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Thread-like tentacles in the Mediterranean corals *Paramuricea clavata* and *Corallium rubrum*

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Abstract

The occurrence of modified tentacles (i.e. thread-like tentacles) in the Mediterranean octocorals *Paramuricea clavata* and *Corallium rubrum* is reported. Colonies of four species of Mediterranean gorgonians were maintained in aquarium conditions for more than five months. The development of thread-like tentacles was observed only in two of the four species. The presence of modified tentacles in other cnidarians has usually been associated with defensive/aggressive behaviour. Our observations show that thread-like tentacles in *P. clavata* and *C. rubrum* can also be used for feeding.

Keywords: Octocorals; thread-like tentacles; Mediterranean Sea; modified tentacles; gorgonians.

Introduction

Research on cnidarian nutrition has demonstrated that many species obtain nutrients through a combination of three processes: incorporation of photosynthetic products of symbiotic zooxanthellae, active transport of dissolved nutrients across epidermal membranes, and suspension feeding (Muscantine, 1973; Johannes, 1974; West *et al.*, 1977). For Mediterranean gorgonians, suspension feeding is the most common food capture strategy (Gili & Coma, 1998). Suspension feeding is based on the presence of waterborne particles which are captured by tentacles with the help of a type of cell (cnidocytes) containing specialised capsules (cnidocysts).

Besides nutrition, tentacles also have a role in the interaction with neighbouring organisms (i.e. intra- and inter-specific competition), as cnidocysts can be used for defence purposes (Patterson, 1991). Among the different ways in which anthozoans interact with neighbouring organisms in defence of the available space, the development of specialised tentacles has been predominantly observed in hexacorals. They are reported as “catch-tentacles” in actinarians and “sweeper tentacles” in some scleractinians and one antipatharian (Williams, 1975). These tentacles have rounded tips, are thicker and longer than feeding-tentacles, have a peculiar “searching” movement, and their epidermis usually has holotrich cnidae.

In octocorals only 3 studies are known (over the ca.

3000 known octocoral species) describing modification of the tentacles as possible defensive / aggressive structures. Sweeper tentacles have been reported only for an encrusting octocoral species, *Erythropodium caribaeorum* (see Sebens & Miles, 1988), while the modified tentacles observed in *Corallium rubrum* (see Abel, 1970) and in a few other gorgonian and soft-coral species [Sebens & Miles' (1988) comments on photographs from Muzik, 1983] have been described as thread-like tentacles. Sweeper tentacles of *Erythropodium* are extremely elongated, do not have pinnules, are only involved in active aggressive behaviour, and their cnidae are different to those in “normal” feeding tentacles. Up to now, thread-like tentacles have been described only in *C. rubrum*. According to Abel (1970) they are three to five times longer than normal tentacles, and they are characterised by a thread-like appearance in the distal part, and the presence of pinnulae. These tentacles are involved in the capture of particles, but they present a different behaviour with respect to normal tentacles (see Abel, 1970, for comparative descriptions). In a recently-described new isidid gorgonian, *Isidella tentaculum*, elongated (up to ~40 cm) tentacle-like modified polyps have been observed surrounding the base of living colonies (Etnoyer, 2008). In this case, true tentacles seems to be absent, but a further histological and cnidae characterisation of these elongated structures is still pending (P.J. Etnoyer, pers. comm.).

Materials and Methods

During the preparation of a series of laboratory experiments on the aggressive behaviour of corals from the Southern Iberian Peninsula, transplants (10-12 cm height) of the endemic Mediterranean octocoral *Paramuricea clavata* were maintained during three months, in relatively high densities, with transplants of *Eunicella* and *Leptogorgia* species (of similar height). Transplants were fed three times per week with newly-hatched *Artemia* nauplii (size ~500 μ m). During the course of an experiment on the fecundity of *C. rubrum*, adult colonies (> 7 mm basal diameter) were collected in the Gulf of Lion (France), fixed to circular concrete bases (5 cm diameter), and maintained in aquarium tanks for five months in open circuit with natural-filtered (5 μ) seawater. No other species apart from *C. rubrum* were present in the aquarium tanks, and colonies were kept in darkness at a temperature of 19-21°C, which is the vertically-averaged temperature in late July-August over a 27m water depth in Banyuls-sur-Mer Bay (Service d'Observation du Laboratoire Arago). Colonies were fed three times per week with 24-hours-old *Artemia salina* nauplii (size ~500 μ) and once a week with a mix of phytoplankton and zooplankton with sizes ranging from 0.2 to 150 μ (Marine Snow®). As the main focus of the experiment was on fecundity, data on the current strength and direction were not recorded.

Results

Thread-like tentacles, similar to the ones described by Abel (1970), were observed only in *Paramuricea clavata* transplants (Fig. 1a, b) and in *Corallium rubrum* colonies (Fig. 1c, d). *Paramuricea clavata* thread-like tentacles were up to 9 mm long in fixed material (four times longer than normal tentacles). The development of the modified tentacles happened in less than three months. Thread-like tentacles observed on *C. rubrum* were ~15 mm long, with pinnules present only on the proximal part, progressively thinning towards the distal part, where pinnulae are absent (Fig. 1d). The concentration of nematocysts was higher in thread-like tentacles than in normal ones, (Fig. 2), especially in the elongated distal portion. In further feeding experiments using *Artemia* nauplii (see Suppl. file, Video 1, ESM 1: Video showing thread-like tentacles of *Paramuricea clavata* and *Corallium rubrum* involved in feeding activity.) Abel's notes were corroborated, observing that these tentacles are capable of capturing prey. Both *P. clavata* and *C. rubrum* thread-like tentacles have been observed killing the *Artemia* nauplii, and stuffing it into the mouth of the polyp.

Discussion

Despite the large bulk of studies on the modified tentacles of scleractinian corals (e.g. Lang, 1971, 1973; Richardson *et al.*, 1979; Sheppard, 1979; Lapid & Chadwick,

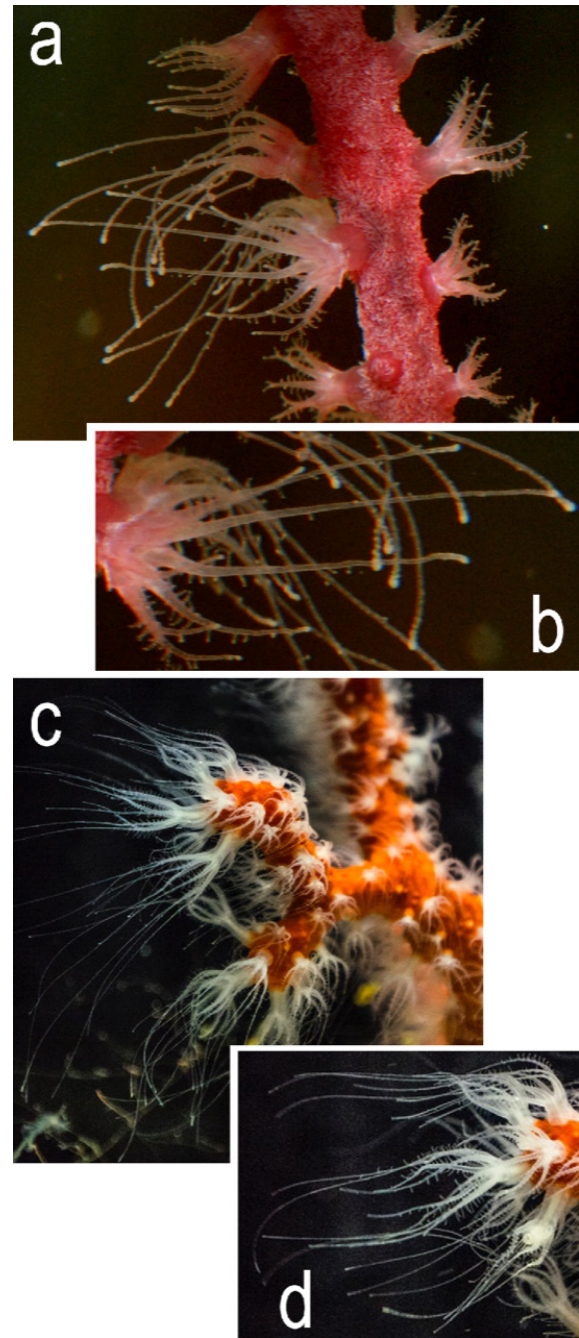


Fig. 1: a: *Paramuricea clavata* transplant with polyps showing thread-like tentacles. b: close up of thread-like tentacles of *Paramuricea clavata*. c: Thread-like tentacles on polyps of a *Corallium rubrum* colony. d: close up of thread-like tentacles of *Corallium rubrum*.

2006) similar studies on octocorals are rare (but see Sebens & Miles, 1988; Abel, 1970). While thread-like tentacles have been previously observed in *C. rubrum*, this paper presents the first report of the occurrence of these modified tentacles in *P. clavata*. The presence of modified tentacles in other cnidarian species (e.g. sweeper tentacles) have usually been associated with aggressive/defensive behaviour (Williams, 1971; Chornesky, 1983)

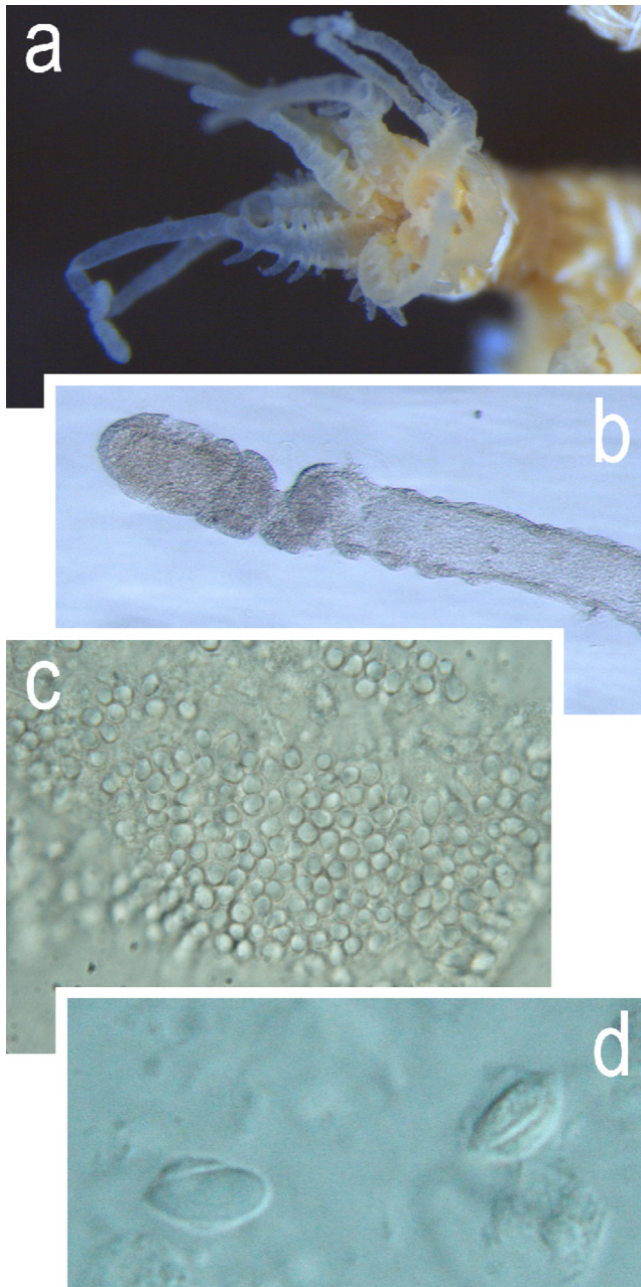


Fig. 2: a: Detail of *Paramuricea clavata* polyps with modified tentacles. b: Distalmost portion of a modified tentacle. c: Detail of the density of nematocysts at the distalmost portion in a modified tentacle. d: Nematocysts.

while new observations suggest that thread-like tentacles can also be used for prey capture.

An important generalisation about the benthic suspension feeding strategy is the importance of the coupling between morphology and flow field in the particle capture process (Patterson, 1991). For this reason, it can be expected that the morphology of tentacles should respond to flow modifications.

According to several authors, a physical property of

the fluids involved in the particle capture is the viscosity (Vogel, 1994), and its relationship with the fluid velocity is described by the Reynolds number (Re):

$$Re = uL/\nu$$

where u is the velocity of the fluid with respect to the object (ms^{-1}), L is a characteristic linear dimension (m), and ν is the viscosity of the fluid ($\text{m}^2 \text{s}^{-1}$).

In order to keep a constant Re, the linear dimension (L) should increase when the fluid velocity (u) decreases. The increase of the size of the tentacles could then be linked to a decrease in fluid velocity.

The formation of modified tentacles required less than three months, which is quite a fast response with respect to the extremely long life span of the species (> 100 years for *C. rubrum* and > 30 years for *P. clavata*).

If these modified tentacles are significantly involved in prey capture in *C. rubrum* and *P. clavata*, the absence of modified tentacles in *Eunicella* and *Leptogorgia* species could be due to the different feeding strategy of those species. The diet of *Paramuricea* and *Corallium* depends more on waterborne prey, being mainly composed of phyto- and zooplankton (Coma *et al.*, 1994; Tsounis *et al.*, 2006). On the other hand, some *Eunicella* species have a mixotrophic strategy, linked to the presence of symbiotic dinoflagellates (Viladrich *et al.*, 2017), and *Leptogorgia* have been reported to be mainly composed of detrital POC, and then more dependent on resuspension events than on flow velocity (Ribes *et al.*, 2003).

However, observations on modified tentacles in octocorals are sporadic; thus, other possible explanations could also be explored for their absence in *Eunicella* and *Leptogorgia* transplants in the tanks, if a main defensive purpose of these structures is maintained. Despite all octocorals species possessing nematocysts, the toxicity of their venoms could differ between species, as occurs in hexacorals and hydroids, as well as chemical defences by the exudation of deterrent secondary metabolites is another way to keep other benthic organisms (included other gorgonian species) distant (see Coll, 1992; Sammarco & Coll, 1992; Stachowicz & Lindquist, 2000; Mariottini & Pane, 2013, among others). Thus, perhaps, the modification of the tentacles of some polyps is another, complementary, strategy of defence-competition developed under determinate conditions.

According to Piraino *et al.* (1993), observations of nematocysts from octocorals are sporadic, as well as very difficult to correctly identify due to their small dimensions. The possible usefulness of the taxonomy of these structures in this group has been neglected because of the more accessible and intensive study of other morphological characteristics such as colony growth form, sclerite arrangement, and sclerite morphology (see Bayer *et al.*, 1983). Piraino *et al.* (1993) described two types of nematocysts in *Corallium rubrum*, and Coma *et al.* (1994) commented on the presence of atrichous (9 to 10 μm) in low densities (less than 50 nematocysts in tentacle frag-

ments of 0.5 mm length). In preliminary observations, two types of nematocyst (similar to those described by Piraino *et al.*, 1993, for *C. rubrum*) were observed in the tentacles of *Paramuricea clavata*, of 10-15 µm in length, being present in much higher densities in those modified tentacles, especially in the elongated distalmost portion.

Further experiments are needed to test all these hypotheses, as well as to understand other potential factors inducing the formation of these modified tentacles (e.g. intra- and inter-specific competition), their histology, types of cnidome, and their possible role as an evolutionary intermediate step in the formation of sweeper tentacle's morphology, as observed in *Erythropodium* and hexacorals.

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