

**Distribution and larval development in the horse mussel
Modiolus modiolus (Linnaeus, 1758) (Bivalvia, Mytilidae)
from the White Sea**

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Modiolus modiolus is an important species in the White Sea benthos. It is widely spread mostly in the Onega and Mezen Bays, but it can be encountered in other regions of the sea as well. In the Dvina Bay, this species has not been found yet. Horse mussel often plays a role of leading form in numerous sea bottom communities and sometimes its biomass reaches 5 kg/m². Nevertheless, there are only few papers dealing with its distribution in the White Sea (Ivanova, 1957; Kudersky, 1962, 1966; Golikov *et al.*, 1985; Fedyakov, 1988).

The reproductive cycle of *Modiolus modiolus* was first described by Seed and Brown (1977) in histological study of specimens from Stranford Lough, Northern Ireland. The reproductive cycle of *M. modiolus* from the White Sea was studied only by Kaufman (1977). As a result of his studies, Kaufman concluded that spawning began in this population in June and July.

First descriptions of *M. modiolus* larvae can be found in the papers of Jørgensen (1946). In his references Jørgensen stated that larvae of this species have not been identified with certainty in plankton samples taken in Danish waters. He thinks that this is due to the very close resemblance of *M. modiolus* to veliger of *Mytilus edulis*.

Later, Rees (1950) stated that in the smallest veligers of *M. modiolus* and *M. edulis* the shape is similar, although in the former the narrow end is less pointed. Nevertheless, in later stages the shapes of two species become more different.

Identification of bivalve larvae and early post-larvae has been extremely difficult. The most detailed description of laboratory cultured *M. modiolus* larvae from the straight-hinge to metamorphosis, including photographic and statistical comparison with *M. edulis*, was given by Schweinitz and Lutz (1976).

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The present study provides distribution and life conditions, an account of reproductive cycle of *M. modiolus* in the White Sea, development of *M. modiolus* larvae from egg to metamorphosis and comparison of *Mytilus* and *Modiolus* post-larvae.

Materials and methods

Material was collected since 1981 from all over the White Sea excluding the Voronka from on board of the White Sea Biological Station R/Vs "Kartesh" and "Professor Vladimir Kuznetsov" using Petersen's grab with working square 0.25 m². The sediment was washed out by seawater on a sieve with the mesh size of 1 mm. The samples were sorted in laboratory; all the organisms were identified, counted and weighted with accuracy within 0.001 g. All data were reduced to 1 m². Depth at the sampling point was measured by echo sounding. The sediment temperature was measured using mercury thermometer to one decimal point. Water for salinity investigation was sampled by Nansen's bathometer within one-meter-thick bottom layer. Salinity was measured by density to 0.1 ‰. All the data obtained were stored in "The White Sea Benthos" database.

Data on *M. modiolus* spat settling were obtained experimentally. The defaunated sea belt *Laminaria saccharina* thalli were put in bags made of nylon net, mesh size 40 mm, which were placed on the sea floor at a depth of approximately 25 m. Five substrata with 6 bags each were installed near the White Sea Biological Station June 26, 2001. Thrice one by one substrata were removed: on October 3 and November 3, 2001 and August 12, 2002.

Fouling organisms settled on the sea belt thalli were washed out using a sieve with mesh size of 0.5 mm, identified, counted and weighted to 0.001 g. Their abundance was reduced to 1 kg of substratum mass. Data obtained in 2001 were pooled.

Sexually mature adult *M. modiolus* were obtained during June and July from various locations of the Chupa Inlet (Kandalaksha Bay) in water depth ranging from 7 to 15 m and were placed in a salt water at approximately 12 °C. Attempts to spawn these bivalves using standard techniques developed for other molluscs (Lossanov & Daevis, 1964) were unsuccessful. In three cases, however, horse mussels kept in aquarium spawned without artificial stimulation.

Larvae were cultured in polyethylene containers at a density of about 15-20 individuals per millilitre, with recurrent aeration. Water temperature ranged from 11.0 to 12.5 °C and conformed to the temperature in the White Sea. Salinity was 25‰, which also conformed to conditions in the sea. Lar-

vae that reached a veliger stage were fed daily with *Dunaliella* sp. and *Isochrysis* sp. (Lossanov & Daevis, 1964). Larvae on a veliger and pediveliger stages were collected from plankton for comparison with artificially reared larvae.

All length measurements and micrographs in this study were obtained from whole larvae or post-larvae, taking care to achieve representative larval orientation. Measurements were made with a compound microscope equipped with an ocular micrometer and are considered accurate within 1 μm . All the data were processed using linear statistics. The diversity statistic in terms of biomass was calculated as Shannon's-Weaver's one.

The oligomixness of communities in terms of biomass was computed using the formula

$$I_0 = \frac{\sigma_B}{B} \sqrt{S} \times 100,$$

where I_0 is an oligomixness statistic, σ_B is a standard deviation in species biomass array, B is a total biomass of the community, S is a species number in the community (Naumov, 1991).

Results and discussion

Life conditions of Modiolus modiolus in the White Sea. Our data do not allow defining a preferable type of sediment for *M. modiolus*. Fedyakov (1986, 1988) points out, that it mostly can be found on the rocky or sandy bottom. Other environmental characteristics according to our material are displayed in Table 1.

Besides few encounters of some small individuals at the depths up to 140 m, the most part of finds are related to depth 7 to 40 m. This depth can be considered as a common one for this species. Kudersky (1962) does not indicate at what a depth he found *M. modiolus* and only points out, that it is associated with the slope between shallows and relatively deep space. According to Golikov's data (Golikov *et al.*, 1985), this species in the Onega Bay can be found at depths 12 to 35 m, while in the Basin at 10 to 55 m. In the Kandalaksha Bay, it was found at depths 4 to 50 m (Fedyakov, 1988).

In our material, the maximum density (276 ind./m²) in *M. modiolus* was found in Zapadnaya Solovetskaya Salma Strait at a depth of 30 m on the silty sands, while the maximal biomass (5420 g/m²) - near Bol'shaya Muk-salma Island at a depth of 10 m on the pebble bottom. The average magnitudes of abundance in *M. modiolus* are presented in Table 2. In our material, average biomass in this species in different communities exceeds val-

ues represented in literature. In community *Modiolus modiolus* + *Verruca stroemia*, Onega Bay, we found its biomass equal to 627 ± 384 g/m² in community *Modiolus modiolus* + *Chlamys islandicus*, Onega Bay, - 2729 ± 1937 g/m²; in community *Modiolus modiolus*, Mezen' Bay, - 579 ± 492 g/m². According to Kudersky's data (1962), its biomass in *Modiolus modiolus* + *Cirripedia* community is 419 g/m². Golikov *et al.* (1985) mark 250 ± 109 g/m² for community *Modiolus modiolus* + *Verruca stroemia*, Basin, and 322 ± 81 g/m² for community *Modiolus modiolus* + *Hydrallmania falcata*, Onega Bay. Fedyakov (1988) notifies its biomass being equal 380 ± 310 g/m² in community *Modiolus modiolus*, Kandalaksha Bay.

Table 1. Living conditions of *Modiolus modiolus* in the White Sea

Region	Depth range (m)	Summer temperature range (°C)	Salinity range (‰)
Kandalaksha Bay	16+98	-1.2+4.6	27.0+29.0
Onega Bay	7+55	6.0+8.5	No data
Dvina Bay		Not found	
Mezen' Bay	16+22	6.1+7.9	25.4+28.1
Basin	10	No data	No data
Gorlo Strait	15+140	4.0+8.7	27.2+30.1
The entire sea	7+140	-1.2+8.7	25.4+30.1

Table 2. Abundance in *Modiolus modiolus* from the White Sea

Region	Number of benthic stations	Number of findings	Occurrence (%)	Average biomass in communities (g/m ²)	Average density in communities (ind./m ²)
Kandalaksha Bay	393	4	1.02	0.047	23.3
Onega Bay	129	10	7.75 ± 2.35	106.149 ± 53.559	7.6 ± 3.2
Dvina Bay	170	0		Not found	
Mezen' Bay	29	5	17.24	579.413	41.4
Basin	46	1	2.17	157.000	20.0
Gorlo Strait	35	6	17.14 ± 6.37	59.633 ± 53.957	25.3 ± 10.2
The entire sea at depth range of 7 to 40 m	300	22	7.33 ± 1.50	847.212 ± 322.354	69.6 ± 17.9

Biotic surrounding of Modiolus modiolus in the White Sea. In the Onega and Mezen' Bays, if found, *M. modiolus* dominates in every benthic station. Two kinds of such communities were encountered in the Onega Bay. One of them includes Cirripedia as subdominant forms, while scallop *Chlamys islandicus* plays this role in the second one. Both of them were found at depths of 7 to 50 m on the gravel sediment. In the Mezen' Bay, only communities with subdominating Cirripedia were found at depths of 16 to 22 m on sandy, pebble and mixed deposits. Kudersky (1962) describes closely related community. On the other side, he did not find the assemblage where scallop is a subdominant species. This author considers such community to be common only for the Barents Sea. Golikov with co-authors (1985) did not find such community as well.

The polymixous communities of *M. modiolus* from the Onega Bay are much richer in species composition and have higher biomass than mesomixous assemblage from the Mezen' Bay (Table 3). The biogeographic structure of these communities is rather similar, widely spread Boreal and Arctic-Boreal species predominating everywhere, although their proportion is different. The trophic structure does not differ in communities found within the scope of observation error. The only exception is, that there were found numerous algae in *Modiolus modiolus* + *Verruca stroemia* community from the Onega Bay. In the all three communities, sessile epifauna makes more than 90% of total biomass. Communities *Modiolus modiolus* + *Verruca stroemia* described by Kudersky (1962) and Golikov with co-authors (1985) resemble that one from our material.

Demographic structure in Modiolus modiolus from the White Sea. It should be stressed that in mentioned above communities, we have never found *M. modiolus* juveniles. Moreover, they are very seldom and thin in our benthic samples at all. Size-frequency plots found in literature (Brown & Seed, 1978; Comely, 1978; Anwar *et al.*, 1990) show, that in most cases molluscs of elder ages predominate in populations inhabiting waters surrounding British Islands.

In our material, this species is represented mostly by big individuals having average mass 12.269 ± 3.220 g. Even molluscs weight about 1 g can be found rather seldom. Juveniles of *M. modiolus* were observed in the Kandalaksha Bay and in the Gorlo Strait in few benthic stations within different polymixous and mesomixous communities (oligomixness statistic 25.58 to 67.55%). In most cases, there were single individuals weighting on average 0.002 g. In two sites only, in Zapadnaya Ryazhkova Salma Strait

Table 3. Main features of bottom communities in the Omega and Mezen' Bays with *Modiolus modiolus* as a dominant species

Characteristics	Omega Bay		Mezen' Bay
	Modiolus + Verruca (in brackets, after Kudersky (1962); Golikov <i>et al.</i> (1985))	Modiolus + Chlamys	
Species number	179 (52; 47)	167	96
Biomass, g/m ²	1770.051 (804.2; 762.3)	4454.840	673.459
Diversity, bit/g	3.829 (0.856; 2.783)	2.264	1.171
Oligomixness, %	38.86 ± 2.15 (53.16 ± 6.18; 47.16 ± 4.86)	64.28 ± 3.76	85.97 ± 6.20
	Biogeographic composition in terms of biomass, %		
Boreal species	4.15 ± 0.47	0.37 ± 0.09	0.08 ± 0.34
Atlantic Boreal species	4.41 ± 0.28	1.74 ± 0.20	2.10 ± 0.55
Widely spread-Boreal species	36.24 ± 1.14	63.15 ± 0.72	86.31 ± 1.32
Arctic-Boreal species	36.09 ± 1.14	31.17 ± 0.69	6.43 ± 0.95
Atlantic Arctic-Boreal species	1.57 ± 0.30	0.35 ± 0.09	0.06 ± 0.09
Pacific Arctic-Boreal species	0.01 ± 0.02	0.09 ± 0.04	0
Arctic species	0.72 ± 0.20	1.02 ± 0.16	0.05 ± 0.09
Species of unknown origin	16.82 ± 0.89	2.11 ± 0.22	4.97 ± 0.84
	Trophic composition in terms of biomass, %		
Autotrophous	9.72 ± 0.70	0.04 ± 0.03	0
Phytophagous	0.04 ± 0.05	0.01 ± 0.01	0.03 ± 0.07
Filter feeders	87.23 ± 0.79	96.91 ± 0.26	97.81 ± 0.56
Deposit feeders	1.08 ± 0.25	2.08 ± 0.21	1.11 ± 0.40
Carnivorous	1.23 ± 0.26	0.25 ± 0.07	0.60 ± 0.30
Omnivorous	0.70 ± 0.20	0.71 ± 0.13	0.43 ± 0.25
Species of unknown feeding	0	0	0.01 ± 0.04

(Kandalaksha Bay) at the place of fairway dragging and at the transection Voronov Cape - Danilov Cape (the Gorlo Strait), a notable number of spat was encountered. In both cases, the depth was 15 to 30 m, rocky or sandy deposits predominating. The sea floor communities consisted of species associated with sites having rather strong bottom currents.

One can consider three reasons to explain, why so rare juveniles are in our material. On the one hand, it is possible that spat passes through the sieve with one-mm large mesh size. On the other hand, spat settling may take place at shallows, where sampling by R/V is impossible. The last reason is that our sampling was carried out during the time when there is no spat settling. All three explanations, however, should be rejected. Even if spat passes through the sieve, juveniles of last year settling should be found in the community. Investigations at a depth less than 7 m (the minimum depth for our R/Vs) by SCUBA diving did not get any evidence neither of *M. modiolus* spat settling nor presence of 1-2-year-old juveniles. If the spat settling takes place, e.g., in winter, nevertheless, the older juveniles should be found. In spite of absence of juveniles in bottom communities, there are a large number of *M. modiolus* larvae in plankton. Thus, the only probable explanation is that spat settling and growth of juveniles take place in narrow localities, which have not been studied yet, and young molluscs migrate towards their definitive sites later.

Taking into account, that we have found some juveniles in places with strong bottom currents at the depth range about 15 to 30 m, we have tried to get *M. modiolus* spat at the similar locality experimentally. Substrata prepared as said above were put on the silty-gravel bottom near base of Sukhaya Cliff in the Chupa Inlet (Kandalaksha Bay). During first three months *M. modiolus* spat settled on the substrata (biomass 0.472 ± 0.466 g/kg_{subst.}, density 6.7 ± 4.9 ind./kg_{subst.}). In 2002, spat settling was recorded as well. Individuals of 2000, 2001 and 2002 years settling were found on the substrata (biomass 0.045 ± 0.005 g/kg_{subst.}, density 54.6 ± 5.7 ind./kg_{subst.}). The presence of 2(+)-years-old juveniles indicates an active migration ability in young horse mussel. For the shell length growth see Fig. 1.

Larval development in Modiolus modiolus from the White Sea. White Sea *Modiolus modiolus* does not appear to become mature until it is 2-3-years old. These bivalves spawned over the whole summer, from the middle of June to September. Larvae were present in plankton from June through November. It is a considerably longer period than Kaufman (1977) stated.

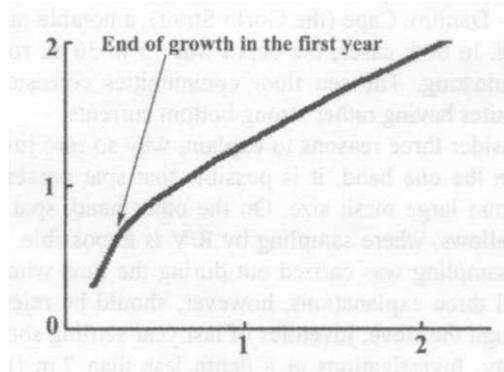


Fig. 1. Growth in *Modiolus modiolus* juveniles, *x-axis* - time (years); *y-axis* - shell length (mm)

The size of the *M. modiolus* eggs was 100 to 100 μm in diameter. According to Jørgensen (1946) the eggs of these bivalves are approximately 100 μm . This size closely agrees with our measurements. However, the size given by Schweinitz & Lutz (1976), 78 to 90 μm , is much smaller than that observed in our cultures.

Early development from cleavage to veliger stage was similar to that described by Malachov & Medvedeva (1985) and Flyachinskaya & Kulakovskiy (1991) for *Mytilus edulis*. The cleavage of *M. modiolus* was unequal spiral and was accompanied by forming of a polar lobe in first, second and third cell-division (Fig. 2, a-g). Unequal blastula without inside cavity was evolved from this cleavage (Fig. 2, h-j). The next stage - conchostome, displayed an archenteron and shell gland (Fig. 2, k). Conchostome is distinctive only for mollusc and corresponding to the gastrula stage of other animals. Trochophore appeared after excurvation of the shell gland and had length 110 μm (Fig. 2, k).

The smallest straight-hinge veliger observed had length and height 170 and 130 μm , respectively (Fig. 3, a). As shell length reached 210 μm , the hinge-line was obscured by the appearance of a low, rounded umbo (Fig. 3, b).

Larval foot became evident within the shell, as larvae attained lengths of 280 μm (Fig. 3, c). Pigmented eyespots appear as larvae exceed 300 μm (Fig. 3, d). The full-grown foot of the pediveliger stage begins functioning as larvae exceed 330 μm (Fig. 3, e).

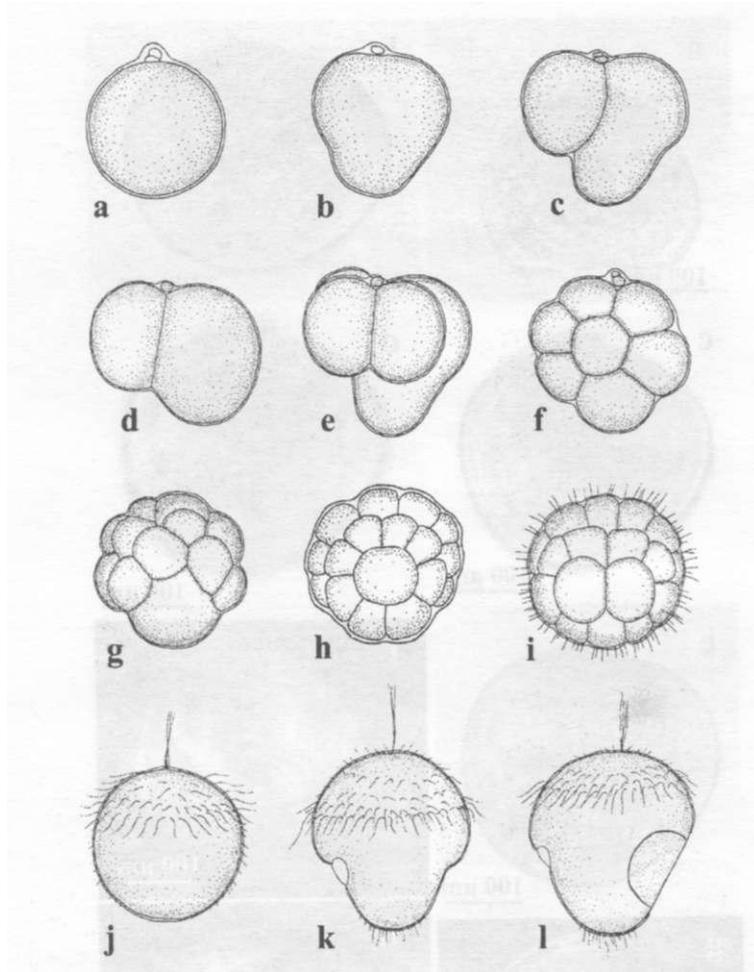


Fig. 2. Cleavage and early embryogenesis of *Modiolus modiolus*. For explanations see page 46

A straight-hinge veliger and pediveliger with functioning foot observed by us were bigger than Schweinitz & Lutz (1976) reported. They found that straight-hinge veliger in their cultures had length and height 105 and 109 μm , respectively. It was much significantly smaller than that observed in our cultures. The length of pediveliger with functioning foot in their cultures was 290 μm , so it was also smaller.

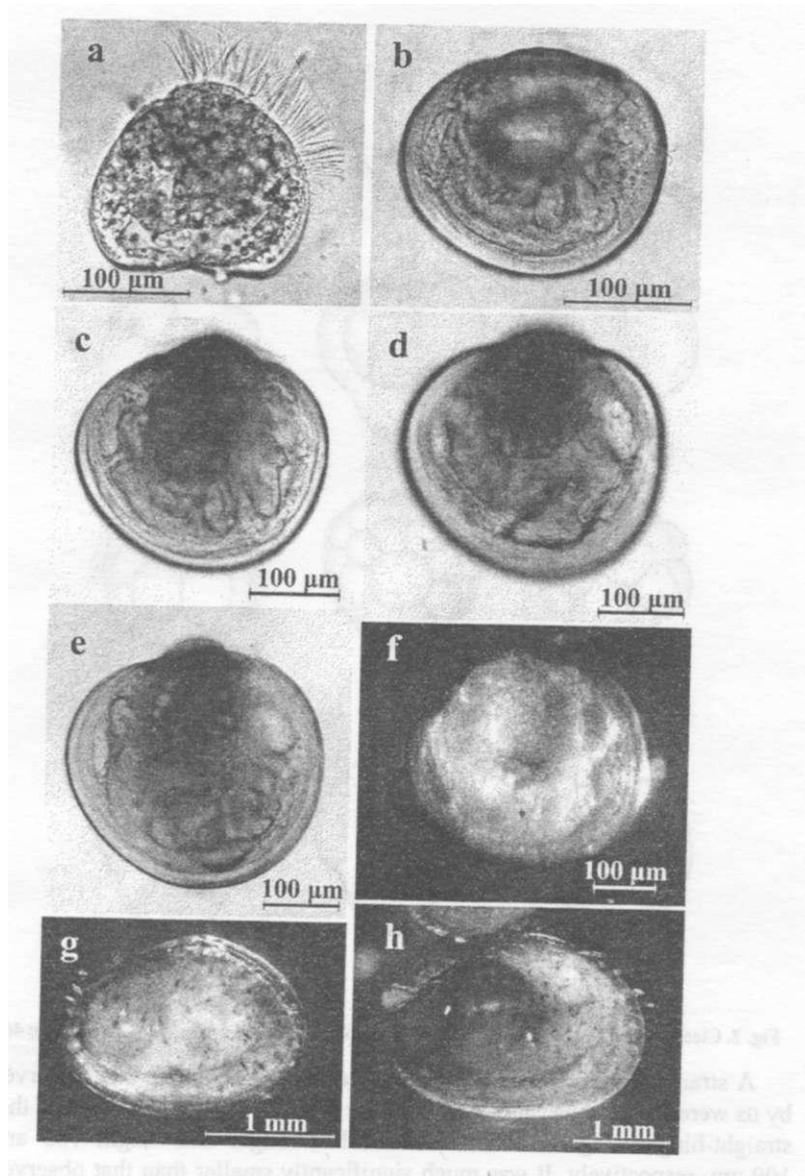


Fig. 3. Metamorphosed juveniles of *Modiolus modiolus*. For explanations see page 46

Although some completely metamorphosed juveniles 350 μm in length were observed in cultures, the majority of the larvae did not lose their velum until they reached 400 μm . All larvae collected from plankton and spat were found on the substrata metamorphosed at size of approximately 400 μm (Fig. 3, f-h). The variation in size at the time of metamorphosis confirms a more critical analysis of the data on growth of larvae in the culture (Lossanov & Daevis, 1964).

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