

Reduction of small-prey capture rate and collective predation in the bleached sea anemone *Exaiptasia diaphana*

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ABSTRACT

Cnidarians may dominate benthic communities, as in the case of coral reefs that foster biodiversity and provide important ecosystem services. Polyps may feed by predating mesozooplankton and large motile prey, but many species further obtain autotrophic nutrients from photosymbiosis. Anthropogenic disturbance, such as the rise of seawater temperature and turbidity, can lead to the loss of symbionts, causing bleaching. Prolonged periods of bleaching can induce mortality events over vast areas. Heterotrophy may allow bleached cnidarians to survive for long periods of time. We tested the reinforcement of heterotrophic feeding of bleached polyps of *Exaiptasia diaphana* fed with both small zooplankton and large prey, in order to evaluate if heterotrophy allows this species to compensate the reduction of autotrophy. Conversely to expected, heterotrophy was higher in unbleached polyps (+54% mesozooplankton prey and +11% large prey). The increase of heterotrophic intake may not be always used as a strategy to compensate autotrophic depletion in bleached polyps. Such a resilience strategy might be more species-specific than expected.

1. Introduction

Cnidarians display a high diversity of feeding behaviours, thus being able to rely on a variety of food resources (Dubinsky and Achituv, 1990; Houlbrèque and Ferrier-Pagès, 2009). Benthic species obtain heterotrophic carbon through the ingestion of waterborne prey (from pico-to mesozooplankton), by absorbing dissolved organic nutrients (Houlbrèque and Ferrier-Pagès, 2009; Geertsma et al., 2022), or by capturing larger animals by active use of their tentacles and pulling the prey inside the mouth (Bos et al., 2011). The latter mainly include benthic fauna (Kruger and Griffiths, 1996; Bos et al., 2011; Ivanova and Grebelnyi, 2017; Sun et al., 2022) and gelatinous macrozooplankton hereafter referred to as jellyfish (medusae, ctenophores and salps) (Fautin and Fitt, 1991; Gili et al., 2006; Hoeksema et al., 2015; Mehrotra et al., 2016; Canovas and Gonzalez-Wanguemert, 2018). In oligotrophic

shallow waters, many cnidarian species establish a facultative mutualistic relationship with dinoflagellates, mainly belonging to the family Symbiodinaceae (LaJeunesse et al., 2018). Microalgae endosymbionts provide the host polyp with photosynthetically fixed carbon, contributing to the energy budget of the heterotrophic animal, which becomes mixotrophic (Allemand and Furla, 2018). Heterotrophy is the way to obtain all the organic carbon in non-symbiotic species (Houlbrèque and Ferrier-Pagès, 2009). In contrast, heterotrophy provides only 15–35% of the organic carbon in mixotrophic tropical corals (Mehrotra et al., 2019). Conversely to the suspension-feeding, where the food particles are carried by water flow (Kaliszewicz, 2013; Geertsma et al., 2022), the capture and ingestion of a large prey involves numerous tentacles, the engulfment of the prey in the gastric cavity, the digestion, and the eventual rejection of remains (Sun et al., 2022; C.G. pers. obs.). The size of polyps and their oral diameter do not influence predation: both

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large-mouthed corals (Mehrotra et al., 2016) and those with relatively small polyps have been reported while ingesting large jellyfish. When small polyps live in proximity to each other (i.e., in a colony or in a group), the large prey could be collectively captured through proto-cooperative interaction, involving the partitioning of prey after its capture (Musco et al., 2018). Colonial species or groups of free-living polyps can capture more than one prey simultaneously (Musco et al., 2018; Ter Horst and Hoeksema, 2021). Evidence indicates that jellyfish are among the most common large prey for anthozoans, their capture and ingestion being reported at several latitudes and depths (Dayton et al., 1970; Berryman, 1984; Jarms and Tiemann, 2004; Hoeksema and Waheed, 2012; Hoeksema et al., 2015; Mehrotra et al., 2016; Canovas and Gonzalez-Wanguemert, 2018; Musco et al., 2018; Ter Horst and Hoeksema, 2021; Gregorin et al., 2022). Several jellyfish species undergo seasonal increments of population density, periodically oscillating from a few to thousands of individuals (Bosch-Belmar et al., 2020). Reports on jellyfish blooms are noticeably increasing in frequency worldwide (Purcell et al., 2007; Báez et al., 2022). Exceptional jellyfish outbreaks are likely promoted by some anthropogenic impacts on the marine environment (e.g., eutrophication, warming of sea water, spreading of submersed artificial substrates, depletion of fish stocks), which mostly occurs in coastal areas (Purcell et al., 2007; Ghermandi et al., 2015). Jellyfish may eventually be carried ashore by the action of currents and wind (Reyes Suárez et al., 2022), there becoming a food resource for coastal species inhabiting the intertidal and subtidal zones (e.g., Canovas and Wanguemert, 2018; Musco et al., 2018; Ter Horst and Hoeksema, 2021). In the open sea, jellyfish can sink onto the seafloor ("jelly-fall"), transferring nutrients from the upper layers to deep ecosystems (Sweetman and Chapman, 2015), where darkness and low temperature hinder photosynthesis by endosymbionts. Large-prey predation could be considered an adaptive trait in anthozoans, substantially contributing to the supply of heterotrophic carbon (Sun et al., 2022). Human activities also directly influence the benthic communities inhabiting the marine coastal areas (Crain et al., 2009; Heery et al., 2018; Bevilacqua et al., 2021). Extreme increases of sea surface temperatures such as marine heatwaves (Oliver et al., 2021) and long-lasting turbidity events due to resuspension of fine sediments caused by e.g., dredging, beach nourishment, coastal construction (Thomas et al., 2003; Erfemeijer et al., 2012; Caballero et al., 2018) induce damage both to anthozoans and to the photosystems of endosymbionts, hindering the supply of autotrophic nutrients, and leading to the break of the symbiotic bond (Szabó et al., 2020). The expulsion or death of endosymbionts from the host tissue leads to their paling to a whitish colour, referred to as "bleaching" (Van Oppen and Lough, 2018). This process could affect all organisms hosting endosymbionts, including corals and sea anemones (Hobbs et al., 2013). Often, bleaching anticipates the deterioration and death of the host species, eventually provoking mass mortality over vast areas, with severe consequences on the eco-system and its biodiversity (Anthony et al., 2009; Levas et al., 2016; Eakin et al., 2019). The recovery of impacted anthozoans is more likely to occur when the stress is exerted for brief periods of time (Anthony et al., 2009; Guest, 2021), although it could be hindered by the synergistic effect of predation exerted on corals by corallivorous taxa (Hoeksema et al., 2013; Moerland et al., 2016; Saponari et al., 2018, 2021; Rice et al., 2019). The intensification of heterotrophic carbon acquisition could allow bleached anthozoans to counterbalance the decrease in the supply of photosynthesized nutrients. Hence, the intensification of the heterotrophic carbon pathway can contribute to the resilience of some coral species (Grottoli et al., 2006; Hughes and Grottoli, 2013). The aim of the present work was to assess the differences in the heterotrophic feeding rate (both suspension-feeding and large-prey predation through proto-cooperation) by unbleached and bleached individuals of the pale sea anemone *Exaiptasia diaphana* (Rapp, 1829) (Actinaria, Aiptasiidae), also represented by *Exaiptasia pallida* (Agassiz in Verrill, 1864) considered a suitable model organism for microalgae-cnidarian symbiosis (Weis et al., 2008; Matthews et al.,

2017; Sproles et al., 2019; Dungan et al., 2020). According to Weis et al. (2008), this species is directly comparable to corals for studies on symbiotic relationships. Bleaching can be artificially induced, and the concentration of endosymbionts could recover to the normal condition following the removal of the sources of stress (Grottoli et al., 2006). Moreover, this species has a worldwide distribution (Grajales and Rodríguez, 2016) and possesses a fast growth and asexual reproduction rate, allowing it to rapidly produce clonal populations (Lehnert et al., 2012). We hypothesize that both heterotrophic modalities (i.e., small-mesozooplankton prey capture, and collective large-prey predation) should be reinforced in bleached individuals.

2. Materials and methods

2.1. Selection of experimental organisms

Exaiptasia diaphana polyps (100 individuals) were sampled by detaching them from the tanks of the Cattolica aquarium (Cattolica, RM, Italy), transferred at the Zoology Laboratory of the Polytechnic University of Marche in tanks filled with Filtered Sea Water (FSW, filtered with mesh net 0.22 μm), at 24 ± 1 °C temperature, 35.0 ± 1.0 Practical Salinity Unit (PSU). In the lab, they were fed three times per week with nauplii of the brine shrimp *Artemia salina*. After the acclimation and the selection of suitable individuals (based on similar body size), bleaching was artificially induced by keeping the sea anemones in the dark for 45 days to exacerbate the negative effects of low-light exposure on endosymbionts. The unbleached anemones were reared with a 12h:12h light/dark cycle, with a 6.3 W LED light source (Amtra Orion LED IPX4) (Fig. 1a). Periodically, the tissue colour of unbleached and bleached anemones was checked with the protocol "Coral Watch – Coral Health Chart" (<https://coralwatch.org>). After 45 days of different light regimes, unbleached anemones corresponded to C5 or C6 category, while bleached ones corresponded to C2 (Fig. 2). To ensure that the loss of endosymbionts did not compromise the health status of all individuals, they were visually checked referring to Dungan et al. (2022). After that, three individuals for each condition were weighed and measured (mouth disc diameter, MDD) to ensure homogeneity of their sizes, and to proceed with the evaluation of the endosymbiont concentration in their tissue. Each sea anemone was pestled and resuspended in a 1.5 ml-Eppendorf vial with 1 ml of FSW and centrifuged at 5000 rpm for 5 min. The so-obtained pellet containing endosymbiont was resuspended in 1 ml FSW (0.22 μm) (Roveta et al., 2023). Evaluation of endosymbionts concentration was estimated by counting cells contained in 10 μl of solution, using a Neubauer hemocytometer (BRAND Tiefe Depth Profondeur 0.100 mm, 0.0025 mm²).

The jellyfish *Aurelia* sp. was used as prey for the evaluation of large-prey predation through proto-cooperation in groups of unbleached and bleached anemones, by virtue of its body length ranging from 5 to 20 or more times larger than the average size of *E. diaphana*. Specimens were either provided by the Cattolica aquarium or collected in the Varano Lake (SE, Italy), where frequent *Aurelia* outbreaks occur (Scorrano, 2014). Based on the average size of the collected sea anemones, 10 individuals of 8 ± 1 cm length were transferred to the laboratory in thermostated containers together with water from the sampling location, to reduce possible stress due to potential differences in water temperature and salinity.

The brine shrimp *A. salina* in its naupliar stage, was used as rearing food for 45 days, and to test the - small-prey capture rate in unbleached vs bleached sea anemones. Cysts of *Artemia salina* can easily be obtained from aquarium and aquaculture markets and used as food for the rearing of cnidarian species in captivity (e.g., Hii et al., 2009). The cysts were rehydrated in 600 mL of FSW at 24 °C and let to hatch after 36–48 h. Newly hatched phototactic nauplii were concentrated under a light source, washed with fresh FSW, filtered through a net (mesh size 200 μm), and provided to the sea anemones.

Before the start of each experiment, sea anemones were selected on

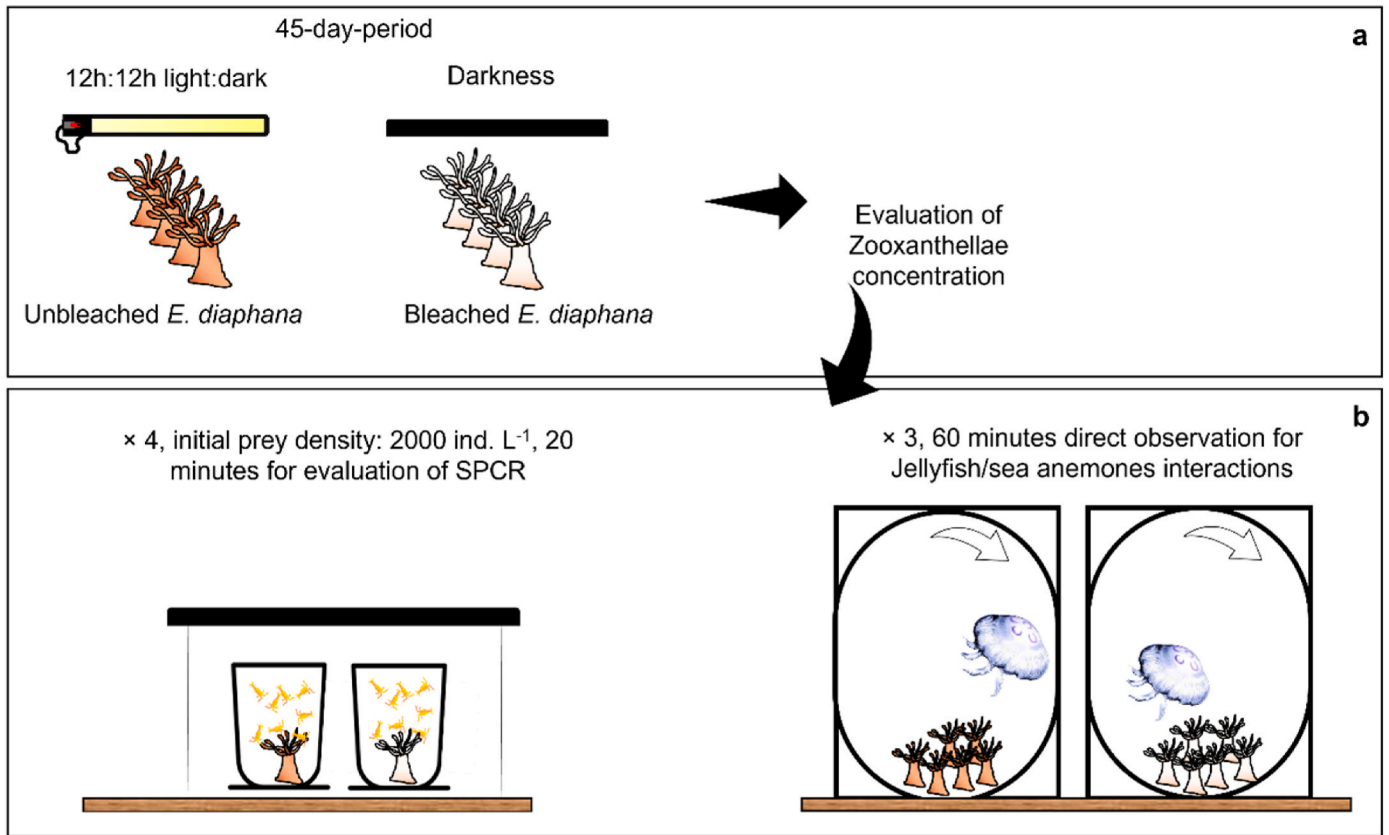


Fig. 1. (a) 45-day-period of light:dark cycle and darkness in order to obtain unbleached symbiotic *Exaiptasia diaphana* sea anemones, and bleached ones after loss of microalgal symbionts. The 45-day-period was assessed through visual evaluation of bleaching status and followed by the measurement of endosymbionts concentration in the tissue of the sea anemones; (b) Graphical representation of the experimental set-up: four replicates of unbleached and bleached sea anemones were used to estimate the small-prey capture rate (SPCR), while three replicates of six grouped sea anemones were tested for the predator-prey interactions with the jellyfish, in a circular tank equipped with slow water flow.

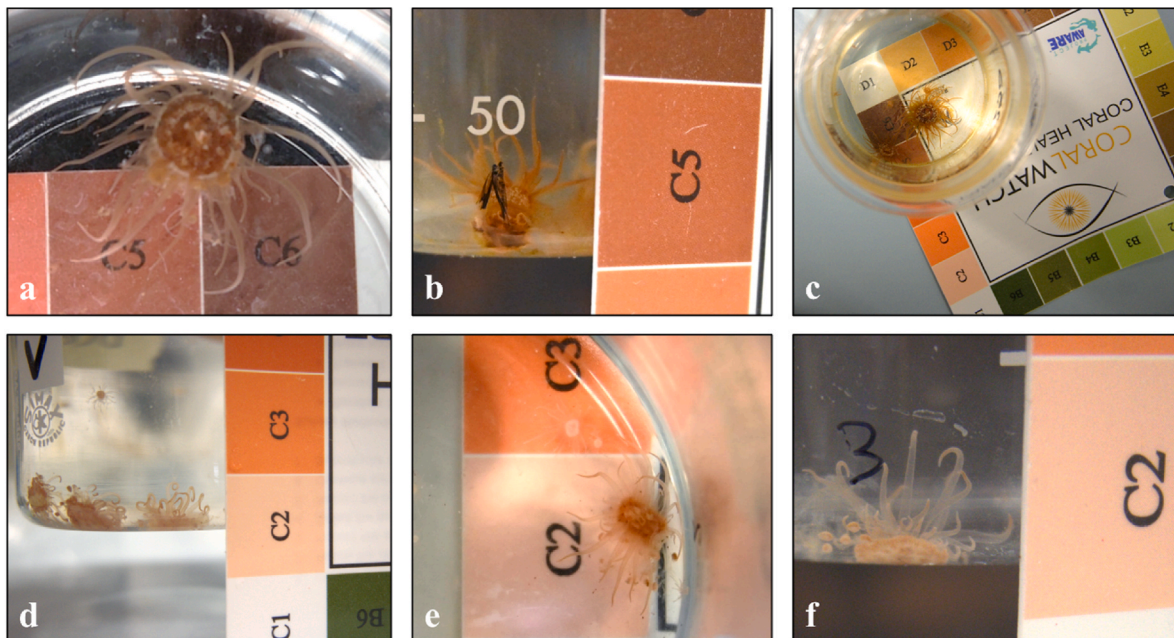


Fig. 2. (a, b, c) Unbleached and (d, e, f) bleached individuals of *Exaiptasia diaphana*, in comparison with the colours of the categories of the Coral Watch Coral Health Chart for the evaluation of tissue bleaching. Unbleached sea anemones referred to the class C5–C6, whilst the bleached ones referred to the class C2/C3 (tentacles/body).

the base of similar MDD, photographed (Nikon Z50 + Nikkor Z DX 16–50 mm f/3.5–6.3 VR), and measured using ImageJ software (Rasband, 2012).

2.2. Evaluation of the small-prey capture rate

To test the small-prey capture rate (SPCR), four unbleached and four bleached individuals were let to settle each one in a 200-ml-volume glass bowl filled with 140 mL of FSW. The sea anemones were allowed to acclimate for 30 min after settlement. At the beginning of the test, 280 *A. salina* nauplii were provided to each polyp in 140 mL of FSW (initial density: 2000 ind. L⁻¹). All individual sea anemones were kept under a black plastic box to ensure darkness. This adaptation was necessary to allow the phototactic nauplii to distribute homogeneously in the available space in the bowl. The suspension feeding was calculated over 20 min (Fig. 1b). Afterwards, the 140 mL FSW water were filtered (200-µm mesh net), the remaining *A. salina* nauplii were recollected and counted, to measure the final density. SPCR was calculated with equation (1) (Hii et al., 2009):

$$SPCR = \frac{D_i - D_f}{\text{Polyps} \times \text{Time}} \quad (1)$$

Where SPCR = small-prey capture rate, D_i = initial prey density (ind. L⁻¹), D_f = final prey density (ind. L⁻¹), Polyps = number of sea anemones feeding, Time = time provided for feeding (minutes).

2.3. Collective predation of large prey

To test the effort of collective predation upon large jellyfish by unbleached and bleached *E. diaphana* polyps, 18 unbleached and 18 bleached individuals with similar MDD were selected. Three replicates were tested for each condition ($n = 3$). Each replicate was constituted by a group of six polyps, which were placed on a 4 × 4 cm² plastic tile, left to settle, and photographed to measure their inter-individual distance (Fig. 1b). The six tiles (three for unbleached condition plus three for bleached condition) carrying the group of six individuals were kept separated during settlement, acclimation, and predation test. In addition to MDD, inter-individual distances were measured prior to starting the experiment to ensure that individual sea anemones were similarly distant to each other. For the predation test, the first tile was inserted onto a plastic support and fixed into a circular tank with water in slow motion, and sea anemones were allowed to acclimate for at least 30 min before providing the group with the large prey. One jellyfish of 8.0 ± 1.0 cm (prey/predator size ratio of ca. 10/1) was entered into the circular tank and the test was run for 1 h. The observation time was decided based on previous experience involving *Astroides calycularis* (Pallas, 1766) *E. diaphana* and to maintain a short experimental period. After 1-h observation, the first tile was removed and replaced by the second, then followed by the third. Each trial was independent from the others. The interaction between the jellyfish and the group of polyps were categorized as (1) No Response: the jellyfish touched the sea anemones while passing over them, they did not react or reacted in a negative way, i.e., by retracting tentacles and body, and avoiding contact; (2) Short Contact: the jellyfish touched the sea anemones while passing and they reacted in a positive way, i.e., trying to grab the prey by folding the tentacles (<60 s); (3) Long Hold: the sea anemones grabbed the prey and held it (>60 s), indicating that they may have started ingestion; (4) Ingestion: the sea anemones started to ingest the prey, parts of the jellyfish were visible inside the gastrovascular cavity of the sea anemones, this phase anticipated digestion and eventual rejection of prey remains; eventually, the body of the polyp became circular, tentacles were retracted and the mouth was closed.

2.4. Statistical analyses

Different response variables were selected to perform comparisons between polyps in the unbleached versus bleached experimental groups. After verifying compliance with the hypothesis of homogeneity of variance, Student's t-tests were used to compare MDD, weight and endosymbionts concentration in unbleached versus bleached sea anemones. Similarly, MDD of single polyps acting as replicates and their SPCRs were tested with Student's t-tests in the experiment for the evaluation of small-prey capture rate. A further analysis was made on both MDD, and inter-individual distances of polyps placed on the tiles, which served as replicates in the second experiment. For this analysis, 2-way Analysis of Variance (ANOVA) was carried out to assess differences within and between tiles. Finally, the type of behavior displayed by polyps between the experimental conditions was analysed by using Welch's test, verifying heterogeneity of variance. The Type I error rate (alpha) was set at 5% for all analyses.

Statistical analyses were performed with the R software environment 4.2.2 Ink (R Core Team, 2022), using the package *car* (Fow and Weisberg, 2019) for homogeneity test, *ggplot2* (Wickham, 2009) and *ggpubr* (Kassambara, 2023) for graphical representation of data.

3. Results

All individuals used for the tests (endosymbionts counts, SPCR, collective predation) corresponded to score 3 and 4 of the health scale proposed by Dungan et al. (2022), representing the best health condition. Exposure to dark conditions led to the expulsion of microalgal endosymbionts, as shown by the significant decrease in endosymbiont concentration (cell mL⁻¹) in bleached compared to unbleached anemones (Fig. 3a). unbleached The MDD and weight of polyps were not significantly different (*t*-test, $n = 3$, $t = 1.226$, $df = 4$, $p = 0.288$; $n = 3$, $t = -0.923$, $df = 4$, $p = 0.408$, respectively). On average, unbleached polyps measured 0.544 ± 0.03 cm [Mean ± Standard Error, SE] and 87.3 ± 2.96 mg; bleached individuals measured 0.501 ± 0.02 cm and 91.00 ± 2.65 mg. Unbleached anemones contained significantly higher concentrations of endosymbionts than bleached ones (unbleached: $7.25 \times 10^5 \pm 2.77 \times 10^4$ cell mL⁻¹; bleached: $1.75 \times 10^5 \pm 7.42 \times 10^4$ cell mL⁻¹; *t*-test, $n = 3$, $t = -6.952$, $df = 4$, $p = 0.002$). Unbleached These preliminary tests allowed to proceed with the evaluation of eventual differences in heterotrophic feeding among unbleached versus bleached sea anemones.

3.1. Evaluation of small-prey capture rate

The MDD was homogeneous between unbleached and bleached anemones (0.485 ± 0.04 cm and 0.434 ± 0.02 cm, respectively; *t*-test, $n = 4$, $t = 1.179$, $df = 6$, $p = 0.283$). unbleached. The density of *A. salina* nauplii provided to unbleached sea anemones passed from 2000 ind. L⁻¹ to 1183.93 ± 21.50 ind. L⁻¹ after 20 min, corresponding to the ingestion of 41% of the total number of nauplii provided and to a SPCR of 816.1 ± 21.05 ind. L⁻¹ × polyp⁻¹ × 20 min⁻¹. The density of *A. salina* nauplii provided to bleached polyps decreased from 2000 ind. L⁻¹ to 1560.79 ± 91.54 ind. L⁻¹, assessing a SPCR of 439.29 ± 91.54 ind. L⁻¹ × polyp⁻¹ × 20 min⁻¹, corresponding to 21.9% of total number of nauplii. The SPCR of unbleached versus bleached sea anemones was significantly different (Welch's test, $n = 4$, $t = 4.0058$, $df = 3.33$, $p = 0.023$) (Fig. 3b).

3.2. Evaluation of collective predation of large prey

The average MDD of the individuals selected for the trial was 0.75 ± 0.04 cm for unbleached and 0.70 ± 0.03 cm for bleached sea anemones, not significantly different from each other ($n = 6$, 2-way ANOVA, $F_1, 32 = 1.038$, $p = 0.316$) and within replicates of the same condition ($n = 6$, 2-way ANOVA, $F_2, 32 = 0.433$, $p = 0.652$). Once settled on the plastic tiles, the average distance of polyps was measured (unbleached: 1.60 ±

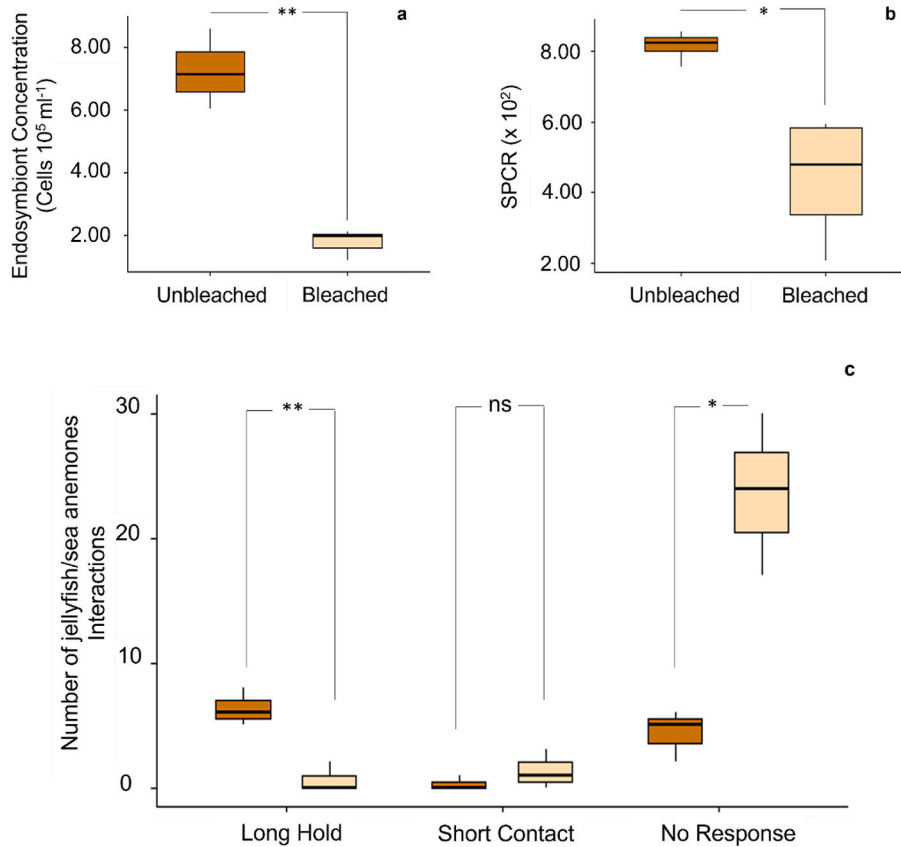


Fig. 3. Graphical representation of (a) e Endosymbionts concentration, (b) small-prey capture rate, SPCR and (c) the predatory responses of unbleached (dark brown) and bleached (light brown) sea anemones *Exaiptasia diaphana*. Asterisks indicate the significance level, where * = $p \leq 0.05$, ** = $p \leq 0.01$, ns = not significant. Boxes indicate the 95% data dispersion, horizontal bars indicate the mean of data, the vertical bars indicate standard error.

0.17 cm; bleached: 1.63 ± 0.11 cm), not different between conditions ($n = 6$, 2-way ANOVA, $F_{1, 32} = 0.292$, $p = 0.593$) nor within replicates of the same condition ($n = 6$, 2-way ANOVA, $F_{2, 32} = 0.155$, $p = 0.857$). During the 1-h direct observation of predatory interactions between the jellyfish and the group of sea anemones (Fig. 3c), the number of “No Response” were 4.3 ± 1.2 for unbleached and 23.7 ± 3.8 for bleached sea anemones (Welch’s test, $t = 4.902$, $df = 2.405$, $p = 0.027$); “Short Contacts” were reported as 0.3 ± 0.3 and 1.3 ± 0.9 for unbleached and bleached sea anemones respectively (Welch’s test, $t = 1.061$, $df = 2.56$, $p = 0.379$), while the number of “Long Holds” was 6.3 ± 0.9 for unbleached and 0.7 ± 0.7 for bleached sea anemones (Welch’s test, $t = -6.952$, $df = 4$, $p = 0.002$). Although the long holds performed by unbleached polyps possibly led to feeding, the “Ingestion” of the large prey or its parts was never reported. In two occasions, one and two polyps

(respectively), detached from the plastic tile and remained attached to the jellyfish for the whole observation period (Fig. 4). Results are summarised in Table 1.

4. Discussion

The prolonged darkness treatment caused the expulsion of microalgal endosymbionts and bleaching of tissues in the sea anemone *Exaiptasia diaphana*. Light limitation is known to represent a stress factor inducing bleaching in symbiotic coral species, as demonstrated for *Acropora millepora* (Ehrenberg, 1834), *Montipora capricornis* Veron, 1985 and *Porites* spp. Link, 1807, *Pocillopora damicornis* (Linnaeus 1758), *Turbinaria reniformis* (Bernard 1896), *Porites lobata* (Dana, 1846) and *Porites lutea* (Milne Edwards and Haime, 1851; Bessell-Browne et al.,

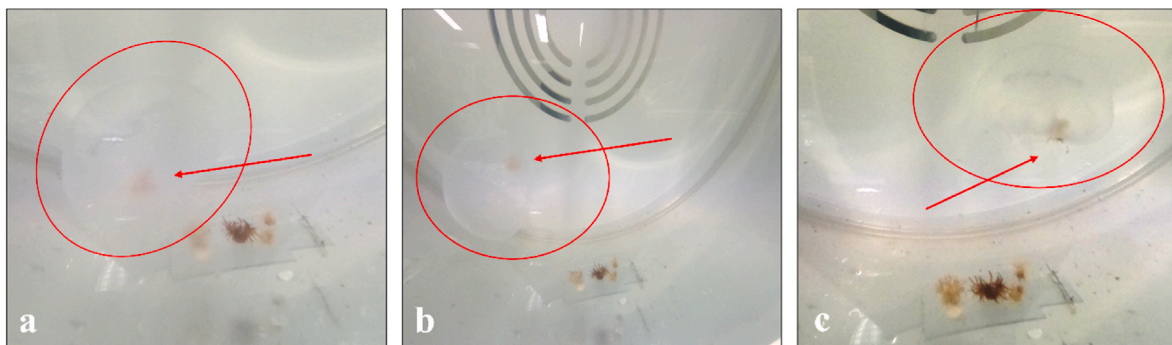


Fig. 4. (a) One polyp (red arrow) detached from the tile while capturing the prey. It remained attached to the jellyfish (indicated with the red circle) until the end of the observation (b, c).

Table 1

Interactions between grouped bleached vs unbleached sea anemones (n = 6) with the large prey *Aurelia* sp. NR = no response; SC = short contact; LH = long hold. SE = standard error. Results of statistical analysis (Welch's tests) are reported as p-values. Significant p-values ($p \leq 0.05$) are indicated in bold.

	Replicate	NR	Mean \pm SE	p-value	SC	Mean \pm SE	p-value	LH	Mean \pm SE	p-value
Bleached	R1	17	24.6 \pm 3.76	0.027	0	1.34 \pm 0.8	0.379	0	0.67 \pm 0.67	0.002
	R2	30			3			0		
	R3	24			1			2		
Unbleached	R1	5	4.34 \pm 1.2		0	0.34 \pm 0.34		6	6.34 \pm 0.88	
	R2	2			1			5		
	R3	6			0			8		

2017; Jones et al., 2020). Despite a 25% reduction in symbiont density upon a 6-week exposure to darkness, the bleached sea anemones tested in this study did not intensify heterotrophic feeding through the ingestion of the brine shrimp *A. salina*. Grottoli et al. (2006) and Palardy et al. (2008) induced starvation and bleaching in coral fragments of three species [*P. lobata*, *Porites compressa* Dana, 1846, and *Montipora capitata* (Dana, 1846)] by increasing temperature and water filtering ($>50 \mu\text{m}$) to exclude zooplankton, and, after bleaching, returned the fragments *in situ* to test their recovery after 2 weeks. Both the above mentioned studies revealed no differences in heterotrophic carbon acquisition between bleached and controls *P. lobata* and *P. compressa* and the increase in exogenous feeding in bleached *M. capitata*. These findings suggested that the two *Porites* species may rely predominantly on photoautotrophic nutrients to support recovery. Bleached *P. compressa* and *M. capitata* underwent a slow recovery that led corals to assimilate more heterotrophic carbon than unbleached controls 4 and 11 months after bleaching (Hughes and Grottoli, 2013). This latter study revealed that heterotrophic feeding is a recovery strategy of starved and bleached anthozoans, allowing the species resilience to future bleaching events (Hughes and Grottoli, 2013). Heterotrophy potentially stimulates the re-establishment of symbiosis, as demonstrated by the density increase of endosymbionts and chlorophyll *a* in the bleached coral *Orbicella faveolata* (Ellis & Solander, 1786) (Towle et al., 2015). Similarly, heterotrophy is positively related to lipid content in stressed *O. faveolata* and *Acropora cervicornis* (Lamarck, 1816) being thus considered an indicator of physiological health in coral species (Towle et al., 2015, 2017). The differences among species responses may depend on many factors such as the bleaching modalities and the recovery time. However, the response of Anthozoa species to bleaching and their recovery may also be species-specific (Palardy et al., 2008), and dependent on the peculiarities of the symbiotic association. The reef-building tropical corals are typically obligate symbiotic (Hiebert and Bingham, 2012), while *E. diaphana* establishes facultative symbiosis. Presumably, obligate symbiotic species rely on photoautotrophic nutrients for their energy demand, more than the facultative ones (Gundlach and Watson, 2019).

To the best of our knowledge, there are no reports about the extent of large-prey predation in artificially or naturally bleached anthozoan species, neither solitarily nor through proto-cooperation. Our findings suggest that proto-cooperative large-prey capture and ingestion was not an alternative to autotrophy in the provision of nutrients, since bleached *E. diaphana* polyps did not increase heterotrophy through proto-cooperation. Although unbleached sea anemones did not ingest the large prey, probably due to the observation time that was not sufficient for polyps of this species, the higher number of long holds of the jellyfish by the group of six unbleached *E. diaphana* compared to those of bleached ones, indicated the differences in large-prey predation effort. The high number of negative responses in the latter (e.g., by retracting the body in a "closed" position), confirmed this result. This outcome could be due to the high energy necessary during the early phases of the process of predation of a large prey (seizing, capturing, pulling towards the mouth). Unbleached sea anemones were able to detect the prey and engaged in proto-cooperative predation by grabbing it with tentacles for up to 8 min, whilst the bleached sea anemones mostly avoided contact with jellyfish. The ingestion of large prey is also a common feature

among Hydrozoa, with reports of the species *Hydractinia angusta* Har- tlaub, 1904; Cerrano et al. (2000) and *Perarella schneideri* (Motz-Kos- sowska, 1905; Bavestrello et al., 2000), Scyphozoa, e.g., *Aurelia coerulea* von Lendenfeld, 1884; Tang et al. (2020), and Anthozoa, such as Acti- naria (Dayton et al., 1970; Ivanova and Grebelnyi, 2017, Canovas and Wanguemert, 2018), Zoantharia (Cerrano et al., 2016; CG pers. obs.), Alcyonaria (Gili et al., 2006), Scleractinia (Mehrotra et al., 2016; Musco et al., 2018; Ter Horst and Hoeksema, 2021; Gregorin et al., 2022) and communication about the jellyfish *Pelagia noctiluca* (Forsskål, 1775) entrapped in Antipatharia branches are reported by Bo et al. (2015). Large-prey capture and engulfment is pre-dominant in azooxanthellate species both in the photic zone, at 15 and 17 m depth Musco et al. (2018), Gregorin et al. (2022) and in deeper ecosystems, at ca. 300 m depth (Sun et al., 2022), 400 m depth (Jarms and Tiemann, 2004) and at 4100 m depth (Lampitt and Paterson, 1987). The paucity of food par- ticles in oligotrophic waters could have driven the adaptation towards the capture and ingestion of macrofauna (Sun et al., 2022), especially where light limitation does not allow symbiosis with microalgae (Goldberg, 2018). However, at tropical and temperate latitudes, sym- biotic species also feed on macrofauna as well, as reported by Ter Horst and Hoeksema (2021), Cerrano et al. (2006), Porter (1974) and Alamaru et al. (2009), among others. In the present study, the capture of the large prey was often hindered by the loss of the jellyfish after few seconds. This negative response could be due to a modification of the cnidom of bleached *E. pallida*. In fact, Gundlach and Watson (2019) evidenced the increase in the quantity of spirocysts and the decline of penetrant nematocysts, along with the decrease in the volume of the individual cnidae in bleached *E. pallida*.

In addition to the duration and intensity of the stress event (Anthony et al., 2009), the tolerance of anthozoans to stress is influenced by other factors such as the morphology and thickness of tissues (Loya et al., 2001), the thermo-tolerance of *Symbiodinium* clades (Diaz-Allymeda et al., 2017), the size of lipids storage before the occurrence of the stress event to be used during photoautotrophic deficiency (Anthony et al., 2009), and the heterotrophic plasticity of the impacted species (Grottoli et al., 2006; Palardy et al., 2008; Anthony et al., 2009; Levas et al., 2016). These differences in tolerance are highly specific to individuals, eventually showing different levels of impacts even when equally sub- jected to a stressor (Diaz-Allymeda et al., 2017; Penin et al., 2007). Photoautotrophic species that show heterotrophic plasticity could be less endangered by the loss of symbionts, especially in food-rich envi- ronments (Anthony et al., 2009; Anthony and Fabricius, 2000). In this perspective, the increase in frequency, duration, and intensity of stress events (e.g., marine heat waves) could favour the survival of species that can shift towards heterotrophy (Grottoli et al., 2006), reflecting in the composition of the community and on the local biodiversity.

In conclusion, bleached *E. diaphana* showed lower values of hetero- trophic intake with both tested feeding modalities when compared to non-stressed conspecifics. These results could be a consequence of the species-specific biological response to bleaching, suggesting that *ad hoc* studies on species suffering from bleaching in the natural environment are needed. Cnidarian species revealed different responses to symbionts establishment and maintenance (Jinkerson et al., 2022), confirming that symbiotic relationship with Symbiodinaceae is highly variable. In the framework of previous studies, these findings suggest that the sea

anemone *E. diaphana* might not be a suitable species to evaluate the increment of exogenous nutrients intake as a strategy to recover from bleaching. However, considering its extensive use as model species for studying the coral-microalgae symbiotic relationship, further investigation of this topic is required.

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CRediT authorship contribution statement

Chiara Gregorin: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marica Di Vito:** Methodology, Investigation. **Camilla Roveta:** Writing – review & editing, Methodology, Investigation. **Torcuato Pulido Mantas:** Writing – review & editing, Formal analysis. **Stefano Gridelli:** Resources. **Federico Domenichelli:** Writing – review & editing, Resources. **Lucrezia Cilenti:** Writing – review & editing, Resources. **Tomás Vega Fernández:** Writing – review & editing, Supervision. **Stefania Puce:** Writing – review & editing, Supervision, Project administration, Conceptualization. **Luigi Musco:** Writing – review & editing, Supervision, Project administration, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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