



It's not where you are, it's what you do after that matters: Tide-in patterns of orientation do not predict where or when limpets forage



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ABSTRACT

A fundamental problem in ecology is to link spatial arrangements of key biota and the scale at which organisms interact with each other to structure communities and influence ecosystem functioning. Limpets are widely acknowledged to play an important role in the ecology of intertidal rocky shores and exert the strongest grazing effect of any marine grazer. As a consequence, to understand rocky shore dynamics it is necessary to understand the processes that control spatial and temporal patterns of limpet foraging. Much is known about how limpets behave and their distribution during low tide while at rest, and where and when limpets forage. However, it is less well understood how the behaviour and distribution of the same individuals within these two phases of activity can interact. At the smallest spatial scale, several species of limpet exhibit population-level biases in orientation during low tide. If orientation influences where and when limpets forage, this bias may lead to a directional bias in foraging direction and location during high tide, and potentially to patchy grazing. On the other hand, foraging location may determine low tide orientation. We tested these ideas by comparing the low tide orientation of individual limpets (*Cellana tramoserica*) with foraging frequency, and the relative direction of travel while foraging. We found that though there was an overall bias in departure angle and foraging location, there was no relationship between low tide orientation of individuals and their departure angle. Instead, prior to departure limpets rotated on their resting site to face a new direction. There was also no link between the direction of travel of limpets returning from foraging and their final low tide orientation, as limpets actively rotated on arrival at their resting site. Our findings suggest that there is little or no direct link between the orientation of an individual and its subsequent foraging, nor the converse. Limpets instead actively select both their orientation and the direction they depart for foraging by rotation on their resting site. These results decouple the small scale tide-out resting distribution and orientation of grazers from their ecological functioning. Therefore noting the location of limpets at low tide has limited use for predicting ecological consequences of their grazing.

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1. Introduction

The behaviour of an organism during one type of activity, for example mating, foraging or resting, is usually thought to directly influence its subsequent behaviour or distribution (Mayor et al., 2009; Picard et al., 2011; Rettie and Messier, 2000; Simpson et al., 2010; Urban and Shugart, 1986). Understanding the ecology of intertidal grazers has taught us many lessons on how the world may work (Menge, 2000; Underwood, 2000). Intertidal limpets play an integral role in the ecology of their ecosystems (Branch, 1981; Coleman et al., 2006; Hawkins and Hartnoll, 1983; Jenkins et al., 2005; Jones, 1946; Underwood, 1978) and grazing by limpets on temperate rocky shores exerts the strongest ecological effect of herbivory in any marine system (Poore et al., 2012). As a consequence, it is important to understand the links

between limpet behaviour and distribution while at rest, and where and when they subsequently forage.

There is an assumption that, for rocky shores in particular, by examining organism distribution during emersion, insight can be gained about tide-in patterns (Bulleri et al., 2004; e.g. Johnson et al., 1997). For example, it has been suggested that grazing in the limpet *Patella vulgata* is patchy as a consequence of their low tide distribution (Burrows and Hawkins, 1998; Hartnoll and Hawkins, 1985; Johnson et al., 1997, 2008). While much is known about the resting distribution and low tide behaviour of limpets (Branch, 1981; Underwood, 1981; Williams et al., 2005; e.g. Wolcott, 1973), and when and where they move during their foraging phrase (e.g. Branch, 1981; Chelazzi et al., 1998a; Della Santina et al., 1995; Santini et al., 2004), the links between the two phases of activity are not well established (but see Aguilera and Navarrete, 2011; Coleman et al., 2004 for exceptions). More specifically, it is unknown whether resting distribution and behaviour are associated with grazing effort and foraging location during the foraging phase, or how differences in foraging may relate to distribution patterns whilst

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at rest. Limpets, in common with other intertidal gastropods, alternate between periods of inactivity, and foraging, which mostly occurs at high tide but can also occur when the tide is out and varies between species and populations (Santini et al., 2005; Williams et al., 1999). During low tide, there are population-level biases in head orientation (Abbott, 1956; Fraser, 2014b; Fraser et al., 2010; Gallien, 1985; Iwasaki, 1993; Williams et al., 1999), and these biases may in turn lead to directional or frequency biases in foraging activity. The aim of the work presented here was to determine whether the orientation of individual limpets (*Cellana tramoserica*) is linked to their behaviour during high tide.

Orientation is defined as the fine-scale directional position of an animal in space at a given point in time, and it often varies greatly among individuals and at different temporal and spatial scales (nightingales Brumm and Todt, 2003; limpets Fraser et al., 2010; black wildebeest Maloney et al., 2005). An animal's orientation can influence its feeding success (Ladau, 2003; e.g. Otway and Underwood, 1987; Zschokke and Nakata, 2010), body temperature (for review see Stevenson, 1985), risk of dislodgment from wave action (e.g. Denny, 1988; Garcia-March et al., 2007) and susceptibility to predation (e.g. Kang et al., 2012; Pietrewicz and Kamil, 1977; Webster et al., 2009). It is possible that an individual's orientation may also have indirect fitness consequences. For example, orientation at one time may influence where and when an organism subsequently forages or conducts mating excursions. Individuals orientating in different directions may vary in the frequency they forage, because certain orientations are more energetically costly and individuals need to refuel to cover those costs (Chelazzi et al., 1998b; Santini and Chelazzi, 1996); individuals that orientate in a more costly manner may need to forage more frequently than those orientated in a more favourable direction. Alternatively only the individuals that orientate in a specific direction can meet the energy requirements needed for foraging. Additionally the angle at which an organism departs to forage may be directly associated with their previous stationary orientation, which may dictate where it forages. If this is true, directional biases in orientation within a population may consequently lead to a directional bias in foraging excursions and a subsequent patchy distribution of grazing activity, with a myriad of downstream ecological consequences.

In highly mobile organisms, including birds and lizards, it can be assumed that patterns of orientation are determined via active selection by individuals. Other explanatory models, such as differences in mortality for individuals orientating in different directions, are unlikely to be supported for highly mobile animals. This is because such individuals can easily change their orientation if it is unfavourable for the conditions they are being exposed to or where they are located. In sessile organisms, like barnacles and ascidians, patterns of orientation may be set by active selection during settlement (Crisp and Barnes, 1954), uneven directional growth patterns (e.g. Crisp and Stubbings, 1957; Young and Braithwaite, 1980), or differential rates of mortality post settlement (as suggested by Otway and Underwood, 1987). Intertidal gastropods are intermediate to sessile and highly mobile animals in

terms of their flexibility in changing orientation. Individuals may be orientated differently each low tide but are unable, or highly unlikely, to alter their orientation once emersed (C. Fraser pers. obv.). *C. tramoserica*, for example, change orientation each low tide cycle (Fraser et al., 2010). Patterns of orientation in intertidal gastropods may be established by a number of different processes, including active selection and differential rates of mortality.

The simplest explanation, and thus should be the first tested, for orientation of an individual limpet is that it is simply a reflection of the direction the limpet was travelling in when it arrived at their resting site and stopped moving. Alternatively limpets may actively select their orientation by active rotation of their body after arrival. This model is partially supported in *P. vulgata* where individuals have been observed to rotate on arrival at their home scar (Cook et al., 1969; Funke, 1968; Little et al., 1990), a behaviour likely to facilitate the tightest fit to the substrata. In contrast to *P. vulgata*, and other homing limpets, *C. tramoserica* does not create a home scar and therefore may not need to actively rotate on their resting site. Finding evidence to support or reject either of these two models will give guidance as to whether future studies should explore resting or active foraging processes when trying to explain patterns of orientation. For example, if selection of orientation is active, then questions would be focused on what benefits limpets may gain from a certain orientation during low tide resting or what abiotic properties of their habitat can influence their orientation. If instead limpet orientation is a function of the direction limpets are moving, then understanding what influences where they forage and how they return to their resting site should be where research is concentrated.

C. tramoserica forages during high tide, although many individuals do not forage every high tide (R. A. Coleman, unpub. data), and exhibits a downwards bias in orientation during low tide (Fraser et al., 2010). We investigated whether low tide orientation influences foraging behaviour, and vice versa, explicitly whether an individual's orientation determines how frequently and where it forages and if an individual's final orientation is dependent on their direction of travel. More formally the following hypotheses in Table 1 (H1–H6) were tested. If orientation is via active selection, individuals could be selecting to face downwards, as at the population level there is a downwards bias in orientation, and therefore only those limpets which are not already facing downwards on arrival at their resting site subsequently rotate, or their rotation may be a response to some other factor (for example habitat properties) (Table 1, H7).

2. Materials and methods

2.1. Study site description

The study was made at two locations near Sydney, Australia; Little Bay (33° 58' S, 151° 15' E) and Cape Banks Aquatic Reserve (34° 59' S, 151° 25' E). Previous work had shown that patterns of orientation were similar at each location (Fraser et al., 2010; C. Fraser unpub.

Table 1
Models and hypotheses tested in this study.

Model	Hypothesis
Frequency of foraging is dependent on orientation	The frequency of limpets foraging will be contingent on whether orientated upwards or downwards (H1)
Population-level bias in foraging departure angle	The frequency distribution of departure angles will be unimodal (H2)
Bias in departure angle is related to observed low tide bias in orientation	There is a relationship between a limpet's orientation during low tide and departure angle (H3)
Individuals select their angle of departure	Limpets rotate on their resting site before departure (H4)
Departure angle is a proxy for where individuals potentially graze	There is a relationship between departure angle and foraging location (H5)
An individual's low tide orientation is the same direction they were previously travelling	There is no difference between a limpet's direction of travel and final orientation (H6)
Only individuals which are not already facing downwards on arrival at their resting site will rotate their body on arrival	The frequency of limpets rotating on their resting is contingent on if they were travelling downwards or not prior to arrival (H7).

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