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The detection of specific prey cues triggers distinct predatory behaviour in *Aurelia coerulea* polyps (Cnidaria: scyphozoa)

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ABSTRACT

Predatory behaviour of cnidarian polyps is poorly described, although their tentacles are equipped with thousands of stinging cells to capture preys. The predatory action is elicited by the tactile stimulation of the tentacles due to the physical encounter between the prey and the polyp. Micro-predation involves low-energetic movements of tentacles and fast ingestion of more small prey simultaneously. In contrast, macro-predation includes expensive actions of the whole body, with a duration of up to 15 min to ingest a large prey. When polyps are spatially aggregated, they can engage in a collective predation in which they first cooperate and then compete for the division of the prey. We hypothesized that an additional stimulation represented by specific prey-produced cues could serve as an additional trigger for predation. We provided three diets (1 large prey, 2 small preys) to groups of five polyps and later stimulated them with prey homogenates as prey-produced cues. Behaviours were first observed and categorized and later used to evaluate feeding activity, together with tentacle contractions and rapid movements. Polyps fed with the large prey and later stimulated with its homogenate showed 2.2 to 6.5 times higher number of tentacle contractions and rapid movements and 55.7% higher occurrence of the category "active feeding" in comparison to all the other combinations of prey/prey cue, resembling the predatory action necessary for macro-predation. These outcomes suggest the ability of polyps to discern the prey cues in the water medium and to modify their behaviour accordingly. Cnidarians are metazoans lacking a central nervous system; however, they are able to detect the presence of prey in their surroundings, process this information and adjust their behaviour accordingly, maximizing the benefits of predation.

HIGHLIGHTS

- Preys of different size are captured by cnidarian polyps with distinct predatory behaviours;
- Collective capture of large prey consists of active grabbing and rapid movements;
- Contact among polyps has been reported during collective large prey capture;
- The detection of prey-produced cues could trigger specific predatory behaviour in polyps;
- In addition to tactile stimulation, olfactory signalling could play a role in eliciting predation in benthic animals.

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1. Introduction

Benthic cnidarians are sessile organisms that settle on the substrate after a short time spent as planktonic planula larvae. After metamorphosis the planula forms a benthic stage (the polyp), which presents a crown of tentacles around the oral opening, oriented upwards (Hickman et al. 2011). Once settled, the polyps form a new population through several pathways of asexual reproduction that lead to the spreading of clones near the parental individuals (Reitzel et al., 2011). In addition to heterotrophic suspension-feeding, polyps are

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specialized in micro-predation, occurring when tentacles touch and capture motile small prey (e.g. mesoplankton; Gregorin et al. 2024a). Moreover, macro-predation, referred to as the predation of prey equal to or larger than the size of the predator, is a widespread feeding modality mainly reported in solitary large-mouthed anthozoans Dayton et al. (1970); Fautin and Fitt (1991); Jarms and Tiemann (2004); Alamaru et al., (2009); Hoeksema and Waheed (2012); Hoeksema et al., (2015); Mehrotra et al., (2016); Ivanova and Grebelnyi (2017); Gregorin et al. (2024a). Macro-predation was also observed within groups (both aggregations and colonies) of small-mouthed polyps that share the capture of large prey (Cerrano et al., 2000; 2016; Musco et al. 2018; Ter Horst & Hoeksema 2021; Gregorin et al., 2022)). This collective predation has been referred to as protocooperation (Skelton, 1979; Musco et al., 2018). With either small or large prey, the predatory reaction of a polyp is elicited by the contact between its tentacle(s) and the prey, and it is accomplished by its ingestion (Houlbrèque & Ferrier-Pagès, 2009; Sun et al., 2022). Predation is a "sit-and-wait" activity carried out by extended tentacles that serve to block the prey incidentally touched, thus requiring an active capture of the prey (Kaliszewicz, 2013). Many relatively small polyps can predate upon large organisms through simultaneous action, as long as they are close enough in space to act on the same prey, as reported in colonial forms (Musco et al., 2018; Ter Horst & Hoeksema, 2021; Gregorin et al., 2022). Besides the contact of the prey with one or more polyps as tactile stimulation that triggers feeding reactions in cnidarian polyps, little is known about the eventual role of additional cues that could interfere with the predation and influence the behaviour of polyps, especially when they act simultaneously in the collective predation.

Cnidarians have been extensively employed as models to decipher the early origins of central nervous systems, being basal metazoans and the sister group of Bilateria (Watanabe et al., 2009; Cheng, 2021). The nervous system of cnidarians consists of nerve nets with longitudinal or circular thickened nerve tracts formed by fused neurons. The presence of the nerve tracts ensures prompt reactions by reason of the enlarged diameter that allows for fast signal transmission (Grimmelikhuijzen & Westfall, 1995, Mackie, 2004, Albert, 2011). Among cnidarians, many model species (e.g. hydras and sea anemones) have been investigated for their ability to detect waterborne molecules released by prey (Ewer & Fox, 1947, Loomis, 1955, Reimer, 1973), and to process the detection of these molecules within their primordial nervous system. Prey metabolites sensed by polyps could represent chemical cues that trigger feeding excitement and feeding behaviour, including predatory action.

The learning capacity of cnidarians was tested by feeding stimulation through laboratory assays by Jennings (1905), Allabach (1905), and Rushforth and Hofman (1972), among others. These studies describe several cnidarian species displaying peculiar behaviours, previously exhibited during a feeding training session, when stimulated with a feeding cue (e.g. prey homogenate; Rushforth and Hofman, 1972). Despite lacking a central nervous system, their cognitive abilities are impressive. Both non-associative and associative learning (or Pavlovian conditioning) have previously been reported in cnidarians. The former implies habituation and sensitization processes, occurring when the responsiveness to a repeated stimulus decreases or increases, respectively. The latter comprises the development of a direct link between a neutral and a non-neutral stimulus (Cheng, 2021; Botton-Amiot et al., 2023). The scyphozoan *Aurelia coerulea* von Lendenfeld, 1884 was selected as a model organism for studying the response to feeding cue stimulation. This species has a worldwide distribution thanks to its resistance to wide ranges of salinity and temperature, and it is frequently found in coastal waters where it breaks out in seasonal blooms (Albert, 2011; Suzuki et al., 2019). It possesses a benthic/planktonic life cycle with the alternance of adult medusae and polyps (Suzuki et al., 2019).

The genus *Aurelia* is the most studied among jellyfish, in both free-swimming and sessile phases. Polyps can implement a population by mean of asexual reproduction (e.g. lateral budding), forming several clones that become fully developed individuals within few days. The benthic phases of Scyphozoa strongly influence the planktonic medusa stage, contributing to determining their population abundance and dynamics (Boero et al., 2008; Lucas et al., 2012).

The first aim of the present work was to provide a detailed description of macro-predatory behaviour performed by cnidarian polyps, and to compare it with micro-predatory behaviour, focusing on both a single polyp and the interactions among individuals. The second aim was to test the ability of polyps to detect prey cues and to learn from previous predation experiences. This ability was assessed by stimulating them with prey homogenates (i.e. feeding cues), in order to trigger different predation strategies (micro- vs. macro-predation). The hypothesis was that after the various prey were presented and consumed (i.e. feeding experience), the prey homogenate (i.e. feeding cue) would trigger the behaviour associated with the predation of that specific prey. The validation of this hypothesis could indicate that the predation: (1) could be triggered by cues other than tactile, detected in the environment; (2) could be prey-specific, meaning that the detection of the cue triggers the behavioural strategy specific to the capture of the prey; (3) could be memorized and linked to the specific prey by means of the nervous system, relating to learning capacity.

2. Materials and methods

2.1. Ethical note

Laboratory trials did not include endangered or protected species. All experimental procedures carried out on animals were in compliance with the guidelines of the European Union (Directive 2010/63/EU).

2.2. Rearing of experimental organisms

Aurelia polyps were provided by the Cattolica Aquarium (Cattolica, Italy) and transferred to the Zoology Laboratory of Marche Polytechnic University, reared in glass bowls filled with filtered sea water (0.22 µm, FSW) at a constant temperature (18.0 ± 0.5°C), with salinity 38 PSU and light:dark cycle 16:8 h. During the rearing period in the laboratory, we proceeded to identify the *Aurelia* species (see Gregorin et al., 2024) as *A. coerulea*. Three times a week, water was renewed, and polyps were fed with newly hatched *Artemia salina* (Linnaeus, 1758) nauplii.

The polyp attaches on the substrate by means of its pedal disc and keeps an erect position thanks to the hydrostatic skeleton that sustains the calyx. The central mouth is oriented upwards, surrounded by a crown of tentacles, and it opens to a gastric cavity where digestion occurs. The mouth disc is constituted by the central mouth and the oral rim, which is the border of the disc. The mouth disc diameter is measured as the longest diameter that joins two opposite points on the oral rim passing through the mouth (Gambill & Jarms, 2014) (Figure 1).

Healthy *Aurelia coerulea* polyps, without swelling tissue indicating ongoing asexual reproduction, were randomly selected from rearing bowls and transferred into 65 small glass capsules (experimental units, EUs: volume 45 mL, bottom area 4.9 cm^2). Between 50 and 60 polyps were deployed in each EU to attain their natural density of between 12 and 20 polyps/cm^2 (Di Camillo et al., 2010). Polyps were left for 1 week to settle

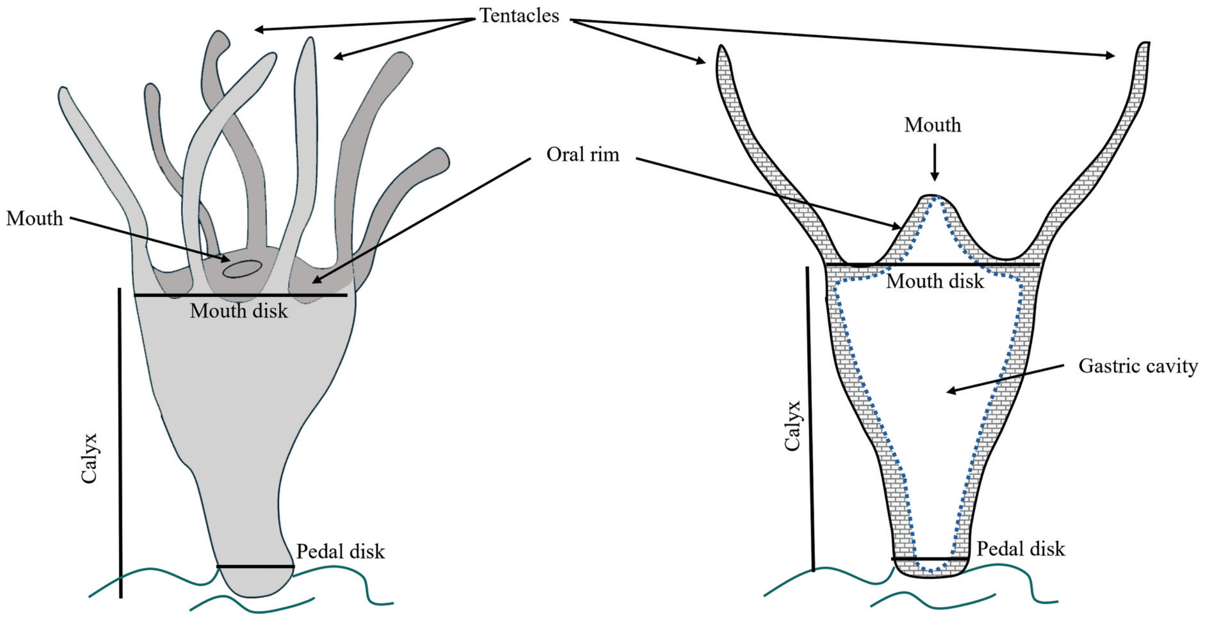

Figure 1. Morphology of *Aurelia coerulea* polyp.

and acclimate to the new environment. FSW renewals and food supply were maintained as indicated above. At the start of the experiment, five polyps were left in the centre of the EU bottom area by removing the others. The five polyps were photographed to measure their individual mouth disc diameter (MDD, Gambill & Jarms, 2014), using ImageJ software (RRID:SCR_003070; Rasband, 2012). Polyps were left fasting for 3 days prior to start the feeding experiment. Eventual buds not completely detached from the parental individual were left in the EU and excluded from the counts and behavioural observations.

Nauplii of the brine shrimp *Artemia salina* (size 0.4–0.5 mm) were used as rearing food for polyps under rearing conditions and considered the usual mesozooplankton food for the feeding experiment. In order to obtain newly hatched nauplii, 0.10 g of *A. salina* cysts were rehydrated in 200 mL FSW at 26°C and 38 PSU. After 24–36 h, the culture containing newly hatched nauplii was washed with the same volume of fresh FSW and positioned under a light source for 5 min, to concentrate the phototactic nauplii. Different aliquots of the so-obtained overcrowded culture were withdrawn, filtered, washed with deionized water, and placed into a stove (72 h at 60°C) on pre-weighted aluminium foils to calculate the mean dry weight.

The rotifer *Brachionus plicatilis* Müller, 1786 was an additional type of mesozooplankton prey (around 0.3 mm size) selected to serve as a control for the potential effects of habituation of polyps to feed on *A. salina* (manipulation control). Live individuals were provided by the aquaculture laboratory of Marche Polytechnic University and reared in a tank (20 L volume), with water at 24°C and 38 PSU. A commercial mixture of dried microalgae was provided to the culture every day. The density (ind./mL) was regularly checked. Several aliquots of the culture (30 ± 12.8 ind./mL) were withdrawn and filtered in a 63-μm mesh strainer. The filtered individuals were collected with a pipette, re-suspended in deionized water, and dried in a stove (72 h at 60°C) on pre-weighted aluminium foils to obtain the dry weight.

The polychaete *Syllis prolifera* Krohn, 1852, around 1 cm length, was selected to serve as large prey thanks to its size ratio in relation to the polyp (1:10 polyp:polychaete). Polychaetes have been reported as an ephemeral feeding resource being predated by benthic cnidarians (Bavestrello et al., 2000; Durden et al., 2015; Maggioni et al., 2017), in addition to other vagile benthic fauna such as echinoderms, molluscs, crustaceans, and gelatinous planktonic organisms (reviewed in Gregorin et al. 2024a). Individuals were sampled at 1–3 m depth off the coast of Ischia Island (Gulf of Naples, Italy), and later transferred to the Zoology Laboratory of Marche Polytechnic University into thermic containers. Polychaetes were maintained in glass bowls filled with FSW and kept in a thermostatic chamber (18.0 ± 0.5°C, 38 PSU, 16:8 h light:dark period). Individuals shorter than 8 mm or longer than 12 mm were discarded to maintain an adequate size ratio with respect to the *A. coerulea* polyps. Six polychaetes were placed in the stove (72 h at 60°C) on pre-weighted aluminium foils to obtain the dry weight.

2.3. Description of macro-predation vs micro-predation

The behaviour of *Aurelia coerulea* polyps was observed for 3–5 h in different sessions while feeding upon two preys requiring different seizing strategies, the brine shrimp *Artemia salina* as zooplanktonic small prey, and the polychaete *Syllis prolifera* as large prey, the former seized through micro-predation and the latter by collective macro-predation. Categorization of polyps typical behaviours was made following some initial observations using a steromicroscope (Zeiss Stemi 305) and through the analysis of videos recorded via a steromicroscope (Nikon SMZ18) equipped with a Nikon D610 digital camera. Observation and categorization of behaviours were used to develop the ethogram.

2.4. Feeding experiment and behavioural trials

Three different food preys were selected for the experiment: (1) *Syllis prolifera*, the large prey ("LP") requiring macro-and collective predation; (2) *Brachionus plicatilis*, a small prey ("SP") never eaten before and accessible through micro-predation; and (3) *Artemia salina*, the usual small prey to serve as control ("cSP"), seized through micro-predation. Preliminary tests allowed the determination of the digestion time required by polyps for the three preys: 10 days for LP, 8 days for cSP, and 4 days for SP (Figure 2 A), determined by providing the different prey items to polyps and counting the time elapsed from ingestion to the complete emptying of the gastric cavity, at 18.0 ± 0.5°C and 38 PSU rearing conditions. The three types of food items were provided to allow polyps from the different experimental groups to end digestion at the same time. In

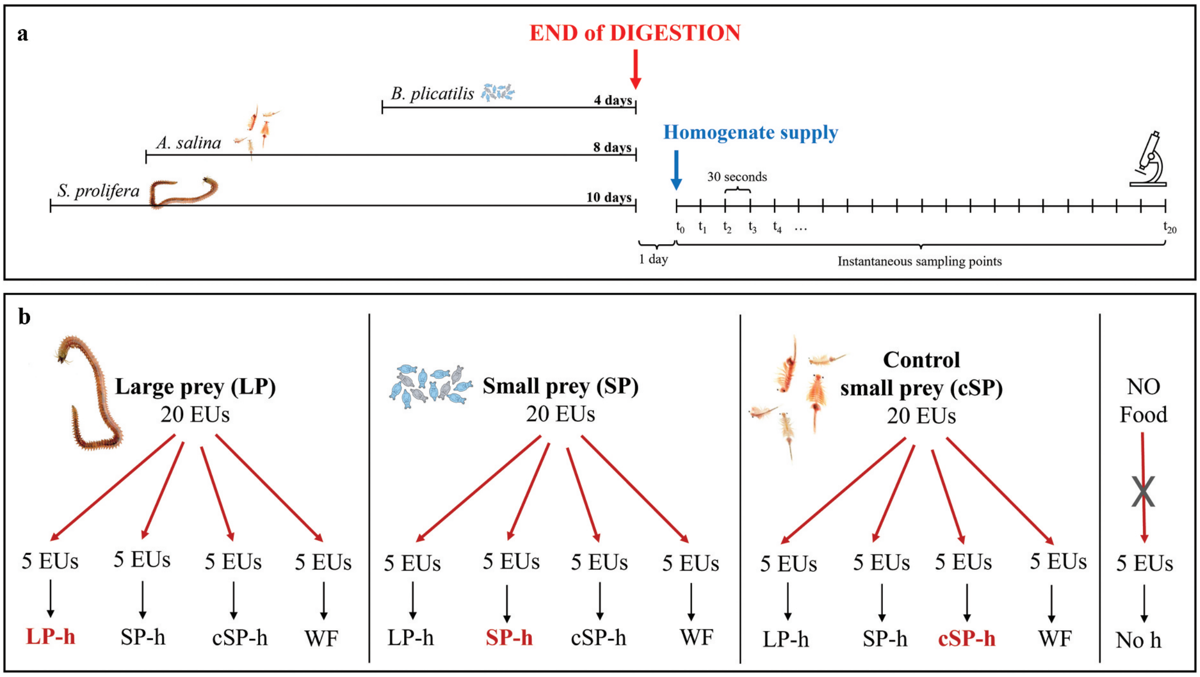

Figure 2. a. Scheme of experimental timing. Days required for the digestion of the three preys by *Aurelia coerulea* polyps are reported. One day after the digestion (red), the prey cue was provided as prey homogenate supernatant at t_0 and the scan instantaneous sampling method with sample points at 30 s intervals was used for the ethological observation using the stereomicroscope. SP = small prey; cSP = control small prey; LP = large prey; t_0 = start of the experiments; t_1, t_2, t_3, … = sample points; t_{20} = end of the experiment. The total duration of the observation was 10 min. b. Scheme of experimental design. EU = experimental unit, LP = large prey, LP-h = homogenate supernatant of the large prey; SP = small prey, SP-h = homogenate supernatant of the small prey; cSP = control small prey, cSP-h = homogenate supernatant of the control small prey; WF = water flow; NO-h = control for manipulation – no stimulation. Homogenate supernatant corresponding to the same alive prey received during the experiment appears in red.

order to ensure that the amount of food provided to distinct experimental groups was comparable, the dry weight of the different prey items was measured: one polychaete between 9 and 11 mm in length weighed 0.22 ± 0.147 mg [mean ± standard error, $n = 6$], which corresponded to the dry weight of 35 µL of *A. salina* overcrowded culture. This aliquot was then filtered through a 200 µm mesh strainer and resuspended in 1 mL FSW. Analogously, 20 mL of *B. plicatilis* culture (30 ± 14.3 ind./mL) was filtered through a 63 µm mesh strainer and resuspended in 1 mL FSW.

The above-mentioned food items were provided to four experimental groups of polyps as follows (Figure 2 B): the first experimental group of 20 EUs received the large prey (LP); the second group of 20 EUs were fed with the small prey (SP); polyps in the third group of 20 EUs were provided with the control small prey (cSP); and an additional group made up of 5 EUs received neither food nor homogenate (NO-h) to control for an eventual absence of response. The day after digestion, each group of 20 EUs was further subdivided into four groups containing 5 EUs each. All EUs were exposed to a feeding stimulus obtained by the three preys (*Syllis prolifera*, *Artemia salina*, *Brachionus plicatilis*). An additional stimulus was made with seawater only (water flow, WF) in order to control for the effect of turbulent mixing of water when the prey cues were injected in the EUs. The prey cues were extracted from a fixed weight of fresh prey homogenate (−h), chopped in 0.5 mL FSW and centrifuged at 13,500 rpm for 5 min at 20°C. Supernatant was collected and stored as feeding stimuli, labelled as “LP-h” (large prey-homogenate), “SP-h” (small prey-homogenate) and “cSP-h” (control small prey-homogenate). For the water flow treatments (“WF”), five aliquots of 0.5 mL FSW were administered. Abbreviations are reported in Table 1.

The response variables were (1) the behaviour of each individual polyp within the EU, ascribed to one of the ethogram categories defined in advance and expressed as a percentage of occurrence, i.e. 1 polyp out of 5 corresponding to 20% and 5 polyps out of 5 to 100%; and (2) the cumulative number of tentacle contractions and mouth movements, also including rapid movements of the calyx (TC-MM) as a proxy for

Table 1. Abbreviations used throughout the manuscript and their description. Hom. = homogenate supernatant used as prey-produced cue.

Prey	Abbreviation	Animal
Large prey	LP	*Syllis prolifera* – polychaete
Small prey	SP	*Brachionus plicatilis* – rotifer
Control small prey	cSP	*Artemia salina* – brine shrimp
Stimulus	**Aabbreviation**	**Cue**
Large prey-homogenate supernatant	LP-h	0.5 mL homogenate supernatant of *S. prolifera*
Small prey-homogenate supernatant	SP-h	0.5 mL homogenate supernatant of *B. plicatilis*
Control for small prey-homogenate supernatant	cSP-h	0.5 mL homogenate supernatant of *A. salina*
Water flow	WF	0.5 mL filtered sea water
Combination Abbreviation	**Description**	**Combinations of prey – prey cue**
LP – LP-h	Polyps fed with large prey and later provided with large prey cue	*S. prolifera* – *S. prolifera*
LP – SP-h	Polyps fed with large prey, and later provided with small prey homogenate supernatant	*S. prolifera* – *B. plicatilis*
LP – cSP-h	Polyps fed with large prey, and later provided with control small prey homogenate supernatant	*S. prolifera* – *A. salina*
LP – WF	Polyps fed with large prey, experiencing water flow injection without food cues.	*S. prolifera* – water flow
SP – LP-h	Polyps fed with small prey, and later provided with large prey homogenate supernatant	*B. plicatilis* – *S. prolifera*
SP – SP-h	Polyps fed with small prey, and later provided with small prey homogenate supernatant	*B. plicatilis* – *B. plicatilis*
SP – cSP-h	Polyps fed with small prey, and later provided with control small prey homogenate supernatant	*B. plicatilis* – *A. salina*
SP – WF	Polyps fed with small prey, experiencing water flow injection without food cues.	*B. plicatilis* – water flow
cSP – SP-h	Polyps fed with control small prey, and later provided with large prey homogenate supernatant	*A. salina* – *S. prolifera*
LP – cSP-h	Polyps fed with control small prey, and later provided with small prey homogenate supernatant	*A. salina* – *B. plicatilis*
LP – LP-h	Polyps fed with control small prey, and later provided with control small prey homogenate supernatant	*A. salina* – *A. salina*
cSP – WF	Polyps fed with control small prey and experiencing water flow injection without food cues.	*A. salina* – water flow

the feeding behaviour of the polyps. The scan instantaneous sampling method by Martin and Bateson (2021) (Figure 2 A) was followed by direct observation through a Zeiss Stemi 305 stereomicroscope, starting immediately before the injection of the homogenate (t_0). The scan of behaviour was performed every 30 s for 10 min, for a total of 20 sample points [t_1–t_{20}], while the number of TC-MM was counted continuously during the whole 10 min observation period.

2.5. Data processing and statistical analyses

Differences among experimental groups were tested through repeated measures (RM) analyses of variance (ANOVAs) after checking the assumption of a normal distribution of data through Shapiro-Wilk's test, as well as homogeneity of variances through Levene's tests. One-way ANOVA was used both to check the homogeneity of size among experimental polyps and to test for the effect of the water flow injection on the number of TC-MM in comparison to the absence of any external stimulation. Two-way ANOVA (factor 1: prey; factor 2: homogenate; factor 1 × factor 2: prey × homogenate) was used to test for the effects of the provision of prey and prey homogenate supernatant on the number of TC-MM. When significant, ANOVA was followed by the *post hoc* Tukey's test for multiple comparisons.

For the analysis of behaviour, focus was on the FM occurrence, which referred to the predatory behaviour. FM occurrence was compared with the occurrence of all the other categories of polyp behaviour via RM-ANOVA. Tests of between-subject effects were corrected for departures from the assumption of symmetry of the variance–covariance matrix, by applying either the Huynd-Feldt correction (if $\varepsilon \geq 0.75$) or the Greenhouse-Geisser one (whereas $\varepsilon \leq 0.75$). The Pillai-Barlett trace was also used to test for between-subject effects, since it is particularly robust to eventual deviations from sphericity, which was checked through the Mauchley's test. Further planned comparisons were made through either t-tests (for similar sample sizes) or

Welch's test (in case of different sample size, thereby assuming heterogeneity of variances) to answer specific questions regarding the timing of polyp response and the cumulative effect of homogenate supernatant supply on polyp behaviour regardless of the type of prey. All tests were two tailed.

The software Statistica (RRID:SCR_014213) and the R software environment 4.2.2 Ink (RRID:SCR_000432; R Core team, 2022) were used for analyses and graphical representations using the packages *car* (Fox et al., 2019), *ggplot2* (Wickham, 2016) and *ggpubr* (Kassambara, 2023).

3. Results

3.1. Description of macro-predation vs micro-predation

The observation of polyps before the provision of prey and during feeding on *Artemia salina* and *Syllis prolifera* allowed for the identification and description of their distinct behaviours, which are summarized in Table 2.

Rest (RE) was the behaviour that polyps displayed in absence of any external stimulus, disturbance, or interaction with conspecifics (Figure 3 A, B); tentacles were extended in the water column, seldom moved with some contractions, the mouth was closed, and the calyx was erected in a vertical position.

Alert and research (AR) was the term adopted for the detection of cues, consisting of a slow movement of tentacles in the water column, particularly the tips, as for searching for prey in the surroundings (Figure 3 C – E, red arrows); the calyx was erect and the mouth was closed.

Feeding and rapid movements (FM) were reported during the provision of prey: it prompted the transport of the prey inside the mouth by one or more tentacles, also characterized by rapid movements of the mouth (opening and closing), of the calyx (e.g. from left to right, vertical to horizontal) and of the tentacles (e.g. marked contractions towards or away from the mouth). Even if FM occurred in the presence of both types of prey, the main differences between FM behaviour with small vs. large prey were (1) the number of tentacles involved in the transport of food inside the mouth; and (2) the duration of the capture and ingestion phases. In the micro-predation, one tentacle was enough to capture *A. salina*, to twist towards the mouth and to transfer the prey inside the gastrovascular cavity, while the large prey was captured by many tentacles simultaneously, most often belonging to more than one polyp, and pulled inside the mouth (Figure 3 F, red circles). The ingestion of the small prey occurred in a few seconds, while for the large prey it lasted from 5 to 15 min, being slowed down by the prey's attempts to escape until the onset of paralysis, which is then followed by its ingestion by polyps.

Closed (CL) polyps (Figure 3 G) was the term used for the behaviour of individuals apparently not interested in feeding, probably reflecting a temporary or permanent ill status. Indeed, it seldom occurred that closed polyps later opened their tentacles and changed their behaviour.

Contact (CO) was seldom observed (Figure 3 H – J); it was the physical interaction of two (or more) polyps while ingesting the large prey, each one pulling the entangled portion of the prey inside its gastrovascular cavity (Figure 3 H). In particular, when two polyps grabbed the prey at opposite extremities of

Table 2. Ethogram reporting observed behaviour of polyps feeding on either small or large prey. The column "strategy" indicates the feeding modality in which the referred behaviour predominantly occurs.

Behaviour	Abbreviation	Description	Feeding strategy
Rest	RE	Polyps are in a resting position, with wide tentacles and closed mouth, tentacles movement and mouth contraction are very rare	None – occurring prior to feeding
Alert and research	AR	Polyps move their tentacles in the water as they are trying to detect some food particles; mouth is closed, tentacles and mouth contractions are very rare	None – occurring prior to feeding
Feeding and rapid movements	FM	Polyps bring their tentacles to the mouth to carry the prey; mouth opens and closes frequently; calyx moves fast and changes its posture (e.g. from vertical to horizontal); tentacle contractions are frequent	Both, with differences in duration and no. of tentacles involved
Contact	CO	Polyps in proximity pull the prey and their oral discs come into tight contact during ingestion	Collective predation
Closed	CL	Polyps have shortened tentacles folded up the oral disc, the mouth is closed, tentacle contractions and mouth movements are absent	None – no feeding is performed
Other behaviours	OTH	Any other behaviour observed	Both

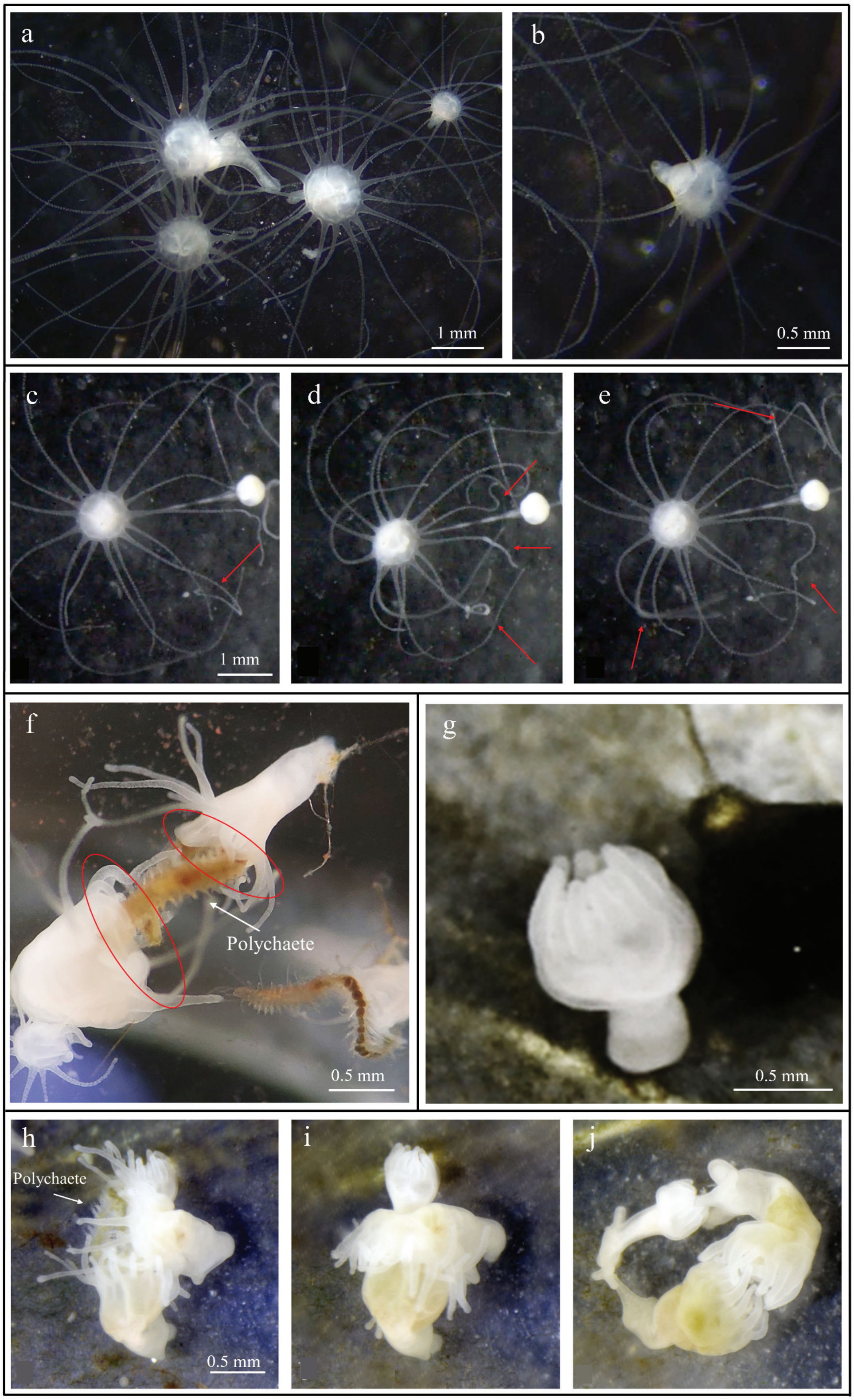

Figure 3. List of categorized behaviours described in Table II. a, b) rest behaviour, RE; c–e) alert and research behaviour, AR. The figures from c to e indicate a time sequence. The red arrows indicate the tips of tentacles moving in the water; f) feeding and

Table 3. Two additional types of behaviour observed after the provision of homogenate supernatant.

Behaviour	Abbreviation	Description
Rest with mouth open	RE-M (OTH*)	Polyps are in a rest position i.e. with tentacles lying on the bottom of the capsule or extended in the water column; their mouth is wide open, kept so for many seconds, the tentacles' contractions towards the mouth are rare
Alert and research with mouth open	AR-M (OTH**)	Tentacles are moving in the water; mouth is wide open for many seconds; tentacles twist and writhe towards the mouth

the prey body (prostomial and pygidial), their oral discs came into tight contact (Figure 3 I), until the prey broke, and they released the contact (Figure 3 J). This behaviour only occurred during collective predation, revealing a sort of intraspecific competition. Often, contact is anticipated by the inclination of the whole body of the polyps (tentacles included) towards the polyp(s) capturing and handling the prey.

The category Other (OTH) included any other behaviour eventually observed.

Two behaviours (OTH* and OTH**, Table 3) were included *a posteriori* in the ethogram because they were frequently observed during the experimental provision of homogenate supernatant and named "RE-M" (eest with open mouth; Figure 4 A, B) and "AR-M" (alert and research with open mouth; Figure 4 C), respectively. These two behaviours implied an extraordinary and long-lasting opening of the mouth (Figure 4 A and C, red arrows), as wide as the maximum external circumference of the oral disc, often followed by the flattening of the polyp to the bottom of the capsule, completely losing its vertical shape as it "melted". With RE-M, tentacles adhered to the bottom of the cup and did not move; while, concerning AR-M, tentacles twisted and crumpled in a very distinctive way towards the oral disc (Figure 4 C, red circles).

3.2. Feeding experiment and behavioural trials

The average size of the population was calculated measuring the MDD of 175 randomly selected polyps from 35 EUs and was 1.05 ± 0.27 mm [mean ± standard error, SE]. The polyps selected for the experiment were homogeneous in size at t_0 (two-tailed one-way ANOVA: $F_{34,140} = 0.882$; $p = .656$), showing small differences reflecting natural populations.

The behaviour "Rest" (RE) was mostly performed by polyps with no stimulation (NO-h) and with water flow injection (WF) in all the EUs, always exceeding 75% of occurrence (except cSP-WF t_1 and t_2) (Figure 5). In SP and cSP groups, WF slightly increased the "Alert and aesearch" (AR) response, as well as the "Feeding, rapid movements" (FM) behaviour, albeit with low occurrence (up to 30% for SP – WF and 40% for cSP – WF) (Figure 5). The net prevalence of RE and AR were related to the low number of TC-MM (Figure 6 A). In both NO-h and WF groups, the number of TC-MM ranged between 17.0 ± 2.3 (SP – WF) and 24.6 ± 1.03 (cSP – WF). The two-tailed one-way ANOVA indicated no significant differences in TC-MM among NO-h and WF treatments ($F_{3,16} = 1.062$, $p = .393$). This result indicates that the mechanical injection of water flow did not affect the behaviour of the polyps for more than the first 60 s (see "Video S1 – cSP-WF" in the Supplementary materials, for example, sped up 4x).

The prey cues triggered different behaviours in relation to the food previously consumed by polyps (Figure 5). Both cSP-h and LP-h had clear effects on polyps, which reacted to the stimulation. AR-M behaviour was recorded with increasing occurrence in SP – LP-h (+12%), SP – cSP-h (+28%), cSP – LP-h (+4%) and LP – cSP-h (+20%) from t_1 to t_{20} (see "Video S2 – SP-LP-h" in the Supplementary material, sped up 4x). Similarly, AR and FM behaviours appeared at t_1 and lasted until t_{20} across these treatments, ranging from 16.84 ± 2.99% to 26.6 ± 6.55%, respectively. In general, the administration of SP-h induced lower percentages of AR and FM behaviours with respect to LP-h and cSP-h (see "Video S3 SP – SP-h" in the Supplementary material, sped up

rapid movements (FM) during collective predation of the polychaete *syllis prolifera* (the large prey). The largest polychaete is captured by two polyps. Many tentacles (red circles) are involved in the ingestion of the prey, each one pulling in its own direction; g) closed polyp (CL), tentacles are shortened and folded on the mouth, which appears closed as well; h–j) contact (CO) between two polyps during collective predation. In h), the polychaete (white arrow) is almost ingested by two polyps. In i), the total ingestion by both polyps resulted in the contact of their oral discs. In j), after some time, when the large prey is divided, the polyps detached and continued digestion.

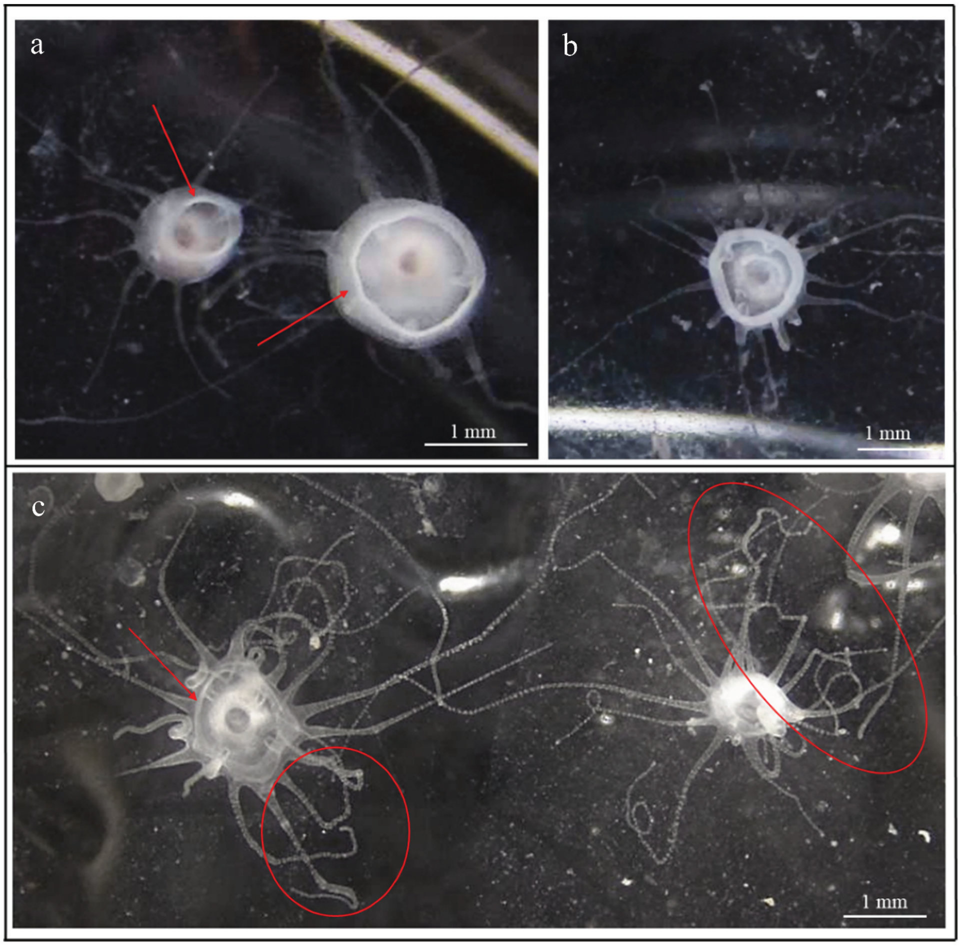

Figure 4. List of categorized behaviours described in Table III. a, b) Rest with open mouth (RE-M) performed by polyps during the administration of homogenates. The mouth is wide open, and tentacles are extended and touching the bottom of the capsule. The oral rim is indicated by the red arrows; c) alert and research with open mouth (AR-M) after the administration of homogenates. The mouth is wide open (red arrow), and tentacles are contracting, twisting, and writhing (red circles).

4x). Particularly, in the LP – SP-h treatment AR occurred 7.6 ± 0.95% of the time, and FM occurred 22.2 ± 6.15% of the time. Conversely, for the LP – LP-h treatment (Figure 5, See "Video S4 LP – LP-h" in Supplementary material, sped up 4x), the highest expression of the FM behaviour was observed. FM increased from 4% to 48% in the first 30 s (t_0 – t_1) and exceeded 60% from t_2 to t_{20}, reaching 92% at t_{11} and from t_{17} to t_{20} (Figure 5, LP – LP-h). The behaviour occurrences described above met those of the TC-MM values (Figure 6 B). Both the prey and the homogenate supernatant had significant effects on the cumulative number of TC-MM, as well as their interaction (two-tailed two-way-ANOVA, Table S1 in the Supplementary material). The significant results of the *post hoc* Tukey's test for multiple comparisons highlighted the differences among groups and treatments (Table S2 in the Supplementary material). The combination LP – LP-h triggered the highest number of TC-MM over the observation period (107.8 ± 10.85), which proved to be significantly different from all the other prey–prey homogenate supernatant combinations (two-tailed Welch's test: $W_{4.67} = 6.44$, $N_1 = 5$, $N_2 = 40$, $p = .002$), and more than doubling the TC-MM elicited by the LP-h on SP and cSP polyps (51.2 ± 11.05 and 48.4 ± 14.05, respectively; Welch's test: $W_{8.0} = 3.66$, $N_1 = N_2 = 5$, $p = .007$ and $W_{7.52} = 3.35$, $N_1 = N_2 = 5$, $p = .011$). This indicated that the homogenate supernatant of the large prey was mostly detected by LP polyps and had no different effects from those from cSP-h for SP and cSP polyps (Welch's test: $W_{23} = 1.53$, $N_1 = 10$; $N_2 = 15$; $p = .14$). The SP-h caused no feeding excitement, with a similar number of TC-MM to those of the WF injection (Welch's test: $W_{23.13} = -0.14$, $N_1 = N_2 = 5$; $p = .888$) and of the NO-h (Welch's test: $W_{6.86} = -0.36$, $N_1 = N_2 = 5$; $p = .728$).

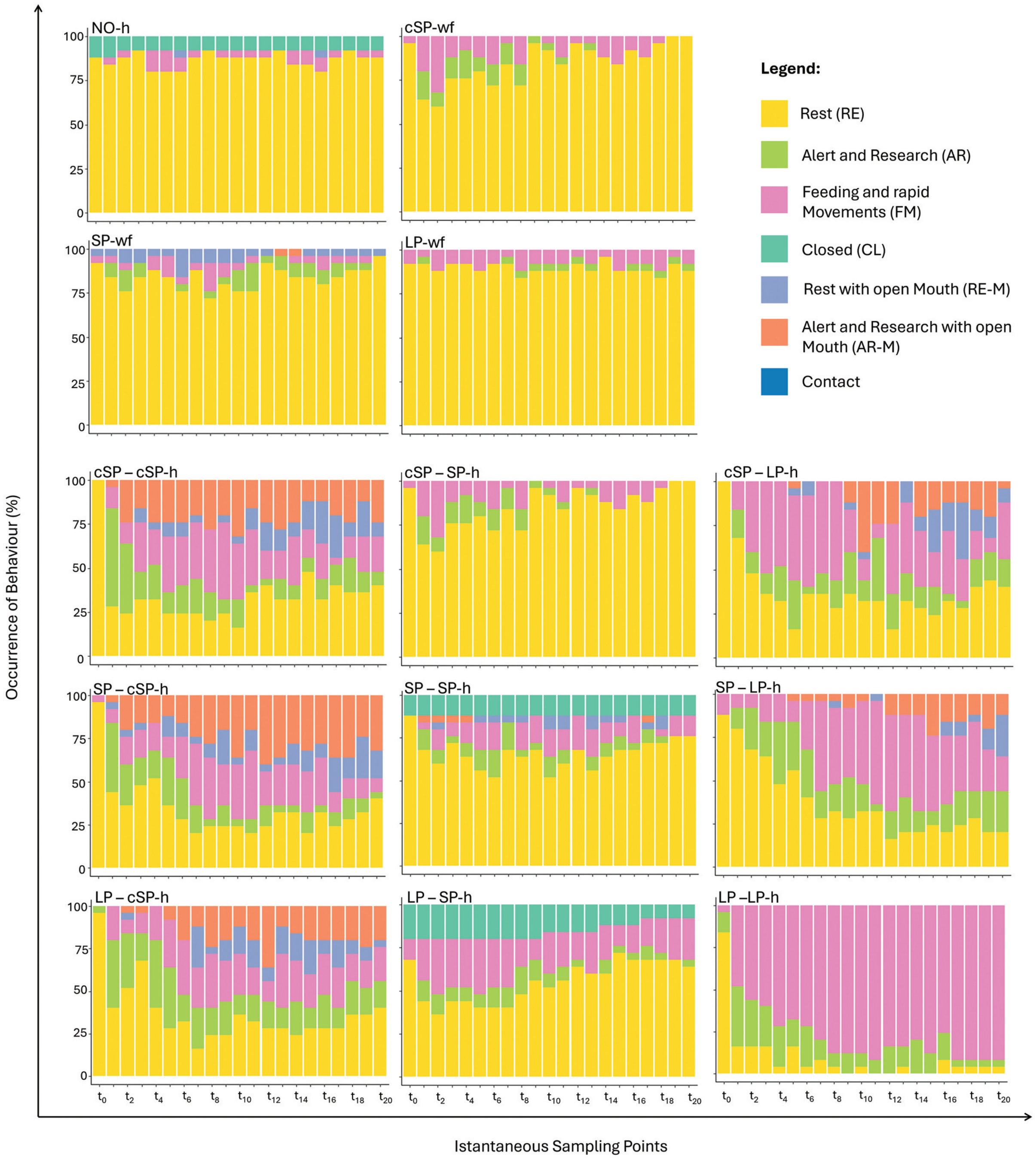

Figure 5. Charts representing the occurrence of alternative behaviours (%, y-axis) following no external stimulation (NO-h), the injection of water flow (WF) or the injection of prey homogenate supernatants (__-h), over the 10 min direct observation period (x-axis). The alternative types of behaviour were RE, rest; AR, alert and research; FM, feeding and rapid movements; RE-M, rest with open mouth; AR-M, alert and research with open mouth; CL, closed. NO-h = polyps do not receive food or homogenate; cSP = polyps fed upon control small prey (*Artemia salina*); SP = polyps fed upon small prey (*Brachionus plicatilis*); LP = polyps fed upon large prey (*Syllis prolifera*); LP-h = large prey homogenate supernatant; SP-h = small prey homogenate supernatant; cSP-h = control small prey homogenate supernatant.

The multivariate RM-ANOVA based on the Pillai's trace as statistics highlighted significant effects of time (10 min observation period) and treatment (prey–prey cue) (Table S3 in the Supplementary material). Further planned comparisons were made to answer specific questions referred to the response of polyps to the large prey-homogenate supernatant (Table 4), hereafter summarized. Polyps that received the LP-h reacted differently from those in the NO-h group ($t_{1,40} = 33.04$, $p < .001$), but the times required for the reactions

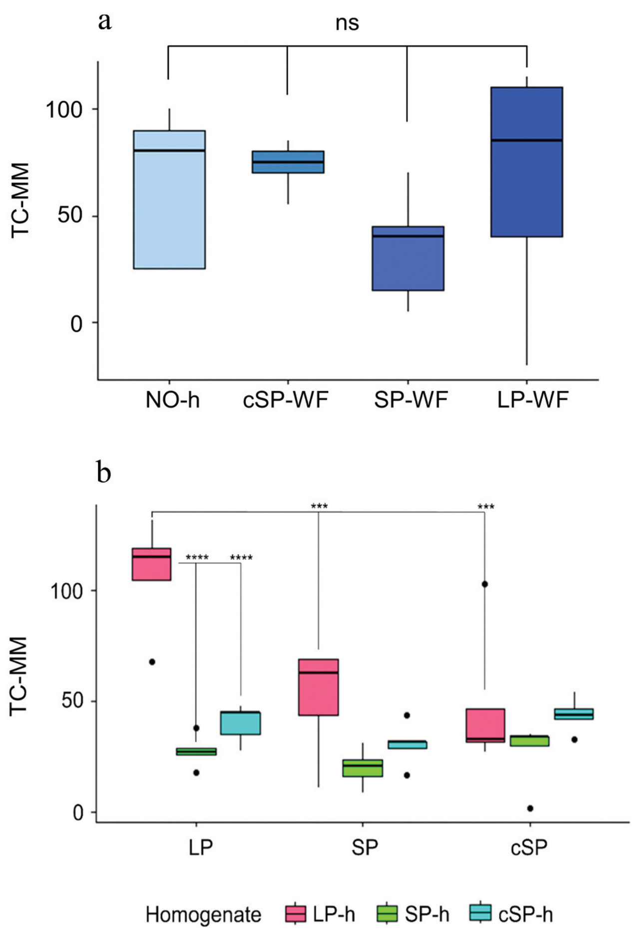

Figure 6. Box plots indicating the total number of tentacle contractions and rapid movements (TC-MM, y-axis) counted during 10 min of direct observation in polyps subjected to different treatments (x-axis). a) comparison between TC-MM of the NO-h group and the water flow treatments. NO-h = polyps did not receive food or homogenate; cSP = polyps fed upon control small prey (*Artemia salina*); SP = polyps fed upon small prey (*Brachionus plicatilis*); LP = polyps fed upon large prey (*Syllis prolifera*); WF = water flow. b) number of tentacle contractions and rapid movements (TC-MM, y-axis) counted during 10 min of direct observation. On the x-axis, prey is reported (LP = large prey; SP = small prey; cSP = control small prey). LP-h = large prey homogenate; SP-h = small prey homogenate; cSP-h = control small prey homogenate). *** = $p \leq .001$ and **** = $p \leq .0001$; ns = not significant. Horizontal bars indicate the median of the groups, the boxes indicate the 95% dispersion of data, and the vertical bars indicate the standard errors, SE.

Table 4. Experimental questions tested though planned comparisons, highlighting the significant differences in FM behaviour between experimental groups in relation to the times of observations.

Experimental question	t-test	Planned comparisons	*p* value	Answer
Do polyps react to LP-h?	NO-h vs. LP-h	All sample points considered	**< .0001**	Yes
How much time is required to see the reaction?	cSP – LP-h	t_0 vs. first time showing significant differences	t_0 vs. t_1: **.04**	30 s
	SP – LP-h		t_0 vs. t_7: **.0006**	3 min and 30 s
	LP – LP-h		t_0 vs. t_1: **.0008**	30 s
Do the polyps of different treatments react in the same way?	LP – LP-h vs. cSP – LP-h	All except t_0	**.0003**	No
	LP – LP-h vs. SP – LP-h		**.0006**	No
	cSP – LP-h vs. SP – LP-h		.84	Yes

Note: Significant p-values are reported in bold. NO-h = no food or homogenate; cSP = polyps fed upon control small prey (Artemia salina); SP = polyps fed upon small prey (Brachionus plicatilis); LP = polyps fed upon large prey (Syllis prolifera); LP-h = large prey homogenate supernatant; SP-h = small prey homogenate supernatant; cSP-h = control small prey homogenate supernatant. Combinations of prey - homogenate are consultable in Table I.

were different at each treatment level. In particular, polyps that fed on cSP and LP reacted immediately (t_0 vs. t_1: $t_{1,40} = 4.67$, $p = .037$ and $t_{1,40} = 13.17$, $p = .001$, respectively), while polyps that fed on SP reacted after 3.5 min(t_0 vs. t_7: $t_{1,40} = 13.97$, $p = .0006$). In contrast, LP – LP-h polyps performed the FM behaviour in a significantly different way with respect to polyps in the cSP – LP-h group ($t_{1,40} = 15.52$, $p = .0003$) and SP – LP-h ($t_{1,40} = 13.94$, $p = .0006$) groups, while the latter two groups did not differ from each other ($t_{1,40} = 0.043$, $p = .838$).

To summarize, the strongest response in terms of FM and TC-MM behaviours was performed by polyps of the combination "LP – LP-h". It was followed in intensity by the reactions triggered by LP-h on the groups SP and cSP as well as by cSP-h on all experimental groups. Finally, the weak reaction in response to SP-h was comparable to those of the WF and no external stimuli (NO-h) groups.

4. Discussion

The outcomes of our observation show that polyps of *Aurelia coerulea* engage in seven feeding/behavioural patterns, each characterized by different movements of tentacles, calyx, oral disc and mouth. The predatory behaviour of *A. coerulea* polyps comprised the capture of the prey through the tentacles and the active transport of the prey inside the gastric cavity, with distinct actions exerted on the small versus large prey. The pre-feeding behaviour, equal for all polyps, consisted mostly in resting, with erected calyx, closed mouth and extended tentacles occasionally moving slowly in the water. In case of micro-predation, one tentacle was employed to bring a single nauplius to the mouth, swallowed in a few seconds. More nauplii could be ingested by one polyp, thanks to the independent movement of the tentacles that allowed simultaneous captures. In contrast, the macro-predatory behaviour involved many tentacles acting simultaneously on the same large prey, to grab and pull it towards the gastric cavity through the mouth, together with rapid movements of the calyx and contractions of the oral disc in a sort of predatory conflict. This behaviour allowed the polyps to entirely swallow the prey in 5–15 min. These observations are in line with previous descriptions of micro-predatory behaviour (Reimer, 1973, Kaliszewicz, 2013, Geertsma et al., 2022)) as well as of the more complex macro-predation (Sun et al., 2022). *Aurelia coerulea* polyps displayed a feeding behaviour similar to the bathyal sea anemone *Urticina* sp. Ehrenberg, 1834 while capturing large prey (up to 25 cm in diameter) such as the brittle stars of the genus *Gorgonocephalus* Leach, 1815 and the sea urchin *Strongylocentrotus pallidus* (Sars , 1872), requiring up to 35 min for the complete engulfment (Sun et al., 2022). In the presence of spatial proximity among polyps, collective predation may occur to capture the large prey. Collective predation implies two or more polyps acting simultaneously on the same prey, and often comprises physical interaction among polyps that merged their oral discs in a sort of competitive interaction to divide the prey. The contact between two or more polyps (or colonies) is common during competitive interactions for space (Chadwick, 1987, Hennessey & Sammarco 2014, Rabelo et al., 2013)), or for food (Gröndahl, 1989, Kaliszewicz, 2013), often associated with aggressive behaviour (Ayre & Grosberg, 1995) During two different field surveys, colonies of the Anthozoans *Parazoanthus axinellae* (Schmidt, 1862) and *Astroides calycularis* (Pallas, 1766) were observed by Cerrano et al. (2016) and Musco et al. (2018) respectively, while feeding on more than one large gelatinous prey (the jellyfish *Pelagia noctiluca* (Forsskål, 1775). These observations suggest that collective predation in cnidarian polyps roughly follows two distinct phases: a first stage in which polyps cooperate to seize and paralyse the large prey, followed by a second step characterized by competition among the involved polyps, with each one singularly trying to engulf, cut and ingest its own part of the bounty. The coexistence of cooperation and competition (defined as "coopetition" *sensu* Bouncken et al., 2015) allows researchers to overcome the classical interpretation of these actions as opposites, since both cooperators and competitors act to maximize the benefit (Klüh, 2022). While the proximity among polyps exacerbates the competition for food in suspension-feeding and micro-predation (Kaliszewicz, 2013), proximity among polyps is necessary for protocooperation to occur (Musco et al., 2018; Gregorin et al., 2022). Engaging in a long-lasting, energy consuming action aimed to capture and ingest the large prey could be counterbalanced by the higher nutritional value of the prey. Sun et al., (2022) reported a higher content of lipids and different fatty acid composition in the sea anemone *Urticina* sp., compared to *Actinostola callosa* (Verrill, 1882) and *Actinauge cristata* (Riemann-Zürneck, 1986), the former adapted to large prey predation and the latter two feeding mostly on small copepods, decapods, and molluscs. It is interesting to note that this kind of interaction occurs in highly related individuals, clones or belonging to the same colony (e.g. Gregorin et al., 2022) as well as in distinct colonies of the same species (e.g. Musco et al., 2018), reflecting on their inclusive fitness. The degree of relatedness of individuals interacting in such feeding events could influence the benefits on the overall fitness of the population. Gregorin et al. (2024b) found that *A. coerulea* polyps grow significantly more when fed with the large prey compared to those feeding on the mesoplankton prey, reflecting on the asexual reproduction rate and, potentially, on the population dynamics not only of the benthic phase but also on the medusa stages. Regarding feeding stimulation, different responses were observed in polyps, suggesting that they effectively discerned the prey cue. The most eliciting cue was represented by the homogenate of the polychaete, followed by that of *Artemia salina*. The homogenized rotifer *Brachionus plicatilis* did not induce a response in polyps. The polychaete homogenate triggered changes in the behaviour of all polyps, with larger response in polyps previously fed with the polychaete. In the sea, chemical signalling is of pivotal importance in shaping and affecting individual behaviours and population dynamics, from unicellular microalgae to more complex multicellular organisms, acting directly on physiological processes such as feeding, mating, competing, and hiding, and lastly influencing community organization and ecosystem functioning (Hay, 2009, Kamio & Derby, 2017). For instance, prey-produced peptides of various types, as well as other primary metabolites such as sugars, respiration products, and metabolic waste compounds, attract generalist consumers that benefit from the detection of prey products for feeding (Hay, 2009; Schaum et al., 2013). In the case of predation, the release of prey-molecules could occur due to its wounding, eliciting the detection of the prey by neighbour predators as well as representing an alarm signal detected by conspecifics, which allows them to promptly respond with risk-avoidance behaviours (Hay, 2009; Schaum et al., 2013). As well, prey organisms can detect predators through their metabolites, as in the case of the burrowing polychaetes *Hediste diversicolor* (Schaum et al., 2013) and *Neanthes virens* (Watson et al., 2005), which can smell the predators via chemical cues and anticipate or prolong the time of retraction in its tube. Former studies on cnidarians demonstrated changes in behaviours related to the chemical stimulation, that also reflected on the external morphology. Ewer and Fox (1947) reported *Hydra* polyps undergoing a “feeding reaction” in the presence of the prey juice, driven by the neuromuscular system, and not involving the discharge of nematocysts. The authors described tentacles that “writhe and twist towards the mouth, while the mouth itself opens widely” (367). Later, Rushforth and Hofman (1972) referred to these peculiar movements of tentacles as “concerts”. Loomis (955) hypothesized that the feeding reaction was driven by a hormone (reduced glutathione, GSH), produced by living animals after being stung by cnidocytes. Fulton (1963), Reimer (1973) and Yamamori (2012) observed feeding reactions in response to the amino acid proline in polyps of *Cordylophora* Allman, 1844, *Calliactis polypus* (Forksål, 1775) and *Aurelia* sp., respectively. During our test, the enlargement of the oral rim (RE-M), often occurring together with tentacle concerts (AR-M), was reported in polyps receiving *A. salina* and *S. prolifera* homogenates. In the presence of these prey cues, polyps “melted” and lost the column shape of the calyx, occasionally turning the mouth upside-down to attach the lip on the glass bottom. The loss of the cylindrical shape of the calyx to a “pancake” shape and the turning of the mouth were both observed by Loomis (1955) in *Hydra vulgaris* Pallas, 1766 (cited as *H. littoralis*), the latter considered as the first phase leading to body-eversion used for waste discharge after feeding (Miglietta et al., 2000). Another hydroid, *Perarella schneideri* (Motz-Kossowska, 1905), settling on bryozoan epidermis, was described adhering the oral rim to it and, in this case, it was considered as a trophic strategy (Bavestrello et al. 2000).

Polyps that experienced the large polychaete as prey showed a distinctive selective response to the large prey homogenate (LP – LP-h), exhibiting the highest occurrence of active feeding, tentacle contractions and rapid movements. This reaction resembled the macro-predatory behaviour needed to capture the large prey. Polyps did not assume the “pancake” shape or evert their body, and RE-M and AR-M were absent as well as concerts. Instead, polyps brought more than one tentacle (often, all of them) inside the mouth, maintaining that position during the whole observation period, changing the calyx orientation, and contracting the mouth very fast. This specific response was elicited by the detection of the prey cue instead of tactile stimulation due to physical encounter. The different behavioural observation obtained during this study may indicate that polyps can actively discern the prey by detecting its molecules and suggests that their feeding behaviour is adjusted according to the type of prey.

Learning abilities are widely recognized in benthic cnidarians, which respond in several ways to different types of stimuli, including olfactive (Allabach, 1905, Ross, 1965), tactile (Johnson & Wuensch, 1994; Watson et al., 2000), electric (Pantin, 1935, Wilson, 1959, Haralson et al., 1975, Botton-Amiot et al., 2023)) and mechanical (Wagner, 1905, Logan, 1975, Logan & Beck 1977). The wide spectrum of responses displayed by polyps includes contraction (Pantin, 1935; Rushforth et al., 1963), mouth movements (Ross, 1965, Hodgson, 1981), escape (Wagner, 1905, Wilson, 1959), extension of body parts, and acrorhagial response together with nematocyst release to show aggressive behaviour (Ayre & Grosberg, 1995). Aggression could be addressed to a single individual, either conspecific or belonging to a different species, and eventually decreases when the polyp becomes accustomed to the new neighbour (Sauer et al., 1986; Brace & Santer, 1991, Ayre & Grosberg, 1995). The selective response of cnidarians to stimulation, for instance by opening the oral rim (Reimer, 1973), showing habituation (i.e. decrease of responsiveness) and sensitization (i.e. facilitation of response), is referred to as non-associative learning and involves the nervous system (Schakner & Blumstein, 2016).

5. Conclusion

In conclusion, our results indicate that prey cues have a role in the detection of different organisms by polyps. The response to feeding cues was represented by changes in behaviour of polyps in relation to the specific prey, since polyps behaved differently when stimulated with rotifer, brine shrimp or polychaete homogenates. Moreover, the previous feeding experience seems to be influential, because the behaviour of polyps fed with distinct preys was different even with the same nature of homogenate provision. These findings suggest that the processing of cue information could occur within the nervous system, relating to learning capacity based on previous feeding experience. Little is known on the prey–predator relationship between benthic cnidaria and organisms larger than their individual size that can also involve cooperation among individuals and that is performed through a different behaviour compared to micro-predation and suspension-feeding. In short, the action of polyps, either solitary or collective, could be elicited by the contact between the prey and the polyp tentacles, although prey cues experienced and memorized during past predation events might play an important role. When polyps are spatially closed, the collective response to the detection of the prey cue could lead them to engage in collective predation. These learning skills allow cnidarians to recognize the prey and to engage the most appropriate behavioural strategy to capture it, with the potential aim of maximizing benefits and minimizing costs. Moreover, as this capacity is shared within the population, it could lead polyps and colonies to coordinate in the collective predation. However, our suggestions are based on ethological observations, and more studies on the nature and functioning of chemical signalling in benthic cnidarians are required. Further *ad hoc* experiments are needed to evaluate the insurgence of habituation or sensitization processes, and the ability of memory retention in organisms subjected to a diet shift after a first prey experience.

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Disclosure statement

The authors declare that they do not have any conflict of interest.

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Author contributions

Conceptualization: Chiara Gregorin, Tomás Vega Fernández, Luigi Musco, Stefania Puce; investigation: Chiara Gregorin; data analysis: Chiara Gregorin, Tomás Vega Fernández; resources: Federico Domenichelli, Stefano Gridelli; writing – original draft preparation: Chiara Gregorin; writing – review & editing: Tomás Vega Fernández, Federico Domenichelli, Stefano Gridelli, Luigi Musco, Stefania Puce; project administration and supervision: Stefania Puce; Luigi Musco.

Data availability statement

Data are available to anyone interested by contacting the corresponding author.

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