OBSERVATIONS ON THE WHITE SEA HYDROID, *SARSIA PRODUCTA* (WRIGHT, 1858) (HYDROZOA: ATHECATA)

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SARSIA

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Polyps of the White Sea hydroid *Sarsia producta* were collected, described and figured, in order to gain new insight into its ecology, morphology, colonial structure, and behaviour. Specific modes of feeding behaviour were observed on hydroids *in situ*, and their diet was examined. The diet of *Sarsia producta* is diverse and based on a wide range of items from different systems: dead organic matter, settled on the substrate or suspended in the water, phytoplankton and zooplankton, and epibenthic animals and algae. Successful capture of such a variety of food items is achieved by the particular feeding movements of the flexible body, well co-ordinated with the movements of hypostome and capitate tentacles. In total, these movements create a complicated feeding behaviour unusual among hydroids.

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INTRODUCTION

Colonial hydroids of the genus *Sarsia* Lesson are reported to grow on various substrata in different areas. Thus, *Sarsia japonica* (Nagao) from Japanese waters live in 3-5 m depth on submerged bamboo, shells of *Mytilus* sp., the red alga *Hypnea* sp., bare rocks, and polychaete tubes (Kubota & Takashima, 1992). The colonies of *S. piriforma* Edwards and *S. striata* Edwards grow on clinker in 15-20 m depth (Edwards 1978, 1983), while *S. tubulosa* (Sars) are found in shallow water on stones, molluscan shells and algae (Naumov 1969; pers. obs.).

In the White Sea, the only species of the genus *Sarsia* recorded so far, are *S. tubulosa* and *S. producta*, the former species being abundant in shallow water. The polypoid stage of the latter species has been recorded from the UK coasts, the English Channel and North Sea coasts of Europe (Hartlaub 1895; Drzewina & Bohn 1916; Russell 1953; Kramp 1935, 1937), from Brazil (Vannucci 1949), Japan (Hirai 1960) and Massachusetts, USA (West 1974). None of these records of *S. producta* include much information on distribution and location, or any data on the behaviour of the hydroid. Moreover, in most cases very few polyps were obtained from the sea, the material usually being supplemented by hydranths reared in the laboratory under controlled conditions (Hincks 1862; Hartlaub 1895; West 1974). The reports from different areas describe the polyps of *S. producta* to vary slightly in proportions, distribution and number of tentacles, location of medusa-buds on the polyp, and colonial structure (Hincks 1862,1868; Hartlaub 1895; Russell 1853; Brinckmann-Voss 1970, 1989; West 1974).

The hydroid has been recorded twice from the White Sea (Mereschkowsky 1878; Shidlowsky 1902) under the name *Stauridium productum*, but these records were not accompanied by any description or drawing, and the specimens were not preserved (Naumov 1969). Medusae of *S. producta* have never been recorded for the Russian coasts except for twenty immature specimens that were once collected in the Sea of Okhotsk by plankton sampling (Naumov 1969). Thus, *S. producta* was announced to be a rare species for Russian seas (Naumov 1969). In Kandalakshsky Bay of the White Sea, colonies of *S. producta* have been accidentally found a few times in the last twenty years by SCUBA-divers, but the colonies were neither described nor preserved, and no data were recorded on their ecology (N. Marfenin & R. Margulis, pers. commn).

The aim of the present study is to describe the polypoid stage of *S. producta*, its colonial structure, behaviour and feeding strategy, in the White Sea.

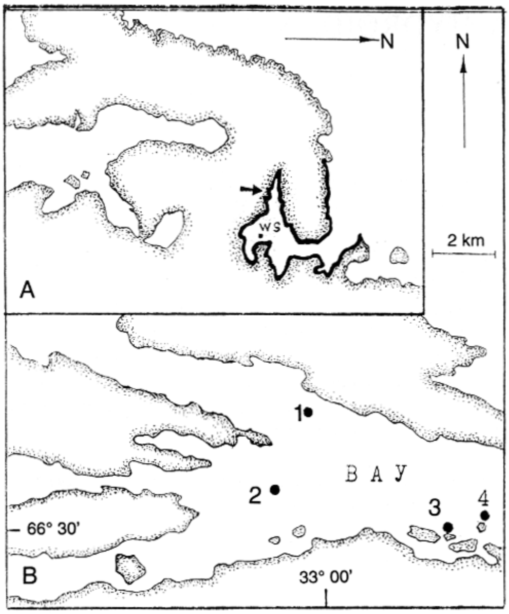

Fig. 1. The locations of *Sarsia producta* collected in Kandalakshsky Bay of the White Sea: 1 - Cape Lobanikha, 15 m deep, 2 - Cape Kindo, 16 m deep, 3 - Kastjan island, 22 m deep, 4 - Kokoikha island, 23-25 m deep.

MATERIAL AND METHODS

In the summer, from June to September, of 1995, a large variety of substrata at various depths was examined using SCUBA in Kandalakshsky Bay of the White Sea (Fig. 1). Gastropod shells with colonies of *S. producta* were found under the thermocline in a nearly constant temperature of 3-5° C, near the islands Kastjan and Kokoikha, and in shallow-water locations subject to seasonal temperature fluctuations, from 8-10° C in summer to 3-5° C in winter, near Cape Lobanikha and Cape Kindo (Table 1).

Colonies were brought to the laboratory and reared in glass vessels under controlled conditions at 10° C. Nematocysts, freshly prepared from living material were identified and measured under an oil immersion objective.

To study the diet of the species, thirty mature polyps of *S. producta* were dissected 2 h after they had been taken from the sea and transported to the lab by boat; their coelenteric contents were examined under a microscope. Other polyps were fed freshly released nauplii of *Artemia salina* once every few days, while their feeding behaviour and life-cycle were observed under a binocular microscope.

RESULTS

Hydroid

Stauridia producta: Wright, 1858 (original description); Hincks 1861; Stechow 1919; Naumov 1969.
Stauridium productum: Hincks 1862, 1868; Allman 1871-1872; Mereschkowsky 1878; Plessis 1881; Crawford 1895; Hartlaub 1895, 1897; Shidlowsky 1902; Bedot 1905; Drzewina & Bohn 1916; Mayer 1910; Kramp 1935.
Coryne productum: Schneider 1898.
Stauridiosarsia producta: Poche 1914; Russell 1953; Rees 1938, 1957; Hirai 1960; Kramp 1961; Kakinuma 1965a, b; West 1974.
Sarsia producta: Mayer 1910; Ranson 1925; Kramp 1937, 1961; Vannucci 1949, 1956; Brinckmann-Voss 1970, 1989; Bouillon 1985; Kubota & Takashima 1992.

The red-coloured hydranth is clavate and slim, 1.5-2.8 mm high (n = 40), with three whorls of four (sometimes five) capitate tentacles each. In every whorl, the length of a relaxed capitate tentacle is 0.4 ± 0.02 mm (n = 30), and of a contracted one - 0.2 ± 0.01 (n = 30). The oral whorl encircles the mouth near the top of the hypostome. The whorls are equidistant, 0.25 ± 0.01 mm (n = 30) apart. Each apical cluster of nematocysts on the tips of the capitate tentacles consists of 50 ± 6 (n = 30) nematocysts, among which stenoteles of two types were identified. The dimensions, length x width, of undischarged capsules of the two types are (14.4-16.6) x (9.5-10.5) µm, and (29.2-30.8) x (18.1-19.9) µm, respectively (Fig. 3).
In the middle of the hydranth, below the basal whorl of capitate tentacles, a single whorl of four filiform tentacles is always present. These tentacles are of the same length as the capitate ones, or shorter, and lack nematocysts. While the distances between the four whorls are constant, the height of the polyp varies due to the length of the stalk

Table 1.Locations of the colonies of *Sarsia producta* collected in Kandalakshsky Bay.

Location	Depth, m	Molluscan shell	Type of shell	Colonies
Cape Lobanikha	15	Neptunea communis	old and empty	+
	15	Buccinum undatum	hermit crab	+ + +
Kastjan island	18	Neptunea communis	old and empty	+ +
Kokoikha island	25	Neptunea despecta	old and empty	+ +
	20	Neptunea despecta	hermit-crab	+ +

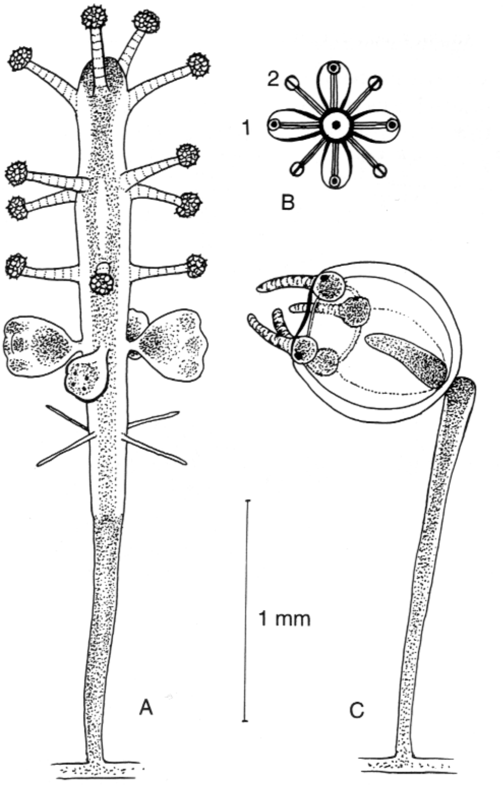

Fig. 2. The hydroid of *Sarsia producta*. A. The mature fertile hydranth. B. Schematic top view of the hydranth: the first plane of symmetry (1) is created by the 1st and 3rd whorls of capitate tentacles plus medusa buds. The second plane of symmetry (2) is organised by the 2nd whorl of capitate and the coinciding filiform tentacles. C. Young medusa detaching from the degenerating polyp.

below the filiform tentacles. The lower part of the mature polyp is covered with a yellow-brown perisarc, which makes the polyp stand upright. Midway between the lowest whorl of capitate and the one of filiform tentacles, two to four medusa buds in different stages of development are attached to the hydranth by short, unbranched stalks (Fig. 2).

All the tentacles and medusa buds are placed symmetrically, creating a radial symmetry of the polyp. The capitate tentacles of the first and third whorls along with the medusa buds are positioned directly above each other, while the capitate tentacles of the second whorl and the filiform tentacles, are positioned at an angle of 45° to the first plane of symmetry (Fig. 2B).

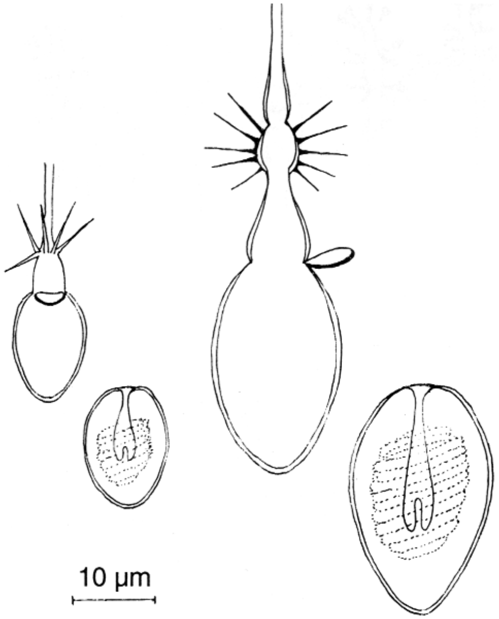

Fig. 3. Nematocysts: stenoteles of the two types.

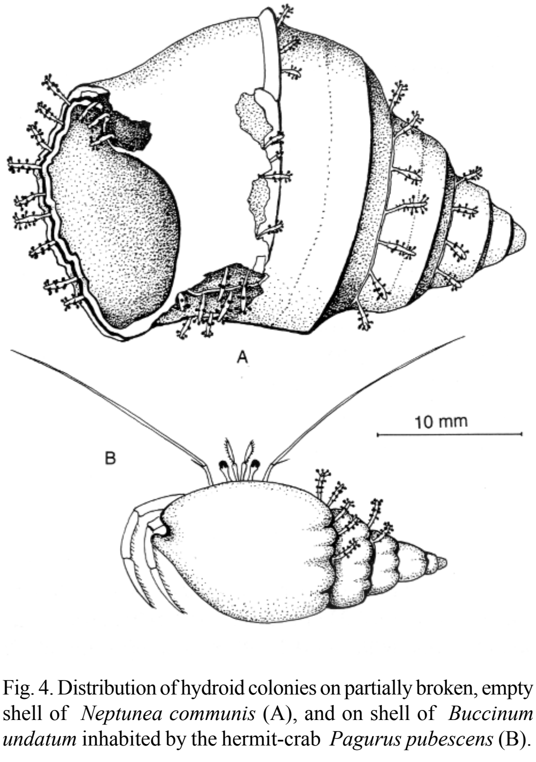

Fig. 4. Distribution of hydroid colonies on partially broken, empty shell of *Neptunea communis* (A), and on shell of *Buccinum undatum* inhabited by the hermit-crab *Pagurus pubescens* (B).

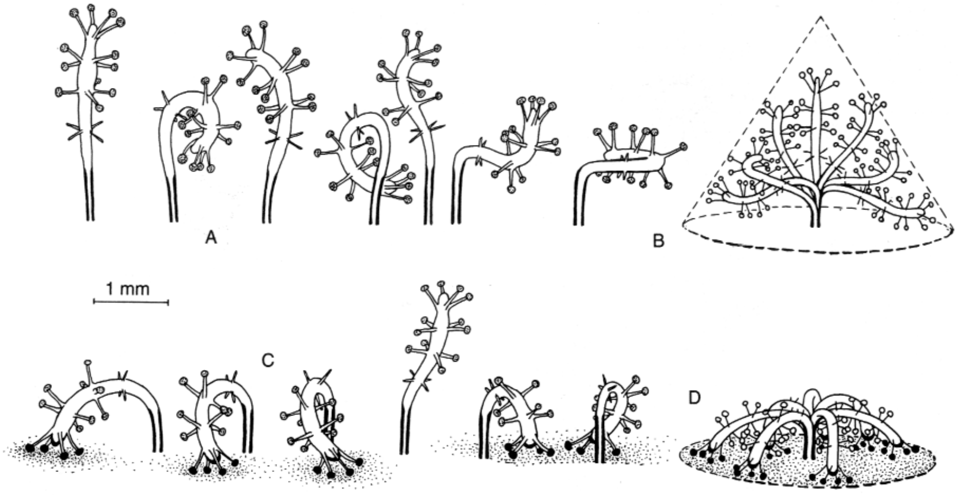

Fig. 5. Feeding behaviour. A. Movements performed by the polyp when searching for planktonic prey. B. Conical volume of water combed by the tentacles og the polyp in search of prey. C. Movements of the oral tentacles when dredging the substrate. D. Circular area of the substrate covered by the tentacles when searching for benthic food particles.

The hydrorhiza of *S. producta* consists of creeping and poorly branched stolons, situated in the sutures between the whorls of the shell, and in hollows and crevices of the shell surface (Fig. 4).

Growth of hydranths and medusae

The hydranth buds are formed 1.2-3 mm from the tips of the growing stolons. The oral whorl appears on the bud on day two after the bud formation; the second whorl is formed on the bud on day five, the third whorl on the next day, while the whorl of filiform tentacles appears on day seven. At this stage, the week old hydranth is able to catch various prey and feed successfully.

During summer, while the male and female medusa buds complete their development, the fertile polyps degenerate and lose all their tentacles, before the last developed medusa detach. At the moment of release, the medusa of *S. producta* with an umbrella height of 0.8 ± 0.05 mm ($n = 9$) from top to velum, possesses a short red-coloured manubrium 0.4 ± 0.03 mm long ($n = 9$), four radial canals and four short tentacles 0.2 ± 0.05 mm long with a black ocellus on each red-coloured tentacular bulb (Fig. 2C). The nematocysts of the recently liberated medusa are stenoteles of the same two types as those of the polyp.

Microhabitat

In Kandalakshsky Bay of the White Sea, ten colonies of *S. producta* were collected on gastropod shells, either old and empty or inhabited by hermit-crabs (Fig. 1).

Six of the best developed colonies were found on empty, old and partially broken large shells of *Neptunea despecta* 100-130 mm long, and *Neptunea communis* 30-60 mm long, while the other four were found on shells of *N. communis*, 40-50 mm long, and *Buccinum undatum*, 20-40 mm long, both inhabited by the hermit crab *Pagurus pubescens* (Table 1).

The habitats were characterized by reduced water movement, there were no tidal currents, and the surface wave movements did not reach down to the bottom. The underwater topography and bottom community from which the colonies had been collected, were of the same type in all the locations. The shells with *S. producta* were found on slight slopes of fine sand covered with a thin layer of silt, through which various boulders, stones and molluscan shells protruded. The communities were characterized by large numbers of live gastropods of *Neptunea* sp. and *Buccinum* spp., and hermit-crabs inhabiting dead shells. Other common hydroids on such shells were the hydractiniids: *Hydractinia allmani* Bonnevie, *Hydractinia carica* Bergh and *Hydractinia serrata* Kramp. However, these were never recorded on the same shells as *S. producta*. The only hydroid found to grow on the same shell with *S. producta*, was *Catablema abyssi* (Sars).

Reaction to light, temperature and mechanical stimuli

The behaviour of *S. producta* is not photodependent. Polyps neither contract nor move immediately after illumination is switched on or off. However, they do react to their substrate being shaken, by quick twisting and bending to the substrate. If the polyps are disturbed by needle-touching, they contract their bodies and all the tentacles. If the temperature is changed from 10° C down to 0° C, or up to 18° C, the polyps swell and contract. It takes about one day for the polyps to reacquire their normal shape and proportions after the temperature has been restored.

Prey searching

The polyps of *S. producta* are very flexible and constantly move, bending and twisting in different directions, searching for prey. The perisarcal hydrocauli in the proximal parts of the polyps are the only parts always remaining upright, though the younger polyps without any perisarc, can bend their entire bodies. While the polyps move or bend to the surface of the substrate, their hypostomes are able to sway or move around in circles (Fig. 5A). The polyps conduct these searching movements regularly, thus combing a conical volume with their twelve tentacles (Fig. 5B). A potential prey, which actively enters or is transported by a water current into this cone, is caught by the clusters of tentacular nematocysts of the constantly moving polyp.

In search for benthic prey, *S. producta* conducts movements of another mode. The polyp bends down to the substrate, forming an arch, and drags the hypostome with extended oral tentacles along a straight line, dredging the substrate by the nematocyst clusters on the tips of the oral tentacles. Then it bends to another side and starts the dredging movement along a parallel line. In this way, the polyp combs the surface in a circle, whose radius depends on the height of the polyp (Fig. 5C). The polyp can also dredge the substrate by its open mouth alone, with the oral tentacles directed backwards (Fig. 5D).

Prey capture

When one of the oral tentacles get into contact with a planktonic protozoan, the polyp quickly joins the other oral tentacles to the first one as if ‘applauding’, whereupon the first tentacle places the prey into the opened mouth. If a protozoan is caught by a tentacle of the lower whorls, the polyp quickly bends down and joins the first tentacle to an oral one, which then takes the prey and puts it into the mouth (Fig. 6A). Observations on the feeding polyps during a total of 48 hours showed that the most common prey of *S. producta* were infusorians (Ciliophora).

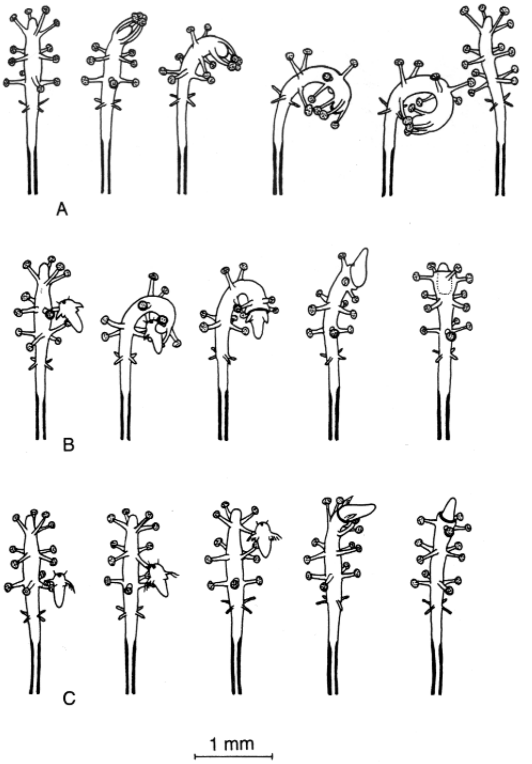

Fig. 6. Transport of prey to the mouth. A. Movements of capitate tentacles when capturing a protozoan. B, C. Two different modes of transport of an *Artemia* nauplius from the basal whorl of capitate tentacles to the mouth.

The behaviour while capturing a bigger planktonic prey, was observed by feeding the polyps *Artemia* nauplii. After an oral tentacle has anchored a nauplius, it rises to the mouth, which then swallows the prey. When a nauplius is caught by a tentacle of the second or third whorl, the polyp bends down, takes the prey into the mouth and straightens up, swallowing the nauplius (Fig. 6B). In another mode of a prey transport, a lower tentacle catching an *Artemia* passes it to a tentacle of the next whorl, this one to an oral tentacle, which finally passes the nauplius into the mouth (Fig. 6C).

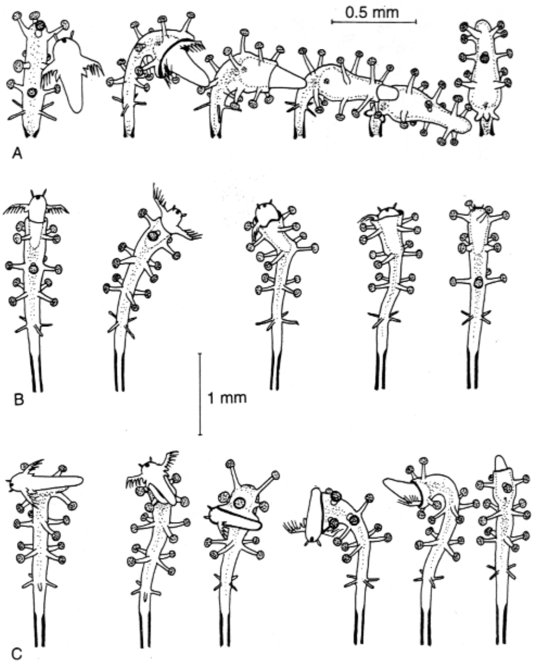

Fig. 7. Swallowing of prey. A. Immature, young polyp swallowing an *Artemia* nauplius with its head downwards. B. Polyp swallowing a nauplius with its head pointing upwards. C. Behaviour of the polyp swallowing a nauplius in a position transverse to the axis of the polyp.

Table 2. Prey items found in the stomach contents of 30 dissected polyps.

	Number of polyps
Planktonic items:	
Flagellata (Protozoa)	16
veligers of Gastropoda	10
trochophores of Polychaeta	8
Rotatoria	7
Copepoda	7
nauplii of Cirripedia	5
Cladocera	1
Ostracoda	1
Benthic items:	
Diatomea	5
Peridinea	2
Polychaeta	4
Nematoda	3
Turbellaria	1

Prey swallowing

The inflexible capitate tentacles of immature polyps can not place a prey directly into the mouth in the most convenient position for swallowing, and the mouth takes the prey in the position it was captured by the cluster of nematocysts of the tentacle. The most convenient orientation of a nauplius for swallowing is with its head downwards in parallel to the axis of the polyp. If the nauplius is inclined at some angle, the mouth changes its position to a more convenient one (Fig. 7A). It takes about one minute for an immature, young polyp to swallow a nauplius that is positioned with its head downwards (Fig. 7A).

A position with the head up and the nauplius in parallel to the polyp's axis, is also suitable. However, developed extremities of the nauplius make swallowing difficult and sometimes even impossible. In such cases, the polyp digests the posterior part of the prey first, and then (5-6 hours later) the rest of the prey (Fig. 7B).

A nauplius located transversely to the polyp's axis, is harder to swallow, particularly if it is relatively big and possess well-developed extremities. In this case, the polyp stretches the mouth in order to swallow the nauplius, and helps this process by regular bending to the substrate and straightening up (Fig. 7C). Sometimes, the polyp can not stretch its mouth wide enough and will then release the nauplius to change its position in parallel to the axis, a process that takes up to 3 hours.

An overfed, mature polyp can catch and swallow one by one, up to eight *Artemia* nauplii in different positions, swelling to an enormous shapeless sack with visible prey inside the coelenteron. Such polyps are able neither to bend nor to move any part of their bodies. Nevertheless, nematocysts are always discharged at the moment a prey is contacted, and the polyp tries to bend its hypostome down to take the prey into its mouth. The polyp succeeds after the first portion of prey is digested (Fig. 8). Thus, *S. producta* feeds as long as it can move and swallow a prey, and there is thus no physiological regulation of the nematocyst discharge or of the feeding process.

Each tentacle can anchor and keep a nauplius, and transport them one after another to the mouth. The polyps full of prey remain motionless, unlike the hungry ones, which always twist and move in their search for prey.

Stomach contents

Various prey items were discovered in 26 of 30 dissected polyp stomachs. The most abundant prey was various developmental stages of copepod nauplii (18 of the 26 stomachs surveyed). The stomach of *S. producta* also commonly contained various planktonic and benthic organisms (Table 2).

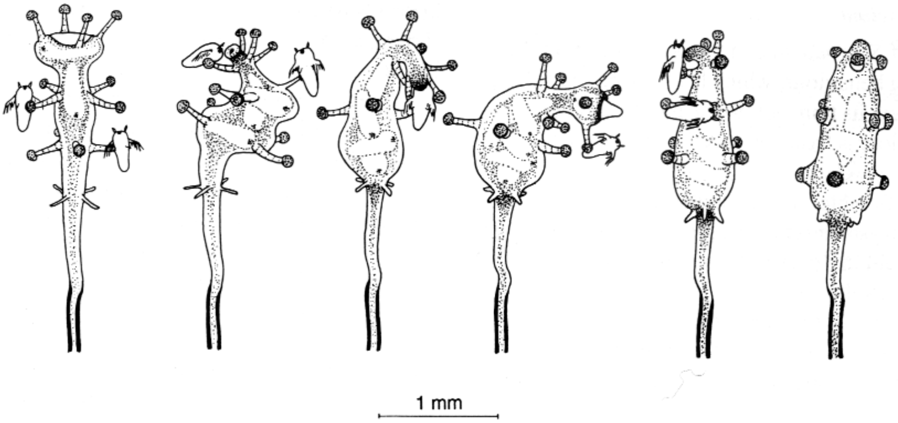

Fig. 8. Polyp morphology and behaviour in the later stages of overfeeding. Polyp at right with eight nauplii in its stomach.

DISCUSSION

Morphological diversity in the polypoid form of Sarsia producta

The morphs of *S. producta* from different areas vary mainly in distribution and number of capitate tentacles, number of whorls, position and number of medusa buds, and the presence and number of filiform tentacles (Table 3). Thus, mature laboratory-reared polyps from Helgoland are reported to possess two complete whorls of capitate tentacles, while the third one is usually replaced by medusa buds, and the whorl of filiform tentacles tends to be missing (Hincks 1868; Hartlaub 1895). In the polyps from the Brazilian coast, up to 15 capitate tentacles are spread without order over the proximal part of the polyp body, while a whorl of five filiform tentacles is always present (Vannucci 1949). American *S. producta* from Massachusetts salt marshes, possess 15 capitate tentacles organised in three whorls, and the basal whorl of four filiform tentacles (West 1974). West (1974) reported also, that the epidermis of the stolon had numerous nematocysts. Between one and five medusa buds are produced either midway between the proximal whorl of capitate tentacles and the basal whorl of filiform tentacles (Hartlaub 1895; West 1974; Orlov, present study) or near, or at the level of the proximal whorl of capitate tentacles (Hincks 1868).

In most previous studies only one or a couple of stolons with very few polyps were obtained by dredging (West 1974), and many of the descriptions of *S. producta* were based on laboratory-reared material. These polyps usually varied slightly from the others collected in the sea, in number of whorls and presence of filiform tentacles (Drzewina & Bohn 1916; West 1974). This paper presents the first description of well-developed colonies of *S. producta* from the sea. Never before have so many mature fertile polyps been discovered on natural substrata.

Table 3. Morphological variation of the polyps of *S. producta* from different sites. c - capitate tentacles; f - filiform tentacles. Use of brackets (1f) signifies that the whorl in question tends to be missing.

Site	Tentacle number	Whorls	Medusa buds	Author
White Sea	up to 15c + 3-4f	3c + 1f	+	Orlov, present study
Massachusetts	15c + 4f	3c + 1f	+	West 1974
England	up to 15c + 3-6f	3c + (1f)	+	Hartlaub 1895
Helgoland	up to 10c + 4-6f	2c + (1f)	+	Hincks 1868
Brasilian coast	12c + 5f	3c + 1f	+	Vannucci 1949
Mediterranean	12c + 4-6f	3c + 1f	+	Brinckmann-Voss 1970
France(Channel)	12-15c + 4-6f	2-3c + 1f	+	Drzewina & Bohn 1916

Feeding behaviour

The polyps of *S. producta* conduct a specific multidirectional feeding behaviour, which leads to successful capture of the prey, its transport to the mouth and ingestion. Such a behaviour is based on specific features in the morphology of *S. producta.*

1. Short, inflexible, capitate tentacles with apical clusters of nematocysts can anchor a prey larger than the polyp itself, and retain this prey until the polyp bends down its hypostome to swallow it.
2. Three levels of tentacle whorls ensure a large prey capture volume, as well as regular transport of a prey from the lowest whorl through the middle and oral ones, to the mouth.
3. Distinct and extensive flexibility of the polyp's body, the hypostome in particular, compensate for the shortness of capitate tentacles and makes it possible to feed on the substrate surface, as well as from the surrounding water. Unlike hydroids of the suborder Filifera and most capitate hydroids with contractile but nearly motionless bodies and active tentacles, the polyps of *S. producta* use their flexible bodies instead of tentacles, for all kinds of multidirectional feeding movements.
4. Plasticity of the hypostome and mouth allow hydranths to swallow prey even bigger than the polyp itself.
5. The colonial structure of *S. producta* is also adapted to the feeding behaviour. Thus, the distances between polyps on a stolon are long enough to prevent them to interfere with the feeding zones of each other.

The stomach content confirms that *S. producta*, like many other hydroids studied, feed on a variety of prey items, and is not specific in diet.

Feeding strategy

Previous studies on feeding biology of hydroids include investigations on physiology and energy budgets (LENHOFF 1974), feeding rates and diets (CHRISTENSEN 1967; PARDY 1971; BARANGE 1988; BARANGE & GILI 1988; MARFENIN & KHOMENKO 1989), behaviour (FULTON 1963; LETUNOV & MARFENIN 1980; CLARK & COOK 1986), and strategy (COMA & al. 1995). All these papers emphasize the biomechanical design of hydroids as being typical of active or passive suspension feeders, with their proportions and sizes adapted to the structure of potential prey and reflecting a trade-off between biomechanical, energetic and ecological constraints (RUBENSTEIN & KOEHL 1977; SEBENS 1982; PETERS 1983; LABARBARA 1984; RYLAND & WARNER 1986; BARANGE 1988).

On the basis of their strategies for capturing prey, colonial hydroids might be divided into four main groups.

1. True planktivores, actively or passively feeding on phyto- and zooplankton. These are modular thecate hydroids with well-developed colonies and small zooids, sieving a prey from moving water by their filiform tentacles.
2. Specialised benthic forms that capture benthic organisms available in their habitat (NAUMOV 1969; BRINCKMANN-VOSS 1970; CALDER 1988; PIRAINO & al. 1992).
3. Commensal hydroids feeding directly on their sessile invertebrate hosts, or on parts of their hosts' food supply (HAND 1957; CAMPBELL 1968; ROBINS 1972; KUBOTA 1983; PIRAINO & al. 1992, 1994)
4. Species with a multidirectional feeding strategy, capturing prey from different sources: zooplankton, sessile organisms dislodged by waves, mobile benthic animals, and dead organic matter (BARANGE 1988; BARANGE & GILI 1988).

Sarsia producta belongs to the last group and exploits different food resources to a far greater extent than most other species studied: phyto- and zooplankton including protozoans; epibenthic animals; benthic sessile or mobile organisms including sessile protozoans and algae; sedimented organic matter, and organic detritus suspended in the water.

REFERENCES

Allman, G.J. 1871-1872. *A Monograph on Gymnoblastic or Tubularian hydroids*. – Ray Society, London. 450 pp.

Barange, M. 1988. Prey selection and capture strategies of the benthic hydroid *Eudendrium racemosum*. – *Marine Ecology Progress Series* 47:83-88.

Barange, M. & J.M. Gili 1988. Feeding cycles and prey capture in *Eudendrium racemosum* (Cavolini, 1785). – *Journal of Experimental Marine Biology and Ecology* 115:281-293.

Bedot, M. 1905. Materiaux pour servir a l'histoire des Hydroides. 2^{e} periode (1821 à 1850). – *Revue Suisse de Zoologie* 13:1-183.

Bouillon, J. 1985. Essai de classification des Hydropolypes - Hydromeduses (Hydrozoa - Cnidaria). – *Indo-Malayan Zoology* 1:29-243.

Brinckmann-Voss, A. 1970. Antomedusae - Athecata (Hydrozoa, Cnidaria) of the Mediterranean. Part I, Capitata. – *Fauna Flora Golfo Napoli* 39:1-96.

— 1989. *Sarsia cliffordi* n. sp. (Cnidaria, Hydrozoa, Antho-medusae) from British Columbia, with distribution records and evaluation of related species. – *Canadian Journal of Zoology* 67:685-691.

Calder, D. 1988. *Shallow-water hydroids from Bermuda: the Athecatae*. – Royal Ontario Museum, Life Sciences division. Contribution No. 148.

Campbell, R. D. 1968. Host specificity, settling and metamorphosis of the two-tentacled hydroid *Proboscidactyla flavicirrata*. – *Pacific Science* 22:336-339.

Christensen, H. E. 1967. Ecology of *Hydractinia echinata* (Fleming) (Hydroidea, Athecata). 1. Feeding biology. – *Ophelia* 4:245-275.

Clark, S.D. & C.B. Cook 1986. Inhibition of nematocyst discharge during feeding in the colonial hydroid *Halocordyle distincha* (= *Pennaria tiarella*): the role of previous prey-killing. – *Biological Bulletin* (Woods Hole, Mass.) 171:405-416.

Coma, R., J.P. Gili & M. Zabala 1995. Trophic ecology of a benthic marine hydroid, *Campanularia everta*. – *Marine Ecology Progress Series* 119:211-220.

Crawford, J. H. 1895. The hydroids of St. Andrews Bay. – *Annual Magazine of Natural History* 16:256-262.

Drzewina, A. & G. Bohn 1916. un changement du type de symetrie (symetrie metabolique) chez un Hydraire, *Stauridium productum*. – *Comptes Rendu des Séances de la Societe de Biologie* 68:131-134.

Edwards, C. 1978. The Hydroids and Medusae *Sarsia occulta* new species, *Sarsia tubulosa* and *Sarsia loveni*. – *Journal of the Marine Biological Association of the United Kingdom* 58:291-312.

— 1983. The hydroids and medusae *Sarsia piriforma* sp. nov. and *Sarsia striata* sp. nov. from the west coast of Scotland, with observations on other species. – *Journal of the Marine Biological Association of the United Kingdom* 63:49-60.

Fulton, C. 1963. Rhythmic movements in *Cordilophora*. – *Journal of Cellular and Comparative Physiology* 61(1):39-51.

Hand, C. 1957. The systematics, affinities, and hosts of the one-tentacled commensal hydroid *Monobrachium* with new distributional records. – *Journal of Washington Academy of Sciences* 47(3):84-88.

Hartlaub, C. 1895. Die Polypen und Quellen von *Stauridium productum* Wright und *Perigonimus repens* Wright. – *Zeitschrift für Wissenschaftliche Zoologie* 61:142-162.

— 1897. Die Hydromedusen Helgoland. 2. Bericht. – *Wissenschaftliche Meeresuntersuchungen*, N. F., II, Abt. Helgoland 1:449-536.

Hincks, T. 1861. A catalogue of the zoophites of South Devon and South Cornwall. – *Annals and Magazine of Natural History* (3) 8:152-161, 290-297.

— 1862. On the production of similiar gonozoids by hydroid polyps belonging to different genera. – *Annals and Magazine of Natural History* (3) 10:459-461.

— 1868. *A history of the British hydroid zoophytes, I-II*. – John van Voorst, London.

Hirai, E. 1960. On the structures of species of Corynidae. – *Bulletin of the Biological Station of Asamushi, Tohoku University* 10:141-144.

Kakinuma, Y. 1965a. On the regeneration of the proximal structures of the hydranth of a hydrozoan, *Stauridiosarsia* sp. – *Bulletin of the Biological Station of Asamushi, Tohoku University* 12:63-68.

— 1965b. On the regeneration of the distal structures of the hydranth of a hydrozoan, *Stauridiosarsia* sp. – *Bulletin of the Biological Station of Asamushi, Tohoku University* 12:69-73.

Kramp, P.L. 1935. Polypdyr (Coelenterata). 1. Ferskvandspolypper og goplepolypper. – *Danmarks Fauna* 41:1-207.

— 1937. Polypdyr (Coelenterata). II. Gopler. – *Danmarks Fauna* 43:1223.

— 1961. Synopsis of the Medusae of the world. – *Journal of the Marine Biological Association of the United Kingdom* 40:1-496.

Kubota, S. 1983. Studies on life-history and systematics of the Japanese commensal hydroids living in bivalves, with some reference to their evolution. – *Journal of the Faculty of Sciences of Hokkaido University*, ser. 6, Zoology 23:296-402.

Kubota, S. & Y. Takashima 1992. Redescription of *Sarsia japonica*(Nagao) (Hydrozoa: Corynidae) from Hokkaido, Japan – *Publications of the Seto Marine Biological Laboratory* 35(6):371-381.

LaBarbara, M. 1984. Feeding currents and particle capture mechanisms in suspension feeding animals. – *American Zoology* 24:71-84.

Lenhoff, H.M. 1974. Chemical perspectives on the feeding response, digestion and nutrition of selected coelenterates. – Pp.157-221 in: Florkin, M. & B. Sheer (eds). *Chemical Zoology*, Part II. Academic Press, New York.

Letunov, V. & N.N. Marfenin 1980. Some characteristics of feeding behaviour in winter colonies of *Dynamena pumila* under various temperature regimes. – *Biologicheskie Nauki* 6:51-55 (in Russian).

Mayer, A.G. 1910. Medusae of the World. Vol. 1. – *Publications of Carnegy Institution* 109:1-230.

Marfenin, N.N. & T.N. Khomenko 1989. The diet of abundant White Sea hydroids. – Pp. 80-84 in: Koltun, V.M., N.N. Marfenin & S.D. Stepanjantz (eds). *Fundamental investigations of the modern spongie and cnidarians*. Russian Academy of Sciences, St Petersburg.

Mereschkowsky, C. 1878. New Hydroida from Ochotsk, Kamtschatka and other parts of the north Pacific Ocean. – *Annual Magazine of Natural History*, ser. 5, II:433-450.

Naumov, D.V. 1969. *Hydroids and hydromedusae of the USSR*. – Israel Program for Scientific Translations, Jerusalem. 160 pp.

Pardy, R.L. 1971. The feeding biology of the gymnoblastic hydroid *Pennaria tiarella*. – Pp. 84-91 in: Lenhoff, H. & al. (eds). *Experimental Coelenterate Biology*. University of Hawaii Press, Honolulu, Hawaii.

Peters, R.H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge.

Piraino, S., J. Bouillon & F. Boero 1992. *Halocoryne epizoica* (Cnidaria, Hydrozoa), a hydroid that 'bites'. – *Scientia Marina* 56(2-3):141-147.

Piraino, S., C. Todaro, S. Geraci & F. Boero 1994. Ecology of the bivalve- inhabiting hydroid *Eumnanthea inquilina* in the coastal sounds of Taranto (Ionian Sea, Italy). – *Marine Biology* 118:695-703.

du Plessis, G. 1881. Catalogue provisoire des Hydroides medusipares observes durant i'hiver 1879/1880 a la station Zoologique de Naples. – *Bulletin de la Societe vaudoise des Sciences Naturelles* (2) 17 (84):108-118.

Poche, F. 1914. Das System der Coelenterata. – *Archiv für Naturschutz und Landschaftsforschung* 80 Abt. A (Heft. 5):47-128.

Ranson, G. 1925. Sur quelques medusa des cotes de la Manche. – *Bulletin of the Museum of Natural History*, Paris 31:323-328, 459-640.

Rees, W. J. 1938. Observations on British and Norwegian hydroids and their medusae. – *Journal of Marine Biological Association of the United Kingdom* 23:1-42.

— 1957. Evolutionary trends in the classification of capitate hydroids and medusae. – *Bulletin of the British Museum of Natural History* 4(9). 534 pp.

Robins, M. W. 1972. A new commensal hydroid from Antarctica. – *British Antarctic Survey Bulletin* 28:75-81.

Rubenstein, D. I. & M.A.R. Koehl 1977. The mechanisms of filter feeding: some theoretical considerations. – *American Naturalist* 111:981-994.

Russell, F.S. 1953. *The medusae of the British Isles: Anthomedusae, Leptomedusae, Limnomedusae, Trachimedusae and Narcomedusae*. – Cambridge: pp. xii + 530, text-figs. 1-319 and pls. i-xxxv.

Ryland, J.S. & G.F. Warner 1986. Growth and form in modular organisms: ideas on the size and arrangement of zooids. – *Philosophical Transactions of the Royal Societe of London (B)* 313:53-76.

Schneider, K C. 1898. Hydropolypen von Rovigno nebst Übersicht über das System der Hydropolypen im Allgemeinen. – *Zoologische Jahrbücher Abteilung für Systematik Ökologie und Geographie der Tiere* 19:472-555.

Sebens K. P.. 1982. The limits to indeterminate growth: an optimal size model applied to passive suspension feeders. – *Ecology* 63:209-222.

Shidlowsky, A. 1902. Materials on Hydrozoan fauna of the Arctic seas. I. Hydroids of the White Sea near the Solovetzkie islands. – *Trudi obschestva estestvoispitatelej Khar'kovskogo Universiteta* XXXVI, 1:3-268 (in Russian).

Stechow, E. 1919. Zur Kenntnis der Hydroidenfauna des Mittel-meers, Amerikas und anderer Gebiete. – *Zoologische Jahrbücher Abteilung für Systematik Ökologie und Geographie der Tiere* 42:1-172.

Vannucci, M. 1949. Hydrozoa do Brazil. – *Publicacio da Faculdade de Filosophicas Ciencias da Universidade do Sao Paolo* 14:219-266.

— 1956. Notes on the Hydromedusae and their distribution in relation to different water masses. – *Publicacao especial do Instituto Oceanografico Sao Paolo* 8:23-109.

West, D.K. 1974. Notes on *Stauridiosarsia producta* (Hydrozoa, Corynidae), a new addition to the New England marine fauna. – *Zoologica Scripta* 3:5-9.

Wright, T. S. 1858. Observations on British zoophytes. 1. *Coryne gravata*. 2. *Stauridia producta*. – *Proceedings of the Royal Society of Edinburgh* 1:338-342.

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