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Skeleton shrimp *Caprella septentrionalis* Krøyer, 1838 (Amphipoda: Caprellidae), an intermediate host of various helminths in the White Sea

I.I. Gordeev[1,2,*], S.G. Sokolov[3]

[1] *Lomonosov Moscow State University, Leninskiye Gory 1/12, Moscow, 119234, Russia.*
[2] *Russian Federal Research Institute of Fisheries and Oceanography, Okruzhnoy Proezd 19, Moscow, 105187, Russia. E-mail: gordeev_ilya@bk.ru*
** Corresponding author*
[3] *A.N. Severtsov Institute of Ecology and Evolution of the RAS, Leninsky pr. 33, 119071, Moscow, Russia. E-mail: sokolovsg@mail.ru*
I.I. Gordeev ORCID: 0000-0002-6650-9120
S.G. Sokolov ORCID: 0000-0002-4822-966X

ABSTRACT: The marine amphipod *Caprella septentrionalis* was examined for helminth infection at four localities in the Velikaya Salma Strait (Kandalaksha Bay, White Sea). A non-zero infection with helminths was found in skeleton shrimps collected at three sampling sites located closest to the White Sea Biological Station (WSBS) of the Lomonosov Moscow State University. The larvae of four parasitic species were found: third-stage juveniles of the nematodes *Hysterothylacium aduncum* and *Pseudoterranova* sp., cystacanths of the acanthocephalan *Echinorhynchus gadi*, and progenetic metacercariae of the digenean *Progonus muelleri*. Skeleton shrimps collected at a distance from WSBS were uninfected. This striking difference seems to be associated with an unusual hydrological regime near WSBS. A high turbulence during tidal motion results in an abundant supply of oxygen and biogenic substances, promoting a high species diversity, biomass and abundance of hosts. Comparison with earlier studies showed a significant reduction in infection rates of skeleton shrimps since the middle of the 20th century.
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KEY WORDS: *Hysterothylacium aduncum*, *Progonus muelleri*, *Pseudoterranova*, *Echinorhynchus gadi*, parasites, infection.

Морская козочка *Caprella septentrionalis* Krøyer, 1838 (Amphipoda: Caprellidae) как промежуточный хозяин гельминтов в Белом море

И.И. Гордеев[1,2], С.Г. Соколов[3]

[1] *Московский государственный университет им. М.В. Ломоносова, Ленинские горы д. 1/12, Москва, 119234, Россия. E-mail: gordeev_ilya@bk.ru*
[2] *Всероссийский научно-исследовательский институт рыбного хозяйства и океанографии, Окружной проезд, д. 19, Москва, 105187, Russia.*
[3] *Институт проблем экологии и эволюции им. А.Н. Северцова РАН, Ленинский пр. 33, Москва, 119071, Россия. E-mail: gordeev_ilya@bk.ru*

РЕЗЮМЕ: Изучена зараженность морской козочки *Caprella septentrionalis* личинками гельминтов в четырех точках пролива Великая Салма (Кандалакшский залив Белого моря). Паразиты выявлены у рачков, собранных на трех ближайших к Беломорской биологической станции МГУ им. М.В. Ломоносова (ББС МГУ) участках отбора проб. Обнаружены личинки III стадии нематод *Hysterothylacium aduncum* и *Pseudoterranova* sp., цистаканты скребня *Echinorhynchus gadi* и прогенетические метацеркарии трематоды *Progonus muelleri*. Козочки, собранные на сравнительно большом расстоянии от ББС МГУ, были свободны от личинок гельминтов. Это разительное отличие, по-видимому, связано с необычным гидрологическим режимом вблизи ББС МГУ. Высокая турбулентность во время приливных движений приводит к обильному снабжению кислородом и биогенными веществами, что способствует высокому видовому разнообразию, биомассе и численности хозяев всех уровней. Сравнение с серединой XX столетия выявило значительное снижение уровня заражения козочек за прошедшее время.

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КЛЮЧЕВЫЕ СЛОВА: *Hysterothylacium aduncum*, *Progonus muelleri*, *Pseudoterranova*, *Echinorhynchus gadi*, паразиты, инфекция.

Introduction

Representatives of the genus *Caprella* Lamarck, 1801 (Amphipoda: Caprellidae), referred to as skeleton shrimps, are common benthic amphipods in the White Sea. Three species are known in the White Sea: *C. dubia* Hansen, 1887, *C. linearis* Linnaeus, 1767, and *C. septentrionalis* Krøyer, 1838, the latter two being the most common (Tchesunov *et al.*, 2008). *Caprella septentrionalis* is the best studied skeleton shrimp. Its life cycle lasts for a year, at the end of which sexually mature males and females reproduce and die. For most individuals, this happens in July (Heptner, 1963). *Caprella* spp. are an important part of the White Sea ecosystem, being a major food source for the White Sea cod, *Gadus morhua marisalbi* Derjugin, 1920 (currently recognized as *Gadus macrocephalus* Tilesius, 1810 by some authors), the navaga, *Eleginus nawaga* (Walbaum, 1792), and other fish (Heptner, 1963; Shulman, Shulman-Albova, 1953; Izvekova, 1964; Valter *et al.*, 1980).

The marine waters around the White Sea Biological Station (WSBS) of the Kandalaksha Bay near the Eremeevsky tidal rapids are well-known for a high species diversity and biomass of all groups of animals, including benthic ones (Tchesunov *et al.*, 2008). This is due to a specific hydrological regime in the area of the station, which is rather unusual for the White Sea. WSBS stands at the narrowing of the Velikaya Salma Strait, at the site of the Eremeevsky tidal rapids between the Velikiy Island and the Small Eremeevsky Island. The passage of large amounts of thoroughly mixed water through the rapids during the tidal motion ensures an increased supply of oxygen and nutrients to demersal communities, while the shallow depth (up to 20 m) ensures good insolation. These factors are conductive to a high species diversity and biomass in the local marine ecosystem. Distribution of *Caprella* spp. in this ecosystem usually reflects the presence of algae, sponges, and hydroids on the sea floor (Heptner, 1963).

Skeleton shrimps, similarly to other marine amphipods, serve as intermediate hosts of many digeneans, acanthocephalans, nematodes and cestodes, which parasitize as adults fish, birds, and mammals (Busch *et al.*, 2012). Their role in infection transmission is associated with their benthic way of life, slow locomotion, feeding on diatoms and smaller crustaceans as well as their great abundance (thousands of individuals per square meter of red algae thickets). Numerous parasitological studies of caprellids in the White Sea and in the adjacent Barents Sea (Valter, 1968, 1976, 1978; Valter *et al.*, 1980; Uspenskaya, 1954; Ouspenskaia, 1960) showed that

Fig. 1. Sampling localities in the White Sea.
Рис. 1. Места отбора проб в Белом море.

C. septentrionalis could be infected with nematodes *Hysterothylacium aduncum* (Rudolphi, 1802) (=*Contracaecum* sp.), *Anisakis* sp., digeneans *Derogenes varicus* (Müller, 1784), *Progonus muelleri* (Levinsen, 1881) (=*Genarches mülleri*), *Podocotyle atomon* (Rudolphi, 1802), *Prosorhynchus squamatus* Odhner, 1905, acanthocephalan *Echinorhynchus gadi* Zoega in Müller, 1776, and cestoda *Hymenolepis microsoma* (Dujardin, 1845). Conservatively high levels of marine fish infection by various helminths recorded throughout the year near WSBS in the last century (Shulman, Shulman-Albova, 1953; Timofeeva, Marasaeva, 1984) and recently (Logvinenko, Gordeev, 2022) suggest that it would be worthwhile the update the data on the infection of *C. septentrionalis*.

In this study, we examined the composition of metazoan parasites of *C. septentrionalis* at several sites in the Velikaya Salma Strait (Kandalaksha Bay, White Sea) with the aim of assessing the current parasitic load on this species. Another aim of our study was to check for the differences in the level of infection in samples taken at various distances from the Eremeevsky tidal rapids, taking into account the unusual hydrological regime in this area.

Material and Methods

SAMPLING AND PROCESSING. Red and brown algae were collected at four sites (Fig. 1) in the Velikaya Salma Strait from a depth up to 15m by the diving team of the White Sea Biological Station (WSBS) of the Lomonosov Moscow State University from July 9 to 19 July 2019. The coordinates of the sites were as follows: 1) Kokoikha Island 66°29′18″N, 33°28′19″E; 2) Velikiy Island 66°33′29″N, 33°06′39″E; 3) Yeremeyeevskiy Island 66°33′16″N, 33°8′23″E; 4) rocky shoal Luda Kamenyuka 66°33′01″N, 33°09′10″E. Sites 2–4 were located near WSBS and Eremeevsky tidal rapids, while site 1 was located closer to the open waters of the White Sea in the coastal area of Kokoikha Island (Kuzakotsky archipelago) in the eastern part of the Velikaya Salma Strait, at a distance of 17 km from WSBS. In total, 4,270 skeleton shrimps were picked from the algae and dissected within a few hours of being removed from the water. All 2,970 specimens collected at sites 2–4 were large (more than 15 mm in length from the anterior end of the cephalon to the posterior end of the abdomen) and were identified as *C. septentrionalis*. Skeleton shrimps (1,300 specimens) collected at site 1 were smaller (less than 15 mm in length). Most of them could be identified as *C. septentrionalis* but in some cases the identification was doubtful. To be on the safe side, we labeled these specimens as *Caprella* sp.

All the segments, including the cephalon, the pereon, the abdomen, and all the appendages of the shrimps were carefully lacerated in the course of parasitological dissection. Special attention was paid to the propodi of the 2nd gnathopods and the brood pouches. Large helminths (length greater or comparable to that of the largest segments of the pereon) were usually recovered alive. All the parasites were rinsed in fresh water and then preserved in 96% ethanol. Digeneans were stained with acetic carmine, dehydrated in an alcohol series, contrasted (cleared) with dimethyl phthalate, and finally mounted in Canada balsam. Nematodes and acanthocephalans were processed with glycerol. Trematodes, acanthocephalans, and nematodes were identified following Moravec (1994), Arai (1989), Gibson (1996), and other sources. Parasitological indices were calculated according to Bush *et al*. (1997). Taking into account the proximity of sites 2–4, we have pooled them together in Table 1.

DNA EXTRACTION, AMPLIFICATION AND ANALYSIS. Total DNA was extracted from 96% ethanol-fixed nematodes and acanthocephalans. Proteinase K and mercaptoethanol in the lysing solution was used for nematodes (Holterman *et al*., 2006) and Wizard SV Genomic DNA Purification System (Promega) for acanthocephalans, as recommended by manufacturers. For nematodes, the ITS1-5.8S-ITS2 locus of rDNA was amplified using the previously described primers NC5 (5'-GTAGGTGAACCTGCGGAAGGATCATT-3') and NC2 (5'-TTAGTTTCTTTTCCTCCGCT-3') (Zhu *et al*., 1998). PCR products were visualized in gel, cut out and cleaned using the SV Gel and PCR CleanUp System kit (Evrogen, Russia). DNA sequencing was performed at the Genome Centre for Collective Use in the Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences (Moscow, Russia). For acanthocephalans, the fragment of 28S rDNA was amplified using the polymerase chain reaction (PCR) with the primers LSU5 (5’-TAG GTC GAC CCG CTG AAY TTA AGC A-3’) and LSUD6-3 (5’-GGA ACC CTT CTC CACTT CAGTC-3’) (Littlewood *et al*., 2000). Unfortunately, our attempts to amplify other genetic markers for acanthocephalans were unsuccessful. All the sequences were amplified using an EncycloPlus PCR Kit (Evrogen, Moscow, Russia), as recommended by the manufacturers. Acanthocephalans were sequenced with additional primers ECD2 (5’-CCTTGGTCCGTGTTTCAAGACGGG-3’), 900F (5’-CCGTCTTGAAACACGGACCAAG-3’), and LSU-1200R (5’-GCATAGTTCACCATCTTTCGG-3’). The sequences were deposited in GenBank of the National Center for Biotechnology Information (NCBI) database with accession numbers: *E. gadi* (~1600bp) — MZ229771, MZ229860, MZ229890, MZ229892, MZ230373, MZ230374; *H. aduncum* (~950bp) — ON014994, ON014995, ON014781, ON014779, ON014942, ON014842, ON014783, ON015047, ON015048.

Partial sequences of the ITS1-5.8S-ITS2 locus of rDNA obtained from the specimens of nematodes to assess their phylogenetic relationships were assembled using the Geneious ver. 10.0.5 software (Biomatters Ltd., Auckland, New Zealand) and aligned with sequences retrieved from GenBank (NCBI) (Table S1) using the ClustalW DNA weight matrix within the MEGA 10.0.5 software alignment explorer (Kumar *et al*., 2018). Indel-rich regions of the alignments were identified and removed in Gblocks (Talavera, Castresana, 2007) with the least stringent settings. The phylogenetic analysis of the nucleotide sequences was carried out using the maximum likelihood (ML) and Bayesian inference (BI) methods. Phylogenetic trees using ML and BI methods were reconstructed using MEGA 10.0.5 software (Kumar *et al*., 2018) and MrBayes v. 3.6.2 software (Ronquist, Huelsenbeck, 2003), respectively. The best nucleotide substitution model for the dataset was estimated using jModelTest version 0.1.1 software (Kumar *et al*., 2018). In both methods, the general time-reversible model GTR + G + I was used based on the Akaike Information Criteria. A Bayesian algorithm was performed using the Markov chain Monte Carlo option with ngen = 10,000,000, nruns = 4, nchains = 4 and samplefreq = 1000. The burn-in values were 2,500,000 for the ‘sump’ and ‘sumt’ options. The robustness of the phylogenetic relationship was estimated using bootstrap analysis with 1000 replications (Felsenstein, 1985) for ML and with posterior probabilities for BI (Ronquist, Huelsenbeck, 2003). The phylogenetic trees of the sequenced nematodes were rooted on *Ascaris lumbricoides* Linnaeus, 1758, based on the findings of Li *et al*. (2018).

Results

Parasite fauna and other symbionts

No parasites were found in any of the 1300 small specimens of *Caprella* sp. from site 1. A total of four parasitic species were found in adult specimens of *C. septentrionalis* from sites

Table 1. Infection of skeleton shrimps *Caprella septentrionalis* (n=2970) by helminths in the WSBS area (data from sites 2–4 taken together).

Таблица 1. Зараженность козочек *Caprella septentrionalis* (n=2970) гельминтами в районе ББС МГУ (точки 2–4 объединены).

Parasite	Prevalence, %	Mean intensity (range)	Site of infection
Hysterothylacium aduncum	4.01	1.01 (1–2)	hemocoel
Echinorhynchus gadi	0.97	1.00 (1)	hemocoel
Pseudoterranova sp.	0.03	1.00 (1)	hemocoel
Progonus muelleri	0.07	1.00 (1)	hemocoel

2–4: progenetic metacercariae of the digenean *P. muelleri*, cystacanths of the acanthocephalan *E. gadi*, and third-stage juveniles of nematodes *Pseudoterranova* sp. and *H. aduncum*. The latter species was the most prevalent (Table 1). In one instance we recovered two specimens of *H. aduncum* from a single host specimen. In all other instances, one parasite per host specimen was found. Only two species were found in all three sites with infected *Caprella* individuals (2–4): *H. aduncum* and *E. gadi*.

Acanthocephalans and trematodes were usually found inside the two largest segments of the pereon, while nematodes migrated freely in the shrimp body. The parasites were not encapsulated.

Hydrozoan epibiont *Obelia* sp. (Hydrozoa: Campanulariidae) were occasionally found on the body surface of large specimens of *C. septentrionalis* but were never seen to penetrate the carapace. These hydrozoans are ubiquitous foulers in the White Sea, inhabiting all kinds of solid substrate.

Numerous free-living nematodes (*Enoplus communis* Bastian, 1865, *Chromadora* sp., *Linhomoeus* sp., *Leptosomatum* sp., *Chromadora* sp., *Pseudocella trichodes* (Leuckart, 1849)) were interwoven between the appendages and segments of the skeletons shrimps in all the four sites. The most abundant of them were *E. communis*. These nematodes were never found in the hemocoel. Apparently, they got entangled with the shrimps while migrating on the sea floor.

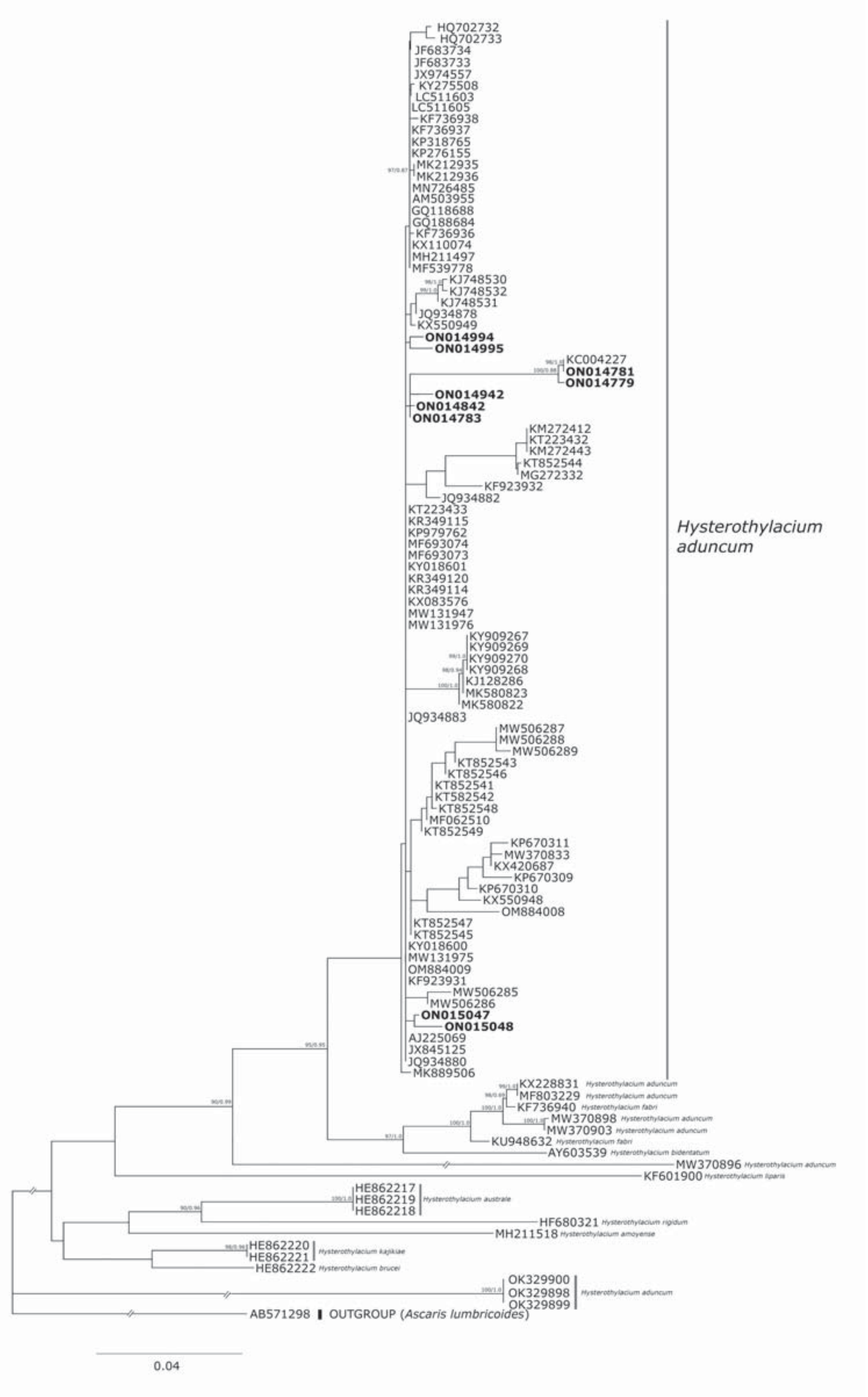
Molecular data

We obtained molecular data for nine specimens of *H. aduncum* and six specimens of *E. gadi.* ML and BI analyses based on the ITS1-5.8S-ITS2 rDNA sequences placed all the newly obtained sequences of *H. aduncum* in a large polytomic clade along with 82 sequences of this nematode species from GenBank (Fig. 2). Four out of the nine sequences, ON015047, ON015048, ON014994 and ON014995, were grouped into two separate subclades, two sequences in each. Sequences ON014779, ON014781, ON014783, ON014942, ON014842 formed a joint subclade with the sequence KC004227 obtained from a sample from the common sole, *Solea solea* (Linnaeus, 1758), in Egypt. However, this subclade was poorly resolved internally.

Several sequences available in GenBank under the name "*H. aduncum*" (KX228831, MF803229, MW370898, MW370896, MW370903, OK329898–OK329900) were grouped into lineages branching outside the

Fig. 2. Phylogenetic position of third-stage juveniles of *Hysterotylacium aduncum ex Carpella septentrionalis* from the White Sea reconstructed based on ML and BI analysis of ITS 1-5.8S-ITS2 rDNA sequences. References for the data retrieved from GenBank are listed in Table S1. The newly obtained sequences are in bold. The bootstrap values exceeding 80% are indicated; in case of smaller bootstrap values, the posterior probability values are also omitted. Scale bar shows the number of substitutions per site.

Рис. 2. Филогенетическое положение личинок III стадии *Hysterotylacium aduncum* из амфипод *Carpella septentrionalis,* отловленных в Белом моря, реконструированное на основе анализа последовательностей ITS1-5.8S-ITS2 локуса рДНК с помощью алгоритмов максимального правдоподобия и Байесовского метода. Ссылки на последовательности, полученные из GenBank, перечислены в таблице S1. Новые последовательности выделены жирным шрифтом. Указаны значения бутстрепа превышающие 80%; в случае меньшей величины бутстрепа значения апостериорной вероятности так же опущены. Масштабная линейка показывает количество замен на сайт.


HQ702732
HQ702733
JF683734
JF683733
JX974557
KY275508
LC511603
LC511605
KF736938
KF736937
KP318765
KP276155
97/0.87
MK212935
MK212936
MN726485
AM503955
GQ118688
GQ188684
KF736936
KX110074
MH211497
MF539778
98/1.0
99/1.0
KJ748530
KJ748532
KJ748531
JQ934878
KX550949
ON014994
ON014995
96/1.0
100/0.98
KC004227
ON014781
ON014779
ON014942
ON014842
ON014783
KM272412
KT223432
KM272443
KT852544
MG272332
KF923932
JQ934882
KT223433
KR349115
KP979762
MF693074
MF693073
KY018601
KR349120
KR349114
KX083576
MW131947
MW131976
KY909267
KY909269
99/1.0
KY909270
98/0.99
KY909268
100/1.0
KJ128286
MK580823
MK580822
JQ934883
MW506287
MW506288
MW506289
KT852543
KT852546
KT852541
KT582542
KT852548
MF062510
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KP670311
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KP670309
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KX550948
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KT852547
KT852545
KY018600
MW131975
OM884009
KF923931
MW506285
MW506286
ON015047
ON015048
AJ225069
JX845125
JQ934880
MK889506
Hysterothylacium aduncum
95/0.95
90/0.99
99/1.0
KX228831 *Hysterothylacium aduncum*
98/0.99
MF803229 *Hysterothylacium aduncum*
100/1.0
KF736940 *Hysterothylacium fabri*
100/1.0
MW370898 *Hysterothylacium aduncum*
MW370903 *Hysterothylacium aduncum*
100/1.0
97/1.0
KU948632 *Hysterothylacium fabri*
AY603539 *Hysterothylacium bidentatum*
MW370896 *Hysterothylacium aduncum*
KF601900 *Hysterothylacium liparis*
100/1.0
HE862217
HE862219
HE862218
Hysterothylacium australe
90/0.96
HF680321 *Hysterothylacium rigidum*
MH211518 *Hysterothylacium amoyense*
98/0.96
HE862220
HE862221
Hysterothylacium kajikiae
HE862222 *Hysterothylacium brucei*
100/1.0
OK329900
OK329898
OK329899
Hysterothylacium aduncum
AB571298 ▌ OUTGROUP (*Ascaris lumbricoides*)
0.04

Table 2. Prevalence (%) of helminths in *Caprella* spp. in the study localities.
Таблица 2. Экстенсивность инвазии гельминтами (%) *Caprella* spp. в изучаемых точках.

Species	Site	Prevalence of infection (%)			
		Hysterothylacium aduncum	*Echinorhynchus gadi*	*Pseudoterranova* sp.	*Progonus muelleri*
Caprella sp.	1. Kokoikha Island, n=1300	0	0	0	0
Caprella septentrionalis	2. Velikiy Island, n=616	2.92	0.81	0.16	0
	3. Yeremeevskiy Island, n=738	4.07	0.14	0	0.14
	4. Luda Kamenyuka, n=1616	4.39	0.87	0	0.06

main *H. aduncum* clade on our tree. Two of these lineages grouped in the same clade with the sequences of congeners *Hysterothylacium fabri* (Rudolphi, 1819) and *H. bidentatum* (Linstow, 1899). This clade appeared as a sister group to the main *H. aduncum* clade. Other lineages of "*H. aduncum*" mentioned above occupied a more basal position on our tree (Fig. 2).

Six partial sequences of the 28S rDNA gene of acanthocephalan cystacanths, morphologically assigned to *E. gadi*, fully coincided with the available sequences of *Echinorhynchus* cf. *bothniensis* Zdzitowiecki et Valtonen, 1987 (KM656143), *Echinorhynchus hexagrammi* Baeva, 1965 (LC625884) and *E. gadi* (MT020861, MT020862).

Discussion

In this study, we found a significant infection of *C. septentrionalis* with the larvae of helminths near WSBS (sites 2–4) and no infection at the site located at a considerable distance from it (site 1). We also provided the second molecular phylogenetic characterization of helminth larvae from caprellids in Arctic waters, after Sokolov *et al.* (2021).

The topology of the phylogenetic tree of *H. aduncum* in our study (Fig. 2) suggests that some specimens, whose sequences were located outside the main *H. aduncum* clade (KX228831, MF803229, MW370898, MW370903, MW370896 and OK329898–OK329900), had been incorrectly identified.

Our results confirm the conclusions that the 28S rRNA gene is inefficient for the identification of acanthocephalans at the species level (Wayland *et al.*, 2015; Kita, Kajihara, 2021; Amin *et al.*, 2021). For a reliable identification, these sequences should be combined with other markers such as cox1. Unfortunately, we failed to obtain these sequences, and so had to rely mainly on the morphological identification of *E. gadi*.

Adult skeleton shrimps die in July aged one year after releasing their young (Heptner, 1963; Kuznetsov, 1964). This means that we examined the population of *C. septentrionalis* when the shrimps had attained their maximal size and thus had accumulated the maximal possible number of parasites. The smaller body size of the shrimps collected near Kokoisha Island seems to be due to the differences in the relative productivity of the local community. The flow velocity in the Velikaya Salma strait is the greatest (1.7 m/sec) in the Eremeevsky tidal rapids (Naumov *et al.*, 2016); in its open parts it is naturally much lower. A high turbulence during the tidal motion results in a constant abundant supply of oxygen and biogenic substances essential for biomass growth (Tchesunov *et al.*, 2008)

The distribution of helminths of *C. septentrionalis* was markedly different between the sites where non-zero infection was recorded

(Table 1). The prevalence of *E. gadi* in large specimens (Table 2) was the same at sites 2 and 4 (0.81 and 0.87%, respectively), and much lower in site 3 (0.14%). The reasons behind these differences remain unclear. They may be due to a rather small sample size (in comparison with, e.g., studies of planktonic crustaceans) and the mosaic distribution of benthic invertebrates.

We cannot describe the distribution pattern of infection of skeleton shrimps with *Pseudoterranova* sp. and *P. muelleri* in the Velikaya Salma Strait because the number of infections was low. *Hysterothylacium aduncum* was the most prevalent parasite species. The prevalence of *H. aduncum* in *C. septentrionalis* was similar in the WSBS area (sites 2–4), varying from 2.92 to 4.39%.

Heptner (1963), in an article on the biology of reproduction and the life cycle of *C. septentrionalis*, made a brief note about a very high prevalence (37%) of infection by nematodes, trematodes, and acanthocephalans in the WSBS area. Unfortunately, he did not give the prevalence values separately for these three groups of parasites. Nevertheless, it is clear that the prevalence values in Heptner (1963) are much higher than those recorded in our study (max. 4.39%). He noted regular co-infections of a nematode and a trematode in skeleton shrimps, while acanthocephalans were always alone in hemocoel. Our research does not support this observation, since only one skeleton shrimp out of 4270 specimens examined was found to be infected by two helminth larvae (those of *H. aduncum*). It should be noted that Heptner (1963) did not indicate the year of collection of the material. The Materials and Methods section of his article and the date of the journal's publication suggest that *Caprella* specimens were most likely collected in 1962 or earlier.

Valter (1968) carefully studied the infection of *C. septentrionalis* by third-stage juveniles of *H. aduncum* (=*Contracaecum* sp.) in a small sample of 378 large and 95 small specimens collected in July, August, and October 1966 near WSBS. According to her records, the prevalence of infection in large females decreased from 19.5% in July to 9.5% in October. The infection in males was much lower: 0, 11.6 and 2.3% in July, August and October, respectively. Small specimens were not infected at all. In 1966–1975, Valter (1968) examined another 3047 skeleton shrimp at the same location mostly in summer and recorded that 9.42% were infected by digeneans *D. varicus*, *P. muelleri* (=*G. mulleri*), *P. atomon*, and *P. squamatus*; 5.15% were infected by third-stage juveniles of *H. aduncum*; 1.01% were infected by *E. gadi* pre-acanthella; and 0.19% were infected by cysticercoids of the cestode *H. microsoma*. It should be noted that the records of *P. squamatus* in *C. septentrionalis* seem to be erroneous. The second intermediate hosts of the bucephalids, to which *P. squamatus* belongs, are teleost fishes (Overstreet, Curran, 2002), not amphipods.

Valter (1976) observed various combinations of worms in *C. septentrionalis*, including combinations with acanthocephalans. This is in contrast with our results and the results of other authors. Later, Valter (1978) found a single specimen of *Pseudoterranova decipiens* (Krabbe, 1878) (=*Terranova decipiens*) in a skeleton shrimp and specified that the *E. gadi* infection rates varied from 0.5 to 6.3% in the WSBS area (Valter *et al*., 1980).

The results of our study and the published data indicate that the level of helminth infection in skeleton shrimps in the WSBS area in July decreased in the course of the recent decades: from 37% in 1962 (Heptner, 1963) to approx. 15% as the average long-term value from 1966–1975 (Valter, 1968; 1976; 1978) to less than 5% in 2019 (our data). The reasons of this dramatic decrease remain unclear. Recent environmental studies indicate a decline in the abundance of fish-associated parasites over the past century due to ocean warming (Wood *et al*., 2022), but no such studies have been conducted in the White Sea.

The data on infection of fish that feed on skeleton shrimps, e.g. the White Sea cod (see Timofeeva, Marasaeva, 1984) suggests that *C. septentrionalis* plays an important role in the transmission of parasites in the WSBS area. Parasites are known to be important drivers of energy flows, and their presence could promote consumption within food chains. They can affect the behavior and some other characteristics such as coloration of their invertebrate hosts, making the infected individual an easier prey to the downstream host (Bakker *et al*., 1997; Knudsen *et al*., 2001; Marcogliese, 2004). So far, however, there is no evidence that infection with any of the parasites recorded in *C. septentrionalis* leads to a decreased mobility, a discoloration or any other changes increasing the chances of this shrimps being eaten by fish. Neither do we know if the skeleton shrimps consumed by the cod or the navaga in the White Sea have an increased level of infection as compared to the mean prevalence of parasites in its population. This matter could be a promising direction of future research.

Conclusion

The larvae of four parasitic species were found: third-stage juveniles of the nematodes *Hysterothylacium aduncum* and *Pseudoterranova* sp., cystacanths of the acanthocephalan *Echinorhynchus gadi*, and progenetic metacercariae of the digenean *Progonus muelleri* in the marine amphipod *Caprella septentrionalis*. Skeleton shrimps collected at a distance from WSBS were uninfected. This striking difference seems to be associated with an unusual hydrological regime near WSBS. A high turbulence during tidal motion results in an abundant supply of oxygen and biogenic substances, promoting a high species diversity, biomass and abundance of hosts. Comparison with earlier studies showed a significant reduction in infection rates of skeleton shrimps since the middle of the 20th century.

Compliance with ethical standards

Conflict of interest. The authors declare that they have no conflict of interest.

Ethical approval. This article does not contain any studies with animals performed by any of the authors.

Sampling and field studies. All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable.

Supplementary data. The following materials are available online.

Table S1 List of species involved in the present phylogenetic analysis based on ITS1-5.8S-ITS2 rDNA sequences.

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References

Amin O.M., Heckmann R.A., Dallarés S., Constenla M., Kuzmina T. 2021. Morphological and molecular description of a distinct population of *Echinorhynchus gadi* Zoega in Müller, 1776 (Paleacanthocephala: Echinorhynchidae) from the pacific halibut *Hippoglossus stenolepis* Schmidt in Alaska // Acta Parasitol. Vol.66. No.3. P.881–898. https://doi.org/10.1007/s11686-021-00361-z

Arai H.P. 1989. Acanthocephala // L. Margolis, Z. Kabata (eds.). Guide to the parasites of fishes of Canada, Part III. Ottawa: Canadian Government Publishing Centre. 95 p.

Bakker T.C.M., Mazzi D., Zala S. 1997. Parasite-induced changes in behavior and color make *Gammarus pulex* more prone to fish predation // Ecology. Vol.78. No.4. P.1098–1104. https://doi.org/10.1890/0012-9658(1997)078[1098:PICIBA]2.0.CO;2

Busch M.W., Kuhn T., Julian M., Klimpel S. 2012. Marine crustaceans as potential hosts and vectors for metazoan parasites // H. Mehlhorn (ed.). Arthropods as Vectors of Emerging Diseases. Berlin: Springer. P.329–360. https://doi.org/10.1007/978-3-642-28842-5

Bush A.O., Lafferty K.D., Lotz J.M., Shostak A.W. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited // J. Parasitol. Vol. 83. No.4. P.575–583. https://doi.org/10.2307/3284227

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using bootstrap // Evolution. Vol.39. No.4. P.783–791.

Gibson D.I. 1996. Guide to the parasites of Canadian fishes. Part IV. Trematoda. Ottawa: NRC Research Press. 373 p.

Heptner M.V. 1963. [Reproduction biology and life cycle of *Caprella septentrionalis* Kroyer (Amphipoda, Caprellidea) in the White Sea] // Zool. Zhurn. Vol.42. No.11. P.1619–1630 [in Russian].

Holterman M., van der Wurff A., van den Elsen S., van Megen H., Bongers T., Holovachov O., Bakker J., Helder J. 2006. Phylum-wide analysis of SSU rDNA reveals deep phylogenetic relationships among nematodes and accelerated evolution toward crown clades // Mol. Biol. Evol. Vol.23. No.9. P.1792–1800. https://doi.org/10.1093/molbev/msl044

Izvekova E.I. 1964. [On the nutrition of cod (*Gadus morhua maris-albi* Der.) in the western part of the White Sea (Great Salma)] // Voprosy Ikhtiologii. Vol.4. No.2. P.354–364 [in Russian].

Kita Y., Kajihara H. 2021. Morphological and molecular characterization of the marine-teleost parasitizing acanthocephalan *Echinorhynchus hexagrammi* (Syndermata: Palaeacanthocephala) from a new host, *Liparis* sp. (Actinopterygii: Scorpaeniformes) // Parasitol. Int. Vol.85. Art.102430. https://doi.org/10.1016/j.parint.2021.102430

Knudsen R., Gabler H.M., Kuris A.M., Amundsen P.A. 2001. Selective predation on parasitized prey — a comparison between two helminth species with different life-history strategies // J. Parasitol. Vol.87. No.5. P.941–945. https://doi.org/10.1645/0022-3395(2001)087[0941:SPOPPA]2.0.CO;2

Kumar S., Stecher G., Li M., Knyaz C., Tamura K. 2018. MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms // Mol. Biol. Evol. Vol.35. No.6. P.1547–1549. doi:10.1093/molbev/msy096

Kuznetsov V.V. 1964. [Biology of the abundant and most common species of crustaceans at the Barents and White seas]. Moscow, Leningrad: Izdatel'stvo "Nauka". 241 p. [In Russian]

Li L., Lü L., Nadler S.A., Gibson D.I., Zhang L.P., Chen H.X., Zhao W.T., Guo Y.N. 2018. Molecular phylogeny and dating reveal a terrestrial origin in the Early Carboniferous for ascaridoid nematodes // Syst. Biol. Vol.67. No.5. P.888–900. https://doi.org/10.1093/sysbio/syy018.

Littlewood D.T.J., Curini-Galletti M., Herniou E.A. 2000. The inter-relationships of Proseriata (Platyhelminthes: Seriata) tested with molecules and morphology // Mol. Phyl. Evol. Vol.16. No.3. P.449–466. https :// doi.org/10.1006/mpev.2000.0802

Logvinenko A.D., Gordeev I.I. 2022. Metazoan parasites of a few marine fish near White Sea Biological Station (Lomonosov MSU) // A.I. Granovich (ed.). Abstracts of the White Sea student scientific session of SPbGU – 2022, 02 February 2022. St. Petersburg: St. Petersburg State University. P.75.

Marcogliese D.J. 2004. Parasites: small players with crucial roles in the ecological theater // EcoHealth. Vol.1. P.151–164. https://doi.org/10.1007/s10393-004-0028-3

Moravec F. 1994. Parasitic nematodes of freshwater fishes of Europe. Praha: Academia. 473 p.

Naumov A.D., Mokievskiy V.O., Chava V.A. 2016. [Tides in the Rugozerskaya Inlet and adjacent water-basins (White Sea, Kandalaksha Bay)] // Trudy Belomorskoy Biostantsii MGU. Vol.12. P.74–90 [in Russian].

Ouspenskaia A.V. 1960. Parasitofaune des crustacés benthiques de la mer de barents-(Exposé préliminaire) // Ann. Parasitol. Hum. Comp. Vol.35. No.3. P.221–242

Overstreet R.M., Curran S.S. 2002. Superfamily Bucephaloidea Poche, 1907 // D.I. Gibson, A. Jones, R.A. Bray (eds.). Keys to the Trematoda, Vol.1. Wallingford: CABI Publishing and the Natural History Museum. P.67–110.

Ronquist F., Huelsenbeck J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models // Bioinformatics. Vol.19. No.12. P.1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Shulman S.S., Shulman-Albova R.E. 1953. [Parasites of fish of the White Sea]. Moscow-Leningrad: Izdatel'stvo akademii nauk SSSR. 200 p. [In Russian]

Sokolov S.G., Atopkin D.M., Gordeev I.I. 2021. Phylogenetic position of the hemiuroid genus *Paraccacladium* Bray & Gibson, 1977 (Trematoda: Hemiuroidea) and the taxonomic status of the subfamily Paraccacladiinae Bray & Gibson, 1977 // Mar. Biol. Res. Vol.17. No.1. P.31–40. https://doi.org/10.1080/17451000.2021.1891252

Talavera G., Castresana J. 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments // Syst. Biol. Vol.56. No.4. P.564–577. https://doi.org/10.1080/10635150701472164

Tchesunov A.V., Kaljakina N.M., Bubnova E.N. (eds) 2008. [A catalogue of biota of the White Sea Biological Station of the Moscow State University]. Moscow: KMK Scientific Press Ltd. 384 p. [In Russian]

Timofeeva S.V., Marasaeva E.F. 1984. [Parasitofauna of two forms of cod of Kandalaksha Bay of the White Sea] // Yu.I. Poljansky (ed.). Ekologo-parazitologièeskie issledovaniya severnykh morei. Apatity: Kol'skiy filial AN SSSR. P.62–76 [in Russian].

Uspenskaya A.V. 1954. [Parasitofauna of benthic crustaceans of East Murman] // Trudy Problemnykh i tematicheskih soveshchaniy. Vol.4. P.123–127 [in Russian].

Valter E.D. 1968. [*Caprella septentrionalis* Kroyer (Amphipoda, Caprellidae) – intermediate host of nematodes of the genus *Contracaecum* Railliet et Henry] // Zool. Zhurn. Vol.47. No.1. P.127–131 [in Russian].

Valter E.D. 1976. [Helminths of the skeleton shrimp *Caprella septentrionalis* Kroyer of the Rugozersky Bay area of the White Sea] // Kratkie tezisy dokladov II-go Vsesojuznogo simpoziuma po parazitam i boleznyam morskikh zhivotnyh. Kaliningrad: AtlantNIRO. P.11–12 [in Russian].

Valter E.D. 1978. [Detection of *Terranova decipiens* (Nematoda, Ascaridata) in the amphipod *Caprella septentrionalis* Kroyer] // Vestnik Moskovskogo Universiteta. Serija Biologièeskaja. Vol.3. P.12–14 [in Russian].

Valter E.D., Kondrashkova A.N., Popova T.I. 1980. [*Caprella septentrionalis* Kroyer – intermediate host *Echinorhynchus gadi* Muller, 1776] // M.A. Babjaskans, O.N. Bauer, T.A. Ginecinskaja, (eds.). Voprosy parazitologii vodnykh zhivotnykh (Tematicheskiy sbornik). Vilnius: Institut zoologii i parazitologii AN Litovskoi SSR. P.19–20 [in Russian].

Wayland M.T., Vainio J.K., Gibson D.I., Herniou E.A., Littlewood D.T.J., Vainola R. 2015. The systematics of *Echinorhynchus* Zoega in Müller, 1776 (Acanthocephala, Echinorhynchidae) elucidated by nuclear and mitochondrial sequence data from eight European taxa // ZooKeys. Vol.484. P.25–52. https://doi.org/10.3897/zookeys.484.9132

Wood C.L., Welicky R.L., Preisser W.C., Leslie K.L., Mastick N., Greene C., Maslenikov K.P., Tornabene L., Kinsella J.M., Essington T.E. 2023. A reconstruction of parasite burden reveals one century of climate-associated parasite decline // Proc. Natl. Acad. Sci. U.S.A. Vol.120. No.3. Art.e2211903120. https://doi.org/10.1073/pnas.2211903120

Zhu X.Q., Gasser R.B., Podolska M., Chilton N. 1998. Characterization of anisakid nematodes with zoonotic potential by nuclear ribosomal DNA sequences // Int. J. Parasitol. Vol.28. No.12. P.1911–1921. https://doi.org/10.1016/S0020-7519(98)00150-7

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