Ruthenica, 2020, vol. 30, No. 4: 195-202.
Published online October 1, 2020.

http: ruthenica.net

Trophic interactions between gall-forming molluscs *Stilifer* spp. (Gastropoda, Eulimidae) and their hosts (Echinodermata)

E.S. MEKHOVA[1], P.Yu. DGEBUADZE [2]

A.N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences, 33, Leninsky prospekt, Moscow, 119071, RUSSIA. E-mail: [1]elena.mehova@gmail.com, [2]p.dgebuadze@gmail.com (corresponding author)

ABSTRACT. The trophic relationships between two species of symbiotic gall-forming molluscs from the genus *Stilifer* (family Eulimidae) and two of their hosts-asteroid species, *Linckia laevigata* and *Culcita noveaguineae,* were investigated using the stable isotope analysis of carbon and nitrogen. The aim of present study was to identify the most preferable host tissue in the symbionts' diet. We analyzed $\delta^{15}N$ and $\delta^{13}C$ values in tube-feet, gonads and digestive glands of the hosts-starfishes and in muscles of the molluscs. Both symbiont species did not differ to each other both in $\delta^{15}N$ and $\delta^{13}C$ values. The average $\delta^{15}N$ and $\delta^{13}C$ values of *Stilifer variabilis* were significantly different from the digestive glands and gonads of their host *Culcita novaeguineae* and did not show differences from the tube-feet of starfishes. A similar pattern was found in the symbiotic association of *Stilifer utinomi* and *Linckia laevigata*. The tube-feet of analyzed starfishes had significantly higher average $\delta^{15}N$ and $\delta^{13}C$ values than the digestive glands and gonads. Obtained isotopic signatures indicate that symbionts do not feed on the host's tissues, but take nutrients from their digestive system. It seems that the proboscis of *Stilifer* spp. absorbs the nutrients from the digestive system of the host-starfish thereby not disturbing significantly the host's immune system.

Трофические взаимодействия между галлообразующими моллюсками рода *Stilifer* (Gastropoda, Eulimidae) и их хозяевами (Echinodermata)

Е.С. МЕХОВА[1], П.Ю. ДГЕБУАДЗЕ[2]

Институт проблем экологии и эволюции им А.Н. Северцова РАН, Ленинский пр-т 33. Москва,. 119071, РОССИЯ. E-mail: [1]elena.mehova@gmail.com, [2]p.dgebuadze@gmail.com (автор-корреспондент)

РЕЗЮМЕ. В данной работе рассмотрены трофические отношения между двумя видами симбиотических галлообразующих моллюсков из рода *Stilifer* (семейство Eulimidae) и их хозяевами – морскими звездами, *Linckia laevigata* и *Culcita novaeguineae,* с использованием метода анализа стабильных изотопов углерода и азота. Целью настоящего исследования было определение наиболее предпочтительной ткани хозяина в пищевом рационе моллюсков-симбионтов. Проанализированы значения $\delta^{15}N$ и $\delta^{13}C$ в амбулакральных ножках, гонадах и пищеварительных железах хозяев-морских звезд, а также в мышцах моллюсков. Оба вида симбионтов не отличались друг от друга, как по азоту, так и по углероду. Средние значения $\delta^{15}N$ и $\delta^{13}C$ в тканях моллюсков *Stilifer variabilis* достоверно отличались от значений пищеварительных желез и гонад их хозяина *Culcita novaeguineae* и не отличались от амбулакральных ножек морских звезд. Аналогичная картина была выявлена в симбиотической ассоциации между моллюсками *Stilifer utinomi* и морскими звездами *Linckia laevigata*. Амбулакральные ножки исследуемых морских звезд имели достоверно более высокие средние значения $\delta^{15}N$ и $\delta^{13}C$, чем пищеварительные железы и гонады. Полученные результаты позволяют говорить, симбионты питаются не тканями хозяина, а компонентами пищи хозяина. Вероятно, что хобот представителей рода *Stilifer* всасывает питательные вещества из пищеварительной системы морской звезды-хозяина, тем самым не сильно раздражая иммунную систему хозяина.

Introduction

Trophic relations between parasites and their hosts are very diverse. In trophic aspect they range from kleptoparasitism, when the symbionts do not feed on their host's tissues, to extremely narrow cases of parasitism, when the parasites feed on specific host's tissue. Identifying these relationships is crucial for understanding the functioning of the symbiotic community and ecosystem as a whole [Lafferty *et al*., 2008]. For a long time, parasites were ignored in the trophic webs studies. Parasites play an important role in benthic communities, but cryptic nature of parasitic relationships requires labor intensive methods to study them.

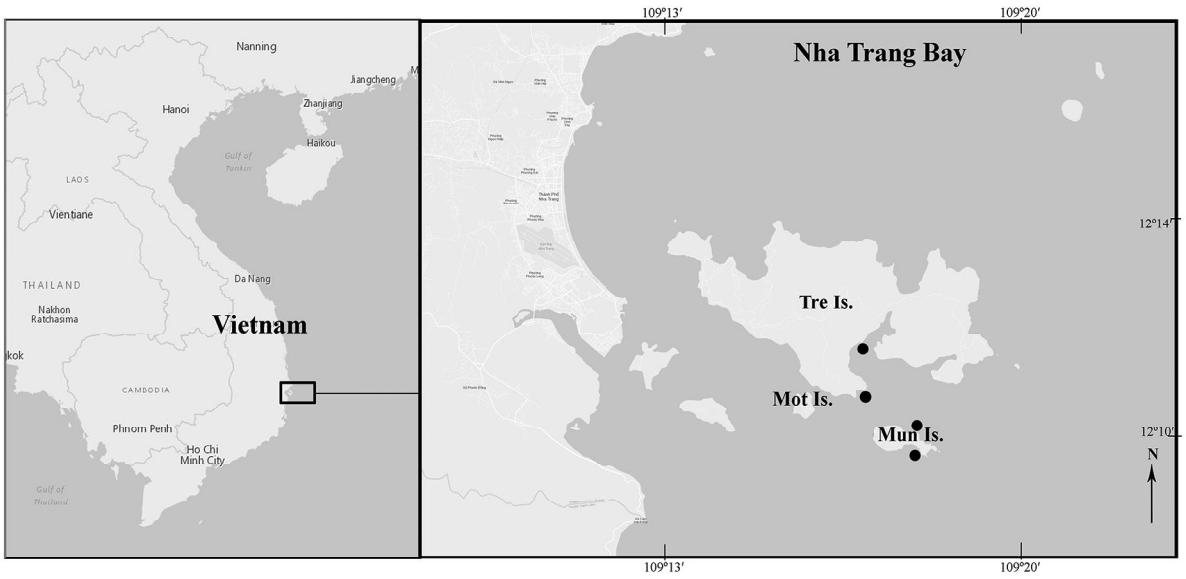

FIG. 1. Schematic map of sampling sites.

РИС. 1. Карта-схема расположения точек отбора проб.

Gastropods from the family Eulimidae are specialized parasites of echinoderms, although the level of specialization varies from strictly species-specific to species with a wide range of hosts [Warén, 1983]. Some details of the symbiont-host relationships are known for a small number of species [e.g. Crossland *et al*., 1991, 1993; Dgebuadze, Kantor, 2015; Queiroz *et al*., 2017]. There are a few papers with the description of eulimids snout morphology, where the sources of their diet are suggested. For example, the proboscis of *Crinophtheiros comatulicola* (Graff, 1875) reaches the coelomic canal of the arm of its host, feather star, and the symbiont absorbs the coelomic fluid [Bacci, 1948]. *Melanella alba* (da Costa, 1778), a temporary ectoparasite of holothurians, drills the wall of the host with its proboscis that secretes a substance which is probably used to quickly relax the host's tissues [Cabioch *et al*., 1978]. Feeding on the host's body fluids was also shown for *Ophieulima minima* (Dall, 1927) and *Peasistilifer edulis* Hoskin, Warén, 1983, and was well studied for *Thyca crystallina* (Gould, 1846) [Warén, Sibuet, 1981; Hoskin, Warén, 1983; Egloff *et al*., 1988]. Since the females of the latter ectoparasitic species are tightly attached to the bodies of their hosts, they lost some anterior parts of the body. Their digestive system is substantially reduced, and the salivary glands are enlarged, so these molluscs can only assimilate food that does not require complex digestion. The degree of penetration of *Th. crystallina* proboscis into its host allows suggesting that its main sources of food are the hemal and perihemal systems of the host, as well as the surrounding fluids and tissues [Egloff *et al*., 1988]. The representatives of the genus *Stilifer* have an elongated proboscis that can be introduced deep into the body or rays of the starfishes. Since these eulimids form galls in body wall of their hosts, the movement of their proboscis is seriously limited as it passes through the host's tissues, including their body wall. Most eulimids have no radula and feed on liquid or semi-dissolved food, which makes it impossible to analyze the composition of the food lump [Lützen, 1972].

Stable isotope analysis (SIA) of carbon and nitrogen has been successfully used to study the trophic relationships for decades [Fry, 2006]. This method can help to overcome some difficulties and understand trophic dynamics between the symbionts and their hosts. The isotopes values differ between organisms due to their diets because of small selective retention of the heaviest isotope and excretion of the lighter one. Typically, with each trophic transfer between a consumer and its diet, $\delta^{15}N$ values increase by approximately 3-5‰ [DeNiro, Epstein, 1981; Minigawa, Wada, 1984]. On the other hand, an animal has $\delta^{13}C$ values close to that of its diet with, however, a slight enrichment of 1‰ [DeNiro, Epstein, 1978; Tieszen *et al*., 1983; Hobson, Clark, 1992].

SIA nowadays allows us to study trophic relationships in different ecosystems, and find some peculiarities, especially in parasitic communities [Deudero *et al*., 2002; Dubois *et al*., 2009]. For example, some authors proposed that the isotope signatures of intestinal parasites (helminths) coincide or are close to the signatures of their hosts [Neilson *et al*., 2005; Navarro *et al*., 2014; Lafferty

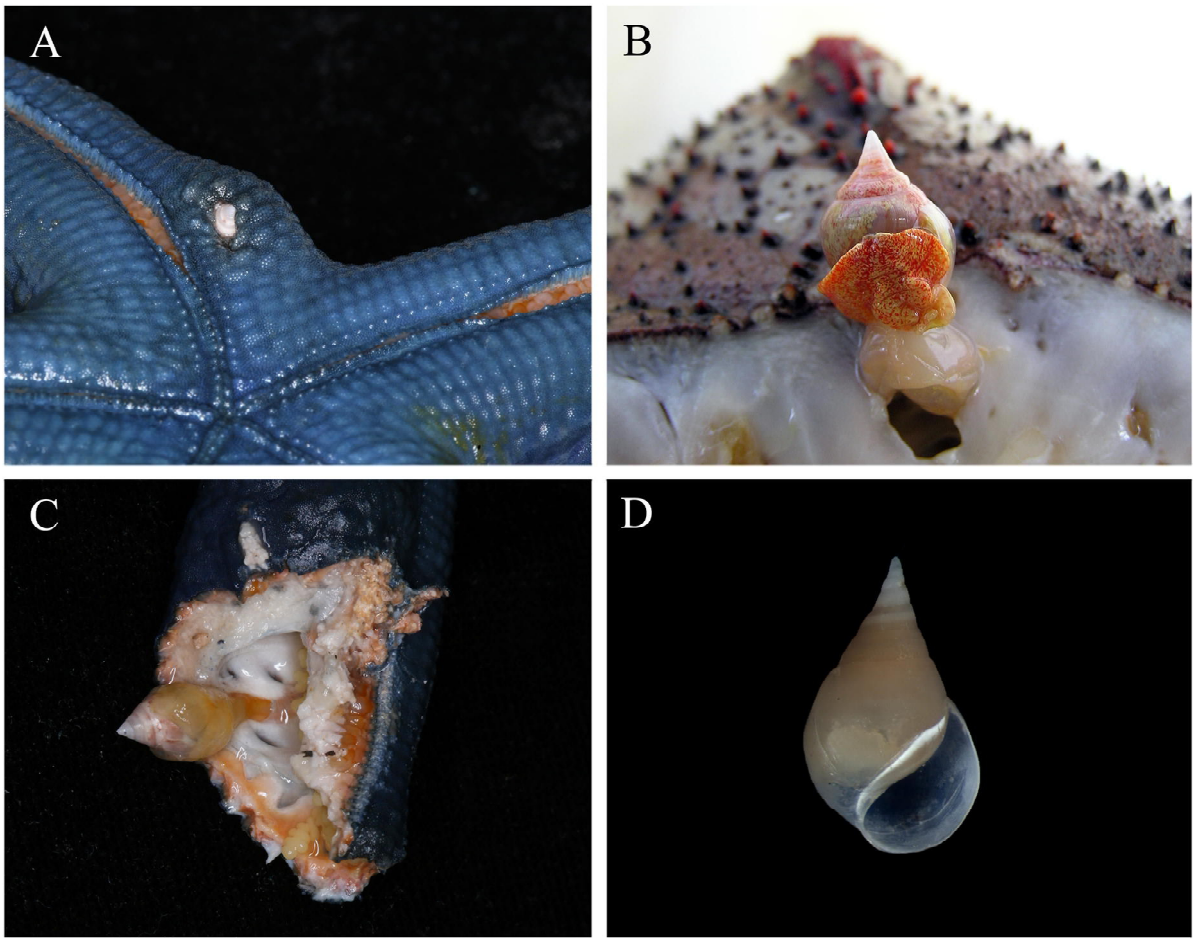

FIG. 2. Gall-forming eulimids and their hosts: **A, C.** *Stilifer utinomi* in the ray of a starfish *Linckia laevigata*; **B, D.** *Stilifer variabilis* in the gall on a starfish *Culcita novaeguineae*.

РИС. 2. Галлообразующие эулимиды и их хозяева: **A, C.** *Stilifer utinomi* в луче морской звезды *Linckia laevigata*; **B, D.** *Stilifer variabilis* в галле в теле морской звезды *Culcita novaeguineae*.

et al., 2008]. For digenean trematodes from marine molluscs no fractionation or low 15N trophic enrichments due to parasite metabolism were detected [Dubois *et al*., 2009]. Parmentier and Das [2004] used the SIA to study the relationships between the Carapidae fishes and their hosts and showed differences in feeding behavior (commensal and parasitic) of these symbionts. So, this method seems appropriate for symbiotic communities, where it is difficult to determine the source of symbionts' diet due to their small sizes, and the food does not contain any solid elements.

The aim of this study is to reveal trophic interactions between the gall-forming eulimids and their hosts – echinoderms. We suppose that these symbiotic gastropods feed on their host and can choose the most preferable tissue.

Materials and methods

Sample processing. The material for the study was collected by SCUBA divers from a depth of 3 to 10 meters in the Nha Trang Bay (South China Sea, central Vietnam) in 2015. Sampling sites are indicated in Fig. 1. All samples were fixed with 80% ethanol. This method of preservation is acceptable since the task of this study is to compare the tissues of symbionts and their hosts [Kaehler, Pakhomov, 2001; Carabel *et al*., 2009]. Some authors noted that the relative trends in fixed samples should be unaffected and thereby they can be used for intercomparison in some ecological analyses [Canuel *et al*., 1995; Gladyshev, 2009].

Two obligate parasitic species of gall-forming eulimids from the genus *Stilifer* associated with starfishes were studied (Fig. 2); *S. utinomi* Habe, 1951 inhabits blue starfishes *Linckia laevigata* (Linnaeus, 1758) and *S. variabilis* O. Boettger, 1893 forms galls in the cushion starfish *Culcita novaeguineae* Müller et Troschel, 1842. Totally five specimens of *S. variabilis* from five host specimens and seven of *S. utinomi* from three host specimens were collected. All molluscs were collected with their hosts. Foot muscles were taken

from the molluscs for the analysis [Fedosov *et al*., 2014; McKinney *et al*., 1999]. Different starfishes' tissues (tube-feet, digestive gland and gonads) were dissected and fixed separately. Each tissue was selected and analyzed in five samples.

Isotopic analysis. Prior to the analysis, all samples were dried for 5-7 days at 50°C, grounded into powder using a mortar and pestle and packed in tin foil (200-500 micrograms each). The SIA was carried out using Thermo Delta V Plus isotope mass spectrometer and Thermo Flash 1112 element analyzer (Thermo Scientific, USA) at the Joint Usage Center "Instrumental Methods in Ecology" at the A.N. Severtsov Institute of Ecology and Evolution of RAS.

The ratio of stable isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) is presented in per mill units (δ, ‰) of deviation from international standards (VPDB for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$). The analytical error in determining the isotope composition (SD in the laboratory standard analysis, n = 6-8) did not exceed 0.2‰. To represent the results, mean values of $\delta^{13}C$ and $\delta^{15}N$ ± 1 standard deviation are reported. The $\delta^{13}C$ values have been corrected for lipid concentration using equation proposed by Post *et al*. [2007] for samples with mass C/N ratio higher than 4.

Statistical analysis. Kolmogorov-Smirnov one-sample test was used to test the normality of the data. One-way ANOVA followed by post hoc multiple comparison tests (Tukey HSD post hoc test) were used to compare the data on the different hosts tissues and symbionts. All statistical analyses were performed with STATISTICA 9.0 (StatSoft, Inc., Tulsa, OK, USA).

Results

Using one-way ANOVA, we found significant differences between echinoderm and symbionts tissues both in $\delta^{13}C$ ($F(3, 33) = 17.629$, $p<0.05$) and in $\delta^{15}N$ ($F(7, 33) = 18.141$, $p<0.05$).

S. utinomi and *S. variabilis* muscles had similar mean $\delta^{15}N$ values, 9.2±0.4‰, Tukey HSD test with d.f. = 33, $p>0.05$ (Fig. 3) The average $\delta^{13}C$ value of *S. utinomi*, -14.1±0.2‰, tended to be lower, than that of *S. variabilis*, -14.5±0.5‰, but the difference was statistically insignificant, $p>0.05$. The mean $\delta^{15}N$ value of *S. variabilis* muscles is significantly different from the digestive glands and gonads of their host *C. novaeguineae:* 9.2±0.4‰, 7.6±0.5‰ and 7.9±0.4‰, respectively, $p<0.01$. Similarly, the mean $\delta^{13}C$ value of *S. variabilis,* -14.5±1.1‰, was higher than that of the digestive glands and gonads of *C. novaeguineae,* -18.3±1.5‰ and -17.0±1.3‰, respectively. These differences were statistically significant, $p<0.01$. The mean $\delta^{15}N$ value of *S. variabilis* was not significantly different from that of the tube-feet of *C. novaeguineae,* 9.8±0.9‰, $p>0.05$; as were the average $\delta^{13}C$ values (-14.7±0.9‰, $p>0.05$).

The mean $\delta^{15}N$ value of *S. utinomi* muscles was significantly different from the digestive glands and gonads of their host *L. laevigata:* 9.2±0.4‰, 7.4±0.2‰ and 8.1±0.3‰, respectively, $p<0.01$. Similarly, the mean $\delta^{13}C$ value of *S. utinomi,* -14.1± 0.6‰, was higher than that of the digestive glands and gonad of *L. laevigata,* -18.5±0.7‰ and -17.4± 0.8‰, respectively. These differences were statistically significant, $p<0.01$. The mean $\delta^{15}N$ value of *S. utinomi* muscles was not significantly different from that of the tube-feet of *L. laevigata,* 9.1±0.9‰, $p>0.05$; as were the mean $\delta^{13}C$ values (-15.5±0.2‰, $p>0.05$).The tube-feet of *C. novaeguineae* had significantly higher mean $\delta^{15}N$ value than the gonads and digestive glands of this species, 9.8±0.9‰, 7.9±0.4‰ and 7.6±0.5‰, respectively, $p<0.01$. The same differences were found for mean $\delta^{13}C$: the tube-feet of *C. novaeguineae* had significantly higher mean $\delta^{13}C$ value than the gonads and digestive glands of this species: -14.8±0.9‰, -17.0±1.3‰ and -18.3±1.5‰, respectively, $p<0.01$. The tube-feet of *L. laevigata* had significantly higher mean $\delta^{15}N$ value than the digestive glands of this species, 9.0±0.3‰ and 7.4±0.2‰, respectively, $p<0.01$. The average $\delta^{13}C$ of tube-feet of *L. laevigata* was significantly higher than that of the digestive glands: -15.5±0.8‰ and -18.5±0.7‰, respectively, $p<0.01$. Between the tube-feet of both echinoderm species the differences were insignificant in both the $\delta^{15}N$ values, $p>0.05$, and the $\delta^{13}C$ values, $p>0.05$.

Discussion

As expected, the starfishes' tissues differ in heavy nitrogen isotope enrichment within a species. The nitrogen variances in the different tissues were shown for some organisms and sometimes such differences can reach up to 4‰ (as for $\delta^{13}C$ – up to 2‰) [Deudero *et al*., 2002]. Parmentier and Das have previously shown such differences of $\delta^{15}N$ for *C. novaeguineae* tissues [Parmentier, Das, 2004]. Indeed, it is known that nitrogen trophic enrichment is the result of transamination and the loss of "light" ^{14}N excretory products [Macko *et al*., 1986]. In addition, gonads have more fatty tissue and are low in carbon heavy isotopes saturation [DeNiro, Epstein, 1978; McConnaughey, McRoy, 1979; Post *et al*., 2007]. The tube-feet are therefore the most indicative of a starfish's diet in comparison to other analyzed organs.

The lack of significant differences in both $\delta^{13}C$ and $\delta^{15}N$ values indicates the similarity of feeding preferences between both species of starfishes in our study. The cushion starfish *C. novaeguineae* primarily prefers corals, but also feeds on algae and

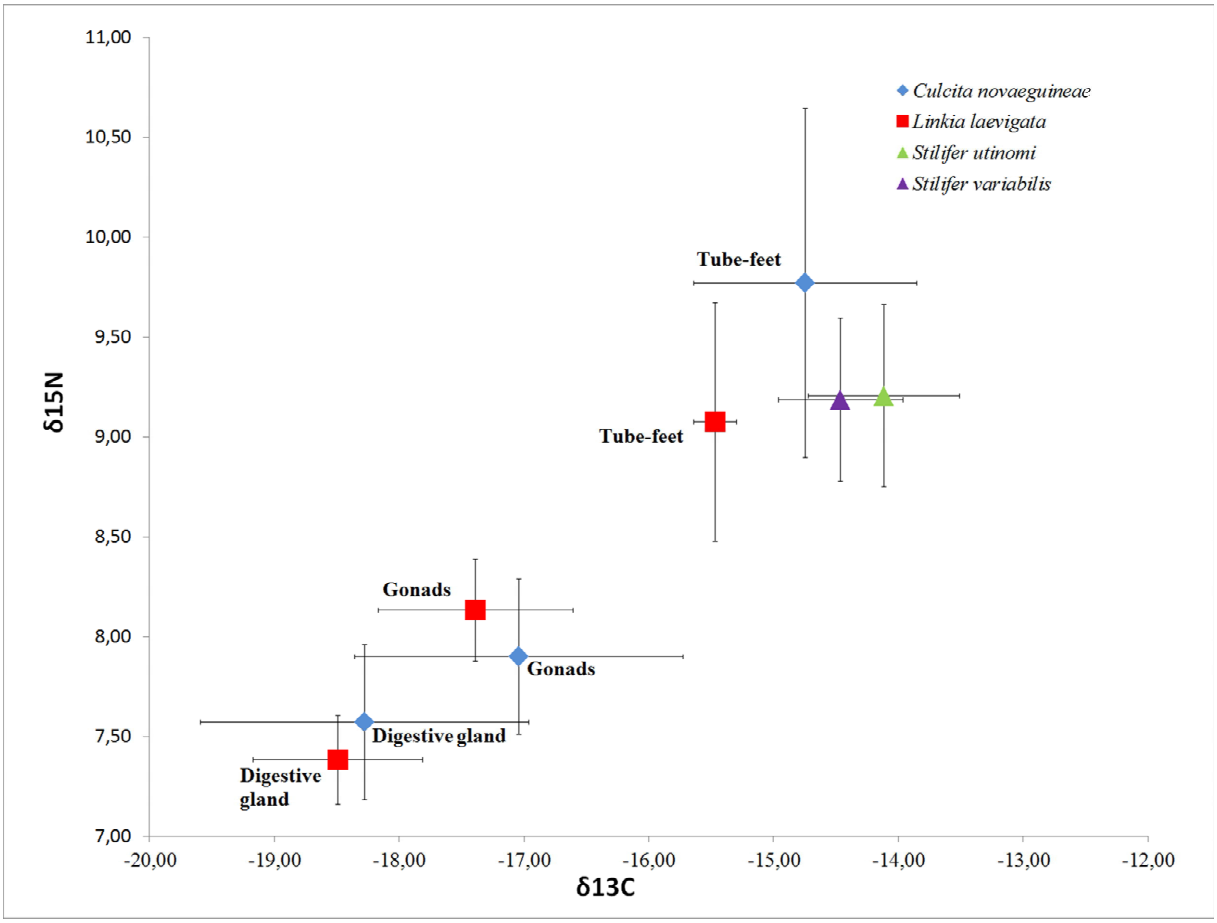

FIG. 3. The average $\delta^{13}C$ and $\delta^{15}N$ values and standard deviations of the muscle tissues of the gall-forming species *Stilifer variabilis* and *Silifer utinomi* and organs of their hosts *Culcita novaeguineae* and *Linckia laevigata* collected in 2015 in the Nha Trang Bay, Vietnam.

РИС. 3. Средние значения $\delta^{13}C$ и $\delta^{15}N$ и стандартные отклонения в мышечных тканях галлообразующих видов *Stilifer variabilis* и *Silifer utinomi,* а также органах их хозяев *Culcita novaeguineae* и *Linckia laevigata,* собранные в 2015 году в заливе Нячанг, Вьетнам.

coral rubble [Bell, 2008]. Another analyzed species *L. laevigata* mainly feeds on coralline algae and detritus [Coleman, 2007; Laxton, 1974]. So, our result may demonstrate on the seasons or local conditions of the bay.

The ratio of $^{15}N/^{14}N$ can indicate an organism's trophic position, but this may not work well for parasites. Although predators are always ^{15}N-enriched in comparison to their prey, parasites are sometimes ^{15}N-depleted when compared with their hosts, as a whole [Pinnegar *et al*., 2001]. Other parasites have a similar enrichment comparing to their hosts, whereas a few parasites are more enriched than expected for a direct consumer [O'Grady, Dearing, 2006]. The level of enrichment can even vary between parasite taxa within the hosts. For example, intestinal nematodes parasitizing rabbits are $\delta^{15}N$-enriched whereas intestinal cestodes in the same host species are $\delta^{15}N$-depleted [Boag *et al*., 1998; Neilson *et al*., 2005]. Further complicating matters, different parasite species on the same host or the same parasite species on different hosts can differ in their isotope enrichment [Deudero *et al*., 2002]. This difference in $\delta^{15}N$ between predators and parasites likely stems from the fact that parasites are relatively selective in which parts of the host they consume. For instance, some parasites may feed on the intestinal contents rather than on the host tissue; others selectively absorb particular biochemical compounds such as amino acids, live in and feed on different host tissues, or have altered metabolism that varies with life stage [Pinnegar *et al*., 2001; Deudero *et al*., 2002]. For these reasons, a topological assessment seems to be the best approach for determining the trophic differences between parasites and their hosts [Lafferty *et al*., 2008].

The obtained data indicates that molluscs tissues are more enriched in heavy nitrogen isotope relatively to the digestive glands and gonads of their

hosts. However, the difference between them was less than 3.4‰, that was also previously shown for other ectoparasites. For example, Pinneagar and co-authors [2001] noted that the blood eating isopod *Anilocra physodes* (Linnaeus, 1758) and larvae of the copepod *Lernaeocera branchialis* (Linnaeus, 1767) did not differ significantly in $\delta^{15}N$ with respect to their hosts: bogue *Boops boops* (Linnaeus, 1758) and flounder *Platichthys flesus* (Linnaeus, 1758). Our data partially correlates with the data on other symbionts of echinoderms: for some carapid species [*Carapus boraborensis* (Kaup, 1856) and *Encheliophis homei* (Richardson, 1846)] the ^{15}N-enrichment was shown compared to different tissues (digestive tract, gonads, digestive glands and tube-feet of starfishes) of their hosts holothurians and starfishes. These symbionts use their host as a shelter and leave it to feed in the environment [Parmentier, Das, 2004]. As with nitrogen isotopes, symbiotic gastropods tissues were consistently enriched in ^{13}C in respect to digestive gland and gonads of their hosts (Fig. 3). This disagrees with the enrichment pattern "$\delta^{13}C < 1‰$ conventionally assumed between consumers and their diets. Meanwhile, the $\delta^{13}C$ values of symbionts tissues and their hosts are almost the same and it demonstrates the absence of differences between host tube-feet and symbionts muscles. All obtained results for both $\delta^{13}C$ and $\delta^{15}N$ allow us to conclude that these gall-forming molluscs feed on what the starfish itself consume and then accumulate in its tube-feet. In that case, symbionts obtain the necessary nutrients of the host from the coelomic cavity without penetrating specific organs and thus causing no fatal damage to their hosts.

But, last year Thieltges and co-authors made an extensive comparative analysis of different host-parasite systems using SIA and showed that the traditional isotope framework does not apply well to parasitic trophic relations. They concluded, that "the average discrimination factors observed in predator–prey and herbivore–plant trophic interactions ($\Delta\ ^{15}N$ of 3.4‰ and $\Delta\ ^{13}C$ of 1.0‰) do not hold true as a general indicator for trophic relationships between parasites and their hosts" [Thieltges *et al.*, 2019: 1335]. Authors suggested that one of the reasons of this situation may be the different metabolic pathways of parasites, especially endobionts.

The morphological features suggest that gall-forming molluscs feed on the host tissues. For example, it was described that the representatives of the genus *Stilifer* have an elongated proboscis that is introduced deeply into the body or rays of the starfish [Lützen, 1972]. However, most researchers did not analyze the method of feeding and the type of absorbed food. In one study of gall-forming species *Paramegadenus arrhynchus* (Ivanov, 1937), it was concluded, based on the structure of the digestive system, that the powerful development of the pharynx's radial muscles, as well as the reduction of the stomach, involves feeding only on gut contents of the host [Ivanov, 1952]. In addition, Queiroz *et al*. [2017] studied the lifecycle of gall-forming eulimid *Sabinella troglodytes* (Thiele, 1925) from sea urchins and additionally observed the feeding mechanisms. They described the feeding process of symbionts on their hosts' spines using an acrembolic proboscis to erode and suck the calcareous matrix to access the scarce spine tissue. It seems amazing why these molluscs do not penetrate the test of sea urchins but make galls and feed on their spines. The morphology and the lifestyle of representatives from the genus *Stilifer* suggest that the mollusc is closely connected with one starfish all its life. Probably, the symbiont proboscis is seriously limited in its movements as it passes through the host's tissues, including the host's body wall [Lützen, 1972]. Hence, such eulimids cannot change the source of food.

Thus, in our study of gall-forming eulimids diet, we conclude that the most feasible food source for *Stilifer* spp. is "a stealing" of nutrients from the celomic cavity of the starfishes, without irritating the host's immune system. Since we do not know the peculiarities of the symbionts' metabolism, our results should be considered preliminary. Further studies are needed to confirm these assumptions, including the investigations of the molluscs' morphology.

Conclusions

SIA is a useful tool to characterize the trophic status in symbiotic associations but should be interpreted with caution. Our results confirm the parasitic feeding of gall-forming eulimids, and the most likely source is the coelomic fluid. It is proved by morphological data, but physiological features of parasites should be further considered, for example selective assimilation by parasites of certain compounds from the food.

Acknowledgements

We thank Dr. A.V. Tiunov, Dr. Prof. Michail I. Gladyshev and Dr. A.K. Zalota for helpful discussions during the sample analysis and manuscript preparation, our colleagues from the Laboratory of Morphology and Ecology of Marine Invertebrates of A.N. Severtsov Institute of Ecology and Evolution (SIEE RAS), the Coastal Branch of the Russian-Vietnamese Tropical Center and Joint Usage Centre "Instrumental Methods in Ecology" (SIEE RAS) for their collaboration during the field sampling and in the laboratory.

The work was suported by the grant from the Russian Science Foundation (grant number 16-14-10118-П; PI Y. Kantor).

References

Bacci G. 1948. *Melanella comatulicola* (Graff), un Gasteropodo parassita della *Antedon mediterranea* (Lam.). *Italian Journal of Zoology*, 15(1–3): 89–98.

Bell J. 2008. Feeding preferences of the cushion star *Culcita novaeguineae* in the presence of the crown of thorns starfish *Acanthaster planci*. *UC Berkeley: UCB Moorea Class: Biology and Geomorphology of Tropical Islands*. *Student Research Papers*, https://escholarship.org/uc/item/97r5p1r3

Boag B., Neilson R., Robinson D., Scrimgeour C.M., Handley L.L. 1998. Wild rabbit host and some parasites show trophic-level relationships for $\delta^{13}C$ and $\delta^{15}N$: A first report. *Isotopes in environmental and health studies*, 33: 81–85.

Cabioch L., Grainger J.N., Keegan B.F., Konnecker G. 1978. *Balcis alba* (Da Costa). A temporary ectoparasite on *Neopentadactyla mixta* Ostergren. In: McHusky D.S., Berry A.J. (Eds) *Proceedings of the 12th European Marine Biology Symposium*. Pergamon Press, Oxford: 237–241.

Canuel E.A., Cloern J.E., Ringelberg D.B., Guckert J.B., Rau G.H. 1995. Molecular and isotopic tracers used to examine sources of organic matter and its incorporation into the food webs of San Francisco Bay. *Limnology and Oceanography,* 40: 67–81.

Carabel S., Verisimo P., Freire J. 2009. Effects of preservatives on stable isotope analyses of four marine species. *Estuarine, Coastal and Shelf Science*, 82: 348–350.

Coleman N. 2007. *Sea stars: Echinoderms of the Asia-Indo-Pacific.* Springwood. Neville Coleman's Underwater Geographic Pty Ltd., 136 p.

Crossland M.R., Alford R.A., Collins J.D. 1991. Population dynamics of an ectoparasitic gastropod, *Hypermastus* sp. (Eulimidae), on the sand dollar, *Arachnoides placenta* (Echinoidea). *Australian Journal of Marine and Freshwater Research*, 42: 69–76.

Crossland M.R., Collins J.D., Alford R.A. 1993. Host selection and distribution of *Hypermastus placentae* (Eulimidae), an ectoparasitis gastropod on the sand dollar *Arachnoides placenta* (Echinoidea). *Australian Journal of Marine and Freshwater Research*, 44: 835–844.

DeNiro M.J., Epstein S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta,* 42: 495–506.

DeNiro M.J., Epstein S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta,* 45: 343–351.

Deudero S., Pinnegar J.K., Polunin N.V.C. 2002. Insights into fish host–parasite trophic relationships revealed by stable isotope analysis. *Diseases of Aquatic Organisms*, 52: 77–86.

Dgebuadze P.Yu., Kantor Yu.I. 2015. The preference of symbiotic *Annulobalcis* gastropods (Eulimidae) for their crinoid hosts. *Symbiosis*, 68(1): 109–114.

Dubois S.Y., Savoye N., Sauriau P.-G., Billy I., Martinez P., de Montaudouin X. 2009. Digenean trematodes–marine mollusc relationships: a stable isotope study. *Diseases of Aquatic Organisms*, 84: 65–77.

Egloff D.A., Smouse D.T. Jr., Pembroke J.E. 1988. Penetration of the radial hemal and perihemal systems of *Linckia laevigata* (Asteroidea) by the proboscis of *Thyca crystallina*, an ectoparasitic gastropod. *The Veliger*, 30(4): 342–346.

Fedosov A., Tiunov A., Kiyashko S., Kantor Yu. 2014. Trophic diversification in the evolution of predatory marine gastropods of the family Terebridae as inferred from stable isotope data. *Marine Ecology Progress Series*, 497: 143–156.

Fry B. 2006. *Stable isotope ecology*. New York, Springer, 308 p.

Gladyshev M.I. 2009. Stable isotope analyses in aquatic ecology (a review). *Journal of Siberian Federal University. Biology,* 2(4): 381–402.

Hobson K.A., Clark R.G., 1992. Assessing avian diets using stable isotope II: factors influencing diet–tissue fractionation. *Condor*, 94: 189–197.

Hoskin G.P., Warén A. 1983. *Peasistilifer edulis*, a new eulimid prosobranch, parasitic on an Indo-Pacific holothurian. *Nautilus*, 97: 23–26.

Ivanov A.V. 1952. The structure of the ectoparasic gastropods of Stiliferidae as a result of their lifestyle. *Trudy Leningradskogo Obschestva Estestvoispytateley*, 71(4): 86–140 [In Russian].

Kaehler S., Pakhomov E.A. 2001. Effects of storage and preservation on the $\delta^{13}C$ and $\delta^{15}N$ signatures of selected marine organisms. *Marine Ecology Progress Series*, 219: 299–304.

Lafferty K., Allesina S., Arim M., Briggs C.J., De Leo G., Dobson A.P., Dunne J.A., Johnson P.T.J., Kuris A.M., Marcogliese D.J., Martinez N.D., Memmott J., Marquet P.A., McLaughlin J.P., Mordecai E.A., Pascual M., Poulin R., Thieltges D.W. 2008. Parasites in food webs: the ultimate missing links. *Ecology Letters*, 11: 533–546.

Laxton J. H. 1974. A preliminary study of the biology and ecology of the blue starfish *Linckia laevigata* (L.) on the Australian Great Barrier Reef and an interpretation of its role in the coral reef ecosystem. *Biological Journal of the Linnean Society,* 6: 47–64.

Lützen J. 1972. Studies on parasitic gastropods from echinoderms II. *Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter*, 19(6): 1–20.

Macko S.A., Estep M.F., Engel M.H., Hare P.E. 1986. Kinetic fractionation of stable nitrogen isotopes during amino acid transamination. *Geochimica et Cosmochimica Acta*, 50: 2143–2146.

McConnaughey T., McRoy C.P. 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. *Marine Biology,* 53: 257–262.

McKinney R.A., Lake J.L., Allen M., Ryba S. 1999. Spatial ability in mussels used to assess base level nitrogen isotope ratio in freshwater ecosystems. *Hydrobiologia,* 412: 17–24.

Minigawa M., Wada E. 1984. Stepwise enrichment of $\delta^{15}N$ along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. *Geochimica et Cosmochimica Acta,* 48: 1135–1140.

Navarro J., Albo-Puigserver M., Coll M., Saez R., Forero M.G., Kutcha R. 2014. Isotopic discrimination of a stable isotopes of nitrogen (for $\delta^{15}N$) and carbon ($\delta^{13}C$) in a host-specific holocephalan tapeworm. *Journal of Helminthology*, 88(3): 371–375.

Neilson R., Boag B., Hartley G. 2005. Temporal host–parasite relationships of the wild rabbit, *Oryctolagus cuniculus* (L.) as revealed by stable isotope analyses. *Parasitology*, 131: 279–285.

O'*Grady* S.P., *Dearing* M.D. 2006. *Isotopic* insight into

host–endosymbiont relationships in liolaemid lizards. *Oecologia*, 150: 355–361.

Parmentier E., Das K. 2004. Commensal vs. parasitic relationship between Carapini fish and their hosts: some further insight through $\delta^{13}C$ and $\delta^{15}N$ measurements. *Journal of Experimental Marine Biology and Ecology* 310: 47–58.

Pinnegar J.K., Campbell N., Polunin N.V.C. 2001. Unusual stable isotopic fractionation patterns observed for fish host–parasite trophic relationships. *Journal of Fish Biology*, 59: 494–503.

Post D.M., Layman C.A., Arrington D. A., Takimoto G., Quattrochi J., Montaña C.G. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, 152: 179–189. doi:10.1007/s00442-006-0630-x

Queiroz V., Neves E., Sales L., Johnsson R. 2017. The gall-former *Sabinella troglodytes* (Caenogastropoda: Eulimidae) and its association with *Eucidaris tribuloides* (Echinodermata: Echinoidea). *Journal of Conchology*, 42(5): 371–377.

Thieltges D.W., Goedknegt M.A., O'Dwyer K., Senior A.M., Kamiya T. 2019. Parasites and stable isotopes: a comparative analysis of isotopic discrimination in parasitic trophic interactions. *Oikos*, 128: 1329–1339

Tieszen L.L., Boutton T.W., Tesdahl K.G., Slade N.A. 1983. Fractionation and turn-over of stable carbon isotopes in animal tissues: implication for $\delta^{13}C$ analysis of diet. *Oecologia*, 57: 32– 37.

Warén A. 1983. A generic revision of the family Eulimidae (Gastropoda, Prosobranchia). *Journal of Molluscan Studies*, 49 (Supplement 13): 1–96.

Warén A., Sibuet M. 1981. *Ophieulima* (Mollusca, Prosobranchia), a new genus of ophiuroid parasites. *Sarsia*, 66: 103–107.