Biodiversity and distribution of epibiontic communities on *Caridina ensifera* (Crustacea, Decapoda, Atyidae) from Lake Poso: comparison with another ancient lake system of Sulawesi (Indonesia)

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**Abstract**


The epibiont communities of the shrimp *Caridina ensifera*, endemic to Lake Poso (Sulawesi, Indonesia), were analysed. Most of the epibiont species were ciliated protozoa belonging to three suctorian genera (*Acineta*, *Podophrya* and *Spelaeophrya*), three peritrich genera (*Zoothamnium*, *Vorticella* and *Cothurnia*), and a haptorid genus (*Amphileptus*). There was also a rotifer epibiont of the genus *Embata*. Epibionts were identified to species level. There were 14 to 1114 epibionts per shrimp. The distribution of the epibiont species on the surface of the basibiont was recorded, calculating the number on the different colonized individuals of *C. ensifera*. The most abundant species, *Zoothamnium intermedium* and *Acineta sulawesiensis*, were also the most widely distributed. There was a significant difference between the spatial distributions of the different epibiont species. The analysis of the number of the epibiont species throughout the anteroposterior axis of the shrimp showed a gradient from the anterior to the posterior end of the body. Data from Lake Poso were compared with those of the Malili lake system (Sulawesi), obtained from its endemic shrimp, *Caridina lanceolata*. Lake Poso had the highest mean diversity, while Lake Mahalona showed the highest maximum diversity. All lakes were correlated with respect to the mean number of epibionts on the anatomical units of the shrimp, which showed a similar general distribution. The distributions of the different epibiont species were compared between the lakes. The possible adaptations of the epibionts as well as the colonization patterns were discussed. From the statistical results and the analysis of the distributions, we propose that in these communities epibiont species have a pattern of colonization in which they follow a behaviour as a whole; each species has a differential distribution, with the species occupying the available substratum with the particular requirements of each functional group, but there is a trend towards maintaining an equilibrium among species and groups, compensating for diversity and number of individuals. In all lakes there was an epibiont distribution model comprising the maintenance of an anteroposterior axis gradient, which was supported by the fluctuation in diversity and number of individuals of the different functional groups of epibiont species. The functional role of the different groups of species seems to tend towards sustainability with little global variation among the lakes.

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Introduction

During the last three decades a number of articles have focused on epibiosis related to Crustacea (Dawson 1957; Eldred 1962; Maldonado and Uriz 1992; Gili et al. 1993; Morado and Small 1995; Dick et al. 1998; Key et al. 1999; Fernandez-Leborans and Tato-Porto 2000a,b). Epibiosis is an association between two organisms: the epibiont and the basibiont. 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 the epibiont (Wahl 1989; Wahl et al. 1997).

Despite the fact that the presence of epibionts (previously referred to as commensals, epizoics, symbionts) on crustaceans has been known for a long time, it is only recently that a new perspective has been brought to their study. This has not only involved a noticeable increase of newly described taxa, but has also highlighted the fact that epibiotic relationships are important in many biological fields: physiological, ecological, evolutionary and those related to conservation and biodiversity.

A number of protozoan ciliate species have been described as epibionts on crustaceans, and unique aspects of the biology and ecology of their basibiont crustacean taxa can be explained by epibiosis (Bottom and Ropes 1988; Abelló et al. 1990; Abelló and Macpherson 1992). Crustacean groups such as cladocerans, copepods, cirripeds, isopods, amphipods and decapods, include species that have been found as basibionts for protozoan and invertebrate epibionts (Ross 1983). Protozoan epibionts are representative of the following groups: apostomatids, chonotrichids, suctorians, peritrichs and heterotrichs (Corliss 1979; Lynn and Small 2000). The invertebrate epibionts include forms that belong to a number of different phyla (including Porifera, Cnidaria, Platyhelminthes, Nemertea, rotifers, the trophi were analysed using the Fernandez-Leborans technique and with methyl green and neutral red. Permanent slides were made for the stained ciliates. To identify the rotifers, the trophi were analysed using the procedure indicated by R.J. Shiel (University of Adelaide, Australia; personal communication), treating isolated specimens, in 10% glycerol/water solution, with 2.5% sodium hypochlorite. Measurements of the epibionts were made with an ocular micrometer. Light microscope images were obtained using KS300 Zeiss IMAGE ANALYSIS software and were used to identify the epibiont species. Statistical analyses were performed using the STATGRAPHICS and SPSS programs.

All epibionts examined are deposited in the Museum of Natural History, Berlin, Germany (ZMB).

Materials and Methods

Specimens of C. ensifera were collected from the south shore of Lake Poso, Central Sulawesi, Indonesia, in March 2004 (Fig. 1). Samples were fixed in 95% ethanol and then transferred to 75% ethanol for light microscopy. In the laboratory, shrimps were dissected and each anatomical unit was observed under a stereoscopic microscope.

For scanning electron microscopy (SEM) of the epibionts, shrimp specimens fixed in 95% ethanol were dehydrated in 100% ethanol for 30 min. Afterwards, they were critical-point dried with a BAL-TEC CPD 030, mounted on aluminium specimen stubs with standard adhesive pads and coated with gold–palladium using a Polaron SC7640 Sputter Coater. Pictures were taken on an LEO 1450VP SEM (software: 32 V02.03) at 10 kV.

Epibionts on the surface of the shrimp were observed and counted on each anatomical unit under stereoscopic and light microscopes. Number of colonial species was indicated by R.J. Shiel (University of Adelaide, Australia; personal communication), treating isolated specimens, in 10% glycerol/water solution, with 2.5% sodium hypochlorite. Measurements of the epibionts were made with an ocular micrometer. Light microscope images were obtained using KS300 Zeiss IMAGE ANALYSIS software and were used to identify the epibiont species. Statistical analyses were performed using the STATGRAPHICS and SPSS programs.

All epibionts examined are deposited in the Museum of Natural History, Berlin, Germany (ZMB).

Results

The epibionts on C. ensifera included the following protozoan ciliates: the suctorians Acinetia sulawesiensis, Podophrya maupasi and Spelacophrya polypondes, the peritrichs Zoanthamnium intermedium, Vorticella globosa and Cothurnia compressa, and the haptorid Amphileptus fusidens. In addition, there was the rotifer Embata lanceps (Fig. 2).
Distribution of the epibionts

Of the infested shrimps, 25% were ovigerous females. The number of epibionts per basibiont fluctuated between 14 and 1114 (mean 314.6). Only 0.45% of these epibionts were rotifers, the ciliate protists comprised the highest proportion of the mean number of epibionts (mean 313.19) (Table 1). Among the ciliate epibionts, the highest number of individuals were either Zoothamnium or Acineta, which represented 94.2% of the mean number of epibionts (Acineta showed the highest proportion, 59.94%). The other ciliates accounted for 5.33% of the mean number of epibionts on the shrimp (Table 1).

Antennulae, antennae, maxillipeds and uropods were the anatomical units with the highest mean number of epibionts. The most abundant epibionts, Zoothamnium and Acineta, were also the most widely distributed on the surface of the shrimp. The rotifer, although rare, was also widely distributed spatially on the basibiont (Table 2).

The statistical comparison between the spatial distributions of the epibiont species on the body of C. ensifera indicated a significant difference between the species (F, 11.05; P ≤ 0.05). The principal component analysis performed using the mean number of epibiont species on the anatomical units of the shrimp showed, in the plot of the two first principal components (Fig. 3), two clusters, one with Amphileptus, Vorticella and Spelaeophrya, and another including Zoothamnium, Acineta, Podophrya and Embata. This second cluster integrated the epibiont species most widely distributed on the basibiont, in contrast to the scarcely present species of the other cluster. The ciliate Cothurnia appeared separately from these clusters because of its presence on the posterior end of the basibiont body in low numbers.

Hierarchical conglomerate analysis produced a dendrogram using the mean number of the different epibiont species on the anatomical units of the shrimp. The units were grouped in five clusters (Fig. 4). A cluster corresponded to the antennulae, antennae and uropods (18.75% of the

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Fig. 1—Geographical area of the study. —A. The Indo-Malaysian Archipelago. —B. Sulawesi. —C. Lake Poso. —D. Lakes of the Malili system.
anatomical units). These units had a high number of epibionts (mean 15.80 epibionts per unit). The second cluster included 46.88% of the anatomical units (rostrum, eyes, second right pereiopod, third, fourth and fifth pereiopods, fourth and fifth pleopods and telson); these units showed the lowest number of epibionts (mean 2.87 epibionts per unit). The third cluster comprised the rest of the pleopods (first, second and third pleopods, 18.75% of the units) and had a moderate number of epibionts (mean 8.27 per unit). In the fourth cluster there were the first and left second pereiopods

The fifth cluster corresponded to the maxillipeds (6.25%), the units with the highest infestation (mean 49.6 epibionts per unit).

Distribution along the anteroposterior axis of \textit{C. ensifera}

Figure 5 shows the mean number of different epibiont species and the total epibiont mean number along the anteroposterior axis of the shrimp. Anatomical units were considered in five groups (rostrum, eyes, antennae and antennulae; maxillipeds; pereiopods; pleopods; uropods and telson). \textit{Zoothamnium} was distributed mainly on the posterior half of the body, especially on the pleopods where it represented 50.48% of the epibionts. It was also found attached to the pereiopods (18.3%) and the maxillipeds (15.4%). In contrast, \textit{Acineta} was more abundant on the anterior part of the shrimp, and 73.90% of the epibionts were located on the maxillipeds (43.2%), rostrum, antennae, antennulae and eyes. \textit{Cothurnia} and \textit{Vorticella} presented a higher number of epibionts towards the posterior end of the body, where they represented 68.8% and 39% respectively, although \textit{Vorticella} showed a remarkable number of individuals on the pereiopods (35.3% of the epibionts). \textit{Spelaeophrya} was more abundant on the anterior part of the body (rostrum, antennae, antennulae and eyes) (77.9%). \textit{Podophrya} colonized mainly the maxillipeds, and \textit{Amphileptus} colonized the ends of the body, while \textit{Embata} colonized the anterior end, pereiopods and pleopods. The epibiont community was distributed following a pattern in which the species occupied the places with behaviour of an ensemble, each species showing a distinctive distribution along the basibiont body. There was a significant difference between the epibiont species considering the mean number of epibionts on the different groups of anatomical units ($F$, 5.98; $P \leq 0.05$), and also considering the

\begin{table}
\centering
\caption{Length and width of the specimens of \textit{Caridina ensifera} analysed and distribution of the epibionts on the crustacean}
\begin{tabular}{lcccr}
\hline
 & Mean & Standard deviation & Minimum & Maximum \\
\hline
Length of the shrimp (mm) & 24.19 & 4.65 & 13.00 & 33.00 \\
Width of the shrimp (mm) & 3.90 & 0.78 & 2.00 & 5.00 \\
Length of ovigerous female shrimp (mm) & 25.40 & 3.91 & 19.00 & 29.00 \\
Width of ovigerous female shrimp (mm) & 4.60 & 0.55 & 4.00 & 5.00 \\
Number of protozoa per shrimp & 313.19 & 305.16 & 12.00 & 1110.00 \\
Number of protozoa per ovigerous female shrimp & 662.20 & 266.05 & 429.00 & 1110.00 \\
Number of rotifers per shrimp & 1.43 & 1.75 & 0.00 & 6.00 \\
Number of rotifers per ovigerous female shrimp & 3.40 & 2.30 & 1.00 & 6.00 \\
Number of epibionts per shrimp & 314.62 & 306.07 & 14.00 & 1114.00 \\
Number of epibionts per ovigerous shrimp & 665.60 & 268.59 & 430.00 & 1114.00 \\
\hline
\end{tabular}
\end{table}

$n = 40$. (9.38% of the units), with a mean of 9.26 epibionts per unit. The fifth cluster corresponded to the maxillipeds (6.25%), the units with the highest infestation (mean 49.6 epibionts per unit).

\section*{Fig. 4}

Dendrogram of the hierarchical cluster analysis (anatomical units) performed using the mean numbers of epibionts on the different anatomical units of the shrimps analysed (metric distance: City Block (Manhattan); method: Ward).
Table 2  Number of each genus of epibiont on the different anatomical units of *Caridina ensifera*

<table>
<thead>
<tr>
<th>Anatomical unit</th>
<th>Acineta</th>
<th>Vorticella</th>
<th>Podophrya</th>
<th>Cothurnia</th>
<th>Zoothamnium</th>
<th>Spealophrya</th>
<th>Amphileptus</th>
<th>Embata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rostrum</td>
<td>3.05 ± 8.43</td>
<td>0.10 ± 0.44</td>
<td>–</td>
<td>0.05 ± 0.22</td>
<td>1.29 ± 5.89</td>
<td>–</td>
<td>0.10 ± 0.30</td>
<td>0.05 ± 0.22</td>
</tr>
<tr>
<td>Left ocular orbit</td>
<td>0.10 ± 0.44</td>
<td>0.05 ± 0.22</td>
<td>0.05 ± 0.22</td>
<td>–</td>
<td>0.52 ± 1.21</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Right ocular orbit</td>
<td>0.29 ± 0.78</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>1.99 ± 5.06</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Left antennule</td>
<td>15.19 ± 19.78</td>
<td>0.10 ± 0.44</td>
<td>–</td>
<td>0.14 ± 0.48</td>
<td>1.43 ± 2.94</td>
<td>0.29 ± 0.90</td>
<td>0.14 ± 0.36</td>
<td>–</td>
</tr>
<tr>
<td>Right antennule</td>
<td>13.86 ± 16.72</td>
<td>0.05 ± 0.22</td>
<td>–</td>
<td>0.29 ± 0.96</td>
<td>0.10 ± 0.44</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Left antenna</td>
<td>13.05 ± 18.80</td>
<td>–</td>
<td>–</td>
<td>0.76 ± 1.41</td>
<td>2.14 ± 4.62</td>
<td>0.10 ± 0.30</td>
<td>0.05 ± 0.22</td>
<td>0.10 ± 0.30</td>
</tr>
<tr>
<td>Right antenna</td>
<td>12.48 ± 17.07</td>
<td>–</td>
<td>–</td>
<td>0.76 ± 2.30</td>
<td>2.10 ± 3.62</td>
<td>0.14 ± 0.48</td>
<td>0.14 ± 0.48</td>
<td>–</td>
</tr>
<tr>
<td>Left maxilliped</td>
<td>40.10 ± 44.51</td>
<td>–</td>
<td>0.86 ± 3.93</td>
<td>–</td>
<td>9.10 ± 16.86</td>
<td>–</td>
<td>–</td>
<td>0.10 ± 0.44</td>
</tr>
<tr>
<td>Right maxilliped</td>
<td>41.29 ± 54.08</td>
<td>–</td>
<td>0.33 ± 1.06</td>
<td>–</td>
<td>7.33 ± 13.19</td>
<td>–</td>
<td>0.10 ± 0.30</td>
<td>0.10 ± 0.44</td>
</tr>
<tr>
<td>Left first pereiopod</td>
<td>6.57 ± 12.43</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>5.81 ± 12.50</td>
<td>0.05 ± 0.22</td>
<td>0.05 ± 0.22</td>
<td>0.14 ± 0.36</td>
</tr>
<tr>
<td>Right first pereiopod</td>
<td>5.38 ± 11.01</td>
<td>0.24 ± 0.89</td>
<td>–</td>
<td>–</td>
<td>3.05 ± 5.30</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Left second pereiopod</td>
<td>4.10 ± 5.74</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>2.52 ± 4.47</td>
<td>–</td>
<td>–</td>
<td>0.05 ± 0.22</td>
</tr>
<tr>
<td>Right second pereiopod</td>
<td>2.14 ± 4.53</td>
<td>0.10 ± 0.44</td>
<td>–</td>
<td>2.57 ± 5.74</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Left third pereiopod</td>
<td>1.95 ± 3.34</td>
<td>–</td>
<td>–</td>
<td>0.57 ± 1.36</td>
<td>–</td>
<td>0.10 ± 0.44</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Right third pereiopod</td>
<td>0.86 ± 2.41</td>
<td>0.05 ± 0.22</td>
<td>–</td>
<td>3.06 ± 7.33</td>
<td>–</td>
<td>0.05 ± 0.22</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Left fourth pereiopod</td>
<td>1.62 ± 4.25</td>
<td>0.43 ± 1.96</td>
<td>0.05 ± 0.22</td>
<td>–</td>
<td>0.76 ± 1.95</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Right fourth pereiopod</td>
<td>1.52 ± 2.80</td>
<td>0.14 ± 0.48</td>
<td>–</td>
<td>0.62 ± 2.40</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Left fifth pereiopod</td>
<td>0.38 ± 1.53</td>
<td>–</td>
<td>–</td>
<td>1.67 ± 3.90</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Right fifth pereiopod</td>
<td>0.38 ± 1.53</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Left first pleopod</td>
<td>0.57 ± 1.40</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>6.10 ± 13.92</td>
<td>0.05 ± 0.22</td>
<td>0.10 ± 0.44</td>
<td>–</td>
</tr>
<tr>
<td>Right first pleopod</td>
<td>1.43 ± 2.60</td>
<td>–</td>
<td>0.10 ± 0.44</td>
<td>–</td>
<td>7.62 ± 13.08</td>
<td>–</td>
<td>0.05 ± 0.22</td>
<td>–</td>
</tr>
<tr>
<td>Left second pleopod</td>
<td>0.57 ± 1.36</td>
<td>0.33 ± 1.53</td>
<td>0.14 ± 0.48</td>
<td>9.62 ± 24.57</td>
<td>–</td>
<td>–</td>
<td>0.10 ± 0.44</td>
<td>–</td>
</tr>
<tr>
<td>Right second pleopod</td>
<td>0.52 ± 1.63</td>
<td>0.14 ± 0.48</td>
<td>9.62 ± 24.57</td>
<td>–</td>
<td>–</td>
<td>0.05 ± 0.22</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Left third pleopod</td>
<td>0.86 ± 1.90</td>
<td>0.14 ± 0.48</td>
<td>5.90 ± 13.46</td>
<td>–</td>
<td>–</td>
<td>0.05 ± 0.22</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Right third pleopod</td>
<td>0.33 ± 0.91</td>
<td>0.05 ± 0.22</td>
<td>7.52 ± 15.74</td>
<td>–</td>
<td>–</td>
<td>0.05 ± 0.22</td>
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<tr>
<td>Left fourth pleopod</td>
<td>0.71 ± 0.71</td>
<td>–</td>
<td>–</td>
<td>3.48 ± 7.98</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Right fourth pleopod</td>
<td>0.48 ± 1.54</td>
<td>0.19 ± 0.51</td>
<td>3.19 ± 8.63</td>
<td>–</td>
<td>–</td>
<td>0.05 ± 0.22</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Left fifth pleopod</td>
<td>0.62 ± 1.83</td>
<td>0.76 ± 2.30</td>
<td>0.67 ± 1.56</td>
<td>0.05 ± 0.22</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Right fifth pleopod</td>
<td>0.10 ± 0.30</td>
<td>0.14 ± 0.65</td>
<td>–</td>
<td>2.33 ± 4.85</td>
<td>–</td>
<td>0.10 ± 0.30</td>
<td>0.10 ± 0.30</td>
<td>–</td>
</tr>
<tr>
<td>Telson</td>
<td>0.33 ± 1.11</td>
<td>0.29 ± 1.31</td>
<td>0.29 ± 1.31</td>
<td>2.62 ± 3.83</td>
<td>–</td>
<td>0.38 ± 1.75</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Left uropod</td>
<td>8.14 ± 11.78</td>
<td>–</td>
<td>5.33 ± 10.91</td>
<td>3.19 ± 5.14</td>
<td>–</td>
<td>0.10 ± 0.30</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Right uropod</td>
<td>9.67 ± 16.37</td>
<td>0.24 ± 1.09</td>
<td>0.10 ± 0.44</td>
<td>2.33 ± 5.15</td>
<td>1.52 ± 5.02</td>
<td>0.05 ± 0.22</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

Data are given as mean ± standard deviation (minimum–maximum); *n* = 40.
The mean number of epibionts on the different anatomical units separately (F, 5.07; P ≤ 0.05). The total number of epibionts indicated that each zone on the anteroposterior axis of the shrimp did not present a remarkable difference in colonization; the areas fluctuated between 11.02% on the posterior end and 31.67% on the maxillipeds. The anterior region (rostrum, antennae, antennulæ, eyes and maxillipeds) of the basibiont represented 54.37% of the epibionts. Pereiopods, pleopods, uropods and telson accounted for 45.63% of the colonization.

Comparison of epibiont communities from Lake Poso and the Malili lake system

The data for the epibiont communities on C. ensifera from lake Poso were compared with those of C. lanceolata from lakes of the Malili system (Fernandez-Leborans et al. 2006), both being shrimp species endemic to their respective lacustrine areas. The specimens of C. ensifera from Lake Poso were larger and had more individual epibionts than the C. lanceolata basibionts from the lakes of the Malili system (Table 3). The most epibiont species were found in Lake Poso, which had 80% of epibiont species. In the Malili system, Lake Mahalona had the most (70%) epibiont species, whereas Lake Towuti had the lowest (30%) of the species. However, if the sum of mean number of individuals of the different epibiont species was considered, Lake Towuti was the most important of the lakes of the Malili system, with 49.34% of the total numbers of individuals in the Malili system. Lake Poso showed the highest mean number of epibionts, accounting for 38.28% of the total number of the four lakes. The different groups of species tended to maintain populations in the diverse lakes. This was the case for the peritrich ciliates. In Lake Towuti, the number of species of peritrich ciliates was low, but this was compensated for by an increase in the number of individuals. In contrast, Lake Mahalona had a higher number of peritrich species, but lower numbers of these ciliates (Table 3).

The mean number of epibionts on the five groups of anatomical units along the anteroposterior axis of the shrimp was considered. We found a significant difference between the different lakes (F, 3.59; P ≤ 0.05), especially between Lake Matano and Lake Poso (t = −2.66; P ≤ 0.05) (Fig. 6). However, there was a significant correlation between the distributions in Lake Mahalona and Lake Poso, and between the mean of all three lakes of the Malili system and Lake Poso (0.90; P ≤ 0.05). The mean number of epibionts on the different anatomical units in all lakes of the Malili system correlated with that in Lake Poso (0.72–0.94; P ≤ 0.05) (Fig. 7).

Considering the distribution of the epibiont species on the basibionts, there were similarities among all lakes: Acineta predominated on the anterior part of the basibiont, whereas
Zoothamnium and Cothurnia tended to appear on the posterior areas of the shrimp. These epibiont species were generally the most abundant. For each anatomical unit and epibiont species, the mean number of epibionts was calculated. The pattern arising from these values with respect to all the colonized anatomical units showed peculiarities in each lake, which are illustrated by the different dendrograms from the hierarchical cluster analysis (Fernandez-Leborans et al. 2006). The epibionts in the three lakes of the Malili system showed a similar colonization pattern with respect to the anteroposterior axis of the shrimp. There were more individual epibionts on the anterior areas of the body, especially on the maxillipeds, antennae and antennulae. The pleopods and uropods are the second most colonized group of appendages, in

<table>
<thead>
<tr>
<th>Malili system</th>
<th>Lake Towuti</th>
<th>Lake Matano</th>
<th>Lake Mahalona</th>
<th>Lake Poso</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Length of the shrimp (mm)</strong></td>
<td>21.26 (14.00–27.00)</td>
<td>16.10 (11.00–21.00)</td>
<td>15.90 (11.00–19.70)</td>
<td>24.19 (13.00–33.00)</td>
</tr>
<tr>
<td><strong>Width of the shrimp (mm)</strong></td>
<td>2.96 (2.00–4.50)</td>
<td>2.65 (2.00–4.00)</td>
<td>3.12 (2.00–4.60)</td>
<td>3.90 (2.00–5.00)</td>
</tr>
<tr>
<td><strong>Number of epibionts per shrimp</strong></td>
<td>250.90 (27.00–971.00)</td>
<td>131.25 (6.00–670.00)</td>
<td>135.75 (2.00–523.00)</td>
<td>314.62 (14.00–1114.00)</td>
</tr>
<tr>
<td>Acineta sulawesiensis</td>
<td>193.08 (4.00–730.00)</td>
<td>11.75 (0.00–31.00)</td>
<td>94.80 (0.00–318.00)</td>
<td>188.62 (1.00–585.00)</td>
</tr>
<tr>
<td>Cothurnia compressa</td>
<td>16.43 (0.00–59.00)</td>
<td>14.55 (0.00–98.00)</td>
<td>1.35 (0.00–23.00)</td>
<td>11.14 (0.00–49.00)</td>
</tr>
<tr>
<td>Zoothamnium intermedium</td>
<td>40.75 (0.00–357.00)</td>
<td>51.25 (0.00–177.00)</td>
<td>2.45 (0.00–42.00)</td>
<td>107.81 (0.00–691.00)</td>
</tr>
<tr>
<td>Vorticella globosa</td>
<td>5.80 (0.00–96.00)</td>
<td>15.15 (0.00–141.00)</td>
<td>1.33 (0.00–22.00)</td>
<td>4.00 (0.00–30.00)</td>
</tr>
<tr>
<td>Opercularia coarctata</td>
<td>48.65 (0.00–523.00)</td>
<td>5.90 (0.00–68.00)</td>
<td>1.30 (0.00–22.00)</td>
<td>2.48 (0.00–18.00)</td>
</tr>
<tr>
<td>Podophrya maupasi</td>
<td>1.30 (0.00–22.00)</td>
<td>0.67 (0.00–4.00)</td>
<td>1.14 (0.00–13.00)</td>
<td>1.43 (0.00–6.00)</td>
</tr>
<tr>
<td>Spelaeophrya polypoides</td>
<td>4.00 (0.00–30.00)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amphileptus fusidens</td>
<td>4.00 (0.00–30.00)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Embata sp.</td>
<td>4.00 (0.00–30.00)</td>
<td>4.00 (0.00–30.00)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

![Fig. 6](image_url) — Distribution of the epibionts (total mean number of individuals) along the anteroposterior axis of the shrimps in the lakes of the Malili system and Lake Poso. Anatomical units are considered in five groups.
comparison with the pereiopods, which contained the fewest epibionts (Fernandez-Leborans et al. 2006). In both lake systems, the maxillipeds and the anterior part of the body (rostrum, antennae, antennulae and eyes), contained the main weight of colonization (54.36%), followed by the pleopods and pereiopods. The posterior end of the body showed the lowest colonization.

With respect to epibiont diversity, the Shannon–Wiener coefficients were calculated for each colonized shrimp. The highest mean value corresponded to Lake Poso (0.744229), and Lake Mahalona presented the highest maximum value (3.7553). There were no significant differences between the lakes and also no significant correlations. However, Lake Mahalona had values of standardized skewness and standardized kurtosis indicating significant departures from a normal distribution, and this fact separated this lake from the rest, being corroborated by the hierarchical cluster and principal component analyses (Fig. 8). In Lake Mahalona

**Fig. 7**—Distribution of the epibionts (total mean number of individuals) along the anteroposterior axis of the shrimps in the lakes of the Malili system and Lake Poso. Anatomical units are considered individually (shrimp images: above, *Caridina ensifera*; below, *Caridina lanceolata*).
Epibiosis on *Caridina* from Lake Poso • Fernandez-Leborans and von Rintelen

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(excepting *Acineta* which was present on all shrimps analysed) the epibiont species appeared in a lower proportion than in the other lakes, and 70% of epibiont species appeared on 10–40% of shrimps.

A multivariate analysis of variance was performed considering the diversity and total number of epibions, and the sex, length and width of the shrimps. This showed that in Lake Poso there was a significant relation between the species diversity of the epibiont community and the length and width of the shrimps. In contrast, sex did not significantly affect the diversity. The number of individual epibions was related to length, width and sex of the host shrimps. In the Malili system, number and diversity of epibions was related to length, width and sex of shrimps in Lake Towuti, whereas in Lake Matano only the number of epibions was related to length, width and sex of shrimps, and in Lake Mahalona there were no significant relationships. Lake Mahalona data reflected the diversity values indicated above.

Taking into account the mean number of epibiont species on the anatomical units of *C. enisfera*, there was a significant correlation between all lakes. The correlation between Lake Poso and the lakes of the Malili system was lowest for Lake Matano (0.70; *P* ≤ 0.05), and highest for Lake Towuti (0.94; *P* ≤ 0.05) (Lake Mahalona 0.89; *P* ≤ 0.05). This contrasts with the facts that, considering the mean number of epibions on the different anatomical units of the shrimp, there was a significant difference between the three lakes of the Malili system (F, 6.23; *P* ≤ 0.05), and that the canonical population analysis performed using the number of epibions on each anatomical unit of all the analysed shrimps, showed a significant difference between these three lakes (F, 3.34; *P* ≤ 0.05) (Fernandez-Leborans et al. 2006). In the canonical correlation analysis using the sum of epibions on each anatomical unit of all the analysed shrimps, there was a significant difference between all lakes, Lake Matano being the most different from the other lakes. The centroid in Lake Matano appeared clearly separated from those of the other lakes.

**Discussion**

The protozoan epibiont species found had not been recorded as epibions on the shrimp *C. enisfera*, although other species of the genera *Acineta*, *Podophrya*, *Zoothamnium*, *Vorticella* and *Cothurnia* had previously been observed as epibions on other crustaceans (Morado and Small 1995; Fernandez-Leborans and Tato-Porto 2000a,b; Fernandez-Leborans 2001). The ciliate species found have been observed as epibions on another shrimp *C. lanceolata* (Fernandez-Leborans et al. 2006). The suctorian species *Spelaephrya polyoides* was found on *Caridina* sp. in Chungking (China) (Nie and Lu 1945), on *Palaemonetes antennarius* and *Atyaephrya desmaresti* (Europa), and on *Xiphocaridina* (Africa and Asia) (Daday 1910; Nozawa 1938; Hadzi 1940). Species similar to *Spelaephrya polyoides* and *Spelaephrya troglocaridis* have been described from the cave shrimp *Troglocaris schmidtii* (Stammer 1935; Matjašič 1956; Matthes et al. 1988). Species of *Amphileptus* have never been found as epibions on crustaceans, although they are not typical sessile ciliates and therefore should be considered as ciliates of the fauna associated with *C. enisfera*. A number of rotifer species have been described as epibions on crustaceans, e.g. *Brachionus rubens* on the cladoceran *Moina brachiata* (Settele and Thalhofer 2003). Other rotifers are epizoic on diverse freshwater crustaceans, such as *Daphnia*, *Asellus*, *Gammarus* (May 1989), or decapods (*Astomatopus*, *Astacus*, *Potamon*, *Chasmagnathus*) (Hauer 1926; Carlin 1939; Wulfert 1957; Hauer 1959; Márquez and Montero 1973; Fontaneto et al. 2004).

The epibiont species observed are similar to others found as epibions or as free-living ciliates. However, in several cases, they exhibit peculiar characteristics, which may constitute adaptations to the epibiont life. For example, *Acineta sulacoensis* has a lorica as a free anterior part over the body enveloping the tentacles, possibly protecting them from damage caused by the movement of the basibiont. Other ciliates, such as *Cothurnia*, are protected by a lorica completely surrounding the body, and have a noticeable short stalk, which allows the ciliate to settle close to the surface of the basibiont. Something similar occurs in *Podophrya*, which has a very short stalk, in contrast to free-living species. *Zoothamnium* has a broad stalk, which is noticeably wider than *C. lanceolata*; this width is not only a protection for the stalk, but also for the colony (Fernandez-Leborans et al. 2006). *Spelaephrya* exhibits the most evident adaptation to the epibiont life. Although it lacks a conspicuous lorica, the body is flattened, and in the posterior area the body can be folded, resting next to the surface of the antennae where these suctorians are most abundant. In several individuals, the macro-nucleus was considerably flattened, and their anterior appeared widened, probably as the result of the adoption of a squashed shape by the ciliate to reduce friction at the...
linkage with the surface of the appendages of the shrimp. These ciliates were only found as epibionts on crustaceans.

The spatial distribution of epibiont species on the *C. ensifera* exoskeleton followed a gradient from the anterior to the posterior end of the body, with the maximum colonization on the anterior parts of the body, without a significant difference between the left and right appendages. This phenomenon was also observed in the epibiont communities of *C. lanceolata* and could be correlated to the behaviour of the shrimp (Fernandez-Leborans et al. 2006). Like *C. lanceolata* in the Malili lake system *C. ensifera* is abundant and widely distributed in Lake Poso and often found in pelagic swarms (K. von Rintelen, personal field observation). Its rapid and characteristic feeding behaviour, as described for *Caridina* in general (Fryer 1960), along with its mobility bring mainly the anterior parts (i.e. the feeding appendages) of the shrimp into contact with different kinds of soft and hard substrates (rocks, wood, sand, macrophytes), which was also observed in *C. lanceolata* from the Malili lakes (Fernandez-Leborans et al. 2006). In addition, the physical characteristics of the surfaces and their morphology were important for colonization. The surfaces of the antennae and antennae provided substrata for the settlement of epibionts, and the movement of these appendages facilitates their colonization. Other units with high number of epibionts, for example the maxillipeds, showed three characteristics as a possible explanation for their remarkable epibiosis: the widely available surface, the protected location of these appendages, and the frequent presence of nutrient particles linked to their function. Other morphological sites with high levels of epibiosis were the uropods, possibly because they have a wide exposed surface, and their position in the body places them close to the important passage of organic material from the digestion and movement of the shrimp.

Many sessile organisms depend upon the characteristics of the living substratum to which they adhered (Gili et al. 1993) and, therefore, the structure, dynamics, physiology and ecology of the basibiont can be reflected in the colonization pattern of the epibiont species, and in the development of epibiont communities. Understanding epibiosis may contribute to understanding the biology of the basibiont. The number and distribution of epibionts on the different anatomical units of the basibiont can indicate terminal moulting, seasonal differences of moult pattern between the two sexes, asynchronous moulting between populations in different geographical areas, burying and feeding behaviours, etc. (Bottom and Ropes 1988; Abelló et al. 1990; Abelló and Macpherson 1992; Gili et al. 1993; Fernandez-Leborans et al. 1997).

Lake Poso had the highest number and diversity of epibiont species, mainly ciliate protozoans, whereas the frequency of other epibionts was less than 1%. The data showed that different epibiont species had distinctive spatial distributions on the basibiont. This fact was reflected in the differential presence of epibiont species on the anatomical units of the shrimp, and it was also defined by the pattern of distribution along the anteroposterior axis of the basibiont, which differed significantly between epibiont species. However, the community seems to behave en masse, which can be verified by the patterns of colonization. We hypothesize that the species tend to occupy the available substratum that has the particular requirements of each functional group, but with a trend towards maintaining an equilibrium among species and groups, compensating through diversity and number of individuals.

All lakes correlated with respect to the mean numbers of epibiont species on the anatomical units of the shrimp, although the three lakes of the Malili lake system differed significantly. Taking into account the number of individual epibionts on the anatomical units of the shrimps, all lakes differed significantly, especially Lake Matano. With regard to the spatial distribution of epibionts along the anteroposterior axis of the shrimp we found similarities between the Malili lakes in general and Lake Poso, but a significant difference between Lake Matano and Lake Poso.

In summary, it can be concluded that all the lakes showed a similar general pattern of epibiont spatial distribution on the hosts, with some peculiar characteristics that separated the lakes of the Malili system from Lake Poso. In the Malili system the lakes Mahalona and Matano showed irregular spatial distribution and diversity patterns. This may be related to the ecological characteristics of these lakes. Lakes of the Malili system are partially isolated, and are located in a string from Lake Matano to Lake Towuti. Deforestation and consequent eutrophication may affect the epibiont communities in these lakes. In all the lakes there was a colonization pattern comprising the maintenance of a anteroposterior gradient, which was sustained by the fluctuation in diversity and number of individuals of the different functional groups of epibiont species. From the data of diversity and proportions of number of species and individuals, it can be deduced that the functional role of the different groups of species seems to tend towards sustainability with little global variation in the diverse lakes. This is the case of the peritrich ciliates; in Lake Towuti, the number of species was low, but this was compensated by an increase in the number of individuals. In contrast, Lake Mahalona had more peritrich species, but fewer individuals. The basibiont represents a dynamic environment on which the epibiont community species acquire a colonization pattern. The species were located following a particular strategy, and this was proved by the results: the species followed a tendency correlated to the different lakes. Independent of the species present and in all cases, each species was established as fitting the same general distribution.

The protozoan ciliate epibionts probably do not harm the basibiont. Within the epibiont community there are diverse trophic links and, therefore, as occurs in free environments, there is an energy feedback (microbial loop or other relations)
and several species can feed on other protozoa in the epibiotic community or on other organisms belonging to the community associated with the host (that have free movement around the basibiont), such as suctorians feeding on other ciliates. Peritrich ciliates could depend on the nutrients arising from the activities of the shrimp. Protozoa of lake environments are considered as a major link in the limnetic food web and they have key functions in energy flow and cycling in freshwater ecosystems. Protozoa are a very important link in the transfer of energy to the higher trophic levels and they are a common nutrient for crustaceans and fish larvae (Porter et al. 1985). The changes in the community structure of protozoa may significantly affect other components of the aquatic food web, and consequently may influence the distribution and abundance of both lower and higher organisms (Beaver and Crisman 1989; Carrick and Fahnsteniel 1992; Cairns and McCormick 1993). Ciliates have important ecological significance in free environments, especially in benthic areas, where they show high growth rates and trophic diversity (Patterson et al. 1989; Fenchel 1990; Fernandez-Leborans et al. 2002). Although on a small scale, these conditions could be transferred to an epibiotic community, which could reflect the biodiversity in the environment (Fernandez-Leborans and Gabilondo 2006).

Lake Poso and the Malili lakes are isolated from each other and harbour both a very distinctive fauna and a high number of endemic taxa living under similar ecological conditions. The various epibiotic communities found on C. ensifera and on C. lanceolata (and on other Caridina species from the Malili lakes; compare Fernandez-Leborans et al. 2006) in the respective lake systems not only represent tendencies regarding the colonization pattern and distribution of different epibionts on their host, but also enhance our knowledge of the lakes’ exceptional fauna. Human impacts (e.g. deforestation around the lakes or introduction of alien species) are a permanent threat to the basibiont shrimps and could harm the epibionts as well. The protection of both lake systems and their unique communities should be a conservation goal.

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