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Evidence of dietary feedback in a facultative association between deep-sea gastropods and sea anemones

Annie Mercier^{a,*}, Meredith Schofield^a, Jean-François Hamel^b^a Ocean Sciences Centre (OSC), Memorial University, St. John's (Newfoundland and Labrador), A1C 5S7, Canada^b Society for the Exploration and Valuing of the Environment (SEVE), 21 Phils Hill Road, Portugal Cove-St. Philips (Newfoundland and Labrador), A1M 2B7, Canada

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ABSTRACT

While epibiotic associations between macrobenthic invertebrates are common, the role they play in the feeding ecology of intervening species is often incompletely understood. The diets of epibiotic sea anemones *Allantactis parasitica* and their gastropod hosts were analyzed using digestive tract contents, lipid biomarkers and observations of live specimens in an attempt to detect dietary feedback from the facultative association. Comparisons were made using symbiotic individuals and asymbiotic counterparts collected at depths of 191–627 m from three neighbouring areas in the northwest Atlantic. Gastropods carrying one or two epibionts had higher stomach indices than those harbouring three epibionts or no epibiont. The diet of symbiotic gastropods was also more diversified based on stomach contents and lipid analysis. Among other things, symbiotic gastropods contained four times more lipids and a greater proportion of $\Sigma n-3$ fatty acids. Gastrovascular cavity content indices of asymbiotic sea anemones were generally lower than those of symbiotic counterparts. Their cavities were more often empty, and their diet less diversified with fewer benthic items, suggesting that foraging of gastropods through the sediments makes more food available to sea anemones living as epibionts. Lipid analysis showed some disparities between symbiotic and asymbiotic sea anemones at the regional scale, including in percent phospholipids and in the proportion of certain fatty acids. Together these findings indicate that mutual protection against predators leads to prolonged and more efficient foraging for gastropods and increased time spent deployed (feeding) in food-rich areas for sea anemones, thus enabling both partners to fully exploit food resources that may be limited at bathyal depths.

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1. Introduction

Epibiotic associations (i.e. involving substrate organisms, the basibionts, and attached species, the epibionts) are the evolutionary result of interactions between environmental factors and benthic life forms. Both benefits and disadvantages to the intervening organisms have been reported from a diverse and widespread array of epibiotic associations (Wahl, 2009). Some of the most ubiquitous examples of epibiosis bring together sea anemones (Cnidaria: Actiniaria) and various benthic invertebrates. The relationship between sea anemones and decapod crustaceans, mainly hermit crabs, has received most of the attention (Faurot, 1910; Ross and Sutton, 1961; Ross, 1971; McLean and Mariscal, 1973; Hand, 1975; Bach and Herrnkind, 1980; Brooks and Mariscal, 1986a; Buckley and Ebersole, 1994; Christidis et al., 1997). Associations between sea anemones and gastropod molluscs have also been reported (Hand, 1975; Ross and Kikuchi, 1976; Ates, 1997, 1998; Reiss et al., 2003; Goodwill et al., 2009), but only rarely studied experimentally (Luzzatto and Pastorino, 2006;

Mercier and Hamel, 2008, 2009). Numerous explanations for the frequent occurrence of sea anemones in epibiotic associations have been proposed. Investigations have mostly focused on the benefits to the basibiont, indicating that hermit crabs (Ross, 1971; McLean and Mariscal, 1973; Bach and Herrnkind, 1980; Brooks and Mariscal, 1986b) or gastropods (Mercier and Hamel, 2008) are protected against predators by the stinging tentacles of the sea anemone(s).

While these symbioses have generally been regarded as examples of mutualism (Ross, 1974; Brooks and Gwaltney, 1993; Mercier and Hamel, 2009) it is not always clear how the sea anemone benefits from the relationship. Some symbiotic sea anemones have been shown to be protected against predators by their host hermit crabs (Brooks and Gwaltney, 1993) and gastropods (Mercier and Hamel, 2008). Benefits to the sea anemone may also include avoidance of poor environmental conditions (e.g. low oxygen or adverse temperature levels) through transportation (Brooks, 1988), decreased chance of being smothered by sediments (Conover, 1975) and greater fertilization success via host aggregations (Mercier and Hamel, 2009). Increased access to food resources resulting from the mobility or feeding activities of the host has also been proposed (Ross, 1974; Stachowitsch, 1980; White et al., 1999; Mercier and Hamel, 2008), but support for this assumption remains limited. Christensen (1967)

* Corresponding author.

E-mail address: amercier@mun.ca (A. Mercier).