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Biological features of symbiotic pea crabs of the genus *Pinnixa* sensu lato (Decapoda: Brachyura: Pinnotheridae) from Vostok Bay of the Sea of Japan

Биологические особенности симбиотических крабов-горошин рода *Pinnixa* sensu lato (Decapoda: Brachyura: Pinnotheridae) из залива Восток Японского моря

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КЛЮЧЕВЫЕ СЛОВА: Симбиоз, морфометрия, репродуктивная биология, размножение, ооциты, яйца, плодовитость.

ABSTRACT. The article describes some biological features (morphometry, sex ratio, reproductive condition, fecundity, egg size and etc.) of symbiotic pea crabs *Pinnixa rathbunae* (main object) and *P. banzu* from Vostok Bay of the Sea of Japan. Despite living in association with different hosts (*Urechis* and *Chaetopterus*) both species are quite similar in biology: females are slightly dominant in number and slightly larger than males, possess the similar relationships between molting and reproductive cycles and the seasonality of reproduction with the possibility of producing more than one clutch of eggs per a season. The average values of morphometric parameters between the two species do not differ significantly, which indicates their close similarity. Different measurements of exoskeleton, presented in the article, as well as their ratios to the width of carapace (REP) for *P. rathbunae* and *P. banzu*, are useful for trophologists reconstructing sizes of these crabs from exoskeleton elements collected in stomachs of different hydrobionts of the Sea of Japan. All these parameters are also compared with other relative representatives of the family Pinnotheridae.

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РЕЗЮМЕ. В статье описаны некоторые биологические особенности (морфометрия, соотношение полов, репродуктивное состояние, плодовитость, размер яиц и т.д.) симбиотических крабов-горошин *Pinnixa rathbunae* (основной объект) и *P. banzu* из залива Восток Японского моря. Несмотря на то, что они живут в ассоциациях с разными хозяевами (*Urechis* и *Chaetopterus*), оба вида довольно схожи биологически: самки немного доминируют по численности и немного крупнее самцов, имеют схожую взаимосвязь между линочным и репродуктивным циклами, сезонность размножения с возможностью производить более одной кладки яиц за сезон. Средние значения морфометрических параметров между двумя видами существенно не различаются, что свидетельствует об их близком сходстве. Различные измерения экзоскелета, представленные в статье, а также их отношение к ширине панциря (REP) для *P. rathbunae* и *P. banzu*, могут быть полезны, к примеру, для трофологов, воссоздающих размеры этих крабов из элементов их экзоскелета, собранных в желудках различных гидробионтов Японского моря. Все эти параметры сравниваются с таковыми для других представителей семейства Pinnotheridae.

Introduction

Pea crabs of the family Pinnotheridae usually live in association with different marine invertebrates. Numerous researches have been focused on their symbiosis with bivalve mollusks, while these crabs also live in polychaetes tubes, burrows of sipunculid and echiuroid worms, thalassinidean shrimps and hemichordates [Stauber, 1945; Christensen, McDermott, 1958; Sastry, Menzel, 1962; Houghton, 1963; Pearce, 1966a, b; Beach, 1969; Kruczynski, 1973; Jones, 1977; Bierbaum, Ferson, 1986; review in Alves, Pezzuto, 1998; McDermott, 2009].

The world fauna of pea crabs of the genus *Pinnixa* sensu lato includes about 70 species, more than 50 of which were found along the American coasts [Sakai, 1934; Manning, Felder, 1989; Coelho, 1997; Zmarzly, 1992; Komai *et al.*, 2014; Marin, 2016]. The taxonomy of subfamilies was recently modified and the genus *Pinnixa* sensu lato was separated for several phylogenetically related genera [Palacios Theil *et al.*, 2016; Palacios Theil, Felder, 2020], but still not all species of the genus *Pinnixa* sensu lato are revised, including our main objects. Taking into account the latest revisions [Palacios Theil *et al.*, 2016; Palacios Theil, Felder, 2020], we believe that these crabs are more or less similar from an ecological point of view and will use the "old" taxonomy in order not to complicate the work with excessive taxonomic details.

Russian fauna includes only 3 species of the genus *Pinnixa* sensu lato, namely *P. tumida* Stimpson, 1858, *P. rathbunae* Sakai, 1934 and *P. banzu* Komai, Nishi et Taru, 2014 (still referring to *Pinnixa* sensu lato), known from the cold-water (northern) part the Sea of Japan and representing the northernmost area of the genus distribution [Marin, Kornienko, 2014; Marin, 2016, 2018]. Only few data on the species composition and some ecological features have been published [Vassilenko, 1990; Marin, 2016, 2018; Burukovsky, Marin, 2018]. At the same time, symbiotic relationships, such data on reproductive biology and ecology have been described from other *Pinnixa* species such *P. chaetopterana* Stimpson, 1860 [McDermott, 2005], *P. tumida* [Takeda *et al.*, 1997], *P. littoralis* Holmes, 1895, *P. faba* (Dana, 1851) [Pearce, 1966a], *P. cylindrica* (Say, 1818) [McDermott, 1981]. *P. tomentosa* Lockington, 1877 [Scanland, Hopkins, 1978], *P. valerii* Rathbun, 1931 [Vargas, 1987], *P. barnharti* Rathbun, 1918, *P. forficulimanus* Zmarzly, 1992, *P. longipes* (Lockington, 1876) [Zmarzly, 1992] and *P. patagoniensis* Rathbun, 1918 [Alves, Pezzuto, 1998].

Thus, the aim of this work is to describe some features of biology (morphometry, reproductive condition, fecundity, egg size and etc.) of *Pinnixa rathbunae* and *P. banzu* from Russian waters (Vostok Bay) of the Sea of Japan. The main object of our study is *P. rathbunae*, the common species in the Vostok Bay, but we also used all sampled specimens of *P. banzu* in the study because such data are also absent for the species.

Material and Methods

Symbiotic pea crabs were collected in Vostok Bay (42°53′35.5″N 132°43′42.1″E) (northern part of Peter the Great Bay) of the Sea of Japan in May and July 2017. Pea crabs *Pinnixa rathbunae* Sakai, 1934 (n=257) (Crustacea: Decapoda: Pinnotheridae) were collected using a hand pump (yabbi-pump) from burrows of echiuroid (spoon-worm) *Urechis unicinctus* (von Drasche, 1881) (Echiura: Echiuroidea: Urechidae) at depths of 0.2–2.0 m at 14–15 July 2017, while rarer pea crabs *P. banzu* (n=9) were collected with SCUBA diving from tubes of polychaete *Chaetopterus* cf. *cautus* Marenzeller, 1879 (Polychaeta: Chaetopteridae) at depths of 3–5 m at 24 May 2017. Polychaete tubes were carefully dug out of the substratum manually not to lose hosts and their symbionts. All symbionts were fixed with 70% alcohol or 4% buffered solution of formaldehyde.

The laboratory biological analysis (after Rodin *et al.* [1979]; Sudnik, Poddueva [1999]) was used for a comprehensive study of biology of pea crabs. The analysis was carried out for 257 specimens of *P. rathbunae* (117 ♂♂, 140 ♀♀) and 9 specimens of *P. banzu* (4 ♂♂, 5 ♀♀) and included: morphometry, sex identification, body weighting, the assessment of phase of the moult cycle (on the condition of cuticle: moulting/intermoulting), in ♀♀ — assigning ovaries maturity stage (OMS) and the development stage of embryos (EDS), counting fecundity of eggs (= embryos) and measurement of their size and of size of mature oocytes. The length of carapace (CL) was measured from the posterior edge of eye orbits to the posterior margin of carapace; width of carapace (CW) — the middle (maximum) width of carapace from one lateral margin to the other; the length of abdomen (AL) — the central length from abdomen proximal margin to distal margin of the telson; the total body length (TBL) was determined summing CL and AL. The length and width of merus of ambulatory pereopods 3 (forth pair of thoracic appendages) (P3), the length and width of palm of chela and the length of chela as well as the ratios between different exoskeleton parts and the width of carapace (REP) were measured according to Rodin *et al.* [1979] and Poddueva [2017, 2018]. We are sure that these ratios are useful, for example, for trophologists in reconstruction of sizes of these crabs from fragments found in the stomachs of aquatic organisms (i.e., fishes) of the Sea of Japan. The measurements were carried out with the help of micrometer on light binocular microscope MBS-10 with an accuracy of 0.1 mm.

The body weight was determined after short-time drying of the specimen on a filter paper with the help of Adventurer ™ Pro analytical scales with the accuracy about 0.01g. The mass of slightly moist ovaries was determined using the torsion weighing-machine Techniprot (0–500 mg) with the accuracy about 0.001g.

The sex determination was accomplished based on the shape of abdomen and the structure of abdominal appendages. The sex determination using secondary sexual characteristics was supported by determining the type of their gonads (testes or ovaries). In a case of identifying gonads as ovaries, their maturity was assessed using a 6-point scale for determination the ovary maturity stage [Sudnik, Poddueva, 2019] based on macroscopic features characterizing the condition of gonads, such as color, shape, structure, relative size, to determine the degree of their maturity: OMS I — the ovaries of immature ♀♀; OMS II — sexually mature; OMS III–V — maturing (OMS III, IV) and mature (OMS V) ovaries; OMS VI–II — gonads in the post-spawning ♀♀.

Table 1. Morphometry of pea crab *Pinnixa rathbunae* (117 ♂♂, 140 ♀♀) in Vostok Bay.
Таблица 1. Морфометрия самцов крабов-горошин *Pinnixa rathbunae* (117 ♂♂, 140 ♀♀) в заливе Восток.

Measured part of exoskeleton (PaEx)	**Min, mm**		**Max, mm**		**Mean±SD, mm**		**Ratio of PaEx to CW (REP)**	
	mm	**ff**	**mm**	**ff**	**mm**	**ff**	**mm**	**ff**
Carapace Width (CW)	4.6	4.2	12.8	12.3	8.31±1.91	8.61±1.79	–	–
Carapace Length (CL)	2.7	2.1	6.2	5.7	4.48±0.88	4.35±0.89	1.85	1.99
Abdomen Length (AL)	2.0	2.2	5.5	8.3	3.74±0.82	4.89±1.45	2.22	1.83
Abdomen Width (AW)	1.4	1.2	3.4	10.8	2.45±0.52	5.87±2.43	3.38	1.70
Total Body Length (TBL)	4.7	4.9	11.4	14.5	8.22±1.68	9.24±2.18	–	–
Length of Palm (left chela)	1.6	1.6	5.0	12.9	2.95±0.75	3.17±1.07	2.90	2.99
Length of Palm (right chela)	0.9	1.0	3.5	3.2	1.98±0.57	2.15±0.47	4.38	9.39
Width of Palm (right chela)	0.5	0.6	2.3	2.1	1.43±0.40	1.27±0.30	6.04	2.84
Length of merus of P3	1.6	1.5	4.7	4.5	2.90±0.66	2.93±0.57	2.89	4.01
Width of merus of P3	0.4	0.3	1.6	1.8	0.93±0.26	0.96±0.87	9.17	7.01

ff — females; mm — males.

Table 2. Morphometry of pea crab *Pinnixa banzu* (4 ♂♂, 5 ♀♀) in Vostok Bay.
Таблица 2. Морфометрия крабов-горошин *Pinnixa banzu* (4 ♂♂, 5 ♀♀) в заливе Восток.

Measured part of exoskeleton (PaEx)	**Min, mm**		**Max, mm**		**Mean±SD, mm**		**Ratio of PaEx to CW (REP)**	
	mm	**ff**	**mm**	**ff**	**mm**	**ff**	**mm**	**ff**
Carapace Width (CW)	14.4	11.8	16.3	14.3	14.9±0.79	13.02±1.02	–	–
Carapace Length (CL)	6.7	5.6	8.0	6.8	7.2±0.49	6.22±0.49	2.07	2.09
Abdomen Length (AL)	5.8	5.2	7.4	5.5	6.3±0.66	5.38±0.13	2.38	2.42
Length of Right Chela	3.9	4.7	5.9	5.4	5.1±0.72	5.08±0.30	3.00	2.56
Length of Palm (right chela)	3.2	3.6	4.3	4.1	3.4±0.68	3.9±0.22	4.59	3.34
Width of Palm (right chela)	1.9	2.4	2.7	2.7	2.3±0.30	2.52±0.13	6.45	5.18
Length of merus of P3	4.0	4.0	4.9	4.5	4.2±0.13	4.3±0.24	3.54	3.01
Width of merus of P3	1.8	1.5	2.1	1.7	1.9±0.13	1.65±0.10	7.93	7.89

ff — females; mm — males.

The gonadosomatic index (GSI) was calculated for mature ovaries as the ratio of their weight to the weight of ♀♀ body in %% (without the total weight of the gonad, stomach and it content, and the mass of eggs from pleopods in a case of ovigerous ♀♀). GSI was evaluated only in females *P. banzu*; we were not able to weigh the mature ovaries of *P. rathbuni* and estimate GSI, since the gonads were extremely loose and we would not be able to weigh them without a significant error.

The stages of embryo development were determined based on a 5-point scale created to determine the stage of embryo development in caridean shrimp [Burukovsky, 1992; Sudnik, Falkenhaug, 2014]. For fecundity estimation, all eggs from pleopods were counted directly under the binocular light microscope but only females with embryos in EDS 1 were used for analysis, in order to avoid bias caused by egg loss during the incubation period.

Mature oocytes and eggs were measured using an ocular microscope with an accuracy of 0.001 mm; larger and smaller diameters (length and width) of at least 10 oocytes/eggs were measured, and the mean values were calculated. The volume of egg with ellipsoid form was quantified by the formula: $V = 4/3 \times \pi \times r1 \times (r2)^2$, where r1 — half the length of the egg, and r2 — half the width of the egg [Oh, Hartnoll, 2004; Bülgü, Samsun, 2006].

Results

Sex ratio. Two studied species of *Pinnixa* clearly differ in population structure: *P. rathbunae* was usually found in groups of adult (mature) and juvenile individuals in burrows of *Urechis unicinctus,* while *P. banzu* was found usually in strictly heterosexual (♂♀) pairs or solitary inside tubes of *Chaetopterus* cf. *cautus*. At the same time, using whole available data, the sex ratio (♂♂/♀♀) was 0.84 (n=257) in *P. rathbunae*, and was 0.8 (n=9) in *P. banzu*.

Morphometry. The results of morphometric analysis and the ratios of exoskeleton parts to the width of carapace (REP) are shown in Tabs 1, 2. The sizes were 4.2–12.8 mm (CW), 2.1–6.7 mm (CL), and 4.7–

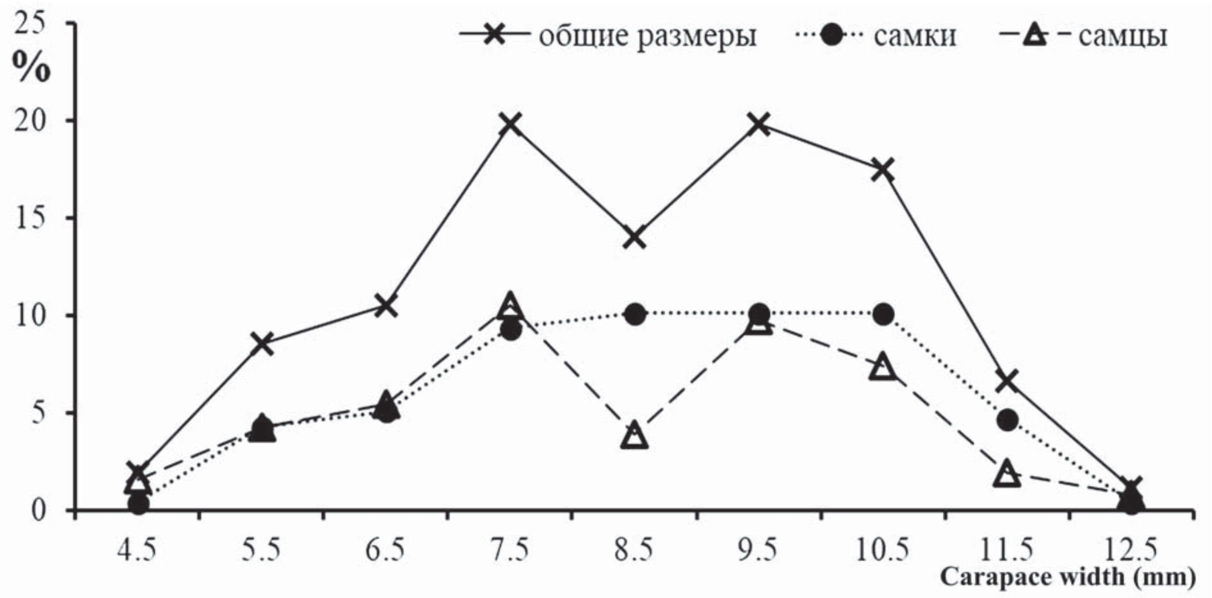

Fig. 1. Size of pea crab *Pinnixa rathbunae* in Vostok Bay.
Рис. 1. Размер крабов-горошин *Pinnixa rathbunae* в заливе Восток.

14.5 mm (TBL) in *P. rathbunae*, the mean (CW, CL, TBL) and the modal sizes (CW) not differ significantly in ♀♀ and ♂♂ (Tabs 1, 2; Fig. 1). The sizes were 11.8–16.3 mm (CW), 5.6–8.0 mm (CL), 10.8–15.4 mm (TBL) in *P. banzu*, while carapace of ♀♀ was smaller than in ♂♂ (11.8–14.3 mm and 14.4–16.3 mm, respectively). However, by the mean values these differences are not significant.

Female reproductive traits, the relationship of moulting and reproduction in ♀♀. Among 257 studied specimens of *P. rathbunae,* 58 individuals were found moulting: 26 ♂♂ (22.2% of all examined ♂♂, CW 4.6–9.9 mm, with the mean 6.86±1.74 mm) and 32 ♀♀ (22.9%, CW 5.1–11.8 mm (7.72±1.79 mm)). The proportion of moulting ♂♂/♀♀ were similar; no significant differences in the sizes of the moulting individuals in both sexes were found. No moulting individuals were found among all studied specimens of *P. banzu*, both ♂♂ and ♀♀ were in the intermoulting period with hard exoskeleton.

The studied ♀♀ of *P. rathbunae* can be divided into 4 groups, based on following criteria – the ovaries maturity stages (OMS), the presence or absence of eggs on pleopods and the development stages of embryos (ESD), and body sizes: non-ovigerous ♀♀ with immature gonads (OMS I–II); non-ovigerous ♀♀ with maturing or mature gonads (OMS III–V); recently spawned ♀♀, i.e. ovigerous with embryos in EDS 1 and immature gonads (OMS VI–II) and ovigerous ♀♀ with embryos in EDS 1–3 and maturing ovaries (OMS III–V) (Tab. 3; Fig. 2). Non-ovigerous ♀♀ greatly prevailed over ♀♀ with eggs (the ratio was 86.4% / 13.6%, respectively). Among 19 ovigerous ♀♀ of *P. rathbunae*, 16 ♀♀ had embryos in EDS 1–2 (i.e., the begin-

Table 3. Reproductive state of ♀♀ of pea-crabs *Pinnixa rathbunae* and *P. banzu* in Vostok Bay.
Таблица 3. Репродуктивное состояние ♀♀ крабов-горошин *Pinnixa rathbunae* и *P. banzu* в заливе Восток.

Non-ovigerous/ ovigerous	Number of females	OMS	State of embryos, EDS	CW (range / mode), mm
Pinnixa rathbunae				
non-ovigerous	40	I, II	–	4.2–9.8 / 7–8
	81	III–V	–	5.8–12.3 / 9–11
ovigerous	3	VI–II	1	10.0–10.8 / 10–11
	10	III–V	1	7.5–10.7 / 8–11
	3		2	
	3		3	
Pinnixa banzu				
non-ovigerous	–	–	–	–
ovigerous	3	IV	1	14.4–16.3
	2	V	2	14.5; 14.6

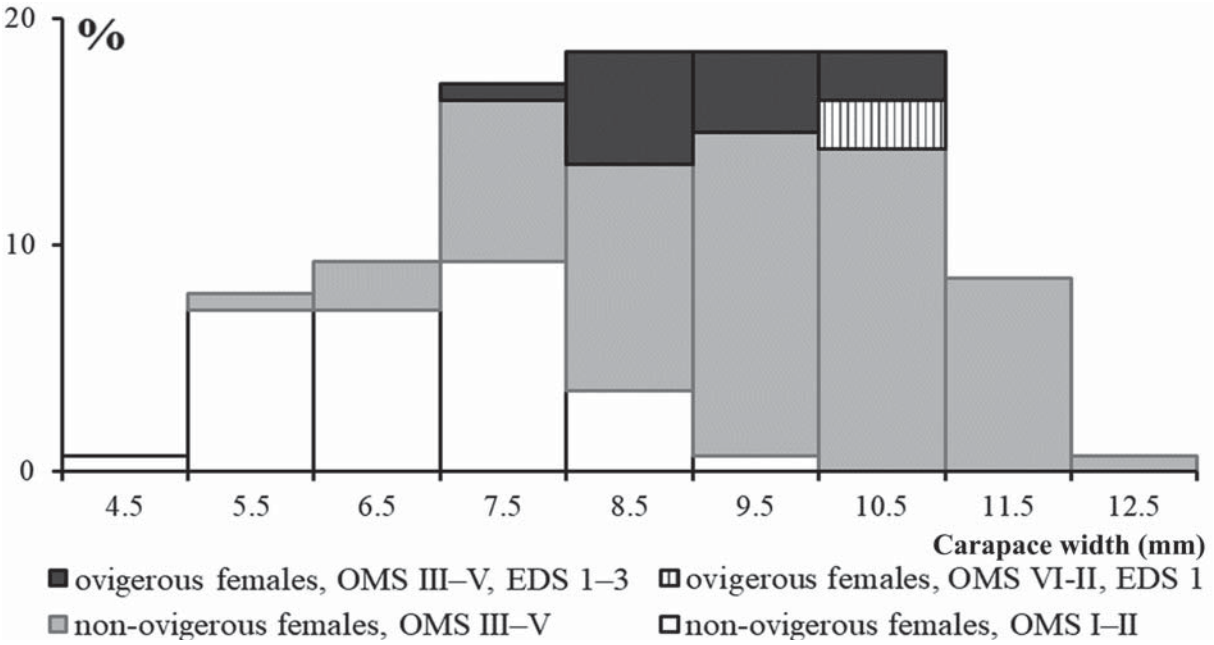

Fig. 2. Size composition of ovigerous (EDS, development stages of embryos 1–3) and non-ovigerous ♀♀ of *Pinnixa rathbunae* with ovaries in different maturity stages in Vostok Bay (%% of all studied ♀♀).

Рис. 2. Размерный состав яйценосных (EDS, стадии развития эмбрионов 1–3) и неяйценосных ♀♀ *Pinnixa rathbunae* с яичниками в различных стадиях зрелости в заливе Восток (в %% от всех исследованных ♀♀).

ning of embryogenesis) and 3 ♀♀ carried embryos in EDS 3 (the middle of embryogenesis) (Tab. 3). All 5 studied ♀♀ of *P. banzu* were ovigerous (Tab. 3), 3 ♀♀ were pre-mature (OMS IV) and have just laid eggs (EDS 1), and 2 ♀♀ have recently spawned (EDS 2) and were again in the pre-spawning state (OMS V) (Tab. 3).

Moulting individuals of *P. rathbunae* were dominating among immature ♀♀ (OMS I), intermoulting ♀♀ with hard exoskeleton prevail among ♀♀ with OMS II, although the proportion of moulting individuals is large (Tab. 4). Moulting individuals were extremely rare among mature ♀♀ with OMS III and the relative number of ♀♀ with soft exoskeleton was increasing among pre-mature and mature ♀♀ (OMS IV–V). Post-spawning ♀♀ (OMS VI–II) possess hard exoskeleton (Tab. 4). The mean sizes of moulting ♀♀ differs significantly in individuals with OMS I (immature) and III–IV (maturing); differences were also observed in the sizes of moulting individuals with OMS I–II and completely mature ovaries at OMS V.

Pre-mature and mature oviparous ♀♀ (OMS IV, V) were found with embryos in the initial development stages (EDS 1, 2) in both *P. rathbunae* and *P. banzu* (Tab. 5) that shows the absence of synchronous development of the ovaries and embryos in these species.

Gonadosomatic index of pre-spawning ♀♀. Gonadosomatic index (GSI) of one spawning was calculated in 2 pre-spawning (OMS V) ♀♀ of *P. banzu* as 9.2 and 11.8%, respectively.

Sizes of mature oocytes. The sizes of mature oocytes in *P. rathbunae* and *P. banzu* not differ significantly, despite the smaller sizes of *P. rathbunae* (Tab. 6).

Table 4. Stages of ovaries maturity in ♀♀ of pea crabs *Pinnixa rathbunae* (intermoulting (with hard exoskeleton) and moulting) in Vostok Bay.

Таблица 4. Стадии зрелости яичников ♀♀ крабов-горошин *Pinnixa rathbunae* (в межлиночном состоянии (с твердым панцирем) и линяющих) в заливе Восток.

Stage of ovary maturity	**Number of females**			**CW of females, mm**			
	total	**intermoulting**	**moulting**	**intermoulting**		**moulting**	
				range	**mean±SD**	**range**	**mean±SD**
I	13	4	9	5.0–9.8	6.5±1.79	5.1–7.2	6.08±1.16
II	28	19	9	4.2–10.0	4.2±1.23	5.1–8.7	6.83±1.17
III	26	24	2	5.8–10.7	8.07±1.18	9.0–9.3	9.15±1.62
IV	47	40	7	9.65–11.8	9.65±1.18	7.0–11.8	9.33±1.7
V	24	19	5	8.1–12.3	8.1±1.03	8.3–10.3	9.48±0.85
VI–II	2	2	–	10.0–10.8	10.4±1.71	–	–

Table 5. The correlation of ovary maturity stage (OMS) / development stage of embryos (EDS) in ovigerous ♀♀ of pea crabs *Pinnixa rathbunae* and *P. banzu* in Vostok Bay.
Таблица 5. Соотношение между стадиями развития яичников (OMS) / стадиями развития эмбрионов (EDS) у яйценосных ♀♀ крабов-горошин *Pinnixa rathbunae* and *P. banzu* в заливе Восток.

OMS	**Number of ovigerous females** ***Pinnixa rathbunae / Pinnixa banzu***					
	EDS 1		**EDS 2**		**EDS 3**	
VI–II	3	–	–	–	–	–
III	5	–	1	–	1	–
IV	3	2	2	–	2	–
V	2	1	–	2	–	–

Table 6. Sizes of mature oocytes (OMS V) in pea crabs *Pinnixa rathbunae* and *P. banzu* in Vostok Bay.
Таблица 6. Размеры зрелых ооцитов (OMS V) крабов-горошин *Pinnixa rathbunae* и *P. banzu* в заливе Восток.

Species	**Number**	**CW, mm**		**Mature oocytes length, mm**		**Mature oocytes width, mm**	
		range	mean± SD	range	mean± SD	range	mean± SD
P. rathbunae	24	8.1–12.3	10.4± 1.62	0.280–0.357	0.312± 0.008	0.238–0.350	0.287 ± 0.008
P. banzu	3	14.5–16.3	15.1± 0.85	0.302–0.312	0.308± 0.058	0.282–0.289	0.285 ± 0.053

Table 7. Egg sizes, egg volume, fecundity (F) and sizes of ovigerous ♀♀ of pea crabs *Pinnixa rathbunae* and *P. banzu* with embryos at different stages of development in Vostok Bay of the Sea of Japan.
Таблица 7. Размер яиц, объем яиц, плодовитость (F) и размеры яйценосных ♀♀ крабов-горошин *Pinnixa rathbunae* и *P. banzu* с эмбрионами на разных стадиях развития в заливе Восток Японского моря.

EDS	**Number**	**CW, mm**		**Fecundity**		**Egg length, mm**		**Egg width, mm**		**Egg volume, mm^3**	
		R	M	R	M	R	M	R	M	R	M
Pinnixa rathbunae											
1	13	8.0–10.8	9.44± 1.69	24–1209	563± 478	0.255–0.310	0.292± 0.022	0.240–0.298	0.275± 0.022	0.008–0.014	0.012± 0.003
2	3	7.5–9.1	8.43± 1.73	551–1048	819± 448	0.283–0.335	0.310± 0.021	0.283–0.320	0.295± 0.021	0.012–0.018	0.014± 0.002
3	3	8.2–10.5	9.33± 1.69	412–1624	945± 520	0.283–0.333	0.300± 0.021	0.250–0.290	0.270± 0.020	0.009–0.015	0.012± 0.002
Pinnixa banzu											
1	3	14.4–16.3	15.1± 0.79	2876–3108	3036 ±89	0.325–0.350	0.342± 0.01	0.300–0.325	0.308± 0.02	0.015–0.019	0.017± 0.003
2	2	14.5; 14.6	–	2917; 3006	–	0.350; 0.350	–	0.325; 0.350	–	0.019; 0.022	–

M — mean±SD; R — range.

Fecundity, egg size. The egg mass was completely laying under the abdomen in ♀♀ of *P. rathbunae* and *P. banzu*. The fecundity was counted for *P. rathbunae* (n=19) and *P. banzu* (n=5) (see Tab. 7). The mean fecundity in *P. rathbunae* (CW 7.5–10.8 mm, EDS 1–3) was 664±448 eggs, ranging from 24 (CW 8.7 mm) to 1624 eggs (CW 10.5 mm), without significant loss of embryos at the stages of EDS 1–3 (from the beginning to the middle of embryogenesis, inclusive) (Tab. 6). The mean fecundity in *P. banzu* (CW 14.4–16.3 mm, EDS 1, 2) was 2974±89 eggs, ranging from 2876 (CW 14.4 mm) to 3108 eggs (CW 16.3 mm) (Tab. 6).

Egg size in *P. rathbunae* ranged from 0.255×0.240 mm (length×width) in ♀ with CW 9.6 mm and embryos development stage (EDS 1) to 0.335×0.320 mm (CW 9.1 mm, EDS 2) and to 0.333×0.290 mm (CW 10.5 mm, EDS 3) (Tab. 6). Egg volume in *P. rathbunae* varied from 0.008 mm^3 (CW 8.7–9.6 mm, EDS 1) to 0.018 mm^3 (CW 9.1 mm, EDS 2). Eggs sizes (volume, diameters) in *P. rathbunae* did not change significantly during the studied part of embryogenesis (EDS 1–3). Eggs of *P. banzu* ranged in size from 0.325×0.300 mm and 0.015 mm^3 (CW 16.3 mm, EDS 1) to 0.350×0.350 mm and 0.022 mm^3 (CW 14.6 mm, EDS 2) (Tab. 6). The size of eggs with embryos on EDS 1–2 in *P. banzu* (CW 14.4–16.3 mm) was slightly larger than in *P. rathbunae* (CW 7.5–10.8 mm) (Tab. 6).

Ectosymbionts of crabs. Ectosymbiotic bryozoans were observed on dorsal surface carapace and on pereiopods in all 4 ♂♂ and 2 of 5 ♀♀ of *P. banzu*, while the remaining 3 ♀♀ had bryozoans in smaller numbers only on pereiopods. No ectosymbionts were observed on carapace and pereiopods in *P. rathbunae*.

Discussion

Recently, for most known pea crabs of the genus *Pinnixa* and other representatives of the family Pinnotheridae, only taxonomic descriptions are known, while data on their biology and ecology are quite rare and fragmentary. However, below we will try to give some general conclusions related to the data presented above.

The sex ratio within the family Pinnotheridae varies greatly. In the studied populations of pea crabs *Pinnixa rathbunae* and *P. banzu*, females somewhat dominated with ♂♂/♀♀ ratio about 0.8–0.84. The ratio is close to equal in *P. patagoniensis* [Alves, Pezzuto, 1998] and it ranged from 0.86 to 1.01 in *P. chaetopterana*, often with males slightly less than females [McDermott, 2005]. Females stronger prevail than males in the studied populations of *P. tumida* [Takeda *et al.*, 1997], *P. cylindrica* [McDermott, 1981], *P. tomentosa* [Scanland, Hopkins, 1978] and related *Pinnaxodes floridensis* H.W. Wells et M.J. Wells, 1961 [Wells, Wells, 1961], while males prevailed over females in *P. littoralis*, *P. faba* [Pearce, 1966a], *Pinnotheres pisum* (Linnaeus, 1767) [Ambariyanto, Seed, 1991] and *Tumidotheres* (*Pinnotheres*) *maculatus* (Say, 1818) [Kruczynsky, 1973]. The absence of juveniles living together with adult crabs was noted earlier for *P. banzu* from tubes of polychaete *C. cautus* [Marin, 2016], while 3.5% of juveniles of *P. chaetopterana* were found together with mature individuals inside tubes of polychaete *Amphitrite ornata* (Leidy, 1855) (Terebellidae) [McDermott, 2005)].

The maximum sizes of *P. rathbunae* were somewhat different: they were slightly smaller in Vostok Bay of the Sea of Japan [present data], compared with Tokyo Bay [Komai *et al.*, 2014]. On the contrary, individuals of *P. banzu* from Vostok Bay were somewhat larger [Komai *et al.*, 2014] (Tab. 8). The size of *P. banzu* from both localities is larger than that of *P. rathbunae* from Vostok Bay and are closer to the sizes of *P. chaetopterana* from the Atlantic coast of the USA [McDermott, 2005] (Tab. 8). The sizes of *P. rathbunae* are closer to those of *P. banzu* species from Tokyo Bay [Komai *et al.*, 2014], *P. tumida* from Mutsu Bay [Takeda *et al.*, 1997] and *P. patagoniensis* from the coast of southern Brazil [Alves, Pezzuto, 1998].

The ♂♂/♀♀ size ratio is also different in pinnotherid crabs. Similar sizes are characteristic of males and females of *P. rathbunae* [present data], *P. patagoniensis* [Alves, Pezzuto, 1998), *P. barnharti*, *P. forficuli-*

Table 8. Sizes of different pea crab species of the genus *Pinnixa* sensu lato.
Таблица 8. Размеры различных крабов-горошин рода *Pinnixa* sensu lato.

Species	Sex	CW, mm		CL, mm		Reference
		min–max	mean±SD	min–max	mean±SD	
P. rathbunae (Vostok Bay)	mm	4.6–12.8	8.31±1.91	2.7–6.2	4.48±0.88	present data
	ff	4.2–12.3	8.61±1.79	2.1–5.7	4.35±0.89	
P. rathbunae (Tokyo Bay)	mm	6.5–14.7	–	3.5–7.2	–	Komai *et al.*, 2014
	ff	4.3–10.5	–	3.7–7.0	–	
P. banzu (Vostok Bay)	mm	11.8–14.3	13.02±1.02	5.6–6.8	6.22±0.49	present data
	ff	14.4–16.3	14.9±0.79	6.7–8.0	7.20±0.49	
P. banzu (Tokyo Bay)	–	7.1–13.1	–	4.1–6.6	–	Komai *et al.*, 2014
P. chaetopterana	mm	1.7–15.5	–	1.0–6.5	–	McDermott, 2005
	ff	1.7–18.3	–	1.1–8.3	–	
P. tumida	mm	9.8–10.5	–	–	–	Takeda *et al.*, 1997
	ff	9.9–12.1	–	–	–	
P. patagoniensis	mm	≤ 11.5	–	–	–	Alves, Pezzuto, 1998

ff — females; mm — males.

manus and *P. longipes* [Zmarzly, 1992]. Contrary, females are larger than males in *P. banzu* from Vostok Bay [present data] as well as most of other species of the genus *Pinnixa* and the family Pinnotheridae [Scanlandt, Hopkins, 1978; McDermott, 1981, 2005; Bell, Stancyk, 1983; Takeda *et al.*, 1997; Alves, Pezzuto, 1998].

Relationship between moulting and reproduction in *P. rathbunae* resemble it in caridean shrimps [Sudnik, 2013]. That allowed us to suppose that young females of these pea crabs, similar to other decapods, pass through moulting of maturation, stimulating development of their ovaries (in Tab. 4, moulting individuals with OMS I–III) [Bhatia, Nath, 1931; Rao *et al.*, 1981; Sudnik, 2013]. Pre-mature and mature females (OMS IV–V) of *P. rathbunae* can molt repeatedly — a complex of moulting hormones, perhaps, stimulates ovary maturation (vitellogenesis in oocytes of the next generation begins), similar to caridean shrimps [Sudnik, 2013].

The size of first female maturity in decapod crustaceans, in our opinion, is characterized by the size of small individuals with immature ovaries (OMS II) without any signs of previous maturation; histological studies of the ovaries in this period of maturation, for example, in a number of malacostracan crustaceans, showed that they were at the end of pre-vitellogenesis, ready for exogenous vitellogenesis [Charniaux-Cotton, 1985; Sudnik, 2013]. Females of some true crabs (Brachyura) in this reproductive state are usually moulting, being ready to mate for the first time. Females of some tropical crabs, for example, *Liocarcinus depurator* (Linnaeus, 1758) from the Mediterranean Sea, *Neohelice granulata* (Dana, 1851) from the waters of Argentina, and *Charybdis variegata (*Fabricius, 1798) near India, molt and mate immediately, with non-developed ovaries (OMS II and VI–II) [Abello, 1989; Ituarte *et al.*, 2004]. Females of New Zealand crab *Ovalipes catharus* (White et Doubleday, 1843) also mates having soft exoskeleton [Ituarte *et al.*, 2004], while the state of their ovaries during copulation is not indicated. Moulting and mating serve as an impetus for the development and maturation of the ovaries in females of brachyuran crabs [Doi *et al.*, 2008; Abello, 1989; Ituarte *et al.*, 2004].

Among the studied females of *P. rathbunae*, about 20% (CW 4.2–10.0 mm, mean±SD 7.08±1.20 mm) had ovaries in OMS II (Tab. 4), and more than 50% of these females had CW 4.2–7.1 mm, which can be interpreted as the size of first maturity in *P. rathbunae*. At the same time, it is difficult to discuss the size of first maturity for other species of the *Pinnixa*, as usually it is not specified. Discussing the size of first maturity, the size of pre-mature and mature individuals is often presented. For example, it is defined as CW 8.0 mm for females of *P. patagoniensis* [Alves, Pezzuto, 1998], while females with CW = 13.4 mm are indicated as sexually mature in *P. faba* and *P. littoralis* [Pearce, 1966a]. The minimum sizes of mature females without eggs (CW 7.2–7.8 mm) and egg-bearing (CW 7.5–10.8 mm) in *P. rathbunae* from Vostok Bay and 2 ♀♀ from Tokyo Bay (CW 8.1 and 7.8 mm) [Komai *et al.*, 2014] are were quite similar that is, probably, the size of the first maturation and spawning in *P. rathbunae*. For example, the majority of oviparous females possess CW = 6–10 mm in *P. chaetopterana* [McDermott, 1981] that probably correspond to the first spawning.

The size of a pre-mature female was CW 7.1 mm in *P. banzu* from Tokyo Bay [Komai *et al.*, 2014] that can be assumed as the size of the first maturing. This size is much smaller than the sizes of re-maturing, already egg-bearing females from Vostok Bay (CW 14.4–14.7 mm) [present data], but it is possible that *P. banzu* from our sampled did not spawn for the first time.

Among our samples, 7 ♀♀ of *P. rathbunae* (36.8% of ovigerous ♀♀) and 5 ♀♀ of *P. banzu* (100%) were recently spawned (EDS 1, 2), but were in a premature or pre-spawning condition again. The possibility of re-spawning a few days after the previous one was described for other species, for example, female of *P. chaetopterana* laid the second clutch with 7269 eggs just 2 days after the first clutch with 10 621 eggs [McDermott, 1981].

Some brachyuran crabs are known to fertilize several clutches from the sperm reserves of a single mating, stored by the female in seminal vesicles, even during the moulting [Warner, 1977; Morgan *et al.*, 1983, 1988; McDermott, 2005]. At the same time, for example, in *P. chaetopterana* under laboratory conditions, females molted several times during the year, but did not mate and produced several clutches of unfertilized eggs, and after copulation they laid fertilized eggs again; another female laid 7 unfertilized clutches during the year, molting only twice during this period; or other female laid 2 clutches, molted, and then laid 3 new clutches without mating, then molted again; there were individuals laid 1–6 clutches in the intermoulting period [McDermott, 2005]. Consequently, copulation is not necessary to run them each gonadal cycle for females of some species of crabs. The relationships between moulting and repeated cycles of gonad maturation in pea crabs of the genus *Pinnixa* are not as obvious as in many caridean shrimps [Sudnik, 2013].

The sizes of mature oocytes in *P. rathbunae* and *P. banzu* (CW 8.1–12.3 and 14.5–16.3 mm, respectively), despite the smaller sizes of *P. rathbunae*, not significantly differ being 0.312±0.008×0.287±0.008 and 0.308±0.058×0.285±0.053 mm, respectively. For comparison, in pre-spawning females of larger leucosiid crab *Lyphira perplexa* Galil, 2009 (Leucosiidae) (CW 17.9–19.0 mm) the size of mature oocytes (0.259±0.02×0.230±0.01 mm) [Sudnik, Poddueva, 2019] were slightly smaller than in *P. banzu* and *P. rathbunae*.

A comparison of the fecundity between the species of the genus *Pinnixa* showed its strong variability and dependence on the body size of females, which was noted for other species of pinnotherids [McDermott, 1981]. In general, the fecundity reaches 8000 and even

Table 9. Fecundity of different pea crab species of the family Pinnotheridae.
Таблица 9. Плодовитость различных крабов-горошин семейства Pinnotheridae.

Species	CW, mm	Fecundity	Egg length, mm	Reference
Pinnixa rathbunae (Vostok Bay)	7.5–10.8	24–1624	0.292±0.022 (EDS 1)	present data
Pinnixa banzu (Vostok Bay)	14.4–16.3	2876–3108	0.342±0.01 (EDS 1)	present data
Pinnixa tumida	10–12.1	93–1846	0.371±0.012 (EDS 1)	Takeda *et al.*, 1997
Pinnixa patagoniensis	8–15.5	830–3000	–	Alves, Pezzuto, 1998
Pinnixa chaetopterana	≥18.3	4000–10621	–	McDermott, 2005
Pinnixa faba*, *P. littoralis	about 26	7000–8000	–	Pearce, 1966a
***Dissodactylus* spp.**	4.6–10.0	<400	0.180–0.450	Telford, 1978; Bell, Stancyk, 1983; George, Boone, 2003

more than 10 000 eggs in genera *Pinnixa* and *Pinnotheres* [Pearce, 1966a; McDermott, 2005]. The fecundity of smaller females of *P. rathbunae* was lower than in large-sized *P. banzu* (Tab. 9).

The significant losses of embryos were not observed both in *P. rathbunae* (EDS 1–3) and *P. banzu* (EDS 1, 2). The maximum fecundity values in *P. patagoniensis* is comparable to it in similar-sized *P. banzu* females (Tab. 8). In smaller species *P. tumida* fecundity was lower [Takeda *et al.*, 1997; Alves, Pezzuto, 1998] (Tab. 9). Species of the genus *Dissodactylus* Smith, 1870, the smallest representatives of the family Pinnotheridae, produce less than 400 eggs [Telford, 1978; Bell, Stancyk, 1983; George, Boone, 2003]. On the contrary, the fecundity in large-sized *P. chaetopterana* reached 10 621 eggs [McDermott, 2005], which significantly exceeds both similar-sized *P. banzu* and smaller-sized *P. tumida*. The fecundity in *P. faba* and *P. littoralis* with larger body sizes was up to 8000 eggs [Pearce, 1966a]. At the same time, females of *P. chaetopterana* can produce 4–5 clutches per spawning season [McDermott, 2005], that explain the wide range in their fecundity due to differences in eggs volume in different clutches. Usually egg clutches decreases with each subsequent clutch in brachyuran crabs, especially, in the absence of repeated copulation [McDermott, 1981; Zalota, 2017; Sudnik, Poddueva, 2019]. For example, in *P. chaetopterana*, fecundity decreased from 10 621 to 7269 eggs in the following egg clutch [McDermott, 1981].

The egg mass was completely lying under the abdomen in females of *P. banzu* and *P. rathbunae* [present study], which has also been described for *P. tumida* [Takeda *et al.*, 1997] and *Dissodactylus mellitae* (Rathbun, 1900) [Bell, Stancyk, 1983]. In other pinnotherids, for example, living in the mantle cavity of bivalve mollusks, egg mass usually goes beyond the abdomen [Silas, Alagarswami, 1967; Jones, 1977].

The size (larger diameter) of eggs in *P. banzu* was slightly larger than in *P. rathbunae* (Tab. 9). At the same time, eggs sizes (diameters, volume) not change significantly during studied beginning part of embryogenesis both in *P. rathbunae* and *P. banzu*. The egg size (large diameter) in *P. tumida* [Takeda *et al.*, 1997] slightly exceeds the egg size of larger-sized *P. banzu* and smaller-sized *P. rathbunae* (Tab. 8). The egg volume is compensated by lesser fecundity and smaller body sizes in *P. tumida* [Takeda *et al.*, 1997], compared with the fecundity large-sized *P. banzu*. Comparing to these species, *P. rathbunae* has the lowest initial fecundity with smallest body size and smallest egg size (Tab. 9). In females of the slightly larger *L. perplexa* (CW 16.2–20.8 mm), the egg size at the beginning of embryogenesis shows even smaller volume — 0.27±0.02 mm which is offset by greater than their fecundity of up to 3282 eggs [Sudnik, Poddueva, 2019].

The reproductive season (spawning and egg-bearing) and its duration are not only species-specific in the pinnotherid crabs, but also geographically variable. Based on all data on reproductive state of *P. rathbunae* and *P. banzu*, it can be assumed that the time of sampling (May for *P. banzu* and mid-July for *P. rathbunae*) was active spawning of females these species in Vostok Bay of the Sea of Japan. Probably, the spawning was not the first for largest egg-bearing females. In addition, the ovaries state (mature or in the middle of maturation) of the recently spawned 36.8% of *P. rathbunae* females and 100% of *P. banzu* females showed that females were soon expected to re-spawn eggs again. Thus, the spawning season in these species includes spring-summer periods. It is possible to assume the existence of portioned spawning in *P. banzu* and *P. rathbunae*, occurring concurrently with embryogenesis, or their ovaries can mature and remain in a mature state until the larvae hatch from the eggs, and then eggs are spawned again. But we need more careful researches for more accurate conclusions. For example, in *P. chaetop*terana, the reproductive season in one of studied localities lasts from May to September, or April–

October in the other, and November–April in the third studied locality; spawning activity in these crabs can be year-round in Florida [McDermott, 2005]. Seasonal spawning activity has been described in a number of other Pinnotheridae species: from February to mid-May in *P. tumida* [Takeda *et al.*, 1997], from May to September in *P. cylindrica* [McDermott, 1981], and from October to March with two spawning peaks in *P. patagoniensis* along the coast of southern Brazil [Alves, Pezzuto, 1998]. Seasonal spawning activity has also been described for *Zaops ostreus* (Say, 1817) [Sandoz, Hopkins, 1947; Beach, 1969], *Tumidotheres* (*Pinnotheres*) *maculatus* [Sastry, Menzel, 1962], *Pinnotheres novaezelandiae* Filhol, 1886 [Jones, 1977], *Pinnixa faba* and *P. littoralis* [Pearce, 1966a], *P. cylindrica* [McDermott, 1981], *P. valerii* [Vargas, 1987], *Fabia subquadrata* Dana, 1851 [Pearce, 1966b] and *Dissodactylus mellitae* [Bell, 1988].

The highest spawning activity in *P. chaetopterana* was observed from the beginning of the spawning season to its middle, after which no more than 36% of females were re-spawned [McDermott, 2005]. Moreover, many species of the family Pinnotheridae produce, as a rule, more than 1 clutch during the spawning season. For example, *P. cylindrica* — at least 2 clutches, *P. chaetopterana* — from 1 to 6 clutches [McDermott, 2005], whereas, according to our data, *P. banzu* and *P. rathbunae* are able to produce at least 2 clutches during the spawning season in Vostok Bay. The portioning of spawning in brachyuran crabs can be ensured by fertilizing of eggs with a reserve of sperm stored by female for some time after copulation, even for a long period. This was noted for *P. chaetopterana*, in which sperm was active for about 10 months in the seminal vesicles of females and they were possible to produce up to 5 egg clutches without repeated copulation [McDermott, 2005]. Females of *Rhithropanopeus harrisii* (Gould, 1841) (Panopeidae) can spawn up to 4 times during 5–9 months following after the copulation [Morgan *et al.*, 1983, 1988].

According to our data, the duration of spawning in *P. banzu* and *P. rathbunae* cannot be directly estimated. Some assumptions about the duration of spawning in *P. banzu* can be made by discussing a single gonadosomatic index (GSI) of one spawning, which was 9.2 and 11.8% in 2 pre-spawning females of *P. banzu*. Comparison with other brachyuran crabs showed that such GSI values are rather high or medium. For example, GSI in mature females of *L. perplexa* with a long, possibly, year-round spawning was 2.96–6.03% with the mean 4.28% [Sudnik, Poddueva, 2018]. In contrast, the mean GSI was about 8.5–9.6%, with maximum reaching 15.5%, in pre-spawning females of *Eriocheir japonica* (De Haan, 1835) (Varunidae) with strict breeding seasonality [Kalinina, Kolpakov, 2008]. There is also evidence of the contribution of females of brachyuran crabs to egg production, accounting for 3–21% in dry weight, with the mean about 11% [Hartnoll, 2006]. Smaller GSI (single spawning) of pre-spawning females in tropical species brachyuran crab can be associated with a long spawning season (possibly year-round), when each individual can spawn several times; they produce more clutches than species of temperate latitudes, and with small one-time reproductive outlays, their total annual reproduction outlays can reach 250% [Hartnoll, 2006]. Based on these discussion, we tentatively suggest the presence of seasonal spawning activity in *P. banzu*.

Conclusion

The studied symbiotic species of pea crab *Pinnixa rathbunae* and *P. banzu*, despite living in association with different hosts (*Urechis* and *Chaetopterus*), show a number of similar biological features. Among other representatives of the family Pinnotheridae, *P. rathbunae* and *P. banzu* have comparable reproductive features: having relatively tiny body sizes (CW 7.5–26 mm), among brachyuran crabs, pea crabs possess fecundity 1600–10 600 eggs with the small size (0.3–0.45 mm at the beginning of embryogenesis). However, taking into account the body size of pea crabs, the relative size of their eggs is not so small and they produce sufficiently developed planktonic zoea.

In both species, females are slightly dominant in number and slightly larger than males; they have common relationships between moulting and reproductive cycles, the seasonality of reproduction with the possibility of producing more than one clutch of eggs per a season. At the same time, *P. banzu* is distinguished by slightly larger body size, and as a consequence, relative slightly larger size of first maturity, larger fecundity, and larger egg size. The average values of morphometric parameters between the two species do not differ significantly, which indicates their close similarity. We suppose to revise the taxonomic status of both species using other methods, for example, molecular genetic analysis.

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References

Abello P. 1989. Reproduction and moulting in *Liocarcinus depurator* (Linnaeus, 1758) (Brachyura: Portunidae) in the North-western Mediterranean Sea // Scientia Marina. Vol.53. No.1. P.127–134.

Alves E.S., Pezzuto P.R. 1998. Population dynamics of *Pinnixa patagoniensis* Rathbun, 1918 (Brachyura: Pinnotheridae) a symbiotic crab of *Sergio mirim* (Thalassinidea: Callianassidae) in Cassino Beach, Southern Brazil // Marine Ecology. Vol.19. No.1. P.37–51. DOI: 10.1111/j.1439-0485.1998.tb00452.x

Ambariyanto A., Seed R. 1991. The infestation of *Mytilus edulis* Linnaeus by *Polydora ciliata* (Johnston) in the Conwy Estuary, North Wales // Journal of Molluscan Studies. Vol.57. No.4. P.413–424. DOI: 10.1093/mollus/57.4.413

Beach N.W. 1969. The oyster crab, *Pinnotheres ostreum* Say, in vicinity of Beaufort, North Carolina // Crustaceana. Vol.17. No.2. P.187–199.

Bell J.L. 1988. Distribution and abundance of *Dissodactylus mellitae* Rathbun (Pinnotheridae) on *Mellita quinquiesperforata* (Leske) (Echinodermata) // Journal of Experimental Marine Biology and Ecology. Vol.117. P.93–114. DOI: 10.1016/0022-0981(88)90220-1

Bell J.L., Stancyk S.E. 1983. Population dynamics and reproduction of *Dissodactylus mellitae* (Brachyura: Pinnotheridae) on its sand dollar host *Mellita quinquiesperforata* (Echinodermata) // Marine Ecology Progress Series. Vol.13. P.141–149. DOI: 10.3354/meps013141

Bierbaum R.M., Ferson S. 1986. Do symbiotic pea crabs decrease growth rate in mussels? // Biological Bulletin. Vol.170. P.51–61. DOI: 10.2307/1541380

Bhatia R.R., Nath V. 1931. Studies in the origin of yolk. VI. The crustacean oogenesis // Quarterly Journal of Microscopical Science. Vol.74. No.2. P.669–701.

Bülgün S., Samsun O. 2006. Fecundity and egg size of three shrimp species, *Crangon crangon, Palaemon adspersus* and *Palaemon elegans* (Crustacea: Decapoda: Caridea), off Sinop Peninsula (Turkey) in the Black Sea // Turkish Journal of Zoology. Vol.30. No.4. P.413–421.

Burukovsky R.N. 1992. [Technique of the biological analysis of some tropical and subtropical shrimps] // Promyslovo-biologicheskie issledovaniya morskih bespozvonochnyh. Moscow: Trudy “VNIRO”. P.77–84 [in Russian].

Burukovsky R.N., Marin I.N. 2018. The food composition of the symbiotic crab *Pinnixa rathbunae* Sakai, 1934 (Brachyura, Pinnotheridae) from burrows of the spoon worm *Urechis unicinctus* (von Drasche, 1881) (Echiurida, Urechidae) in Vostok Bay of the Sea of Japan // Arthropoda Selecta. Vol.27. No.4. P.319–324. DOI: 10.15298/arthsel.27.4.06

Charniaux-Cotton H. 1985. Vitellogenesis and its control in malacostracan crustaceans // American Zoology. Vol.25. P.197–206. DOI: 10.1093/icb/25.1.197

Christensen A.M., McDermott J.J. 1958. Life-history and biology of the oyster crab, *Pinnotheres ostreum* Say // Biological Bulletin. Vol.114. No.2. P.146–179.

Coelho P.A. 1997. Revisão do gênero *Pinnixa* White, 1846, no Brasil (Crustacea, Decapoda, Pinnotheridae) // Trabalhos Oceanográficos da Universidade Federal de Pernambuco. Vol.25. P.163–193.

Doi W., Masashi Y., Strüssmann C.A., Watanabe S. 2008. Growth and reproduction of the portunid crab *Charybdis bimaculata* (Decapoda: Brachyura) in Tokyo bay // Journal of crustacean biology. Vol.28. No.4. P.641–651. DOI: 10.1651/07-2964.1

George S.B., Boone S. 2003. The ectosymbiont crab *Dissodactylus mellitae* – sand dollar *Mellita isometra* relationship // Journal of Experimental Marine Biology and Ecology. Vol.294. P.235–255. DOI: 10.1016/S0022-0981(03)00271-5

Hartnoll R.G. 2006. Reproductive investment in Brachyura // Hydrobiologia. Vol.557. No.1. P.31–40. DOI: 10.1007/s10750-005-9305-6

Houghton D.R. 1963. The relationship between tidal level and the occurrence of *Pinnotheres pisum* (Pennant) in *Mytilus edulis* // Journal of Animal Ecology. Vol.32. P.253–257.

Ituarte R.B., Spivak E.D., Luppi T.A. 2004. The reproductive cycle of the Southwestern Atlantic estuarine crab *Chasmagnathus granulatus* (Brachyura: Grapsoidea: Varunidae) // Scientia marina. Vol.68. No.1. P.127–137.

Jones J.B. 1977. Post-planktonic stages of *Pinnotheres novaezelandiae* Filhol, 1886 (Brachyura: Pinnotheridae) // New Zealand Journal of Marine and Freshwater Research. Vol.11. P.145–158.

Kalinina M.V., Kolpakov N.V. 2008. [Features of the reproductive cycle of the Japanese mitten crab *Eriocheir japonica* in the rivers of Primorye] // Sovremennoe sostoyanie vodnykh bioresursov. Materialy nauchno-prakticheskoi konferentsii. Vladivostok. P.112–114 [in Russian].

Komai T., Nishi E., Taru M. 2014. A new species of *Pinnixa* (Crustacea: Decapoda: Brachyura: Pinnotheridae) associated with a tube worm, *Chaetopterus cautus* (Annelida: Polychaeta), from Tokyo Bay, Japan // Zootaxa. Vol.3793. No.1. P.119–132. DOI: 10.11646/zootaxa.3793.1.5

Kruczynski W.L. 1973. Distribution and abundance of *Pinnotheres maculatus* Say, in Bogue Sound, North Carolina // Biological Bulletin. Vol.145. No.3. P.482–491. DOI: 10.2307/1540632

Manning R.B., Felder D.L. 1989. The *Pinnixa cristata* complex in the Western Atlantic, with a description of two new species (Crustacea: Decapoda: Pinnotheridae) // Smithsonian Contributions to Zoology. No.473. 26 pp. DOI: 10.5479/si.00810282.473

Marin I.N. 2016. The species composition and ecological features of pea crabs of the genus *Pinnixa* White, 1846 (Brachyura: Pinnotheridae) in Peter the Great Bay, the Sea of Japan // Russian Journal of Marine Biology. Vol.42. No.2. P.139–145. DOI: 10.1134/S1063074016020061

Marin I. 2018. New records of holothurian-associated pea crab *Pinnixa tumida* Stimpson, 1858 (Crustacea: Decapoda: Pinnotheridae) from the Russian coastal waters of the Sea of Japan // Ukrainian Journal of Ecology. Vol.8. No.4. P.307–310.

Marin I.N., Kornienko E.S. 2014. [Decapoda of Vostok Bay of the Sea of Japan] // Biodiversity and Environment of Far East Reserves. No.2. P.50–72 [in Russian with English abstract].

McDermott J.J. 1981. Biology of the symbiotic crab *Pinnixa cylindrica* (Say) (Decapoda. Pinnotheridae) // Proceedings of the Pennsylvania Academy of Science. Vol.55. P.23–27.

McDermott J.J. 2005. Biology of the brachyuran crab *Pinnixa chaetopterana* Stimpson, 1860 (Decapoda: Pinnotheridae) symbiotic with tubicolous polychaetes along the Atlantic coast of the United States, with additional notes on other polychaete associations // Proceedings of the biological society of Washington. Vol.118. No.4. P.742–764. DOI: 10.2988/0006-324X(2005)118%5B742:BOTBCP%5D2.0.CO;2

McDermott J.J. 2009. Hypersymbioses in the pinnotherid crabs (Decapoda: Brachyura: Pinnotheridae): a review // Journal of Natural History. Vol.43. No.13–14. P.785–805. DOI: 10.1080/00222930802702480

Morgan S.G., Goy J.W., Costlow J.D. 1983. Multiple ovipositions from single matings in the mud crab *Rhithropanopeus harrisii* // Journal of Crustacean Biology. Vol.3. No.4. P.542–547. DOI: 10.2307/1547949

Morgan S.G., Goy J.W., Costlow J.D. 1988. Effect of density, sex ratio, and refractory period on spawning of the mud crab *Rhithropanopeus harrisii* in the laboratory // Journal of Crustacean Biology. Vol.8. No.2. P.245–249. DOI: 10.2307/1548316

Oh C.-W., Hartnoll R.G. 2004. Reproductive biology of the common shrimp *Crangon crangon* (Decapoda: Crangonidae) in the central Irish sea // Marine Biology. Vol.144. No.2. P.303–316. DOI: 10.2307/1548316

Palacios Theil E., Cuesta J.A., Felder D.L. 2016. Molecular evidence for non-monophyly of the pinnotheroid crabs (Crustacea: Brachyura: Pinnotheroidea), warranting taxonomic reappraisal // Invertebrate Systematics. Vol.30. No.1. P.1–27. DOI: 10.1071/is15023

Palacios Theil E., Felder D.L. 2020. Phylogeny of the genus *Pinnixa* White, 1846 (Crustacea, Brachyura, Pinnotheridae) and allies inferred from mitochondrial and nuclear molecular markers, with generic reassignment of twenty-one species // Zoosystema. Vol.42. No.6. P.85–103. DOI: 10.5252/zoosystema2020v42a6

Pearce J.B. 1966a. On *Pinnixa faba* and *Pinnixa littoralis* (Decapoda: Pinnotheridae) symbiotic with the clam, *Tresus capax* (Pelecypoda: Mactridae) // Barne H. (ed.). Some contemporary studies in marine science. London: Allen and Unwin Publ. P.565–589.

Pearce J.B. 1966b. The biology of the mussel crab, *Fabia subquadrata*, from the waters of the San Juan Archipelago, Washington // Pacific Science. Vol.20. No.1. P.3–35.

Poddueva E.A. 2017. [Determination of first maturity size of male crabs *Lyphira perplexa* Galil, 2009 (Crustacea: Malacostraca: Decapoda: Brachyura: Leucosiidae) of the Nha Trang Bay, Vietnam] // Dni nauki. Materialy nauchno-tekhnicheskoi konferentsii studentov i kursantov. Kaliningrad: FSBE HP “KSTU”. P.5 [in Russian].

Poddueva E.A. 2018. [Analysis of morphometry and first maturity size of males and females of crab *Lyphira perplexa* Galil, 2009 (Crustacea: Malacostraca: Decapoda: Brachyura: Leucosiidae) of the Nha Trang Bay, Vietnam] // Dni nauki. Materialy nauchno-tekhnicheskoi konferentsii studentov i kursantov. Kaliningrad: FSBE HP “KSTU”. P.132 [in Russian].

Rao C.N., Shakuntala K., Reddy S.R. 1981. Moult-reproduction relationship in the freshwater prawn *Macrobrachium lanchesteri* (de Man) // Proceedings of the Indian Academy of Sciences: Animal sciences. Vol.90. No.1. P.39–52.

Rodin V.E., Slizkin A.G., Myasoedov V.I. *et al*. (eds.) 1979. [Manual for Investigation of Decapoda of the Far-Eastern Seas]. Vladivostok: TINRO. 60 pp. [In Russian]

Sakai T. 1934. Species of the genus *Pinnixa* (Pinnotherid crab) found in the Far East // Science Reports of the Tokyo Bunrika Daigaku. Sect.B. Vol.2. No.29. P.37–43.

Santoz M., Hopkins S.H. 1947. Early life history of the oyster crab, *Pinnotheres ostreum* (Say) // Biological Bulletin. Woods Hole: Marine Biological Laboratory. Vol.93. P.250–258.

Sastry A.N., Menzel R.W. 1962. Influence of hosts on the behavior of the commensal crab *Pinnotheres maculatus* Say // Biological Bulletin. Woods Hole: Marine Biological Laboratory. Vol.123. P.388–395.

Scanland T.B., Hopkins T.S. 1978. A supplementary description of *Pinnixa tomentosa* and comparison with the geographically adjacent *Pinnixa tubicola* (Brachyura: Pinnotheridae) // Proceedings of the Biological Society of Washington. Vol.91. P.636–641.

Silas E.G., Alagarswami K. 1967. On the instance of parasitisation by the pea-crab (*Pinnotheres* sp.) on the backwater clam [*Meretrix casta* (Chemnitz)] from India, with a review of the work on the systematics. Ecology, and ethology of pea-crabs of the genus *Pinnotheres* Latreille, 1802 // Proceedings of the Symposium on Crustacea (Ernakulam, 12–15 January 1965). Symposium Series 2. Marine Biological Association of India. Part 3. P.1161–1227.

Stauber LA. 1945. *Pinnotheres ostreum*, parasitic on the American oyster, *Ostrea* (*Gryphaea*) *virginica* // Biological Bulletin. Vol.88. P.269–291.

Sudnik S.A. 2013. [On the relationship between molt cycles and reproduction in female shrimps (Crustacea. Decapoda. Natantia)] // Vodnye bioresursy, akvakul’tura i ekologiya vodoemov. Materialy nauchnoi konferentsii. Kaliningrad: FSBE HP “KSTU”. P.290–293 [in Russian].

Sudnik S.A., Poddueva E.A. 2019. [Biology of the crab *Lyphira perplexa* Galil, 2009 (Crustacea: Brachyura: Leucosiidae) in the South China Sea] // KSTU News. Scientific Journal. No.52. P.43–60 [in Russian].

Sudnik S.A., Falkenhaug T. 2014. The method of biological analysis for caridean shrimps (Decapoda: Natantia: Caridea) with emphasis on pelagic shrimps. The science and society in the conditions of globalization // Materialy Mezhdunarodnoi nauchno-prakticheskoi konferentsii (Ufa, 21–22 April, 2014). Ufa: RIO ICIPT. P.7–11.

Takeda S., Tamura S., Washio M. 1997. Relationship between the pea crab *Pinnixa tumida* and its endobenthic holothurian host *Paracaudina chilensis* // Marine Ecology Progress Series. Vol.149. P.143–154.

Telford M. 1978. Distribution of two species of *Dissodactylus* (Brachyura: Pinnotheridae) among their echinoid host populations in Barbados // Bulletin Marine Science. Vol.28. P.652–658.

Vargas J.A. 1987. The benthic community of an intertidal mud flat in the Gulf of Nicoya, Costa Rica. Description of the community // Revista de Biologia Tropical. Vol.35. P.299–316.

Vassilenko S.V. 1990. [On systematics and ecology of commensal crabs of the family Pinnotheridae (Crustacea: Decapoda: Brachyura) in the Sea of Okhotsk and northern Sea of Japan] // Sistematika i ekologiya bespozvonochnykh dal’nevostochnykh morei i estuariev. Trudy Zoologicheskogo Instituta AN SSSR. Vol.218. P.75–95 [in Russian].

Warner G.F. 1977. The biology of crabs. New York: Van Nostrand Reinhold Company. 202 pp.

Wells H.W., Wells M.J. 1961. Observations on *Pinnaxodes floridens*, a new species of pinnotherid crustacean commensal in holothurians // Bulletin Marine Science. Vol.11. P.267–279.

Zalota A.K. 2017. [Alien species of marine decapods. (Crustacea: Decapoda) in the Russian seas and adjacent waters]. Diss. kand. … biol. nauk. Moscow: IO RAN. 255 pp. [In Russian]

Zmarzly D.L. 1992. Taxonomic review of pea crabs in the genus Pinnixa (Decapoda: Brachyura: Pinnotheridae) occurring on the California shelf, with descriptions of two species // Journal of Crustacean Biology. Vol.12. No.4. P.677–713. DOI: 10.1163/193724092X00166

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