Arthropoda Selecta 24(4): 401–416

Maturation, fecundity and embryos development in three deep-water shrimps (Decapoda: Caridea: Pasiphaeidae, Oplophoridae) along the mid-Atlantic Ridge from Iceland to the Azores

Созревание, плодовитость и развитие эмбрионов у трех глубоководных креветок (Decapoda: Caridea: Pasiphaeidae, Oplophoridae) со Срединно-Атлантического хребта от Исландии до Азорских островов

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KEY WORDS: pelagic shrimps; reproductive strategies; sex identification; fecundity; embryos development.

КЛЮЧЕВЫЕ СЛОВА: пелагические креветки, репродуктивные стратегии, определение пола, плодовитость, развитие эмбрионов.

ABSTRACT. The aim of this study is description of the reproductive characters of three species of deep-water caridean shrimps. Ovarian maturity staging and staging of embryos development in these species are described for the first time. Ovarian maturation, fecundity and eggs size, type of spawning and characteristics of embryos development integrally reflect reproductive patterns in *Parapasiphae sulcatifrons*, *Acanthephyra pelagica* and *A. purpurea*. All these species generally have K-strategy traits. However the two *Acanthephyra* spp. which live in shallower water layers and possess morphological plesiomorphies show K-strategy with important components of r-strategy (i.e. relatively large number of small but lecithotrophic larvae). *P. sulcatifrons* which is a bathypelagic species characterized by some apomorphies has extreme K-strategy traits and produces small numbers of large lecithotrophic larvae.

РЕЗЮМЕ. Цель данной работы — описание репродуктивных характеристик трех видов глубоководных каридных креветок. Стадии зрелости яичников и стадии развития эмбрионов у этих трех видов описываются впервые. Созревание яичников, величина плодовитости и размер яиц, тип нереста и развитие эмбрионов интегрально отражают специфику воспроизводства *Parapasiphae sulcatifrons*, *Acanthephyra pelagica* и *A. purpurea*. Всем видам присущи, главным образом, черты К-стратегии. Однако, оба вида *Acanthephyra*, более мелководных и имеющих ряд морфологических плезиоморфий, демонстрируют К-стратегию с тенденцией к r-стратегии (производят относительно большое количество лецитотрофных, но мелких личинок). Батипелагическая и характеризующаяся рядом апоморфий *P. sulcatifrons* имеет черты сильно выраженной К-стратегии с формированием небольшого количества крупных лецитотрофных личинок.

Introduction

Pelagic decapod shrimps often comprise a significant portion of biomass in midwater collections from the open ocean and play an appreciable role in the pelagic food web [Omori, 1974; Jamieson et al., 2009]. Despite a number of studies on the taxonomy and distribution of such pelagic shrimp species as *Parapasiphae sulcatifrons* Smith, 1884, *Acanthephyra purpurea* A. Milne-Edwards, 1881 and *Acanthephyra pelagica* Risso, 1816 [Vinogradov, 1968; Foxton, 1972; Crosnier, Forest, 1973; Hargreaves, 1984; Tchesunov, 1984; Kikuchi, Omori, 1985; Krygier, Wasmer, 1988; Hendrickx, Estrada Navarrete, 1989; Komai et al., 2000; Martin, 2003] there is still limited knowledge on their reproduction [Chace, 1940; Omori, 1974; Burukovsky, 1993, 1998; Burukovsky, Andreeva, 2011]. The aim of this paper is to describe traits of the reproductive system maturation (development of the primary and secondary sexual characters, maturation of ovaries), fecundity and embryos development in these deep-water species from the North Atlantic along the Mid-Atlantic Ridge from Iceland to the Azores and to discuss interspecific differences of their reproductive strategies.

Table 1. Size of examined shrimp specimens.
Таблица 1. Размер исследованных особей креветок.

Species	Juveniles			Males		
	No.	TL, mm (in aver.)	CL, mm (in aver.)	No.	TL, mm (in aver.)	CL, mm (in aver.)
P. sulcatifrons	43	14.9–44.1 (30.4)	4.9–14.6 (10.1)	305	22.4–74.9 (54.6)	7.4–24.8 (18.0)
A. pelagica	106	16.2–37.8 (28.7)	3.8–8.8 (6.7)	568	25.1–124.9 (70.1)	5.9–29.3 (16.4)
A. purpurea	5	18.8–28.5 (25.6)	3.4–6.6 (5.8)	89	29.4–90.3 (59.3)	6.8–21.0 (13.9)

Species	Females								
	Total			Non-oviparous			Oviparous		
	No.	TL, mm (in aver.)	CL, mm (in aver.)	No.	TL, mm (in aver.)	CL, mm (in aver.)	No.	TL, mm (in aver.)	CL, mm (in average
P. sulcatifrons	500	20.6–98.9 (60.3)	6.8–32.7 (19.7)	356	20.6–85.6 (55.4)	6.8–28.3 (18.3)	144	32.7–98.9 (72.6)	15.2–32.7 (24.1)
A. pelagica	664	26.4–106.1 (68.9)	6.2–24.8 (16.1)	653	26.4–106.1 (68.7)	6.2–24.8 (16.1)	11	68.6–98.0 (80.9)	16.07–22.9 (18.9)
A. purpurea	163	30.5–91.4 (58.3)	7.2–21.2 (13.6)	96	30.5–91.4 (53.1)	7.2–21.3 (12.3)	67	51.9–77.7 (65.9)	12.1–18.1 (15.4)

Material and Methods

Sampling was conducted during the Census of Marine Life (CoML) field project MAR-ECO (www.mar-eco.no) from 5 June to 3 July 2004 along the mid-Atlantic Ridge (MAR) area from Iceland (~60°N – 26°W) to the Azores (~41°N – 28°W). The material was obtained using a pelagic "krill trawl" [see Wenneck et al. 2008 for details]. Hauls were performed in the depth range from 1.5 to 3008 m. All samples were initially preserved in 4% borax neutralized formalin in seawater and later transferred to 75% ethanol for further storage. In order to study shrimp reproductive parameters in detail we use standard methodology for biological analysis [Burukovsky, 1992], that has been adopted for the pelagic shrimps [Sudnik, Falkenhaug, 2014]. These methods include: measuring of the total body length (TL) and of the carapace length (CL), sex identification, weighting of individual, ovary and egg clutches, identification of the ovary maturity stage (6-stages, included both macroscopic and some microscopic features), identification of the stage of embryo development (5-stages), counting the absolute batch fecundity (ABF, total amount of mature oocytes per prespawning female ovary) and the real [Burukovsky, 1994] batch fecundity (RBF), measuring of diameters of ripe oocytes and of eggs with embryos at the different development stages. To identify sex in Caridea the shape of the endopodite lobe of the first pleopod (which is regarded as a «copulatory appendage» (CA) for instance in pandalids) and the condition of *appendix masculina* (AM) on the endopodite of the second pleopod between appendix interna and the endopodite lobe were assessed [Allen, 1959; Burukovsky, 1992; Krol et al., 1992].

A total of 1338 specimens of *A. pelagica* (106 juveniles, 568 males, 664 females), 257 of *A. purpurea* (5 juveniles, 89 males, 163 females), and 874 of *P. sulcatifrons* (43 juveniles, 305 males, 500 females) were examined (Table 1). In twenty six specimens of *P. sulcatifrons* sex identification was not possible because of bad condition of their exoskeleton (Table 2). In 3 of 500 females of *P. sulcatifrons* and in 2 of the 828 of *Acanthephyra* spp. identification of ovarian maturity stages was not possible because of the bad condition of the material (Table 3). The absolute individual fecundity (AIF) is defined as the total number of ripe oocytes in the mature ovary (stage V) produced by a female during the entire reproductive season. AIF could not be determined in this study because of the limited sampling period (one month). ABF was determined in *P. sulcatifrons* but it was not assessed in *Acantephyra* spp. because of too small and crumbled vitellogenic oocytes which could not be separated in the ethanol fixed ovary. In *P. sulcatifrons* (having large eggs) ripe oocytes sizes were measured in ovaries of 11

Table 2. Primary and secondary characters for sex identification in studied shrimps species.
Таблица 2. Первичные и вторичные признаки для определения пола у изучаемых видов креветок.

Species	Juveniles			Males						Females				
	No. of samples	CL, mm	Main characteristics	No. of samples	CL, mm	Copulatory appendage on pleopods 1 (CA)	A.M. on pleopods 2		Testes	No. of samples	CL, mm	CA	A.M. on pleopods 2	Ovaries at maturity stage II
P. sulcatifrons	43	less 10 – sometimes up to 13	gonads not recognizable. A.M. not developed	35	7–13	present	absent		weakly developed	16	less 10	present	absent	not recognizable
				31	13–15	present	small lobe		weakly developed, not bent	66	10–14	present	absent	seen with removed carapace
				94	15–19	present	normally developed		normally developed, weakly bent	418	14–15 and more	present	absent	distinguished through carapace
				145	19–25	present	normally developed		normal, bent, visible through the carapace					
A. pelagica	106	less 6, less often 10	CA, A.M. not developed; gonads not recognizable	15	6–8	began to develop	begin to develop	A.I.' length (A.I.) larger A.M.' length (A.M.)	not recognizable visually	120	6–12	absent	absent	not recognizable
				4	8–9	continues to develop	continues to develop	A.I. equal or some less A.M.	recognizable visually					
				377	9–19	normally developed	normally developed	A.I. less A.M.	recognizable visually	544	12–14 and larger			distinguished without carapace cutting
				172	19–30	fully developed	normally developed	A.I. twice less A.M.	bent, of maximum length					
A. purpurea	5	3–7, less often 9	the same as in *A. pelagica*	26	less 10–12	weakly developed	began to develop	A.M. 25–100% of A.I.	slightly bent, weakly developed	43	less 12	absent	absent	began to develop
				10	12–13	normally developed	developing	A.M. 70–150% of A.I.	not fully developed	62	12–15			recognizable
				53	13–14 and larger	normally developed	fully developed	A.M. exceeded twice A.I.	well developed, bent	58	15–18 and larger			easily recognizable

Table 3. The staging of ovaries maturity in *P. sulcatifrons*.
Таблица 3. Стадии зрелости яичников *P. sulcatifrons*.

Ovarian maturity stage	No. of samples	Ovaries shape	Ovaries color and condition	Ovaries size	Ovaries characteristics
I	46	Resembling a triangle, paired shape is not visible	Transparent, slightly whitish, hardly distinct on a background of other tissues	Very small (about 15–20% of CL and 25% of carapace width (CW))	
II	249	H-like shape, long and narrow or round-triangular	Jellylike, dim, whitish, a clearly distinct on a background of other tissues	Ovary occupies up to 60% of CL	Most developed protoplasmic oocytes lay in a single layer above the smaller ones
III	88	H-like shape	Light orange color of ovaries is changed to reddish-orange; the vitellogenic oocytes are easily separated from each other	Ovary occupies up to 70% of CL and up to 50–60% of CW	Ovary is at the beginning of active vitellogenesis; vitellogenic oocytes lay above protoplasmic ones
IV	57	H-like shape	Vitellogenic oocytes become reddish-orange in color, are hardly separated from each other; protoplasmic oocytes remain white in color	Ovary occupies up to 80% of CL and up to 70% of CW	Well-developed granular structure; vitellogenic oocytes are filled by a liquid fatty yolk, lay in one layer above the layer of the protoplasmic oocytes. The proliferation zone (PZ) lay ventro-medially in the ovary, consists of the tiny protoplasmic oocytes and oogonia
V	56	H-like shape	Same as for the stage IV	Ovary occupies the cephalothorax	Lateral branches of ovary — completely reduced, the anterior branches — weak rudiments, the posterior branches — barely reach the 1st abdominal segment; the PZ has a triangular shape; no middle sized vitellogenic oocytes between the ripe and the protoplasmic oocytes in ovary; the ripe oocytes polygonal shaped
VI–II (the post spawning ovaries)	1	Weakly developed H-like shape	Jellylike limp, a clearly distinguished on a background of other tissues; the ovarian granular structure is not clearly visible	Ovary is little wider than in the stage II	Ovary consists of the PZ and the more developed protoplasmic oocytes, sometime contains some ripe oocytes that had not been laid on the pleopods during previous spawning

females. The size of ripe oocytes was possible to measure in one prespawning female of *A. pelagica*. A total number of 203 females of three species were investigated for the identification of embryos development stages (144 of *P. sulcatifrons*, 11 of *A. pelagica* and 48 of *A. purpurea*). RBF defined as the number of eggs with embryos found on pleopods of an ovigerous female, was counted and eggs sizes were measured in 151 females of *P. sulcatifrons*, in 61 females of *A. purpurea* and in 21 specimens of *A. pelagica.* There were no *A. pelagica* females with newly laid eggs on pleopods in the material. Images of copulatory organs, eggs and sometimes gonads were made with the aid of a microsystem of Leica DFC420 camera. Images of shrimp body, gonads were made using a digital photo camera (Sony DSC-T10).

Results

Parapasiphae sulcatifrons

Total body length (TL) of the investigated specimens of *P. sulcatifrons* varied from 14.9 mm to 98.9 mm, 56.2 mm in average, the carapace length (CL) — from 4.9 to 32.7 mm, 18.6 mm in average (Table 1). Sex identification in *P. sulcatifrons* was possible using the shape of pleopod 2 but not the shape of pleopod 1 (its primary and secondary characters used for sex identification are presented in Table 2). The copulatory appendage (CA or copulatory organ) on pleopod 1 was observed both in males and in all females but *appendix masculina* (AM) on pleopod 2 was always absent in females (Fig. 1, 2). Specimens with CL less than 10 mm were regarded as juveniles (they had no visually distinguished primary and secondary sexual characteristics). In males the primary (*testis* and *vas deferens*) and the secondary (CA and AM) sexual characters began to develop nearly simultaneously (at CL 13–15 mm) and were fully developed yet at CL 19–21 mm (Fig. 7). Sizes of males and females (separately for non-oviparous and oviparous females) are presented in Table 1. The ratio of males to females was 1:1.6.

Description of ovarian maturity stages including the main macroscopic characters, including relative ovaries size, their condition, shape and color are presented in Table 3. Some microscopic features (the mutual disposition of oocytes of different developmental stages, indications of vitellogenesis in the ovary, oocytes size data) were added in the stage description for *P. sulcatifrons* (its large oocytes could be distinguished visually).

Shrimp females are ready for the first copulation at ovarian maturity stage II [Burukovsky, 1992]. Such females of *P. sulcatifrons* had CL 10–14 mm which could be defined as pubertal size. In females with CL larger 14–15 mm ovaries at maturity stage II could be identified without dissection of the carapace (Fig. 10, 11). Ovaries at this stage consisted of only protoplasmic oocytes that were clearly distinguished even without a microscope magnification and did not show visual indications of vitellogenesis. This previtellogenic condition was also confirmed by the histological study [Sudnik, 2008]. The ovaries increased considerably in length during stage III but they did not reach to the abdomen (Fig. 12). They had a light orange coloration owing to the beginning of active vitellogenesis. There were two types of oocytes in the ovary: one generation of vitellogenic oocytes (orange or reddish-orange in color, polygonal-shaped, approximately equal sized) was located dorsally and a thin layer of protoplasmic oocytes (much smaller and whitish in color) underlaid it ventrally. The vitellogenic oocytes have been increasing in size during stage IV owing to filling with liquid fatty yolk. Beneath the vitellogenic oocytes a band of protoplasmic oocytes with the proliferation zone was found ventro-medially in each ovary (Fig. 13, 14). The vitellogenic oocytes were about ten times larger than the most developed protoplasmic ones. No intermediate sized vitellogenic oocytes were found between the large sized vitellogenic and small sized protoplasmic oocytes in the ripe ovary (Fig. 15). Ripe oocytes lay in specific polygonal “cells” (Fig. 16). Postspawning ovaries (Fig. 17) often contained single large ripe orange oocytes that had not been laid on the pleopods during previous spawning. The average size of ripe oocytes in *P. sulcatifrons* ovaries was 3.44 ± 0.28 × 2.57±0.21 mm and the average ABF in *P. sulcatifrons* was 19±4 ripe oocytes.

The main characteristics for five stages of embryos development and description of newly hatched larvae in *P. sulcatifrons*, the data on RBF values and eggs sizes are presented in Table 5 and illustrated in Figs 27, 28, 30, 33, 35.

A. purpurea and *A. pelagica*

TL of the investigated specimens of *A. purpurea* ranged between 14.8 and 91.4 mm, 58.4 mm in average, CL: 3.4–21.3 mm, 13.5 mm in average; in *A. pelagica* TL was 16.2–124.9 mm, 66.2 mm in average, CL ranged from 3.8 to 29.3 mm, 15.5 mm in average (Table 1). Sex identification in *Acanthephyra spp.* was possible based both on the shape of CA of pleopod 1 and on the shape of AM on pleopod 2 (their primary and secondary traits for sex identification are presented in Table 2). Sizes of males and females (separately for non-oviparous and oviparous females) for both species are presented in Table 1. Sex ratio (males:females) was 1:1.8 in *A. purpurea* and 1:1.2 — in *A. pelagica*.

Specimens with CL of 6–9 mm and less in *A. purpurea* and those with CL less than 10 mm in *A. pelagica* were identified as juveniles (Table 2).

In the males of *A. pelagica* secondary sexual characters began to develop some time earlier then the primary ones (testis) (Table 2). Males with CL 9–19 mm had well developed CA and AM (Fig. 3); their bended testes attained maximum length and were located along the entire dorsal side of cephalothorax, in particular covering the hepatopancreas (Figs. 8, 9). In the males of *A. purpurea* secondary and primary char-

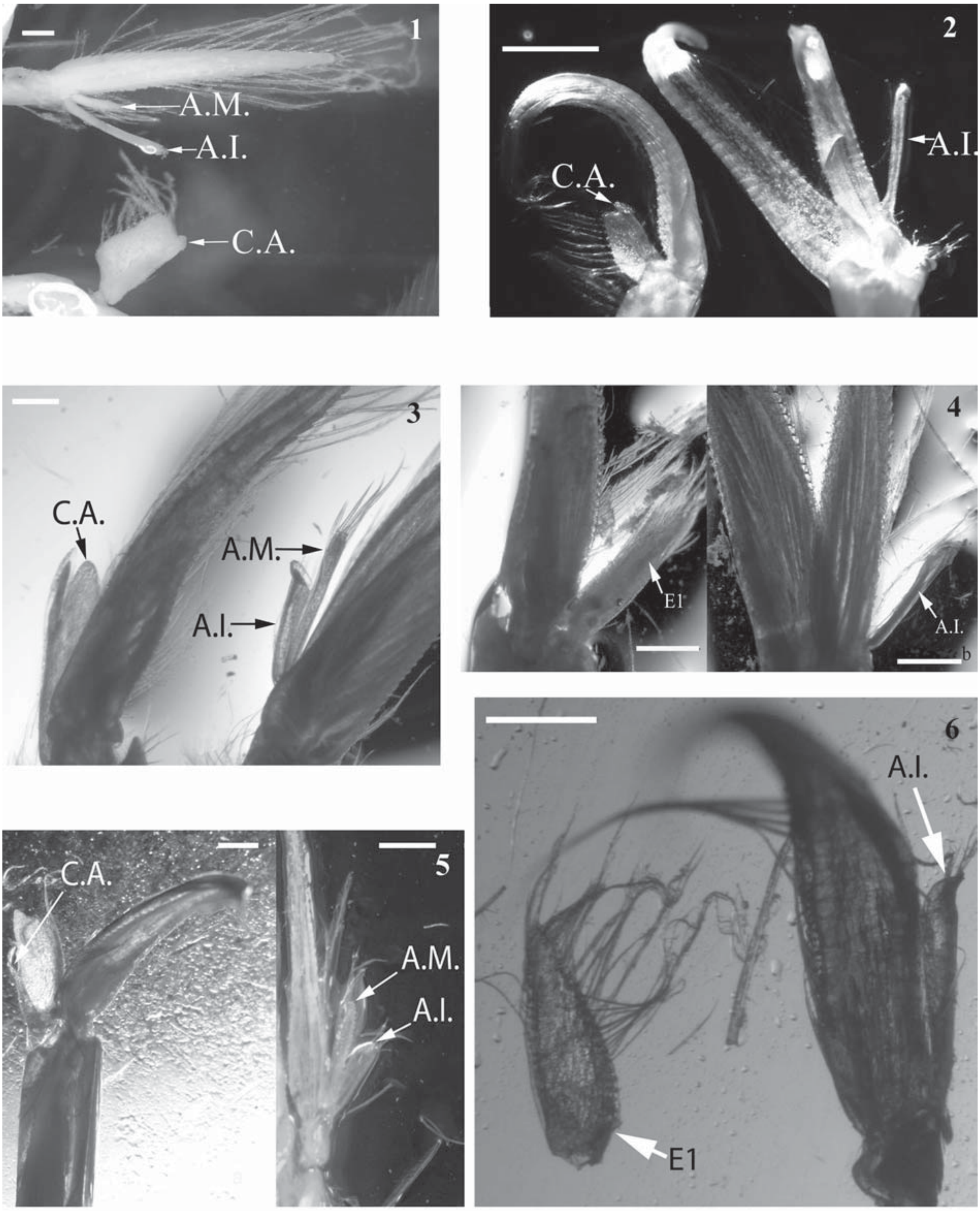

Fig. 1–6. Characters used for sex identification in *Parapasiphae sulcatifrons*, (1, 2)*,* in *Acanthephyra pelagica* (3, 4), in *A. purpurea* (5, 6): 1, 3, 5 — in males; 2, 4, 6 — in females. Abbreviations: E1— endopodite of 1st pleopods; C.A. — copulatory appendage on E1; A.I. — *a.interna* on pleopod 2; A.M. — *a.masculina* on pleopod 2. Scale bars: 1–3, 5, 6 — 1 mm; 4 — 0.5 mm.

Рис. 1–6. Признаки, использованные для определения пола у *Parapasiphae sulcatifrons*, (1, 2)*,* у *Acanthephyra pelagica* (3, 4), у *A. purpurea* (5, 6): 1, 3, 5 — у самцов; 2, 4, 6 — у самок. Сокращения: E1 — эндоподит плеопод 1; C.A. — копуляторный вырост на E1; A.I. — *a.interna* на плеоподах 2; A.M. — *a.masculina* на плеоподах 2. Масштаб: 1–3, 5, 6 — 1 мм; 4 — 0,5 мм.

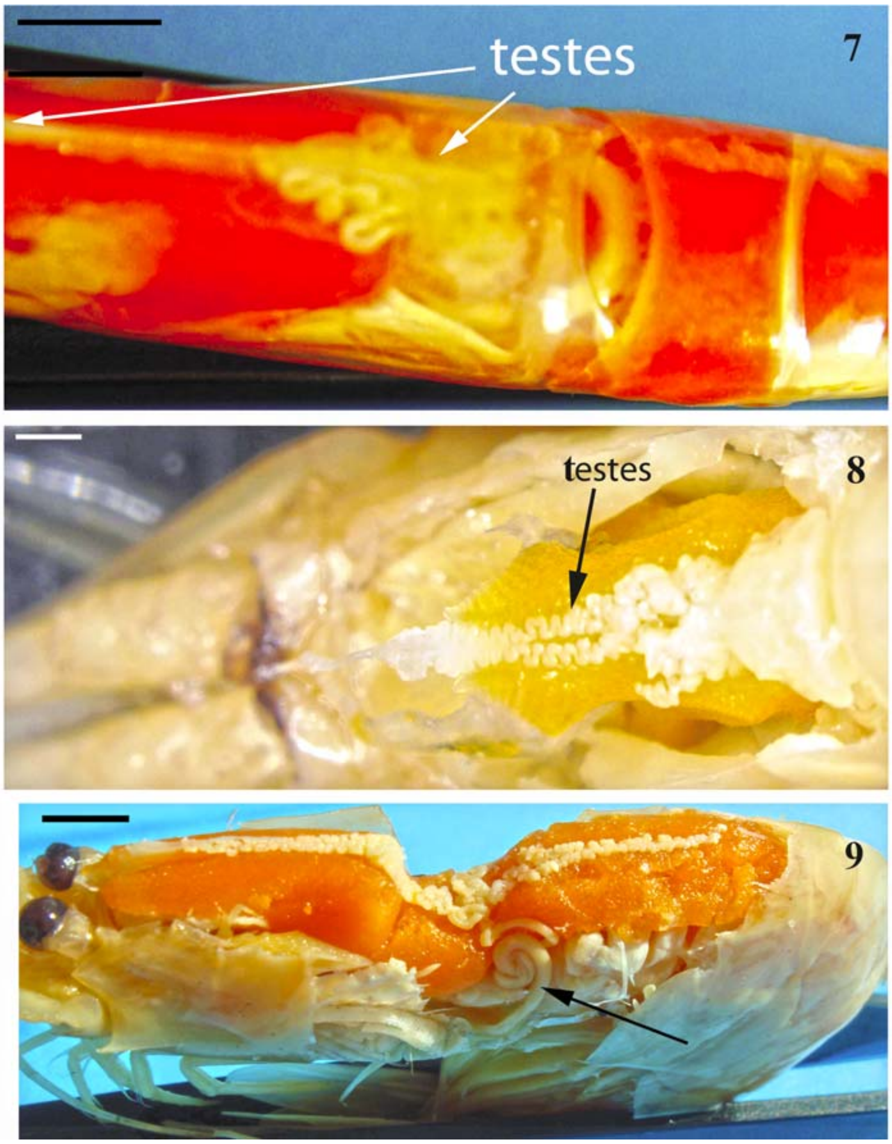

Fig. 7–9. Testes: 7 — of *Parapasiphae sulcatifrons*, dorsal view through the carapace; 8, 9 — of *A. pelagica*: 8 — dorsal view; 9 — lateral view, arrows show spiral vas differences. Scale bars: a — 5 mm; b — 10 mm; c — 3 mm.

Рис. 7–9. Семенники: 7 — *Parapasiphae sulcatifrons*, вид сверху через карапакс; 8, 9 — *A. pelagica*: 8 — вид сверху; 9 — вид сбоку, стрелки показывают спиральные семяпроводы. Масштаб: a — 5 мм; b — 10 мм; c — 3 мм.

acters showed nearly simultaneous development at CL 9–10 mm. Males with CL larger than 12–13 mm usually had CA and AM fully developed (Fig. 5) but their testes became fully developed and reached a characteristic bended shape only in males with CL 13–14 mm and larger. The testes are set along the entire dorsal side of the cephalothorax covering the hepatopancreas and reach to the end of 2nd abdominal segment. Males larger than CL 16.5 mm had thicker and whiter testis, clearly visible through the carapace.

As a rule no CA on the endopodite lobe of pleopod 1 and no AM on pleopod 2 were found in females of *Acanthephyra* spp. (Figs 4, 6). In few cases of an abnormal development of female sexual characteristics a well-developed CA was found in *A. pelagica* females. However, this abnormality had not prevented these specimens to be functional females. *A. purpurea* and *A. pelagica* females were beginning to mature (ovaries on maturity stage II) at CL 12–14 mm, but more frequently at CL 15–18 mm. We identified six stages of ovarian maturity in *Acanthephyra spp.* The main macroscopic characters including relative ovaries size, their condition, shape and color are presented in Table 4. The ovaries became visible on the background of other tissues at early maturity stage II (Fig. 18, 19) At this stage ovaries extended in size in the lateral and the abdominal directions. At the stages III–IV they continue to increase considerably in their length and width (Figs 20–23). Ripe ovaries had a visible granular structure and were extended nearly over entire length of the carapace (Figs 24, 25). A characteristic size of ripe oocytes in *A. pelagica* ovaries was about 0.35 × 0.09

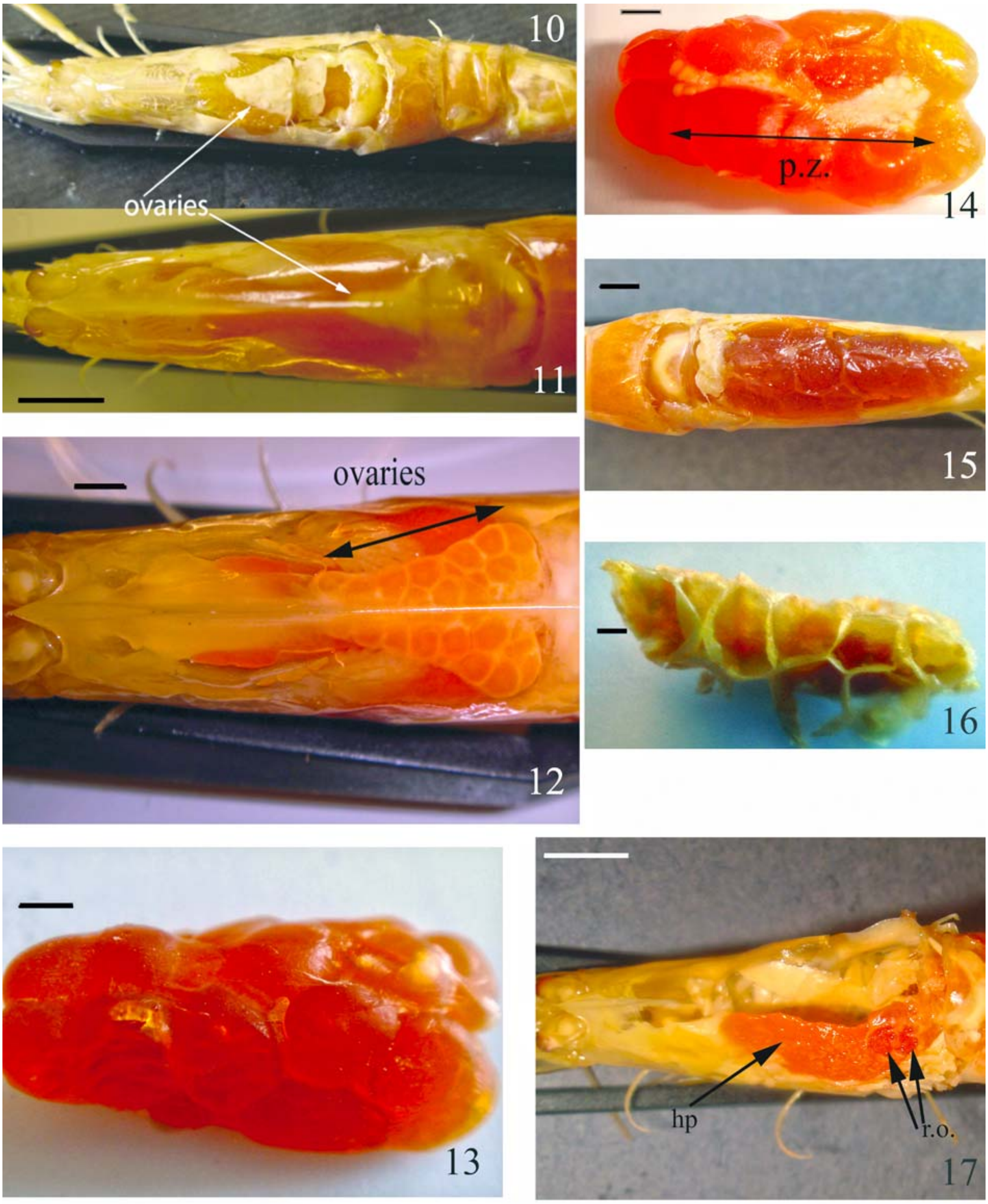

Fig. 10–17. *Parapasiphae sulcatifrons*, ovaries at different maturity stages: 10, 11 — stage II: 10 — without carapace; 11 — through the carapace; 12 — stage III; 13, 14 — stage IV; 15 — stage V; 16 — empty ovarian “cells” for ripe oocytes; 17 — stage VI–II (postspawning). 10–13, 15 — dorsal; 14 — ventral; 17 — lateral views. Abbreviations: p.z. — proliferation zone; hp — hepatopancreas; r.o. — ripe oocytes. Scale bars: 10, 11, 17 — 5 mm; 12, 13, 14, 15 — 2 mm; 16 — 1 mm.

Рис. 10–17. Яичники *Parapasiphae sulcatifrons* на разных стадиях зрелости: 10, 11 — стадия II: 10 — вид без карапакса; 11 — вид сквозь карапакс; 12 — стадия III; 13, 14 — стадия IV; 15 — стадия V; 16 — пустые ячейки яичника для зрелых ооцитов; 17 — стадия VI–II (посленерестовые самки). 10–13, 15 — дорсально; 14 — вентрально; 17 — латерально. Сокращения: p.z. — зона пролиферации; hp — гепатопанкреас; r.o. — зрелые ооциты. Масштаб: 10, 11, 17 — 5 мм; 12, 13, 14, 15 — 2 мм; 16 — 1 мм.

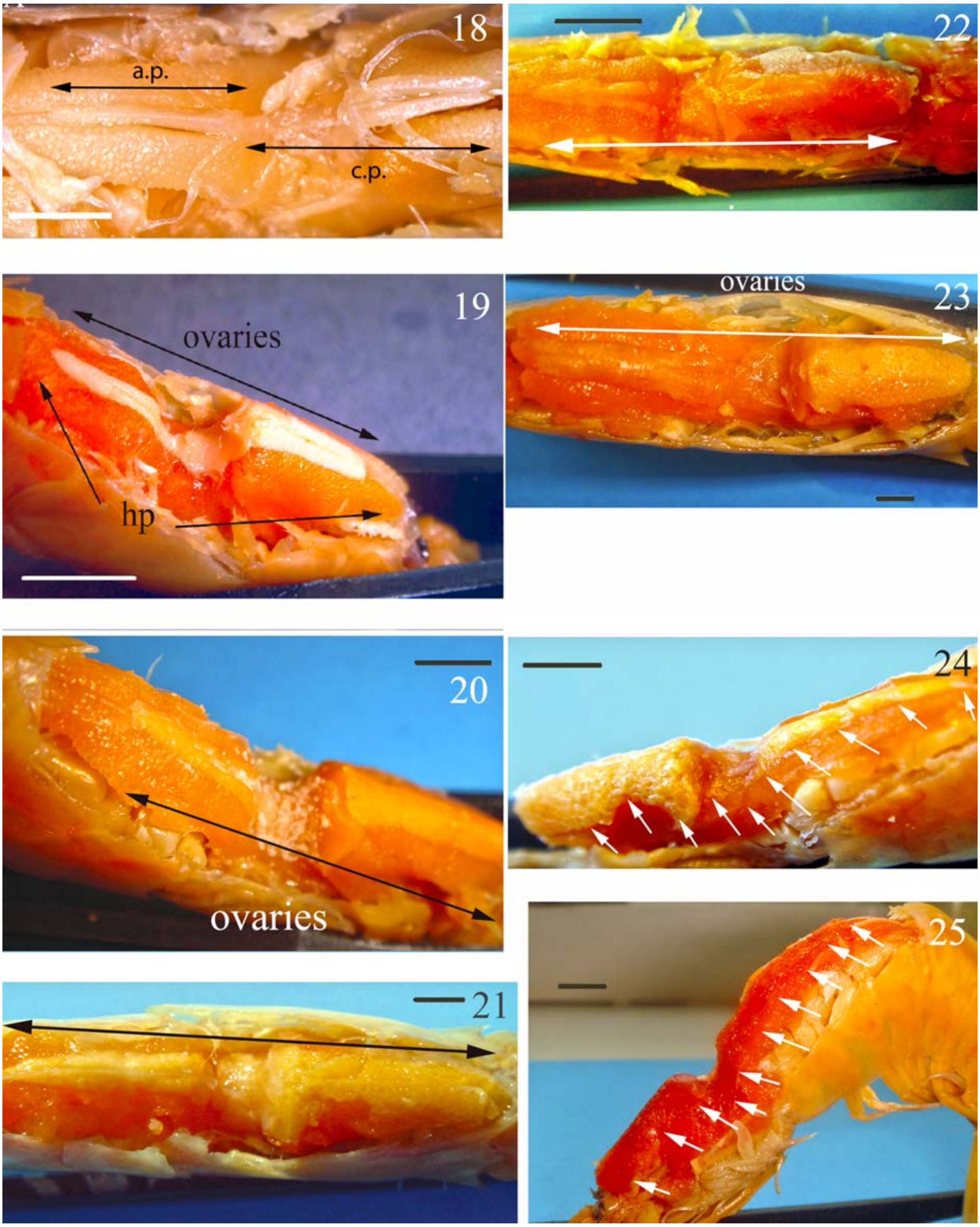

Fig. 18–25. *Acanthephyra* spp.' ovaries at different maturity stages: 18, 19 — stage II; 20, 21 — stage III; 22, 23 — stage IV; 24, 25 — stage V (arrows show the ovaries location). 18, 20, 22, 24 — *A. purpurea*; 19, 21, 23, 25 — *A. pelagica*. 18, 21, 22, 23 — dorsal; 19, 20 — dorsolateral; 24, 25 — lateral views. Abbreviations: a.p. — abdominal part; c.p. — cephalothoracal part; hp — hepatopancreas. Scale bars: 18, 24, 25 — 5 mm; 19–23 — 4 mm.

Рис. 18–25. Яичники *Acanthephyra* spp. на разных стадиях зрелости: 1 — стадия II; 2 — стадия III; 3 — стадия IV; 4 — стадия V (стрелки показывают расположение яичников). 18, 20, 22, 24 — *A. purpurea*; 19, 21, 23, 25 — *A. pelagica*. 18, 21, 22, 23 — дорсально; 19, 20 — дорсолатерально; 24, 25 — латерально. Сокращения: a.p. — абдоминальная часть; c.p. — головогрудная часть; hp — гепатопанкреас. Масштаб: 18, 24, 25 — 5 мм; 19–23 — 4 мм.

mm. The main characteristics for five stages of embryos development and morphological observations on just hatched larvae in *Acanthephyra* spp., the data on RBF values and eggs sizes are presented in Table 5 and illustrated in Figs 26, 29, 31, 32, 34.

Discussion

The specimens of *A. pelagica* had a greater maximum total length (up to 125 mm) then those of *A. purpurea* (up to 91.4 mm) and of *P. sulcatifrons* (up to 98.9 mm). The maximum sizes (TL) of females and males of *A. pelagica* (7–15 mm in females and 35–50 mm in males) were also larger than in the two other species. Average sizes (TL) of females and males of *P. sulcatifrons* and of *A. purpurea* were similar being by 10–15 mm less than the average TL of *A. pelagica*. The investigated area (60–41º N, 26–28º W) is located somewhat north to the North Atlantic Subtropical Convergence (NASC) zone. In the NASC zone (55–30º N, 2–35º W) [Burukovsky, Andreeva, 2010] external sexual characters of *A. pelagica* had developed (at larger size in both males and females, beginning from 55 mm TL) while the maximum male size (TL) was less (99 mm *vs*. 125 mm in our material). In *P. sulcatifrons* from the neighboring area (46–37º N, 15–30º W) [Burukovsky, 1993] visual sex identification was possible in shrimps larger than 45 mm TL on, as compared to 21–22 mm in our material) and the maximum size (TL) of males and females was smaller than in our materials (up to 60 and 84 vs. 75 and 99 mm, respectively). Development of sexual characters in *A. purpurea* from the same area (46–37º N, 15–30º W) [Burukovsky, 1998] took place at larger size (TL), i.e. up to 57 mm vs. 29–31 mm in our specimens and the maximum sizes of both sexes were somewhat less than those from our material (up to 87 mm and 90–91.4 mm respectively). In a separate study we intend to discuss whether these differences are due to faster growth or longer (> 3 years) life span.

The study of functional maturation of an individual includes development of its reproductive system: gonads, copulatory and accessory organs, and secondary sexual characteristics, allowing the male to copulate and the female to be copulated and spawn. Difficulties with sex identification are common in the studies of shrimp biology, especially when dealing with sequential hermaphrodites changing their sex during the life history. Then it is necessary to examine gonads in addition to the condition of secondary (external) sexual characters.

In males of all investigated species (*P. sulcatifrons* and *Acanthephyra* spp.) we observed simultaneous development of the primary and the secondary sexual characteristics. The morphology of pleopod 1 was not indicative for sex identification in *P. sulcatifrons*. This has also been documented in the crangonids *Crangon crangon* (Linnaeus, 1758) and *Argis dentata* (Rathbun, 1902) [Frechétte et al., 1970] and in the freshwater atyid shrimp *Neocaridina denticulata* (De Haan, 1844) [Oh et al., 2003]. However, in oplophorids of the genus *Acanthephyra,* sex identification is possible by using the shape of both pleopods 1 and 2 as described for instance for Nematocarcinidae by Burukovsky [1992]. Oplophorid shrimps (*Acanthephyra* spp.) with their numerous morphological plesiomorphies in digestive, respiratory, reproductive systems, a structure of some exoskeleton elements [Martin, Davis, 2001; Burukovsky, 2003; Sudnik, 2008; De Grave, Fransen, 2011] are closer to nematocarcinids and may be considered as evolutionary old groups while the pasiphaeids with their morphological apomorphies in those systems are closer to crangonids, atyids and palaemonids, which are probably evolutionary advanced caridean groups.

The majority of carideans have H-like shaped ovaries, where two lateral parts are connected by a transverse part. Comparison of ovarian morphology using available literature indicated that ovaries of such meso- to upper bathypelagic species as *A. pelagica*, and *A. purpurea* are most similar to the ovaries of Nematocarcinidae, the epibenthic inhabitants of the continental slope. *Nematocarcinus'* ripe ovaries have the most primitive construction among carideans, showing some similarities to ovaries of penaeids: the anterior and the lateral branches (2 pairs) are rudimentary (typical for carideans), and the posterior branches reaches up to the end of abdomen (similar to peneids) [Burukovsky, 1992]. The species of *Acanthephyra* have a rather similar ovary morphology, where the posterior branches of ripe ovary reaches to the half of 3rd abdominal segment (Table 4). In interzonal meso-bathypelagic *Parapasiphae sulcatifrons* as in other Pasiphaeidae such as *Glyphus marsupialis* Filhol, 1884 and *Pasiphaea tarda* Krøyer, 1845 [Sudnik, 2008] ovaries are very compact, including the central part, the anterior branches are rudimentary; their lateral branches are completely reduced and the posterior branches are possible to distinguish only in ripe condition, when they barely reach the 1st abdominal segment (Table 3). The same was shown for *Macrobrachium rosenbergii* De Man, 1879 (Palaemonidae) [Jayachandran, 2001]. In the interzonal bathypelagic oplophorid shrimp, *Systellaspis debilis* A. Milne-Edwards, 1881 the ovary was compact, without any lateral and posterior branches and it barely reached to the 1st abdominal segment [Sudnik, 2007]. Similar ovarian morphology was found in species of epibenthic pandalid shrimps (*Plesionika ensis* A. Milne Edwards, 1881, *Plesionika edwardsii* Brandt, 1851, *Pandalus montagui* Leach, 1814, *Pandalus borealis* Krøyer, 1838) [Mistakidis, 1957; Allen, 1959; Schultze, 1993; Sudnik, 2008] from the shelf and the upper part of continental slope: extremely weakly developed anterior branches were only met in the ripe ovary. In crangonid *Argis dentata* (Rathbun, 1902) [Frechétte et al., 1970] the ovaries are also very compact, and do not reach to the abdomen. Considering a general interpretation of shrimps evolutionary pathways [Burukovsky, 2003] we suppose the existence of evolutionary tendency to reduction the ovaries branches.

The ovarian structure in *Acanthephyra* spp. was difficult to study without histological investigation due

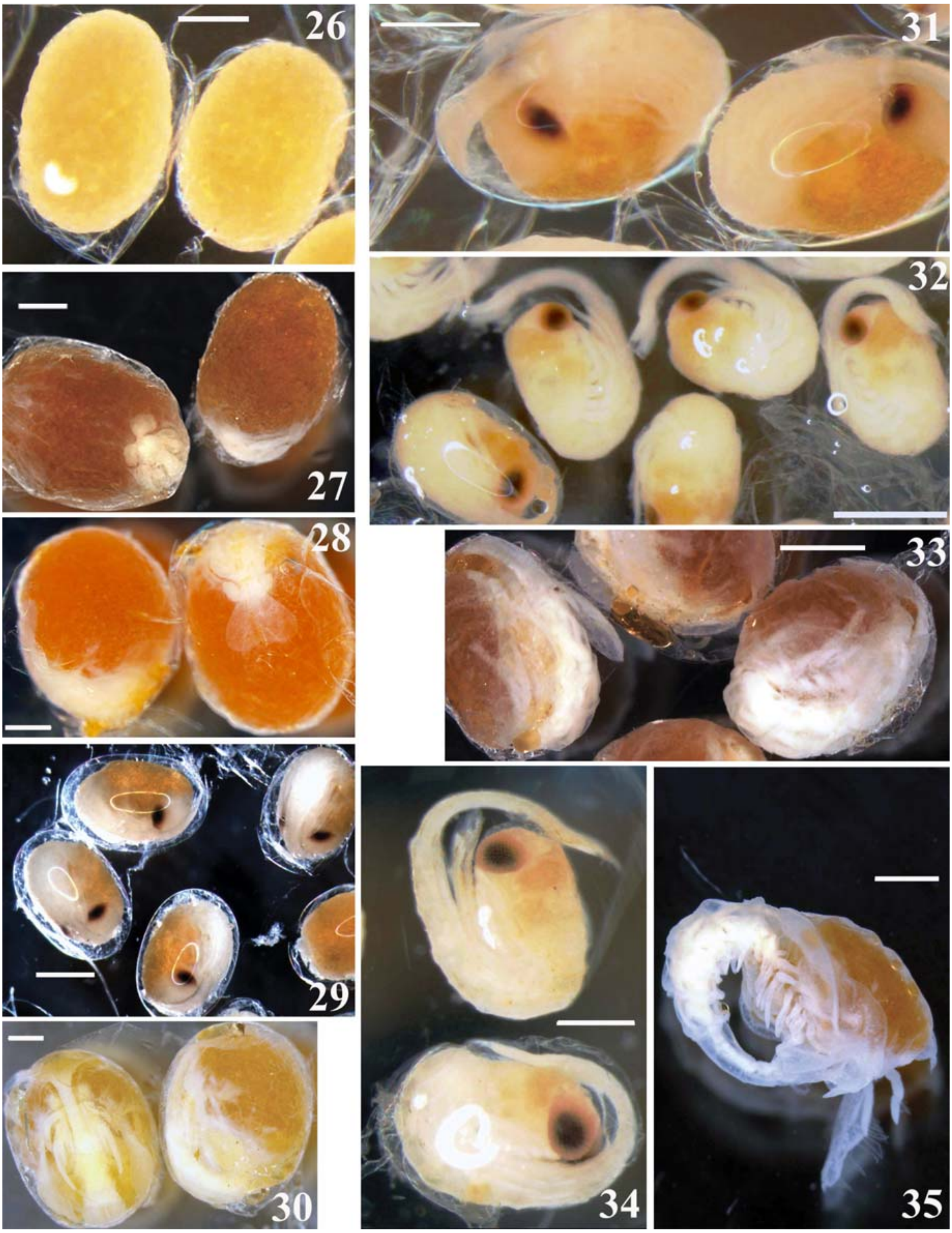

Fig. 26–35. The stages of embryos' development: 26 — stage 1; 27 — stage 2; 28 — stage 3; 29, 30 — stage 4; 31–33 — stage 5; 34, 35 — just hatched larvae; 26, 31 — *Acanthephyra pelagica purpurea*; 29, 32, 34 — *A. pelagica*; 27, 28, 30, 33, 35 — *Parapasiphae sulcatifrons*. Scale bars: 26 — 0.25 mm; 27, 28 — 1 mm; 29 — 0.5 mm; 30, 35 — 0.8 mm; 31 — 0.3 mm; 32 — 0.7 mm; 33 — 1.5 mm; 34 — 0.4 mm.

Рис. 26–35. Стадии развития эмбрионов: 26 — стадия 1; 27 — стадия 2; 28 — стадия 3; 29, 30 — стадия 4; 31-33 — стадия 5; 34, 35 — только что вылупившиеся личинки; 26, 31 — — *Acanthephyra pelagica purpurea*; 29, 32, 34 — *A. pelagica*; 27, 28, 30, 33, 35 — *Parapasiphae sulcatifrons*. Масштаб: 26 — 0,25 мм; 27, 28 — 1 мм; 29 — 0,5 мм; 30, 35 — 0,8 мм; 31 — 0,3 мм; 32 — 0,7 мм; 33 — 1,5 мм; 34 — 0,4 мм.

Table 4. The staging of ovaries maturity in *Acanthephyra* spp.
Таблица 4. Стадии зрелости яичников *Acanthephyra* spp.

Ovaries maturity stage	No. of samples	Ovaries shape	Ovaries condition	Ovaries characteristics
I	16	Very narrow; its paired shape not visible	Transparent, hardly distinct on a background of other tissues	Ovary covers up to 25% of the distal part of the stomach
II	440	Narrow in the proximal cephalothoracal and in the abdominal parts; enlarged in the central cephalothoracal part	Jellylike, opaque, visible distinguished on a background of other tissues	In proximal part ovary occupies up to 50–70% of CL, in central part – up to 25–40% of CW; in distal part reaches to the beginning of 2nd abdominal segment; covers up to 50% of distal part of the stomach
III	198	Same as for stage II; H-like shape	Weak granular structure, light orange in color	Ovary occupies up to 70–90% of CL and up to 60% of CW in its central part; its distal part reaches to the half of 2nd abdominal segment; covers up to 70% of distal part of the stomach
IV	104	H-like shape, narrower in its abdominal part, a narrow enough — in the proximal cephalothoracal part and an enlarged in the central cephalothoracal part	Clearly granular structure, orange in color	Ovary occupies up to 100% of CL and up to 80% of CW; distal part reaches to the end of the 2nd abdominal segment
V	67		Distinct granular structure, orange in color	Ovary occupies cephalothorax and up to 80% of CW in its central part; its anterior and lateral branches (2 pairs) are rudimentary, the posterior branches of ripe ovary extend up to the half of 3rd abdominal segment. Distinguishing of ripe vitellogenic oocytes is possible without dissection of the carapace.
VI–II (the post spawning ovary)	1	Ovary shape narrower than it was in stage II	Jellylike, limp, distinguished on a background of the other tissues; granular structure not visible	The size of post spawning ovary varies in the same limits as it is in the stage II; differences are possible due to some not laid large ripe oocytes

to their small oocyte sizes. In contrast to this, in ripe females of *P. sulcatifrons* the oocytes of previtellogenic and vitellogenic growth were clearly distinguished even without using a microscope. In their ovaries the proliferation zone lies ventro-medially, as it was shown for other shrimp species [Leloup, 1936; Mistakidis, 1957; Burukovsky, 1970; Relini, Semeria, 1983; Levi, Vacchi, 1988; Krol et al., 1992; Sudnik, 2008]. The maturity stages I and II correspond to immature ovaries in the period of protoplasmic growth of oocytes and possibly in the period of endogenous vitellogenesis [Sudnik, 2008, 2015; Burukovsky, Sudnik, 2014]. The period of active vitellogenesis (stages III–IV) is characterized by accumulation of exogenous yolk in most developed oocytes and changes of ovary color from whitish to orange. Our data showed that in *P. sulcatifrons* (similarly to another species with large oocytes, *Oplophorus novaezelandiae* (de Man, 1931) [Burukovsky, 1994]) the mature vitellogenic oocytes were filled with liquid fatty yolk. All vitellogenic oocytes in the ripe ovaries of *P. sulcatifrons* were mature, they were about 10 times larger than protoplasmic oocytes, and there were no middle sized vitellogenic oocytes in the ripe ovary of *P. sulcatifrons*. After spawning the ovaries returned to the immature condition (stage VI–II). All this indicates a type of ovarian maturation where an asynchronic growth of oocytes without follicle (previtellogenic oocytes and oocytes with the indications of endogenous vitellogenesis) proceeds by a synchronic vitellogenesis of the most developed oocytes [terms by Burukovsky, Sudnik, 2014, Sudnik, 2015]. Similar situation was found in *Farfantopenaeus notialis* Burkenroad, 1939 [Burukovsky, 1970], *Aristeus varidens* Holthuis, 1952 [Burukovsky, Sudnik, 2004], in *Nematocarcinus affricanus* [Burukovsky, Sudnik, 2014], *Systellaspis debilis*, *Glyphus marsupialis* [Sudnik, 2007, 2015], in 11 species of penaeid and caridean shrimps [Sudnik, 2008] on the basis of histological investigations of ovaries. This is expected in *Acanthephyra* spp., but needs to be confirmed through histological analyses of the ovary.

In most caridean shrimps and in some other decapods all ripe oocytes are described to be simultaneously laid on the pleopods [Heldt, 1938; Aoto, 1952; Burukovsky, 1970; Levi, Vacchi, 1988; Krol et al., 1992; Gorny, George, 1997; Kobayashi, 2003; Ramirez-Llodra, Segonzac, 2006; Sudnik, 2008, 2015]. This is in agreement with our results on *P. sulcatifrons*, *A.*

Table 5. The staging of embryos development, the real batch fecundity (RBF) and the egg sizes in studied shrimps.
Таблица 5. Стадии развития эмбрионов, величина реализованной плодовитости и размеры яиц у изучаемых креветок.

Stage	Species	No. of females with eggs on pleopods	RBF, no. of eggs, +/–SD	Egg diameter (short-and long-axis diameters), mm, +/–SD	Main characteristics		
					Eye	Telson	Others
1	*P. sulcatifrons*	35	12±2	4.4±0.1/3.2±0.1	No visual indications of embryo development; eggs are semitransparent		
	A. purpurea	6	944±417	0.8±0.02/0.6±0.02			
	A. pelagica	0	–	–			
2	*P. sulcatifrons*	65	10±1,4	4.2±0.1/3.2±0.1	Eggs are semitransparent; embryo having a shape of semi moon band is on the animal egg pole (probably, at nauplius or postnauplius stage)		
	A. purpurea	10	1720±656	0.83±0.03/0.52±0.05			
	A. pelagica	0	–	–			
3	*P. sulcatifrons*	20	7±2	4.3±0.1/3.2±0,3	Eye spot of embryo has a thin semi moon shape; eye cornea is not pigmented	Embryo is curled and its tail overlapped the head by 10% of the total embryo length	Embryo (broader) thoracic part and its (narrower) abdominal part with a weak transversal lines of segments are distinguished
	A. purpurea	12	1094±584	0.82±0.04/0.58±0.05	Eye spot of embryo has a thin semi moon shape; eye cornea is partly pigmented	Embryo is curled and the tip of its tail reached its head	
	A. pelagica	0	–	–			
4	*P. sulcatifrons*	17	12±3	4.2±0.1/3.3±0.3	Eye cornea has an oval shape and is not pigmented	Embryo is curled and its tail overlapped the head by 10–15% of the total embryo length	Embryo is at the zoea stage; its size is increased, amount of yolk is reduced; thoracic appendages are well developed, abdominal segments are weakly determined
	A. purpurea	7	1888±623	0.88±0.05/0.59±0.03	oval shaped eye cornea is well pigmented		
	A. pelagica	4	1278±664	1.37±0.03/0.85±0.06			
5	*P. sulcatifrons*	7	9±4	4.3±0.2/3.4±0.4	Larvae inside eggs are prior to or during hatching; females may carry both eggs with a full developed zoea inside and newly hatched larvae		Larvae have liquid lipids inside cephalothorax, free body appendages, and free tail
	A. purpurea	13	862±284	0.96±0.05/0.67±0.06			Larvae have no liquid lipids inside cephalothorax
	A. pelagica	7	898±665	1.22±0.10/0.87±0.08			
Just hatched larvae	*P. sulcatifrons*	7	–	Larva' approx. length 6.45–6.88	Thoracopods and pleopods of larvae are not yet developed; liquid lipid yolk inside cephalothorax		
	A. purpurea	13	–	Larva' approx. length 2,21–2,4	Thoracopods and pleopods of larvae are not yet developed; no liquid lipid yolk inside cephalothorax		
	A. pelagica	7	–	Larva' approx. length 2,81–3,05			

pelagica and *A. purpurea* where a synchronic vitellogenesis guarantees the onetime laying of all ripe oocytes during each spawning and we saw only equally developing oocytes on pleopods. Single portion of oocytes that have not been laid during a spawning event (see description of stages VI–II in Tab. 3, 4) have to be resorbed during the next gonadal cycle as it for many other decapod shrimp species [King, 1948; Aoto, 1952; Cummings, 1961; Burukovsky, 1970; Ville, 1972; Levi, Vacchi, 1988; Tan-Fermin, 1991; Demestre, Fortuno, 1992; Ramirez-Llodra, Segonzac, 2006; Sudnik, 2008] and for other animals [Eisenstadt, 1977; Ivankov, 1985; Kasyanov, 1989; Nigmatullin, 2000].

The RBF and egg sizes on each embryos development stage differed by orders of magnitude between *P. sulcatifrons* and *Acanthephyra* spp. The interzonal bathypelagic species *P. sulcatifrons* (600–2100 m and deeper) had a rather compact ovary and its fecundity (RBF) was less than 20 eggs per female in average. On the contrary, the interzonal mesopelagic-upper bathypelagic species *Acanthephyra* spp. (100–200 to 1800–2000 m), had well-developed distal branches in the ripe ovary and their RSF attained more than 2000 eggs per female in average (Tab. 5). In addition, considerable differences in eggs sizes were noted. The sizes of newly laid eggs in pasiphaeid shrimps *P. sulcatifrons* (4.4 ± 0.1 × 3.2 ± 0.1 mm; Tab. 5) and *Glyphus marsupialis* (4.8–6.5 × 3.9–5.1mm) [Sudnik, 2007], as in oplophorids *Oplophorus novaezilandie* (2.6–2.8 × 1.6–2.7 mm) [Burukovsky, 1994] and *Systellaspis debilis* (3.4–3.6 × 1.97–2.2 mm) [Sudnik, 2015] were much larger than in the oplophorid *A. purpurea* (0.8 ± 0.02 × 0.6 ± 0.02 mm: Tab. 5). The sizes of the newly hatched larvae in *P. sulcatifrons* were more than twice as large as larvae of *Acanthephyra* spp. (approximately 6.5–7 mm and not more than 3.2 mm, respectively: Tab. 5) and had storage of liquid lipids inside the cephalothorax. A more compact shape of the ovary coincides with a decrease in fecundity and increase in the egg size, which is found in caridean shrimps that have adapted to a mode of bathypelagic life.

Both *Acanthephyra* spp. and *Parapasiphae sulcatifrons* demonstrate the K-strategy traits typical for all carideans (a well-developed care of offspring), i.e. the shrimps carry their eggs on the pleopods and evolve in the direction to develop larger eggs and larger lecithotrophic larvae, compared to penaeids. The aristeids and penaeids show indications of r-strategy and release their numerous small eggs in the water, where mainly planctotrophic larvae develop. *Acanthephyra* spp. have more numerous and smaller eggs and smaller lecithotrophic larvae compared to pasiphaeids, other oplophorids and other caridean species [this study; Sudnik, 2008, 2015]. *Acanthephyra* spp. show indications of both K-strategy (incubations of embryos on pleopods) and the tendency to r-strategy (numerous small embryos and newly hatched larvae), which was classified as K-r-strategy according to Sudnik [2008]. *A. pelagica* and *A. purpurea* have a more shallow distribution range than *P. sulcatifrons* and are probably morphologically closer to the older evolutionary shrimp groups (nematocarcinids, penaeids: [Burukovsky, 2003]). *P. sulcatifrons* has few large eggs and large lecithotrophic larvae which can be regarded as components of KK-strategy (extreme K-strategy: [Sudnik, 2008]). *P. sulcatifrons* is a bathypelagic species and, according to Burukovsky [2003] and our results, it morphologically corresponds to evolutionary younger shrimp groups. The decrease in fecundity in species adapted to the deepwater life is related to the reproductive strategy which is directed towards formation of large well developed lecithotrophic larvae. Both large and advanced larvae with the storage of liquid lipids inside the cephalothorax are considered to increase the chances of survival at low temperatures and limited food availability in the bathypelagic waters.

ACKNOWLEDGEMENTS. This study was an element of MAR-ECO (2001–2010), an international field project under the Census of Marine Life. We thank the crew and scientists on the R/V GO Sars for help during collecting and sorting of crustacean catches. We are indebted to Hege Øverbø Hansen (IMR, Norway) for her help during species identification. V. Laptikhovsky (the Falklands, UK), R.N. Burukovsky (KSTU, Kaliningrad, Russia) for the help in locating relevant literature. We wish to thank all colleagues and especially Ch.M.Nigmatullin (AtlantNIRO, Kaliningrad), V.A. Spiridonov (IO RAS, Moscow) who provided helpful advices and critical reading of the manuscript.

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Responsible editor V.A. Spiridonov