



First report of ciliate (Protozoa) epibionts on deep-sea harpacticoid copepods



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ABSTRACT

We report the first observations of ciliate epibionts on deep-sea, benthic harpacticoid copepods. One ciliate epibiont species belonged to class Karyorelictea, one to subclass Suctorina, and one to subclass Peritrichia. Our samples came from the continental rise off central California (36.709°N, 123.523°W, 3607 m depth). We found that adult harpacticoids carried ciliate epibionts significantly more frequently than did subadult copepodids. The reason for the pattern is unknown, but it may involve differences between adults and subadult copepodids in size or in time spent swimming. We also found that the ciliate epibiont species occurred unusually frequently on the adults of two species of harpacticoid copepod; a third harpacticoid species just failed the significance test. When we ranked the 57 harpacticoid species in our samples in order of abundance, three species identified were, as a group, significantly more abundant than expected by chance if one assumes that the abundance of the group and the presence of ciliate epibionts on them were uncorrelated. High abundance may be among the reasons a harpacticoid species carries a ciliate epibiont species disproportionately frequently. For the combinations of harpacticoid species and ciliate epibiont species identified, we found one in which males and females differed significantly in the proportion that carried epibionts. Such a sex bias has also been reported for shallow-water, calanoid copepods.

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1. Introduction

Benthic harpacticoid copepods (hereafter harpacticoids) occur in essentially all shallow-water, marine sediments (reviewed by Hicks and Coull, 1983). They are also ubiquitous in deep-sea sediments, where they are abundant (see, e.g., Vincx et al., 1994) and species rich (see, e.g., Baguley et al., 2006; Rose et al., 2005; Shimanaga et al., 2004; Thistle, 1978). By analogy with their shallow-water relatives, deep-sea harpacticoids are expected to be important in the transfer of energy and materials from microbes to larger organisms (reviewed by Hicks and Coull, 1983; Pace and Carman, 1996). Ciliate epibionts (hereafter epibionts) are protozoans a few tens of microns long. They attach themselves to many substrates, including harpacticoids (Carman

and Dobbs, 1997), where their presence may affect the harpacticoid's performance (see, e.g., Puckett and Carman, 2002).

While identifying deep-sea harpacticoids for an ecological study, we found that some individuals carried epibionts. Although this phenomenon has been observed in shallow-water harpacticoids (e.g., by Batisse, 1992, 1994; Herman et al., 1971; Utz, 2003), our search of the literature revealed no examples from the deep sea. Here, we report its existence, give some natural-history information, and describe the results of our searches for patterns in the occurrence of epibionts on deep-sea harpacticoids. Patterns reported from shallow-water calanoid copepods guided our search.

We asked (1) whether copepodids carry a particular epibiont species more or less frequently than adults (see, e.g., Herman and Mihursky, 1964; following Huys and Boxshall, 1991, we use copepodid to refer to the postnaupliar stages I–V); (2) whether the adults of a particular harpacticoid species carry a particular species of epibiont unusually frequently (see, e.g., Turner et al., 1979; Wahl and Mark, 1999); (3) whether the adults of harpacticoid species that carry epibionts unusually frequently are also unusually abundant when considered as a group; and (4) whether, for the adults of the harpacticoid species that carry epibionts

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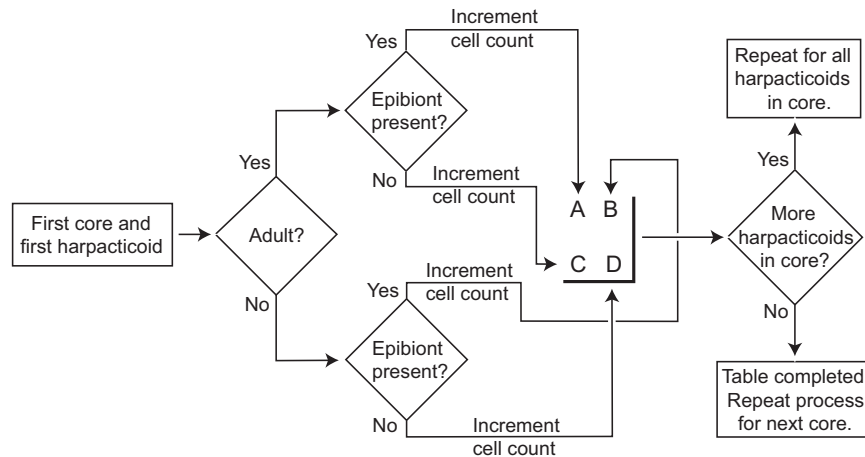


Fig. 1. A flow diagram showing how harpacticoid adult and copepodid individuals were assigned to 2-by-2 tables for each core.

unusually frequently, the sexes carry epibionts in different proportions (see, e.g., Nagasawa, 1988; Ohtsuka et al., 2004).

2. Materials and methods

Our samples came from 36.709°N, 123.523°W at 3607 m on the continental rise off central California. The bottom-water temperature, salinity, oxygen, and pH were 1.55 °C, 34.39, 120 μmol, and 7.78 respectively. The average current speed 15 m above the seafloor was 3 cm s⁻¹ (Barry et al., 2005).

We took four sediment cores of 7 cm inner diameter with the remotely operated vehicle *Tiburon* of the Monterey Bay Aquarium Research Institute. (They were the control samples from the experiment designated CO₂-5 in Barry et al., 2005; Sedlacek et al., 2009.) Processing was quantitative for harpacticoids (Sedlacek et al., 2009). Briefly, a 1.9-cm-diameter subcorer was inserted into the center of a core. We studied the sediment between the corer and the subcorer. The 0- to 0.5-cm, 0.5- to 1-cm, 1- to 2-cm, and 2- to 3-cm layers were preserved separately in a solution of one part formalin and nine parts artificial seawater (salinity 35) buffered to neutrality with sodium borate.

In the laboratory, we stained the harpacticoids with rose bengal and removed them from the sediment under a dissecting microscope. We counted the copepodids and adults from each sample. We determined the sex of each adult and used standard morphological characters to identify it to working species, i.e., a group of individuals believed to belong to a single species. We used a working-species approach because we anticipated that fewer than 5% of our species would have scientific names (see, e.g., Rose et al., 2005), which was the case.

Ciliates are best identified alive, but our samples had to serve multiple purposes and were preserved with formalin. As Ólafsdóttir and Svavarsson (2002) found, formalin preservation made the identification of ciliates difficult. We erected working species using light and scanning electron microscopy and identified them to the lowest possible taxon using standard, morphological characters and the relevant literature (e.g., Curds, 1987; Dragesco, 1999; Lynn and Small, 2000; Warren, 1986). We used a compound microscope to assign each epibiont individual to a working species.

In statistical tests, we took alpha to be 0.05 and made no correction for multiple testing. For some questions, we analyzed 2-by-2 tables; Fig. 1 shows an example of how we filled such a table.

3. Results

3.1. The fauna

We recognized 57 working species of harpacticoids from 13 families (Sedlacek, 2007). None of the species was known to science.

Three epibiont species were abundant enough to study (i.e., found on at least three harpacticoid adults). One was from class Karyorelictea near *Trachelolophos* (Fig. 2), one from subclass Suctorina near *Loricophrya* (Fig. 3), and one from subclass Peritrichia near *Vorticella* (Fig. 4). We refer to them as the karyorelictid, the suctorian, and the peritrich, respectively. See Fig. 5 for taxonomic affinities.

We found some patterns in epibiont attachment. The suctorian (28 individuals) and the karyorelictid (12 individuals) occurred primarily on harpacticoid antennules, although we found one harpacticoid with a suctorian on its cephalosome. The karyorelictid was observed only on harpacticoid individuals that carried at least one suctorian. The peritrich (15 individuals) occurred on harpacticoids in approximately equal numbers on the cephalosome, near the mouth parts, and on the body between the swimming legs.

In scanning electron micrographs, we observed no damage to a harpacticoid's exoskeleton, even when the epibiont had been dislodged during processing, and no concentrations of microbes around the locations where the epibionts had been attached.

3.2. Question 1. Do copepodids carry a particular epibiont species more or less frequently than do adults?

We would have preferred to ask this question for individual harpacticoid species, but we could not identify copepodids to species (a frequent problem in studies of deep-sea harpacticoids; see, e.g., George and Schminke, 2002, but see Menzel and George, 2012, for an exception). Rather, we classified each harpacticoid individual (regardless of species) from a given core as a copepodid or as an adult. To determine whether a given epibiont species occurred on copepodids in a different proportion than it did on adults, we created (Fig. 1) a 2-by-2 table for that epibiont species for each core. Using the tables from the four cores as replicates, we found (two-tailed Mantel–Haenszel test, Sokal and Rohlf, 1995) that the proportion of adults that carried epibionts was significantly greater than that of copepodids for the karyorelictid ($p = 0.004$) and the suctorian ($p < 0.001$). In addition, we found a strong trend ($p = 0.063$) for the peritrich to follow this pattern.

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