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Size composition, reproductive characteristics and food composition in crabs *Seulocia vittata* (Ortman, 1858) and *Lyphira perplexa* Galil, 2009 (Decapoda: Brachyura: Leucosiidae) from Nha Trang Bay (South Vietnam)

Размерный состав, репродуктивные характеристики и состав пищи крабов *Seulocia vittata* (Ortman, 1858) и *Lyphira perplexa* Galil, 2009 (Decapoda: Brachyura: Leucosiidae) из залива Нячанг (Южный Вьетнам)

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KEY WORDS: *Seulotia vittata*, *Lyphira perplexa*, Nha Trang Bay, sizes, reproductive biology, fecundity, oocytes, eggs, food composition, benthic predators.

КЛЮЧЕВЫЕ СЛОВА: *Seulotia vittata*, *Lyphira perplexa*, залив Нячанг, размеры, репродуктивная биология, плодовитость, ооциты, яйца, состав пищи, хищники-бентофаги.

ABSTRACT. Data on the size composition, reproductive parameters and food composition of two widespread Indo-Westpacific crabs from the family Leucosiidae (Crustacea: Decapoda: Brachiura) were described: *Seulotia vittata* (244 specimens, carapace length 29.5–43.3 mm and body weight 1.80–5.72 g) and *Lyphira perplexa* (318 specimens, respectively 26.7–40.9 mm and 1.50–6.42 g). Crabs were collected in Nha Trang Bay (South Vietnam) in February 2007. They were found on sandy and silty bottom of the sublittoral at depths from 7 to 85 m. Juveniles were not found; the sex ratio (male to female) was close to one to one in *S. vittata* and 1.7 : 1 in *L. perplexa*. Both among males and females of both species were predominated specimens with similar carapace width (CW, near 18–22 mm). The size at first maturity of males was 19–20 mm CW in *S. vittata* and 21–24 mm CW in *L. perplexa*; in both species females this trait could not be determined: all of them were maturing or ripe.

The main reproductive features of both species in Nha Trang Bay were quite similar. February was the time of their active spawning: egg-bearing specimens predominated; there were up to 40–55% of almost mature and pre-spawning females many. In *S. vittata*, fecundity was up to 3014 eggs with size of newly laid eggs 0.220 ± 0.01 × 0.245 ± 0.02 mm; in *L. perplexa* — 3282 eggs with size 0.230 ± 0.01 × 0.259 ± 0.02 mm; egg volume was 0.005–0.006 mm^3. In females of both species, there is a possibility of repeated spawning event in given reproductive period. Slightly larger fecundity and larger egg size in *L. perplexa* may contribute to its more successful reproduction in Nha Trang Bay, active dispersal and some numerical dominance.

Judging by the contents of the stomachs, both species can be tentatively attributed to predator-gatherers or even attacking predators. In both species, decapod crustaceans play a significant role in food: in *S. vittata* these were peneid shrimps and Stomatopoda, i.e. bury and burrowing animals, and in *L. perplexa* — some kind of crab (possibly epibenthic). In *S. vittata*, bivalves (mainly infauna representatives) were present among the eaten mollusks, and in *L. perplexa*, epibenthous gastropods, as well as plant remains. At this level of knowledge of the composition of the food of these two species, it can be assumed that both of them are predators-benthophages that do not neglect necrophagy, but *S. vittata* is also a detritophagus that feeds mainly on infauna, and *L. perplexa* is rather an epibentophagus. Due to these crabs probably do not compete with each other.

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РЕЗЮМЕ. Описаны размерный состав, репродуктивные параметры и состав пищи двух широко распространенных индо-западнотихоокеанских крабов из семейства Leucosiidae (Crustacea: Decapoda: Brachiura): *Seulotia vittata* (244 особи, длина карапакса 29,5–43,3 мм, масса тела 1,80–5,72 г) и *Lyphira perplexa* (318 особей, соответственно 26,7–40,9 мм и 1,50–6,42 г). Крабы собраны в бухте Нячанг (Южный Вьетнам) в феврале 2007 года. Они обитают на песчаных и илистых грунтах сублиторали на глубинах от 7 до 85 м. Ювенильные особи не обнаружены, соотношение полов (самцы / самки) было близко к 1 : 1 у *S. vittata* и 1,7 : 1 у *L. perplexa*. Как среди самцов, так и среди самок обоих видов преобладали особи со сходной шириной карапакса (ШК, около 18–22 мм). Размер первого полового созревания самцов состав-

лял 19–20 мм ШК у *S. vittata* и 21–24 мм ШК у *L. perplexa*; у самок обоих видов его определить не удалось: все они были созревающими ими зрелыми. Основные репродуктивные черты обоих видов в заливе Нячанг были достаточно сходными. Февраль — время активного нереста: преобладали яйценосные особи, среди которых было до 40–55% практически зрелых и преднерестовых самок. У *S. vittata* плодовитость достигала 3014 яиц при размере отложенных яиц 0,220 ± 0,01 × 0,245 ± 0,02 мм; у *L. perplexa* — 3282 яиц размером 0,230 ± 0,01 × 0,259 ± 0,02 мм; объем яиц составлял 0,005–0,006 мм^3. У самок обоих видов существует вероятность повторного нереста в данный репродуктивный период. Несколько большая плодовитость и больший размер яиц у *L. perplexa* могут способствовать более успешному размножению вида в заливе Нячанг, активному расселению и некоторому численному доминированию.

Судя по содержимому желудков, оба вида можно предварительно отнести к хищникам-собирателям или даже нападающим хищникам. У обоих видов значительную роль в питании играют десятиногие ракообразные: у *S. vittata* это были пенеидные креветки и Stomatopoda, т.е. зарывающиеся и норные животные, а у *L. perplexa* — какой-то краб (возможно, эпибентосный). У *S. vittata* среди съеденных моллюсков присутствовали двустворчатые (преимущественно инфауна), а у *L. perplexa* — эпибентосные брюхоногие, а также растительные остатки. На данном уровне изученности состава пищи этих двух видов можно предположить, что оба они хищники-бентофаги, не пренебрегающие некрофагией, но *S. vittata* к тому же детритофаг, питающийся преимущественно инфауной, а *L. perplexa*, скорее, — эпибентофаг. Благодаря этому крабы, вероятно, не конкурируют друг с другом.

Introduction

Biology of crab family Leucosiidae is actually not studied. In the literature there are literally single works devoted to one or another of biology aspects in several species. In addition, the taxonomic status of the family was finally established quite recently, thanks to a series of works performed by B. Galil in 2001–2009 as part of the revision of this family. Both species, which served as the objects of our research, were studied by her to one degree or another.

The first studied species *Lyphira perplexa* Galil, 2009 appeared in the process of re-examination of the genus *Phylira* Leach, 1817 [Galil, 2009]. From this genus there were created seven new genera, including the species *P. heterograna* Ortmann, 1892 transformed into the genus *Lyphira* with three new species. Due to this, information about all species of the genus, including *L. perplexa*, turned out to be limited only by the materials of the collections that were examined by the author of the revision [Galil, 2009], i.e., the description of specimens belonging to this genus stored in the museum collections.

The second species *Seulocia vittata* (Ortman, 1858) has a longer history. It was described in the second half of the 19th century and it belonged to the genus *Leucosia* Weber, 1795. During the above-mentioned revision of the family Leucosiidae, this species, along with a number of others, was separated from the genus *Leucosia* into the newly created genus *Seulocia* [Galil, 2005].

In the Nha Trang Bay, South Vietnam, where materials for our work were collected, both crabs serve as an object of stable artisanal fishery. Despite the fact that both species are not rare, the first data on their biology were obtained only recently [Poddueva, 2018; Sudnik, Poddueva, 2018, 2019, 2021]. The composition of food has been studied previously only in *L. perplexa* [Burukovsky, 2019].

The aim of this work is to compare some biological characteristics in *S. vittata* and *L. perplexa*. The study was carried out within the framework of the international project of the A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow and the Russian–Vietnamese Scientific and Technical Tropical Center (Nha Trang, Vietnam) “Analysis of the species and functional structure of associations of mangrove crabs (Brachyura) in some bays of the South China Sea”.

Material and Methods

The studied crabs were purchased by I.N. Marin, a researcher at the Institute of Problems of Evolution and Ecology of the Russian Academy of Sciences, at the local fish market in the mouth of the Be River near the city of Nha Trang (Vietnam) in February 2007. Crabs were fixed with 70% ethanol.

The number of studied crabs was following: *L. perplexa* — 318, and *S. vittate* — 244 specimens. For study the composition of the food in *L. perplexa* was used 214 specimens of which 59 ones had food in their stomachs, and only in 5 specimens had full stomachs, and in *S. vittate* — 188 specimens, of which 55 had food remains, and 8 stomachs were full. This number of material exceeds the sufficiency criterion (30 stomachs), which guarantees that at least 80% of food objects diversity that will be found in them [Cartes, Sarda, 1989].

The method of crab laboratory biological analysis [Rodin *et al*., 1979; Burukovsky, 1992; Sudnik, Falkenhaug, 2014; Sudnik, Poddueva, 2019, 2021] included: determination of the individual weight, body size (total body length (**TL**, length from the posterior edge of the eye orbits to the posterior edge of the telson), width (**CW**) and length of the carapace (**CL**, length from the posterior edge of the eye orbits to the posterior edge of the carapace), sex, the stage of maturity of the gonads (for ovaries — on a six stages scale: stage I — non-developing; stage II — in the beginning of development without signs of maturation; stage III — in the beginning of maturation; stage IV — in the middle of maturation; stage V — ripe; stage VI–II — post-spawning); for testes (performed for *S. vittata*) — on a three stages scale (stage I — in the beginning of development; stage II — in the middle of development; stage III — full developed); in egg-bearing females: single-time realized fecundity (direct counting of the number of embryos), the stage of embryo development used a five stages scale; the size of mature oocytes in ovaries, the eggs size were estimated (large and small diameters in 10 oocytes or eggs, with an accuracy of 0.01 mm, average values were calculated) and egg volume. A technique from Microsoft office package was used for statistical processing.

The study of the composition of food was carried out according to the method [Burukovsky, 2017, 2022]. After opening the stomach, the degree of its filling was first determined on a 4-point scale: 0 — the stomach is empty; 1 — food occupies

less than half of the volume of the stomach; 2 — food occupies about half (from 1/3 to 2/3) of the volume of the stomach; 3 — the stomach is full. The food lump was then placed in a drop of water in a Petri dish. Identification of the taxonomic affiliation of the victims by their remains, as a rule, was carried out up to the level of a class or order (for example, Gastropoda, Bivalvia, Polychaeta, Amphipoda, etc.).

The components of the food lump that could be counted and measured were recalculated and measured with an accuracy of 0.01 mm using the ruler of the eyepiece micrometer of the binocular microscope MBS-10. Regardless of their filling, the composition of the contents of the stomachs was identified in all stomachs with food. In full stomachs, the volume of individual components of the food lump was determined visually with an accuracy of up to 10% of the volume of the entire food lump. The food and inedible components of the food lump, which make up less than 10% of the volume of the food lump of a full stomach, were simply listed. Then the frequency of occurrence was calculated (the percentage of the occurrence of this component of food from the total number of studied stomachs with food) and the Froerman coefficient was calculated. It represents the average number of food objects in the stomach, excluding sand and other inedible components of the food lump [Burukovsky, 2022]. To do this, all the frequencies of occurrence of food objects were sum up, and divide the resulting amount by 100. According to the data obtained during the analysis of full stomachs, the reconstructed average (virtual) food lump was calculated, that is, the average share of each component of the food lump in its volume, expressed as a percentage [Burukovsky, 2022]. The name "components of the food lump" refers to the totality of all objects encountered in the possessed stomach including sand etc., as opposed to "food objects", that is, the part of it that is used as food.

The characterization of the contents of the stomachs is carried out in three steps. (1) A description of the residues themselves. This allows us to assess the features of the crab habitat, the way it consumes food and their state. (2) Determination of the frequency of occurrence (**FO**) of each component of the food lump in all stomachs with food, regardless of its amount in them. (3) Calculation of volume ratios of food components in full stomachs and reconstruction of the average virtual food lump (**VFL**). This allows you to really assess the role of each food object in the crab's feeding.

The results obtained at each stage of the description of the composition of food in the studied object complement each other. Separately, they give a preliminary and "planar" idea on the feeding of the studied object. For example, the frequency of occurrence of foraminifera in some species can reach 60–70%, but their share in the volume of a virtual food lump usually does not exceed 0.1–0.2%. This means that foraminifera, no matter how often they occur, enter the stomach in negligible quantities, and they cannot play any important role in the diet of given species. There is a certain behavioral aspect in assessing the relationship between the crab and its food objects, in this case foraminifera. For example, when analyzing ontogenetic changes in the frequency of occurrence and the ratio of components of a virtual food lump, the frequency of occurrence of a victim with a change in the size of crabs may decrease, and its share in the virtual food lump may increase. Consequently, the crab feeds on this victim less often, but in greater numbers [Burukovsky, 2017, 2022].

Results

Seulocia vittata

SIZE COMPOSITION AND REPRODUCTIVE TRAITS. The sex ratio of crabs in the sample was close to one to one (56% of males and 44% of females); juveniles were not found. In general, the TL of crabs was 38.4 ± 2.1 (29.5–43.3) mm. The values of the three size characteristics of females and males are presented in Table 1. There were no significant differences in the average CW of males and females (t stat. = 0.54, t crit. = 1.97, p = 0.05) (Table 1). Both among males and females were predominated specimens with CW 18–21 mm (87% and 82%, respectively); the share of smaller specimens of both sexes did not exceed 6–7%, and the share of specimens larger than 21 mm in males was 6%, in females — 12%. The average body weight was 3.77 ± 0.83 (1.80–5.72) g, the weight of females on average slightly exceeded that of males (3.90 ± 0.70 and 3.65 ± 0.98 g, respectively, t stat. = 2.77, t crit. = 1.97, p = 0.05).

Among males predominated (53%) large specimens (CW 19.7–21.7 mm) with well-developed testes, who reached maturity (stage of maturity 3), which was confirmed by morphometric data [Sudnik, Poddueva, 2021]. Slightly less (40%) were smaller males (CW 18.1–19.6 mm) with testes at the stage of maturity 2. Males with less developed testes (stage 1) were rare (7%), their CW was the smallest (17.2–18.0 mm). The size at maturity of males was 19–20 mm CW; in females from this material it cannot be determined: all of them were maturing or ripe, individuals with CW less than 16 mm are needed.

Egg-bearing specimens prevailed among females (6:1), most of which (CW 16.3–22.1 mm), having maturing ovaries, carried embryos at stages of development from 1 to 3. Females with gonads at the beginning of matura-

Table 1. Sizes, body mass of crabs *Seulocia vittata* and *Lyphira perplexa* in Nha Trang Bay.
Таблица 1. Размеры, масса тела крабов *Seulocia vittata* и *Lyphira perplexa* в заливе Нячанг.

Sizes, body mass of crabs	***Seulocia vittata***		***Lyphira perplexa***	
	♂♂	♀♀	♂♂	♀♀
TL, mm	37.9 ± 1.8 (32.3–42.9)	39.0 ± 2.4 (29.5–43.3)	34.6 ± 3.2 (26.7–40.9)	33.0 ± 1.8 (27.5–37.9)
CW, mm	19.6 ± 0.97 (17.2–21.7)	19.7 ± 1.08 (16.3–22.1)	20.7 ± 1.64 (15.2–25.0)	18.4 ± 0.94 (16.0–22.5)
CL, mm	22.7 ± 1.06 (19.1–24.9)	22.4 ± 1.33 (16.7–25.1)	21.2 ± 1.84 (16.0–25.1)	18.6 ± 1.03 (16.0–22.6)
Body mass, g	3.65 ± 0.90 (1.94–5.74)	3.93 ± 0.70 (1.8–5.54)	4.10 ± 0.86 (1.50–5.92)	2.68 ± 0.48 (1.67–5.09)

Table 2. Carapace width, egg size and fecundity at different stages of embryogenesis in *Seulocia vittata* and *Lyphira perplexa* in Nha Trang Bay.
Таблица 2. Ширина карапакса, размер яиц и плодовитость на разных стадиях эмбриогенеза у *Seulocia vittata* и *Lyphira perplexa* в заливе Нячанг.

Stages of embryogenesis	*Seulocia vittata*			*Lyphira perplexa*		
	carapace width, mm	fecundity	egg volume, mm^3	carapace width, mm	fecundity	egg volume, mm^3
1	19.0 ± 0.76 (16.3–19.8)	2181 ± 252 (1715–2754)	0.005 ± 0.001 (0.003–0.007)	18.5 ± 0.94 (16.2–20.9)	2903 ± 178 (2525–3208)	0.007 ± 0.002 (0.003–0.011)
2	19.8 ± 0.91 (17.9–21.3)	2334 ± 381 (1513–3157)	0.008 ± 0.001 (0.007–0.011)	18.3 ± 1.00 (16.8–20.0)	2967 ± 116 (2690–3200)	0.014 ± 0.001 (0.011–0.016)
3	19.8 ± 1.26 (17.3–22.1)	2348 ± 360 (1769–3023)	0.010 ± 0.001 (0.007–0.011)	18.1 ± 0.92 (16.0–19.8)	2863 ± 246 (2289–3282)	0.018 ± 0.009 (0.005–0.059)

Table 3. Sizes of mature oocytes in *Seulocia vittata* and *Lyphira perplexa* in Nha Trang Bay.
Таблица 3. Размеры зрелых ооцитов у *Seulocia vittata* и *Lyphira perplexa* в заливе Нячанг.

Seulocia vittata			*Lyphira perplexa*		
carapace width, mm	sizes of mature oocytes, mm		carapace width, mm	sizes of mature oocytes, mm	
	large diameter	small diameter		large diameter	small diameter
19.7 ± 1.04 (17.3–22.1)	0.245 ± 0.020 (0.225–0.253)	0.220 ± 0.010 (0.210–0.250)	18.3 ± 1.00 (16.5–20.3)	0.263 ± 0.020 (0.260–0.287)	0.230 ± 0.010 (0.215–0.256)

tion (stage III, 36 spec., CW 19.6 ± 1.07 (16.3–21.3 mm)) had embryos at one of the first three stages of development, but more often at stage 1 (58%) or stage 2 (39%). Females with ovaries in the middle of maturation (stage IV, 34 spec., CW 19.7 ± 0.98 (17.5–21.3 mm)) carried embryos at stages of development 2 or 3. In females with mature ovaries (stage V, 21 spec., CW 19.6 ± 1.32 (17.3–22.1 mm)), embryos were developed before the middle of embryogenesis (stage 3). One female with undeveloped ovaries (stage I–II) had just laid eggs. Consequently, the processes of embryos development in clutches and gonad maturation proceeded quite synchronously ("continuous cycle of reproduction": Burukovsky, 2010: 678).

Half of females (51%), carrying embryos in the first half of development, had pre-mature and mature ovaries, which indicates the possibility of their repeated spawning this year.

The fecundity values reached 3157 eggs (Table 2). The volume of eggs from the first to the third stage of embryogenesis significantly increased by 2 times (t stat. = 16.5, t crit. = 2.02, p = 0.05) (Table 2). Females carrying embryos at the stage of development 3 showed slightly greater fecundity than ones that had just laid eggs (Table 2; t stat. = 2.11, t crit. = 2.00, p = 0.05), which may be due to the larger size of females of the first group (t stat. = 3.30, t crit. = 2.00, p = 0.05).

Females without eggs were rare, half of them (7 spec., CW 19.8 ± 1.04 (18.4–21.2) mm) had maturing and mature gonads, the rest, with similar sizes (8 spec., CW 20.3 ± 1.03 (18.9–21.4) mm), were post-spawning.

The large and small diameter of mature oocytes in the ovaries of pre-spawning females was 0.245 ± 0.02 and 0.220 ± 0.01 mm (Table 3).

FILLING THE STOMACHS. Most crabs (71%) had empty stomachs. Among those that had at least traces of food in their stomachs, specimens with a stomach filling of 1 point (21%) prevailed, and only 4% of crabs had full stomachs (Fig. 1).

GENERAL CHARACTERISTICS OF STOMACH CONTENTS. The composition of food lumps included both inorganic components (grains of sand) and organic detritus (a complicated complex of dead organic matter suspended in the water column in the form of particles of

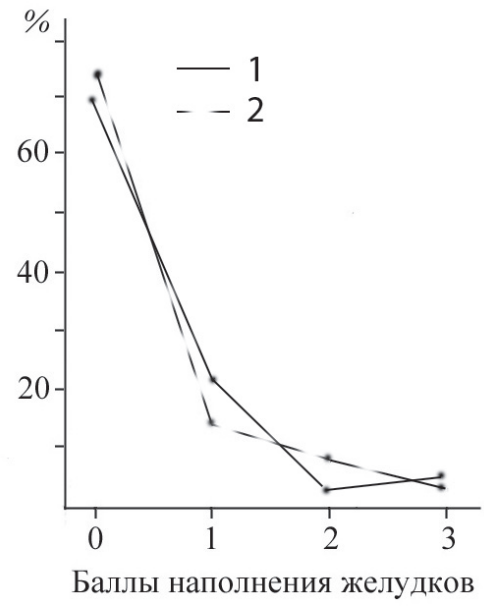

Fig. 1. Feeding intensity of crabs *Seulotia vittata* (1) and *Lyphira perplexa* (2) in Nha Trang Bay (0–3 — score values of gastric filling).
Рис. 1. Интенсивность питания крабов *Seulotia vittata* (1) и *Lyphira perplexa* (2) в заливе Нячанг (0–3 — значения баллов наполнения желудков).

Table 4. Comparative characteristics of food composition in *Seulocia vittata* and *Lyphira perplexa* in Nha Trang Bay.
Таблица 4. Сравнительная характеристика состава пищи у *Seulocia vittata и Lyphira perplexa* в заливе Нячанг.

Food composition	Frequency, %		Reconstructed average (virtual) food lump, %	
	S.vittata	***L. perplexa***	***S. vittata***	***L. perplexa***
detritus	16. 4	13.6	15.0	–
fish	14.5	20.3	26.2	32.0
decapods	9.1	18.7	33.8	20.0
stomatopods	3.6	–	25.0	–
other malacostracans	3.6	3.4	–	–
molluscs, total	5.4	18.7	–	40.0
bivalves	5.4	–	–	5.4
gastropoda	–	18.7	–	18.7
polychaetes	3.6	–	–	–
eggs	1.8	8.5	–	8.0
insect	–	1.7	–	–
ostracoda	–	1.7	–	–
ophiura	–	8.5	–	–
plant remains	–	5.1	–	–
unindefied remains	23.6	18.6	–	–
“something fibrous”	49.1	59.3	–	–
grains of sand	12.7	6.8	–	–
substrate	–	6.8	–	–
Froermann coefficient	1.07	1.10		

various sizes or deposited on the bottom, and microorganisms living on it [Burukovsky, 2022]), undefined residues and food objects that were identifiable.

Grains of sand were found, as a rule, singly or in small quantities. Only once in the stomach with a filling of 1 point there were more than a dozen of sand granes. The sizes of the sand grains did not exceed 0.07 mm, i.e. they are large siltstones, a sedimentary rock intermediate between sand and silt [Petelin, 1967]. Small siltstones were not found. Once a fragment of carbonate composition (0.07 mm) was found, as well as, an opaque flat particle with a diameter of 0.2 mm.

The organic components of a food lump can be divided into three groups. The first group includes fragments of chitin, which cannot be identified, and semicircular tubes with a cross-section of 0.3 mm and a length of 1.2 mm. Similar tubes are inhabited by amphipods from the family Corophiidae [Burukovsky, 2010]. They were found in small numbers. The second group includes a loose mass resembling a half-decomposed or half-digested pulp. This mass sometimes included fragments of the bristles of errant polychaetes (acicles) or small fragments of fish bones. They are found in small numbers. The third group of indeterminate residues is a coarse-fibrous, elastic and dense substance of light gray or dark gray color. It was found either in empty or almost empty stomachs, usually in the posterior part of the cardiac stomach, adjacent directly to the entrance to the pyloric appendage. More often than not, there was nothing in those stomachs but it. We do not refer it to food objects. In order not to overload Table 4, which contains information about the composition of food in the stomachs of crabs, we conditionally called it “fibrous substance”.

Food objects included detritus, fish remains, decapod crustaceans and juvenile mantis crayfish (order Stomatopoda). Detritus is a loose substance. In a drop of water, it disintegrated into characteristic flakes. As a rule, it was found in small quantities, but in one case it filled 90% of the volume of a full stomach. The remains of the fish were usually represented by small fragments of bones from 0.15–0.2 to 5 mm length and 0.15 mm thick. Once, an eye lens with a diameter of 1.2 mm was encountered. The bones were always in varying degrees of destruction, unlike what we observed in the study of shrimp food [Burukovsky, 2022]. In one of the full stomachs, against the general background of the half-digested contents, a large number of very small irritating and black fragments were observed. Our experience suggests that these are most likely fragments of fish scales and (or) the lining of their body cavities; perhaps they are the remains of dead fish.

Shrimp were found in four stomachs. In two of them, half-empty, they could hardly be identified by clear characteristic details of the exoskeleton. In the third, complete, they accounted for 80% of the volume of the food lump. According to the branched structure of the gills, it was possible to recognize a shrimp from the suborder Dendrobranchiata and, most likely, from the family Penaeidae. In the other stomach, the undoubted fragments of the shrimp could not be identified even to suborder level. Of the other crustaceans, the remains of a crab were encountered once. They occupied 80% of the volume of a full stomach, but were so badly destroyed that belonging to the Brachyura infra-order could be established only by the characteristic structure of the third maxillipeds and mandibles. Of the other crustaceans, characteristic Stomatopoda remains were found in two full stomachs, and

some higher cancers were found in two more stomachs, but they could not be determined more precisely. In addition, remains of polychaetes were found in two stomachs in the form of fragments of acicles and bundles of other types of 0.75 mm length bristles belonging to errant polychaetes, possibly from the families Onuphiidae or Eunicidae. Small fragments of bivalve shells were found three times, and four spherical eggs with a diameter of 0.4 mm, probably a harpacticid copepod, were found in one almost empty stomach.

FREQUENCY OF OCCURRENCE OF FOOD OBJECTS, THEIR SHARE IN THE VIRTUAL FOOD LUMP. The frequency of occurrence was dominated by "fibrous substance" (FO 49.1%), indeterminate remains (23.6%), detritus (16.4%), fish (14.5%), grains of sand (12.7%) and decapod crustaceans (9.1%), that is, non-food objects prevailed (Table 4). The Froerman coefficient turned out to be equal to 1.07. There were only five food objects in the virtual food lump. All its other components were found in literally negligible quantities. Among these dominant by share in full stomachs were: fish (26.2%), stomatopods (25.0%), shrimp (23.8%), detritus (15%) and crabs (10%).

Lyphira perplexa

SIZE COMPOSITION AND REPRODUCTIVE TRAITS. The number of males in the sample exceeded that of females (63 and 37%, respectively); juveniles were not found. The values of the three-dimensional characteristics of females and males are presented in Table 1. In general, the TL of crabs was 34.0 ± 2.84 (26.7–40.9) mm. The average CW of males was significantly slightly larger than that of females (t stat. = 14.26, t crit. = 1.97, p = 0.05). Males with a CW of 18–22 mm (72%) and females with a CW of 18–19 mm (51%) prevailed. The share of smaller specimens in females was greater (37% compared to 5% in males), but the share of larger specimens in males and females were similar (23 and 26%). The body weight was 3.26 ± 0.97 (1.50–5.92) g. The average weight of males exceeded that of females by 1.5 times (t stat. = 13.7, t crit. = 1.98, p = 0.05), which corresponded to their larger sizes (Table 1). The size at maturity of males was 21–24 mm CW; in females it couldn't be determined: all of them were maturing or ripe, individuals with CW less than 16 mm are needed.

The number of egg-bearing females was almost 4.5 times more than females without eggs. The sizes of the females of these two groups were similar (16.0–20.9, 16.5–22.5 mm).

Among the females without eggs, maturing and pre-spawning specimens (stages IV–V, CW of 18.5 ± 1.1 (16.5–22.5) mm dominated (91%), the rest (2 spec., CW 18.0 and 18.8 mm), were post-spawning with undeveloped ovaries (stage VI-II). The large and small diameter of mature oocytes in the ovaries of pre-spawning females was 0.263 ± 0.020 and 0.230±0.010 mm (Table 3).

More than half of the egg-bearing females (57%, CW of 18.3 ± 1.05 (16.0–20.5) mm), having maturing gonads (stages III–IV), carried embryos at the initial and middle stages of development. The rest females with similar size (CW of 18.5 ± 0.98 (16.2–20.9) mm) with undeveloped ovaries (stage VI-II) carried recently laid eggs. There was an expressed synchronization of the processes of embryogenesis and ovarian maturation, i.e. a continuous cycle of reproduction, as in the previous species.

The fecundity value in studied 97 females reached 3282 eggs (Table 2). The volume of eggs from the first to the third stage of embryogenesis significantly increased by 2.5 times (t stat. = 4.34, t crit. = 2.07, p = 0.05) (Table. 2), egg losses were not detected during this period (t stat. = 0.69, t crit. = 2.03, p = 0.05). The reproductive state of a relatively large group of females (38% of all females of the sample) indicated the possibility of re-spawning this year: they bearing embryos at the beginning and middle of development, had maturing, pre-mature and mature ovaries, preparing for the next spawning event.

FILLING THE STOMACHS. Two-thirds of the crabs (75%) had empty stomachs. Among other, specimens with traces of food in their stomachs predominated – 15%, and stomachs filled with half their volume was in 8%, and only five specimens (2%) had full stomachs (Fig. 1).

GENERAL CHARACTERISTICS OF STOMACH CONTENTS. We have divided the components of the food lump into the following groups: grains of sand, soil, detritus, "fibrous substance", remains of plant origin, unidentified remains of animal origin, and, finally, the remains of animals whose taxonomic status can be determined at least to a class or order.

The grains of sand were found 4 times only (FO of 7.4%) as part of detritus and only in single quantities. The sizes of the grains of sand are 0.05–0.07 mm and one grain of sand is 0.7 mm. Fine grains of sand on the Petelin granulometric scale belong to large siltstones.

By bottom soil (or substrate) means the mineral component of a food lump of the smallest size (but do not refer to grains of sand as "soil"). Previously, "clean" soil was rarely found in the stomachs of the decapod crustaceans (mainly in shrimp) studied in our study [Burukovsky, 2022]. It is well distinguishable from detritus and its specific gravity is probably greater. This is revealed because the soil quickly settles to the bottom of the Petri dish, while detritus is suspended in water above the bottom of the Petri dish and still has a flake-like consistency. In fact, "soil" is found in almost every stomach of benthophages, but in negligible quantities. Because of this, we usually left it out of the used data, not taking into account together with other components of the food lump. In *L. perplexa*, the soil has a dark gray color and inclusions of carbonate composition. It was caught in three stomachs with a FO of 6.8%.

Detritus was found in 8 half-empty stomachs with a FO of 13.6%. It had an almost black color and a loose consistency. It always contained skeletal remains of food objects (see below).

In addition to bottom soil and detritus, in all stomachs that had a stomach filling score of 1 ("traces of food"), only "something fibrous" was found, which we called a fibrous substance (see above). It was a homogeneous and relatively viscous mass, having a grayish-brown

color in the incident light. As a rule, there were no other components of the food lump in the stomach besides it. It was located ventrally in the posterior part of the cardiac part of the stomach, near the cardio-pyloric valve. It is possible that these were remnants from food objects of the previous act of feeding that did not have time to enter the pyloric division of the stomach. This component of the food lump was found in 35 stomachs (FO of 59.3%).

The remains of plant origin were found three times. Once (FO of 1.7%) in the form of a very small piece of fiber belonging to some representative of higher plants. Twice more (FO of 3.4%) tangles of threads similar to dead rhizomes of anfel algae were found.

Unidentified animal remains can be divided into two groups. The first group includes shapeless fragments of chitin. Among them there are very thin films and relatively thick shapeless pieces belonging, apparently, to some crustaceans. This is also hinted at by the coincidence of the frequency of their occurrence and the remains of crustaceans that can be identified at least up to the order (FO of 18.6%, and see below). The second group includes spindle-shaped objects and rich brown color in a passing beam of light. At first glance, they resemble dinoflagellates. In their most expanded place there is a transverse groove. However, one side of them is convex, and the other is slightly concave. In addition, they are much larger than dinoflagellates: their length varies from 0.23 to 1.6 mm, most often 0.8 mm or more. Usually they were caught singly, but in individual stomachs their number reached 6 specimens.

Fish, crustaceans, primarily decapods, and mollusks stand out among the food objects. The first is represented by finely chopped bones. Only once was found a vertebra with a length of 0.5 mm and an eye lens with a diameter of 1.3 mm. One of the stomachs was completely filled with a pulp of soft tissues, crushed bones, among which were several cycloid fish scales 1.5 mm length.

Decapod crustaceans were represented by scraps of limbs and a cephalothorax. Among them, penaeid shrimps, well identified by the gills of dendrobranchia. There were also trichobranchia, which are found in various groups of decapods, including small lobsters (Scyllaridae), hermit crabs, etc. Crab pleopods were also encountered. The size of the food remains could not be measured. According to the state of the remains, it is impossible to determine whether these victims were eaten alive or not.

From other crustaceans, thoracopoda of amphipods and a whole ostracoda with a length of 1 mm were found once. Of the other arthropods, a fragment of the anterior part of the insect's body was found in one of the stomachs. Judging by this fragment, the length of the whole victim should have been 5–6 mm. Apparently, a dead individual that got into the water was eaten.

Mollusks in the stomachs of *L. perplexa* were represented by gastropods, judging by shell fragments belonging to the one species. In cases where it was possible to approximately reconstruct the shape and size from the fragments, these were shells of very thin-walled mollusks of approximately spherical shape with a size of about 1.5 mm. Twice, the stomachs were filled with fragments of mollusk soft tissues. A comparison of the shape of the fragments, their thinness, and the shape of the fragments of soft tissues, allows us to assume that the victims of the crab were young mollusk *Hydatina physis* (L. 1758). In addition, the smallest fragments of mother-of-pearl, enclosed in detritus, were encountered. It was impossible to find out which group of mollusks they belonged to. Finally, individual spherical eggs, fragments of clutches, as well as eggshells were found in the stomachs. Perhaps they were the eggs of some small gastropods. In addition, typical skeletal elements of the arms of ophiura and very small foraminifera (0.07–0.2 mm) were found singly.

THE FREQUENCY OF OCCURRENCE AND THE PROPORTION OF FOOD OBJECTS IN THE VIRTUAL FOOD LUMP (Table 4). According to the frequency of occurrence in the stomachs of *L. perplexa*, "something fibrous" completely dominates (FO of 59.3%). This almost corresponds to the proportion of stomachs with a filling score of 1. As a rule, apart from this mass, there was nothing in the stomachs. Fish (FO of 20.3%), decapod crustaceans (FO of 18.6%) and mollusks (FO of 18.6%) are found with approximately the same frequency among food objects. They are accompanied by detritus (FO of 13.6%), which is most likely the result of "sloppy feeding". Other food items can probably be attributed to sporadic and accidental victims.

The virtual food lump is formed by the three most common food objects: mollusks (40%), fish (32%) and decapod crustaceans (20%). The role of mollusks in nutrition will increase even more if the eggs found in the stomachs of *L. perplexa* really belong to mollusks.

Discussion

As mentioned above, *S. vittata*, as member of the genus *Leucosia*, has been known since the late 19th century, and *L. perplexa* is a relatively "young" species [Galil, 2005, 2009]. Faunistic information about *S. vittata* finds is available from the waters of Mauritius, India — from the Malabar coast to the Bay of Bengal, Thailand, Malaysia, Singapore, China (including Hong Kong), Indonesia (Java, Surabaya), the Philippines (Sulu Sea and Berhala Strait). This species was found at depths of 5–36.5 m [Galil, 2005; Checklist …, 2008], i.e. it is a typical Indo-Westpacific, sublittoral-upper shelf species.

Data on the distribution of *L. perplexa* were limited to museum materials used in the revision of the family Leucosiidae [Galil, 2009]. But relatively recently, this species was mentioned in the atlas of crabs of the Persian Gulf [Naderloo, 2017] and its morphology was described from the province of Khuzistan — the northernmost part of the same Gulf [Ebadi *et al*., 2017]. In 2014, it was discovered in Indian waters near Calcutta, Cochin [Jijith *et al*., 2014]. Based on this, we can conclude that *L. perplexa* is an inhabitant of the Indian Ocean, known in the Persian and Oman Gulfs, the waters of Pakistan and India up to the Bay of Bengal. However, our materials collected in the waters of Nha Trang Bay (South China Sea, Vietnam) noticeably push the eastern boundary of its range beyond the Indian Ocean. Consequently, *L. perplexa*, like *S.*

vittata, belongs to the typical Indo-Westpacific species. Both inhabits at the bottom of the sublittoral and the upper part of the shelf at depths from 5 to 85 m, on sandy and silty soils [Galil, 2009; Jijith *et al*., 2014; Naderloo, 2017]. Consequently, both objects of our study are quite close faunistically.

The main features of the biology of *S. vittata* and *L. perplexa* of the Nha Trang Bay were generally comparable. Marked dominance of males in the sample of *L. perplexa* may be related to the method of collecting material, or with different mortality of males and females at juvenile stages, or with their spatial segregation in the littoral zone. An interspecific comparison of the sizes of males and females (Table 1) showed that the maximum and average values of the total body length, the average length of the carapace, were greater in both males and females of *S. vittata* (for TL: males t stat. = 12.2, t crit. = 1.97, p = 0.05; females t stat. = 21.3, t crit. = 1.97, p = 0.05; for DC: males t stat. = 9.07, t crit. = 1.97, p = 0.05; females t stat. = 23.9, t crit. = 1.97, p = 0.05). According to the width of the carapace (Table. 1) the largest individuals were found among males of *L. perplexa*, and on average they were slightly larger than males of *S. vittata* (t stat. = 7.07, t crit. = 1.97, p = 0.05). In females, on the contrary: the average width of the carapace was greater in *S. vittata* (Table 1; t stat. = 9.07, t crit. = 1.97, p = 0.05).

The sizes of males and females were quite similar in both species, in *L. perplexa* males are on average slightly larger than females. In addition, we found in the Nha Trang Bay *S vittata* males were the largest of the previously known sizes (CW 24.9 mm, as opposed to CW 23.9 mm in males from the Indian Ocean [Galil, 2009]. Both species were dominated by males and females of similar sizes (CW 18–21 mm). The average body weight of males in *L. perplexa* was slightly greater than in *S. vittata* (Table 1; t stat. = 3.72, t crit. = 1.97, p = 0.05). There were no significant differences in the average body weight of female (t stat. = 1.65, t crit. = 1.97, p = 0.05). There were no significant differences in the average body weight of crabs of different sexes of both species.

The size at maturity in males of both species were close (CW 19–20 mm in *S. vittata* and 16–20 mm in *L. perplexa*), and in females of both species — at smaller sizes (CW less than 16 mm; for clarification, material on small females is needed). The female sizes at first-time spawning of both species in different parts of the range are similar — CL 16–20 mm (our data are for the South China Sea; Galil [2005, 2009] — for the waters of the Indian and Pacific Oceans); the smallest egg-bearing females in the Nha Trang Bay had CW 16.0–16.3 mm.

Analysis of data on the reproductive state of females of both species showed that February is the time of active spawning of these crabs in the Nha Trang Bay: egg-bearing females with embryos at different stages of development predominated, up to 40–55% of almost mature and pre-spawning females were encountered. Up to 38–51% of egg-bearing females of both species were going to spawn again soon. In both species, there was a fairly synchronous maturation of the ovaries and the development of embryos on pleopods, which allows them to produce several clutches during the spawning season, which takes January–February in the waters of this Bay. A few females (2–7%) missed the current mass spawning, which may be due to the peculiarities of mating and storing their sperm and (or) the qualitative characteristics of such specimens. The sizes of mature oocytes in ovaries of both species are close — on average large and small diameters were 0.24–0.26 and 0.22–0.23 mm (Table 3).

The maximum fecundity of both species reached close values — up to 3157–3282 eggs (Table 2), which demonstrates a comparable level of reproductive capabilities. The initial realized fecundity (the number of recently laid eggs, stage of embryogenesis 1) in *L. perplexa* was 1.3 times greater than that in *S. vittata* (Table 2; t stat. = 12.18, t crit. = 2.04, p = 0.05) with larger (1.4 times) eggs in *L. perplexa* (Table 2; t stat. = 5.58, t crit. = 2.00, p = 0.05).

The CW of recently spawned *L. perplexa* females was significantly slightly less than that in females of *S. vittata* (Table 2; t stat. = 2.14, t crit. = 2.01, p = 0.05). *L. perplexa* females with slightly smaller average body sizes laid a larger number of larger eggs in comparison with *S. vittata*. The volume of eggs from the beginning to the middle of embryogenesis in *L. perplexa* increased by 2.5 times, compared with a twofold increase in *S. vittata*. It can be assumed that larger egg sizes and higher fecundity contribute to more successful reproduction of *L. perplexa* in the waters of the Nha Trang Bay than in *S. vittata*.

In the literature, data on the feeding of crab family Leucosiidae is absent. Probably, our previous publication devoted to the food composition of *L. perplexa* [Burukovsky, 2019], and this paper represents the first information about it. Therefore, the discussion is necessarily limited only to our own results.

In both species not only specimens with empty stomachs absolutely predominate, but also the frequency of occurrence of specimens with different filling of stomachs practically coincide (Fig. 1). Complete dominance among the sample of specimens with empty stomachs is a phenomenon quite characteristic of predators, especially attackers. The most striking example is the shrimp *Glyphus marsupialis* Fihol, 1884, in which, in more than 1,000 stomachs studied, only 29 contained food, and 10 were full [Burukovsky, 2022]. On the contrary, in the detritophagous *Nematocarcinus africanus* Crosnier et Forest, 1973, all 379 studied stomachs contained food, and 177 of them were full [Burukovsky, 2012]. Approximately the same is observed in the shrimp *Alpheus lobidens* De Haan, 1849 (myco-, phyto- and detritophagus), which out of 872 studied stomachs in 861 had food, of which 602 stomachs were full [Burukovsky *et al*., 2018].

This is also reflected in the Froerman coefficient, which is less than two in attacking predators, close to two in grazing predators, and closer to three or four in predator–gatherers and gatherers (detritophages–necrophages) [Burukovsky, Trunova, 2007; Burukovsky, 2017, 2022]. In *S. vittata* and *L. perplexa*, even if we consider a “fibrous” mass as a food object, the frequency of occurrence of which, respectively, is 49 and 59% (Table 4), the Froerman coefficient is less than two.

In fact, the effect described above is nothing more than an artifact. This, to some extent, is evidenced by the distribution of the frequency of occurrence of stomachs with varying degrees of fullness of food (Fig. 1). In this case, the time interval between the capture of crabs and their fixation turned out to be such an impact, since they were caught at night and bought early in the morning at the fish market at the place where the catches were unloaded (personal information of the late V.A. Spiridonov), and only after that crabs were fixed with an ethanol solution. Three-quarters of the crabs, whose stomachs were completely devoid of any signs of food, were probably caught before all the others. In about 15% of specimens, a loose mass was found in the stomachs near the pyloric valve — half-digested food ready to enter the pyloric filter of the stomach. And only about 10% of the specimens had quite distinguishable food objects in their stomachs. Probably, these crabs were caught last and did not have time to digest their victims. Based on this, the comparative characteristics of the composition of the food in these two species are not very correct, but this is the first such study on crabs family Leucosiidae, so the following arguments can be considered a "starting point" and, hopefully, can be useful to other researchers.

Judging by the contents of full stomachs, both species can be tentatively attributed to predator-gatherers or even attacking predators (classification — according [Burukovsky, 2017]), feeding on the most common representatives of bottom or demersal hydrobionts — fish fry, young mollusks, stomatopod and decapod crustaceans.

Despite the clear taxonomic differences of the generic level, the crabs are similar in appearance. They do not differ much in size, as well as in the general parameters of the habitat: silty-sandy bottom soils on the sublittoral and upper part of the shelf (see above). The question arises: are there any signs of the overlap of their food spectra? They are revealed when comparing the composition of the contents of the stomachs of both types of crabs (Table 4). First of all, the general similarity of the composition of food is noticeable. For example, the fact that both species do not neglect necrophagia, at least in relation to fish. Morphological features of both species are unlikely to contribute to the hunt for fry. And the shape of the remains of fish in the stomachs of crabs also indicates that they ate dead fish. Their frequency of occurrence in both species is very close, and in terms of the share in the volume of the virtual food lump (VFL) in one species, they occupy a quarter, and in the second species — almost a third of the volume of the VFL. But they consume detritus in different ways, which differs little in their frequency of occurrence. But in *S. vittata* it occupies 15% of the volume of the VFL, and in *L. perplexa* is present there only in the form of traces, sometimes accompanied by the presence of the smallest inorganic substance, which we call "substrate". This suggested that in *L. perplexa*, the appearance of detritus in the stomach is the result of "sloppy nutrition" [Burukovsky, Trunova, 2007).

In both species, decapod crustaceans have some role in food, but in *S. vittata* they are peneid shrimp, i.e. burrowing animals, and in *L. perplexa* they are crabs (possibly epibenthous). A quarter of the volume of the VFL in *S. vittata* is occupied by Stomatopoda — burrowing ambush predators, i.e. also partly member of infauna.

Such parallels can be traced in relation to other food items. In *S. vittata*, bivalves (mainly infauna) are present among mollusks, and in *L. perplexa*, epibenthous gastropods are present. They also have plant remains in their diet.

Conclusion

The studied Indo-Westpacific species of purse crabs *Seulocia vittata* and *Lyphira perplexa*, living, often together, on sandy and silty bottom of sublittoral-upper shelf zones adjacent to seagrass beds and coral reef flats [Prakash, Kumar, 2020; Sudnik, Poddueva, 2021], had been some similar biological features. It is important to note that both samples of two species were represented by adults with no juveniles present that probably related to the method of collecting material. In both species males were slightly or significantly more abundant than females, herewith in *L. perplexa* males were on average slightly larger than females. In February females of both species actively participated in spawning. They had close values of maximum fecundity and possibility of producing more than one clutch of eggs per a season. Their males have close values of size at maturity. At the same time, *L. perplexa* females, having slightly smaller carapace width than in *S. vittata* females, is distinguished by larger values of fecundity, larger egg size, and more pronounced increase in egg volume during embryogenesis, which should result in more developed larvae. Successful reproduction may contribute to *Lyphira perplexa* more active dispersal and some numerical dominance in Nha Trang Bay than to *Seulocia vittata*.

At this level of knowledge of the composition of the food of these two species, it is impossible to make categorical conclusions, but it is quite acceptable to assume that both of them are benthic predators that do not neglect necrophagia, but *S. vittata* is also a detritophagus that feeds mainly on infauna, and *L. perplexa* is rather an epibentophagus. Due to this, most likely, their food spectra do not overlap. These bentophagous predators should have a significant impact on ecosystem due to their mass abundance.

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