Journal of Experimental Marine Biology and Ecology 451 (2014) 9–15

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

The effects of limpet morphology on predation by adult cancrid crabs

Carrie L. Tyler [a,*], Lindsey R. Leighton [b], M. Kowalewski [a]

[a] Florida Museum of Natural History, Museum Road, P. O. Box 117800, Gainesville, FL 32611-7800, USA
[b] Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E3

ARTICLE INFO

Article history:
Received 19 February 2013
Received in revised form 11 October 2013
Accepted 15 October 2013
Available online 19 November 2013

Key words:
Cancer productus
Gastropoda
Lottiidae
Functional morphology
Shell ornament

ABSTRACT

Limpets are important prey for some crab species, yet little is known about the role of the limpet shell in defense against crab predation. In an effort to identify limpet shell morphologies that decrease vulnerability to predation by adult cancrid crabs, laboratory feeding trials using three common species of Pacific Northwest limpets (*Lottia digitalis, L. pelta* and *L. scutum*) were conducted to assess how different shell morphologies affect mortality and handling time. Large size, shell ornament (radial ridges), and low-spired geometry were expected to result in increased survivorship, and/or longer handling times. Although mortality varied between species, no relationship between size and increased survivorship was observed. Contrary to the expectation that radial ribs resist predation, individuals with smooth morphologies experienced lower mortality. Furthermore, binomial logistic regression indicated that the presence of shell ornament was the only significant explanatory variable in predicting mortality. As species possessing high-spires and ridges may typically occur high in the intertidal where predation risk due to crabs is relatively lower, shell ornament is likely an adaptation to physical factors such as thermal stress, and does not appear to be antipredatory for limpets.

1. Introduction

Durophagous (shell crushing) crabs play an important role in shaping intertidal gastropod communities (e.g., Burrows et al., 1999; Cannicci et al., 2002; Silva et al., 2008, 2010c; Yamada and Boulding, 1996), and morphological adaptations to predation pressure have been well documented for many species of gastropod prey (e.g., Bertness and Cunningham, 1981; Dalziel and Boulding, 2005; Palmer, 1977; Vermeij, 1977, 1983, 1987). Although crab predation is thought to regulate intertidal limpet populations (Silva et al., 2008, 2010a), and limpets are important prey for many crab species (Cannicci et al., 2002; Chapin, 1968; Lowell, 1986; Silva et al., 2008, 2010c; Thompson et al., 2000), little is known about the effects of limpet shell morphology on durophagous predation relative to spirally coiled gastropods. This study aims to explore the role, if any, of limpet morphology in regards to predation by cancrid crabs.

A variety of anti-predatory morphologies have been proposed for limpets including size, shape, tenacity, shell ornament, and shell thickness. A limpet's primary means of defense is attachment to the substrate (Coleman et al., 2004; Iwasaki, 1993; Silva et al., 2008), and high tenacity is thought to be particularly important in resisting predation (Denny, 2000; Silva et al., 2008; Vermeij, 1987). As large limpets require considerably greater force to be removed from the substrate (Branch and Marsh, 1978; Silva et al., 2008), they may be less vulnerable to some types of predatory attack behavior (e.g., prying), and size may also provide a refuge from crab predation (Vermeij, 1976).

Shell ornament has received very little attention in limpet predation studies (but see Lowell, 1987). In some shells, corrugations increase stiffness preventing the shell from buckling when compressed (Boulding, 1984; Pennington and Currey, 1984), and strong sculptures decrease the shell surface area in contact with the crushing apparatus, restricting the application of force to the thickest parts of the shell (Miller and LaBarbera, 1995; Vermeij, 1974). Shell shape may also be important (Bulkley, 1968; Chapin, 1968; Lowell, 1986), and limpet shells with relatively low spires may be less vulnerable to durophagy: crabs attacking limpets with low-spired geometry ("flat") are often unsuccessful in attempts to crush the shell, due to difficulty in attaining purchase with the chela on the low-angle, sloped sides (Denny, 2000; Lowell, 1986, 1987). While shell thickness varies across limpet species and is not uniform throughout the shell, thicker shells can typically withstand greater and repeated loading and are more resistant to predation (Boulding, 1984; Grefsrud and Strand, 2006; Miller and LaBarbera, 1995; Boulding and LaBarbera, 1986).

In addition to confounding attacks, anti-predatory morphologies may also deter predators by decreasing energy gains. Although biological systems may frequently be too complex for optimal foraging to apply, energy gain remains an important factor in prey selection. If we assume that predators forage optimally to maximize energy gain (Clark et al., 2000; Enderlein et al., 2003; Krebs, 1977; MacArthur and Pianka, 1966; Stephens and Krebs, 1986), then predators will prefer prey that are the most profitable in regards to energy gained per unit handling time. Foraging crabs may select prey based on handling time either by maximizing the number of prey gained during the available foraging time, or by minimizing the time taken to acquire the prey

* Corresponding author.

0022-0981/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.jembe.2013.10.022

(Elner and Hughes, 1978; Rovero et al., 2000). Adult cancrid crabs move onshore with high tide to forage, and back to deeper water during low tide, most likely due to physiological constraints (Yamada and Boulding, 1996). Thus, handling time could be particularly important for adult cancrids living in the shallow intertidal, as foraging time is limited to times of submergence. Prey with morphologies that increase handling times (e.g., thicker shells, or larger size) may, therefore, be rejected by adult crabs in favor of prey with shorter handling times (Boulding, 1984; Grefsrud et al., 2003; Miller and LaBarbera, 1995). Shorter handling times may also serve to minimize the predator's exposure to risk from their own predators (birds, raccoons, other crabs, octopuses, otters, fishes, etc.).

Here we test vulnerability of three species of common Pacific Northwest limpets, *Lottia digitalis* (Rathke), *Lottia pelta* (Rathke), and *Lottia scutum* (Rathke), to predation by *Cancer productus* (Randall). Laboratory feeding experiments were performed to determine whether differential mortality results from variations in limpet shell morphology: (a) large size (i.e., increased tenacity and shell thickness, and exceeding maximum gape), (b) shell ornament (increased shell strength and/or handling time), and (c) low-spired geometry (difficulty attaining purchase). Morphologies that reduce vulnerability to predation should result in: (1) a lower proportion of successful attacks, or (2) longer grappling times (increasing cost-benefit ratio, increasing likelihood of disruption by predator). Crabs will utilize different attack strategies based on prey morphology, and success will vary across strategies.

The identification of limpet morphologies that decrease vulnerability to crab predation could prove useful in exploring the role of predation in the spatial variation of limpet abundance and diversity, as morphology can serve as a proxy for predation intensity in both modern and ancient communities (Lowell, 1987; Vermeij, 1987). Furthermore, as these mollusks can be crucial in regulating algal abundance on rocky shores (Guerry et al., 2009; Hawkins and Hartnoll, 1983), understanding the role of predation in controlling limpet populations is directly relevant to ecosystem assessment and management.

2. Materials and methods

Laboratory feeding trials were conducted to investigate the effect of limpet shell morphology on predation by adult cancrid crabs using three species of limpets (Patellogastropoda: Lottiidae): *Lottia digitalis*, *Lottia pelta*, and *Lottia scutum* (Fig. 1). Trials were conducted at Friday Harbor Laboratories during July of 2006. These species were chosen as they are abundant in the Pacific Northwest, and represent a range of morphologies facilitating the measurement of a variety of quantitative variables with potential consequences for predatory encounters. Such variation cannot be found represented within a single species, and is necessary when examining multiple morphological variables in concurrence. The finger limpet, *L. digitalis*, is relatively high spired for a limpet, has pronounced radial ridges extending to the anteriorly located apex, and its aperture is small and oval, reaching lengths of up to 3 cm. The shield limpet, *L. pelta*, has a shell geometry comparable to *L. digitalis* but with a high apex slightly off-center toward the anterior margin of the shell. *L. pelta* can be either smooth or moderately ribbed at the margin, has an oval aperture, and can reach 4 cm in length. The plate limpet, *L. scutum*, is very flat, with a low, rounded centrally located apex, its shell is smooth, has a larger, more circular aperture, and can reach up to 6 cm in length. All three species coexist not only locally in False Bay, but also broadly, along the Pacific Coast of North America. While vertical zonation of these species has been observed, there is substantial overlap of the species across these zones (Shotwell, 1950; personal observation): *L. scutum* ranges from −0.3 to 1.8 m (from LLW), *L. pelta* from 0.15 to 1.8 m, and *L. digitalis* ranges predominantly from 1 to 1.8 m, but does occur sparsely up to as high as 2.7 m.

Whereas species are morphologically distinct in multiple ways summarized above, the specimens used in experiments represent comparable range of shell sizes (Fig. 2). Furthermore, whereas species are distinct in shell geometry, substantial intraspecific variation in height/length ratios can be observed so that the bivariate morphospaces of the three species overlap (Fig. 2).

All limpets were collected from the rocky intertidal areas of False Bay on the southwest shore of San Juan Island (Washington, U.S.A.). As it was not logistically feasible to remove very small limpets from the substrate without damaging the organism, no individuals with a length < 10 mm were collected. As 94% of *Patella vulgata* surveyed by Silva et al. (2010a) were of a size vulnerable to predation by the crab *Necora puber* (a somewhat smaller species than *Cancer*), the size range of limpets employed here in experimental trials is likely a reasonable range of prey encountered by crabs in natural settings. Limpets were numbered and measured in the lab, and housed in an open circulation sea-table for a minimum of one week before utilization in feeding trials. As all limpets were measured before use in trials, prey sizes were standardized within species across all trials. All limpets were examined for evidence of damage (e.g., chipped shells, failure to adhere to the substrate), and only robust, undamaged individuals that could withstand attempts to remove them from the substrate by hand after

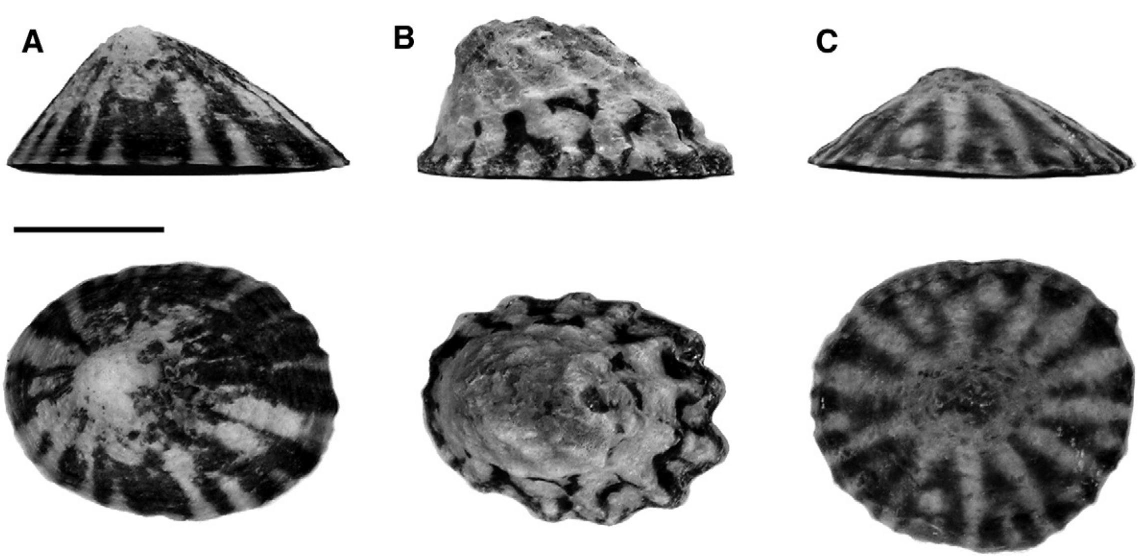

Fig. 1. Three limpet species collected from False Bay, San Juan Isl., WA: (A) *Lottia pelta*, (B) *Lottia digitalis* and (C) *Lottia scutum*. Top row is a lateral view; second row shows a dorsal view. Scale (1 cm).