Some aspects of the life history and ecology of *Oncholaimium ramosum* (Nematoda: Oncholaimidae) in the polluted harbour of the Sea of Japan

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Summary. *Oncholaimium ramosum* (Nematoda: Oncholaimidae) occurs in the heavily polluted harbours of the Sea of Japan. The life history of *O. ramosum* has been studied in the laboratory and in the habitat over a two-year period. Observations on the embryonic and postembryonic development, and also the moulting processes are presented. Egg laying was observed on 35 occasions, and 400 eggs and approximately 1000 nematodes of this species were investigated. *O. ramosum* has two generations in the Sea of Japan. Egg deposition continues from February to July (spring generation) and from September to November (autumn generation). Females of *O. ramosum* were observed from egg deposition to death. Eggs are laid either singly or in batches of 2-38. The cleavage of 43-50% of eggs was observed immediately after eggs had been laid. The development of the remaining eggs was delayed for 8-10 days. The process of hatching of the first to last egg to be laid also occurred over 8-10 days. The stages of 2, 4, 8 blastomeres, late gastrula, and vermiform juveniles are described. The average time of development of *O. ramosum* from the beginning of cleavage to hatching was 1-1.5 months. The size and developmental time of *O. ramosum* juveniles (J1-J4) and adults was determined. Reproduction and duration of the life cycle are discussed.
Key words: free-living marine nematodes, embryonic, postembryonic development, Sea of Japan.

Marine free-living nematode development has not been studied in depth. Most of the research that has been done so far has been directed at describing the development of some of the commonest parasitic nematodes that influence human health and agriculture. There are general descriptions of embryonic development of free-living marine nematodes of some species (e.g. Malakhov, Cherdantzev, 1975; Vranken *et al.*, 1981; Jensen, 1983; Malakhov, 1983; Voronov *et al.*, 1989; Voronov, 1999). However, the information about the postembryonic development is very limited (Malakhov, 1980; Voronov *et al.*, 1989).

The postembryonic development of nematodes involves four moults (Bird, 1984; Malakhov,1994). Over the past 20 years there has been a number of reviews on moulting and growth, notably by Bird (1984). Unfortunately, these reviews only emphasized the gaps in our knowledge of the physiology of nematode moulting.

Information on the life cycles and development of the free-living marine nematodes has been presented by Filipjev & Michailova (1924), Wieser & Kanwisher (1960), Tietjen & Lee (1973), Malachov (1972), Bergolz & Brenning (1978), Smol *et al.* (1980), Vranken *et al.* (1981) and Jensen (1983). Some of these results were summarized by Heip *et al.* (1985). Not much is known about the reproduction biology of marine Japanese nematode species (Kito, 1979).

Oncholaimium ramosum occurs at high densities in heavily polluted harbours of the Sea of Japan (Fadeev & Fadeeva, 1999; Fadeeva *et al.*, 2003). The abundance of certain taxa of benthic marine invertebrates is known to increase dramatically when levels of particulate organic and toxic enrichment become abnormally high, and these groups have become known as 'pollution indicator' species.

This paper contains the initial information on embryonic and postembryonic development, the moulting process and some aspects of the growth of *O. ramosum*.

This study is part of a project on the ecology of Japanese nematodes carried out at the Ecology Department, Far Eastern National University.

MATERIAL AND METHODS

The life cycle of oncholaimid nematodes extends over a long period of time. It is extremely difficult to obtain satisfactory data throughout the life cycle of the species in laboratory conditions; therefore, to investigate the reproductive biology experimental observations and seasonal data of natural populations development were used.

Quantitative sediment samples were collected from the seasonal station in Golden Horn Bay (Vladivostok Port) in 1997 (March-October) and from March 2000 to March 2001, at 13 m depth by scuba divers, and qualitative samples were taken with a 0.025 m^2 Petersen Grab. In our work we also used additional material of *O. ramosum* collected from Melkovodnaya Bay, Boisman Bay and Golden Horn Bay (Peter the Great Bay of the Sea of Japan) and stored in the Faculty of the Ecology of Far Eastern National University.

Oncholaimium ramosum did not survive through a whole life cycle in the laboratory. The nematodes were raised under laboratory conditions that approximated to those in nature. During experiments, the nematodes were kept in the dark in 35 and 87 mm Petri dishes with 10–15 and 25–30 ml seawater, respectively, from the same habitat (30–32 S and 4°–10° C). In previous tests, the worms die when kept in the light at room temperature (20–23°C).

Eight gravid females were separated from the muddy sediment and transferred into Petri dish with sterile seawater. Seven replicates were made during these experiments. The water was changed every 5–7 d by adding 1–3 ml fresh non-sterile interstitial seawater from the original samples used as food sources. Such food source contained organic matter, bacteria and ciliates. Sterile seawater was prepared by autoclaving at 1.5 kg/cm2 pressure for 20–30 min. The absence of any substratum simplified the observation of egg laying and development. During the experiment the development of 35 clusters of eggs was observed.

Females that had just laid eggs were transferred into a Petri dish with seawater and some sediment from the same habitat. Water was changed every 5–7 d by adding 1–3 ml fresh interstitial seawater as food source. Virgin females were held separately in another Petri dishes with some fine sand. When transferred into the new environment, old females were maintained in conditions approximating to those in nature. The embryological development of eggs was studied with a microscope (Axiostar, Zeiss) in Petri dishes without transferring the eggs on the glasses. In total, during two series of experiments, the development of approximately 400 eggs was studied. Development of juveniles was observed on a daily basis at 4–10°C and 30–32°. The hatching process was repeatedly observed under the microscope during experimental cultivation. Illustrations of embryos and stages of juvenile development were taken with digital camera Olympus.

Some nematodes were fixed with 4% formalin for the following measurements; 420 individuals were measured. The morphometric analysis was used to define the life cycle stages of *Oncholaimium ramosum*. Some most important specific features were selected: length of the body, pharynx, tail, spicules, distance to vulva; head and maximum diameter and also 4 De Man indices (a, b, c, V). The number of circles of cephalic setae, presence or absence of sexual structures (spicules, ovaries, vulva, demanian system), peculiarities of cuticle, pharynx and intestine were also recorded.

RESULTS

Some nematologists do not recognize the genus *Oncholaimium*. Therefore, some species of nematodes having features of the genus *Oncholaimium* are included in the genus *Oncholaimus*. The basic features of generic distinctions are connected with the form of the female reproductive system.

The demanian system of *Oncholaimus* includes two terminal ducts and two pores located bilaterally, and three or more ducts and pores in *Oncholaimium* located asymmetrically (Belogurov & Belogurova, 1989; Smolyanko & Belogurov, 1987). According to our observations, *Oncholaimium* has two groups from 3-4 ducts and pores located anterior to the anus.

After the last (fourth) moult, females accumulate sperm in the uterus. Primary oocytes fuse with spermatozoa in the distal end of the uterus. The fertilized oocytes of *O. ramosum* accumulate in the uterus, change to zygotes and immediately enter the mitotic prophase of the first cleavage. Meiosis is arrested at the telophase stage of the first division and continues only after eggs have been laid. The number of *O. ramosum* synchronous eggs is 2 – 32. The females deposited individual eggs

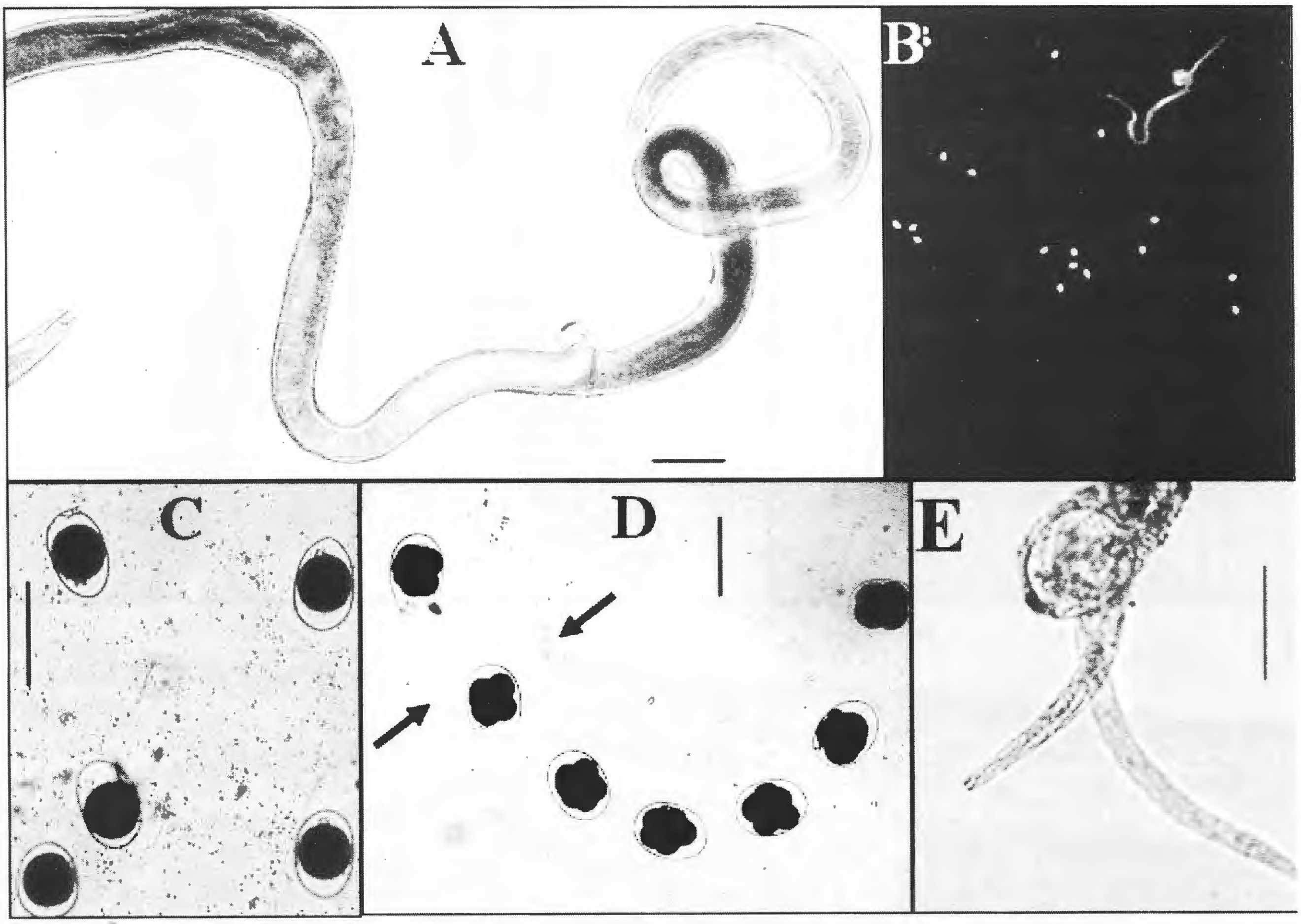

Fig. 1. Photomicrographs of *Oncholaimium ramosum* Smolyanko et Belogurov, 1987. A & B: Eggs deposited by female; C: Zygote before the first division of cleavage (two polar bodies); D: Some stages of the development of living embryos in the egg after being laid; E: Hatching of the first stage juvenile. Scale bars: A – 50 µm; C-E – 100 µm.

one-by-one, squeezing them through a vulva at short intervals (Fig. 1A, B). Laying each ègg lasted some seconds. Usually, females laid a sequence of 6-8 eggs and then, after a delay, more fertilized eggs were added to the uterus. After deposition, eggs have either an elongated or oval form, repeating the form of uterus tube, or they have a teardrop form. They have average measurements of 50–94 x 95–120 µm (Fig. 1C). Under laboratory conditions, 100% mortality of females occurred after completion of egg laying.

The deposited eggs were covered with a viscous secretion and stuck easily to the bottom of Petri dishes, grains of sand or to needles. Probably, the secretion helps the formation of egg-clusters, which are formed immediately isolated eggs come in contact with each other. The deposition of isolated eggs that do not form clusters was also observed in the laboratory (Fig. 1D). The eggs were laid in the form of a chain, a lump or a cluster of eggs pasted together. They always had the general thin capsule seen clearly under the microscope. The number of eggs laid by each female varied from 2 to 38 (frequently 8).

The development of eggs after laying was irregular. Cleavage of 46 – 50 % of eggs began immediately but the development of the remaining eggs was delayed for 8–10 days. However, the time interval between egg deposition and hatching was the same for all eggs.

The embryonic development of *O. ramosum* eggs occurred within the egg-clusters. The peeling of the cytoplasm from the eggshell occurred immediately after eggs were deposited. In a few

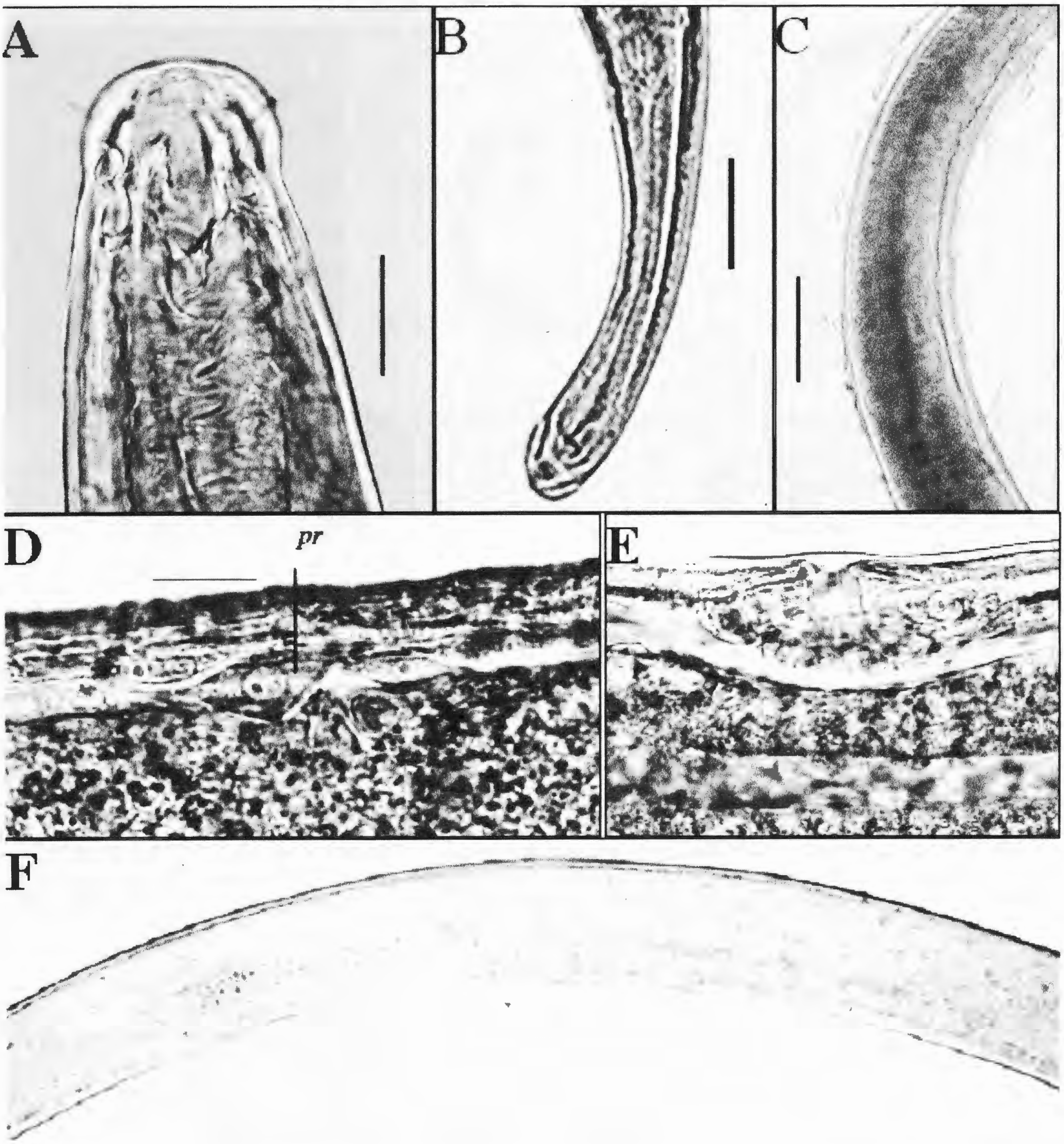

Fig. 2. Examples of the juveniles of *Oncholaimium ramosum* during moult. A & B: The anterior and posterior end of juvenile during second moult; C: Cuticular moulting; D: Genital primordium during the second moult, pr - primordium; E: Genital primordium of the third-stage female juvenile; F: Vulva of the fourth-stage female juvenile, lateral view. Scale bars: A – 20 µm; B – 40 µm; C – 100 µm; D,E – 10 µm; F – 40 µm.

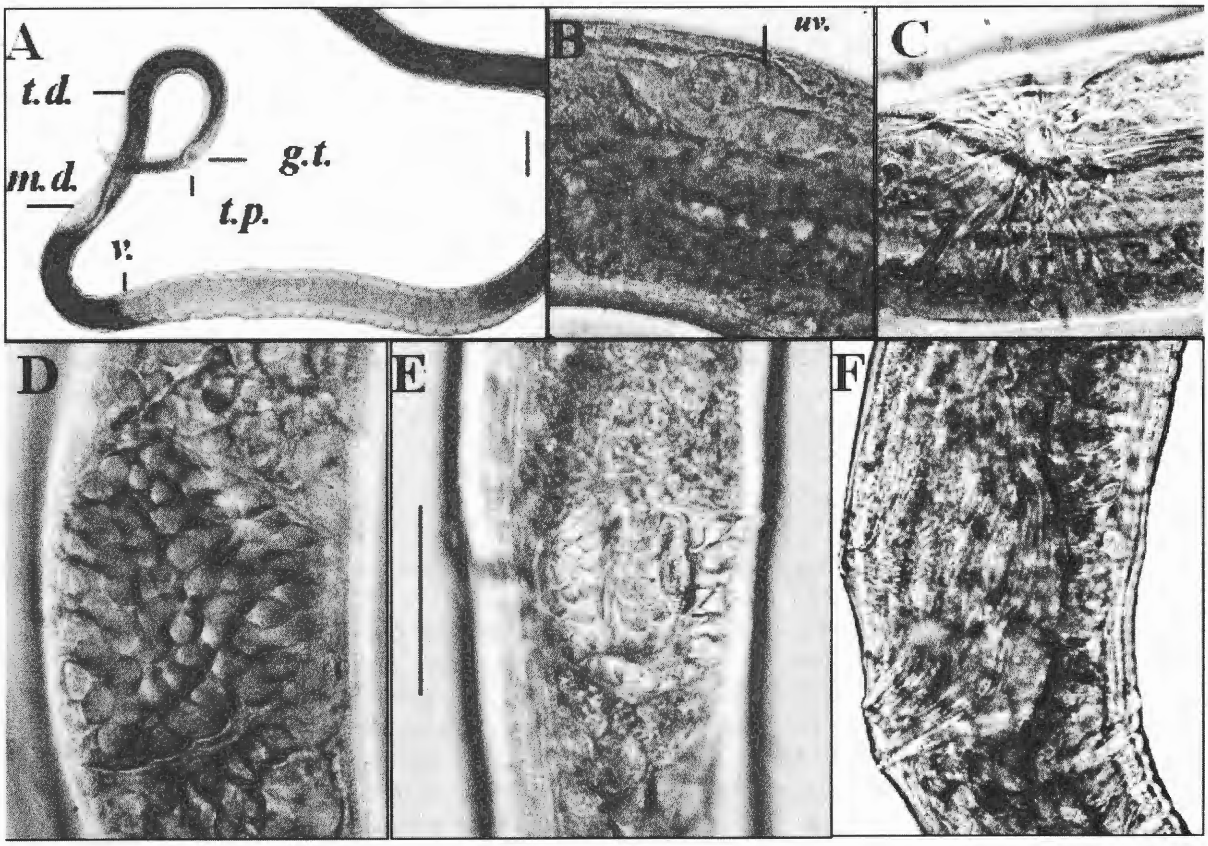

Fig. 3. Photomicrographs of *Oncholaimium ramosum* female. A: Entire demanian system; B: Detail of the region around the uvette; C: Vulvar region, ventral view; D & E: Epidermal glandular tissue; F: Terminal pores. g.t. - glandular epidermal tissue, m.d. - main duct, t.d. — terminal duct, t.p. - terminal pore, uv. - uvette, v. - vulva. Scale bars: A — 100 μm; B — 20 μm; C — 10 μm; D, E, F — 100 μm.

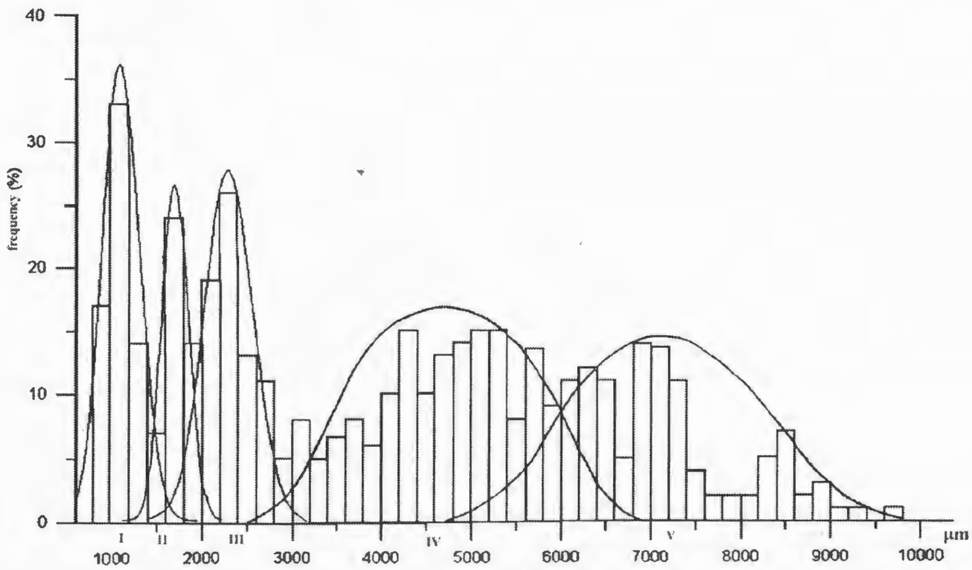

Fig. 4. Frequency - dimensional histograms of nematode population of *Oncholaimium ramosum*.

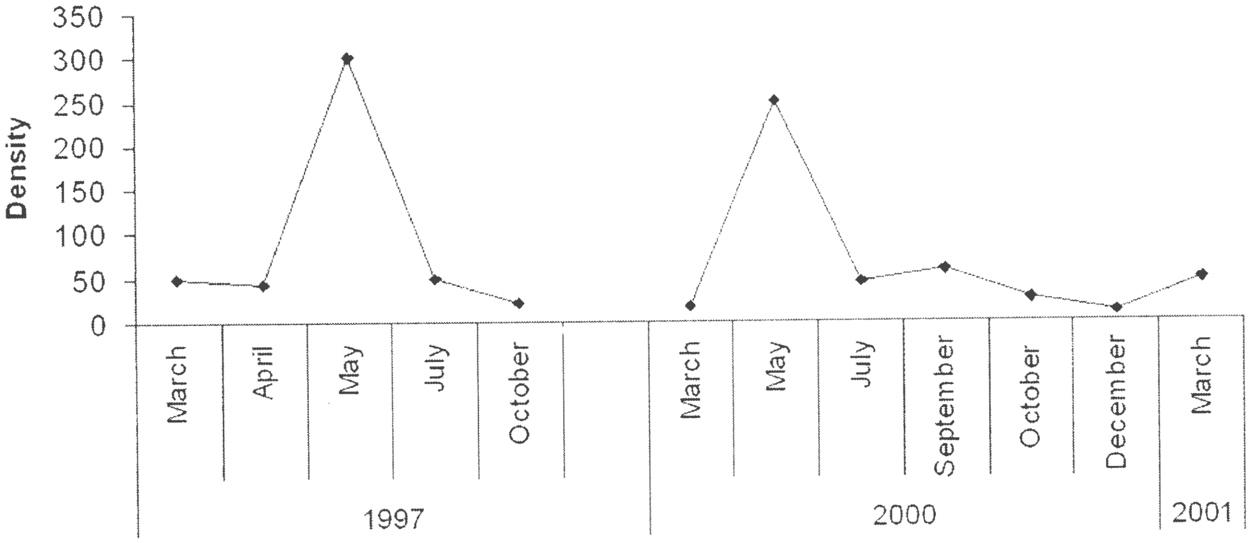

Fig. 5. Seasonal fluctuations of density of *Oncholaimium ramosum* (ind. m $^{-2}$).

minutes the eggs become absolutely spherical in form and remained in the same state on average for 1 – 2 days. At the end of the delay before cleavage, two polar bodies were formed (Fig. 1C).

Their position, relative to the longitudinal egg shell axis, is polar. The two-cell stage shows the usual arrangement of blastomeres along the longitudinal egg-shell axis. The second division occurs approximately in 2 h after the first and results in 4 blastomeres, which have the tetra-hedron form (Fig. 1D). Approximately 1 – 2 h later, the third cleavage was observed, resulting in the formation of 8 blastomeres, much smaller in size compared with the initial ones. Prominent cytoplasmatic movement was observed for the interphase blastomeres. Gastrulation starts on the second or third day from the deposition of the eggs or in 1 day from the beginning of the first cleavage. The embryo of the 4th day had the organization of a gastrula; a' tadpole' stage was formed on 8-9-th day, and on 18–20th day after deposition of the eggs passive juvenile rotation inside the eggs was noted. The hatching of the first-stage juveniles was recorded approximately 30 - 43 days after egg deposition (Fig.1E). The first postembryonic stage of *O. ramosum* is a vermiform juvenile that is structurally very much like the adult.

Thus, the average time of development of an embryo of *O. ramosum* is 1-1.5 months (Table 1).

The postembryonic development. Postembryonic development is accompanied by periodic cuticular moults between successive stages. *Oncholaimium ramosum* is a species where the nematodes undergo all four moults after hatching.

The first- stage juveniles. The mean body length of first-stage juveniles (J1) after hatching is 1079.6±119 μm (Table 2). They are very pale, almost transparent. Cephalic sensillae in two circles. The trophic-sense and caudal parts of the body have the large distinct hypodermal cells. Characteristic large gonadal primordium (a pair of cells without yolk in cytoplasm and condensed chromatin in a nucleus) lay in pseudocoelom near the intestine. Oesophagus is 281.2±40.0 μm, tail = 86.8±9.4 μm. a = 24-37.7; b = 2.6–4.8; c = 10.3–15.6. The hatched juveniles increase their body length by 1.5–2 times on average, and then they moult

The second-stage juveniles. Similar to J1. The mean body length of second-stage juveniles (J2) is 1537.7±184.9 μm. J2 have only one circle of cephalic sensillae and the large well appreciable hypodermal cells. Oesophagus is 364.9±41.6 μm, tail = 99.7±7.9 μm . Gonadial primordia is more developed than in J1. a = 30.7-38.5; b = 3.3-5.5; c = 10.1-20.0. Moulting J2 are presented in Fig. 2 A,B,C & D.

The third-stage juveniles. The mean body length is 2245.3±303.7 μm. Oesophagus is 374.2±53 μm, tail part = 109.7±10.8 μm. a = 34.9-46.5; b = 4.5-8.6; c = 15.4-29.5. By the end of the third stage the sizes of the hypodermal cells of the anterior body and caudal parts have decreased appreciably. The reproductive system starts to develop at this stage. The gonadal primordium is ovoid, few-celled, 24-236 μm (Fig. 2F).

The forth-stage juveniles. Differentiation of females and males is observed this age. Sexual dimorphism is more prominent in the structure of gonads. Oesophagus is 440.3±70.5 μm, tail part =126.4±12.4 μm. a = 40.7–61.1; b = 6.0–10.1; c = 26.6–48.4. Two size classes can be differentiated: 2124-6452 μm (females) and 2380-6140 μm (males). Most somatic growth is recorded for forth-stage juveniles. The basic attribute of the end of the fourth juvenile stage is the formation of female and male reproductive system. Gonads are still rudimentary, represented by oval ovary; the uterus is not clearly differentiated (Fig. 6A). The vagina is not completely formed; the vulva is closed by the cuticle (Fig. 2E).

Adult characteristics. Body length of the mature males is 4836-9172 μm, mature females – 4128-9694 μm. Mature females are virgins and gravid. The virgin female length is 4128-6452 μm. The vulva of nematodes is open after the last moult (Fig. 3C). The first gravid females appear in 120 – 140 days after hatching. Oesophagus is 497.6 ± 88.1 μm, tail – 152.1 ± 28.1 μm. a = 57.5-69.8; b = 14.0-17.5; c = 41.4-49.9; V = 62.6 – 68.0% (females). a = 64.3-77.0; b = 8.1-14.5; c = 52.7-59.9 (males). The female reproductive system of *O. ramosum* is monodelphic, ovary is reflexed; the germinal tip of the ovary is characterized by oocytes located in two lines, in the other part of the ovary in one line. The oncholaimid demanian system is well developed and constitute a complex spermatheca (Fig. 3A). The parts of demanian system of *O. ramosum* are formed in the virgin females. However, they are poorly visible because the walls of the ducts are often collapsing in absence of sperm. The transparent sticky secretion is produced by glandular epidermal tissue for the attraction of the males. The uvette is an oval structure on the right side of the body, made up of about 2 elements surrounding a minute pore (Fig. 3B), 160-180 μm posterior to vulva; the osmosium anterior to uvette. Gravid females have *ductus intericus*, the part of the main dorsal tube between osmosium and uvette, filled with sperms. *Efferentus principalis* is part of the main dorsal tube between uvette and lateral tubes. *Ductus terminals* at the end has two lateral dilatation containing glands, two series of about 20 – 25 cells (Fig. 3D, E). The number of terminal ducts and pores is generally not less than three, situated 300-460 μm anterior of the anus (Fig. 2A). Distal parts of terminal ducts are cuticular and well observed (Fig. 3F). The male reproductive system is diorchic, with anterior and posterior testis and a pair of spicules. The spicules of mature males are similar to fourth-stage juveniles but larger (Table 2). The precloacal supplement is shaped as a folded funnel.

The recognition of J1 to J3 has been carried out on the basis of histogram analysis of the frequency - size structure of the nematode population (Fig. 4). This analysis was based on the assumption that linear body sizes of nematodes of a single age class tend to normal distribution. Five well separated size groups corresponding to the five nematode stages were defined. The data of histograms of polymodal frequency - size distributions of *O. ramosum* population are in good agreement with the moult sizes and data shown in Table 2. The fourth and fifth age stages were defined by the degree of development of the reproductive system. The body length of the mature males is smaller than the mature females. Somatic growth is most pronounced for fourth-stage juveniles and adults.

Population seasonal dynamics of *Oncholaimium ramosum*. The nematode density of *O. ramosum* fluctuates seasonally (Fig. 5). Its highest densities are recorded in May and low densities from summer to winter months. Juveniles are found throughout the year, whereas mature females and males are nearly absent at the end of July and in winter. The total population consists of 60% (in spring) to 95% juveniles towards the end of July and in winter. Females are abundant from March to June and from September to October. At least 50% of them are gravid. Mature nematodes had disappeared at the beginning of August. The sex ratio over the period of main reproduction is 1:1 but it moves in favour of females (1:1.2) at the end of this period.

The females deposited eggs from February to July. The peak of juvenile numbers was in May-June. J1 to J3 were abundant in March–April and in September-October. J3 and J4 were dominant in May-June and November-December. The maximum number of nematodes moulting from J4 to adult was noted in July. By the end of August nematodes of the first generation were mature and started to deposit eggs. The juveniles of the II generation hatched in 1-1.5 months. These juveniles may be termed the "autumn" generation. The number of J1-J3 increased but not so as rapidly as in the spring. Only immature nematodes were found in December. Obviously these are juveniles that appeared in autumn. They survive in adverse environmental conditions and become mature in the early spring.

Thus, the simultaneous existence of two cohorts of juveniles in the population is observed in the spring and in the early autumn. The death of adults at the end of reproductive period testifies to the fact that each nematode survives for only one reproductive cycle. Therefore, the generation time of this species can reach 6 –7 months.

DISCUSSION

Most studies on embryonic and postembryonic development have focused on shorter-living species of marine nematodes (Tietjen *et al.*, 1970; Tietjen & Lee, 1972; Bergholz & Brenning, 1978; Vranken *et al.*, 1981; Jensen, 1983; 1995) rather than on longer-living species (Malakhov, 1974; Malakhov & Cherdantsev, 1975; Voronov *et al.*, 1989; Voronov, 1999). One of the earliest formations of genital primordia among all animals is described for nematodes (Malakhov, 1998). Postembryonic development of nematodes is accompanied by periodic moulting. Juvenile development of *O. ramosum*, like of other free-living species of nematodes, is accompanied by the modifications of cephalic setae at the early stages of development, and the formation and rapid growth of trophico-genital part at the last stages. The moult, as well as of the degree of development of the female reproductive system are good markers for juvenile stages. The demanian system of *O. ramosum* develops after the last moult. Terminal ducts and pores of virgin females are not quite evident. After insemination, the tubular female reproductive system is filled with sperm, and two symmetric spermathecae (with 3 – 4 ducts in each) are clearly visible on both body sides. The secretion of glandular epidermal tissue surrounding spermathecae attracts the males. Some authors (Coomans *et al.*, 1988) proved that terminal parts of the demanian system of *Oncholamus oxyuris* form during traumatic insemination. Precopulatory and mating behaviours of females and males of *O. ramosum* were not investigated.

The results of laboratory studies show the fast rate of oocyte maturation of *O. ramosum*. It was noted that the number of eggs in the uterus increased from 10 to 17 in 4 days. In the parallel experiment the female, after having deposited 20 eggs, produced another 6 eggs in 4 days. It proves that sperm are preserved in the tubular organ for an extended period of time and they are gradually used during the fertilization of maturing oocytes.

It is known that the duration of marine nematode development varies from a few days (for the small rhabditids) to several months (for the large oncholaimids) (Heip *et al.*, 1985). The generation time of the related species *Oncholaimus brachycercus* lasts approximately 360 days (Heip *et al.*, 1985), and *O. oxyuris* – 480 days (Smol *et al.*, 1980). Males of *O. oxyuris* become mature earlier than females, live longer and therefore outnumber the females (Smol *et al.*, 1980). The sex ratio during the main period of reproduction is 4:6 in favour of males but by the end of summer it changes to 2:8 (Smol *et al.*, 1980). On average, the entire population of this species consists of 70% juveniles.

Males of *O. ramosum* have smaller body length, become mature and die earlier. The mortality rate of the adults registered both in laboratory conditions and in natural populations has also been noted by other researchers and for other species of nematodes (Tietjen *et al.*, 1970; Tietjen & Lee, 1972; Bergholz & Brenning, 1978; Smol *et al.*, 1980; Jensen, 1995). A high percentage of juveniles has been recorded by Meyers *et al.* (1970) for *Metoncholaimus scissus*. The dominance of juveniles in *Sabatieria pulchra* populations through all seasons has been shown by Heip *et al.* (1985). The constant presence of *Eudiplogaster pararmatus* juveniles in seasonal samples has also been noted by Romeyn *et al.* (1983).

Table 1. The average duration of embryonic development of *Oncholaimium ramosum* (t=4°-10°C, S=30-32 ‰).

Embryonic development	Duration
From deposited inseminated egg to the first cleavage	1 - 2 d
2-cell stage	2 hr
4-cell stage	1-2 hr
From the beginning cleavage to the gastrula (15 - 16-cell stage)	1 d
From deposited eggs to the stage of tadpole	8 - 9 d
From deposited eggs to the stage of embryo rotation	18 - 20 d
From deposited eggs to the hatching of juveniles	30 - 43 d

Table 2. Age stages of *Oncholaimium ramosum*.

Age stage		Diameter head (μm)	Length body (μm)	Index				Features
				a	b	c	V%	
J1		12.5-16	808 - 1664	36.97±0.76	4.10±0.06	12.91±0.25	–	Two circles of cephalic seta
Moulting		16	1582					Two circles of cephalic setae, 4 amphidial foveas
J2		15-18	1500 - 2000	37.62±0.88	4.17±0.08	14.21±0.41	–	One circle of cephalic setae
Moulting		20	1988					One circle of cephalic setae, 4 amphidial foveas
J3		17-22.5	1700 - 2864	45.74±0.78	5.91±0.11	20.50±0.35	–	Primordia of ovary (24-236 μm)
J4	♀♀	23 - 28	2124 - 6547	58.99±1.66	9.50±0.30	32.81±1.11	–	Formed reproductive system; closed vulva
	♂♂		2380 - 6140					Length of spicules (58-68 μm)
Moulting		32	4836 - 6080					4 amphidial foveas
Adult	♀♀	30 - 36	4128 - 9694	59.27±1,29	15.65±0.27	45.68±1.50	65.3	Opened -top vulva
	♂♂		4836 - 9172	69.17±1,23	11.78±0.31	44.70±2.00	–	Length of spicules (up to 86 μm)

The number of annual generations depends on the length of time of animal development, which is a function of worm body size (Heip *et al.*, 1985). The small species have short life cycles and, therefore, a large number of annual generations. The larger species become mature later, have a longer life cycle and a smaller number of annual generations. According to estimates of many researchers the number of annual generations varies from 0.5–1 (oncholaimids) to 17 (monhysterids) (Heip *et al.*, 1985).

Field studies show that the number of *Oncholaimium ramosum* annual generations is two. *O. oxyuris* has 1.6 generations per year (2 annual generations or 2 generations in three years). Another species of this family, *O. brachycercus* has 1 or 2 annual generations depending on the temperature (Smol *et al.*, 1980). The development rate of female oocytes, the fecundity and the longevity determine the reproductive potential of the species that allows it to maintain a high abundance of nematodes under the anthropogenic stress and absence of competition.

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Фадеева Н.П., Давыдкова И.Л. Некоторые особенности жизненного цикла и экологии *Oncholaimium ramosum* (Nematoda: Oncholaimidae) в загрязненных бухтах Японского моря.
Резюме. Нематоды *Oncholaimium ramosum* (Nematoda: Oncholaimidae) встречаются в загрязненных бухтах Японского моря. Жизненный цикл *O. ramosum* был изучен в лаборатории и в среде обитания в течение двух лет. Проведены исследования эмбрионального и постэмбрионального развития, а также процессов линьки. Исследовано около 35 кладок и 400 яиц, 1000 нематод этого вида. В течение года нематоды *O. ramosum* имеют два поколения в Японском море. Откладка яиц продолжается с февраля до июля (весеннее поколение) и с сентября до ноября (осеннее поколение). В лаборатории наблюдения за самками проводились почти непрерывно от откладки яиц до гибели. Самка откладывала либо отдельные яйца, или делала кладки из 2-38. Развитие яиц в кладках проходило неравномерно. У 46-50 % яиц дробление начиналось раньше, а остальные 50 % яиц отставали в развитии на 8-10 дней. Описываются стадии 2, 4, 8 бластомеров, последняя гаструла, и червеобразная личинка. Среднее время развития эмбриона нематод *Oncholaimium ramosum* от момента откладки яиц до выхода сформированной личинки из яйца равно 1-1.5 месяца. Определены размеры и время развития неполовозрелых особей J_1 – J_4 и взрослых особей для *O. ramosum*. Обсуждаются продолжительность цикла жизни и особенности формирования половой системы этого вида.