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Protocooperation among small polyps allows the coral *Astroides calycularis* to prey on large jellyfish

The coral *Astroides calycularis* (Scleractinia: Dendrophylliidae) is endemic to the Mediterranean Sea (Terrón Sigler et al. 2016), where it can be reef forming (Musco et al. 2017: Fig. 1). In shallow water, it may cover up to 90% of rocky substrate from the surface down to 15 m depth where it is found in caves and on vertical walls. *Astroides calycularis* colonies frequently occur in dense aggregations (Goffredo et al. 2011), possibly favored by limited dispersion ability of both sexual (Goffredo et al. 2010) and asexual propagules (Serrano et al. 2017). High water movement promotes massive colony shapes with closely connected polyps usually forming continuous orange surfaces, leaving little space for the settlement of other benthic organisms (Casado Amezua et al. 2013). *Astroides calycularis* is “polystomatous,” forming small colonies composed of polyps connected to each other as a single organism bearing several mouths. Colony morphology is also strongly controlled by food availability (Goffredo et al. 2011). Polyps are typically 4–5 mm in length but larger polyps can grow up to 8 mm long. Like other azooxan thellate corals, *A. calycularis* is an obligate suspension feeder (Cebrian and Ballesteros 2004) and it is assumed to feed primarily on zooplankton transported by water movement, although the identity of its most preferred prey is unknown.

The venomous mauve stinger *Pelagia noctiluca* is a holoplanktonic jellyfish with a phosphorescent bell 3–12 cm wide. It is typical of warm water but currents may transport swarms of jellyfish into temperate and cold seas. Thus, it can be found from the tropics to the north Pacific and Atlantic, including the Mediterranean Sea. *Pelagia noctiluca* is usually pelagic and performs diel vertical migrations, albeit occasionally reaching the coast in large quantities. In the western Mediterranean, it forms persistent populations where it can be a nuisance to bathing people during periodic blooms in the warm season, raising increasing concerns as these blooms become more frequent (Canepa et al. 2014). *Pelagia noctiluca* is known to be preyed upon by fishes and turtles and parasitized by crustaceans. So far only one published picture of *P. noctiluca* seized by a polyp of a polystomatous coral is known (Aguilar 2007:30).

Observations of predation of the mauve stinger, *P. noctiluca*, by the orange coral, *A. calycularis*, were made in 2010, 2014, and 2017 during three field survey campaigns carried out in different localities of the Mediterranean Sea (Appendix S2). Capture and ingestion of 20 observed jellyfish involved several polyps belonging to different colonies

(Fig. 1a, Appendix S1: Fig. S1A–D, Video S1). The feeding behavior begins when a *P. noctiluca* jellyfish becomes trapped under an overhang with abundant *A. calycularis*. The pulsating swimming of the jellyfish moves the bell repeatedly against the overhang ceiling. Here *A. calycularis* polyps first adhere to the bell after which several polyps rapidly engulf the oral arms of the jellyfish, a process lasting between 1 and 5 minutes. Single polyps are able to ingest the oral arm tips preventing the jellyfish from escaping, while other polyps collaborate in ingesting pieces of jellyfish arms and umbrella (Fig. 1b, Appendix S1: Fig. S1D). Some jellyfish escape these attacks or become released as many were observed lying dead on the seafloor, with a hole on the top of the bell possibly caused by the predators. A similar behavior is shown when jellies are pushed by waves or currents onto colonies living on vertical walls along the shore (Appendix S1: Fig. S1A–D).

Present data and available information do not allow us to quantify the predation pressure exerted by *A. calycularis* on the mauve stinger. It seems unlikely that predation by the

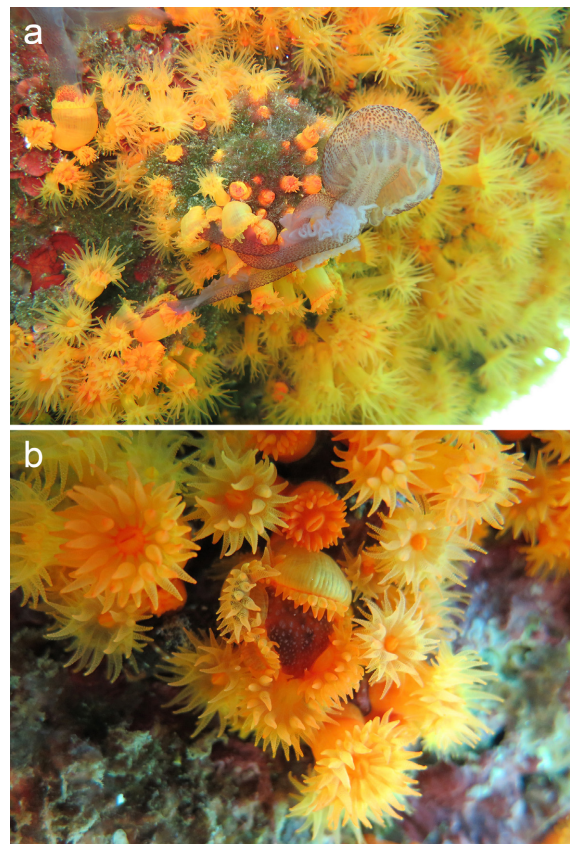


FIG. 1. *Pelagia noctiluca* jellyfish trapped among coral colonies of *Astroides calycularis* during *P. noctiluca* blooms in Italy. (a) Polyps preying singularly or in groups of the same or different colonies at Favignana Island (8 May 2017). (b) Close up view of coral polyps swallowing a piece of jellyfish umbrella at Pantelleria Island (23 May 2014).

coral significantly affects jellyfish populations, since these normally complete their life cycle in the pelagic realm. However, the incidental availability of *P. noctiluca* accumulated along the shoreline is arguably an important resource for the coral, as there may also be other macroscopic gelatinous plankton, such as ctenophores and salps.

Previous observations of monostomatous mushroom corals have reported their ability to eat large gelatinous plankton owing to their big mouth or large gape in the Red Sea (Alamaru et al. 2009), Malaysia (Hoeksema and Waheed 2012), and Thailand (Mehrotra et al. 2016). Capture of *P. noctiluca* by the polystomatous coral *Phyllangia mouchezii* has been illustrated (Aguilar 2007:30). However, the provided picture is hardly interpretable and it is unclear if collective behavior is involved. Here we describe how several small colonies of a polystomatous coral with tiny mouths and small gapes cooperate to do so analogously. Indeed, the ecological and evolutionary advantage for some Dendrophylliidae of having many small polyps has remained elusive (Arrigoni et al. 2014). Collective predation among relatively small polyps allows *A. calycularis* to access food resources well beyond its gape, thereby exploiting ephemeral, highly abundant patches of large prey.

The coral colonies display synchronized capture of the jellyfish. Collective synchronization of foraging provides immediate benefits to the fitness of engaged individuals with relatively little cost. These attributes allow for the selection of the observed behavior over evolutionary time (Clutton Brock 2009) through, e.g., the tendency of colonies to form aggregations. Thus, we consider the observed facultative mutualistic behavior a case of “proto-cooperation” (sensu Allaby 1998).

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