



RESEARCH NOTE

Rasping patterns of the high-shore limpet *Cellana grata*

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Patellid limpets are dominant grazers on many rocky shores around the world, strongly influencing intertidal community structure as a result of their feeding on the epilithic biofilm and macroalgae (Branch, 1981; Lubchenco & Gaines, 1981; Hawkins & Hartnoll, 1983). To quantify grazing pressure, many studies have examined the temporal and spatial patterns of limpet foraging excursions (e.g. Chelazzi, Della Santini & Santini, 1994; Santini, Ngan & Williams, 2011). In general, these studies include assessments of when and/or where limpets move, often with the assumption that grazing (i.e. rasping the rock surface with their radula and ingesting material) takes place throughout this movement phase (see Williams & Little, 2007). There is, however, little empirical evidence to support this assumption, creating a gap in the understanding of how much food limpets are ingesting and therefore the intensity of, and variation in, grazing pressure during their foraging excursions. Such knowledge is important for attempts to determine subsequent impacts on intertidal communities, and for parameterization of energetic models of spatio-temporal patterns of grazing (see Santini *et al.*, 2011).

Limpets exhibit complex patterns of when and where they feed (Williams & Little, 2007), which have been extensively studied (Little *et al.*, 1990; Gray & Williams, 2010; Santini *et al.*, 2011); nevertheless, integrating rasping intensity with observed movement patterns is rare (but see Chelazzi *et al.*, 1994b), primarily due to difficulties involved in making such measurements. As a result, spatial and temporal variation of grazing has mostly been assessed during random sampling periods within a foraging excursion or in aquariums under laboratory conditions (Newell, Pye & Ahsanullah, 1971; Zeldis & Boyden, 1979; but see Chelazzi *et al.*, 1994a, b).

The limpet *Cellana grata* (Gould) is an abundant grazer in the upper intertidal zone of Hong Kong (Morton & Morton, 1983). This species forages while awash (Williams & Morritt, 1995) and typically follows a triphasic movement pattern (Davies, Edwards & Williams, 2006): rapid movement up the shore with the flood tide, followed by a brief period of reduced or limited movement at high tide, and then rapid movement down the shore with the ebbing tide, before coming to rest at a specific height (Williams & Morritt, 1995). As *C. grata* follows the tidal cycle, its vertical position on the shore is closely associated with the water level and the total distance of its foraging excursion can exceed 1 m (Williams & Morritt, 1995; Davies *et al.*, 2006). Despite the general movement patterns of this limpet having

been described in detail, grazing patterns are speculative because identifying when the animal is rasping the rock surface has proved difficult due to wave action (Williams & Morritt, 1995). Here we report the use of a contact microphone to record the rasping of *C. grata* individuals *in situ* and to describe the spatial and temporal variation of the limpets' rasping.

Recordings of limpet rasping were made with a contact microphone based on a LIS352AX MEMS inertial sensor (ST Microelectronics, Geneva, Switzerland). A 10-m length of paired and insulated 24 AWG wires with 50-cm leads (33 AWG wire wrap) was soldered to the sensor and the sensor was water-proofed with a small amount of Instant Mix 5 minute epoxy (Loctite, Westlake, OH, USA). The thin leads gave flexibility for the limpet to move freely and reduced drag from wave action. The 24 AWG wires were connected to a 3.5-mm stereo phone plug and the whole system was powered by a 3 V battery pack. Recordings were made on a digital audio recorder (VN-6200 PC, Olympus, San Jose, CA).

Continuous recordings were made of *C. grata* individuals ($n = 7$; 30.8–56.2 mm shell length; Table 1) at Cape d'Aguilar, Hong Kong (22°13'N, 114°12'E) in July, September and October 2012 during spring tides. Hong Kong experiences mixed, semi-diurnal spring tides (see Williams, 1994, for a description of tidal patterns in Hong Kong) with a maximum amplitude of the high, high tide at Cape d'Aguilar of about 2.5 m above chart datum (+CD). Since *C. grata* moves up and down the shore following the tide, one tidal cycle represents one activity period. Microphones were attached at low tide while the limpets were inactive and, for each limpet, recordings commenced before movement began (or within about 15 min) and ended after movement ceased on the following ebb tide. Microphones were attached to the shell over each limpet's head with a mixture of adhesive putty and cyanoacrylate glue (Aron Alpha Gel, Japan). Hourly, real-time tidal heights were obtained from the Hong Kong Observatory station at Waglan Island, 5 km south-east of Cape d'Aguilar.

Distinct rasping sounds were clearly distinguishable from wave swash or other background noises on the audio recordings (Fig. 1; Supplementary Material). Rasping rates were calculated from audio recordings following Petraitis (1992) and converted to rasps per minute (rpm). Rasping rates were calculated at 2-min intervals for the duration of each recording (i.e. 30 measurements per hour).

Table 1. Tidal information, recording times, and shell lengths (± 0.1 mm) of *Cellana grata* recorded at Cape d'Aguilar, Hong Kong.

Limpet no.	Date	Shell length (mm)	Recording time	Nearest hour and height (m + CD) of high tide	Nearest hour and height (m + CD) of low tide
1	20 July	55.8	04:53–13:40	10:00–2.40	17:00–0.81
2	22 July	56.2	04:45–12:05	11:00–2.53	18:00–1.08
3	18 September	32.5	05:45–20:45	11:00–2.31	16:00–1.31
4	19 September	31.4	07:00–21:26	12:00–2.10	17:00–1.25
5	13 October	36.0	16:00–00:30	20:00–2.34	01:00–1.47
6	15 October	30.8	05:15–12:45	08:00–2.33	14:00–1.27
7	15 October	34.8	05:15–13:20	08:00–2.33	14:00–1.27

Times and heights of high and low tides are taken from the hourly recorded tidal height data at Waglan Island, thus times and tidal heights of high and low tide are given to the nearest hour.

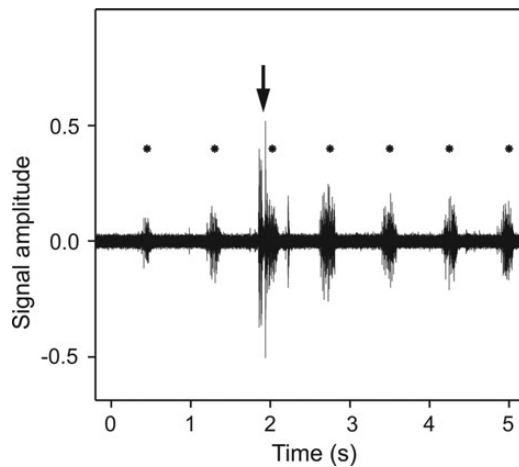


Figure 1. A 5-s sample audio recording of a grazing *Cellana grata* from which rasping rates could be calculated. Individual rasps are indicated with an asterisk. The signal from a wave breaking on the limpet momentarily before $t = 2$ s can be seen (arrow), but the rasping signal is still visible.

Because *C. grata* moves while awash, the times and tidal heights of rasping measurements can be associated with the vertical position of limpets on the shore (Williams & Morritt, 1995; Davies *et al.*, 2006). To assess the spatial variation in rasping, we calculated the amount of time each limpet rasped between hourly tidal heights by pairing the time stamp of the audio recording with the time of the tidal heights. The phase of the tidal cycle was also considered in this analysis, to determine at what tidal heights and phases the limpets were rasping continuously (i.e. all 30 measurements per hour showed rasping), rasping sporadically (fewer than 30 measurements per hour showed rasping), or not rasping at all.

The mean rasping rates of each limpet were calculated separately for periods of sporadic rasping and for periods of continuous rasping. We tested for differences in the sporadic and continuous rasping rates with a paired Student's *t*-test after tests for assumptions of equal variance were confirmed with Bartlett's test. Variation in rasping rates between ebb and flood tides were tested in the same manner, except that two individuals were excluded because they did not exhibit continuous rasping during the recording period. Mean and maximum rasping rates were calculated for each limpet, taken from all measurements where rasping occurred, regardless of sporadic or continuous rasping. All statistical tests were conducted with R statistical software.

Mean rasping rates for each individual ranged from 61 to 108 rpm and maximum rasping rates ranged from 103 to 138 rpm (Fig. 2). Rasping was typically continuous as the

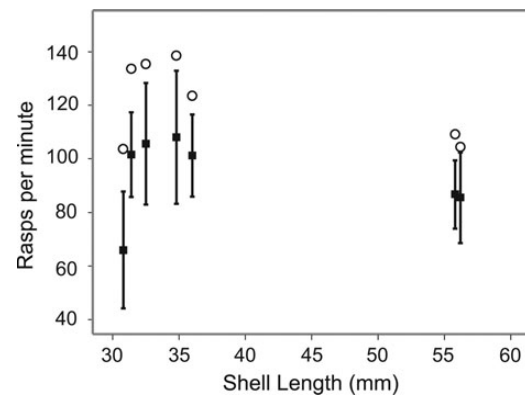


Figure 2. Mean (squares) rasping rates \pm SD and maximum rasping rates (open circles) for seven *Cellana grata* individuals as a function of shell length.

limpets moved up the shore with the flood tide and down the shore with the ebb tide (Fig. 3). There were many periods of continuous rasping ranging from 2 to 3 h (Fig. 3A–C, E, G), although rasping was sometimes limited to periods < 1 h (Fig. 3F) or > 7 h (Fig. 3C, D). Variation in the duration of continuous rasping followed changes in the tidal cycle (Fig. 4). All limpets rasped continuously at tidal heights below 2 m + CD, but rasping gradually became more sporadic above 2 m + CD, until finally stopping at tidal heights above 2.4 m + CD. This pattern was mirrored on the ebb tide where rasping changed from sporadic to continuous as the tidal height decreased (Fig. 4).

Rasping rates were similar between ebb and flood tides (98.5 ± 22.2 and 85.3 ± 14.1 rpm for ebb and flood, respectively; paired Student's *t*-test: $t = 1.62$, $df = 5$, $P > 0.05$). Limpet 2 (Table 1) did not experience an ebb tide and so was not used in the tidal phase comparison. Rasping rates were faster during continuous as opposed to sporadic rasping (106.6 ± 8.9 and 80.4 ± 6.8 rpm, respectively; paired Student's *t*-test: $t = 4.69$, $df = 4$, $P = 0.009$). Overall, there was some variability in these patterns on a daily basis according to variation in tidal patterns. When the tide remained unusually high for over 3 h, for example, no rasping was recorded for the duration of this period (Fig. 3B). Similarly, limpets may continue rasping for many hours when the tide is below a certain upper limit (i.e. 2.4 m + CD) and above the lower resting height of the limpet (Fig. 3D).

Due to the small sample size of this study, generalization of the observed rasping patterns is limited. However, maximum and mean rasping rates of *C. grata* were considerably faster than previously measured rates for other rocky shore limpets: *Patella caerulea*, 35.9 ± 7.4 rpm (Chelazzi, Parnagnoli & Santini, 1998);

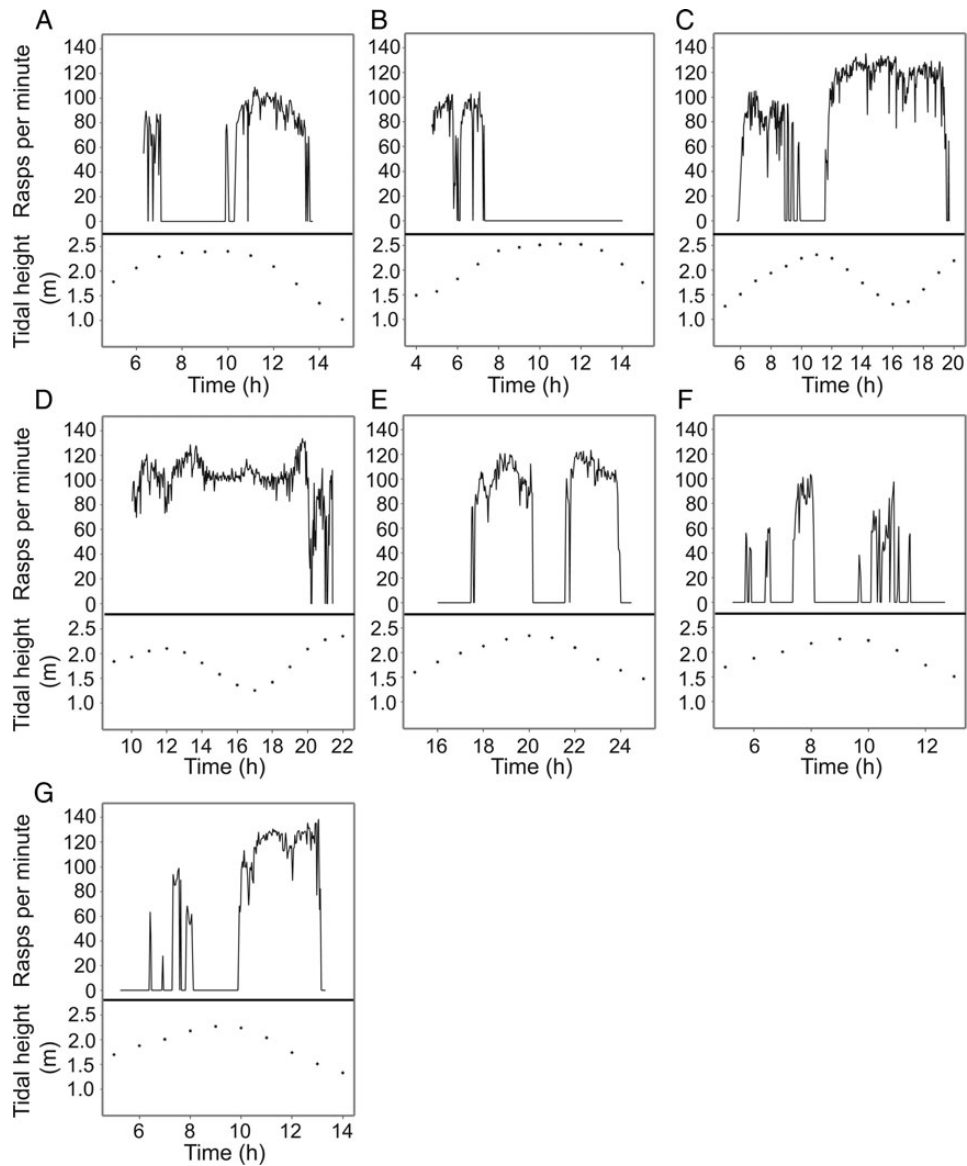


Figure 3. Rasping rate profiles (above) with hourly tidal height data (below) for each *Cellana grata* examined (profiles A – G correspond to limpets 1–7 in Table 1). Note that the x-axis scale changes for each profile.

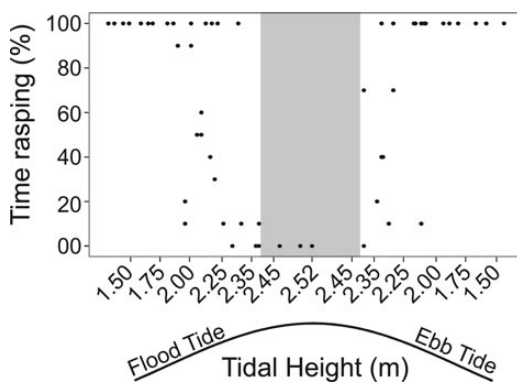


Figure 4. Percentage of time each *Cellana grata* spent rasping between the observed hourly tidal heights. The shaded area represents the tidal heights where no rasping occurs. Each point represents one hourly measurement of time spent rasping.

P. vulgata, 12.8 ± 7.3 rpm (Chelazzi *et al.*, 1994) and 34–51 rpm (Little & Stirling, 1985); *C. tramoserica*, 80 rpm (Petraitis, 1992); and *C. ornata*, 60 rpm (Boyden & Zeldis, 1979). Rasping occurs while *C. grata* moves up the shore with the flood tide and down the shore with the ebb tide (Williams & Morritt, 1995; Davies *et al.*, 2006) and is constrained by tidal height, because rasping stopped when the limpets passed a fairly consistent upper tidal height limit (about 2.4 m + CD), which approximates to the extreme high, high-water mark (Hong Kong Observatory). *Cellana grata* gradually slows its rasping rate and percentage of time rasping as it approaches this upper tidal height, which corresponds to the period of reduced movement observed by Williams & Morritt (1995) at the time of maximal tidal height.

Tidal cycles that remained within the bounds of the upper and lower tidal height limits of grazing resulted in feeding bouts longer than 7 h, suggesting that *C. grata* is an opportunistic grazer. One question is, why is *C. grata* confined to these vertical, spatial limits? One possibility is variability in the epilithic biofilm, which has a patchy distribution and is less abundant in

the high-shore area (Williams & Morritt, 1995; Nagarkar & Williams, 1997; Chapman, 2000). This patchy food source may, therefore, represent a risk of relatively low energy returns, so it benefits the limpet to move and graze in areas of the shore where the epilithic biofilm is more abundant or more evenly distributed. Regardless of tidal phase (ebb *vs* flood), rasping was more sporadic when individuals were higher on the shore, which may be a result of the limpet encountering substrata with lower quantities or qualities of food (Williams & Morritt, 1995).

When the limpets are inactive at their lower resting height, stimuli such as wave splash can act as a cue for the limpet to initiate movement and feeding (Ngan, 2006; Santini *et al.*, 2011). In the absence of such cues, *C. grata* has an endogenous, semi-diurnal activity pattern, corresponding with the tidal cycle (Gray & Williams, 2010). This endogenous rhythm suggests that *C. grata* is 'prepared' to be active during every tidal cycle, but uses physical cues to commence movement and rasps when environmental conditions permit, to maximize its potential activity phase (see Ngan, 2006; Santini *et al.*, 2011) according to variation in physical conditions, such as magnitude and timing of tidal cycle, and wave splash (e.g. Parpagnoli, Pecchioli & Santini, 2013).

Cellana grata, therefore, exhibits a suite of behavioural adaptations (i.e. resting height on midshore, triphasic temporal organization of grazing, moving only while awash), including temporal variation in rasping rates, that play a role in allowing the limpet to maximize energy intake within a variable window of foraging opportunities (Chapman, 2000; Santini *et al.*, 2011), while minimizing exposure to potential abiotic stressors (Williams & Morritt, 1995). Such an integrated understanding of grazing patterns across space and time can facilitate more accurate modelling of the energy budgets of these grazers and provide insights into which behavioural modifications (e.g. rasping rate, time of foraging excursions, duration of continuous rasping) are most important for optimal performance of grazers in their respective habitats (Evans & Williams, 1991; Santini, Chelazzi & Della Santina, 1995; Santini & Chelazzi, 1996).

SUPPLEMENTARY MATERIAL

Supplementary Material is available at *Journal of Molluscan Studies* online.

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