The life cycle of Catablema vesicarium (A. Agassiz, 1862) (Hydrozoa, Pandeidae)

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The life cycle of *Catablema vesicarium* (A. Agassiz, 1862) (Hydrozoa, Pandeidae)

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Abstract

The hydrozoan classification systems often rely on limited character sets of either polyp or medusa stages, and these classifications stay non-consistent in many cases because of lack of life cycle data. This is usual for hydrozoans with tiny inconspicuous colonies and intermittent medusae production period such as pandeid in the polar latitudes. In this study, the previously unknown life cycle of boreal-arctic pandeid hydrozoan *Catablema vesicarium* was elucidated under experimental conditions. Medusae *C. vesicarium* were found near the Pertsov Biological Station in the White Sea and maintained in a laboratory till spawning. Morphological descriptions of development stages including medusae, eggs, planulae, polyps, and medusae buds are represented. Hydroid *C. vesicarium* was also collected on the shell with live *Astarte elliptica*. Identification of this colony was confirmed by comparing the sequences of the mitochondrial *CO1*, *16S*, and nuclear *18S-ITS1-5.8S* gene fragments of medusae and polyps. Hydroids *C. vesicarium* have almost sessile polyps with perisarc cup only at the base, and newborn medusae have rudimentary marginal bulbs which alternate with four

marginal tentacles. Identification characters of the cultivated hydrozoan are discussed in comparison with other known pandeids. The data on temperature range of medusae appearing in experiments may be potentially useful for studying seasonality of jellyfish in the sea.

AQ1

AQ2

Keywords

Hydrozoa
Pandeidae
Catablema vesicarium
Life cycle
Astarte elliptica
White Sea

Introduction

The medusae *Catablema vesicarium* inhabit the North Atlantic and Arctic Seas (Kramp 1961; Schuchert 2007). This cold-water species can be found in the Barents and White seas during the summer months (Zelickmann 1972; Pertsova 1979; Slobodov and Marfenin 2005). Pacific records are uncertain (Arai and Brinckmann-Voss 1980; Schuchert 2007). Medusa *Catablema* has occurred in lists of marine species since the nineteenth century. One and a half hundred years has passed since the first description of the species by A. Agassiz as *Turris vesicaria* (Agassiz 1865). Only little information was added in later studies (Haeckel 1879; Nutting 1901; Hartlaub 1914). The biological peculiarities such as reproduction and life cycle of *Catablema* species are unknown (Schuchert 2007). Some authors considered the polyps of *Catablema* are probably *Perigonimus abyssi* G.O. Sars, 1874 (Naumov 1960). This guess has no proof.

In this paper, the life cycle of *Catablema vesicarium* (A. Agassiz, 1862) from the White Sea was elucidated as a result of successful cultivation, some lucky finds in the sea, and molecular comparative analysis of the collected specimens.

Methods

Hydrozoan material was collected near the Pertsov Biological Station in Kandalaksha Bay of the White Sea in 2012–2014 (Fig. 1). Medusae were scooped up by a small jar from the surface of the sea. They were maintained in a small aquarium at 10–12 °C, 2–3 weeks till spawning. The water in the aquarium was changed every other day. The medusae *Catablema vesicarium* were fed by copepods *Calanus glacialis* Jaschnov, 1955, *Metridia longa* (Lubbock, 1854), ~~Dead~~lifeless ~~Sea arrow~~chaetognath *Parasagitta elegans* (Verrill, 1873), and by the soft tissues of the mollusc *Mytilus edulis* Linnaeus, 1758, which were cut into small pieces. The medusae were placed in a finger bowl shortly before spawning when the eggs were evident over female gonads (Fig. 2d). The newborn planulae were placed in dishes with a flat bottom at 10–12 °C. Glass microscopical slides were placed at the bottom of the dishes beforehand. In the summer months and in September, the colonies of *C. vesicarium* were kept in an aerated finger bowl. The water in the bowl was changed every other day, and the polyps were fed using concentrated zooplankton from the sea. In the other months, the colonies were maintained in aquaria in Moscow State University without changing the water and were fed by Artemia nauplii. The colonies grew well all year. The hydroid *C. vesicarium* is easy to handle in the laboratory. The species is not very demanding to quality of the water or food, and it requires only low temperature to release medusae. To encourage the release of medusae, the colonies were placed into aquaria with the temperature of 0–2 or 4–6 °C. The medusae buds were evident in a month after the temperature change. Newborn medusae were fed by Artemia nauplii.

Fig. 1

Scheme of the sampling area: a location of the Pertsov Biological Station in the White Sea

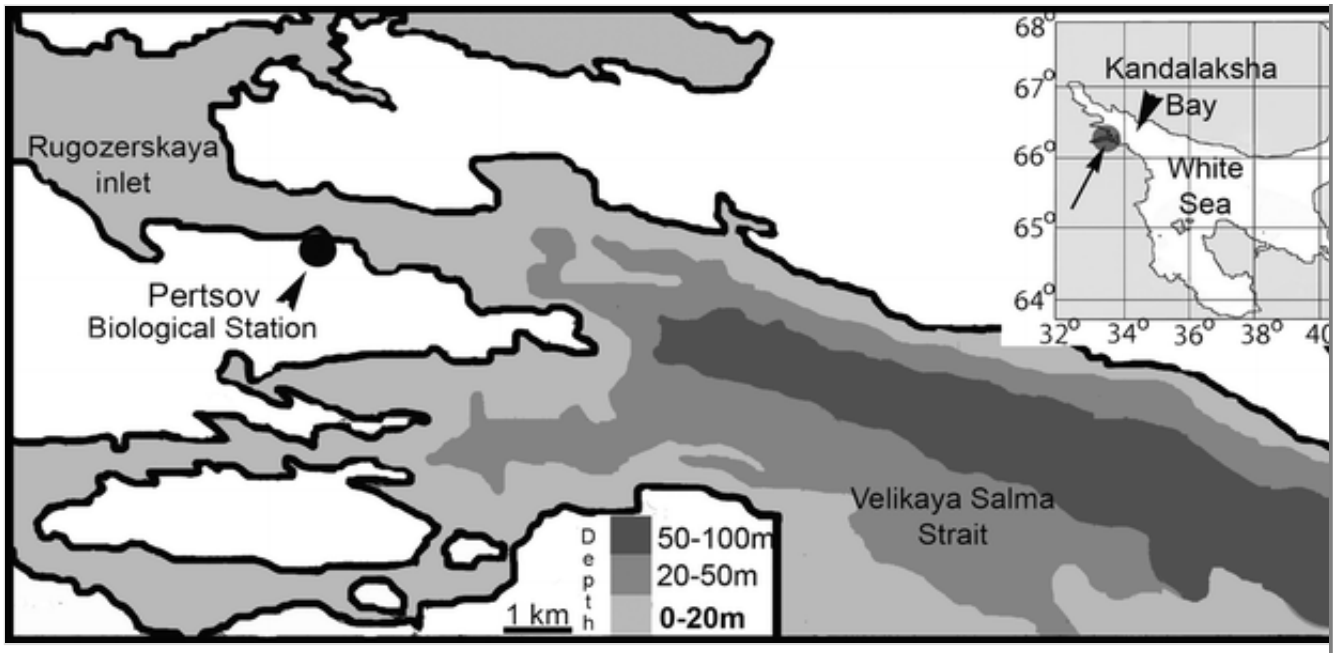
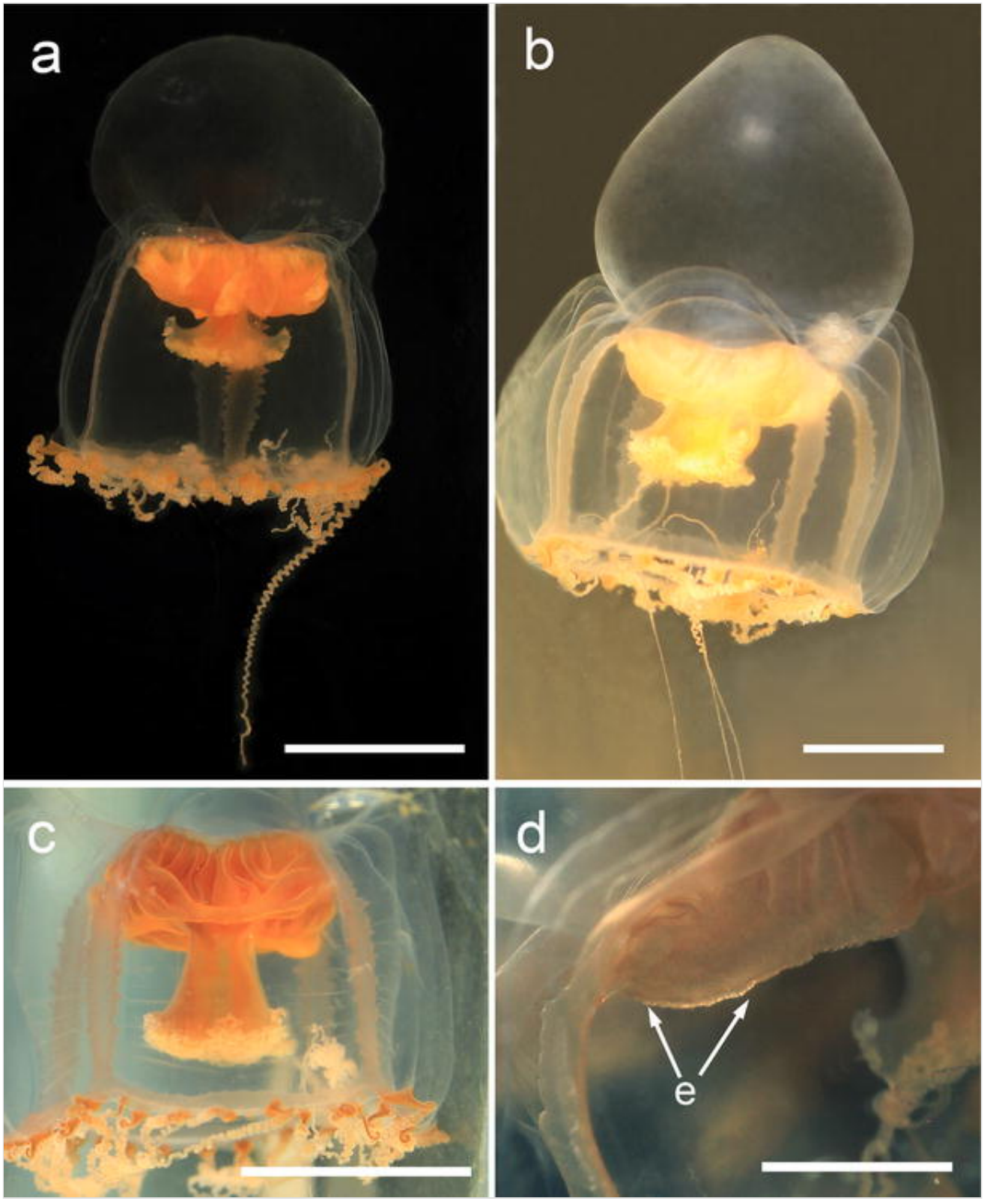


Fig. 2

Adult medusae *Catablema vesicarium* from the sea: **a** male, *scale bar* 10 mm, **b** female, *scale bar* 5 mm, **c** manubrium of the male, *scale bar* 10 mm, **d** manubrium of the female with eggs-~~**e**~~, *scale bar* 2 mm, *e* eggs



All life history stages were photographed alive, including colonies, individual polyps, medusa buds, and newly released and adult medusae. Photographs were taken with a Canon camera with a 100-mm MP-E macrolens. Photographs of nematocysts were taken with a microscope Leica equipped with Nomarski interference contrast optics.

DNA extraction and sequencing

For DNA amplification and sequencing, two samples of medusae and two samples of polyps were fixed in 96 % ethanol and kept at −20 °C. DNA was extracted with the Promega Wizard SV Genomic DNA Purification (Promega Corporation, Madison, USA) and was used for tissue lysis and DNA purification in accordance with the manufacturer's protocol. DNA concentration and purification efficiency were determined by the electrophoresis on a 1.2 % agarose gel. Polymerase chain reaction (PCR) amplification of nuclear *18S-ITS1-5.8S-ITS2-28S* rDNA and mitochondrial *16S* rDNA fragments were accomplished with the primers given in Table 1. Loci were amplified using the Encyclo PCR kit (Evrogen Joint Stock Co., Moscow, Russia). Amplification was done with a Veriti Thermal Cycler (Applied Biosystems, Foster City, CA, USA) in a 25-μL reaction mix containing 1 × PCR buffer, 1 μL of 10 μM of primer pair mix, 1 μL of template, 0.2 mM of each dNTP, and 0.5 U of Taq polymerase. Reaction mixtures were heated to 94 °C for 120 s; followed by 35 cycles of 15 s at 94 °C, 30 s at 50 °C for the 28S rRNA fragment, and 60 s at 72 °C; and then a final extension of 7 min at 72 °C. The Promega PCR Purification Kit protocol (Promega) was used to purify the amplification products. Amplification products were sequenced in both directions. Each sequencing reaction mixture contained 1 μL of BigDye (Applied Biosystems, PerkinElmer Corporation, Foster City, CA), 1 μL of 1 μM primer, and 1 μL of DNA template; sequencing reactions were run for 40 cycles of 96 °C (15 s), 50 °C (30 s), and 60 °C (4 min). Sequences were subjected to ethanol precipitation to remove unincorporated primers and dyes. Products were resuspended in 12 μL of formamide and were electrophoresed in an ABI Prism 3500 sequencer (Applied Biosystems). All new sequences are available in GenBank (KT288205-KT288208).

Table 1

Primers used in amplification reactions and accession number of obtained fragments

Gene fragment	Primer and reference	Accession number	Length of amplified fragment	Sequence
18S-ITS1-5.8S-ITS2-28S region	SR6R White et al. (1990)	KT288207	688 bp	AAGWAAAAGTCGTA
	LR1 White et al. (1990)	KT288208	688 bp	GGTTGGTTTCTTTTC

Mitochondrial 16S rDNA fragment	16SAR Cunningham and Buss (1993)	KT288205	613 bp	TCGACTGTTTACCAA
	16SBR Cunningham and Buss (1993)	KT288206	613 bp	ACGGAATGAACTCA

Our amplifications of *ITS* and *16S* loci yielded fragments of approximately 700 and 608 bp, respectively. We amplified a 25-μL reaction mix containing 1 × PCR buffer, 1 μL of 10 μM of primer pair mix, 1 μL of template, 0.2 mM of each dNTP, and 0.5 U of Taq polymerase. Reaction mixtures were heated on Veriti® Thermal Cycler to 94 °C for 300 s, followed by 35 cycles of 15 s at 94 °C, 30 s at a specific annealing temperature, and 45–60 s at 72 °C, depending on the length of the fragment, and then a final extension of 7 min at 72 °C. Annealing temperature was set to 49 °C for the 16S primer pairs and 52 °C for the *ITS* primer pair.

Data analysis

Sequences were assembled and checked with CodonCode Aligner software (www.codoncode.com/aligner). Then, DNA sequences were aligned using ClustalW method implemented in the Molecular Evolutionary Genetic Analysis, version 5.1 (MEGA 5.1), software (Tamura et al. 2011).

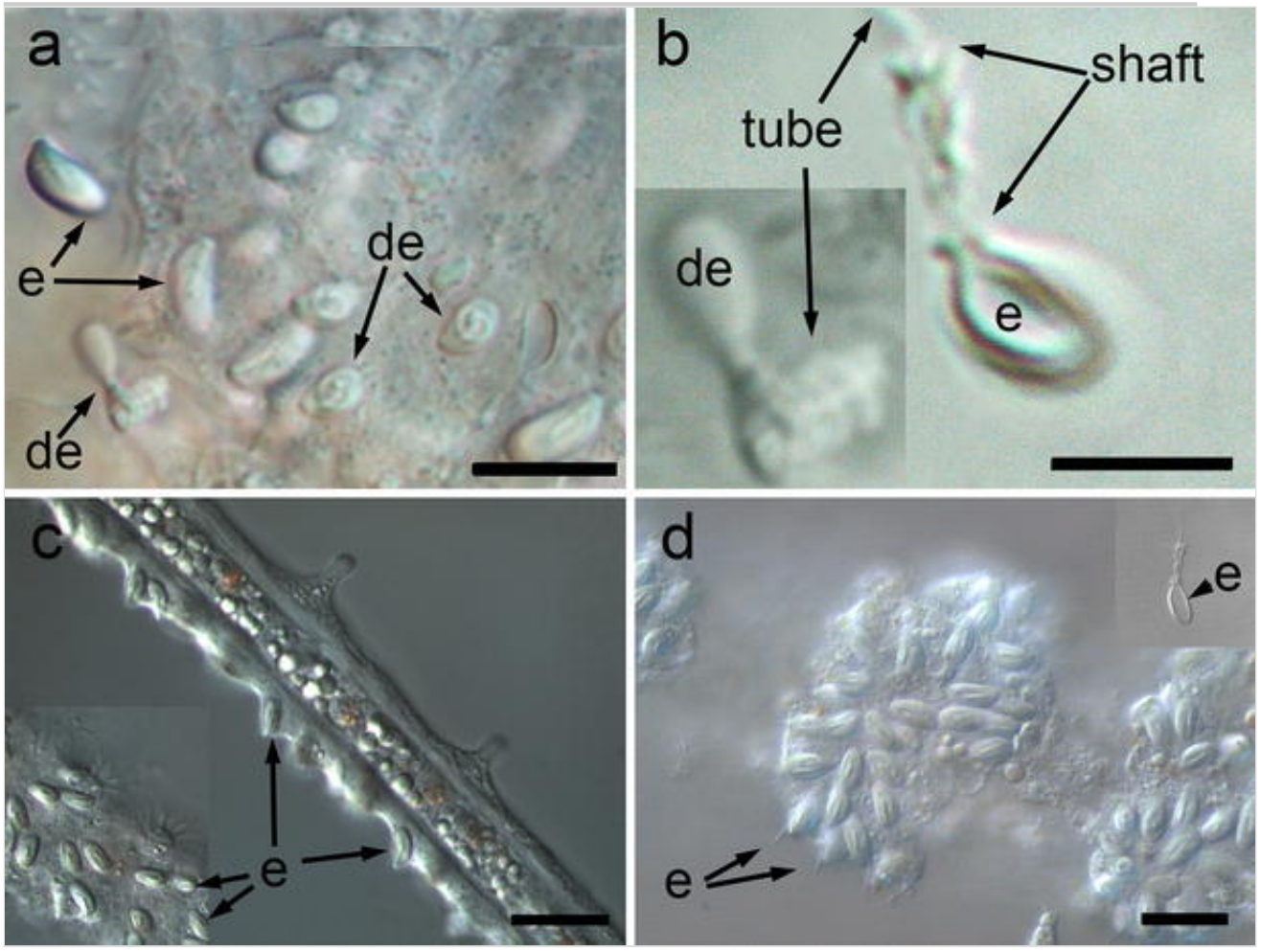
Results

The medusae *Catablema vesicarium* are a rare species near the Pertsov Biological Station. Only three specimens, two female and one male, were collected in June 2012, and a young pandeid medusa supposedly *C. vesicarium* was collected on May 12, 2014. The young specimen had four tentacles and eight tentacle bases with red eyes (Fig. 7c). The adult medusae had 28 tentacles and were similar in morphology (Fig. 2a, b). The female medusae had the bells about 20 mm in height. The colour of their manubrium was citrine at first, but changed to light orange shortly before spawning. A transparent layer of eggs appeared on folds of the manubrium at the same time (Fig. 2d). The medusae released eggs in batches over a 2- to 3-week period in July. The only male had a height of 25 mm. The colour

of its manubrium was light orange at first and changed to dark orange before spawning. There were nematocysts euryteles on the tentacles of the young and adult medusae. The length of the nematocysts varied in the range of 5.5–8.5 μm (Fig. 3c, d).

Fig. 3

Nematocysts of *Catablema vesicarium*: **a** tentacle of polyp, *scale bar* 10 μm, **b** discharged desmoneme (de) and eurytele (e) from the tentacle of polyp, *scale bar* 5 μm, **c** tentacle of newborn medusa in the distal and proximal (*insertion*) parts, *scale bar* 20 μm, **d** tentacle of adult medusa with discharged eurytele (*insertion*), *scale bar* 10 μm

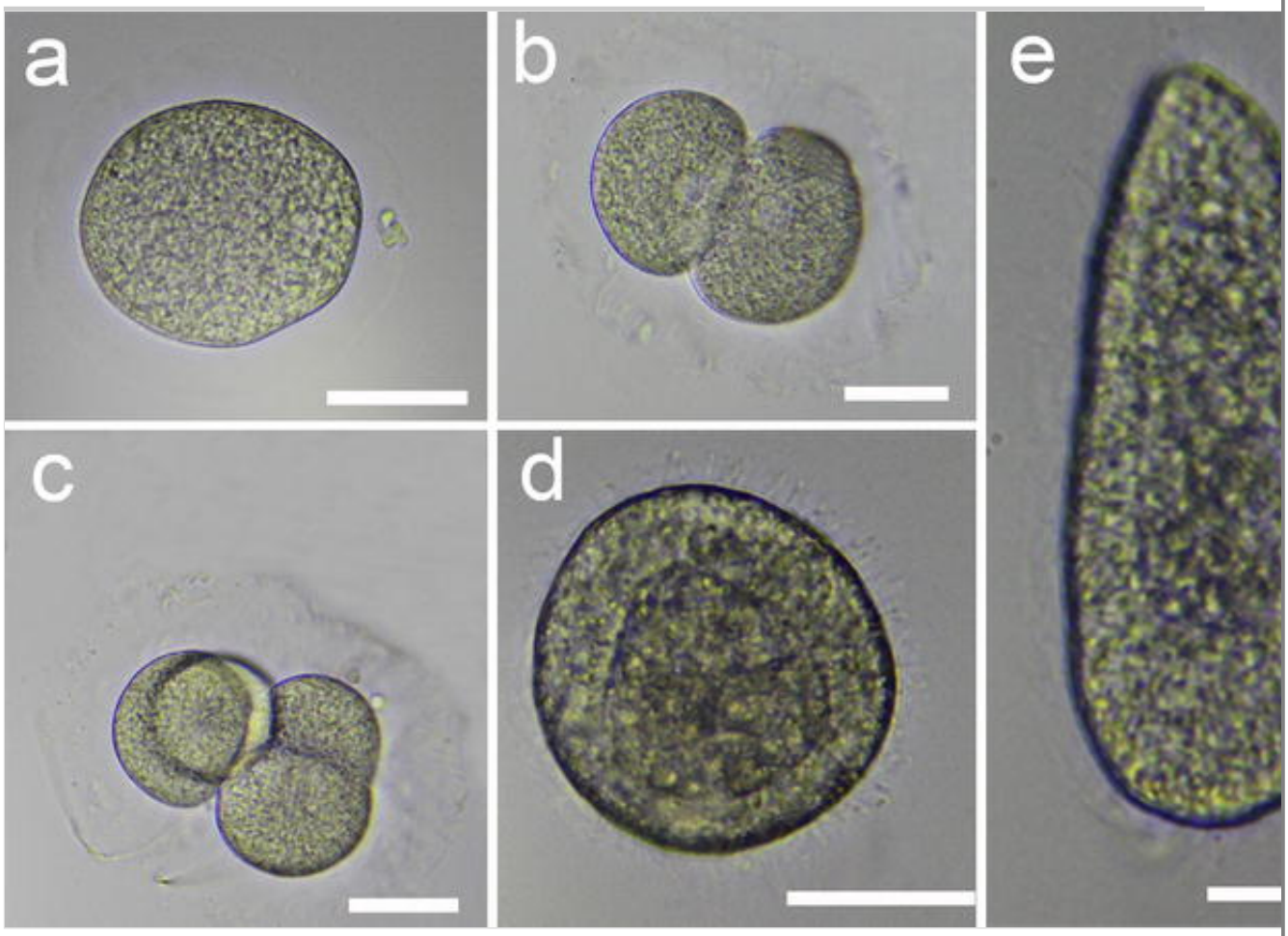


The eggs of *C. vesicarium* had a size of about 50 μm. They had a transparent jelly cover and adhered to the bottom of the bowls after being liberated. Cleavage began on the 10th of July, and the planulae were swimming on the 12th of July (Fig. 4). The planulae were contractile with the largest length of about 60 μm. Their shape changed from spherical to elongated. They had pointed posterior and obtuse anterior ends. There was a vast cavity inside each planula. The planulae slowly crawled over the

bottom of a bowl over a long period of time. Sometimes the planulae rotated about their axis near by the substratum or they became spherical for a while.

Fig. 4

Early development of *Catablema vesicarium* (*scale bar* 20 μm): **a** egg with jelly cover, **b, c** early cleavage of the egg, **d**, **e** planula



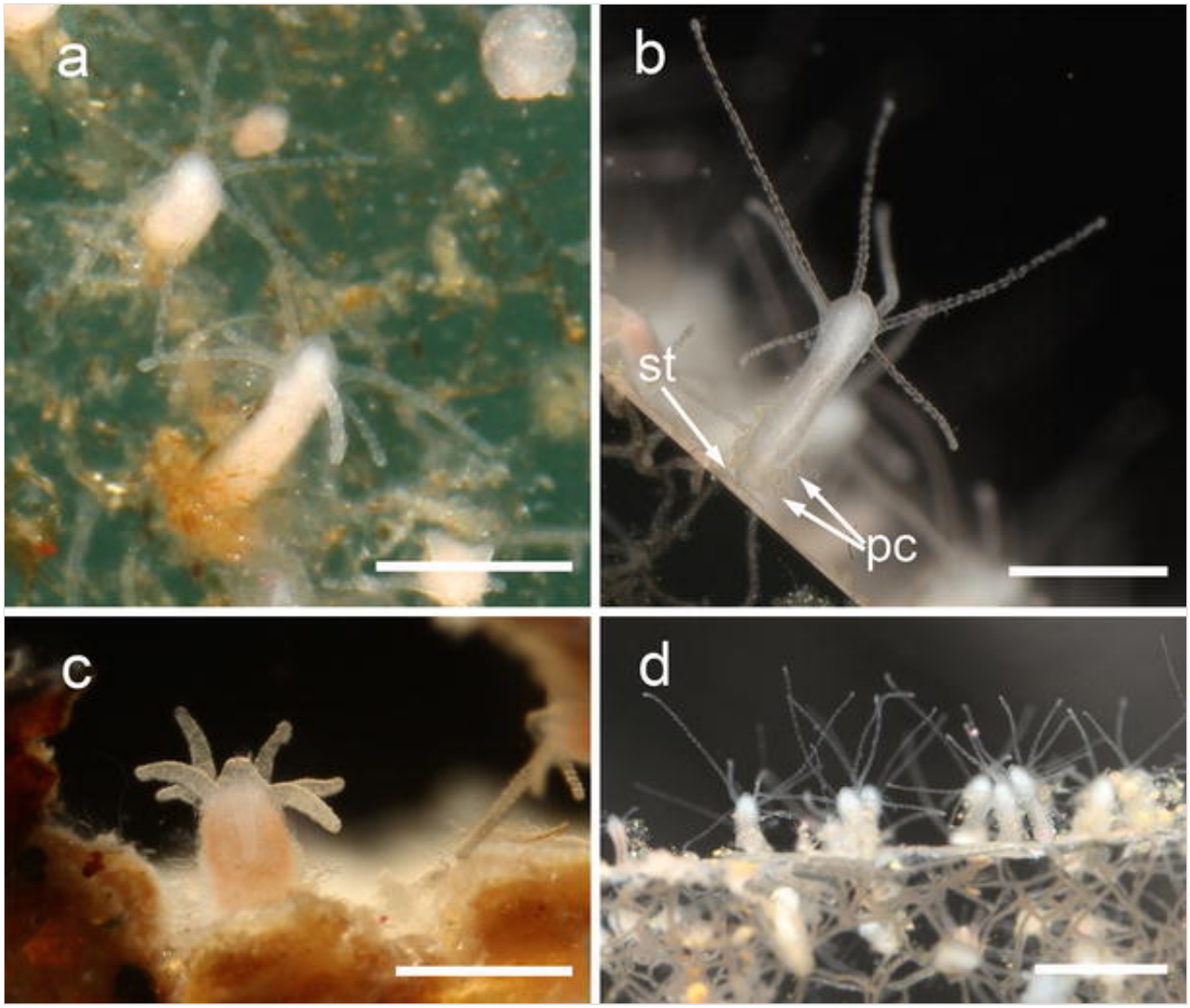
After 2 weeks, some planulae settled to a slide and the others perished. Only one colony *C. vesicarium* was maintained afterwards. At first, the colony grew very slowly, because tiny young polyps could seize only small copepoda nauplii and fed rarely. Ten polyps had grown on a linear hydrorhiza by the beginning of September. Later, the size of some polyps increased and they now fed on various plankton prey such as copepods and cladocerans. As a result of increased food supply, hydrorhiza began to ramify over the glass and send up many new polyps.

The hydroids *C. vesicarium* formed creeping colonies with many ramified stolons (Fig. 5). Some stolons ran up over various substrata in developed colonies. But the stolon tips never tore off the hydrorhiza for spreading.

The polyps possessed very short pedicels, being almost sessile. Only the base of the polyps was surrounded by a membranous perisarc cup (Fig. 5b, 8a). The body of the polyps was spindle shaped with a diameter of about 1/3–1/5 in height. The conical hypostome was encircled by a single whorl of 3–8 filiform amphicoronate tentacles with nematocysts. The size of the undischarged nematocysts was 6.5–7.5 µm long and 2.5–3.5 µm wide (microbasic euryteles), 4–5 µm long and 2–3 µm wide (desmonemes) (Fig. 3a, b). The polyps appeared whitish-grey to beige with whitish coloured hypostome. After being fed Artemia, they gained a light brown shade. But they lost the colour after evacuation of undigested matter. The young polyps with 3–4 tentacles had a length of 100–200 µm. The largest polyps had a length of 750 µm. They were clustered very densely (Fig. 5d), and a pair of polyps often seized the only food item together.

Fig. 5

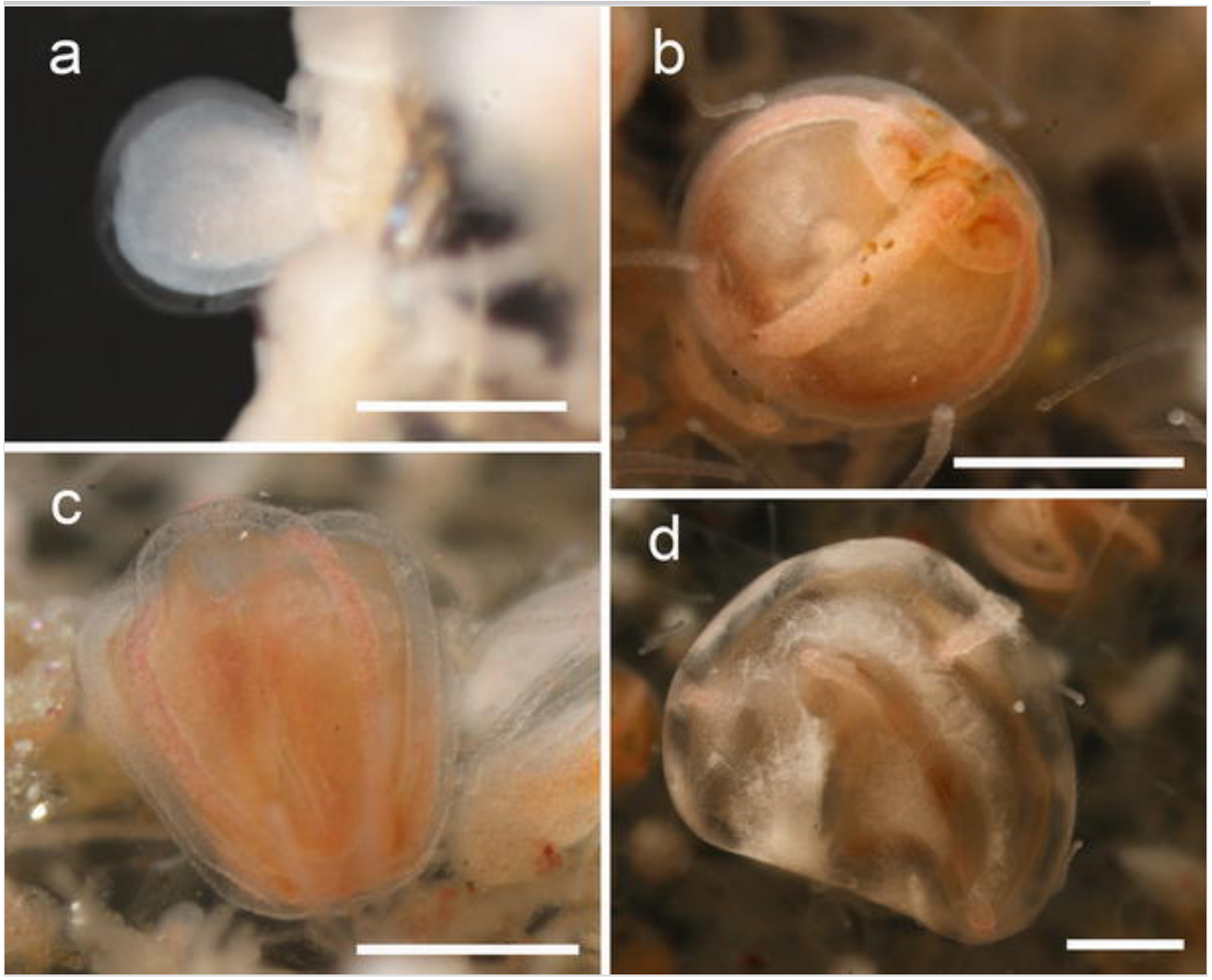
Polyps and colonies of *Catablema vesicarium*. **a** young polyp, **b** large polyp, **c** polyp on the shell *Astarte elliptica* collected in the sea in June 2014, **d** cultivated colony on glass slide. *Scale bar* 0.5 mm (**a**, **b**, **c**), 1 mm (**d**). *p* pedicel of polyp, *pc* perisarc cup at the base of polyp



The medusa buds of *C. vesicarium* arose directly from the creeping stolons (Figs. 6, 8a). The early buds were pyriform, covered with a transparent perisarc, and had a length of about 200–250 μm (Fig. 6a). There was a pair of developing radial canals inside the buds. After 2 weeks of development, the buds had four radial canals, eight tentacular bulbs (four large bases and four small ones), and a short pedicel. These buds were orange with beige radial canals and tentacular bulbs. Later, a light-coloured ring (circular gastric canal) appeared around the bulbs and spiral tentacles appeared inside the buds. The bases of the tentacles had a thick transparent ectodermal layer (Fig. 6b, c). The four large tentacular bases were folded in the direction of the centre and formed a cruciform figure upside the buds. The largest size of the buds was about 0.8–0.9 mm. After a month of development, the perisarc of the buds became soft and disappeared soon after (Fig. 6d). During dissolution of the perisarc, the size of the buds increased significantly. Finally, this process resulted in medusae liberation.

Fig. 6

Medusae buds of *Catablema vesicarium*: **a** small medusa bud, *scale bar* 200 µm, **b** advanced bud, *scale bar* 0.5 mm, **c** mature bud, *scale bar* 0.5 mm, **d** bud during perisarc dissolution, *scale bar* 0.5 mm



The newly liberated medusae of *C. vesicarium* often were as high as they are wide with a size of about 1–1.5 mm (Fig. 7a–c, 8b). The bell at the apex was interrupted by the remains of an attachment structure. There was no apical process up by the bell. The whole surface of the bell was slightly opaque because of numerous tiny pits and furrows. The manubrium had a length 1/3–1/2 of the bell cavity. It was cylindrical with four prominent lips. The circular gastric canal and four radial ones were broad and smooth. Four larger tentacle bulbs with four tentacles were present. Sometimes medusae had two opposite long tentacles and two opposite short ones. Rudimentary marginal bulbs disposed between adjacent tentacles. Each tentacle bulb carried an ocellus on its abaxial side. A small apical process appeared the next day after the medusa was born. The size of the medusae in the experiment was about 6 mm after a month of development (Fig. 7d).

The base of the stomach had elongated connections (mesenteries) with the radial canals. The apical process consisted about a half of a bell in size. The cultivated medusae usually had only four long tentacles independent of age. Afterwards, the medusae development was not normal and resulted in death of medusae before maturation.

Fig. 7

Newborn (**a**, **b**) and 1-month-old (**d**) medusae *Catablema vesicarium* from the laboratory, and young medusa (supposedly *C. vesicarium*) from the sea (**c**). *Scale bar* 1 mm (**b**, **c**), 2 mm (**a**, **d**). *m* mesentery

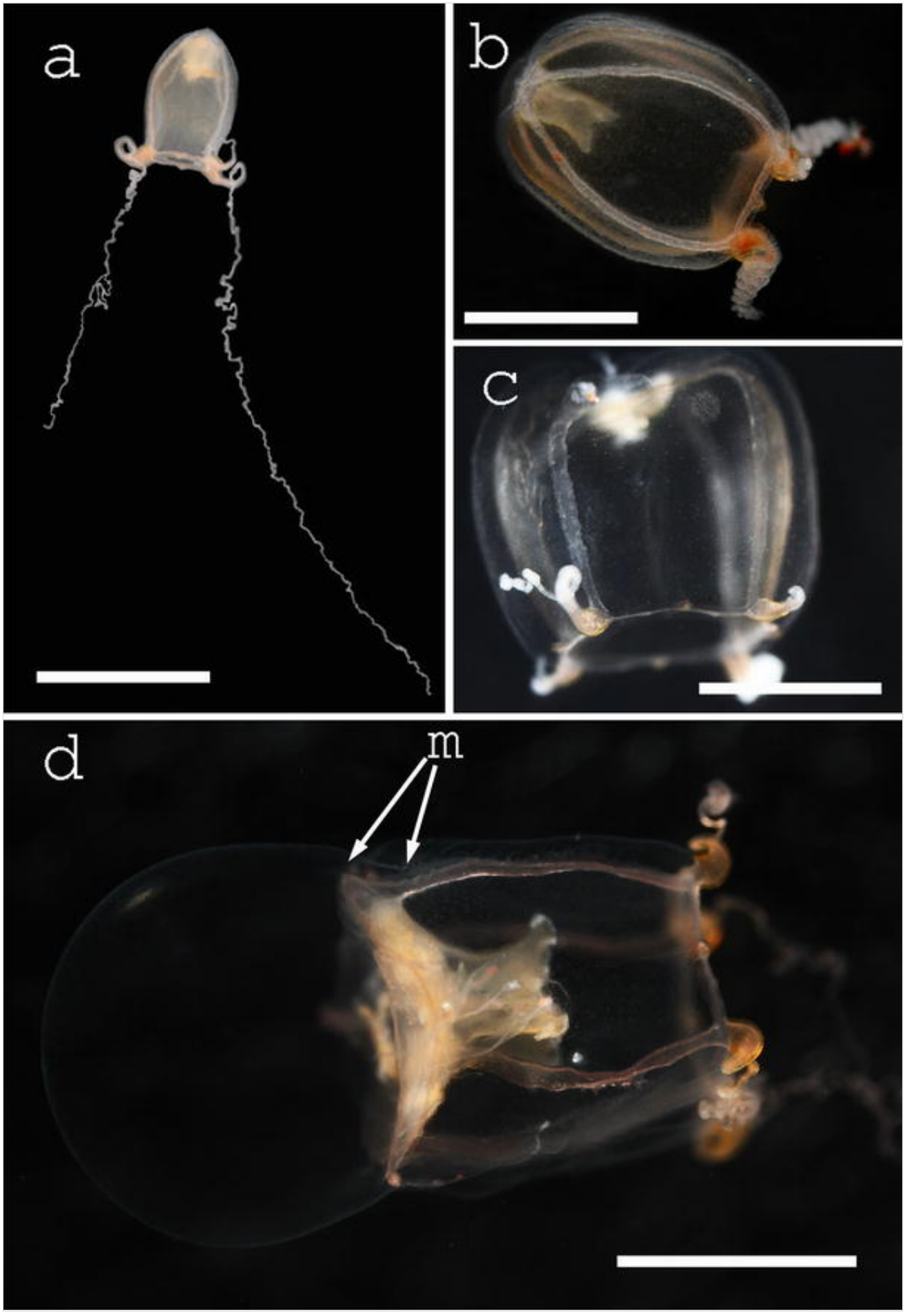
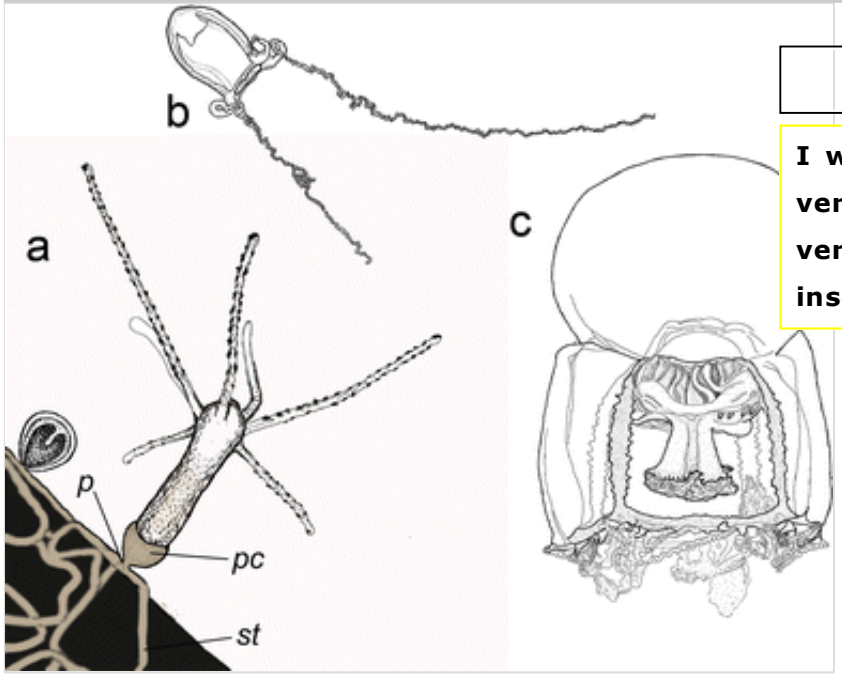


Fig. 8

Development stages of *Catablema vesicarium* (schematic drawings): **a** polyp

with medusae bud, **b** newborn medusa, **c** adult medusa. *Scale bar* 0.5 mm (**a**), 1 mm (**b**), 10 mm (**c**). *m* mesentery, *p* peduncle, *pc* perisarc cup, *s* stolon



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Several polyps of *C. vesicarium* were found in the sea too (Fig. 3c). A hydrozoan colony over an *Astarte elliptica* (Brown, 1827) shell with live mollusc was collected in June 2014 with a trawl in the marine part of the Velikaia Salma Strait at depth of about 20–40 m. The colony was not similar with other pandeid hydroids from the White Sea because the polyps had a whitish colour and lacked a pedicel.

Molecular tools were used to compare *C. vesicarium* medusa and polyps. There were no data for this species in GenBank, so we could only compare sequences obtained for medusae and for polyps. The nuclear ribosomal internal transcribed spacer (ITS) region contains two highly variable spacers (ITS1 and ITS2) which are usually species specific. The comparison of ITS region sequences obtained for medusae and polyps samples has shown the 100 % identity. The same result was obtained for mitochondrial 16S fragments. We used MEGA to calculate the *p*-distances for 16S sequences between *C. vesicarium* and some other Pandeidae species. It consists of 0.054 for *Neoturris brevicornis* (EU448103), 0.061 for *Hydrichthys boycei* (EU448102), 0.062 for *Leuckartiara octona* (AM411422.1), and 0.076 for *Leuckartiara nobilis* (AM183135). So as a result of molecular analysis, we concluded the collected hydroid colony over the mollusc shell was *C. vesicarium* species.

Discussion

Pandeidae hydrozoan (in the strict sense) is a large family which contains 20 genera and about 70 species (Bouillon and Boero 2000). Life cycles of most species are known fragmentary. Only about fifteen species were maintained in the laboratory previously (Table 2). Some genera need a revision (Schuchert 2007). In the Eurasian Arctic seas, the fauna of pandeid medusae consists of five genera: *Catablema*, *Halitholus*, *Leuckartiara*, *Neoturris*, and *Pandea* (Stepanjants and Svoboda 2013). Two pandeid medusae (*Catablema vesicarium* and *Halitholus cirratus* Hartlaub, 1913) are known from the White Sea (Pertsova 1979). The life cycles of *Leuckartiara octona* (Fleming 1823), *Neoturris pileata* (Forsskål, 1775), and *Pandea conica* (Quoy & Gaimard, 1827) are known from previous studies (Table 2). But our knowledge of life cycle of *H. cirratus* is incomplete, and the life cycle of *C. vesicarium* was unknown till now (Schuchert 2007).

Table 2

List of pandeid life cycles reconstructions

Species	**Region**	**References**
Amphinema sp.	East Pacific (California, Bodega Harbor)	Rees (2000)
Amphinema dinema	North Atlantic (Plymouth)	Rees and Russell (1937)
Amphinema dinema	New Zealand (Wellington Harbour)	Schuchert (1996)
Amphinema rollinsi	East Pacific (California, Monterey Bay)	Widmer (2007)
Amphinema rugosum	North Atlantic (Plymouth)	Rees and Russell (1937)
Amphinema rugosum	New Zealand (Drake's Island)	Schuchert (1996)
Halitholus cirratus (?)	Baltic Sea	Hartlaub (1914)
Halitiara inflexa	Bismarck Sea (Papua New Guinea)	Bouillon (1985)
Hydrichthys cyclothonis	East Atlantic	Damas (1934)
Hydrichthys mirus (?)	North Atlantic (USA, Newport)	Fewkes (1887, 1888)

Hydrichtys mirus (?)	Caribbean Sea (Central America, Belize)	Larson (1982)
Hydrichtys mirus (?)	Bismarck Sea (Papua New Guinea)	Boero et al. (1991)
Leuckartiara sp. (*Tiara pileata, Perigonimus repens*)	North Atlantic (Helgoland)	Hartlaub (1895) (synonyms in Rees 1938)
Leuckartiara octona	North Atlantic (Plymouth)	Rees (1938)
Merga galleri	Mediterranean (Italy, Gulf of Naples)	Brinckmann (1962); Schuchert (2007)
Merga tergestina	Mediterranean (Italy, Gulf of Naples)	Vannucci and Yamada (1959)
Neoturris sp.	Weddell Sea (Antarctic)	Piraino et al. (2003)
Neoturris pileata	Clyde Sea Area	Edwards (1965)
Octotiara russelli	Papua New Guinea (Laing Island, Wuvulu Island)	Boero and Bouillon (1989)
Pandea conica	Villefranche-sur-Mer (France)	Picard (1956); Schuchert (2007)
Pandeopsis ikarii	Bismarck Sea (Papua New Guinea)	Bouillon (1985)
Pelagiana trichodesmiae	Tropical Atlantic (West Indies, Barbados)	Borstad and Brinckmann-Voss (1979)
Stomotoca atra	Papua New Guinea (Laing Island)	Boero and Bouillon (1989)

Pandeid medusae usually have enough morphological characters to enable species identification (Bouillon and Boero 2000; Schuchert 2007). The collected medusae *C. vesicarium* were similar to ones in previous descriptions (Agassiz 1865; Haeckel 1879; Hartlaub 1914; Kramp 1961; Schuchert 2007). The medusa has a large apical projection (Fig. 8c). Four radial canals are broad and strongly jagged. The broad base of the stomach has elongated connections (mesenteries) with radial canals. Tentacles are numerous. Each tentacle bulb carried an ocellus on its abaxial side. Gonads form long folds on the manubrium that tend to be vertical in the interradial region (Schuchert 2007). We assigned the young specimen collected in the field (Fig. 7c) to *C. vesicarium* because only two pandeid medusae are

known for the White Sea area, and a tentacle bulb of *H.cirratus* does not carry an ocellus.

Pandeid hydroids live on mollusc shells or other substrata in the sea. They have a few morphological features. Usually, it is a difficult task to tell one species from another. Some authors considered the polyps of *C. vesicarium* are probably *Perigonimus abyssi* (Naumov 1960). We can reject this guess now. More probably, *P. abyssi* relates to *Leuckartiara* or *Neoturris* species (Rees 1938, 1956; Schuchert 2007). The hydroid *C. vesicarium* is unlike the most known Arctic Pandeidae hydroids (own dates; Schuchert 2007; Stepanjants and Svoboda 2013). The characteristic features of *C. vesicarium* hydroid are that the polyps are almost sessile and perisarc cup is placed only at the base of polyps and that the medusa buds arise directly from creeping stolons (Fig. 8a). These characters of the hydroid are similar to *P. conica* ones (Picard 1956; Schuchert 2007). But hydroid *P.conica* inhabit other substrata [pelagic gastropod *Clio cuspidata* (Bosc, 1802)], and newborn medusae have only two tentacles and four tentacle bases with dispersed red pigment present in the bulbs (Schuchert 2007). On the contrary, the newborn medusae of *C. vesicarium* have four tentacles and eight bulbs with red pigment (Fig. 8b).

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Medusae *C. vesicarium* usually appear in the White Sea during the period from May till July (our data; Pertsova 1979; Slobodov and Marfenin 2005). Hydroids inhabit the shell of *Astarte elliptica* with live molluscs and can be collected in the cold water under the thermocline. As a result of our laboratory experiments, we assume the hydroids can produce medusae all year round in such conditions. But there were no catches of medusae in the period from August till April. It is possible that the seasonality of medusae appearing in the sea depends on food supply. Zooplankton abundance in the surface layer of the sea is low during the period from November till March. The larval stages of some zooplankton species such as barnacle *Semibalanus balanoides* (Linnaeus, 1767) larvae and copepods *Pseudocalanus sp.* are abundant in the sea in April and May. The hydroids and newborn medusae can feed with this nutritious food.

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Compliance with ethical standards

Conflicts of interest The authors have no potential conflicts of interest.

Ethical standards The experiments comply with the current laws of the Russian Federation.

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