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SIZE DEPENDENT RESISTANCE TO WAVE ACTION IN THE INTERTIDAL GASTROPOD *LITTORINA LITTOREA* (L.)

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ABSTRACT

Within species of littoral gastropods changes in size frequency distributions along exposure gradients are often observed. Size dependent susceptibility to wave action has been offered as an explanation for these patterns. However, the literature contains conflicting views on the relative susceptibility of small and large individuals. A simple experimental design allowing for controlled exposure of snails to turbulent water flow was tested. The experiment supported the claim that large individuals of *Littorina littorea* are more resistant to wave action than small ones. The drag force exerted on shells in flowing water was measured over a range of shell sizes. Coefficients of drag suggest that large individuals can withstand higher water velocities of steady flow. The results are discussed in the context of the hydrodynamic regime normally experienced by littorinids.

INTRODUCTION

Wave impact is an important physical factor with which littorinid gastropods have to cope. If the animals try to avoid wave impact by moving down, predation, especially by crabs, and possibly competition will increase. If they move up the shore they will be exposed to desiccation and extreme temperatures as well as terrestrial predators. Dislodgement by waves will prevent the animals from feeding in the preferred zone and expose them to predation.

On exposed shores, zones of high and moderate wave impact offers escape from pressures on survival. Adaptation for life in this zone, however, involves tradeoff which may lower fitness in more protected environments.

This paper re-addresses the seemingly simple question: is the ability of intertidal gastropods to withstand wave impact related to their size, and if so, is the correlation positive or negative? Due to the complex nature of hydrodynamic forces acting on an object in flowing water, the question is not as simple as it may seem at first.

Variation in mean size of littoral snails with shore level of exposure gradients are frequently reported (Vermeij 1972; Raffaelli 1982). Size dependent resistance to the impact of waves has been suggested as one factor involved in the development and maintenance of these differences in intraspecific size-frequency distributions along exposure gradients. Any pattern related to exposure, however, may be affected by substrate structure (availability and size distribution of crevices) (Emson & Faller-Fritch 1976; Hylleberg & Christensen 1978; Raffaelli & Hughes 1978) as well as selective predation by crabs (Heller 1976; Reimchen 1982; Chilton & Bull 1984; Branwood 1985).

Attempts have been made to elucidate the relationship between size and resistance to wave force experimentally (North 1954; Struhsaker 1968; Behrens 1972; Chow 1975; Hylleberg & Christensen 1978; McQuaid 1981; Boulding & Van Alstyne 1993). The results, however, are ambiguous. Denny *et al.* (1985) used a more theoretical approach in which the components of the hydrodynamic force were analyzed separately. Like any model, their model is based on simplifying assumptions.

The present paper reports the result of testing of a simple experimental apparatus for the measurement of relative resistance. The influence of shell size on drag force in steady flow is determined and the conflicting views in the literature briefly discussed.

MATERIAL AND METHODS

A random selection of 35 periwinkles (*Littorina littorea*) were collected along the southern pier of Rønbjerg Harbour in the central part of the Limfjord, Denmark (56° 53,47'N; 9° 10,14'E), and were kept in an aquarium with running sea water prior to the experiment.

The experimental apparatus consisted of a 160 cm PVC-tube with an inner diameter of 8 cm. The tube could be fixed at different angles to the horizontal. At the lower 20 cm the upper half of the tube was cut away. 150 cm from the top of the tube a piece of slate tile was fixed at a 45° angle to the tube axis. This platform was cut to fit precisely into the lower half-tube. From a container at the top of the tube, an amount of sea water could be released by the rapid opening of a large valve at the bottom of the container.

At the beginning of each test the tube was fixed at a 25° angle, and a gentle flow was directed down the tube. The experimental animal was placed on the slate at the point of intersection of the tube's longitudinal axis, with the anterior end facing the stream of water. When the snail had extended its foot, it was exposed to bursts of water released from the container. These bursts were gradually increased until 500 ml were reached, showing that the snail had attached to the substratum. Between each burst of 500 ml of water the angle of the tube was increased by 5° until the snail was dislodged. The angle of the tube was then recorded along with the shell height (largest linear measurement) of the experimental animal. The slate was scrubbed to remove mucus before a new animal was tested. After testing, the animals were preserved in alcohol.

The force of drag experienced by a snail in flowing water was measured in the following way (Fig. 1):

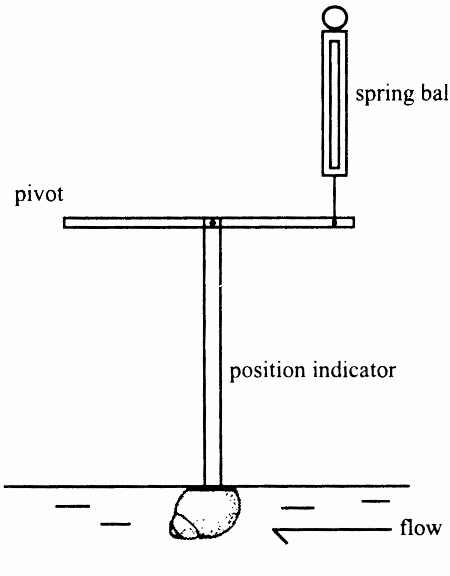

Figure 1. Experimental setup for the measurement of drag force on shells. For explanation see text.

Five *L. littorea* shells of different sizes were fixed on small metal discs with epoxy resin. To measure drag on each specimen it was fixed upside down to a magnet mounted at the end of a 50 cm hollow aluminum rod. At the other end the rod was mounted on a pivot allowing it to swing freely in the direction of flow. Two 3 cm perspex arms were mounted perpendicular to the rod at level with the pivot. A spring balance was fixed to one arm by thin wire 2 cm from the pivot. The rod was lowered so as to precisely submerge the shell in the flowing seawater, and the force was calculated from the momentum necessary to bring the rod back to its resting position (in the absence of flow).The magnet allowed specimens to be inter-changed easily. Drag force was measured at a water velocity of 0.5 m/s in a rotating container of 34 cm diameter and with the anterior end of specimens towards the flow. The effect of changing orientation was also measured. The outlines of shells were projected onto paper, and the projections cut out and weighed to determine the area of projection perpendicular to the flow.

RESULTS

In the dislodgement test two of the 35 snails (26.2 and 31.1 mm shell height) resisted dislodgement even at 90 degrees. The test procedure was then repeated with 1,000 ml of water, resulting in dislodgement at 75 and 60 degrees, respectively. For the remaining 33 test animals the angle of dislodgement following exposure to bursts of 500 ml of water is plotted against shell height in Fig. 2.

Since actual force on the snails was not measured, and two of the animals were above the 90 degrees maximum with 500 ml bursts, a non parametric method was employed in testing correlation. The Spearman rank correlation coefficient, $r_S = 0.536$, was significant ($P < 0.01$) indicating a strong association between shell height and force of dislodging water. There was, however, considerable variation in the angle of dislodgement among individuals of comparable size.

The force of drag, F_D, in a steady flow of 0.5 m/s ranged from 3.49×10^{-3}N on a 10.8 mm shell to 1.5×10^{-2}N on a 31.8 mm shell. Comparisons were made on the basis of coefficient of drag obtained from the relationship:

$$F_D \cong \frac{1}{2} C_D \rho u^2 A$$

(Mann & Lazier 1991) where C_D is the coefficient of drag, ρ is the density of the water, u is the speed of flow and A is the projected area of the object (onto a plane perpendicular to the direction of flow).

The coefficient of drag of the smallest shell was more than twice that of the largest (Fig. 3), indicating that the force per unit area of adhesive surface in the large individual would be only half that experienced by the small individual.

Changing orientation of the shell so that the posterior end was facing the flow resulted in an 8.6 % increase in drag force, whereas orienting the shell perpendicular to the flow direction increased drag force by 38 %.

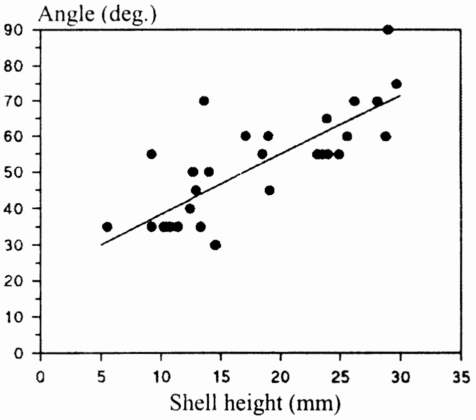

Figure 2. The response of 33 *Littorina littorea* to 500 ml bursts of sea water of increasing energy as measured by the angle of the experimental tube. Angle at dislodgement is plotted against the height of the shell.

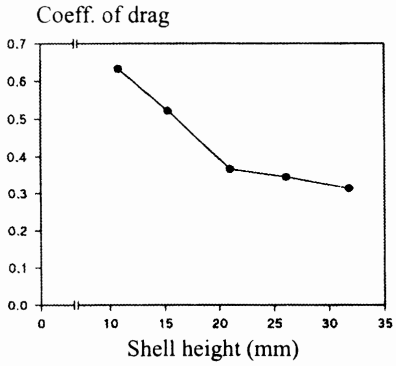

Figure 3. The relationship between size and coefficient of drag in *Littorina littorea* measured at a flow velocity of 0.5 m/s.

DISCUSSION

Various experimental methods have been employed in evaluating the size *vs.* exposure-resistance question. North (1954), Struhsaker (1968), and Chow (1975) put snails into tubes with flowing water and studied the percentage of snails of different size classes being washed off. The two former authors found small individuals to be more resistant than large ones (*Littorina planaxis* and *L. picta* (= *Nodilittorina picta*), respectively) whereas the latter author found the opposite in *L. scutulata*. Behrens (1972) used a jet of seawater to test resistance to dislodgement in *L. sitkana* and *L. scutulata*. She found small individuals of the former species to be most resistant, whereas small and large individuals were equally resistant in the latter species. However, Boulding & van Alstyne (1993) did not detect any difference between small and large *L. sitkana* in their flow tank experiment.

Hylleberg & Christensen (1978) showed experimentally, that adhesive tenacity in *Littorina littorea* was proportional to the length squared (*i.e.* roughly proportional to the area of the foot), and McQuaid (1981) found a largely similar relationship in *L. africana*, though with a power of 2.23 to length. While the former authors used a theoretical argument to predict that large individuals, therefore, would do better than small under conditions of wave exposure, McQuaid (*op. cit.*) was able to show this in field experiments with tethered animals, using a "turbulometer" (Field 1968) to measure exposure.

Denny *et al.* (1985) made a deeper theoretical study of the problems facing wave-swept organisms. They focused on the acceleration reaction component of force in breaking waves in which large organisms are relatively more prone to dislodgement than small organisms. This is due to the acceleration reaction being proportional to the third power of linear dimension. Under shallow water waves, however, accelerations are relatively small and flow forces depend largely on fluid velocity (Carstens 1968). Such flows are dominated by drag and lift forces, in which an important component is the drag force. The drag coefficient, C_D, is a complex function of Reynolds number and must be empirically determined for a given object. The Reynolds number, $Re = u\ d/\nu$, is a dimensionless number determining the relative importance of inertial and viscous forces (u is the velocity of flow, ν is the kinematic viscosity of the fluid, d is a characteristic dimension of the object).

Denny *et al.* (1985) argued that since snails like *L. scutulata* did not live in habitats where the acceleration reaction was a major force component, wave exposure would not affect size distributions. However, they used fixed values for coefficients of drag and lift in their model while their own empirical data demonstrated a dependence of at least the drag coefficient of hemispheres on Reynolds number similar to that found in the present study. The projected area of a *L. littorea* shell facing the flow is hemicircular. However, the backward projecting spire will probably result in a reduced drag on the shell compared to that of a true hemisphere.

The force of lift has not been considered here. Its dependence on flow velocity is similar to that of drag, but the coefficient of lift may be less dependent on Reynolds number (Denny *et al.* 1985).

Littorinids do not expose themselves to the full strength of large breaking waves. Their adhesive tenacity is not sufficient to withstand the forces involved. They are absent from highly exposed shores, and move down or hide in crevices during periods of violent wave action. Thus, in the hydrodynamic regime in which they move, forces of drag and lift are dominant, and here large individuals are favoured, being able to feed for a longer time, provided flows are rough so that small individuals cannot partly shelter in a boundary layer. In sheltered and more crowded situations, density of food may set a limit to size due to larger absolute food requirements of large individuals. Thus, hydrodynamic forces and intraspecific competition may act together to produce patterns of size distribution.

It is evident from a theoretical analysis of components of hydrodynamic forces acting on organisms, that the size-selective effect of these forces is depending on the hydrodynamic flow pattern. This may at least partly explain the different outcomes of empirical studies. The large variation in response within size classes is another factor which may have contributed to conflicting results.

The hydrodynamic flow pattern in the bursts of water used in the small dislodgement experiment reported here was not quantified, but is thought to emulate non-breaking waves washing up a rock surface or over boulders, a situation often experienced by feeding littorinids. The experiment demonstrates that even under such hydrodynamic regimes large individuals will on average be better off than small ones.

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