

Review

Epibiotic Communities of Common Crab Species in the Coastal Barents Sea: Biodiversity and Infestation Patterns

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Abstract: Crabs are important ecosystem engineers in marine habitats worldwide. Based on long-term data, we analyzed the species composition and infestation indices of epibionts and symbionts colonizing the great spider crab, *Hyas araneus*, and two lithodid crabs—the northern stone crab, *Lithodes maja*, and the red king crab, *Paralithodes camtschaticus*—in the coastal zone of the Barents Sea. The epibiotic communities found on great spider crabs were closer to northern stone crabs (33%) compared to red king crabs (25%). The prevalence of mobile symbionts (amphipods, *Ischyrocerus*, and polychaetes, *Harmothoe*) and common epibionts, such as barnacles and hydrozoans, was low on great spider crabs and high on the body and in the gills of lithodid crabs. Epiphytes were abundant on great spider crabs but not present on both species of lithodid crabs. Egg symbionts found on *H. araneus* and *P. camtschaticus* do not affect their local populations. Differences in the fouling communities found on the three crab species are associated with host size range, surface properties of their carapaces, and behavior patterns.

Keywords: Barents Sea; epibionts; symbionts; *Hyas araneus*; *Paralithodes camtschaticus*; *Lithodes maja*



Citation: Dvoretzky, A.G.; Dvoretzky, V.G. Epibiotic Communities of Common Crab Species in the Coastal Barents Sea: Biodiversity and Infestation Patterns. *Diversity* **2022**, *14*, 6. <https://doi.org/10.3390/d14010006>

Academic Editors: Michael Wink and Piero G. Giulianini

Received: 13 December 2021

Accepted: 21 December 2021

Published: 23 December 2021

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1. Introduction

Only a few species of relatively large crustaceans occur in the coastal zone of the Barents Sea. Among them, the highest abundance and biomass are registered for one member of the family Oregonidae, the great spider crab, *Hyas araneus* (Linnaeus, 1758), and two members of the family Lithodidae, the red king crab, *Paralithodes camtschaticus* (Tilesius, 1815), and the northern stone crab, *Lithodes maja* (Linnaeus, 1758). Unlike to the true crab, *Hyas araneus*, which has the normal five pairs of legs, lithodid crabs are considered to be a crab-like species because their 5th pair of legs is reduced and hidden under the carapace where it is used to clean the crab gills. In the literature, however, *L. maja* and *P. camtschaticus* are also referred to as “crabs”. Great spider crabs and northern stone crabs are native inhabitants of the Barents Sea and both have no commercial value [1], while red king crabs were introduced into the Barents Sea from the North Pacific and are considered to be a highly valued delicacy on the international market [2,3] and a source for producing valuable biochemical substances [4]. Although, in the coastal Barents Sea, each species has specific ecological and ethological features [1,2,5–7], these crabs often occur at the same locations.

Epibiosis is a common phenomenon in aquatic systems, especially in marine environments where wave turbulence has caused many mobile and sessile organisms to evolve a system of settlement and attachment to hard, relatively stable surfaces provided by other organisms [8–10]. The calcified body surface of decapod crustaceans is known to be a suitable substrate for many species of marine animals and plants [8,11–13]. Investigations have focused on studying the nature of epibiosis. This is important because they can contribute to basic knowledge on important aspects of the hosts' biology including molting and growth patterns, behavior, and migration activity [14]. In many cases, studies on the flora and fauna associated with living marine invertebrates can provide new information on

Table 1. Cont.

Taxa	<i>Hyas araneus</i>			<i>Lithodes maja</i>			<i>Paralithodes camtschaticus</i>		
	Pr 95%C.I.	Int X ± SE	Range	Pr 95%C.I.	Int X ± SE	Range	Pr 95%C.I.	Int X ± SE	Range
<i>Ulvaria obscura</i> (Kützing) P.Gayral ex C.Bliding, 1969	<u>23.1</u> 10–36	–	–	–	–	–	–	–	–
Hydrozoa									
<i>Coryne hincksi</i> Bonnevie, 1898	<u>2.6</u> 0–8	–	–	–	–	–	–	–	–
<i>Halecium beanii</i> (Johnston, 1838)	<u>2.6</u> 0–8	–	–	–	–	–	<u>2.4</u> 0–7	–	–
<i>Obelia geniculata</i> (Linnaeus, 1758)	<u>10.3</u> 1–20	–	–	<u>48.6</u> 33–65	–	–	<u>4.8</u> 1–11	–	–
<i>Obelia longissima</i> (Pallas, 1766)	<u>17.9</u> 6–30	–	–	<u>94.6</u> 87–100	–	–	<u>66.7</u> 52–81	–	–
Turbellaria									
<i>Peraclistus oophagus</i> (Friedmann, 1924)	<u>23.1</u> 10–36	–	–	–	–	–	–	–	–
Nemertini									
Nemertini g. sp.	<u>10.3</u> 1–20	15.8 ± 10.1	4–46	<u>10.8</u> 1–21	4.3 ± 2.6	1–12	<u>2.4</u> 0–7	1.0 ± 0.0	1–1
Polychaeta									
<i>Bushiella (Jugaria) similis</i> (Bush, 1905)	–	–	–	<u>2.7</u> 0–8	2.0 ± 0.0	2–2	–	–	–
<i>Circeis armoricana</i> Saint-Joseph, 1894	<u>38.5</u> 23–54	23.9 ± 6.5	3–93	<u>59.5</u> 44–75	89.4 ± 32.5	4–345	<u>33.3</u> 19–48	5.3 ± 2.3	1–33
<i>Eumida sanguinea</i> (Oersted, 1843)	–	–	–	<u>5.4</u> 0–13	1.5 ± 0.5	1–2	<u>2.4</u> 0–7	1.0 ± 0.0	1–1
<i>Harmothoe imbricata</i> (Linnaeus, 1767)	–	–	–	<u>70.3</u> 56–85	1.3 ± 0.2	1–3	<u>33.3</u> 19–48	1.4 ± 0.2	1–3
<i>Lepidonotus squamatus</i> (Linnaeus, 1758)	–	–	–	<u>2.7</u> 0–8	1.0 ± 0.0	1–1	–	–	–
<i>Placostegus tridentatus</i> (Fabricius, 1779)	<u>43.6</u> 28–59	–	–	<u>64.9</u> 49–80	–	–	–	–	–
<i>Protula tubularia</i> (Montagu, 1803)	<u>7.7</u> 1–16	1.3 ± 0.6	1–2	–	–	–	–	–	–
<i>Spirobranchus triqueter</i> (Linnaeus, 1758)	<u>20.5</u> 8–33	1.9 ± 0.5	1–5	<u>8.1</u> 1–17	–	–	–	–	–
Hirudinea									
<i>Crangonobdella fabricii</i> (Malm, 1863)	–	–	–	–	–	–	<u>2.4</u> 0–7	2.0 ± 0.0	2–2
<i>Johanssonia arctica</i> (Johansson, 1898)	–	–	–	<u>2.7</u> 0–8	3.0 ± 0.0	3–3	<u>11.9</u> 2–22	1.4 ± 0.2	1–2
<i>Platibdella olriki</i> (Malm, 1863)	<u>2.6</u> 0–8	1.0 ± 0.0	1–1	–	–	–	–	–	–
Bivalvia									
<i>Heteranomia squamula</i> (Linnaeus, 1758)	<u>7.7</u> 1–16	3 ± 1.5	1–6	<u>48.6</u> 33–65	13.9 ± 9.4	1–79	<u>9.5</u> 1–18	2 ± 0.7	1–4
<i>Hiatella arctica</i> (Linnaeus, 1767)	–	–	–	<u>13.5</u> 2–25	4.4 ± 2.4	1–5	<u>4.8</u> 1–11	1.5 ± 0.5	1–2
<i>Mytilus edulis</i> Linnaeus, 1758	<u>10.3</u> 1–20	1.3 ± 0.3	1–2	<u>32.4</u> 17–48	1.4 ± 0.2	1–3	<u>26.2</u> 13–39	2.1 ± 0.6	1–8
Gastropoda									
<i>Margarites</i> sp.	<u>5.1</u> 1–12	4.5 ± 3.5	1–8	–	–	–	–	–	–
Copepoda									
<i>Calanus finmarchicus</i> (Gunner, 1765)	<u>2.6</u> 0–8	1.0 ± 0.0	1–1	–	–	–	–	–	–
<i>Ectinosoma neglectum</i> Sars G.O., 1904	<u>25.6</u> 12–39	44.5 ± 25.5	1–269	<u>2.7</u> 0–8	2.0 ± 0.0	2–2	–	–	–
<i>Harpacticus uniremis</i> Krøyer, 1842	<u>46.2</u> 31–62	10.8 ± 5.6	1–101	–	–	–	<u>2.4</u> 0–7	1.0 ± 0.0	1–1
<i>Tisbe furcata</i> (Baird, 1837)	<u>30.8</u> 16–45	79.3 ± 18.3	7–235	<u>8.1</u> 1–17	2.0 ± 0.6	1–3	<u>2.4</u> 0–7	17.0 ± 0.0	17–17

Table 1. Cont.

Taxa	<i>Hyas araneus</i>			<i>Lithodes maja</i>			<i>Paralithodes camtschaticus</i>		
	Pr 95% C.I.	Int X ± SE	Range	Pr 95% C.I.	Int X ± SE	Range	Pr 95% C.I.	Int X ± SE	Range
<i>Zaus abbreviatus</i> Sars G.O., 1904	<u>2.6</u> 0–8	1.0 ± 0.0	1–1	–	–	–	–	–	–
Amphipoda									
<i>Ampelisca</i> sp.	–	–	–	–	–	–	<u>2.4</u> 0–7	1.0 ± 0.0	1–1
<i>Gammarellus homari</i> (Fabricius, 1779)	<u>10.3</u> 1–20	1.0 ± 0.0	1–1	<u>5.4</u> 0–13	2.0 ± 1.0	1–3	<u>2.4</u> 0–7	1.0 ± 0.0	1–1
<i>Hippomedon propinquus</i> G.O. Sars, 1890	<u>5.1</u> 1–12	2.5 ± 1.5	1–4	–	–	–	–	–	–
<i>Ischyrocerus anguipes</i> Krøyer, 1838	<u>12.8</u> 2–23	5.8 ± 4.1	1–22	<u>48.6</u> 33–65	9.1 ± 1.2	1–23	<u>52.4</u> 37–67	9.4 ± 3.4	1–70
<i>Ischyrocerus commensalis</i> Chevreux, 1900	<u>5.1</u> 1–12	5.5 ± 1.5	4–7	<u>94.6</u> 87–100	26.5 ± 3.5	8–109	<u>100.0</u> 100–100	79.8 ± 11.6	5–492
Cirripedia									
<i>Balanus balanus</i> (Linnaeus, 1758)	<u>2.6</u> 0–8	9.0 ± 0.0	9–9	<u>35.1</u> 20–51	1.7 ± 0.2	1–3	<u>4.8</u> 1–11	1.5 ± 0.5	1–2
<i>Balanus crenatus</i> Brugiere 1789	–	–	–	<u>32.4</u> 17–48	3.2 ± 0.6	1–8	<u>26.2</u> 13–39	2.9 ± 0.8	1–9
<i>Verruca stroemia</i> (O.F. Muller, 1776)	<u>2.6</u> 0–8	3.0 ± 0.0	3–3	–	–	–	–	–	–
Bryozoa									
<i>Bugula harmsworth</i> Waters, 1900	<u>5.1</u> 1–12	–	–	–	–	–	–	–	–
<i>Callopora lineata</i> (Linnaeus, 1767)	<u>7.7</u> 1–16	–	–	<u>29.7</u> 15–44	–	–	<u>4.8</u> 1–11	–	–
<i>Crisia denticulata</i> (Lamarck, 1816)	–	–	–	<u>10.8</u> 1–21	–	–	–	–	–
<i>Disporella hispida</i> (Fleming, 1828)	<u>7.7</u> 1–16	–	–	<u>27.0</u> 13–41	–	–	<u>4.8</u> 1–11	–	–
<i>Patinella verrucaria</i> (Linnaeus, 1758)	<u>15.4</u> 4–27	–	–	<u>13.5</u> 2–25	–	–	<u>2.4</u> 0–7	–	–
<i>Porella smitti</i> Kluge, 1907	<u>2.6</u> 0–8	–	–	–	–	–	–	–	–
<i>Tricellaria arctica</i> Busk, 1855	<u>10.3</u> 1–20	–	–	<u>18.9</u> 6–32	–	–	<u>4.8</u> 1–11	–	–

Note: Pr—prevalence of infestation (% of infested crabs, above the line), 95% C.I.—95% confidence interval (below the line), Int—intensity of infestation (individuals per infested crab), X—mean, SE—standard error.

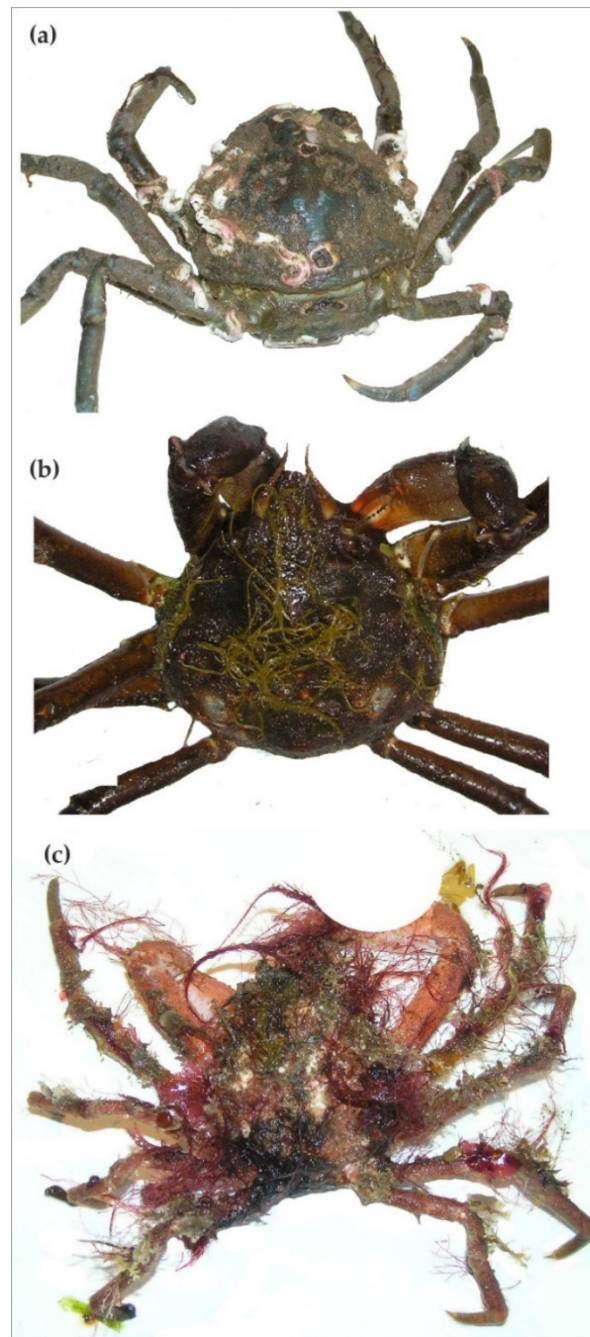


Figure 1. *Hyas araneus*. Adult great spider crabs colonized by the brown algae, *Dictyosiphon foeniculaceus*, (a) the polychaete, *Spirobranchus triqueter* (b), and a young crab decorated with epiphytes (c).

2.2. *Lithodes maja*

A total of 26 taxa were registered on the northern stone crabs (Table 1) with the highest prevalence found for typical epibionts [5,30,36]. Attached species were presented by the hydrozoans, *Obelia*, and the polychaetes, *Placostegus tridentatus* and *Circeis armoricana* (Figure 2a). Mobile species were presented by the symbiotic amphipods, *Ischyrocerus commensalis*, which predominantly colonized the mouthparts and gills, and by polynoid polychaetes, *Harmothoe imbricata*. The mean CW of *L. maja* was 91.9 ± 1.3 , ranging from 77.0–101.0 mm.

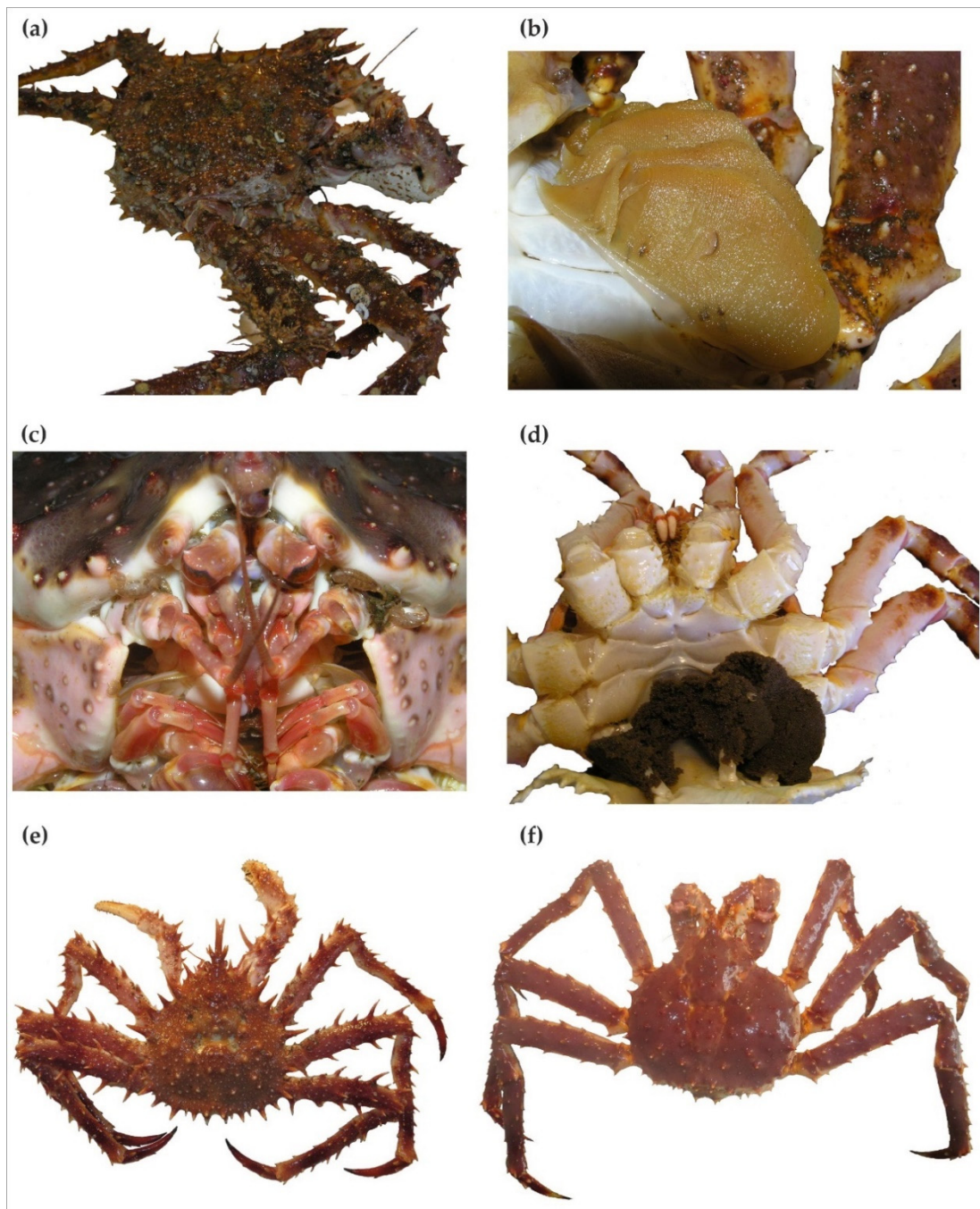


Figure 2. *Lithodes maja* and *Paralithodes camtschaticus*. Typical epibiotic community of northern stone crabs (a). Symbiotic amphipods, *Ischyrocerus commensalis*, in the gills (b), on the mouthparts (c), and on the egg masses (d) of red king crabs. Carapaces of a recently molted northern stone crab (e) and red king crab (f).

2.3. *Paralithodes camtschaticus*

Among 25 taxa of associated species found on red king crabs in the coastal Barents Sea, the amphipods, *Ischyrocerus commensalis* (in the gills and on the mouthparts, Figure 2b,c) and *Ischyrocerus anguipes* (on the carapace and limbs), as well as the hydrozoan, *Obelia longissima* (on the carapace and limbs), had the highest frequency of occurrence (Table 1). Symbiotic amphipods were also registered on the female egg clutches, but these findings were rare (Figure 2d). The mean CW of *P. camtschaticus* was 154.9 ± 3.2 , with a size range of 121.5–227.0 mm.

3. Comparison of Epibiotic Communities

3.1. General Patterns

The epibiont prevalence differs significantly among the three crab species [30]. The maximum similarity was seen in the case of congeneric species, *L. maja* and *P. camtschaticus* (Bray–Curtis similarity index 64%), and the minimum similarity was registered for *P. camtschaticus* and *H. araneus* (25%).

In the case of *L. maja* and *H. araneus*, this index was 33%. In the case of *H. araneus* and *L. maja*, the maximum contribution to the dissimilarity was registered for *Ischyrocerus commensalis*, *Obelia longissima*, *Harmothoe imbricata*, and *Harpacticus uniremis*. In the case of *H. araneus* and *P. camtschaticus*, the most important species were *Ischyrocerus commensalis*, *Obelia longissima*, *Harpacticus uniremis*, *Placostegus tridentatus*, and *Ischyrocerus anguipes*. Dissimilarity between fouling communities of *L. maja* and *P. camtschaticus* was attributed to nine species (each had a contribution of 5% or higher): *Placostegus tridentatus*, *Obelia geniculata*, *Heteranomia scuamula*, *Harmothoe imbricata*, *Balanus balanus*, *Obelia longissima*, *Circeis armoricana*, *Callopora lineata*, and *Disporella hispida* (Table 2). These results are also supported by Chi-square tests (Table S1).

Table 2. Results of the SIMPER analysis on infestation indices: contributions of main taxa (%) to dissimilarities within different crab species in the coastal Barents Sea.

Taxa	Comparisons		
	<i>Lithodes</i> vs. <i>Hyas</i>	<i>Paralithodes</i> vs. <i>Hyas</i>	<i>Paralithodes</i> vs. <i>Lithodes</i>
<i>Acrosiphonia</i> sp.	1.94	2.42	–
<i>Chordaria flagelliformis</i>	2.77	3.46	–
<i>Desmarestia aculeata</i>	1.39	1.73	–
<i>Dictyosiphon foeniculaceus</i>	2.49	3.11	–
<i>Palmaria palmata</i>	3.05	3.80	–
<i>Ptilota gunneri</i>	3.33	4.15	–
<i>Saccharina latissima</i>	–	1.38	–
<i>Ulvaria obscura</i>	2.49	3.11	–
<i>Obelia geniculata</i>	4.15	–	10.02
<i>Obelia longissima</i>	8.29	6.57	6.37
<i>Peraclistus oophagus</i>	2.49	3.11	–
Nemertini g. sp.	–	1.06	1.92
<i>Circeis armoricana</i>	2.27	–	5.96
<i>Harmothoe imbricata</i>	7.60	4.50	8.43
<i>Placostegus tridentatus</i>	2.30	5.88	14.81
<i>Protula tubularia</i>	–	0.84	–
<i>Spirobranchus triqueter</i>	1.34	2.77	1.85
<i>Johanssonia arctica</i>	–	1.61	2.10
<i>Heteranomia scuamula</i>	4.43	–	8.93
<i>Hiatella arctica</i>	1.46	–	2.00
<i>Mytilus edulis</i>	2.40	2.15	1.42
<i>Ectinosoma neglectum</i>	2.48	3.46	–
<i>Harpacticus uniremis</i>	4.99	5.90	–
<i>Tisbe furcata</i>	2.45	3.83	–
<i>Gamarellus homari</i>	–	1.06	–
<i>Ischyrocerus anguipes</i>	3.87	5.34	–
<i>Ischyrocerus commensalis</i>	9.67	12.80	–
<i>Balanus balanus</i>	3.52	–	6.93
<i>Balanus crenatus</i>	3.51	3.53	1.42
<i>Callopora lineata</i>	2.38	–	5.70
<i>Crisia denticulata</i>	1.17	–	2.47
<i>Lichenopora hispida</i>	–	–	5.08
<i>Lichenopora verrucaria</i>	2.09	1.75	2.54
<i>Scrupocellaria arctica</i>	–	0.74	3.23

The mean intensity of *Ischyrocerus commensalis* on great spider crabs is significantly lower than on lithodid crabs, while this index calculated for *Ischyrocerus anguipes* is similar on all three crab species [37,38,42]. The same results were found for the bivalve mollusks, *Mytilus edulis* and *Heteranomia squamula*, and the barnacle, *Balanus crenatus* (Table S2). The

mean intensity of *Circeis armoricana* did not vary significantly between great spider crabs and northern stone crabs, but was significantly higher compared to red king crabs [5,30,36].

3.2. Factors: Ecology and Behavior of Hosts

The most diverse assemblage of fouling organisms was registered on great spider crabs. This result is linked to the presence of algae on their carapaces. In contrast to *Hyas araneus*, no algae species were found on red king crabs and northern stone crabs. It is most likely that this pattern is associated with the ecology of *H. araneus* in the coastal Barents Sea where these crabs usually occur at 5–25 m depths in laminarian kelps. At deeper sites, *H. araneus* is distributed on rocky or muddy bottoms [26]. In contrast to adult lithodid crabs, algae play an important role in the ration of great spider crabs [1,43]. This increases a chance to be fouled by algae for *H. araneus*.

In addition, some authors classify *H. araneus* as decorators, i.e., crabs which actively attach foreign matter to their bodies or external structures aiming to protect themselves against predators and/or abiotic forces [44,45]. In *Hyas*, this behavior pattern seems to take place at the early stages of ontogenesis (Figure 1c) because epibiotic algae were rarely seen on great spider crabs that reached a terminal molt, suggesting only passive settlement of algal zoospores on the carapace [38]. Similar behavior was registered for other spider crabs such as *Maja squinado* [46] and *Maja crispata* [47].

We registered a relatively high incidence of infestation of the turbellarian worm, *Peraclistus oophagus*, on *H. araneus*. This species is known to be an egg predator [48] and, therefore, it was found only on the female egg masses. However, negative effects for the host are negligible due to the high fecundity of *H. araneus* [48]. *Peraclistus* were not recorded on the egg clutches of northern stone crabs and red king crabs in contrast to the symbiotic amphipods, *Ischyrocerus commensalis*. The last species, however, is considered to be a scavenger rather than a true egg predator; its presence could have a positive effect because *Ischyrocerus commensalis* ingests dead eggs and, therefore, may be responsible for sanitary tasks [17].

3.3. Factors: Ecology and Behavior of Epibionts

Heavy fouling by epiphytes on the exoskeleton of great spider crabs leads to lower infestation levels of other attached species [38]. This explains the rare occurrence of hydrozoans on *H. araneus*. In older crabs, epibiotic algae are replaced by sedentary polychaete worms, which are also preventing other epibionts to settle on the host carapaces [38]. This fact partially explains the low infestation indices of symbiotic amphipods on the great spider crabs compared to red king crabs. However, the main reason is that the amphipods cannot find suitable food on great spider crabs; this is confirmed by the rare localization of these symbionts on the mouthparts of *H. araneus*. An opposite pattern is registered for lithodid crabs, especially for red king crabs. The ischyrocerid amphipods are known to feed on the crab food remnants and detritus concentrated on the mouthparts and limbs of their hosts [16,34,42]. Both inter- and intra-specific competition was reported for *Ischyrocerus commensalis* [49,50], confirming its adaptation to symbiotic lifestyle on king crabs [42]. Similar relationships were described for the amphipod, *Caprella unguilina*, on the subantarctic false king crab, *Paralomis granulosa* [51].

We found a less frequent occurrence of the symbiotic amphipods in the gills of great spider crabs but higher prevalences of small copepods compared to lithodid crabs. This result is explained by the fact that the carapace of *H. araneus* is more tightly attached to the body than in the case of lithodid crabs, preventing colonization of their respiration organs by large amphipods [1,25]. In contrast, small copepods may easily occupy great spider crabs as a result of being drawn into the gills during the host respiration activity; they can live here without competition with other symbionts, in contrast to the gill community of red king crabs, where large amphipod specimens can feed on harpacticoid copepods [35].

3.4. Factors: Host Size and Carapace Properties

Although the diversity of associated organisms is higher on great spider crabs, they have lower infestation indices than we registered on both species of lithodid crabs: the maximum prevalence of each epibiont is 50% on *H. araneus*, and 100% on *L. maja* and *P. camtschaticus*. Most likely, this pattern reflects the size differences observed among the crab species: the smallest CW is registered for great spider crabs and the largest size for red king crabs [52]. Smaller hosts have less surface area for settling, and a positive association between body size and infestation indices was reported for many decapod–crustacean–epibiotic associations across the world’s oceans [8,11,53–56].

The fouling community of the great spider crab is closer to that observed on another native species, the northern stone crab, rather than the red king crab. This result is associated with the higher prevalence of sedentary polychaetes on *L. maja* compared to *P. camtschaticus*. It is known that juvenile northern stone crabs have a great number of spines, most of which become reduced as the crabs mature [1]; hence, the carapace and limbs of northern stone crabs are rough in comparison to the smooth body surface of red king crabs (Figure 2e,f) [36]. Irregular rough surfaces have been shown to be a more favorable substrate for settlement of typical attached taxa [57,58] and, therefore, support the highest species richness, abundance, and diversity [59,60], explaining the higher proportions of tubular polychaetes, hydrozoans, and bryozoans on *L. maja*.

The chemical composition of the body surface also differs significantly between great spider crabs and lithodid crabs so that the green- and brown-green-colored carapaces of *H. araneus* consist of higher proportions of N and P than the red-colored carapaces of *L. maja* and *P. camtschaticus* [61]. Such surfaces are more favorable for algal zoospores because they have been shown to demonstrate positive chemotaxis to substrata rich in N and P [62].

4. Conclusions

Our comparative study has shown that great spider crabs harbored lower numbers of mobile symbionts (the corophioid amphipods, *Ischyrocerus commensalis* and *Ischyrocerus anguipes*, and the polynoid polychaetes, *Harmothoe imbricata*) than the crabs in the family Lithodidae. Typical attached taxa, such as barnacles and hydrozoans, were also less abundant on the great spider crabs. The main feature of the *Hyas araneus* fouling community is the presence of epiphytes, which were not found on the lithodid crabs analyzed. The main differences in the structure of epibiotic assemblages on the three crab species are linked with differences in their body size, surface properties of the carapace, and behavior patterns. Egg symbionts, such as the tubellarian worm, *Peraclistus oophagus*, on *Hyas araneus* and the amphipod, *Ischyrocerus commensalis*, on *Paralithodes camtschaticus*, seem to have no or a negligible impact on the host populations.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d14010006/s1>, Table S1: Differences among the prevalences of associated organisms on great spider crabs (*Hyas araneus*), northern stone crabs (*Lithodes maja*), and red king crabs (*Paralithodes camtschaticus*) as revealed by Chi-square tests; Table S2: Differences among mean intensities of common associated organisms on great spider crabs (*Hyas araneus*), northern stone crabs (*Lithodes maja*), and red king crabs (*Paralithodes camtschaticus*), as revealed by Kruskal–Wallis tests, followed by Bonferroni tests for medians.

Author Contributions: Conceptualization, A.G.D.; methodology, A.G.D.; validation, A.G.D. and V.G.D.; investigation, A.G.D. and V.G.D.; visualization V.G.D.; writing—original draft, A.G.D. All authors have read and agreed to the published version of the manuscript.

Funding: This study was funded by the Ministry of Science and Higher Education of the Russian Federation.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

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