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NOTE

Increased drag reduces growth of snails: comparison of flume and *in situ* experiments

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ABSTRACT: Snails *Littorina littorea* with and without artificial epibionts were exposed *in situ* for nearly 1 mo. Measurement of individual shell length increase over this period revealed that clean snails grew 3 times faster than fouled snails. These results compare well with previously conducted flume experiments (Wahl 1996). This epibiosis effect is thought to be due to increased drag—the only feature distinguishing the 2 treatment groups—caused by the presence of epibionts on the shell. Increased drag probably entails higher energy expenditure for pedal activities (attachment and locomotion) and a reduced allocation of resources towards growth and, possibly, reproduction.

KEY WORDS: *Littorina littorea* · Drag · Simulated epibiosis · Growth rates · *In situ* experiments · Energetic trade-offs

Pedal activities such as attachment and locomotion represent a substantial part of the gastropod metabolic budget (e.g. Grenon & Walker 1981, Davies et al. 1992). Attachment and up-stream locomotion must counteract drag encountered by the snail due to water flow. Previously, I have shown that epibionts may substantially increase drag on the periwinkle *Littorina littorea* (Wahl 1996). This effect was hypothesised to increase costs of pedal activities. Indeed, working on snails equipped with artificial epibionts in a flume, it could be shown that increased drag did reduce growth rates. In this *in vitro* experiment, some parameters were controlled artificially. Flow was maintained at a constant velocity of 8 cm s^{-1}. Grazing area per snail was confined to a circle with a radius of 7 cm. Additionally, the availability of food was periodically limited. Under these conditions, fouled snails grew significantly slower, 35% on average, than clean snails. Presumably, fouled snails facing increased drag were forced to invest more energy into locomotion and attachment. The energy thus spent was lost for growth. While these flume results hint at an epibiosis effect of great ecological potential, some doubt always remains about the reliability of *in vitro* experiments in reflecting natural processes.

How, then, do the flume results relate to 'real life'? Does epibiosis also reduce growth of the basibionts under natural conditions? In order to answer these questions, I followed the growth of (artificially) fouled and clean snails in their original habitat.

Material and methods. *In situ* experiments were run during summer 1996 in the Western Baltic. A total of 400 *Littorina littorea* were collected near the test site at 3 to 4 m depth (200 m off Strande, Kiel Fjord, Germany, 54° 26'N, 10° 11'E). Shell length was measured to the nearest $^1/_{10}$ mm as the longest distance between the apex and the far rim of the aperture. Average shell length was 13.7 mm (SE: ±0.2 mm, range: 10.8 to 16.6 mm), which can be regarded as indicative of a half-grown snail, the largest locally found individuals measuring about 24 mm in length (Wahl 1996).

The snails were thoroughly cleaned of epibionts by brushing. Each individual was tagged by gluing a numbered plastic disk (diameter 2.7 mm) onto the shell. Numbers were assigned randomly to snails. Subsequently, odd numbers were assigned to a 'fouled', even numbers to a 'clean' batch (200 individuals each). As the physical properties of 'epibionts' should remain constant during the experiment, I chose to glue artificial algae (a 2 cm long palmtree-shaped, neutrally buoyant segment of a plastic aquarium plant) by means of a drop of Z-Spar Splash Zone cement onto the apical end of the 'fouled' snails, while clean snails received a drop of cement only in the same shell location. The 2 resulting batches of snails resembled each other in all parameters except drag. The treatments cement-plus-palmtree (= 'fouled') and cement-only (= 'clean') increased drag as compared to pre-treat-

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ment snails by the factors 5.3 and 1.4, respectively. Thus, the artificial aufwuchs closely matched the effect of natural *Ectocarpus* sp. fouling on *Littorina littorea* (for details see Wahl 1996). To increase the retrieval rate in the field, snails were marked with a fluorescent yellow dot on the top of the shell.

All snails were then returned to a stony patch (4 m^2) within their original habitat. After 26 d, SCUBA divers collected all marked snails they could find in a 1600 m^2 area centred around the stony patch. The individual increase in shell length during the 26 d of the field experiment (July–August 1996) was used as a parameter of snail growth.

Growth rates of fouled and clean snails were compared by 1-way ANOVA (after having applied Cochran's Test to ensure that variances were homogeneous).

Results. A total of 60 fouled (30% of originally exposed) and 51 clean (26%) *Littorina littorea* were collected, identified by number and measured at the end of the experiment. On average, shell length had increased by 0.065 (SE 0.03) mm for fouled snails and by 0.195 (SE 0.03) mm for clean snails, corresponding to a growth rate of 2.5 µm d^{-1} and 7.5 µm d^{-1}, respectively. Thus, clean snails grew 3 times faster than fouled snails (Fig. 1, 1-way ANOVA. F = 9.64, p = 0.0024).

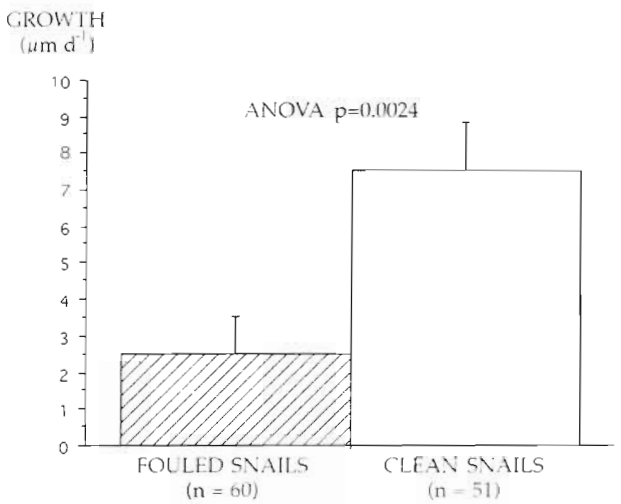

Fig. 1. *Littorina littorea*. Difference in growth rates between clean and fouled snails expressed as mean daily shell length increase (µm d^{-1} ± SE) during the 26 d *in situ* experiment

Discussion. The treatment-caused difference between the 2 snail batches consisted of the presence of an artificial epibiotic alga on the members of the 'fouled' batch. Apparently, this treatment caused a 3-fold difference in growth rates between the 2 groups. As snails were retrieved in similar proportions, it does not seem to have affected mortality or emigration of the snails.

In a previous experiment (Wahl 1996) I showed that a variety of epibionts may substantially increase drag on the snail host. Further, simulated epibiosis led to a decrease in growth rates when fouled and clean snails were exposed to constant flow (8 cm s^{-1}) in a flume. During periods when snails had to roam for grazing, clean snails grew 2 to 12 times faster. This trend was reversed when food was so abundant that snails no longer depended on locomotion for feeding and became sedentary. Growth rates were substantially lower than those reported for other snail populations (Ekaratne & Crisp 1984, Kemp & Bertness 1984) by factors 4.5 and 7 for clean and fouled snails, respectively. At that time, I hypothesised that a reason for this difference might lie in one particular aspect of the flume conditions: continuous rather than intermittent exposure to flow.

To check for this and other possible artefacts of the *in vitro* experiment, the study was repeated under natural *in situ* conditions. The results were surprisingly similar The mean growth rate for all snails was slightly lower (by 7%) than under flume conditions. The 3-fold decrease of *in situ* growth rates induced by the addition of artificial aufwuchs closely resembled the mean growth difference (2.5-fold) between clean and fouled snails (mean daily growth during periods C1 and C2 = 6.4 vs 2.6 µm d^{-1}, respectively) during summer in the flume experiment.

Consequently, the growth-reducing effect of epibiosis in non-stationary water can be regarded as realistic. The generally slow growth of all snails was not an artefact due to experimental conditions in the flume, but seems characteristic for Baltic *Littorina littorea* of the size class examined. As the 2 studies reporting faster growth rates were conducted in fully marine habitats (>30‰ salinity; Ekaratne & Crisp 1984, Kemp & Bertness 1984), salinity stress may play some part in explaining the discrepancy. Typical local salinity values range between 15 and 20‰.

Thus, epibiosis via increased drag may affect snails negatively in several ways. If reduced growth rates are caused by an energetic trade-off between growth and enhanced foot-muscle activity in fouled snails, the same mechanism may hamper gonadal maturation and reproductive output of these snails. Additionally, slower growth may increase mortality by postponing the moment when a snail outgrows the prey-spectrum of local predators, such as *Carcinus maenas*. This factor could, on the other hand, be counterbalanced by an associational resistance effect of certain epibionts which reduce predation on the host (e.g. Wahl et al. in press)

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