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Reduced tenacity during “high-speed” territorial encounters in the intertidal owl limpet, *Lottia gigantea*: Agonistic escalation increases risk of wash-off

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ABSTRACT

The dislodging effect of breaking waves is among the critically important factors structuring rocky intertidal communities. Because behavior is so difficult to study in the field, the interaction of wave force with behavior of intertidal organisms is poorly understood. Here, we present a field study of the interaction of breaking waves with the natural behavior of individuals of *Lottia gigantea*, an intertidal limpet with a complex territorial behavioral ecology. We hypothesized that limpets engaging in fast-moving territorial chase in response to intraspecific contact are more vulnerable to wash-off by a passing wave than are slowly foraging limpets that do not take part in such chase. We measured the lift force required to dislodge limpets while they were engaged in three natural behavioral responses to intraspecific contact in the field: 1.) continued foraging, 2.) retreat, and 3.) territorial pursuit. We divided the measured force-to-remove by aperture area to estimate resistance to wave-induced lift force, or tenacity. Tenacity (Newtons·cm^{-2}) in slowly foraging limpets was 2–4 times stronger than previously reported for moving limpets (retreating at high speed from sea stars). Small foraging limpets showed stronger tenacity than did large limpets. Tenacity was significantly reduced by high-speed territorial and retreat responses, especially in small limpets. We compounded the wash-off probabilities of tenacity during the expected number of high-speed chases in the face of an entire year of reported waves at a nearby ocean buoy, and estimated that limpets should suffer substantially greater mortality (11.5%) than do limpets that refrain from all territorial chase (2.9%). Overall, these data support our hypothesis that dislodgement by breaking waves comprises a significant risk attendant to territorial chase. The fact that limpets nevertheless engage in these chases suggests that the resources gained by this behavior are substantial.

1. Introduction

Biomechanical analyses have provided key insights into the impact of ocean waves on the ecology of near-shore organisms. Models developed by Denny (1987, 1989, 2000, 2006; Denny and Gaines, 1990; Denny and Gaylord 2002, 2010; Denny, 1994; Denny, 1999) and others (Holbrook et al., 1991; Bell and Gosline, 1997; Gaylord et al., 2003, 2006; Koehl 1999, 2006) address the interaction of the dislodgement forces of waves with the distributions, sizes, and shapes of organisms. Less attention has been paid to the interaction of these forces with the behavior of marine organisms. One exception is the early discovery that prosobranch gastropods are more easily dislodged when moving than when stationary (Miller, 1974). Although qualitatively important, these observations were performed in the laboratory, out of the context of the particular habits and habitats of the study species. More recently, Denny and Blanchette (2000) performed field observations on the owl limpet, *Lottia gigantea*, in its habitat, the mid to high intertidal zone of wave-exposed rocky coastlines. They sought to measure the adhesion strength of limpets, but because the intertidal zone at their study site (Hopkins Marine Station) is treacherous, these measurements were only made at low tide, when individuals of *L. gigantea* are stationary. Thus, our knowledge of the adhesion strength of limpets during their normal foraging behavior as the water washes over them is indirect at best. Furthermore, *L. gigantea* is a territorial limpet with a rich complex behavioral ecology (Galbraith, 1965, Stimson, 1970, 1973, Wright, 1982, 1985, 1989, Wright and Shanks, 1993, Shanks, 2002, Fenberg and Roy 2012; see below); raising the question of how its territorial behavior interacts with risk of dislodgement.

1.1. *Territorial behavior of L. gigantea*

When the tide is in, and owl limpets are wetted, large individuals

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(50–90 mm) can be observed to slowly forage (ca 0.2 cm·min^{-1}, Wright unpublished) in their 1000 cm^2 gardens of microalgae, from which they actively exclude other competitors (intra and interspecific) for food and space (Stimson, 1970, 1973; Wright, 1982, 1985, 1989; Wright and Shanks, 1993; Shanks, 2002). Such territory holders respond to contact with an intruding limpet by delivering a strong territorial response, consisting of abrupt thrusting and rapid (average speed, 8 cm·min^{-1}, Wright, 1982) pursuit of the intruder, until it has either been forced outside the territory perimeter or dislodged from the substratum (Stimson, 1970). Established territory holders are thus able to reduce competition with other limpets for their micro-algal food, which they evenly graze (Shanks, 2002; see also Branch, 1975, 1976). A single, medium to large limpet, foraging within an isolated territory with clear boundaries, will consistently (ca 80–95% of the time; Wright pers. obs.) respond to intraspecific contact with a high-speed territorial response.

Smaller individuals of *L. gigantea* are commonly found resting on home scars just outside the perimeter of the territories of large individuals. When wetted by the tide, they regularly leave these home scars to intrude into the adjacent territory. The grazing of these intruders is much more exploitative than that of a territory resident (Shanks, 2002), and they respond to intraspecific contact during this intrusion with a quick turn and rapid retreat (average velocity, 6 cm·min^{-1}) away from the contacted limpet (Wright, 1982; Shanks, 2002). Small limpets grazing inside an isolated territory containing another larger (by > 20 mm) individual, will consistently (50–70% of the time, Wright pers. obs.) respond to limpet contact with this high-speed retreat.

In addition to the territorial and retreat responses described above in response to contact with a conspecific, foraging individuals of *L. gigantea* will sometimes show neither response to contact. Instead they simply continue foraging at their usual very slow pace (0.1–0.3 cm·min^{-1}) more than an order of magnitude slower than territorial or retreat behavior (Wright, 1982). Unlike the territorial and retreat responses, which are relatively predictable in the field, this "continued foraging" behavior is observed in many different territorial settings, including the ones described above. It is most common when there are several nearby (< 0.5 m) neighboring owl limpets of approximately the same size as the subject limpet. Virtually all foraging limpets respond to limpet contact in one of the above three ways (A very small proportion of subjects, < 5%, pull their shell tightly against the substratum, retracting their cephalic tentacles underneath it. Such limpets were not studied here).

We hypothesized that high-speed territorial and retreat behaviors are high-risk strategies. This hypothesis predicts that limpets engaged in high-speed behavior should be more easily dislodged from the substratum by passing waves than if they continued slowly foraging. Furthermore, it predicts even greater risk of dislodgement during particularly rapid territorial or retreat behaviors. We tested these predictions by presenting naturally foraging subject limpets in the field with a conspecific "bait" limpet to induce one of the three responses (continued foraging, retreat, or territorial), and then measured the lift force required to remove these limpets from the substratum while engaged in these different behaviors. We predicted that behavior associated with rapid locomotion (rapid retreat and rapid territorial response) would reduce tenacity and increase risk of dislodgment, relative to continued slow foraging.

2. Materials and methods

2.1. Background on wave-induced lift, force to remove, and their dependence on aperture area

In the high-energy rocky intertidal zone of California, individuals of *Lottia gigantea* are exposed to breaking ocean waves and swells. Each incoming wave creates at least four different stresses on limpets (Denny, 1988, Gaylord, 1999), but lift force, analogous to that created by an airplane wing, is the most likely to exceed the resistance capacity of a limpet (Denny, 1988, Gaylord, 1999, Denny and Blanchette, 2000), thereby dislodging it. For any given flow parallel to the substratum surface, lift force is expected to increase proportionally to planform area. The biological resistance to this lift force tends to also be proportional to the planform area of the foot adhering to the substratum, a measure nearly the same as the planform area of the shell. Thus, if a small limpet barely resists the lift from a passing wave, a large one should as well. These considerations have led to the use of a key variable, tenacity (Grenon and Walker, 1981, Miller, 1974, Branch and Marsh, 1978, Hahn and Denny, 1989), defined as force-to-remove an individual divided by its planform area. Tenacity most directly estimates the resistance to the lift force induced by a passing wave, and is thus widely used in the present study.

2.2. Measuring "force to remove" in naturally moving limpets (see video)

Observations of limpet behavior were performed at Inspiration Point, Corona Del Mar, California (33.590317, −117.870516), after dark, in conditions that allowed extended observations of moving limpets. If tidal heights are too low to wet the limpets, they cease moving. If they are too high, turbulent water prevents observation. We found that, at this site, predicted high-low tides of 0.3–0.5 m above mean lower-low water were ideal.

Prior to our behavioral observations, during negative daytime low-low tides, we identified individual limpets that were most likely to engage in the two high-speed chase behaviors: territorial or retreat response. A prospective territorial limpet has relatively few neighbors (within 0.5 m) larger than 30 mm. A prospective retreater usually has one or more neighbors whose shell lengths are at least 20 mm longer than its own. Onto the top of each of these limpets we glued a small (15 mm diameter) screw eye and a permanent numbered tag using water-proof two-part epoxy ("Splash Zone", *Z*-spar Inc).

In order to estimate the overall lift force required to remove moving limpets, we visited the intertidal zone during night-time high-low tides, when limpets were still wetted by waves. There we identified foraging subject limpets, containing a previously glued screw-eye and tag. Foraging is readily confirmed by observing anterior cephalic tentacles extended beyond the shell of a subject limpet (Wright, 1982). We touched the cephalic tentacles of the foraging subject with the tentacles of a "bait" limpet, a small individual of *L. gigantea* obtained from a different site. Subject limpets performed one of three behaviors defined here: 1.) territorial response (accelerate for more than one shell length toward the bait limpet), 2.) retreat response (turn at least 90° and accelerate away from the bait limpet), or 3.) continued foraging (movement during 90 s of contact < 1 shell length; turn < 90 degrees, cephalic tentacles still extended).

If a subject showed territorial or retreat behavior, we maintained contact (tentacles of bait limpet held in contact with either the tentacles of territorial subjects or the posterior body-wall of retreating subjects) in an attempt to maximize the subject-limpet's speed for 1–2 shell lengths. After recording the minimum time the limpet traversed 1 shell-length (used to estimate speed, see below), or after 90 s in limpets that showed continued foraging behavior, we briskly pulled (not jerked), on a spring scale attached with a line to the screw-eye glued to the shell of the subject limpet, in a direction perpendicular to the substratum. This spring scale (spring constant = 3.56 N·cm) had a "weight marker" that recorded the maximum force, i.e., the "force to remove" the subject limpet. We estimate the time of application of increasing force to be 0.8–1.2 s. We also measured force to remove in limpets that continued foraging. Based on previous research (foragers move at 0.1–0.3 cm·min^{-1}, Wright, 1982) limpets that continued foraging were assigned a speed of 0.2 cm·min^{-1}. The longest shell length of each subject limpet was measured to the nearest mm. For territorial and retreat responses, speed (cm·min^{-1}) was calculated from the time required for the subject to move one shell length. Force to remove subject limpets was

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