ELSEVIER

Journal of Experimental Marine Biology and Ecology 354 (2008) 231–240

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

Metabolic consequences of living in a wave-swept environment: Effects of simulated wave forces on oxygen consumption, heart rate, and activity of the shell adductor muscle of the abalone *Haliotis iris*

D.A. Donovan [a],*, H.H. Taylor [b]

[a] *Department of Biology, Western Washington University, 516 High St., Bellingham, WA 98225, USA*
[b] *School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8020, New Zealand*

Received 28 February 2007; accepted 26 November 2007

Abstract

Animals in wave-exposed habitats must constantly contend with the hydrodynamic forces of lift and drag. In this study, we investigated aspects of the metabolic response of *Haliotis iris* to simulated wave forces varying in magnitude up to 9.6 N applied to the shell at 69° to horizontal, alternately from anterior and posterior directions, with a period of 10s. Shell adductor muscle activity (electromyogram, EMG), heart rate, and oxygen consumption were monitored during force application and during extended recovery. EMG spiking was absent at zero force, but increased markedly with increasing force, in synchrony with the wave cycle. In contrast, heart rate was unaffected by wave forces and varied by only 5% over the whole range of applied forces. During force application, oxygen consumption increased by 10–25% above resting rates and remained elevated throughout a 5-hour recovery period, indicating a switch to anaerobic metabolism. It is concluded that living in a wave-swept environment is metabolically costly for abalone although this may be compensated by improved food availability and more efficient ventilation induced by external flow.

Keywords: Abalone; *Haliotis iris*; Metabolism; Wave force

1. Introduction

The rocky intertidal zone is a high-energy environment that can support high levels of productivity (Leigh et al., 1987) and species diversity (Dayton, 1971; Connell, 1972; Levin and Paine, 1974; Paine and Levin, 1981). It is also a very complex environment with several factors that affect organism size and abundance. On one hand, organism size can be enhanced by wave action. This is often the case for algae and sessile invertebrates for which wave action can increase food and nutrient availability, enhance gas exchange, and reduce predation and competition (Leigh et al., 1987). Conversely, the size of sessile organisms may be restricted in very exposed habitats due to mechanical limits imposed by hydrodynamic forces (Denny et al., 1985). Motile animals are similarly affected in the wave-swept intertidal and face additional challenges due to the effects of hydrodynamic forces on locomotion. Many animals are less tenacious while moving and face a greater chance of being dislodged while foraging (Menge, 1974; Menge, 1978; Denny et al., 1985; Denny and Blanchette, 2000).

Abalone (family Haliotidae) exist worldwide and are found in a range of habitats from temperate rocky coasts to tropical reefs (Geiger, 1998; Lindberg, 1992). There are approximately 56 species of abalone (Geiger, 1998) that vary widely in maximum length. The largest species, which include *Haliotis iris* (Martyn), occur in high-energy temperate shorelines where there is an abundance of drift macroalgae (Estes et al., 2005). In this environment, abalone employ a "sit-and-wait" foraging strategy in which they remain relatively sessile and trap algae that drift by under the large foot. *H. iris* inhabits rocky coasts of New Zealand.

---

* Corresponding author. Tel.: +1 360 650 7251; fax: +1 360 6503148.
E-mail address: donovan@biol.wwu.edu (D.A. Donovan).

0022-0981/$ - see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.jembe.2007.11.011

The adults are typically found on flat boulder bottoms, low rocky shelves, and the bottom of vertical walls (Poore, 1972a) and thus are exposed to the constant hydrodynamic forces that bring drift algae to it.

Although abalone tend to grow larger in more exposed habitats, they may be the exception rather than the norm. Marine snails inhabiting exposed sites generally tend to be smaller than those found in protected areas, with thinner shells and larger feet (Boulding, 1990). These adaptations presumably help them avoid dislodgement. A number of studies have documented size differences and growth rates between conspecific gastropods in different habitats (Brown and Quinn, 1988; Etter, 1988, 1989; Boulding and Van Alstyne, 1993; Hobday, 1995) and have also shown that snails transplanted from exposed sites to more protected habitats exhibit increased growth (Brown and Quinn, 1988; Etter, 1988, 1989; Boulding and Van Alstyne, 1993).

Although differences in size have been well documented in gastropods, the physiological or mechanical bases for these differences are unresolved and probably multiple. Gastropods adhere less tenaciously to the substratum during locomotion (Miller, 1974) and wave forces can limit the ability of mobile animals to forage (Menge, 1974; Menge, 1978). Thus, some authors suggest that reduced caloric intake limits growth in gastropods that actively forage (Brown and Quinn, 1988). Denny et al. (1985) attribute size variations of organisms in wave-swept areas to increased mortality rates of larger individuals due to increased mechanical forces of drag and lift causing higher levels of dislodgement (but see Denny, 1999). However, differences in size of wave-exposed gastropods could also be due to the increased metabolic demands of resisting dislodgement by hydrodynamic forces. Even for abalone, with their efficient “sit-and-wait” foraging, living in a wave-swept environment must have metabolic costs.

Gastropods adhere to the substratum by secreting from the sole of their muscular foot a thin layer of adhesive mucus which acts as a glue when the animal is stationary (Denny and Gosline, 1980; Denny, 1984). In limpets and abalone, the tarsos muscle of the foot is closely associated with an adductor or columellar muscle which dorsally attaches to the shell and is responsible for clamping the shell tightly against the substratum (Trueman and Brown, 1985; Voltzow, 1990). In limpets, adhesion is accomplished by an interaction between the mucus layer and contraction of the columellar muscle resulting in both suction and mucus-derived adhesion (Smith, 1991, 1992). The extent to which muscular contraction contributes to adhesion and the energy costs associated with these different mechanisms are unknown.

The purpose of this study was to investigate the effects of simulated hydrodynamic forces on the metabolism of gastropods. The abalone, *H. iris*, was chosen for its preferred habitat and large size. It is a large gastropod, reaching 180 mm length (Poore, 1972c; Geiger, 1998), which enabled us to monitor multiple aspects of its metabolic response. Specifically, we measured heart rate and adductor muscle activity while a range of forces were applied at constant period, mimicking waves of various magnitudes. We also measured oxygen consumption during application of forces and during an extended recovery period to investigate the prolonged effects of wave exposure.

2. Materials and methods

2.1. Animal collection and maintenance

Abalone were collected from South Bay, Kaikoura, New Zealand and transported in moist air to the University of Canterbury, Christchurch, where they were held in a recirculating seawater system at 15 °C and a salinity of 34–35‰. All experiments were conducted within 6 weeks of collection. The abalone were fed a mixture of artificial abalone food and powdered seaweed.

2.2. Morphometric measurements

To determine average areas required for estimating lift and drag on the abalone, morphometric measurements were made on a representative size range of *H. iris* used in our study ($N=15$; 102–141 mm length). Shell height, width, and length were recorded directly using Vernier calipers; measurements of width and length were taken at the largest appropriate diameter of the inferior shell margin. Measurements of shell areas were made by digitally photographing each animal from the front, back, and ventral aspect (taken through a glass aquarium onto which they were allowed to adhere). The calibrated photographs were traced using ImageJ (National Institutes of Health, Bethesda, Maryland, USA). The measurements of area included shell aperture area (A_a) and shell frontal area (A_f, the projected area of the face of the shell in the plane perpendicular to the direction of flow). All areas from photographs were traced twice, recalculated, and averaged.

2.3. Experimental apparatus and determination of experimental forces

To test the effects of wave force action on abalone metabolism, a machine was constructed to mimic oscillatory wave forces in a laboratory setting (Fig. 1). Period, force, and the angle at which the force was exerted could all be manipulated. Briefly, individual abalone were held in a temperature-controlled seawater bath under the machine. Two lengths of wire with springs (A) attached to them were connected, at one end, to a hook attached mid-dorsally to the shell and, at the other end, to a peg (C) on each of two motors (B) clamped to a metal rod arching over the seawater bath. The pegs traveled in separate circles producing a sinusoidally varying tension on the springs.

“Wave” period was manipulated by controlling the time for each motor to complete one revolution. In the present study, each motor alternately completed its revolution in 5 s, simulating a wave washing over the animal and back again with a period of 10 s, which is a typical period for the east coast of New Zealand (Pickrill and Mitchell, 1979). “Wave” force was manipulated by using springs of different stiffness and by adjusting the distance of the attachment peg from the motor axis. The diameter of the circle traveled by the peg on the motor was kept as small as possible to minimize deviations from the desired angle as the force was exerted. Angle deviation was