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SYMBIOTIC RELATIONS AND FEEDING BIOLOGY OF *SYMBION PANDORA* (CYCLIOPHORA) AND *TRITICELLA FLAVA* (BRYOZOA)

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COMMENSALISM
EPIBIOSIS
FILTER-FEEDING

ABSTRACT. – Norway lobsters (*Nephrops norvegicus*) with epizoans were held in tanks with seawater and ¹⁴C-labelled microalgae (*Rhodomonas baltica*) for 24 h. The isotopic activity of two epizoans on the mouth parts of the host, the bryozoan *Triticella flava* and the cycliophoran *Symbion pandora*, were compared by liquid scintillation counting. There was no isotopic activity recovered in *Symbion pandora* but *Triticella flava* actively ingested the labelled algae and accumulated isotopic activity over time. The cycliophoran feeding activity was assessed further by direct observation of detached feeding stages in a recirculation system. Feeding stages did not respond when algae were offered, but immediately began feeding when diluted hemolymph or homogenized mussel was offered. The results explain why cycliophorans only occur on the mouthparts of the host and support the notion that cycliophorans are obligatory commensals that solely depend on the food provided by their host. Cycliophorans start feeding when the host begins to feed and high concentrations of food particles become available. It is likely that cycliophoran feeding individuals have developed sensory mechanisms to synchronize their food supply with the feeding activity of the host but the precise mechanism is still unknown. In contrast *T. flava* is a facultative commensal that can sustain on plankton independent of host feeding activities. In agreement with this *T. flava* often occurs on other parts of the host than the mouth parts.

INTRODUCTION

The microscopic *Symbion pandora* Funch & Kristensen 1995 is an ectosymbiont living on the mouthparts of the Norway lobster, *Nephrops norvegicus* (Linnaeus, 1758). The species was described as the first member of the new phylum Cycliophora (Funch & Kristensen 1995), a group of marine protostomes with uncertain phylogenetic affinities (Funch *et al.* 2005). Since its first discovery a number of additional cycliophoran species have been recognized from the mouth appendages of the American lobster *Homarus americanus* H. Milne-Edwards, 1837 (Baker *et al.* 2007, Baker & Giribet 2007, Obst *et al.* 2005, 2006) and the European lobster *H. gammarus* (Linnaeus, 1758). Six different stages are known from the cycliophoran life cycle (Funch & Kristensen 1997, Obst & Funch 2003). The most prominent stage, the polyp-like feeding individual is permanently attached to the integument of the host (Fig. 1). It is the only stage equipped with an alimentary tract and it ingests food with a ciliated ring-like filter apparatus, the so-called buccal funnel. Young feeding stages typically reproduce asexually with non-feeding larvae. Such larvae immediately settle on the mouth parts and develop into new feeding stages. This asexual reproduction results in a colonization of the mouth parts of the host

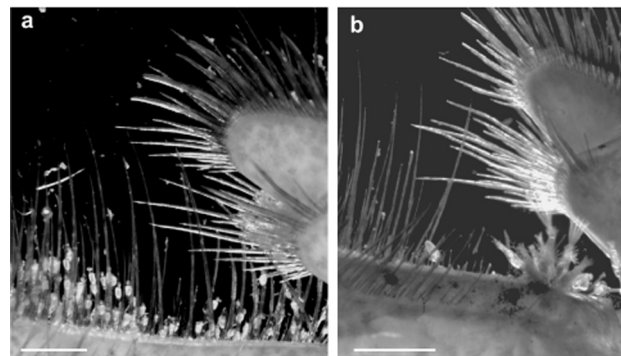


Fig. 1. – Medial rim of the mouth appendage (Mxp II) of *Nephrops norvegicus*. Typical epibionts in this microhabitat are the feeding individuals of *Symbion pandora* (a) and the polypids of *Triticella flava* (b). Scale bar: 1 mm.

(Obst & Funch 2006). All cycliophoran species known today have this type of very complex life cycle (Obst & Funch 2003) which is almost entirely taking place on the mouthparts of three nephropid lobsters. This suggests intense symbiotic relations between the epibionts and their host. However, few studies have so far examined this relationship closer (Obst & Funch 2006) and the most critical host-epibionts interactions remain to be identified. It is still unclear for example what restricts the epibionts to the narrow habitat on the lobster's mouth

parts or which part of the epibionts complex life history has evolved in adaptation to the host moulting cycle. Such features are well studied in other invertebrates with complex life cycles. In the present study we use an experimental approach to investigate cyclophoran feeding biology in order to better define the relationship to their hosts. We wish to address the question of whether suspension feeding in cyclophorans is similar to other filter feeding epibionts (Di Camillo *et al.* 2008, Fernandez-Leborans 2003). The bryozoan *T. flava* is ideal for comparison due to similarities in habitat and feeding mechanism with *S. pandora*. Both species often co-occur on the mouth parts of *Nephrops norvegicus* where they are permanently attached, and both species are suspension feeders that use ciliated structures surrounding the mouth to collect food particles.

MATERIALS AND METHODS

Tank experiment

For the following experiments *Nephrops norvegicus* was collected in cages from Gullmarsfjorden in July 2001 and retained in running seawater without any food supply. Adult healthy lobsters with epizoic fauna on the integument were selected and placed in closed aquaria (size 50x30x20 cm) with filtered seawater. Microalgae (*Rhodomonas baltica* Karsten, 1898) were labelled with ^{14}C by incubation in *f/2* growth medium added 600 $\mu\text{Ci NaH}^{14}\text{CO}_3 \text{ l}^{-1}$ in 500 ml Erlenmeyer flasks during 3 algal generations. Subsequently, the algae were rinsed for non-incorporated labelled material in the water by centrifugation (1000 g for 5 min) and resuspension in *f/2* growth medium. The algae were then added to the aquaria holding lobsters at a concentration of 5000 cells ml^{-1} . After 24 hours all lobsters were killed and their mouthparts removed. Individuals of the cyclophoran *Symbion pandora* and the bryozoan *Triticella flava* were removed from the mouth parts and placed individually in scintillation vials and Ultima Gold scintillation cocktail (Perkin Elmer) was added. The isotopic activity was then measured by liquid scintillation counting in a Beckman LS5000TD liquid scintillation counter.

Direct observations of feeding

In a separate experiment three to six feeding stages of *Symbion pandora* attached to a small piece of cuticle were dissected from the mouth parts and placed in a Petri dish filled with 30 ml of filtered seawater and connected to a recirculation system allowing temperature control and addition of different feeding substrates. Feeding stages with an open buccal funnel or a degenerating buccal funnel were excluded and only non-feeding individuals were chosen for this experiment. The cyclophoran feeding activity was assessed in response to three different substrates in the water, a) live algal cells (*Rhodomonas baltica*), b) 25 μl of hemolymph from *Nephrops norvegicus* mixed with 25

μl of distilled water, and c) homogenized mussel (*Mytilus edulis* Linnaeus, 1758). The filtering activity was observed and recorded with a Nikon Coolpix digital camera attached to an S-VHS and mounted on a Zeiss Stereomicroscope at 50x magnification.

RESULTS

Tank experiment

There was no isotopic activity recovered in *Symbion pandora* after exposure to radio labelled *Rhodomonas* algae for 24 hours (Fig. 2a). In contrast, the nearby attached bryozoan *Triticella flava* actively ingested the labelled algae and accumulated isotopic activity over time (Fig. 2b).

Direct observations of feeding

None of the feeding individuals responded when algae were offered. In contrast feeding stages reacted instantly to the addition of either diluted hemolymph or homogenized mussel by opening the buccal funnel and feeding for several minutes without pause. In young individuals the feeding response to hemolymph and mussel was so strong that even deterring the animal with a pincer did not

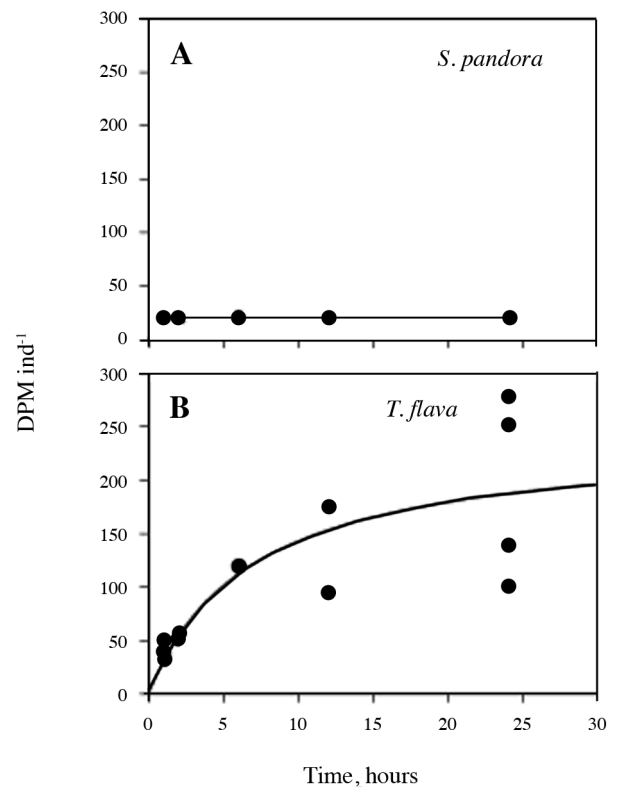


Fig. 2. – Feeding experiment tracing the incorporation of ^{14}C from labelled *Rhodomonas baltica* over time. A. *S. pandora* does not accumulate any ^{14}C from algae with time whereas B. *T. flava* do accumulate ^{14}C over time.

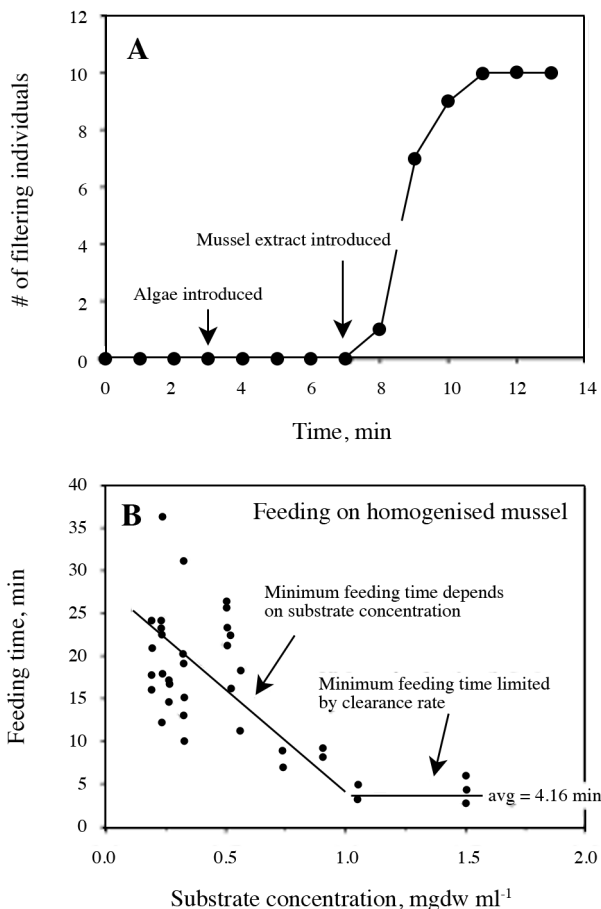


Fig. 3. – Feeding experiment tracing the feeding activity of *S. pandora*. A. Adding *Rhodomonas baltica* to the water did not stimulate a feeding response, while the addition of mussel extract directly triggered feeding activity. B. A high concentration of protein rich food stimulates a short intense feeding response, while decreasing concentrations cause extended feeding periods.

disturb the feeding activity. Following the cycliophoran feeding activity for 15 min after successively adding different substrates to the water showed that live algal cells (added 3 min after the start) did not initiate feeding while homogenized mussels (added 7 min after start) caused all individuals to start filtering (Fig. 3a). Once the feeding was initiated, *Rhodomonas baltica* and other particles in the water then also became ingested. Measuring feeding time of cycliophoran individuals as a function of food concentration of homogenized mussel in the surrounding water showed a clear relationship in which feeding time increased in a linear manner with declining food concentration (Fig. 3b).

DISCUSSION

In the present experiments *Symbion pandora* feeds exclusively on particles and suspended matter with high energy contents like homogenized mussel and host hemo-

lymph. Although particles with low energy contents such as algae or scattered detritus particles are not rejected once feeding is initiated such nutrients do not trigger any feeding response in the epibionts. With this behavior cycliophorans show a feeding strategy different from that of other sessile filter feeders which sieve the water column continuously and unspecifically (Jeffries *et al.* 1982, Larsen & Riisgård 2002, Riisgård *et al.* 2000, 2002, 2004 Riisgård 2002, Riisgård & Manriquez 1997, Riisgård & Nielsen 2006). This was already suggested by Obst & Funch (2006) based on the distribution patterns on the mouth appendages. The results presented here suggest that the cycliophorans strongly depend of the food provided by the host. Such “food sharing” is probably initiated as the host begins to feed and high concentrations of food particles become available. It is likely that cycliophoran feeding individuals have developed sensory mechanisms to synchronize their food supply with the feeding activity of the host. This could be experimentally tested by exposing feeding individuals to certain amino acids typically contained in nutrient rich tissue.

In conclusion, the relationship between cycliophorans and their hosts is commensalistic, as there seems to be a great benefit for the epibionts while the host seems largely unaffected. However, in some cases cycliophorans (e.g. on *Homarus*) can grow extremely dense and therefore maybe cause clogging of the sensory setae. The experiments presented here suggest that cycliophorans are obligatory commensals adapted to feed on short and high concentration of food particles provided by their host. It is likely that the feeding stages during one feeding event can fill the digestive system after which they become inactive and utilise the ingested food.

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