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Biology of the basket star *Gorgonocephalus caputmedusae* (L.)

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Abstract Ophiurid basket stars belonging to the family Gorgonocephalidae are distributed from the Arctic to the Antarctic and from the shallow subtidal to the deep sea, but their biology remains poorly known. In situ observations at the mouth of the Oslofjord by a remotely operated vehicle showed that *Gorgonocephalus caputmedusae* had a patchy distribution at 85 to 120 m water depth and frequently occurred in association with the gorgonian *Paramuricea placomus* and the coral *Lophelia pertusa*. Morphological and histological studies show that *G. caputmedusae* is well adapted to capture macroplanktonic prey. Histological examination of the arms revealed the presence of a thick layer of dermal mutable connective tissue which is probably an energy-efficient way to maintain its feeding posture against the current. This layer is connected to the nerve cord suggesting that the passive mechanical properties (stiffness) is controlled by the nervous system. In the distal parts of the arms, each segment has a pair of sticky tube feet and a sophisticated system of spines and hooks, which are connected to muscles and collagenous tendons. In combination, these features were shown, in an experimental flume study, to be used for capturing the locally abundant krill species *Meganycitiphanes norvegica*. This

is the first documentation of *G. caputmedusae* of this kind.

Introduction

Gorgonocephalid basket stars have fascinated scientists since their discovery more than 100 years ago. They were then occasionally obtained in dredges or fishnets from great depths. Five gorgonocephalid species have been identified from European waters, of which four occur in Scandinavian waters. *Gorgonocephalus caputmedusae* (L.) was found first by Mortensen (1924) at around 300 m depth in the Skagerrak. Subsequently, this species was reported also from the Swedish Skagerrak coast (Jägerskiöld 1933). However, it is only recently, with the development of remotely operated vehicles (ROVs), that this species has been observed in situ in the Skagerrak. In addition, ROVs make it possible to bring intact animals to the laboratory for experimental studies.

In an earlier experimental laboratory study, Patent (1970) examined the biology of *G. eucnemis* from the East Pacific. She described how this basket star was able to capture plankters with their armoured arms. Later, Emson et al. (1991) described in great detail the feeding mechanism in *G. arcticus*, a species found in New Brunswick, Canada. This latter species uses highly specialised spines and hooks on the distal parts of the arms to trap and, by coiling the arms, wrap the prey, which is then transported to the mouth. Emson et al. (1991) showed that *G. arcticus* was a macroscopic suspension feeder, and that most of the food in the stomach of captured specimens were krill of the species *Meganycitiphanes norvegica*.

The present study is the first detailed description of morphological and histological structures associated with the feeding biology in *G. caputmedusae*. In addition, the feeding mechanism of *G. caputmedusae* was studied in an experimental flume tank using live *Meganyciti-*

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phanes norvegica. We demonstrate that their feeding mechanism is more elaborate than previously shown for gorgonocephalids and suggest that it involves active regulation by the nervous system.

Materials and methods

Collection, video recording and behavioural studies

In situ observations were made using a Phantom S4 ROV. The width of view that the camera recorded was generally between 0.5 m and 4.0 m. The specimen of *G. caputmedusae* studied experimentally in this work was collected in December 2003 at the southern entrance of the Oslofjord at 86 m depth at N 59°06'030; E 10°47'992. A frame with a net was attached to the front of the ROV allowing collection of an intact specimen.

The specimen was transported in a cool box to Kristineberg Marine Research Station in Sweden, where it was maintained in a flume tank (4-m long, 0.5-m wide) with continuous water supply and adjustable water current (0–50 cm s⁻¹) at a temperature of 4–6°C and a salinity of ~34‰, i.e. conditions similar to where it was caught. The behavioural study was made in January and February 2004. *G. caputmedusae* was given a set of horizontally orientated bars where it attached orientated with its aboral side against the current. Video recordings were made horizontally through a window in the flume tank by using Videotronic Infosystems. Filming in darkness was made in IR-light.

Virtually no information was available on the feeding biology of *G. caputmedusae*. Live krill (*Meganctiphanes norvegica*) was collected as food in the deeper part (~100 m) of the Gullmarsfjord adjacent to the marine station.

Scanning electron microscopy

Distal pieces of arms of *G. caputmedusae* and entire specimens of *M. norvegica*, after they had been caught by arms of *G. caputmedusae*, were fixed in glutaraldehyde in seawater (4%). Fixation was followed by dehydration in a graded ethanol series. Samples were critical point dried using a CPD20 (Balzers Union). In order to isolate skeletal elements, pieces of arms of *G. caputmedusae* were boiled in saturated KOH. The isolated skeletal elements were then washed ten times in distilled water and air-dried. All samples were coated with gold in an Ion Sputter JFC-1100 (JEOL) and viewed in a JSMT220A (JEOL).

Histology and microscopy

Pieces of *G. caputmedusae* arms were fixed in 4% paraformaldehyde in filtered seawater (FSW) for 2 h at room temperature or 4°C overnight. They were then rinsed in

FSW and decalcified in 0.5 M EDTA for 24 h. The pieces were subsequently dehydrated in an ethanol series, then embedded in paraffin wax with melting temperature 55–58°C (Merck, Darmstadt, Germany). Sections (6–8 µm) were obtained using a Leica microtome (Leica Microsystems, Milton Keynes, UK) and mounted on slides coated with an egg white/glycerol mix and/or poly-L-Lysine. In order to visualize the connective tissue, sections were stained with Domagk's method after dewaxing and rehydration then permanently mounted using Poly Mount (Polysciences Europe, Eppeheim, Germany).

In order to identify nervous tissue in *G. caputmedusae*, we used the pan-neuronal monoclonal NeuN antibody (Chemicon international, Temecula, CA, USA), commonly used to identify neurons in vertebrates (Casella et al. 2004). Wax sections were processed for immunohistochemistry according to standard protocols. Specifically, blocking was performed in 10% normal goat serum in phosphate buffered saline (PBS: 136.9 mM NaCl, 2.7 mM KCl, 1.5 mM KH₂PO₄, 8.0 mM and Na₂HPO₄ at pH 7.4). The sections were incubated overnight at 4°C with the NeuN antibody diluted 1:100 in blocking solution. Secondary antibody and the following detection reaction were performed using the mouse IgG Vectastain elite ABC peroxidase kit (Vector laboratories, Burlingame, CA, USA) according to manufactures instructions. Diaminobenzidine (DAB) (Amersham Biosciences, Buckinghamshire, UK) was used as the peroxidase substrate in combination with nickel (Vector laboratories) for colour enhancement. A pretreatment of 10 min in 0.3% H₂O₂ in PBS was performed to quench the activity of endogenous peroxidase. The labelled sections were counterstained in eosin yellow (Sigma Aldrich, Poole, UK) for optimal contrast.

Slides were analysed using a Leica microscope adapted for digital imaging with a Canon S40 colour camera and Canon imaging software, all provided by Leica Microsystems. Images were processed by using Adobe Photoshop.

Results

Video recording in situ

Video recordings in situ by a ROV have been made in many deep-sea areas around the Norwegian–Swedish border, but to date *Gorganocephalus caputmedusae* has only been observed in three rather restricted areas at the mouth of the Oslofjord (T. Lundälv, personal observations). In November and December 2003, *G. caputmedusae* was found on four ROV inspected transects in the outer Oslofjord at 85 to 120-m depth. The distribution was generally patchy. Sometimes several individuals could be observed at the same spot, but basket stars could also be absent over large parts of the transects.

A strong association was observed between *G. caputmedusae* and the gorgonian *Paramuricea placomus* (L.)

where 35 of 90 gorgonocephalids were attached to the gorgonian on one 400-m long transect. *G. caputmedusae* was also found associated with, e.g. the coral *Lophelia pertusa* (L.) and the sponges *Geodia baretii* (Bowerbank) and *Phakellia* sp. In addition, *G. caputmedusae* was found on dead *L. pertusa* and coral rubble. Notably, however, *G. caputmedusae* was never observed in frequently occurring *Lophelia* and sponge habitats where gorgonians were lacking. The basket star was always attached with the oral side to the objects and the arms extended, forming the shape of a concave fan against the current. Krill, *Meganyctiphanes norvegica* (M. Sars), was abundant in the investigated areas.

Morphology and histology

The disc of *G. caputmedusae* was 6.5 cm in diameter and pentagonal in outline. The aboral side of the disc was light yellow in coloration with a granulated surface (Fig. 1). The five arms were highly branched and divided in a dichotomous way up to eight times. Several arms of the freshly captured specimen showed signs of regeneration.

The distal part of each arm was armoured by incomplete circles of spines and hooks. The spines appear pair-wise on the oral side close to the tube feet (Fig. 2a). The hooks, about 15 in each circular row, were on the aboral side of the arm regularly opposing each other with only the tips penetrating the epidermis (Fig. 2b). The spines were equipped with three to five spikes (Fig. 2c, d), whereas hooks only had two spikes (Fig. 2e). Note the extensive trabecular organization of the stereome at the proximal side of the spines, whereas the hooks were almost entirely smooth and joint-like on their proximal surface. Figure 2f shows a small hook penetrating the carapace of a krill (*M. norvegica*). The krill, which was trapped by the distal part of an arm of

G. caputmedusae, was immediately fixed for examination by scanning electron microscopy.

A cross section in an arm revealed the typical morphology of ophiuroids belonging to the order Phyrnophiuoidea (Fig. 3) with an epidermis overlying a thick layer of dermal connective tissue, four intervertebral muscles and a neural cord. The connective tissue layer is innervated and connected to the neural cord (Fig. 4). Each arm segment bears a pair of simple elongated tube feet (without bulb) adjacent to the arm spines. Tube feet present a classical organization with four layers: epidermis, connective tissue layer, nervous tissue, and coelomic epithelium. The nerve cord is connected to a ring ganglion at the base of each tube foot (Fig. 4). The NeuN antibody labelled the entire nerve cord and showed that the tube feet were heavily innervated (Fig. 5). Spines and hooks are attached to the lateral arm plate by both collagenous tendons and a single muscle. Some of the collagenous bundles connect to the adjacent spines (Fig. 6).

Feeding and general behaviour

In the experimental flume tank, *G. caputmedusae* was generally attached to the grid with some arms curled tightly on the bars. Most branches of the arms were stretched out (Fig. 1) in a parabolic arrangement facing the current with the aboral side. This position was interpreted as the active feeding position of the animal.

G. caputmedusae was in active feeding position both day and night as indicated by the arms bending against the current. On some occasions the basket star was found to have moved against the current and attached to an object at the other end of the flume, a distance of ~3 m covered in less than 8 h, illustrating the basket star's potential for mobility. The animal could change its position on the bar, probably in relation to current

Fig. 1 *Gorgonocephalus caputmedusae* attached to stones in the flume tank

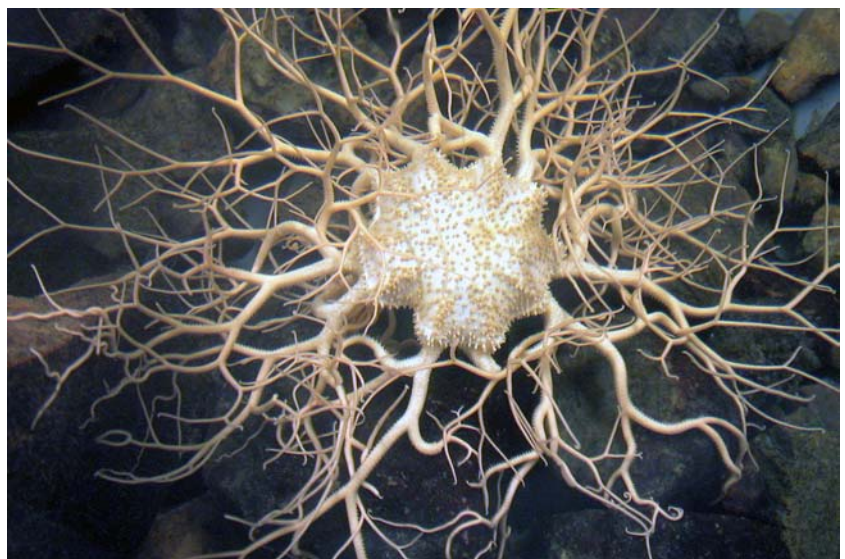
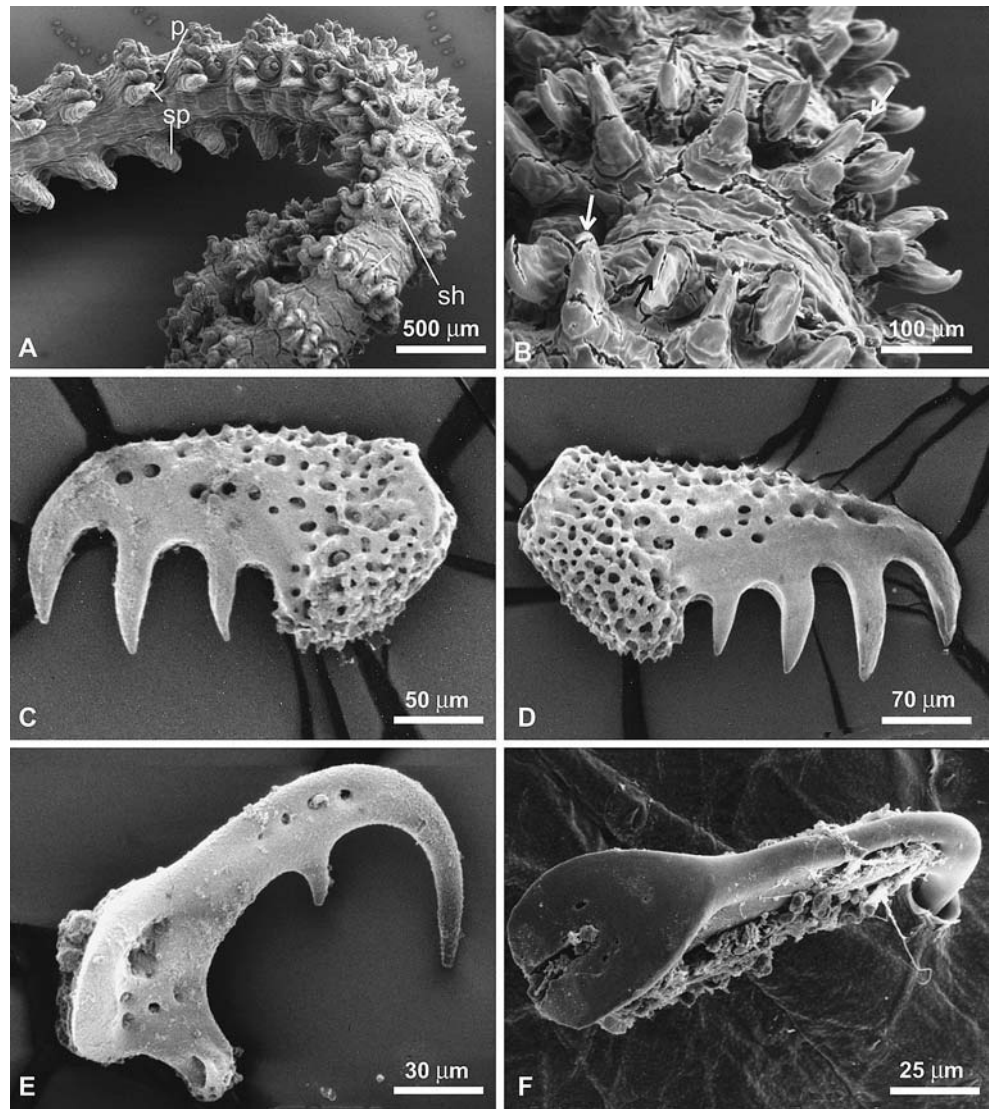


Fig. 2 Scanning electron micrographs of *Gorgonocephalus caputmedusae*. **a** Distal end of an arm to show the arrangement of spines and hooks. Each incomplete circle of hooks consists of a pair of spines (*sp*) on the oral side and about 15 small hooks (*sh*) on the aboral side; position of tube feet (*p*). **b** Enlarged view of dorsal rows of small hooks. Only the tips of the hooks are penetrating the epidermis. Note the regularly opposing arrangement of neighboring hooks. **c, d** Spines are equipped with two to five teeth. Note the extensive trabecular organization of the stereome at the proximal side of the spine. **e** Small hooks never possess more than two teeth. Note that at the proximal end the small hooks do not show the extensive trabecular skeleton structure. The proximal surface in small hooks is smooth and joint-like. **f** Hook penetrating the carapace of *Meganyctiphanes norvegica*. Note the joint like appearance of the proximal surface of the hook



speed, but without any obvious pattern. In high current speeds, 50 cm s^{-1} , it seemed to have difficulties to keep the arms stretched out and the number of curled arms increased, presumably to decrease drag.

Gorgonocephalus caputmedusae showed interest in food consumption every second or third day; when fed at closer intervals, the food was occasionally caught but released after some minutes. *G. caputmedusae* captured and ingested krill that was released in a flume tank at a distance of about 1 m up-stream from the basket star. The krill usually encountered some branches of the arms of the basket star within 30 s in different current speeds of 0, 20, 40 and 50 cm s^{-1} . When a food item touched an arm, generally the arm tip, the activity of that arm increased instantly. That arm branch or adjacent branches entangled the prey rather fast and within a few minutes the prey was entirely wrapped and could hardly be seen. As soon as a krill touched an arm, it could not escape even if swimming frantically with its pleopods. It was probably attached to the arm by the tube feet, which are sticky, and/or by the hooks that can penetrate through

the exoskeleton (Fig. 2f). On a piece of cut arm where a krill recently had been attached, 10–15 hooks were observed (in a dissecting microscope) to be erect whereas those away from the attached site were not.

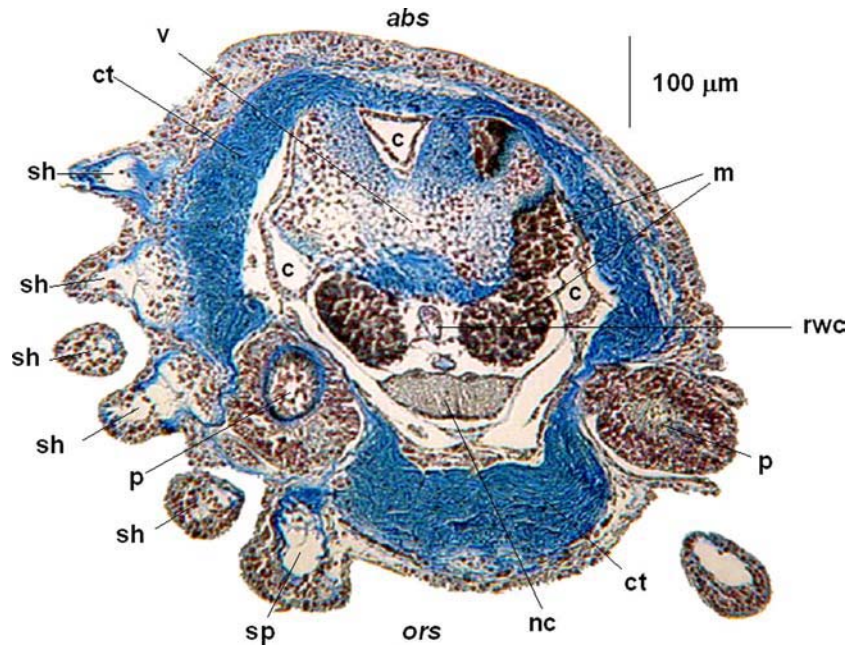
In most cases the prey was transported to the mouth. The time for this transport was measured to be between 11 min and 77 min for six specimens of trapped krill. It was not possible to observe how the prey was transferred into the mouth, because too many arm branches were hiding the prey and the mouth. After a while, in that position close to the mouth, the arm branches uncoiled and no prey was visible.

Discussion

Distribution

Gorgonocephalus caputmedusae seems to have specific habitat requirements, and in this study it was found to live in association with, e.g. *Paramuricea placomus*,

Fig. 3 *Gorgonocephalus caputmedusae* transversal section of an arm stained with Domagk's method. Aboral side (*abs*); oral side (*ors*); arm coelom (*c*); connective tissue (*ct*); spines (*sp*); intervertebral muscle (*m*); neural cord (*nc*); tube foot or podium (*p*); radial water canal (*rwc*); small hook (*sh*); vertical ossicle (*v*)



Lophelia pertusa and several species of Porifera, but always in proximity to *P. placomus*. This is in agreement with other studies of deepwater corals where gorgonocephalids have been found associated with *Lophelia* reefs in the Faroe Isles (Jensen and Fredriksen 1992) and with *Primnoa* spp. in the Gulf of Alaska (Krieger and Wing 2002). The habitat in the present study is characterised by rather uniform annual temperatures (4–8°C) and salinities (~34‰), and probably rather constant bottom currents. The distribution of *G. caputmedusae* seemed to be restricted to particular bottom areas with a patchy distribution. The congeneric *G. arcticus* was also found to have an irregular distribution in New Brunswick,

Canada. It was found in shallower water, 14–20 m (Emson et al. 1991), whereas *G. caputmedusae* in the present study was found at 85 to 120 m depth.



Fig. 4 *Gorgonocephalus caputmedusae* longitudinal section of an arm stained with Domagk's method showing the connection between neural cord and connective tissue layer (*arrow*) and the tube foot ring ganglion. Connective tissue (*ct*); intervertebral muscle (*m*); nerve (*n*); neural cord (*nc*); tube foot or podium (*p*); vertical ossicle (*v*)

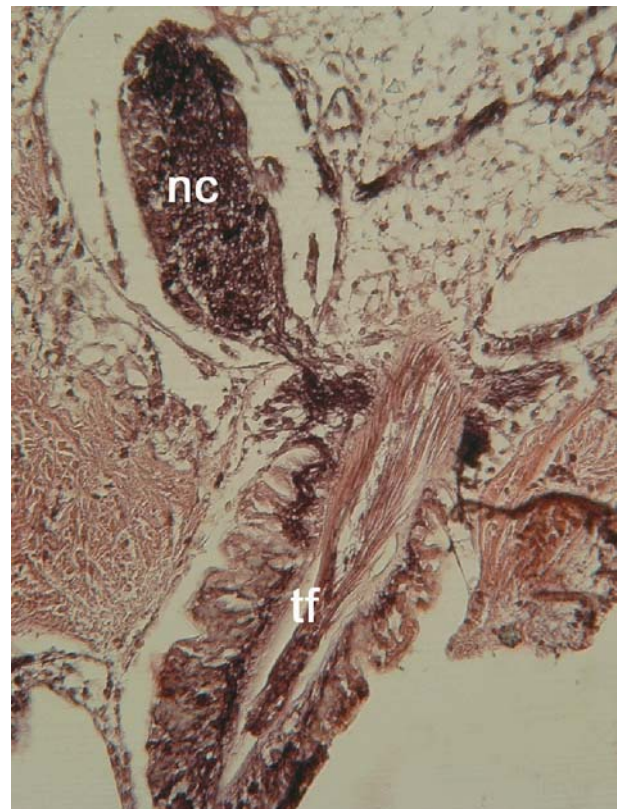


Fig. 5 Innervations of a tube foot (*tf*) of *Gorgonocephalus caputmedusae*. The nerve cord (*nc*) and its neuronal processes labelled by using a pan neuronal monoclonal NeuN antibody and a peroxidase mediated colour reaction that stains labelled structures black/brown in a transversal section. Eosin was used to stain the background reddish

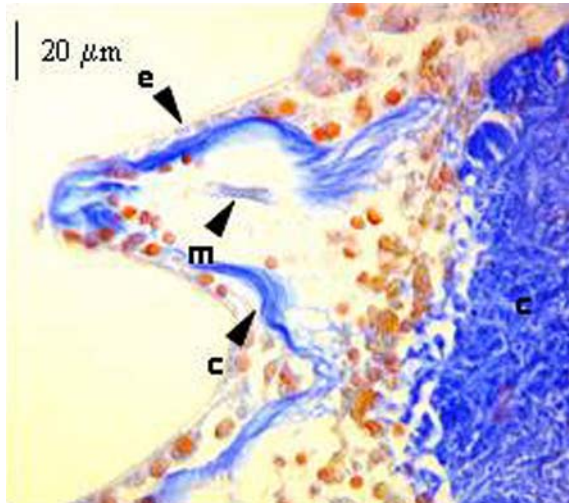


Fig. 6 Longitudinal section of hook articulation in *Gorgonocephalus caputmedusae* stained with Domagk's method showing muscle (*m*) and collagenous ligament (*c*). *e* epidermis

Feeding mechanisms

The feeding biology of *G. caputmedusae* has not been described before. The robust and armoured arms of *G. caputmedusae* most probably form too crude a filter apparatus for microscopic food and the structure rather suggests that macrophagy prevails, which relates to the classification by Warner (1982). The in situ observations made using a ROV showed that krill was abundant in the areas inhabited by the basket stars, which suggests that krill could be a main prey. Our experimental studies demonstrated that the arm tips of *G. caputmedusae* could trap krill; then the arm tips coiled around the prey, and the krill was subsequently moved to the mouth. Thus, the feeding behaviour can be traced to three steps: the feeding posture, the capture of the prey, and the transport to the mouth. These procedures were similar to those described in detail for *G. arcticus* (Emson et al. 1991). Similarly, Patent (1970) observed that *G. eucnemis* could catch plankters and move them to the mouth. Emson et al. (1991) found mainly krill in the stomach of *G. arcticus* collected from the sea and concluded that the anatomy and feeding behaviour of this species and in *G. eucnemis* are ill-adapted for efficient acquisitions of small prey. They could, therefore, be macroscopic suspension feeders just as *G. caputmedusae* in the present study. *G. caputmedusae* was, like *G. arcticus*, actively feeding both day and night, whereas the other described basket stars are nocturnal feeders (Emson et al. 1991).

Emson et al. (1991) found that many stomachs from *G. arcticus* were empty and suggested that prey encounter could be occasional. Thus, the basket star has to maintain a feeding posture with arms bending against the current for extended periods of time. Histological sections revealed the presence of a thick layer of dermal connective tissue innervated by the nerve cord together with small intervertebral muscles. Ophiuroids belonging

to Phrynophiuroida usually have a fleshy integument due to the preponderance of connective tissue in their dermis playing the role classically fulfilled by calcified skeleton in other ophiuroids (Byrne and Hendler 1988; Byrne 1994). This connective tissue is mutable, it is able to rapidly alter (time course less than 1 s to few minutes) its mechanical properties (Motokawa 1984; Wilkie 1984). The stiffness is under neural control (Wilkie 1984, 2002) by a sophisticated system of neurotransmitters (e.g. acetylcholine) and neuromodulators (e.g. neuropeptides) (Motokawa 1981, 1984, 1987; Mladenov et al. 1989; Birenheide et al. 1998). This mutable connective tissue, unique to echinoderms, is used in Phrynophiuroida for reversible modification of stiffening/softening behaviour (Sides 1987; Byrne & Hendler 1988) in order to control the feeding posture without the need of muscular activity and thus without investment in energetically demanding muscle cells (Wilkie 1978; Emson and Woodley 1987; Byrne and Hendler 1988).

Tube feet, spines and hooks

Since prey encounter could be occasional (Emson et al. 1991), it is vital to retain encountered prey. Tube feet, spines and hooks are most probably used for capturing and holding prey. Tube feet play many roles in echinoderms: feeding, locomotion, gas exchange and sensory perception (Byrne 1994). Basket stars have minute podia and some authors suggest that they mainly function as sensory structures and in gas exchange (Wolfe 1982; Emson et al. 1991). Our observations on *G. caputmedusae* suggest that the tube feet might also be used for prey capture. The tube feet are very sticky and the fact that krill were attached to an arm tip so tightly that they could not swim away, suggests that tube feet, probably in combination with hooks (Fig. 2f), are instruments for initial capture. Since no terminal bulb is visible on tube feet, an adhesive mucous is probably secreted by mucous podial gland (as described by Emson et al. 1991 for *G. arcticus*).

Spines (large hooks) and small hooks of *G. caputmedusae* are clearly modified lateral spines. As with any ophiuroid spines, they are attached to the lateral arm plate by a ring of collagen and a single spine muscle (Byrne 1994). Contraction of this muscle causes the spine to move proximally downward and serves to re-erect the spine after it has been deflected by external forces (Wilke pers. com. in Byrne 1994). Patent (1970) stated that each hook had muscles, but showed no evidence for this. In contrast, Emson et al. (1991) found no proof that muscles were attached to the hooks. In the present study, it is shown for the first time that muscles are indeed connected to the spines and hooks of *G. caputmedusae*. The muscles are suggested to fit to the joint-like appearance on the hooks (Fig. 2e, f). Therefore, it is likely that spines and hooks play a much more active role in the capturing of macroscopic plankton organisms than hitherto believed. Spines and hooks of

G. caputmedusae can be moved actively, which makes the arms much more useful in catching prey.

In Euryalinids, the hook-shaped spines help to secure prey caught by the arms (Mortensen 1932; Patent 1970; Hendler and Miller 1984; Dearborn et al. 1986; Emson and Woodley 1987; Emson et al. 1991). Also in other phyla, hook-like appendages have developed for food capture. For example sponges of the genus *Asbestoplu-ma*, living in nutrient-deprived environments, have evolved carnivory and capture small crustaceans passively by means of hook-shaped spicules (Vacelet and Boury-Esnault 1995). In *G. caputmedusae*, the hooks on the aboral side of the arm can penetrate the exoskeleton of crustaceans and initially help to keep the prey attached to the arm. Later, during the coiling of the arm, the spines on the oral side also could help holding the prey.

When the prey is captured at an arm tip, the activity of that arm increased instantly, coiling around the prey. Such movements were also described in crinoids after mechanical stimulation. Arm flexure resulted from the contraction of large flexor muscles, and the recovery from the elastic recoil of ligaments (Young and Emson 1995). The presence of a similar thick layer of connective tissue suggests a similar process in *G. caputmedusae*.

The shape and morphology of spines and hooks in *G. caputmedusae* (Fig. 2) and *G. arcticus* (Emson et al. 1991) showed an astounding resemblance suggesting that the two species use the same mechanism for feeding. This suggests that the species have a common origin, but have maintained a successful technique for being macroscopic predators.

Conclusions

This is the first documentation of *G. caputmedusae* feeding behaviour. This species is able to hold arms extended in the feeding posture for long periods at low energy costs thanks to the presence of dermal connective tissue. The prey is captured by using both sticky tube feet and hooks that can move by muscular action and penetrate the exoskeleton of krill. After contact with the prey, neurally mediated signals may induce a change in the mechanical properties of the connective tissue that becomes soft and flaccid. Contraction of the muscles allows the arm to entangle the prey and transport it to the mouth. Spines and hooks help to secure the prey caught by the arms.

Our data on behaviour and functional anatomy show that *G. caputmedusae* is well adapted for catching large prey such as *M. norvegica*.

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