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Morphology of antennular sensors in *Clausocalanus furcatus* (Copepoda: Calanoida)

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The success of planktonic copepods in aquatic environments is dependent on efficient sensing of their three-dimensional surroundings. The detection of external cues is of importance for the localization of other organisms (prey, predators and mates), and is mediated by an array of mechano- and chemoreceptors located on the paired antennules (A1).

We investigated the morphology and distribution pattern of A1 sensory structures in the adult female of Clausocalanus furcatus *(Copepoda: Calanoida) using different techniques (camera lucida, scanning and transmission electron microscopy and laser scanning confocal microscopy) each focusing on a specific aspect of the structures analysed. Integration of the information collected shows that* C. furcatus *possesses an array of mechanical, chemical and dual-function sensors over its A1, by which the copepod can detect different stimuli from the environment. Results are discussed in the light of the unique swimming behaviour displayed by this widespread epipelagic copepod.*

Keywords: *Clausocalanus furcatus*; antennules; mechanosensors; chemosensors; ultrastructure

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INTRODUCTION

Like most crustaceans, copepods rely primarily on mechanical and chemical stimuli to gain information from the environment (Laverack, 1968). The detection of external cues is assured by different receptors, whose role is to convey a signal to the central nervous system. Planktonic copepods have numerous sensors on their body, but mainly along their antennules (A1), whose role has been demonstrated by ablation experiments (Mullin & Brooks, 1967; Landry, 1980; Gill & Crisp, 1985), direct stimulation (Gill, 1985; Fields & Yen, 1996, 2002) and electrophysiological recordings (e.g. Yen *et al.*, 1992; Lenz & Yen, 1993; Fields *et al.*, 2002; Fields & Weissburg, 2004).

Setae are the most common supracuticular mechanoreceptors in crustaceans (Watling, 1989). Mechanical stimuli are important in the detection of prey (e.g. Landry, 1980; Buskey, 1984), predators (e.g. Lenz & Hartline, 1999) and mates (e.g. Strickler, 1998; Yen *et al.*, 1998). Mechanoreceptors possess a thick cuticle, and may either move in all directions or be directionally-sensitive (Bush & Laverack, 1982). Setae with different morphotypes (Factor, 1978) are associated with specific functional roles (Yen *et al.*, 1992), while apical pore bearing setae are likely involved in the dual detection of mechanical and chemical stimuli (Jacques, 1989).

Chemoreception is crucial for copepods’ sensing of their environment (Ache, 1982; Jackson & Kiørboe, 2004) and is involved in communication between a mating couple (e.g. Katona, 1973), in detection of feeding stimuli (e.g. Poulet & Marsot, 1978; Poulet & Ouellet, 1982) and in predator avoidance (e.g. Folt & Goldman, 1981). Antennular chemosensitivity is ascribed to aesthetascs (Ache, 1982), formed by the aggregation of a large number of chemoreceptors (Laverack, 1988). Aesthetascs are thin-walled (Laverack & Ardill, 1965) tubular sensory filaments (Huys & Boxshall, 1991), with a spongy cuticle that facilitates instantaneous odorant absorption from the surrounding medium (Shelton & Laverack, 1970; Lenz *et al.*, 1996). Usually, aesthetascs are more abundant on the basal segments of the A1s (Boxshall *et al.*, 1997; Boxshall & Huys, 1998; Moore *et al.*, 1999), where the flow of the feeding currents is stronger.

The aim of the present work was to acquire the basic information on the sensory modalities used by the small calanoid *Clausocalanus furcatus* to interact with prey. *Clausocalanus furcatus* is abundant in tropical and subtropical areas of both hemispheres (Frost & Fleminger, 1968) and displays a peculiar swimming behaviour with fast motion along convoluted tracks (Mazzocchi & Paffenhöfer, 1999). In the present study we investigated the sensory structures displayed by the A1s of adult female *C. furcatus* by means of different techniques. Integration of the information collected by each approach provided a full account of the external and internal features of antennular sensors, providing important insights into the way this small copepod interacts with its surrounding environment.

MATERIALS AND METHODS

Clausocalanus furcatus adult females (~1 mm total length) were sorted from zooplankton samples collected in the Gulf

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of Naples by gentle vertical hauls using a Nansen net (200 μm mesh size), with a 5 l glass jar as cod-end bucket. Only specimens in perfect condition with fully intact antennules were chosen for this study.

Individuals utilized for morphological analyses were either narcotized with MS222 (tricaine methane sulphonate) (1 g l^{-1}) (Mullin & Brooks, 1967) or fixed and preserved in 4% buffered formalin solution. Four study methods were employed: camera lucida drawings (CLDs), scanning electron microscopy (SEM), transmission electron microscopy (TEM) and laser scanning confocal microscopy (LSCM), each focusing on different features of the A1 and its sensors.

For a concise description of A1 morphology, CLDs were made using a Zeiss Axioskop 2 plus microscope equipped with a Zeiss Axioskop camera lucida tube at 40X magnification.

Scanning electron microscopy allowed the reconstruction of the three-dimensional distribution of sensors along the entire antennule, as well as the investigation of microscale structures. Selected specimens were dehydrated in a graded ethanol series, with a procedure modified from Huys & Boxshall (1991). Individuals were then critical point dried using liquid carbon dioxide (5 h), mounted on an aluminium stub and platinum coated, and observed with a Jeol JSM-6700F.

Transmission electron microscopy permitted the determination of the finest details of internal structure, with two-dimensional images of ultrathin section of the material analysed. In the present study, specimens were prepared following a modification of the procedure described in Weatherby *et al.* (1994). Ultrathin sections (500 Å) were cut with a Leica Ultracut UCT and examined with an EFTEM LEO 912AB.

Laser scanning confocal microscopy allowed targeting of mechano- and chemoreceptors (Bundy & Paffenhöfer, 1993), as well as muscular bands and other anatomical details (Carotenuto, 1999). Sensillae were rapidly stained by a fluorescent carbocyanine dye (DiI), which penetrates into the lipid bilayer of neuronal cell membranes (Honig & Hume, 1986). Material was prepared following the method described by Carotenuto (1999); specimens were then incubated for 1 h in dark conditions in a 70% ethanol solution enriched with four drops of DiI for each ml of solution. Prior to observations, copepods were rapidly rinsed in bidistilled water to wash out excess DiI. The observations were performed using a Zeiss LSM 510 Meta ($\lambda = 543$ nm) at 100X magnification.

Table 1. The distribution of sensory structures along the antennules of *Clausocalanus furcatus* female, obtained by comparative analysis of camera lucida drawings, scanning electron microscopy micrographs and laser scanning confocal microscopy reconstructions.

Ancestral segmentation	Actual segmentation	Simple setae	Modified setae	Aesthetascs
I	1	1 + 2s	0	0
II–IV	2	6	0	1
V	3	1	1	1
VI	4	2	0	1
VII	5	2	0	1
VIII	6	2	0	1
IX	7	1	1	1
X–XI	8–9	3	1	1
XII	10	1	0	1
XIII	11	1	0	1
XIV	12	2	0	1
XV	13	1	0	1
XVI	14	1	1	1
XVII	15	1	0	1
XVIII	16	1	1	1
XIX	17	1	0	1
XX	18	1	1	1
XXI	19	1	0	1
XXII	20	1	0	0
XXIII	21	0	1	0
XXIV	22	1 + 1*	0	1
XXV	23	1 + 1*	0	0
XXVI–XXVIII	24–25	2s + 1* + 3**	0	1

*, on the posterior margin; **, on the distal tip, grouped in a tuft; s, serrulate seta.

RESULTS

The A1 of *Clausocalanus furcatus* had aesthetascs and three different kinds of setae: simple, serrulate and modified (Table 1). All sensory structures were aligned along the anterior margin of the A1s (Figure 1); only segments 22, 23 and compound segments 24–25 had one seta each on the posterior margin. Following the scheme applied by Lenz & Yen (1993), the A1s of *C. furcatus* could be divided into three sectors: the basal sector (segments 1 to 8–9), where setae were more closely spaced; the median sector (segments 10 to 18), where setae became sparse; and the distal sector (segments 19 to 24–25) bearing a reduced number of setae. The antennules also carried single aesthetascs on all segments except 1, 20, 21 and 23; on segments 3, 7, 14 and 16 aesthetascs were arranged as part of a trithek (the basic antennulary armature unit comprising 2 setae and 1 aesthetasc) typical of female copepods (e.g. Boxshall, 1983). All tritheks were arranged as described by Giesbrecht (as cited in Boxshall, 1983) with one seta almost in the middle of the segment, and another seta close to the aesthetasc on the distal part. When modified setae were present on a segment, it was always the seta closer to the aesthetasc that was modified. The sensory arrangement on the distal tip comprised: two serrulate setae and one aesthetasc on the anterior margin, one seta on the posterior edge and a tuft of three outwardly projecting setae sharing a common origin.

Simple setae (Figure 2A) were pure mechanoreceptors, with a smooth external surface and a tapered tip. They originated from a symmetrical circular (approximately 4 μm in diameter) socket which, coupled with the lack of any one-point innervation at the base of the sensor, provided indirect evidence of the absence of directional sensitivity (Bush & Laverack, 1982). Simple setae had the typical characteristics of the copepod mechanosensor, i.e. a thick cuticle enveloping a large proliferation of microtubules (Figure 2B).

Segment 1 and compound segments 24–25 carried two setae ornamented with short setules (1–2 μm) (serrulate setae) each. In addition, segment 1 had a pore between two neighbouring setae (Figure 3A). Another pore was sometimes visible close to the socket of the seta on the anterior margin of segment 23, but this character was not discernible in all individuals investigated. The ultrastructure of serrulate setae (Figure 3B) was similar to that of simple setae (thick cuticle,

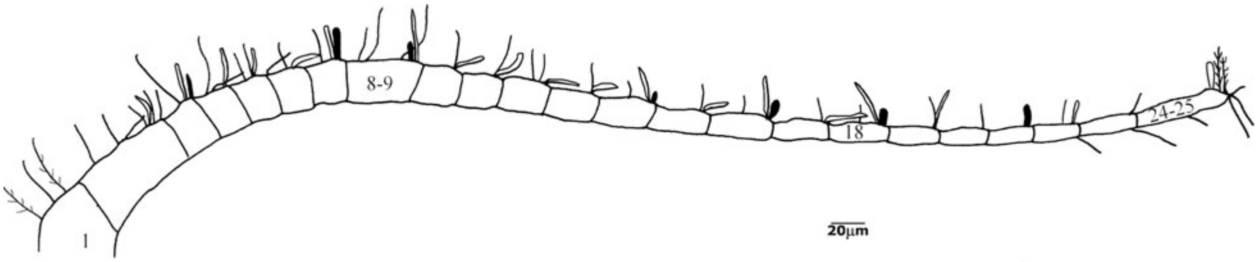

Fig. 1. Alignment of setae and aesthetascs along the margins of the A1 of *Clausocalanus furcatus* female. Camera lucida drawing (40X magnification) shows the setation pattern, and the arrangement of aesthetascs (cylindrical-like structures) and modified setae (in black) along the segments.

presence of microtubules). In addition, small setules did not have any sort of innervation, indicating that they were just chitinous extensions of the mechanosensor.

Modified setae were presumed to be chemosensory or dual-function sensors (Figure 4A). They were characterized by a smooth texture, as in simple setae, whilst the median and distal part of the sensor possessed a spongy-like structure typical of copepod aesthetascs (Figure 4B). Modified setae were attached to the A1 via a socket larger (5–7 µm) than that of simple setae. Their base was characterized by a clearly recognizable neck constriction, and the tip lacked any apical pore. The internal structure of modified setae possessed characters typical of simple setae (Figure 4C): the cuticle was rather thick and consisted of consecutive layers of chitin, while the internal cavity was partly filled with a relatively large number of microtubules.

The aesthetascs of *C. furcatus* had the characteristic bulbous shape with a spongy external texture (Figure 5A). The root of the sensor protruded directly from the chitinous surface of the A1, the base having a diameter of nearly 2 µm. Unlike the same receptors found in other species (Kurbjeweit & Buchholz, 1991; Bundy & Paffenhöfer, 1993), the aesthetascs of *C. furcatus* did not show any neck

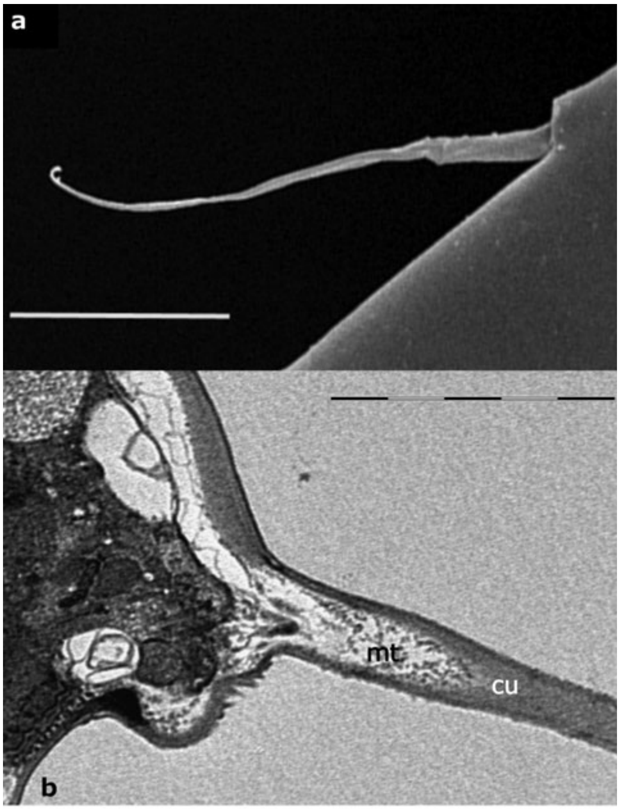

Fig. 2. (A) Scanning electron microscopy detail of a naked seta present on segment 14 of the left A1 of a *Clausocalanus furcatus* adult female. The picture shows the smooth texture of the sensor, its tapering shape and the characteristic anchor socket (scale bar = 10 µm); and (B) longitudinal transmission electron microscopy section of simple seta on distal part of the A1 of *C. furcatus*. The simple seta is characterized by a thick cuticle (cu), recognizable by its compact structure formed by overlapping layers of chitin, and by the presence of numerous microtubules identified as small black dots (mt) (scale bar = 5 µm).

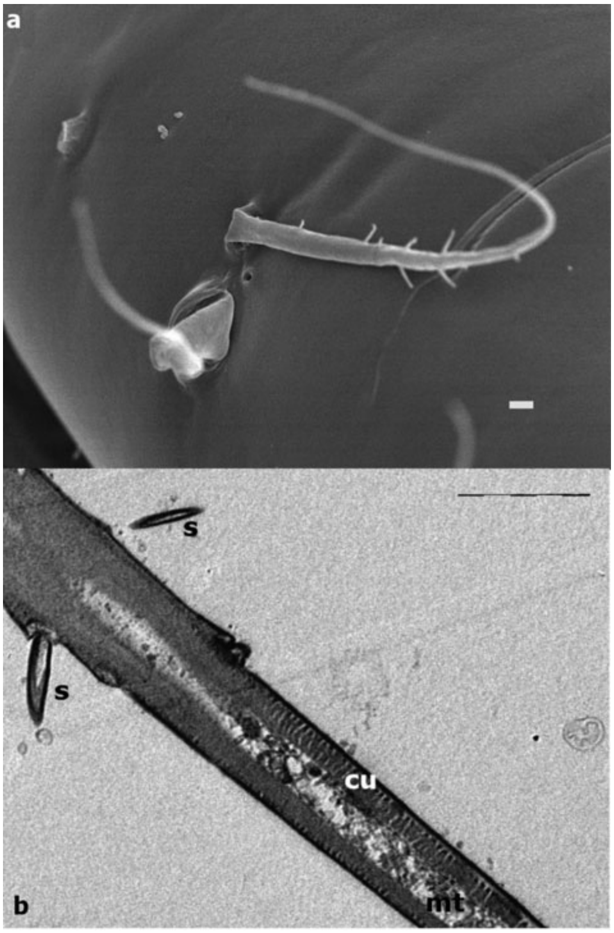

Fig. 3. Segment 1 of the right antennule of *Clausocalanus furcatus* female. (A) Details of one serrulate seta, of the naked seta and of the pore between them (scale bar = 1 µm). Setule length is approximately 1 µm; and (B) longitudinal section of serrulate seta. The setules (s) are not provided with any nervous termination, but are projections from the chitinous outer surface of the seta. As in simple setae, the serrulate seta shows a thick cuticle (cu) and numerous microtubules (mt) (scale bar = 2 µm).

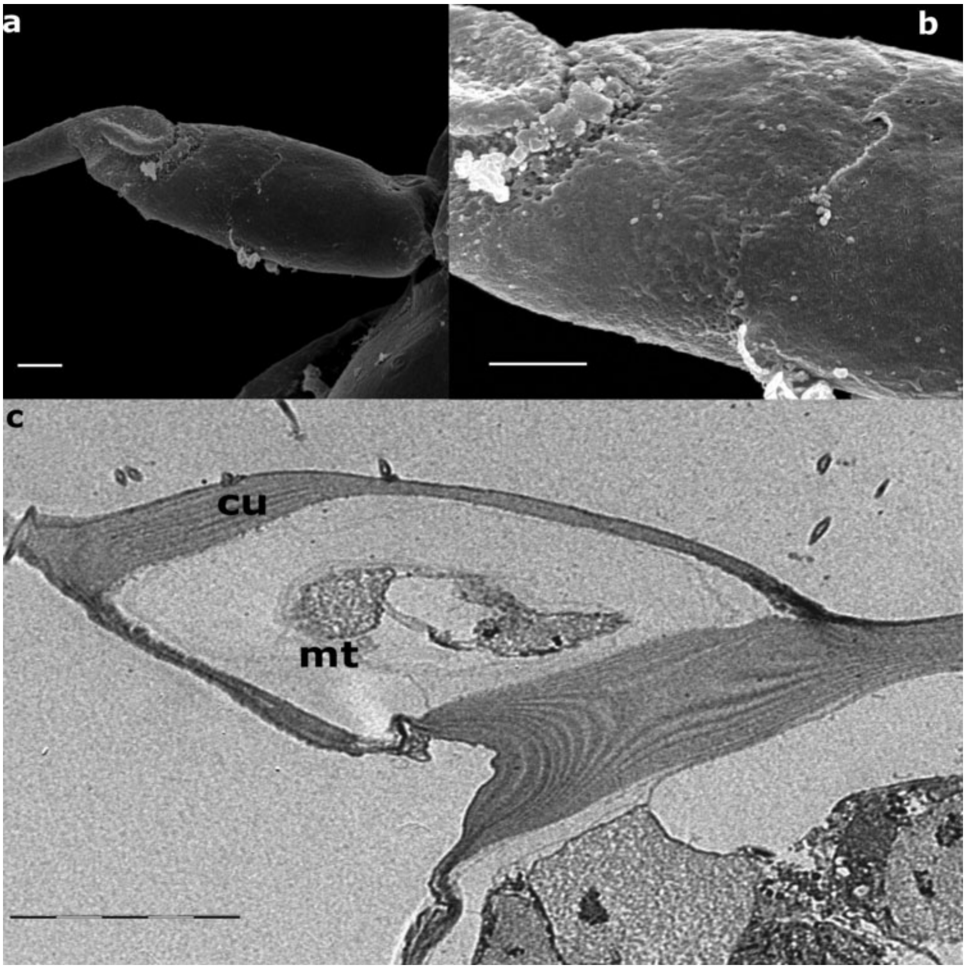

Fig. 4. (A) Morphological features of the modified seta on segment 14 of the antennule of *Clausocalanus furcatus* (scale bar = 1 μm); (B) detail of the spongy cuticular structure along the body of the sensor (scale bar = 1 μm); and (C) longitudinal section of the base of modified seta, showing typical features of mechanosensory setae: a thick cuticle (cu) enveloping numerous microtubules (mt). Note also the width of the structure, which is much larger than normal setae (scale bar = 4 μm).

constriction. The tip lacked a pore (Figure 5A). The base of the aesthetasc on segment 2 was always accompanied by a pore; this association was occasionally noted also for other aesthetascs (segments 14, 16, 19 and 24–25), but did not represent a common feature in all specimens analysed. All pores reported for the A1 of *C. furcatus* were circular shaped, as described for other calanoids (e.g. Blades & Youngbluth, 1979; Gill, 1986). From an ultrastructural point of view (Figure 5B), the aesthetascs of *C. furcatus* were characterized by the lack of a cluster of microtubules and a very thin and apparently perforated cuticle, through which chemical odorants might permeate, coming into contact with the nervous structures of the sensor. The dark circular profiles evident in the TEM section might be the ends of forked dendrites, whose presence further supports the chemosensory function of this structure (Lenz *et al.*, 1996).

Compiled confocal images showed brightly fluorescent aesthetascs and weakly non-uniformly fluorescent modified setae, while simple setae did not fluoresce at all (Figure 6A). Aesthetascs fluoresced as a consequence of the absorption of DiI through their spongy cuticle (Figure 6B); the assimilation of the dye occurred somewhat uniformly along the entire length of the sensor. Simple setae did not fluoresce at all (Figure 6C) indicating that their thick chitinous cuticle was almost impermeable to DiI. Modified setae showed spots of fluorescence localized on the median/distal part, corresponding to the spongy texture noted using SEM (compared with Figure 4A). By contrast, no fluorescence was noticed at the base of the modified seta, where the cuticle was thick (Figure 4B).

Table 1 summarizes the distribution of the sensory array along the A1 of *C. furcatus* female, obtained from comparative observations using CLDs, SEM micrographs and LSCM reconstructions.

DISCUSSION

The antennules of adult female *Clausocalanus furcatus* are equipped with different kinds of mechano- and chemoreceptors by which this small calanoid copepod can acquire information from the surrounding environment.

The analysis of the characteristics of the different receptors, as well as the identification of a pattern of distribution along the A1, provide important cues to improve our knowledge about the mechanisms by which *C. furcatus* interacts with the fluid medium. Firstly, with the only exception of the distal segments, all sensors are aligned along the anterior

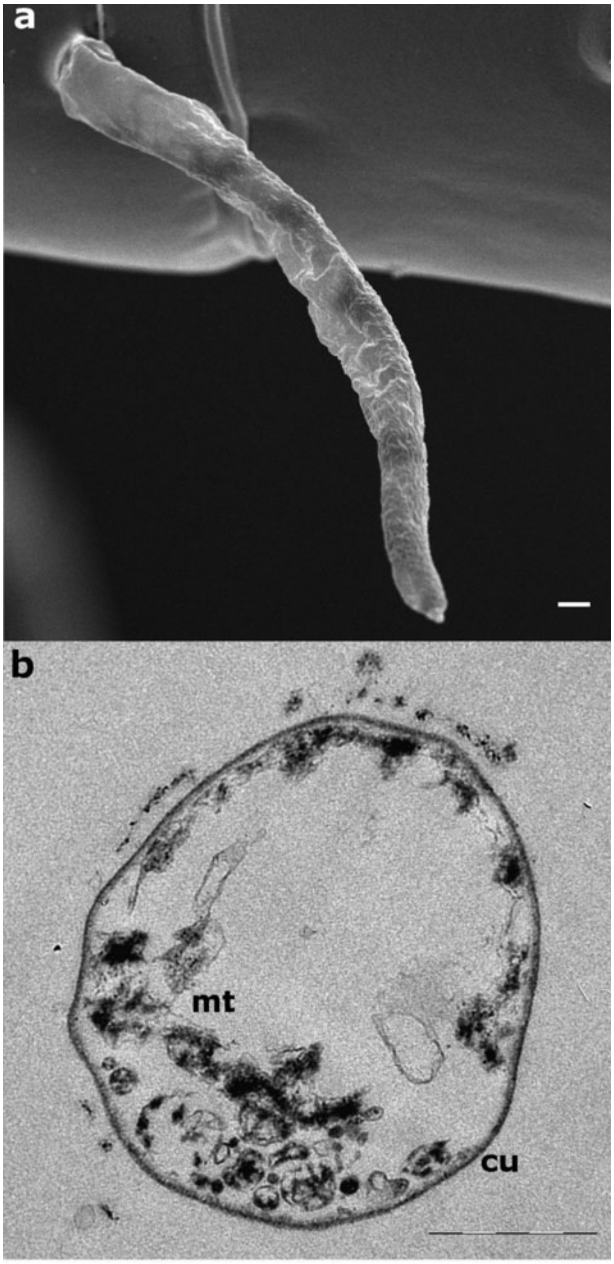

Fig. 5. (A) Aesthetasc on segment 2 of the left antennule of *Clausocalanus furcatus* female. Scanning electron microscopy shows the cylindrical shape, with crenulated texture along its entire length (scale bar = 1 μm); and (B) transmission electron microscopy cross-section of aesthetasc located on the distal tip of the A1 of *C. furcatus*. The chemosensory function of this structure is underlined by the presence of a thin cuticle (cu) and by the presence of few microtubules (mt) (scale bar = 1 μm).

margin of the A1, an arrangement fitting the continuous active motion of this species, which would benefit from scanning the fluid in front of the organism. The presence of sensors along the posterior margin from segment 22 to compound segments 24–25 likely improves the sensitivity of the distal tip area, which usually acts as an early warning system (e.g. Gill, 1985; Fields & Weissburg, 2004).

Analysis of video recordings (Uttieri, 2006) shows that *C. furcatus* captures dinoflagellate prey only when they are inside an area of $0.16\ \text{mm}^2$ centred on the rostrum and extending approximately 0.4 mm from it. This area overlaps

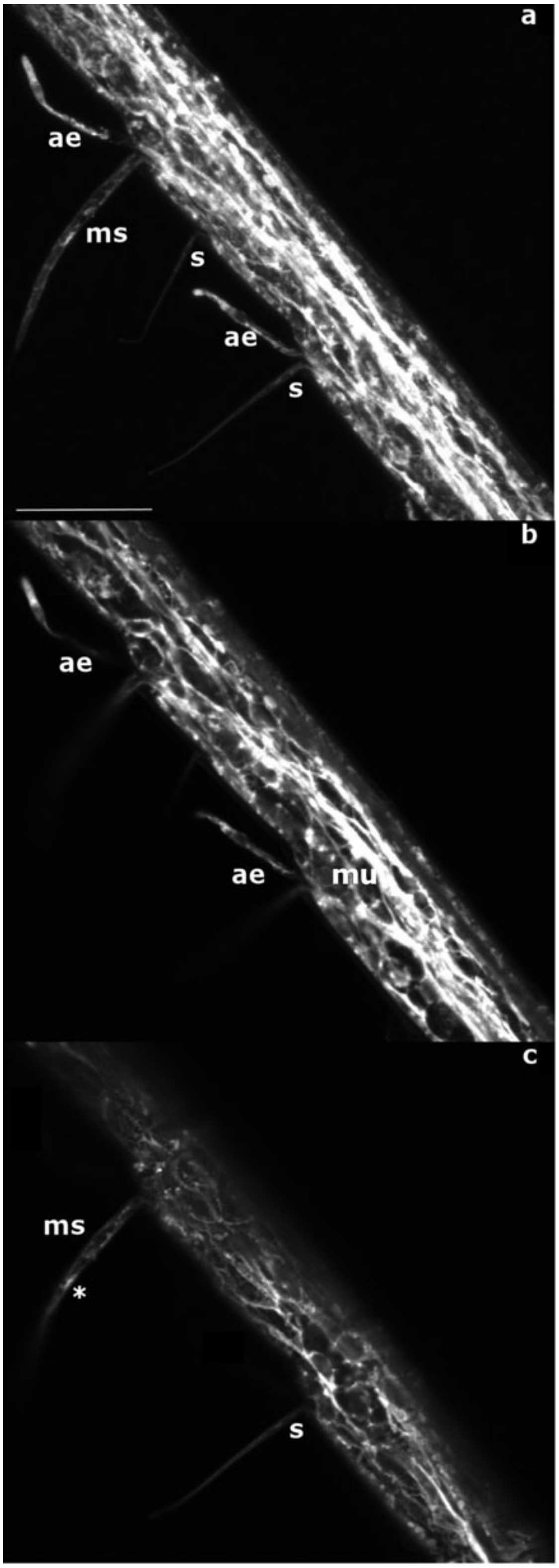

Fig. 6. Laser scanning confocal microscopy pictures of segments 15 and 16 of the A1 of *Clausocalanus furcatus*. (A) Compiled image of the optical sections taken, showing brightly fluorescent aesthetascs (ae), modified setae (ms) with bare fluorescence and non-fluorescent simple setae (s); (B) optical section (optical thickness = 1 μm) showing fluorescent aesthetascs (ae) as a result of uniform fluorescent carbocyanine dye absorption throughout the sensor; muscle bands (mu) are also evident in the section; and (C) optical section (optical thickness = 1 μm) highlighting the localized spot of fluorescence (*) along the modified seta (ms); by contrast, the simple seta (s) does not show any fluorescence. Scale bar = 20 μm for all panels.

with the proximal segments of the A1 where purely mechanosensory setae are more abundant, including the first segment which bears two serrulate setae. This evidence suggests that setae are directly involved in the near-field detection of mechanical stimuli from a potential prey just before its capture. This point is strengthened by comparison with similar-sized cruising species (e.g. *Paracalanus parvus* and *P. aculeatus*; personal observation), which bear much longer sensors allowing these species to better localize a potential item in the far field. The short setae carried by *C. furcatus* may be tuned to detect stimuli only in the near vicinity, thus explaining the reduced dimensions of the capture area. In addition, the short setules present on serrulate setae likely increase the surface of the sensors and consequently their ability in detecting weak mechanical stimuli from potential prey.

The presence of chemoreceptors (aesthetascs and modified setae) along the entire A1, and more particularly on the segments outside the capture area, hints at the exploitation of chemical cues to perceive the presence of potential food items externally to the capture area. *Clausocalanus furcatus* keeps its peculiar swimming motion during feeding and non-feeding events (Uttieri, 2006); mediated by its numerous chemoreceptors, the copepod may be able to detect the presence of chemical cues released by prey items outside the capture area, and approach them by its looping behaviour until they are inside the capture area. The hypothesis proposed here is confirmed by video observations showing *C. furcatus* looping around a prey without capturing as long as it is outside the capture area (personal observation).

The effectiveness of chemoreception would be enhanced by the typical swimming motion of *C. furcatus*. Detection of chemical cues occurs when an odorant molecule comes into contact with the sensitive surfaces of a chemosensory detector; by swimming continuously and at high speed, the copepod increases the net flux of water across the sensor array, thus increasing the probability of detecting a suitable cue. Moreover, even at the low Reynolds number regime where copepods usually live, the fast swimming may reduce the boundary layer around the sensor, further improving the flux to the sensor.

Paffenhöfer & Loyd (2000) noticed that the setae of the maxilliped and second antenna of *Centropages velificatus, Eucalanus pileatus, Paracalanus aculeatus* and *Temora stylifera* possessed an opening at their end, indicating a putative olfactory perception of food particles. Preliminary investigations (personal observation) show apical pores on the setae of second antennae in *C. furcatus* which would effectively enlarge its prey-perceiving area, with beneficial effects on its feeding success.

In conclusion, *C. furcatus* seems to depend to a large extent on the detection of chemical cues from its prey. The densely aggregated mechanoreceptive setae on the basal sector of the A1 allow the copepod to sense potential prey items only when they are located inside its capture area, and consequently in the near field interactions. This is supported by recordings of intense neurophysiological responses from the basal segments of the A1 (personal observation). In contrast, the mid and distal parts of the A1 do not appear involved in the process of prey capture, but are rather utilized by the copepod to re-orient towards prey located outside the capture area. The sensory apparatus displayed by *C. furcatus* seems to be compatible with its swimming and predatory behaviour (Uttieri, 2006) and to be suited to life in stratified oligotrophic waters, where phytoplankton aggregations may occur. These aggregations, in fact, often release chemical exudates that could be perceived by the distal chemoreceptors (aesthetascs and modified setae) of *C. furcatus*. By using the chemoreceptors distributed along the A1, the copepod can discriminate gradients of odorant molecules and consequently modify its swimming towards the patch. Once inside, the copepod can efficiently collect food particles utilizing its restricted capture area. The proposed hypothesis, corroborated by the results in the present work, provides an explanation for the success of this small calanoid in oligotrophic areas of both hemispheres.

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