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Marine protozoan epibionts on the copepod *Lepeophtheirus salmonis*, parasite of the Atlantic salmon

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Abstract

Two species of ciliate suctorian protozoa belonging to the genus *Ephelota*, *E. gemmipara* and *E. gigantea*, were found as epibionts on the marine copepod *Lepeophtheirus salmonis* (salmon louse), an ectoparasite of marine salmonid fish, including the Atlantic salmon, *Salmo salar*. Epibionts were distributed over the cephalothoracic shield, genital segment, abdomen and caudal branches of the copepods. Individuals from both species possessed two types of tentacles: long, prehensile, pointed tentacles and short, adhesive, capitate feeding tentacles. Both species contained a highly ramified and lobated macronucleus. *E. gemmipara* showed a rounded cellular body attached to a stalk possessing longitudinal and transversal striations but lacking a suprastylar extension. *E. gigantea* had an umbrella-shaped cellular body significantly larger than in *E. gemmipara*, the stalk showing only longitudinal striations but possessing a conspicuous suprastylar extension. This is the first time that the presence of ciliate epibionts has been recorded at species level on the copepod *Lepeophtheirus salmonis*. Statistical data about the distribution of both species on the surface of the copepod are detailed and a new geographical distribution for *E. gigantea* is proposed.

Keywords: *Ephelota*, *epibiosis*, *Lepeophtheirus salmonis*, *parasite*, *salmon*

Introduction

Epibiosis is a facultative association of two organisms: the epibiont and the basibiont (Wahl 1989). The term epibiont includes organisms that, during the sessile phase of their life cycle, are attached to the surface of a living substratum, while the basibiont lodges and constitutes a support for the epibiont (Threlkeld et al. 1993). Both concepts describe ecological functions (Wahl 1989).

Epibiosis between ciliated protozoa and crustacea is widely reported and occurs across most crustacean orders. However, ciliated protozoa from the peritrichs, suctorina and chonotrichs are more frequently reported as epibionts of crustacea (Morado and Small

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1995; Sprague and Couch 1971; Fernandez-Leborans and Tato-Porto 2000a, 2000b; Fernandez-Leborans 2001).

Lepeophtheirus salmonis (Kroyer, 1838) is a copepod crustacean, subclass Copepoda Milne-Edwards 1840, order Siphonostomatoida Thorell 1859, family Caligidae Burmeister 1834. The order Siphonostomatoida contains the sea louse and other freshwater and marine species, parasitic in their adult phase on fish and invertebrates. This parasitic marine copepod is often referred to as the salmon or sea louse, and is commonly found on species of wild and sea-farmed salmonids of the genera *Oncorhynchus*, *Salmo* and *Salvelinus* in the northern hemisphere (Kabata 1979). The feeding action of this parasite over the host skin results in the removal of mucus, leading to broken skin and ultimately the exposure of muscle and other tissues (Kabata 1974). Fish deaths due to lice damage have been recorded (Wooten et al. 1982), but in less extreme cases, lice damage results in poorer growth, increased susceptibility to disease and morphological damage, resulting in a decrease in the market value of the fish. *L. salmonis* continues to be a major problem for salmon farmers in Scotland, costing the industry millions to control each year.

Specimens of *Lepeophtheirus salmonis* collected from farmed Atlantic salmon from the west coast of Scotland were populated with suctorian epibionts of the genus *Ephelota*. The morphological features, taxonomic position and distribution on the basibiont of these suctorian epibionts are described.

Material and methods

Adults *L. salmonis* from farmed Atlantic salmon were collected from the west coast of Scotland (salinity 34 psu, water temperature 8°C). Samples were fixed immediately in 10% neutral buffered formalin. In the laboratory, copepods were dissected and viewed using a microscope. The presence and distribution of different suctorian ciliates from each copepod body section were recorded.

Suctorians were isolated and viewed using a compound light microscope. Samples were stained with methyl green, bright green, neutral red and silver carbonate to assist in identification (Fernandez-Leborans and Castro de Zaldumbide 1986). Biometric data of the suctorians were obtained using a graduated eye-piece. Statistical analyses were performed with Statgraphics program. Sixty individuals of each species were considered for biometrical features.

For scanning electron microscopy (SEM), whole adult sea lice were fixed at 4°C for 1 h in 1% glutaraldehyde. Initial fixation was followed by a 2–3-day immersion in 3% glutaraldehyde at 4°C, followed by a rinse in 0.1 M cacodylate buffer (pH 7). Samples were then post-fixed in 1% osmium tetroxide for 2 h, before dehydration through a graded ethanol series. From 100% ethanol, samples were transferred to a 50:50 mix of ethanol and hexamethyldisilazane (HMDS) for 30 min before being transferred to 100% HMDS for a further 30 min. Samples were air-dried at room temperature, mounted on aluminium stubs and coated with gold. Samples were viewed using a Philips 500 SEM at 15 kV. Figures were made from light and electron microscope images using an Image Analysis System (KS300 Zeiss).

Results

Lepeophtheirus salmonis populated with suctorians from the genus *Ephelota* were examined. Figure 2 shows the distribution of the ciliates over the cephalothoracic shield, genital

segment and abdomen. Two types of suctoria epibionts were observed, both had differing morphologies and one was substantially larger than the other.

Small suctoria

Morphologic features (Table I; Figures 1, 3–5). The body of the smaller suctoria was rounded, between 97.4 and 348.5 μm in length and 71.8–410.0 μm in width. There was an anteriorly positioned ring of tentacles, consisting of two types: (1) long, thin, pointed, prehensile tentacles (9.6–153.8 μm in length), carrying numerous haptocysts, varying in number from 2 to 51 tentacles per specimen; (2) short, thick, adhesive capitate tentacles, that were extensions of the endoplasm (3.8–67.2 μm in length), varying in number from 2 to 36 tentacles per specimen.

The macronucleus occupied a large area in the cellular body and is highly ramified with numerous lobes. This macronucleus was between 63.4 and 235.8 μm in length and 46.1 and 184.5 μm in width. There were from one to four spherical micronuclei situated close to the macronucleus. A contractile vacuole was situated laterally, in an anterior position, close to the macronucleus, and had a diameter of between 5.8 and 51.8 μm .

The stalk was considerably longer than the body (four to five times), and had longitudinal and transverse striations. The stalk was 123–2173 μm in length and between 30.8 and 112.8 μm in width (the width of the stalk varied little between the two extremes). Numerous thin structures protruded from the external surface of the stalk; they were perpendicularly disposed to the longitudinal axis of the stalk. These structures (possibly trichocysts) measured over 100 μm in length. The distal part of the stalk joined directly on to the copepod surface without the aid of a specialized structure. The proximal part joined to the cellular body in a bell-shaped area surrounded by a double membrane structure that continued inside the cell.

Different phases of division of these suctoria were observed. Budding was exterior, multiple and transversal. Buds (4–14) developed simultaneously from the apical pole. Each bud, oval in shape, had a length of 19.2–92.3 μm and a width of 30.7–92.3 μm . The buds showed a longitudinal central area on the ventral surface where ciliature was situated. This ciliature was composed of a right ciliary field bending to the centre at the apical end, and a lengthened left ciliar field that was interrupted by the right field bending. In the bud, the

Table I. Biometric features of *Ephelota gemmipara* (in μm).

	Mean	SD	SE	Minimum	Maximum
Length	222.90	62.70	9.70	97.40	348.50
Width	215.10	76.90	11.70	71.80	410.00
Stalk length	1058.80	513.40	93.70	123.00	2173.00
Stalk width	70.90	23.30	4.50	30.80	112.80
Macronucleus length	123.20	53.10	16.00	63.40	235.80
Macronucleus width	101.20	48.70	16.20	46.10	184.50
Micronucleus diameter	16.90	11.90	3.20	5.80	51.80
Bud number	6.00	3.54	1.30	2.00	14.00
Bud length	54.70	26.10	9.90	19.20	92.30
Bud width	48.70	21.70	8.20	30.70	92.30
Pointed tentacle number	23.00	11.40	2.00	2.00	51.00
Pointed tentacle length	59.10	31.30	7.20	9.60	153.80
Capitate tentacle number	7.60	6.60	1.20	2.00	36.00
Capitate tentacle length	16.40	16.00	4.00	3.80	67.20

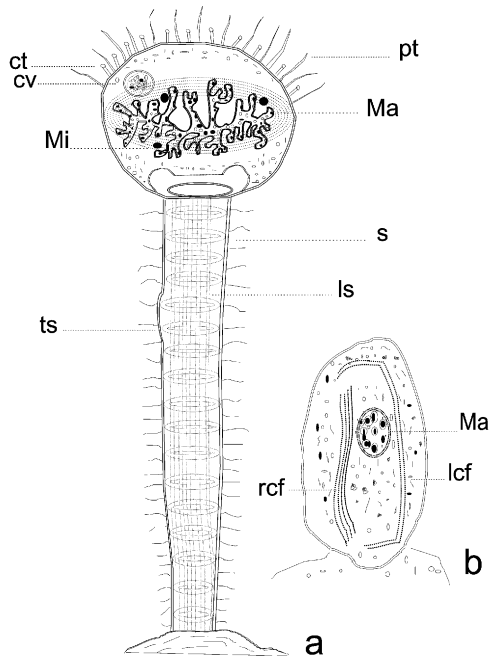
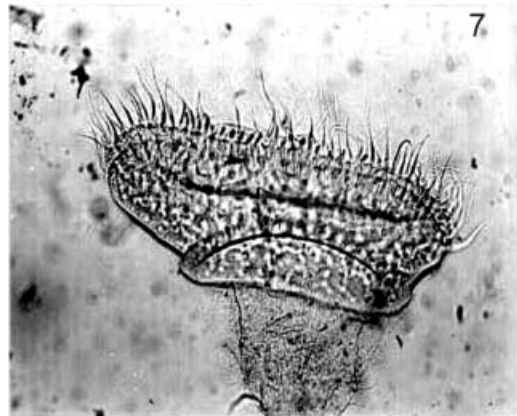
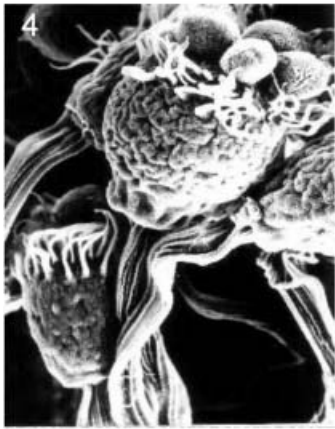
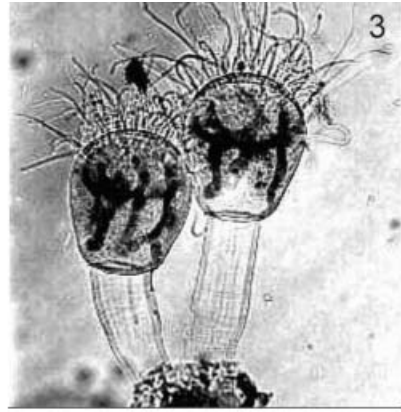


Figure 1. *Ephelota gemmipara*. (a) Schematic diagram of the body. ct, capitata tentacles; pt, prehensile tentacles; cv, contractile vacuole; ls, longitudinal striations; Ma, macronucleus; Mi, micronucleus; s, stalk; ts, transversal striations. (b) Schematic diagram of a bud of *Ephelota gemmipara*. rcf, right ciliar field; lcf, left ciliar field; Ma, macronucleus.

macronucleus initially consisted of different spherical masses, that later, during budding combined to form an oval macronucleus. This oval macronucleus subsequently lengthened to form a lobed structure that was located at the periphery of the cell. In addition, tomites were observed, in many cases attached to the copepod, near the adult suctorian attachment sites.

Taxonomic position. The examined suctorians belong to genus *Ephelota* Wright, 1858 (class Phyllopharyngea De Puytorac et al., 1974, subclass Suctorina Claparède and Lachmann, 1858, order Exogenida Collin, 1912, and family Ephelotidae Kent, 1882) (Batisse 1994; Lynn and Small 2000). As members of this genus, they showed the two types of tentacles: shorter, extensible, feeding, capitata tentacles, and a ring of long, pointed, prehensile tentacles (Batisse 1994; Lynn and Small 2000). Within the genus *Ephelota*, the species with characteristics most similar to that of the analysed ciliates is *Ephelota gemmipara* (Hertwig, 1875). *Ephelota gemmipara* and the present ciliate share similar morphology both in the shape and measurements of the body, the possession of transverse striations on the stalk and similar stalk lengths, and they both lack an extension in the suprastylar end of the stalk (Collin 1912; Kahl 1934; Grell and Benwitz 1984; Grell and Meister 1984; Matthes et al. 1988).

Distribution on the basibiont. The suctorians were found colonizing most parts of the dorsal surface of *L. salmonis*. They were predominately located on the genital segment and on the abdomen. However, they were also observed on the cephalothoracic shield and on the



Figures 2–7. (2) A specimen of the copepod *Lepeophtheirus salmonis* showing the suctoria attached to its surface ($\times 11$). (3) Two individuals of *Ephelota gemmipara* showing the lobulate macronucleus, the tentacles and the stalk ($\times 112$). (4) *Ephelota gemmipara*. SEM photomicrography showing buds ($\times 224$). (5) *Ephelota gemmipara*. SEM photomicrography showing the distal part of the stalk and the body ($\times 224$). (6) *Ephelota gigantea*. General view of the body ($\times 108$). (7) *Ephelota gigantea*. Aspect of the anterior area of the body ($\times 149$).

caudal branches (high densities can also colonize the copepod egg strings, data not shown) (Table II).

Larger suctoria

Morphological features (Table III; Figures 6–8). Ciliates were umbrella-shaped with a cellular body between 82.0 and 512.5 μm in length. The apical zone was notably wider (153.8–666.3 μm), in comparison to the posterior pole (153.8–430.5 μm) that joined the stalk. In the apical region of the body, there were two types of tentacles: (1) long, thin, pointed prehensile tentacles (7.7–134.4 μm in length) carrying numerous haptocysts, varying in number from 10 to 65 tentacles per individual; (2) short, thick, capitate tentacles (5.8–32.6 μm in length), varying in number from 4 to 38 tentacles per individual.

The macronucleus was highly ramified and lobate, occupying a high proportion of the cellular volume, and was between 51.3 and 615.0 μm in length and 71.8–410.0 μm in width. Between one and four spherical micronuclei were situated close to the macronucleus. The contractile vacuole was situated laterally in the anterior part of the body, and it had a diameter of 5.8–51.8 μm .

The stalk was approximately four times the length of the body (307.5–1947.5 μm in length, 35.9–256.3 μm wide). The stalk showed pronounced longitudinal striations and numerous trichocysts. The anterior part of the stalk (suprastylar) joined the cellular body with a large and conspicuous extension. This part of the stalk had a length of 51.3–410.0 μm and width in the medium part of 30.8–276.8 μm . In the area where this large extension of stalk joined the cellular body, there were three fibrillar structures forming three

Table II. Distribution of *Ephelota gemmipara* on the basibiont.

	Mean	SD	SE	Minimum	Maximum
Cephalothorax	16.40	26.20	9.90	0.00	59.00
Genital segment	42.60	48.00	18.10	0.00	123.00
Abdomen	37.10	27.90	10.50	5.00	88.00
Caudal branches	18.00	27.90	10.60	0.00	80.00

Table III. Biometric features of *Ephelota gigantea* (in μm).

	Mean	SD	SE	Minimum	Maximum
Length	221.10	120.00	21.90	82.00	512.50
Maximum width	307.20	110.70	19.90	153.80	666.30
Minimum width	243.30	66.80	13.90	153.80	430.50
Stalk length	823.40	460.50	88.60	307.50	1947.50
Extension length	190.10	100.40	21.40	51.30	410.00
Minimum stalk width	80.50	48.20	9.30	35.90	256.30
Extension width	146.40	64.80	12.20	30.80	276.80
Macronucleus length	114.40	126.80	29.10	51.30	615.00
Macronucleus width	217.20	84.40	18.40	71.80	410.00
Micronucleus diameter	16.90	11.90	3.20	5.80	51.80
Pointed tentacle number	34.50	14.90	3.20	10.00	65.00
Pointed tentacle length	68.50	28.90	6.20	7.70	134.40
Capitate tentacle number	17.60	10.60	2.30	4.00	38.00
Capitate tentacle length	17.90	6.00	1.30	5.80	32.60
Longitudinal striation number	50.30	16.50	3.50	22.00	80.00

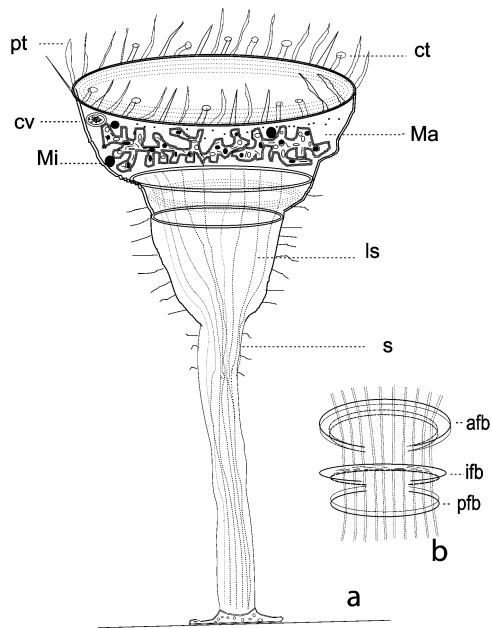


Figure 8. *Ephelota gigantea*. (a) Schematic diagram of the body. pt, prehensile tentacles; ct, capitate tentacles; cv, contractile vacuole; Ma, macronucleus; Mi, micronucleus; ls, longitudinal striations; s, stalk. (b) Schematic diagram of the fibrillar bands of the suprastylar area of the stalk. afb, anterior fibrillar band; ifb, intermediate fibrillar band; pfb, posterior fibrillar band.

concentric bands. From these three bands, the two more exterior showed longitudinal fibres (the anterior and the posterior fibrillar bands, afb and pfb), while the intermediate fibrillar band (ifb) contained transversally disposed fibres.

Taxonomic position. The suctoria examined belong to the genus *Ephelota*. As members of this genus, they showed two typical types of tentacles: (1) capitate, shorter, extensible, thick tentacles; (2) long, pointed, prehensile tentacles, constituting a ring in the apical area of cellular body (Batisse 1994; Lynn and Small; 2000). Within the genus *Ephelota*, the species with characteristics most similar to that of the analysed ciliate is *Ephelota gigantea* Noble, 1929. *Ephelota gigantea* and the present ciliate share similar morphology both in the shape and measurements of the body, the possession of prominent longitudinal striations on the stalk, similar stalk lengths and the possession of the suprastylar extension of the stalk. Another species of *Ephelota*, *E. plana* Wailes, 1925 (epibiont on algae and bryozoans), is similar to *Ephelota gigantea* and considered by Noble (1929) as a synonym of this species. According to Kahl (1934), the dimensions of *E. gigantea* are larger than those of *E. plana*.

Distribution on the basibiont. The distribution of *Ephelota gigantea* on the basibiont (Table IV) showed that the greatest number of suctoria were located on the cephalothoracic shield, their density being considerably lower on other parts of the body.

Statistical analyses performed using the suctorian density of each species in the different areas of the copepod showed that there was no significant correlation between the two species with respect to their anatomical distribution. However, there was a significant difference ($t=4.11$, $P=0.06$) between both species with respect to their distribution in each anatomical unit.

Table IV. Distribution of *Ephelota gigantea*.

	Mean	SD	SE	Minimum	Maximum
Cephalothorax	3.40	9.10	3.40	0.00	24.00
Genital segment	0.10	0.40	0.10	0.00	1.00
Abdomen	0.40	1.10	0.40	0.00	3.00

Occasionally, specimens of *Ephelota gemmipara* were observed attached to the stalk of individuals of *Ephelota gigantea*.

Discussion

The genus *Ephelota* has been found as epibionts in many different crustacean groups: decapods, amphipods, euphausiaceans and copepods. *Ephelota gemmipara* has been found as an epibiont on the copepods *Calanus finmarchicus* (Gunnerus, 1765) and *Candacia armata* (Boeck, 1872) (cf. Rose 1924), as well as on *Pleuromamma borealis* (F. Dahl, 1893) and *Pleuromamma gracilis* (Claus, 1863) (cf. Steuer 1928). Except for *Ephelota gemmipara* and *Ephelota crustaceorum* Haller, 1880 (that were observed on an unidentified copepod by Lebour 1917), no other species of *Ephelota* have been observed as epibionts on copepods. However, Stone and Bruno (1989) reported an unidentified suctorian from the genus *Ephelota* on sea lice from Scotland, and researchers frequently observe these unidentified suctorians as epibionts of sea lice (personal observation).

Ephelota gigantea was described by Noble (1929) and this description was recorded by Kahl (1934). This species was found as an epiphyte on algae in Monterey Bay (California, USA). Since then, no references to *Ephelota gigantea* has appeared. Moreover, the presence of *Ephelota gigantea* on the copepod *Lepeophtheirus salmonis* in Scotland noticeably extends the geographical distribution of this suctorian ciliate.

Ephelota gemmipara appeared on the carapace of copepods in significantly higher densities than *Ephelota gigantea*, 26–161 individuals per copepod to 0–28, respectively.

The presence of *Ephelota gemmipara* colonizing the stalk of *Ephelota gigantea* represents a hyperepibiosis. This phenomenon has been previously described in suctorians from the genus *Trichophrya* (some species of which have been described as epibionts of crustacea) on the stalk of the peritrich ciliate *Epistylis*, itself an epibiont of crustacea (Lynn and Small 2000). The development of buds was similar to that described by Guilcher (1951), the two ciliar fields described by this author being observed although with a lower number of kineties.

Although *Ephelota* sp. has been previously observed as an epibiont of sea lice, this is the first time that a formal identification to a species level has been achieved. In this epibiosis the copepod could not possibly obtain any benefit. However, the epibiont could potentially benefit from the basibiont. The basibiont provides a substratum, protection and a potential food supply from the salmonid epidermis. It is possible that protozoa graze on particles released from the salmon skin during the feeding activities of the copepod. In addition, the presence of the ciliate epibionts could be favoured by the fact that, in contrast to the constant motility of free-living copepods, a parasitic copepod basibiont is usually attached to its salmonid host; hence their time spent free in the water column is greatly reduced.

Epibiont suctorians have been previously described from 46 copepod crustacean species belonging to 37 genera (Fernández-Leborans and Tato-Porto 2000b). Suctorians constitute a special group of ciliate protozoa. Their sessile behaviour and the presence of tentacles with

a feeding function in place of a mouth, determine the life strategy for these organisms. Suctoria show a strong tendency to commensalism and can establish associations with a wide range of hosts including other protozoa, algae, molluscs, rotifers, annelids, crustacea, insects, fish, and turtles (Corliss 1979).

Hosts (basibionts) are used as a substratum, as well as means of dispersion and protection, and in many cases, they contribute to the provision of food for the suctoria. Although most suctoria are ectocommensal, some are endocommensal or endoparasites (Fernández-Leborans and Tato-Porto 2000b). Some of the copepods analysed had a high density of suctoria epibionts, approximately 160 suctoria per copepod. Such high densities could represent a negative impact for the basibiont, due to a reduction in mobility (Overstreet 1983), inhibition in moulting (Glynn 1970; Reaka 1978), and an increase in the risk of predation (Willey et al. 1990). However, heavily colonized *L. salmonis* were not observed to have their mobility impaired, either on or off their fish host, hence the suctorian ciliates are suggested to have a harmless phoretic relationship with their sea lice basibionts.

In summary, this is the first record and definitive description to species level of identity of two suctorian species, *Ephelota gemmipara* and *Ephelota gigantea*, found as epibionts on the salmon louse *Lepeophtheirus salmonis*. In addition, this is the first record of protozoan ciliate epibionts at species level on *L. salmonis*. *Ephelota gemmipara* has been found previously on only three other genera of copepods. *Ephelota gigantea* has only previously been reported as an epiphyte on algae on the Pacific coast of Californian. This study is the first report of this epibiont in the Atlantic, which extends its geographical distribution, and also the first report of a copepod basibiont for this species.

Conclusions

- This is the first definitive description to species level of identity of two suctorian species, *Ephelota gemmipara* and *Ephelota gigantea* found as epibionts on the salmon louse *Lepeophtheirus salmonis*.
- *Ephelota gemmipara* has been found previously on only three other genera of copepods. *Ephelota gigantea* has only previously been reported as an epiphyte on the Pacific coast of Californian. This study is the first report of this epibiont in the Atlantic, which extends its geographical distribution, and also the first report of a copepod epibiont for this species.
- The morphological features and distribution of epibionts on the copepod are described.

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