

Dynamic measurements of black oystercatcher (*Haematopus bachmani*) predation on mussels (*Mytilus californianus*)

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Abstract

Intertidal zone mussels can face threats from a variety of predatory species during high and low tides, and they must balance the threat of predation against other needs such as feeding and aerobic respiration. Black oystercatchers (*Haematopus bachmani*) on the Pacific coast of North America can depend on the mussel *Mytilus californianus* for a substantial portion of their diet. Observations suggest that oystercatchers tend to focus on mussels beginning to gape their valves during rising tides, following periods of aerial emersion. We present detailed, autonomous field measurements of the dynamics of three such predation events in the rocky intertidal zone. We measured accelerations of up to 4 g imposed on mussels, with handling times of 115–290 s required to open the shell and remove the majority of tissue. In each case a single oystercatcher attacked a mussel that had gaped the shell valves slightly wider than its neighbors as the rising tide began to splash the mussel bed, but no other obvious characteristic of the mussels, such as body temperature or orientation, could be linked to the oystercatcher's individual prey choice.

KEYWORDS

accelerometer, black oystercatcher, mussel, predation

1 | INTRODUCTION

Among the many stresses of life in the intertidal zone, responding to the threat of predation must often be balanced against the need to carry out basic life functions such as aerobic respiration, feeding, and waste removal. The sea mussel *Mytilus californianus* CONRAD 1837, found along the western coast of North America, must contend with a number of different predators, including sea stars (Paine, 1974), muricid whelks (Dayton, 1971), crabs (Hull & Bourdeau, 2017), lobsters (Robles, Sweetnam, & Eminike, 1990), sea otters (Estes, Riedman, Staedler, Tinker, & Lyon, 2003), and bird predators such as oystercatchers (Hartwick, 1973, 1976). These predators can attack by prying, crushing, or drilling, and the mussel's primary defense is to hold the shell valves tightly closed, cutting itself off from water, oxygen, and food in the process. The need to eventually reopen the valves to pump seawater and release wastes can be exploited by mussels' predators, particularly following long periods of emersion.

The black oystercatcher *Haematopus bachmani* AUDUBON 1838 represents one such threat to intertidal mussels. Found along the west coast of North America, this long-billed bird preys on a variety of intertidal fauna such as limpets and mussels, using a variety of methods to attack its prey (Garza, 2005; Hartwick, 1976). Descriptions of predation methods are common for black oystercatchers and related species such as the Eurasian oystercatcher, *Haematopus ostralegus* (Hartwick, 1976; Norton-Griffiths, 1967; Webster, 1941; Wootton, 1997), but direct measurements of the dynamics of attacks are rare.

Hartwick (1973, 1976, 1978) produced extensive observations of black oystercatcher predation behavior from a population near Vancouver Island. Oystercatchers tend to switch prey species throughout the course of a falling or rising tide, turning their attention to *Mytilus* mussels as the mussel beds transition in or out of the water and mussels gape their valves, then moving to limpets or crabs when gaping mussels are not available. The proportions of mussels, limpets, and other prey in the diet of black oystercatchers vary among

sites, with mussels making up a trace amount of the diet at Cape Arago, Oregon, 10% of the adult diet at Tatoosh Island, WA, and up to 29% of the diet at Vancouver Island (Frank, 1982; Hartwick, 1973; Wootton, 1997).

Mussels form dense aggregations and anchor themselves to the substratum and their neighbors using proteinaceous byssal threads, so they can present a greater challenge for the oystercatcher to remove than other prey items. However, mussels represent a substantial energetic payoff (Hartwick, 1976). Among oystercatcher species preying on mussels in the genus *Mytilus*, there are two primary avenues of attack: hammering a crack in a dislodged mussel's ventral shell margin, or stabbing the beak between the gaped shell valves of a mussel in order to sever the posterior adductor muscle (Hulscher, 1996; Norton-Griffiths, 1967; Webster, 1941). Hartwick (1973, 1976) observed that black oystercatchers only used the stabbing method to attack mussels. Studies by Norton-Griffiths (1967) and Nagarajan, Lea, and Goss-Custard (2002) estimated the number of hammering bouts needed by Eurasian oystercatchers to crack the ventral margin of *Mytilus edulis* mussel shells, but no data exist on the forces exerted upon mussel prey during the stabbing attacks of black oystercatchers.

Here, we provide new insight into the dynamics of black oystercatchers feeding on *M. californianus* at a field site at Hopkins Marine Station (HMS hereafter) in Pacific Grove, CA (36.6217°N, 121.9043°W). During a field experiment designed to measure mussel behavior and physiology in *M. californianus* (Gleason et al., 2017; Miller & Dowd, 2017), we recorded incidental observations of oystercatcher predation events on three focal mussels. Using gape sensors and accelerometers attached to those mussels, we were able to record the accelerations and time course of oystercatcher predation events in the field. We were also able to compare the focal mussels with adjacent, instrumented mussels to discern possible means by which oystercatchers select their specific prey targets.

2 | METHODS

The instrumentation and datalogging systems used for the mussels in this experiment are described in Miller and Dowd (2017). Briefly, we created an artificial mussel bed comprising 12 instrumented live mussels and several dozen additional live mussels (adult body size 40–70 mm shell length, harvested from the mid-intertidal zone at HMS) on a 45 × 30 cm acrylic plastic plate (Figure 1). Mussels anchored themselves to the plate and to neighboring mussels with byssal threads.

The instrumented mussels each had a 3-axis accelerometer and 3-axis magnetometer orientation sensor (LSM303D; ST Microelectronics, Fairport, NY) attached to the right shell valve, with full-scale acceleration set to a maximum of 4 g per axis, and set to record at 4 Hz with a 50 Hz low-pass filter applied to the analog accelerometer signal prior to digitization by the sensor. We measured the gape between the two shell valves using a magnetic Hall effect sensor (Allegro A1393; Allegro MicroSystems, Worcester, MA) attached to

the posterior end of the left valve, and a magnet glued opposite it on the right valve. For body temperature measurements, a 30-gauge K-type thermocouple was implanted in a hole drilled through the shell at the mid-ventral margin of the left valve. Valve gape and body temperature were sampled at 1 Hz. Each sensor had a cable running back to a waterproof box housing the data logger, so that the instrumented mussels were partially tethered by these cables, but the main attachment of the mussels to the plate was via their own byssal threads.

The experimental plate was deployed in the high intertidal zone at HMS at 1.7 m above mean lower low water, near the upper extent of natural mussel beds on the wave-exposed end of the rocky point. The plate was deployed from July 15 to August 6, 2015.

The body orientation of each mussel during an attack was reconstructed using the 3-axis accelerometer and magnetometer data (Videos S1–S3) using the methods described in Miller and Dowd (2017). We note that only orientation, not translational movements, could be accurately represented in the video reconstructions. The instantaneous total acceleration (g) in all three axes of the accelerometer sensor was calculated at each time point as

$$\text{total acceleration} = \sqrt{(a_x)^2 + (a_y)^2 + (a_z)^2} \quad (1)$$

We generated estimates of forces applied to the mussel by the oystercatcher using a range of potential masses for mussels in the size range of each attacked mussel (expressed as a 95% prediction interval around the average mass of a mussel of the given lengths). We derived the length (mm) to mass (g) relationship ($\text{Mass} = (1.47 \times \text{Length}) - 62.1$) from a sample of 261 live mussels from HMS with shell lengths in the range from 50.3 to 95.0 mm. The maximum acceleration during each of the three attacks was converted from g to m/s^2 using the local gravitational acceleration for Monterey, CA (9.7991 m/s^2). Forces were estimated using the range of masses and the maximum acceleration imposed on each mussel using the relationship $F = m \times a$. Analyses were carried out using R 3.4.3 (R Core Team, 2017).

3 | RESULTS

Three instrumented individuals of *M. californianus* (shell lengths of 71.5, 62.9, and 71.1 mm) were attacked and consumed by black oystercatchers during the field trial. We found the shells of additional mussels from the experimental bed that had been consumed on days prior to the first recorded attack.

In each case, the attack happened during a rising afternoon high tide, following a multi-hour aerial exposure of the mussels during low tide. The combination of tide heights and offshore wave heights (Table 1) would have been splashing the plate intermittently at the time of each attack, but not enough to continuously submerge the plate, thus leaving it accessible to oystercatchers for several minutes between sets of waves. Small movements of individual instrumented mussels were detected in the accelerometer data in the two hours

FIGURE 1 Overhead view of the experimental mussel bed comprising 12 instrumented individuals of *Mytilus californianus* and additional live mussels. Inset: close-up of an instrumented mussel showing the gape sensor (posterior end, top of photo), accelerometer/magnetometer (right valve), and thermocouple (small black wire leading to ventral midpoint of the left valve)



before the attacks (Figure 2), which are most likely attributable to isolated splashes or wave impacts. The initial two attacks (July 21 and 25) were not directly witnessed, but oystercatchers were observed near the experimental plate prior to the attacks on both afternoons, and the mussel shells, still tethered by the sensor cables, were found completely empty, save for small pieces of tissue, the next day. Prior to the third attack on July 28, 2015, we placed a time-lapse camera near the experimental plate, and over 1.5 min captured five images of an oystercatcher with its beak on or in the instrumented mussel at times that corresponded to the beginning and cessation of the high acceleration values recorded for that mussel using the data logger. Based on this evidence, we are confident that the recorded events on July 21 and July 25 also represent oystercatcher attacks.

During the low-tide period prior to the July 21 and 28 attacks, the consumed mussels had been the coolest instrumented mussels on the plate (20 and 22°C maximum temperatures, respectively) and had the shell valves closed for ~8 and 4 hr, respectively, before

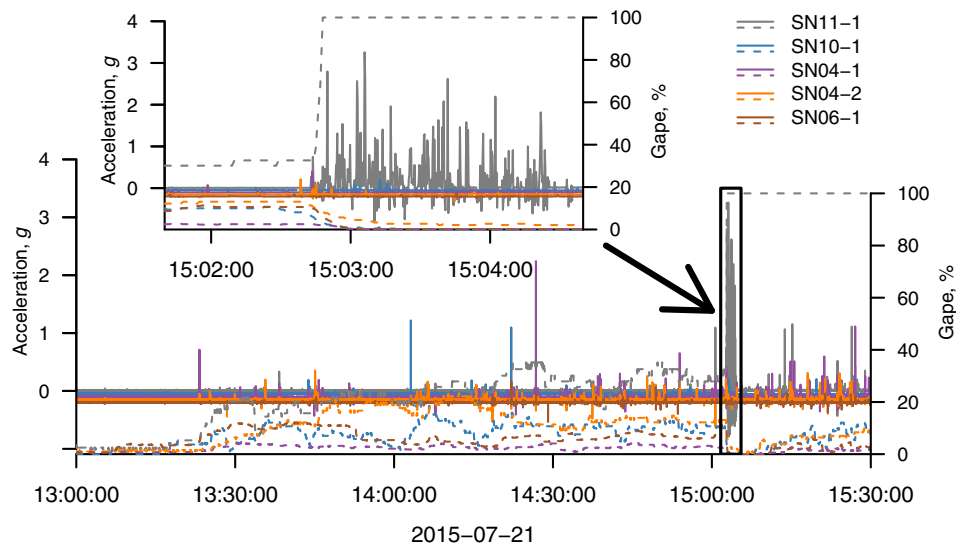
starting to gape prior to the attack. For the attack on July 25, the consumed mussel had been closed for ~5 hr before starting to gape, but had been the second warmest of the instrumented mussels on the plate, reaching a maximum internal temperature of 31°C. At the start of the attack on July 21, the mussel was oriented with the ventral surface facing down against the plate, and the posterior end of the shell tilted downward slightly (Video S1). For the July 25 attack, the mussel was initially oriented with the right valve facing down towards the plate, potentially exposing the ventral margin of the shell to attack, with the posterior end of the body pointing slightly downward (Video S2). For the third recorded attack on July 28, the mussel was also resting with the right valve facing down toward the plate, and with the posterior end tilted upwards slightly (Video S3).

In all three predation events, the valves of the mussels were gaped between 9 and 31% of their full opening immediately prior to the attack, potentially providing an initial entry point for the oystercatcher. Compared to the other instrumented mussels on the experimental plate, the mussels attacked on July 21 and 28 were the widest-gaped mussels immediately prior to the attacks, while the mussel attacked on July 25 was the second-most widely gaped mussel on the plate (Figure 2). While neighboring instrumented mussels were slightly gaped at the start of each attack, they often closed their valves during the initial 10–20 s of the attack on the focal mussel, presumably as a response to the movement induced in the mussel matrix by the activity of the oystercatcher. That movement was recorded as small accelerations, less than 0.5 g, in four to five neighboring mussels that were not attacked. No chipping of the empty shells was visible, indicating that penetration between the gaped valves was the likely method of entry. The oystercatchers took between 2 and 4.8 min to open the shell valves and pull the tissue out of the shells (Table 1). All three attacks consisted of bouts of vigorous movement of the mussel, interspersed with brief 2–3 s pauses during which the mussel was not moving (Figure 2). There were longer pauses during each attack during which the mussel did not move, presumably because the oystercatcher had paused to

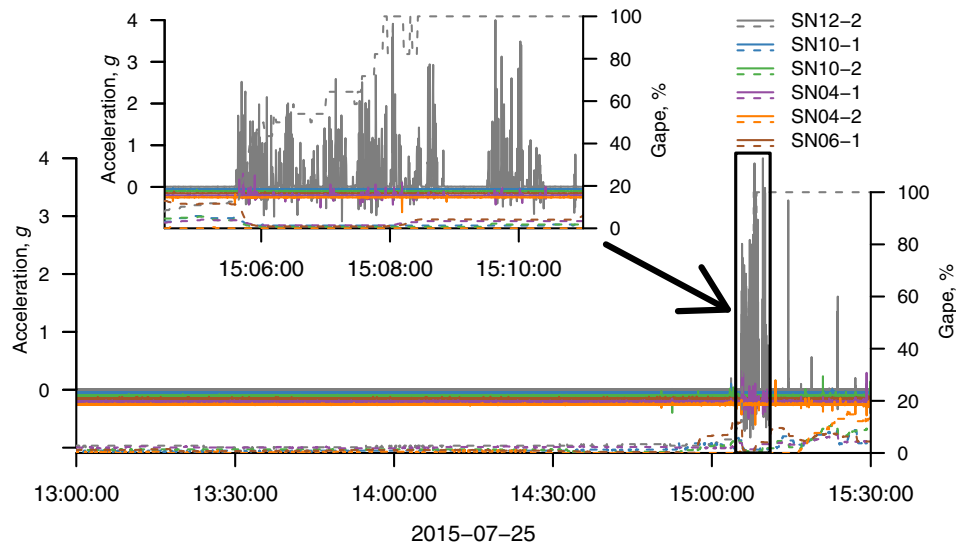
TABLE 1 Time and duration of three mussel predation events by individuals of *Haematopus bachmani*. The combination of tide height and offshore wave heights prior to each attack would have been sufficient to occasionally splash the mussels, which were located 1.7 m above mean lower low water. Tide data were retrieved from the Monterey Harbor tide station (National Oceanic and Atmospheric Administration station 9413450), and ocean wave height data were collected by a waverider buoy situated ~400 m north of the field site (Coastal Data Information Program buoy 158, Scripps Institute of Oceanography). Time values given are local time (Pacific Daylight Time)

Mussel ID	Time of attack	Duration of attack (s)	Tide height (m)	Wave height (m)
SN11-1	2015-07-21 15:02:42	115	1.46	0.51
SN12-2	2015-07-25 15:05:35	290	1.20	0.80
SN05-2	2015-07-28 15:13:39	121	0.97	0.85

A



B



C

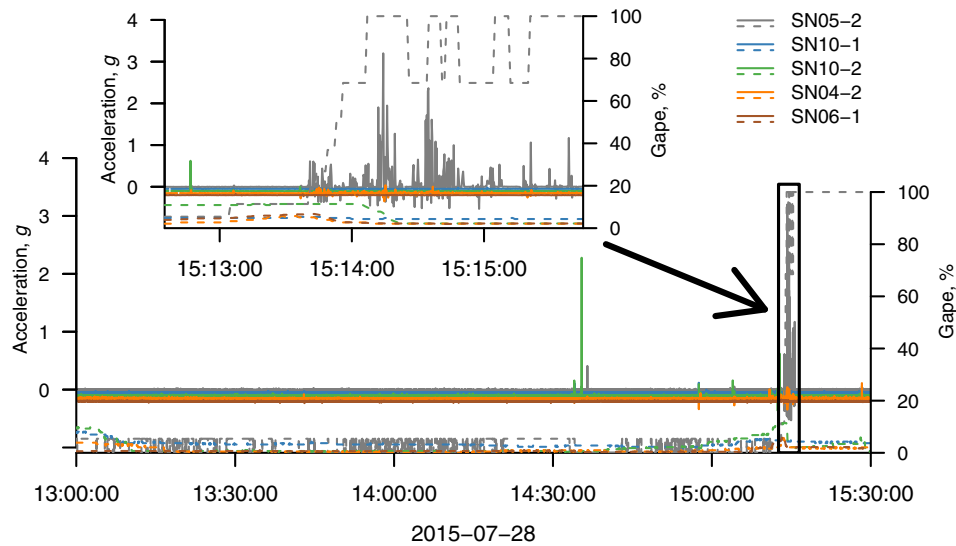


FIGURE 2 Time series illustrating acceleration and gape data in individuals of *Mytilus californianus* attacked by black oystercatchers (*Haematopus bachmani*). Data show the 2 hr leading up to the attacks on July 21 (A), July 25 (B), and July 28 (C), and a close-up of the time of attack (inset A–C). Each plot shows net acceleration for the focal mussel being attacked (solid grey line) and nearby mussels that were not being attacked (solid colored lines). Acceleration values have gravitational acceleration removed, and data for the surviving mussels in each plot have been offset slightly below the zero acceleration line for clarity. Gape values are shown with dashed lines using the same color as the respective acceleration data for each mussel. The gape percentage scale is shown on the right-hand ordinate axis. Black rectangles in the main plots (A), (B), and (C) mark the shorter periods of time shown in each respective inset plot

swallow tissue (Hartwick, 1973). Based on the reconstructed orientations (Videos S1–S3), the mussel shells were turned over repeatedly and were swung back and forth while the oystercatcher removed tissue, although we caution that orientations derived from instances of high accelerations can only provide approximate body positions.

The maximum net accelerations imposed by the oystercatchers on the mussel shells ranged 3.2–4 g (Figure 2, Table 2), after subtracting acceleration due to gravity (1 g). Based on a range of potential mussel masses, we estimated peak forces of 0.76–1.74 N exerted on the mussels, although we note that these estimates may be affected substantially by the changing mass of the mussel through the course of the attack.

4 | DISCUSSION

Black oystercatchers at HMS attacked and opened mussels in our experimental mussel bed in a manner similar to that described for a black oystercatcher population near Vancouver Island, British Columbia (Hartwick, 1973, 1976). The serendipitous choice by the birds to attack mussels with attached electronic sensors allowed us to make unique measurements of the progression of each predation event. In addition to the instrumented mussels, numerous additional live mussels on the plate were removed, consumed, and left as empty shells near the plate over the course of the 3-week deployment. Based on the fact that these other mussels were also consumed, we suspect that the instrumentation attached to the focal mussels was not the primary reason for the oystercatchers to choose to attack these

mussels. Neighboring natural mussel beds in this zone of the high shore are primarily composed of smaller mussels that would yield less tissue, so this plate of large adult mussels in an easy to reach location on the high shore may have represented a particularly attractive target for oystercatchers.

Among the predators that attack and eat *M. californianus*, black oystercatchers may be exploiting a unique vulnerability when mussels gape the valves slightly while exposed to air. Tightly closing the shell valves is the primary method of protection from a variety of predatory threats. For example, during high tide submerged mussels may be attacked by relatively fast-moving predators, such as lobsters or crabs, that crush mussel shells to gain access to the mussel's tissue. The mussel's primary protection comes from closing the shell valves tightly and relying on overall size and shell thickness to resist these crushing forces (Hull & Bourdeau, 2017; Robles et al., 1990). High tide can also bring slow-moving predators, including sea stars, which slowly pull the shell valves apart over the course of hours (Paine, 1974), or whelks, such as members of the *Nucella* genus, that drill and dissolve their way through the shell using a radula and secretions from an accessory boring organ (Dayton, 1971; Miller, 2013). For both sea stars and whelks, predation events may extend through high and low tides, subjecting mussels to the added stress of oxygen limitation and waste accumulation stemming from prolonged valve closure.

Compared to the other common predators of mussels, oystercatchers use a strategy that avoids having to break the mussel shell or engage in prolonged attacks, and that focuses instead on a relatively narrow window of opportunity when mussels are accessible during low-tide aerial emersion, and have gaped their valves. Each of the three feeding events in our experiment took place during a rising tide when waves had begun to splash the experimental site, but the mussels were still primarily exposed to the air and accessible to the birds, similar to the behavior described by Hartwick (1973, 1976). During aerial emersion at low tide, individuals of *M. californianus* typically keep the shell valves tightly closed, likely to minimize desiccation risk (Dowd & Somero, 2013). Prolonged valve closure over several hours often leads to a shift to anaerobic metabolism as internal oxygen stores decrease (Bayne, Bayne, Carefoot, & Thompson, 1976). Consequently, mussels will often open their valves slightly to begin taking in oxygen late in the tide cycle, as soon as they are splashed by the rising tide but before they are fully submerged. Based on the timing of our observed attacks and the mussel shell-gape data, it appears that the oystercatchers at HMS waited for the mussels on our experimental plate to begin gaping before initiating their attacks, and chose mussels that were relatively widely gaped

TABLE 2 Mussel length, estimated mass, maximum acceleration, and estimated maximum force exerted on each mussel during the predation events. Mussel mass is an estimate based on the mass of similar-sized mussels containing all of their tissue and water trapped in the shell. Acceleration values are the net acceleration of all three axes (x, y, z), with gravitational acceleration (in the z-axis) removed. The estimated maximum force varies due to the range of possible masses of the mussels, which likely declined over the course of feeding. 95% prediction intervals are given for mass and force estimates

Mussel ID	Length (mm)	Estimated mass (g ± 95% PI)	Maximum acceleration (g)	Estimated maximum force (N, 95% PI)
SN11-1	71.5	43.3 ± 11.3	3.26	1.02–1.74
SN12-2	62.9	30.6 ± 11.3	4.04	0.76–1.64
SN05-2	71.1	42.7 ± 11.3	3.20	0.98–1.69

compared to neighboring mussels on the plate. There was no clear indication that mussel body orientation, prior maximum temperature, or time spent with valves closed prior to the attack had any effect on the choice of mussel prey, but many more observations would be required to identify which of these characteristics might play a role in prey selection.

We estimated handling time based on the length of time from the first registered high acceleration of the mussel shell until the cessation of shell movement. Hartwick (1976) reported a mean handling time to attack and consume a mussel of 45 s, with a range of 7–125 s, while our three observations were somewhat longer at 115, 121, and 290 s. The relatively larger size of the three mussels (62.9–71.5 mm) compared to the mean observed by Hartwick (49 mm) might have led to longer handling times, but we note that the longest handling time came from the smallest mussel in our sample. The sensor wires attached to the mussels and the underlying plate may have slowed down the rate of tissue extraction by limiting the bird's ability to manipulate the shell position easily.

Oystercatchers were able to impart sizeable accelerations of more than 3 g on the mussels during handling, with peak accelerations observed several seconds after the shell valves had been opened. We estimated relatively small maximum forces being imparted during these attacks (0.76–1.74 N), similar to the force estimated to be necessary for oystercatchers to dislodge some limpet prey (Hahn & Denny, 1989). As a point of comparison, woodpecker species are estimated to impart much larger forces (maximum values between 23 and 32.4 N) and undergo larger accelerations (3,612–9,790 m/s²) while drumming (Vincent, Sahinkaya, & O'Shea, 2007; Wang et al., 2011; Yoon & Par, 2011). It is highly likely that our available acceleration data underestimate the forces imposed by the bird, particularly during the initial stabbing of the beak between the two shell valves. If the mussel was situated so that the shell was braced against the substratum along the axis of the stabbing motion, accelerometers would have registered lower acceleration due to constrained movement of the mussel, despite the imposition of a large force necessary to cut the adductor muscles and pry the shell valves apart. Based on these data, it is unclear at what stage during the attack the birds might impart the greatest forces on the mussel, and a full accounting of the forces imposed by an oystercatcher on a mussel during the attack would require a different style of sensor on the prey item, such as a force transducer.

Through the use of accelerometers and magnetic Hall effect sensors on the prey mussels, we provide novel insight into the accelerations imposed by oystercatchers on prey mussels and the potential forces being generated while the bird removes tissue from the interior of the mussel. Our data corroborate earlier descriptions of the stabbing method and timing of attacks by black oystercatchers on mussels in the field (Hartwick, 1973, 1976; Webster, 1941), and these illustrate the strategy by which oystercatchers exploit mussels' gaping behavior during the splashing of a rising tide, when other mussel predators would be less of a threat. Beyond the application of recording oystercatcher predation events,

the orientation sensor and magnetic Hall effect valve gape sensor package could be used in a similar manner to track the progression of predation events by sea stars such as *Pisaster ochraceus*. While in some instances time lapse cameras could provide information about the time course of mussel shell valve opening by sea stars, the orientation sensor and Hall effect gape sensor would allow measurements even in cases where the view of a mussel might be obscured by the body of the sea star or by wave action. The low cost and long life of the sensor and data logger package permit their usage in field settings where tide cycles and wave action might make other forms of long-term observation such as human observers or cameras impractical. More generally, the types of sensor packages described here are providing new insights into bivalve feeding behavior (Riisgård, Lassen, & Kittner, 2006), growth (Ballesta-Artero, Witbaard, Carroll, & van der Meer, 2017), responses to water quality (Sow, Durrieu, Briollais, Ciret, & Massabuau, 2011; Tran, Ciret, Ciutat, Durrieu, & Massabuau, 2003), and can allow researchers to better link the organism's interaction with the environment to its physiological status (Dowd & Somero, 2013; Gleason et al., 2017; Miller & Dowd, 2017).

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PERMITS

The data presented here were derived from incidental observations of individuals of *Haematopus bachmani* interacting with mussels that were part of a field trial focused on mussel behavior and physiology, and as a result these observations were made without specific permits for vertebrate subjects.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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