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, suctoria and chonotrichs are more frequently reported as epibionts of crustacea (Morado and Small...
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.

Suctoria 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 suctoria 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 suctoria 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| 4.00   | 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   |
The 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 suctoria belong to genus *Ephelota* Wright, 1858 (class Phyllopharyngea De Puytorac et al., 1974, subclass Suctoria 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, capitate 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 suctoria 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 (×11). (3) Two individuals of *Ephelota gemmipara* showing the lobulate macronucleus, the tentacles and the stalk (×112). (4) *Ephelota gemmipara*. SEM photomicrography showing buds (×224). (5) *Ephelota gemmipara*. SEM photomicrography showing the distal part of the stalk and the body (×224). (6) *Ephelota gigantea*. General view of the body (×108). (7) *Ephelota gigantea*. Aspect of the anterior area of the body (×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 |
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.
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 suctoria 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 suctoria 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 ciliolar 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 suctoria have been previously described from 46 copepod crustacean species belonging to 37 genera (Fernández-Leborans and Tato-Porto 2000b). Suctoria constitute a special group of ciliate protozoa. Their sessile behaviour and the presence of tentacles with

|                | 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    |

Table IV. Distribution of *Ephelota gigantea*. 

594  G. Fernandez-Leborans et al.
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 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 epibiont for this species.
- The morphological features and distribution of epibionts on the copepod are described.

References

Batisse A. 1994. Sous-Classe des Suctoria Claparède et Lachmann, 1858. In: Grassé P-P, editor. Traité de Zoologie 2, (2). Paris: Masson. p 433–473.

Claparède E, Lachmann J. 1858–1859. Etudes sur les Infusoires et les Rhizopodes. Mémoires Institute Nationale Génevois 5:1–260.

Collin B. 1912. Etude monographique sur les Acinétiens. Morphologie, Physiologie, Systématique. Archives Zoologie experimentelle générale 51:1–147.

Corliss JO. 1979. The ciliated protozoa: characterisation, classification and guide to the literature. New York: Pergamon Press.

Fernandez-Leborans G. 2001. A review of the species of protozoan epibionts on crustacea. III. Chonotrich ciliates. Crustaceana 74:581–607.
Fernandez-Leborans G, Castro de Zaldumbide M. 1986. The morphology of Anophrys arenicola sp. nov. (Ciliophora, Scuticociliatida). Journal of Natural History 20:713–721.

Fernandez-Leborans G, Tato-Porto ML. 2000a. A review of the species of protozoan epibionts on crustacea. I Peritrich ciliates. Crustaceana 73:643–683.

Fernandez-Leborans G, Tato-Porto ML. 2000b. A review of the species of protozoan epibionts on crustacea. II Suctorian ciliates. Crustaceana 73:1205–1237.

Glynn PW. 1970. Growth of algal epiphytes on a tropical marine isopod. Journal of Experimental Marine Biology and Ecology 5:88–93.

Grell G, Benwitz G. 1984. Die Ultrastruktur von Ephelota gemmipara Hertwig und E. plana Wailes (Suctoria): ein Vergleich. I. Die Adulte Form, 1984. II. Der Schwärmer. Protistologica 20:205–233.

Grell G, Meister A. 1984. Beiträge zur Ultrastruktur der Konjugation von Ephelota gemmipara R. Hertwig (Suctoria). Protistologica 20:65–86.

Guilcher Y. 1951. Contribution a l'étude des ciliés gemmipares, chonotriches et tentaculifères. Annales des Sciences Naturelles, Zoologie 13:33–132.

Kabata Z. 1974. Mouth and mode of feeding of Caligidae (Copepoda), parasites of fishes, as determined by light and scanning electron microscopy. Journal of Fisheries Research Board Canada 30:1583–1588.

Kabata Z. 1979. Parasitic copepoda of British fishes. London: The Ray Society.

Kahl A. 1934. Ciliata entocommensalia et parasitica Suctoria. In: Grimp G, Wagler E, editors. Die Tierwelt der Nord und Ostsee. Leipzig: Geest & Portig. p 185–228.

Lebour MV. 1917. The microplankton of Plymouth Sound. Journal of the Marine Biological Association of the United Kingdom 1:133–182.

Lynn DH, Small EB. 2000. Phylum Ciliophora. In: Lee JJ, Leedale GF, Bradbury P, editors. The illustrated guide to the protozoa. New York: Allen Press. p 371–656.

Matthes D, Guhl W, Haider G. 1988. Suctoria und Urceolariidae. Stuttgart: Gustav Fischer.

Morado JF, Small EB. 1995. Ciliate parasites and related diseases of crustacea, a review. Reviews in Fisheries Science 3:275–374.

Noble AE. 1929. Two new species of the protozoan genus Ephelota from Monterey Bay, California. University of California, Publications Zoology 33:13–26.

Overstreet RM. 1983. Metazoan symbionts of crustacea. In: Bliss DE, editor. The biology of crustacea. London: Academic Press. p 155–250.

Reaka ML. 1978. The effects of an ectoparasitic gastropod, Caledoniella montrouzieri, upon moulting and reproduction of a stomatopod crustacean, Gonodactylus viridis. Veliger 21:251–254.

Sprague V, Couch J. 1971. An annotated list of protozoan parasites, hyperparasites and commensals of decapod Crustacea. Journal of Protozoology 18:526–537.

Stone J, Bruno DW. 1989. A report on Ephelota sp. a suctorian found on sea lice Lepeophtheirus salmonis and Caligus elongatus. Bulletin of European Association of Fish Pathology 9:113–115.

Threlkeld ST, Chiavelli DA, Willey RL. 1993. The organization of zooplankton epibiont communities. Trends in Ecology and Evolution 8:317–321.

Wahl M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. Marine Ecology Progress Series 58:175–189.

Willey RL, Cantrell PA, Threlkeld ST. 1999. Epibiotic flagellates increase the susceptibility of some zooplankton to fish predation. Limnology and Oceanography 35:952–959.

Wooten R, Smith JW, Needham EA. 1982. Aspects of the biology of the parasitic copepods Lepeophtheirus salmonis and Caligus elongatus on farmed salmonids and their treatment. Proceedings of the Royal Society of Edinburgh 81B:185–197.