over time, indicating a progressively more dispersed distribution of the population (Permdisp, F (10,682), $P=0.029$).

The MDD of polyps at t_0 were similar among diets ([mean ± SE, $n=8$] SP: 0.87 ± 0.04 mm., LP: 0.81 ± 0.04 mm, MIX: 0.80 ± 0.04 mm; ANOVA, F (2,69) = 0.796; $P=0.455$). During time, polyps MMD increased by 0.22 ± 0.06 mm in the SP group, 0.37 ± 0.05 mm in LP, and 0.37 ± 0.05 mm in MIX (Fig. 3b; Table 1). The 37.5%of the cumulative number of MDDs decreased in SP, while in both LP and MIX the percentage of reduced MDDs over time were 4.2%. The Pillai's test highlighted the significant effect of Time (Pillai, H = 0.616, $P<0.001$), while the interaction Time · Group (Pillai, H = 0.337, $P=0.237$) was not significant. The size of polyps started to diverge in the second period of the experiment, from t_5 to t_{10} (Fig. 3b). The comparisons between the first *versus* the second time sub-sets (t_0-t_4*versus* t_6-t_{10}) highlighted significant difference in growth rates of SP polyps compared to those of MIX polyps (Welch's test, W211.12= −2.01, $P=0.046$).

The population RRs were [mean ± SE, n = number of experimental units = 3] 62.5 ± 12.5% for SP, 54.2 ± 18.2% for LP, and 100 ± 12.5% for MIX, respectively (Fig. 3c; Table 1). The Huyhn-Feldt test revealed the significant effect of Time (F(8,48) = 26.70, $P<0.001$) and no significant interaction of Time · Group (F(16,48) = 1.34, $P=0.214$). However, from the profile analysis (Fig. 3c) polyps belonging to the MIX group showed a more pronounced increase in RR from t_7 to t_{10}, compared with SP and LP (Fig. 3c). In this time sub-set, Welch's tests highlighted significant differences in RR between MIX and SP (W 16 = −4.165, $P=0.001$), and between MIX and LP (W 13.26 = −3.726, $P=0.003$).

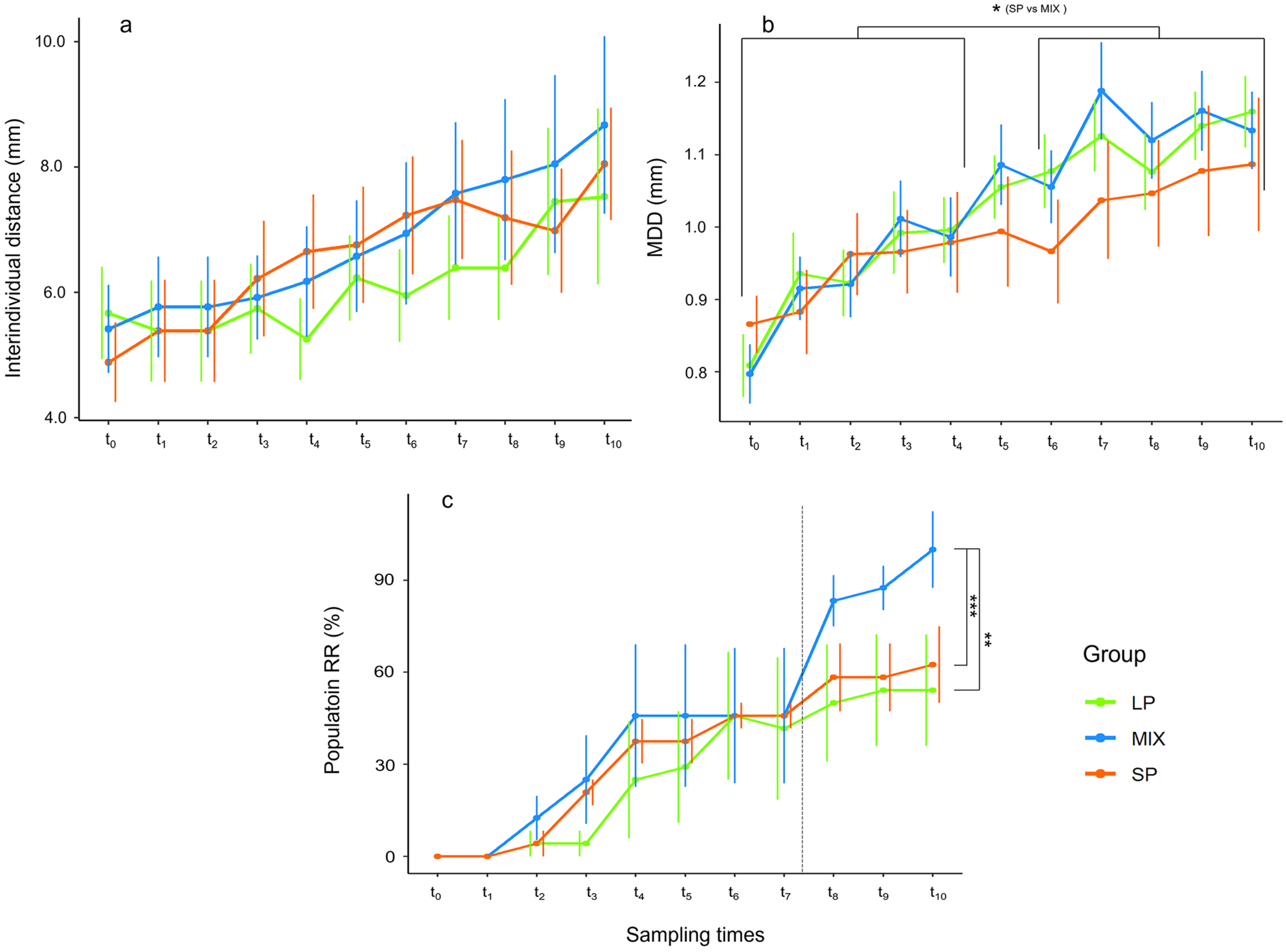

Fig. 3 Line charts showing population ($n=8$) trends, from t_0 to t_{10}. **(a)** Interindividual distances among polyps (mm); **(b)** Mouth disc diameter (MDD) of polyps, (mm). Analyses were performed on the two sub-sets (t_0-t_4 vs. t_6-t_{10}) to test the differences of MDD of SP *versus* LP and MIX polyps; **(c)** Reproduction rate in percentage. Statistical analyses were performed to compare the groups in the last three sampling times (t_8-t_{10}), corresponding to the steep trajectory of the MIX line. SP, orange line; LP, green line; MIX, blue line. Error bars represent Standard Error (SE). ns = not significant; * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$

Table 1 Summary of increments/decrements (t_{10} – t_0) of distances ($n=21$), Mouth Disc Diameters (MDD, $n=24$), Population Reproduction Rate (pop. RR, $n=3$) and Individual Reproduction Rate (Ind. RR, $n=3$). Mean values ± SE are reported

Experimental Groups	DISTANCE (mm)	MDD (mm)	Pop. RR (%)	Ind. RR (%)
SP	+3.17 ± 0.86	+0.22 ± 0.06	62.5 ± 12.5	133.5 ± 16.67
LP	+2.87 ± 1.50	+0.37 ± 0.05	54.2 ± 18.2	/
MIX	+3.26 ± 4.19	+0.37 ± 0.05	100 ± 12.5	/
LP- Eat	+1.47 ± 2.85	+0.38 ± 0.12	/	144.4 ± 44.4
LP-Excl.	+4.53 ± 1.91	+0.15 ± 0.06	/	0
MIX-Eat	+2.27 ± 1.7	+0.24 ± 0.06	/	183.33 ± 16.7
MIX-Excl.	+3.59 ± 2.55	+0.21 ± 0.16	/	55.6 ± 29.4

Effects of prey type on the aggregation and fitness of polyps at individual level

The sub-group that fed upon the large prey for more than 6 times (“Eat”) was formed by 2, 4 and 3 polyps in the LP experimental units and by 3 polyps in each MIX experimental unit. The comparison of these sub-groups showed no differences (t-test, T 4 = 0, $P=1$).

The interindividual distances within both LP-Eat and MIX-Eat differed from SP (Fig. 4a, b). At t_0, distances of all polyps were homogeneous (Welch, SP vs. LP: W 38.96 = −0.9161, $P=0.366$; SP vs. MIX: W 39.64 = −0.5754, $P=0.578$) (Fig. 4a). The 76% of the cumulative number of distances among SP polyps increased showing an overall average of 3.17 ± 0.86 mm from t_0 to t_{10}. Among LP-Eat and MIX-Eat polyps, distances increased by 1.47 ± 2.85 mm and 2.27 ± 1.7 mm, respectively (Table 1). There were no

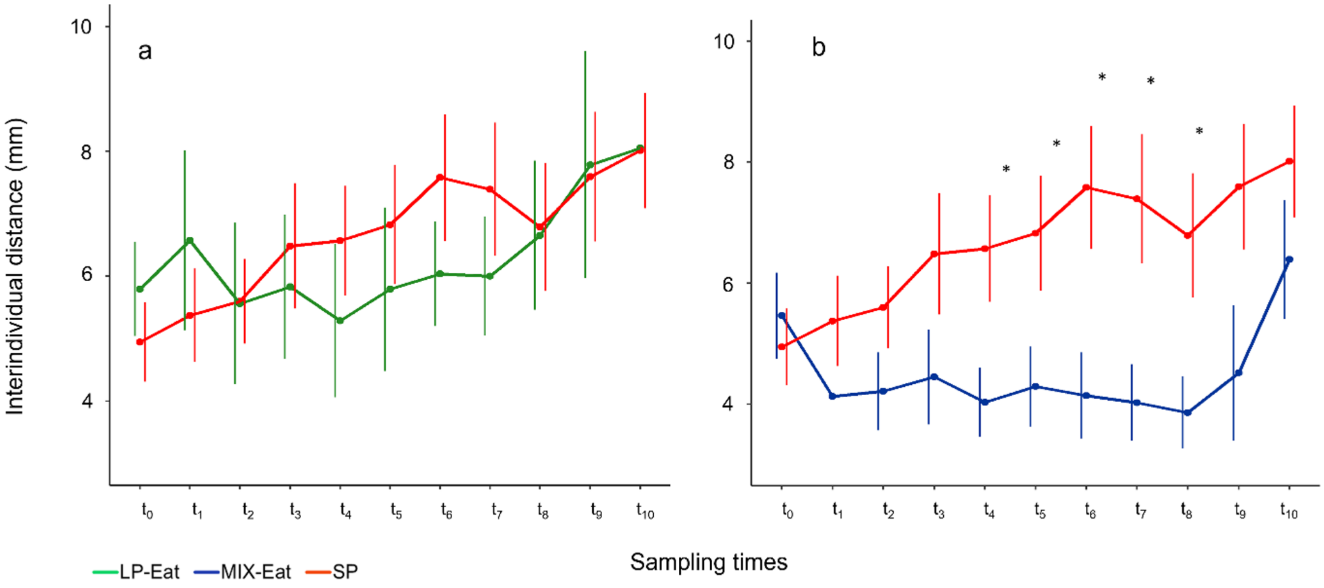

Fig. 4 Interindividual distances measured between group-foragers LP-Eat (**a**) and MIX-Eat (**b**), compared with SP (orange line). Vertical bars = standard error; * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$

Table 2 Welch's test (two-tailed) for comparisons between SP, LP-Eat and MIX-Eat polyps, from t_1 to t_{10}. P-- values are reported, considered significant when ≤ 0.05, written in bold. For tests results and number of samples, see supplementary materials, Table S1

Comparison	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}
DISTANCE										
SP vs. LP-Eat	0.48	0.973	0.675	0.415	0.536	0.256	0.131	0.934	0.929	0.988
SP vs. MIX-Eat	0.389	0.156	0.125	**0.023**	**0.039**	**0.011**	**0.0119**	**0.021**	0.063	0.248
MDD										
SP vs. LP-Eat	**0.009**	**< 0.0001**	**0.002**	**0.0006**	**0.0001**	**0.004**	**0.001**	**< 0.0001**	**0.0005**	**0.0043**
SP vs. MIX-Eat	0.126	**0.012**	**0.032**	0.058	**0.049**	**0.014**	**0.012**	**0.002**	**0.0125**	0.1191
% RR										
SP vs. LP-Eat	0.524	0.102	0.698	0.698	0.698	0.674	0.674	0.925	0.925	0.834
SP vs. MIX-Eat	0.230	0.352	0.930	0.930	0.930	0.442	0.442	0.262	0.262	0.102

significant differences in distances between SP *versus* LP-Eat (Fig. 4a; Table 2), while the comparison between SP *versus* MIX-Eat was significant in some sampling times (Fig. 4b; Table 2). LP-Excluded and MIX-excluded polyps increased their distances by 4.53 ± 1.91 mm and by 3.56 ± 2.56 mm, respectively (Table 1). In both cases, excluded polyps diverged more than those capturing the large prey (+ 68% for LP group and + 34% for MIX group, see example in Fig. 7).

The type of prey influenced the growth of polyps. LP-Eat (Fig. 5a) and MIX-Eat (Fig. 5b) grew on average by + 0.38 ± 0.12 mm and + 0.24 ± 0.16 mm, respectively (Table 1). The SP polyps also showed a growing trend (Fig. 5a, b), but the increment was lower (+ 0.23 ± 0.05 mm, Table 1). The LP-Eat polyps were significantly larger than SP polyps in all sampling times, as well as MIX-Eat polyps except for t_1, t_4 and t_{10} (Table 2). LP-excluded polyps increased their MDD by 0.15 ± 0.06 mm, while the MIX-Excluded increased by 0.21 ± 0.06 mm (Table 1), with no difference with SP (SP vs. MIX-Excl.: Welch at t_{10}, W 31.87 = 1.653, $P = 0.108$).

The number of SP parent polyps (Fig. 6a, b) were 4, 3 and 4, producing respectively 6, 3 and 6 clones. The average RR of SP polyps was 133.3 ± 16.67%, and the number of producers was on average 45.8 ± 4.2% of the starting population. The number of LP-Eat polyps that reproduced were 3, 4 and 3 in the three LP experimental units (Fig. 6a). These polyps produced 3, 4 and 7 clones, respectively (RR = 144.4 ± 44.4%, varying within a range between 100% and 233.3%). The percentage of reproductive polyps with respect to the initial population was 41.7 ± 4.2%, slightly lower than SP polyps, but it is noteworthy that the reproducers were exclusively LP-Eat polyps (the LP-Excl. polyps never reproduced). The RR of MIX-Eat polyps was 183.33 ± 16.7%. The number of MIX-Eat producers were 4, 3, and 3 in each experimental unit (Fig. 6b) and produced 6 clones each. The percentage of producers in the initial population was 41.7 ± 4.2%. In this case, the

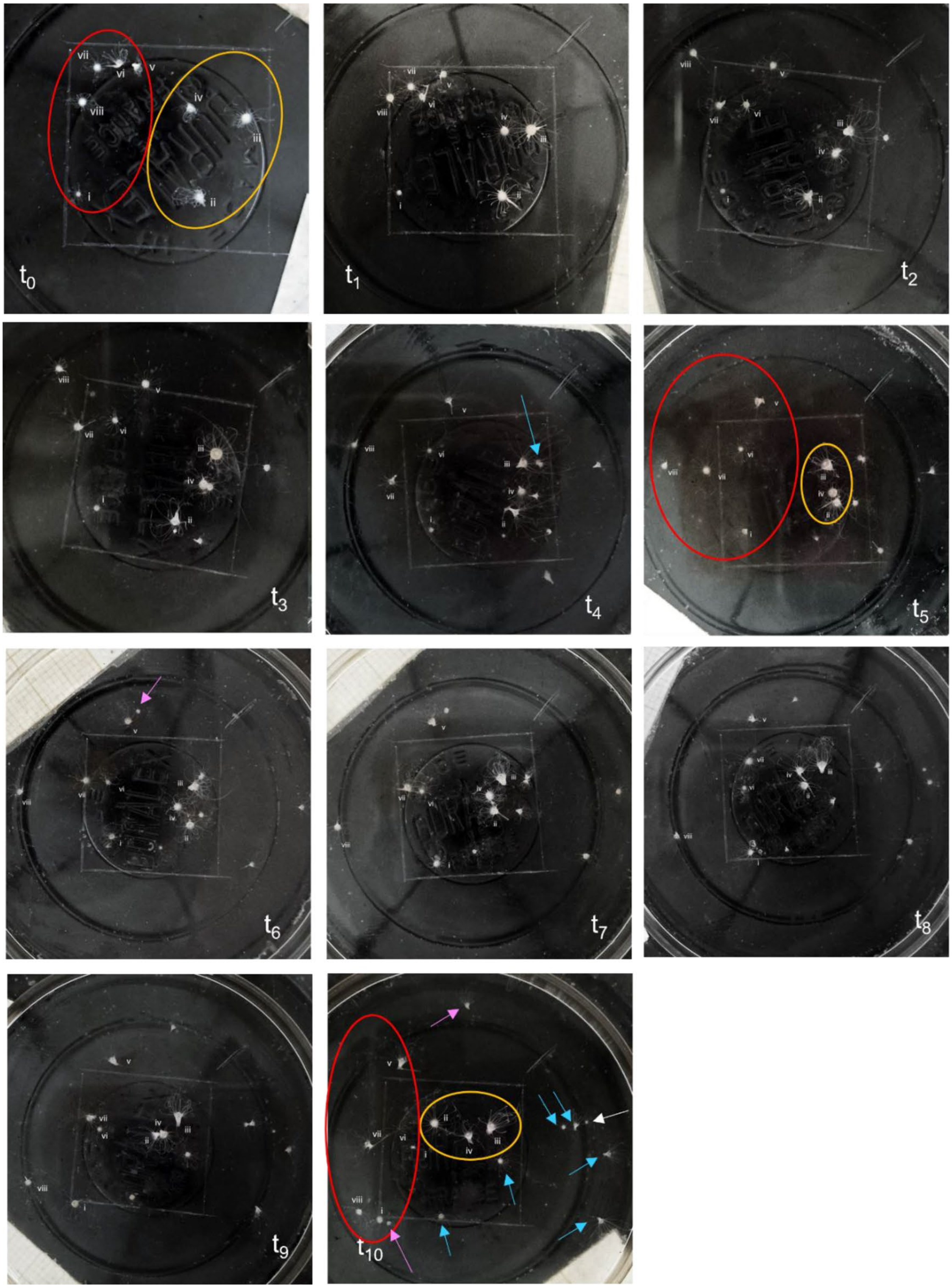

Fig. 7 MIX experimental group, experimental unit No. 3. t_0: polyps in red circle fed upon *A. salina*, becoming MIX-Excluded; Polyps in the orange circle captured the polychaete and ingested *A. salina*, becoming MIX-Eat. t_5: MIX-Eat are much closer and bigger than MIX- Excl, getting dispersed instead. t_{10}: MIX-Excl. are more dispersed; Blue arrows indicate clones produced by MIX-Eat, pink arrows indicate clones produced by MIX-Excl; White arrow indicates a polyp produced by a newborn, excluded from the analyses

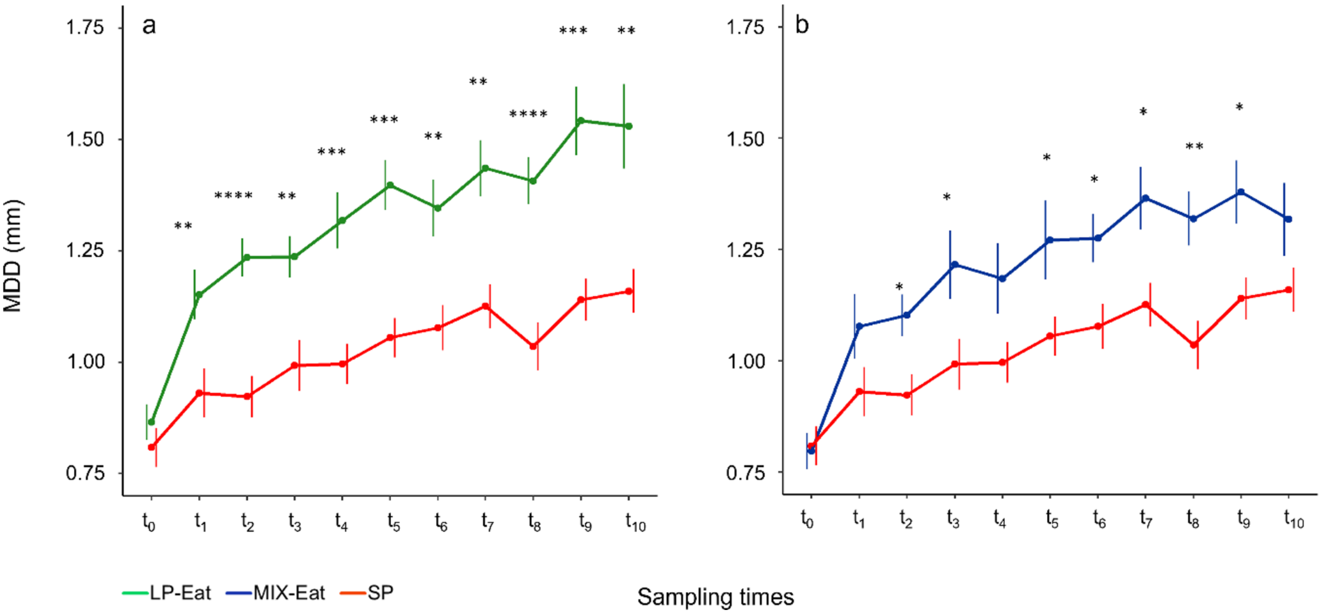

Fig. 5 Mouth Disc Diameter (mm) of LP-Eat (**a**) and MIX-Eat (**b**), compared with SP (a and b). Vertical bars = standard error; * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$

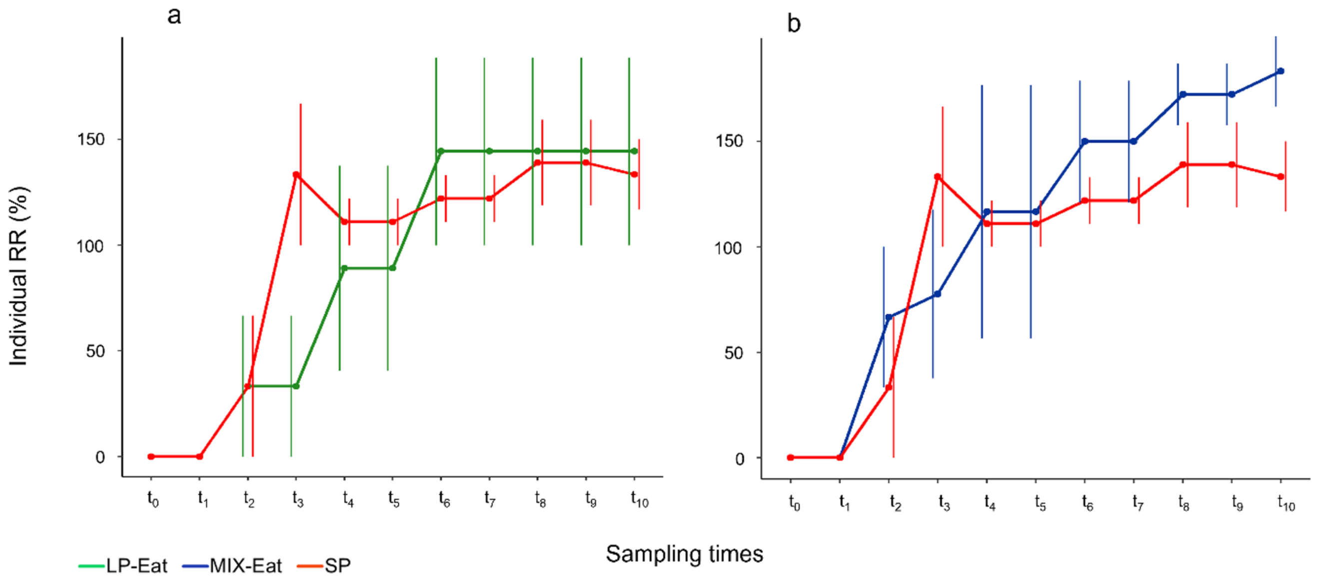

Fig. 6 Individual reproduction rate (RR, %) of SP polyps compared with that of LP-Eat (**a**) and MIX-Eat (**b**); Error bars = Standard Error

MIX-Excluded polyps also reproduced, possibly because they were not starved. However, they did to a lesser extent, with a RR of 55.6 ± 29.4% (MIX-Eat vs. MIX-Excl.: Welch, W 3.17 = 3.781, $P = 0.03$). The total number of reproduced polyps in the MIX group accounted for 66.7 ± 8.3% of the initial population. One clone produced a polyp of second generation. There were no significant differences between the groups SP *versus* LP-Eat parents, as well as between SP *versus* MIX-Eat parents (Table 2).

A summary of statistic results for distances, MDDs and RRs for comparison of Eat and Excluded sub-groups are reported in Supplementary materials S2.

Discussion

Benthic Cnidarians colonize substrates from the surface to the deep sea-bottom, where they contribute to the structural architecture of marine animal forests, create ecosystems representing biodiversity hotspots and perform several ecological roles (Bo et al. 2015; Rossi et al. 2017). The population dynamics of sessile stages of Scyphozoa are thought to profoundly influence the variation of abundance of their planktonic counterparts (i.e., the medusae populations), with consequent effects on plankton ecology and several human maritime activities (Purcell et al. 2007). Studying the factors that regulate the abundance, growth and reproduction of sessile polyps may be crucial for the proper management of jellyfish blooms and the prevention of the impact they may cause (Arai 2009).

Our outcomes highlighted different response in polyps of *Aurelia coerulea* exposed to three different diets i.e., large prey, small prey and both prey types. At population level, the simultaneous provision of large prey and small prey (MIX diet) led to higher growth and asexual reproduction rates, being beneficial to the population. Polyps accessing two preys could have benefited from complementarity of nutrients brought by each prey type. However, no differences were reported in any response variable between polyp populations eating only large or only small prey. Regarding distances, in all experimental populations the interindividual distances between polyps increased. It is noteworthy that polyps feeding upon small prey got more dispersed compared to those feeding upon the large prey. These results could have been influenced by the spatial arrangement of excluded polyps. Indeed, by not considering excluded polyps and analysing "Eat" polyps only, the outcomes highlighted clear differences. .

Many predators acting together on the same prey were beneficial to the population. Polyps seized the large prey simultaneously, hindering its escape ability and succeeding in its capture. Uetz (1988) described higher individual predation rates in group-foraging spiders building their webs in proximity to each other. By creating a net, spiders were able to capture larger prey that bounced multiple times on different webs (Uetz 1988). Similarly, overlapped tentacles belonging to neighbour individuals resemble the spiders' strategy with same intent and outcome. Cnidarians are voracious "sit-and-wait" predators (Kaliszewicz 2013). The web of tentacles formed by polyp aggregations could enhance the speed of paralysis in large prey due to larger number of nematocysts involved. Moreover, the surface available for large prey capture increases proportionally with the level of aggregation, as well as the number of possible capture sites (Tardent 1995; Corrales-Ugalde et al. 2017).

The experimental set-up allowed to distinguish two sub-groups in the same populations based on the feeding behavior, with individuals capturing the large prey (sub-group "Eat") and others that were excluded from the action (sub-group "Excluded"). We hereafter refer to the former as group-foragers, and to the latter as solitary-feeders. Group-foragers depended on protocooperative intraspecific interactions for large prey capture, while solitary-feeders were rather influenced by intraspecific competition and relied on themselves for feeding (upon small prey). The number of group-foragers was similar in the two experimental groups LP and MIX, indicating an optimal group size probably determined by the morphology and size of the prey. Selectivity based on prey characteristics (also including behavior, escape ability and detectability) is common among predators in relation to their feeding strategy, since it enhances the foraging efficiency (Greene 1986). Prey selectivity is well reported in cnidarians at all developmental stages from adult scyphozoan medusae (Zeman et al. 2016), ephyrae (Sullivan et al. 1997) and polyps (e.g., Kamiyama 2011) but also among other classes (e.g., Purcell et al. 2012; Rivera-De La Parra et al. 2016).

In the present study, group-foragers and solitary-feeders clearly differed in size, the first becoming larger probably due to the higher amount of food availability for each polyp. However, the number of polyps that effectively reproduced (asexually) was similar irrespective of their diet, apart from starving ones, indicating that the amount of food provided was sufficient to allow reproduction. The reproduction rates of *Aurelia* sp. polyps are strongly affected by the quantity of provided food, and the absence of reproduction during starvation was previously reported (Schiariti et al. 2014; Purcell et al. 2019).

Group-foragers also tended to converge, achieving a slightly higher level of aggregation in respect to t_0, whilst solitary-feeders doubled their interindividual distances. This trend was significant in MIX diet but absent in LP diet and requires further investigation. Nonetheless, the tendency to converge in group-foragers fed with both preys was possibly determined by the amelioration of competition for food towards conspecifics. Their ability to access prey much larger than those affordable by solitary polyps appears as an emerging property of the group resulting from a combination of spatial proximity and individual size of polyps. Smaller polyps, even if close enough to fit the large prey, did not engage in collective predation probably because their size was too small to counteract the escape of the large prey. Hence, the different sizes of the individuals both as effect of the diet and intrinsic population variability, and their distance from the location of the capture, determined unequal foraging abilities, driving polyps to be group-foragers or not. Such "decision" reflected on the individual and the population fitness. In a population of several organisms, the formation of clusters is more likely to occur among cooperating individuals, while those not actively taking part in the action are spatially excluded (Nowak 2006). In this case, the benefits received by neighbouring polyps were primarily driven to phenotypic characteristics of polyps (the optimal size and location).

The olfactory cues released by the injured prey during predation may have played a role in the group foraging performed by *A. coerulea* polyps. When dealing with such basal animals it is not appropriate to refer to explicit decision-making processes, the joint predatory action seeming rather driven by several features including size and position in space, and intra-specific interactions. Thus, the decision on whether to join or leave a foraging-group is not based on cognition, as it is instead the case for animals with cognitive ability (Giraldeau and Pyke 2019). However, the ability to detect predatory cues is well known in cnidarians (Abe 1938; Pantin and Pantin 1943; Ewer and Fox 1947; Loomis 1955; Lenhoff and Schneiderman 1959; Fulton 1963; Pierobon et al. 1997; Yamamori 2012). Although lacking a centralized nervous system, their neural abilities are orchestrated within ganglion-like structures (Satterlie 2011), several layers of neural nets in tentacles and oral rim (Cheng 2021), and synapses are spread in the whole body (Holland 2003). The so-called "skin brain" (Holland 2003) allows cnidarians to exhibit the most basic form of decision-making through the detection and processing of mechanical and chemical stimulation (Huang and Bechtel 2020), as herein observed. Learning processes, habituation, inhibition, sophisticated and coordinated behaviours in general have been well studied in cnidarians (Mackie 1990; Cheng 2021).

To conclude, according to the theory of social foraging, if the collective exploitation of resources is advantageous for most individuals, it could turn into an evolutionary stable strategy, that aims at maximizing the individual biological fitness of group members (Giraldeau and Pyke 2019). Cnidarians are considered at the base of the evolutionary tree-of-life and sister-group of Bilateria (Dunn et al. 2008; Collins 2009; Zapata et al. 2015) with whom they share genes related to neurotransmission and neuronal activity (Watanabe 2017). The observed patterns of group foraging with clear benefits on the fitness, may recall a precursor of the social behavior performed by higher bilaterians, possibly developed from basal and non-cognitive forms of "decision-making", as those herein observed, and later evolved into cognitive processes.

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Author contributions CG, TVF, SP and LM conceived and designed the study; CG and DS performed the experiment and the data analyses; SG and FD assisted for organisms' provision and maintenance; GF provided the molecular characterization of specimens, and phylogenetics and haplotype analysis of *A. coerulea*; CG wrote the article draft; TVF, DS, SP, LM, GF, SG and FD contributed to the editing and preparation of the final version. SP, TVF and LM provided the funds for material and sampling. All authors read and approved the final manuscript.

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Data availability Data are available to anyone interested, by contacting the Corresponding Author.

Declarations

Ethical statement The experiments were carried out following the International ethical standards.

Conflict of interest The authors declare no conflict of interest.

References

Abe N (1938) Feeding behavior and the nematocyst of *Fungia* and 15 other species of corals. Palao Trop Biol Stn Stud 1:369–521

Anderson MJ (2006) Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62(1):245–253. https://doi.org/10.1111/j.1541-0420.2005.00440.x

Arai MN (1997) A functional biology of Scyphozoa. Chapman & Hall, London

Arai MN (2009) The potential importance of podocysts to the formation of scyphozoan blooms: a review. In: Jellyfish Blooms: Causes, Consequences, and Recent Advances: Proceedings of the Second International Jellyfish Blooms Symposium, held at the Gold Coast, Queensland, Australia, 24–27 June, 2007 (pp. 241–246). Springer Netherlands

Bavestrello G, Puce S, Cerrano C, Balduzzi A (2000) Life history of *Perarella schneideri* (Hydrozoa, Cytaedidae) in the Ligurian Sea. Sci Mar 64(S1):141–146. https://doi.org/10.3989/scimar.2000.64s1141

Bo M, Bavestrello G, Angiolillo M, Calcagnile L, Canese S, Cannas R, Cau A, D'Elia M, D'Oriano F, Follesa MC, Quarta G, Cau A (2015) Persistence of pristine deep-sea coral gardens in the Mediterranean Sea (SW Sardinia). PLoS ONE 10(3):e0119393. https://doi.org/10.1371/journal.pone.0119393

Boero F (1984) The ecology of marine hydroids and effects of environmental factors: a review. Mar Ecol 5(2):93–118. https://doi.org/10.1111/j.1439-0485.1984.tb00310.x

Boero F, Bouillon J, Gravili C, Miglietta MP, Parsons T, Piraino S (2008) Gelatinous plankton: irregularities rule the world (sometimes). Mar Ecol Prog Ser 356:299–310

Brown JL (1982) Optimal group size in territorial animals. J Theor Biol 95(4):793–810. https://doi.org/10.1016/0022-5193(82)90354-X

Brown KM, Alexander JE Jr (1994) Group foraging in a marine gastropod predator: benefits and costs to individuals. Mar Ecol Prog Ser 112(1/2):97–105

Cash KJ, Wrona FJ, Scrimgeour GJ (1995) The effects of group size on per capita ingestion in flatworms. Freshw Biol 34(3):477–483. https://doi.org/10.1111/j.1365-2427.1995.tb00905.x

Cerrano C, Puce S, Chiantore M, Bavestrello G (2000) Unusual trophic strategies of *Hydractinia Angusta* (Cnidaria, Hydrozoa) from Terra Nova Bay, Antarctica. Polar Biol 23(7):488–494. https://doi.org/10.1007/s003000000110

Cheng K (2021) Learning in Cnidaria: a systematic review. Learn Behav 49(2):175–189. https://doi.org/10.3758/s13420-020-00452-3

Clark PJ, Evans FC (1954) Distance to nearest neighbor as a measure of spatial relationships in populations. Ecol 35(4):445–453. https://doi.org/10.2307/1931034

Clark CW, Mangel M (1986) The evolutionary advantages of group foraging. Theor Popul Biol 30(1):45–75. https://doi.org/10.1016/0040-5809(86)90024-9

Cochran WG (1941) The distribution of the largest of a set of estimated variances as a fraction of their total. Ann Eugen 11(1):47–52

Collins AG (2009) Recent insights into cnidarian phylogeny. Smithson Contrib Mar Sci 38:139–149

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Corrales-Ugalde M, Colin SP, Sutherland KR (2017) Nematocyst distribution corresponds to prey capture location in hydromedusae with different predation modes. Mar Ecol Prog Ser 568:101–110. https://doi.org/10.3354/meps12059

De Waal FB (2005) How animals do business. Sci Am 292(4):72–79. https://doi.org/10.1098/rstb.2019.0663

Di Camillo CG, Betti F, Bo M, Martinelli M, Puce S, Bavestrello G (2010) Contribution to the understanding of seasonal cycle of *Aurelia aurita* (Cnidaria: Scyphozoa) scyphopolyps in the northern Adriatic Sea. J Mar Biolog Assoc U K 90(6):1105–1110. https://doi.org/10.1017/S0025315409000848

Di Camillo CG, Bavestrello G, Cerrano C, Gravili C, Piraino S, Puce S, Boero F (2017) Hydroids (Cnidaria, Hydrozoa): a neglected component of animal forests. Mar Anim Forests 20:397–427. https://doi.org/10.1007/978-3-319-21012-4_11

Dong Z (2019) Blooms of the moon jellyfish Aurelia: causes, consequences and controls. World seas: an environmental evaluation, Elsevier, pp. 163–171. https://doi.org/10.1016/B978-0-12-805052-1.00008-5

Duineveld GC, Lavaleye MS, Bergman MJ, De Stigter H, Mienis F (2007) Trophic structure of a cold-water coral mound community (Rockall Bank, NE Atlantic) in relation to the near-bottom particle supply and current regime. Bull Mar Sci 81(3):449–467

Dunn CW, Hejnol A, Matus DQ, Pang K, Browne WE et al (2008) Broad phylogenomic sampling improves resolution of the animal tree of life. Nature 452:745–749. https://doi.org/10.1038/nature06614

Ewer RF, Fox HM (1947) On the functions and mode of action of the nematocysts of Hydra. Proc Zool Soc Lond 117(2–3):365–376. https://doi.org/10.1111/j.1096-3642.1947.tb00524.x

Fernández-Juricic E, Erichsen JT, Kacelnik A (2004) Visual perception and social foraging in birds. Trends Ecol Evol 19(1):25–31. https://doi.org/10.1016/j.tree.2003.10.003

Fitzgerald MR, Ives AR (2017) Conspecific attraction drives intraspecific aggregations by *Nephila clavipes* spiders. Ethol 123(1):51–60. https://doi.org/10.1111/eth.12577

Fox J, Weisberg S (2019) An {R} companion to Applied Regression, 3rd edn. Sage Publication, Thousand Oaks CA

Forskål P (1775) Descriptiones Animalium, Avium, Amphibiorum, Piscium, Insectorum, Vermium; quae in Itinere Orientali Observavit Petrus Forskål. Post Mortem Auctoris editit Carsten Niebuhr. Adjuncta est materia Medica Kahirina. Mölleri, Hafniae, 19 + xxxiv + 164 pp

Frank ET, Linsenmair KE (2017) Flexible task allocation and raid organization in the termite-hunting ant *Megaponera Analis*. Insectes Soc 64(4):579–589. https://doi.org/10.1007/s00040-017-0579-2

Fulton C (1963) Proline control of the feeding reaction of *Cordylophora*. J Gen Physiol 46(4):823–837. https://doi.org/10.1085/jgp.46.4.823

Gambill M, Jarms G (2014) Can *Aurelia* (Cnidaria, Scyphozoa) species be differentiated by comparing their scyphistomae and ephyrae? Eur J Taxon 107:1–23. https://doi.org/10.5852/ejt.2014.107

Goldstein J, Augustin CB, Bleich S, Holst S (2017) A matter of tolerance: Distribution potential of scyphozoan polyps in a changing environment. Mar Ecol 38(5):e12457. https://doi.org/10.1111/maec.12457

Giraldeau LA, Pyke G (2019) Group foraging. In: Choe JC (ed) Encyclopedia of animal behavior. Elsevier Academic, pp 191–200

Greene CH (1986) Patterns of prey selection: implications of predator foraging tactics. Am Nat 128(6):824–839. https://doi.org/10.1086/284608

Greenhouse SW, Geisser S (1959) On methods in the analysis of profile data. Psychometrika 24(2):95–112

Gregorin C, Musco L, Puce S (2022) Protocooperation in *Tubastraea* cf. *Micranthus* to catch large planktonic prey. Mar Biodivers 52(3):1–2. https://doi.org/10.1007/s12526-022-01276-2

Gregorin C, Di Vito M, Roveta C, Mantas TP, Gridelli S, Domenichelli F, Cilenti L, Vega Fernández T, Puce S, Musco L (2024a) Reduction of small-prey capture rate and collective predation in the bleached sea anemone *Exaiptasia diaphana*. Mar Environ Res 106435. https://doi.org/10.1016/j.marenvres.2024.106435

Gregorin C, Vega Fernández T, Di Camillo CG, Musco L, Puce S (2024b) Big enough for an extra-large meal: a review on predation upon large animals by benthic cnidarians. Hydrobiologia:1–17. https://doi.org/10.1007/s10750-024-05523-4

Gröndahl F (1989) Evidence of gregarious settlement of planula larvae of the scyphozoan *Aurelia aurita*: an experimental study. Mar Ecol Prog Ser 56(1):119–125

Herbert-Read JE, Romanczuk P, Krause S, Strömbom D, Couillaud P, Domenici P, Kurvers RHJM, Marras S, Steffensen JF, Wilson ADM, Krause J (2016) Proto-cooperation: group hunting sailfish improve hunting success by alternating attacks on grouping prey. Proc R Soc B Biol Sci 283(1842):20161671. https://doi.org/10.1098/rspb.2016.1671

Hoff KVS, Blaustein AR, McDiarmid RW, Altig R (1999) Behavior: interactions and their consequences. University of Chicago Press, pp 215–239

Holland ND (2003) Early central nervous system evolution: an era of skin brains? Nat Rev Neurosci 4(8):617–627. https://doi.org/10.1038/nrn1175

Houlbrèque F, Ferrier-Pagès C (2009) Heterotrophy in tropical scleractinian corals. Biol Rev 84(1):1–17. https://doi.org/10.1111/j.1469-185X.2008.00058.x

Huang LTL, Bechtel W (2020) A Phylogenetic Perspective on Distributed Decision-Making Mechanisms. Preprint at PhilSci Archive. https://philsci-archive.pitt.edu/id/eprint/17250

Hutto RL (1988) Foraging behavior patterns suggest a possible cost associated with participation in mixed-species bird flocks. Oikos 51(1):79–83. https://doi.org/10.2307/3565809

Huynh H, Feldt LS (1970) Conditions under which mean square ratios in repeated measurements designs have exact F-distributions. J Am Stat Assoc 65(332):1582–1589. https://doi.org/10.1080/01621459.1970.10481187

Huynh H, Feldt LS (1976) Estimation of the Box correction for degrees of Freedom from Sample Data in Randomized Block and Split-plot designs. J Educ Behav Stat 1(1):69–82. https://doi.org/10.3102/10769986001001069

Ishii H, Katsukoshi K (2010) Seasonal and vertical distribution of *Aurelia aurita* polyps on a pylon in the innermost part of Tokyo Bay. J Oceanogr 66(3):329–336. https://doi.org/10.1007/s10872-010-0029-5

Kaliszewicz A (2013) Is larger better in sit-and-wait predators? Competitive superiority in Hydra. Hydrobiologia 714(1):105–114. https://doi.org/10.1007/s10750-013-1527-4

Kamiyama T (2011) Planktonic ciliates as a food source for the scyphozoan *Aurelia aurita* (s.l.): feeding activity and assimilation of the polyp stage. J Exp Mar Biol Ecol 407(2):207–215. https://doi.org/10.1016/j.jembe.2011.06.016

Kassambara A (2023) _ggpubr:“ggplot2’ Based Publication Ready Plots_. R package version 0.6.0, URL https://CRAN.R-project.org/package=ggpubr

Kiørboe T (2011) What makes pelagic copepods so successful? J Plankton Res 33(5):677–685. https://doi.org/10.1093/plankt/fbq159

Krause J, Ruxton GD (2002) Living in groups. Oxford Series in Ecology and Evolution, Oxford University Press

Krohn A (1852) Über die Erscheinungen bei der Fortpflanzung von *Syllis prolifera* und *Autolytus prolifer*. Archiv für Naturgeschichte, Berlin. 18(1):66–76, plate III Fig. 1., available online at https://biodiversitylibrary.org/page/7061053

Kurta A (1982) Social facilitation of foraging behavior by the hermit crab, *Coenobita compressus*, in Costa Rica. Biotropica 14:132–136. https://doi.org/10.2307/2387742

Laidre ME (2013) Foraging across ecosystems: diet diversity and social foraging spanning aquatic and terrestrial ecosystems by an invertebrate. Mar Ecol 34(1):80–89. https://doi.org/10.1111/j.1439-0485.2012.00527.x

Lendvai AZ, Barta Z, Liker A, Bokony V (2004) The effect of energy reserves on social foraging: hungry sparrows scrounge more. Proc. R. Soc. London, B 271(1556): 2467–2472. https://doi.org/10.1098/rspb.2004.2887

Lenhoff HM, Schneiderman HA (1959) The chemical control of feeding in the Portuguese man-of-war, *Physalia physalis* L. and its bearing on the evolution of the Cnidaria. Biol Bull 116(3):452–460. https://doi.org/10.2307/1538954

Licandro P, Conway DV, Daly Yahia MN, Fernandez de Puelles ML, Gasparini S, Hecq JH, Tranter P, Kirby RR (2010) A blooming jellyfish in the northeast Atlantic and Mediterranean. Biol Lett 6(5):688–691. https://doi.org/10.1098/rsbl.2010.0150

Liu Y, Passino KM (2002) Biomimicry of social foraging bacteria for distributed optimization: models, principles, and emergent behaviors. J Optim Theory Appl 115(3):603–628. https://doi.org/10.1023/A:1021207331209

Loomis WF (1955) Glutathione control of the specific feeding reactions of hydra. Ann N Y Acad Sci 62(9):211–227. https://doi.org/10.1111/j.1749-6632.1955.tb35372.x

Lucas CH, Graham WM, Widmer C (2012) Jellyfish life histories: role of polyps in forming and maintaining scyphomedusa populations. Adv Mar Biol 63:133–196

Mackie GO (1990) The elementary nervous system revisited. Am Zool 30(4):907–920. https://doi.org/10.1093/icb/30.4.907

Maggioni D, Puce S, Galli P, Seveso D, Montano S (2017) Description of *Turritopsoides marhei* sp. nov. (Hydrozoa, Anthoathecata) from the Maldives and its phylogenetic position. Mar Biol Res 13(9):983–992. https://doi.org/10.1080/17451000.2017.1317813

Marambio M, Canepa A, Lòpez L, Gauci AA, Gueroun SK, Zampardi S, Boero F, Yahia OK-D, Daly Yahia MN, Fuentes V, Piraino S, Deidun A (2021) Unfolding jellyfish bloom dynamics along the Mediterranean basin by transnational citizen science initiatives. Diversity 13(6):274. https://doi.org/10.3390/d13060274

Marques R, Bonnet D, Carré C, Roques C, Darnaude AM (2021) Trophic ecology of a blooming jellyfish (Aurelia coerulea) in a Mediterranean coastal lagoon. Limnol Oceanogr 66(1):141–157. https://doi.org/10.1002/lno.11593

Massa-Gallucci A, Gambi MC (2014) *Syllis prolifera* (Krohn, 1852) (Annelida, Syllidae): A standardised protocol. Technical report at ResearchGate. https://www.researchgate.net/publication/268075415

Mauchly JW (1940) Significance test for sphericity of a normal n-variate distribution. Ann Math Stat 11(2):204–209

Miyake H, Terazaki M, Kakinuma Y (2002) On the polyps of the common jellyfish *Aurelia aurita* in Kagoshima Bay. J Oceanogr 58:451–459. https://doi.org/10.1023/A:1021628314041

Montseny M, Linares C, Viladrich N, Capdevila P, Ambroso S, Díaz D, Gili J-M, Gori A (2020) A new-large-scale and cost-effective restoration method for cold-water coral gardens. Aquat Conserv: Mar Freshw Ecosyst 305(2020):977–987. https://doi.org/10.1002/aqc.3303

Motz-Kossowska S (1905) Contribution à la connaissance des hydraires de la Méditerranée occidentale. I. Hydraires gymnoblastiques. Archives de Zoologie Expérimentale et générale, 4me série. 43:39–98

Musco L, Fernández TV, Caroselli E, Roberts JM, Badalamenti F (2018) Protocooperation among small polyps allows the coral *Astroides calycularis* to prey on large jellyfish. Bull Ecol Soc Am 99(4):1–6. https://doi.org/10.1002/bes2.1445

Nowak MA (2006) Five rules for the evolution of cooperation. Science 314(5805):1560–1563. https://doi.org/10.1126/science.1133755

Oksanen J (2012) Vegan: community ecology package. R package version 2.0–3 http://CRAN.R-project.org/package=vegan

Pantin CFA, Pantin AMP (1943) The stimulus to feeding in *Anemonia sulcata*. J Exp Biol 20(1):6–13. https://doi.org/10.1242/jeb.20.1.6

Pallas PS (1766) Elenchus zoophytorum sistens generum adumbrationes generaliores et specierum cognitarum succintas descriptiones, cum selectis auctorum synonymis. pp. 451

Phillips JA, Peacock SJ, Bateman A, Bartlett M, Lewis MA, Krkošek M (2018) An asymmetric producer-scrounger game: body size and the social foraging behavior of coho salmon. Theor Ecol 11(4):417–431. https://doi.org/10.1007/s12080-018-0375-2

Pierobon P, De Petrocellis L, Minei R, Di Marzo V (1997) Arachidonic acid as an endogenous signal for the glutathione-induced feeding response in Hydra. Cell Mol Life Sci 53(1):61–68. https://doi.org/10.1007/PL00000580

Pillai KCS (1965) On the distribution of the largest characteristic root of a matrix in multivariate analysis. Biometrika 52(3–4):405–414

Polyakov AY, Quinn TP, Myers KW, Berdahl AM (2022) Group size affects predation risk and foraging success in Pacific salmon at sea. Sci Adv 8(26):eabm7548. https://doi.org/10.1126/sciadv.abm7548

Purcell JE, Uye SI, Lo WT (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Mar Ecol Prog Ser 350:153–174. https://doi.org/10.3354/meps07093

Purcell JE, Clarkin E, Doyle TK (2012) Foods of *Velella velella* (Cnidaria: Hydrozoa) in algal rafts and its distribution in

Irish seas. Hydrobiologia 690:47–55. https://doi.org/10.1007/s10750-012-1052-x

Purcell JE, Bondyale-Juez DR, Romero-Kutzner V, Martínez I, Caprioli R, Tames-Espinosa M, Almunia J, Alonso E, Packard TT, Gómez M (2019) Food supply effects on the asexual reproduction and respiratory metabolism of *Aurelia aurita* polyps. Hydrobiologia 846(1):135–146. https://doi.org/10.1007/s10750-019-04057-4

Quijano N, Passino KM (2010) Honey bee social foraging algorithms for resource allocation: theory and application. Eng Appl Artif Intell 23(6):845–861. https://doi.org/10.1016/j.engappai.2010.05.004

Rasband WS (2012) ImageJ: image processing and analysis in Java. Astrophysics Source Code Library, pp ASCL–1206

Ritz DA (1997) Costs and benefits as a function of group size: experiments on a swarming mysid, *Paramesopodopsis rufa* Fenton. In Animal groups in three dimensions, JK Parrish and MH Hamner, eds. (Cambridge University Press), pp.194–206

Rivera-De la Parra L, Sarma SSS, Nandini S (2016) Effects of predation by *Hydra* (Cnidaria) on cladocerans (Crustacea: Cladocera). J Limnol 75:39–47. https://doi.org/10.4081/jlimnol.2016.1368

Riyas A, Dahanukar N, Krishnan KA, Kumar AB (2021) Scyphozoan jellyfish blooms and their relationship with environmental factors along the South-eastern Arabian Sea. Mar Biol Res 17(2):185–199. https://doi.org/10.1080/17451000.2021.1916034

Rossi S, Bramanti L, Gori A, Orejas C (2017) An overview of the animal forests of the world. In: Rossi S (ed.) Marine animal forests: the ecology of benthic biodiversity hotspots, Springer international publishing, pp. 1–28. https://doi.org/10.1007/978-3-319-17001-5_1-1

Ruppert EE, Fox RS, Barnes RD (2004) Invertebrate Zoology: a functional evolutionary approach. Brooks/Cole Pub Co

Satterlie RA (2011) Do jellyfish have central nervous systems? J Exp Biol 214(8):1215–1223. https://doi.org/10.1242/jeb.043687

Schiariti A, Morandini AC, Jarms G, von Glehn Paes R, Franke S, Mianzan H (2014) Asexual reproduction strategies and blooming potential in Scyphozoa. Mar Ecol Prog Ser 510:241–253. https://doi.org/10.3354/meps10798

Schiariti A, Melica V, Kogovšek T, Malej A (2015) Density-dependent effects control the reproductive strategy and population growth of *Aurelia aurita* s.l. Scyphistomae. Mar biol 162:1665–1672. https://doi.org/10.1007/s00227-015-2704-y

Schmitt RJ, Strand SW (1982) Cooperative foraging by yellowtail, Seriola lalandei (Carangidae), on two species of fish prey. Copeia 1982(3):714–717. https://doi.org/10.2307/1444679

Sebens KP (1981) The allometry of feeding, energetics, and body size in three sea anemone species. Biol Bull 161(1):152–171. https://doi.org/10.2307/1541115

Shapiro SS, Wilk MB (1965) An analysis of variance test for normality (complete samples). Biometrika 52(3/4):591–611

Sheppard CE, Heaphy R, Cant MA, Marshall HH (2021) Individual foraging specialization in group-living species. Anim Behav 182:285–294. https://doi.org/10.1016/j.anbehav.2021.10.011

Silk JB (2007) The adaptive value of sociality in mammalian groups. Philos Trans R Soc Lond B Biol Sci 362(1480):539–559. https://doi.org/10.1098/rstb.2006.1994

Siokou-Frangou I, Christaki U, Mazzocchi MG, Montresor M, Ribera d'Alcalá M, Vaqué D, Zingone A (2010) Plankton in the open Mediterranean Sea: a review. Biogeosciences 7(5):1543–1586

Skelton PW (1979) Gregariousness and proto-cooperation in rudists (Bivalvia). Biology and systematics of colonial organisms. In: Larwood G, Rosen BR, eds. Biology and systematics of colonial organisms, Proceedings of the International Symposium held at the University of Durham, Academic Press Inc., London, pp 257–279

Sukhoputova AV, Kraus YA, Kirillova AO, Markov AV (2019) Differentiation of the oral–aboral axis and body parts during life cycle transitions in Scyphozoa. Biol Bull Rev 9:412–431. https://doi.org/10.1134/S2079086419050086

Sullivan BK, Suchman CL, Costello JH (1997) Mechanics of prey selection by ephyrae of the scyphomedusa *Aurelia aurita*. Mar Biol 130:213–222. https://doi.org/10.1007/s002270050241

Sun J, Hamel JF, Shikon V, Cossignani EF, Mercier A (2022) Trophic ecology, diet and feeding behaviour of three bathyal sea anemones (Actiniaria: Cnidaria) in the Northwest Atlantic. Deep-Sea Res I: Oceanogr Res Pap 179:103678. https://doi.org/10.1016/j.dsr.2021.103678

Sutton GJ, Hoskins AJ, Arnould JP (2015) Benefits of group foraging depend on prey type in a small marine predator, the little penguin. PLoS ONE 10(12):e0144297. https://doi.org/10.1371/journal.pone.0144297

Syazwan WM, Rizman-Idid M, Low LB, Then AYH, Chong VC (2020) Assessment of scyphozoan diversity, distribution and blooms: implications of jellyfish outbreaks to the environment and human welfare in Malaysia. Reg Stud Mar Sci 39:101444. https://doi.org/10.1016/j.rsma.2020.101444

Tardent P (1995) The cnidarian cnidocyte, a high-tech cellular weaponry. BioEssays 17(4):351–362. https://doi.org/10.1002/bies.950170411

Ter Horst LJ, Hoeksema BW (2021) Salpivory by colonial reef corals at Curaçao, Southern Caribbean. Diversity 13(11):560. https://doi.org/10.3390/d13110560

Uetz GW (1988) Group foraging in colonial web-building spiders. Behav Ecol Sociobiol 22:265–270 (1988)

Uetz GW (1992) Foraging strategies of spiders. Trends Ecol Evol 7(5):155–159. https://doi.org/10.1016/0169-5347(92)90209-T

Von Lendenfeld R (1884) The scyphomedusae of the southern hemisphere. Part III. Proc Linn Soc N S W 9:259–306

Watanabe H (2017) Back through time: how cnidarians and basal metazoans shed light on ancient nervous systems. In: Shigeno S, Murakami Y, Nomura T (eds) Brain evolution by design, diversity and commonality in animals. Springer, Tokyo, pp 45–75. https://doi.org/10.1007/978-4-431-56469-0_3

Welch BL (1938) The significance of the difference between two means when the population variances are unequal. Biometrika 29:350–362

Welch BL (1947) The generalization of 'Student's' problem when several different population variances are involved. Biometrika 34:28–35

Wilson E (1975) Sociobiology: the new synthesis. Harvard University Press

Yamamori L (2012) The Trigger for Feeding in *Aurelia aurita*. The 3rd International Symposium on Libera Arts and General Education, Kyoto University, p 13

Zapata F, Goetz FE, Smith SA, Howison M, Siebert S, Church SH, Sanders SM, Ames CL, McFadden CS, France SC et al (2015) Phylogenomic analyses support traditional relationships within Cnidaria. PLoS ONE 10(10):e0139068. https://doi.org/10.1371/journal.pone.0139068

Zeman SM, Brodeur RD, Daly EA, Sutherland KR (2016) Prey selection patterns of *Chrysaora fuscescens* in the northern California Current. J Plankton Res 38(6):1433–1443. https://doi.org/10.1093/plankt/fbw065