

# Up or down? Limpet orientation on steeply sloped substrata

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**ABSTRACT:** Variation in the distribution of animals across the landscape, within and between habitats, can occur at a variety of scales. At the smallest scale, individuals can either be positioned randomly or can be orientated in regard to variables. Differences in orientation can, for many animals, directly affect their reproductive success and/or survivorship, and these effects may have downstream ecological consequences. Organisms may orientate themselves in a specific way in response to varying environmental conditions or habitat properties; alternatively they may consistently orientate in a specific direction. The present study investigated patterns of orientation during low tide in the intertidal marine limpet *Cellana tramoserica* on steeply sloped rocky surfaces ( $>60^\circ$  to the vertical). We also examined whether individual limpets consistently orientated in the same direction or if orientation was dependent upon their orientation during the previous low tide. There was a downward bias in orientation. Mensurative and manipulative experiments measuring limpet orientation over different days showed that individual limpets did not consistently orientate in the same direction and that their orientation was independent of their orientation during the previous low tide. Thus, whilst limpets on slopes often orientate with their heads downwards, there is much inherent individual variation in the orientation patterns exhibited by resting limpets. Simple mechanistic explanations such as responses to desiccation are unlikely to be sufficient to explain why limpets choose different orientations at the end of foraging excursions. These findings have implications for understanding limpet distributions on rocky shores and downstream ecological consequences.

**KEY WORDS:** *Cellana tramoserica* · Direction · Consistency of orientation · Behaviour · Circular statistics · Intertidal habitat · Australia

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## INTRODUCTION

One of the main aims of ecology is to understand and explain organism distribution patterns. The distribution of animals can occur as a response to the availability of food and other resources (e.g. Bennett et al. 1991, Jowett & Richardson 2003, Farris et al. 2010), to variations in habitat characteristics (e.g. Branch 1975, Dunham et al. 2003), and to interactions between individuals (e.g. De Santo et al. 2003). These patterns can occur at a number of scales, within and between habitats and microhabitats. At the scale of an individual, animals can position themselves in a specific orientation within a given habitat. These patterns of distribution can be maintained by animals consistently choosing to position themselves in a similar manner (e.g. Chapman 1994,

McNett & Rypstra 2000, Olabarria et al. 2002, Laurel et al. 2003). Alternatively, some characteristic of the environment may encourage individuals to distribute themselves in a certain way, and so organisms may then select different microhabitats, depending on the macrohabitat in which they are located (Frank 1982, De Santo et al. 2003). Patterns of orientation may be similarly explained, with individuals consistently orientating in the same direction (e.g. Ladau 2003, Zschokke & Nakata 2010) and responding to variations in habitat properties or environmental variables (e.g. Spurr 1975, Wood & Lustick 1989, Fortin et al. 2000). Unfortunately, patterns of orientation by organisms have not often been examined in such a way. Instead, studies have either drawn conclusions from correlations between variations in the environment and an individual's orien-

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tation, or assumed, without explicit testing, that individuals consistently orientate in the same direction.

Many organisms orientate in certain directions during different situations and at varying stages in their life history. A wide range of organisms, including several species of bird, insect, spider and reptile, have been observed to orientate in specific directions during roosting, foraging, migration and times of rest. The ability of an organism to adopt a particular orientation at a given time/place may have survival and health implications. Specific orientations have been suggested to confer benefits in terms of thermoregulation (Bartholomew 1966, DeWitt et al. 1967, Lustick et al. 1978, Brodsky & Weatherhead 1984, Fortin et al. 2000), predation success (Walguarnery et al. 2009), vulnerability to predation (Coleman et al. 1999), waste disposal (Williams et al. 1999), hatchling success (Butler et al. 2009) and health (Goodenough et al. 2008). Often these orientations function through varying exposure of the body to the stimulus of interest, to increase or decrease the surface area sensitive to the factor.

We have limited knowledge about patterns of orientation shown by species which commit to a specific direction and then cannot change until environmental conditions permit (but see Zschokke & Nakata 2010 for work done on spiders). The commitment to a given orientation means that for such an individual, the choice of an initial orientation may be more important than for organisms that can modify their orientation if needed. Limpets are a good species to properly examine this. Limpets offer an ideal study system both for examining orientation in sedentary organisms and for testing hypotheses in regards to whether organisms consistently orientate in a similar direction or if orientation is dependent on variations in the environment. We can easily change the position and/or orientation of limpets, so manipulative experiments are tractable. As a significant proportion of the population forages each tidal cycle and individual orientation may then vary over each low tide, patterns of consistency in orientation can be determined after very short periods of time.

Rocky shores have long been used as a test bed for developing general theories about ecological phenomena. In particular, the role of limpets in controlling the development of macroalgae has been understood for >60 yr (Jones 1946). Limpets graze the biofilm as they move across what is, to an individual limpet, a largely 2-dimensional habitat. The ingestion of biofilms by limpets also includes taking in the juvenile stages of marine macroalgae. Across a wide range of locations, temperate rocky-shore communities have been shown to be fundamentally structured by limpet grazing (see Hawkins et al. 1992, Underwood 2000, Paine 2002 for review). In one of the few continental-scale manipulative experiments done, Coleman et al. (2006) demon-

strated that in the absence of limpet grazing, not only do macroalgae increase in abundance, but also the spatial variability of both macroalgae and marine organisms on the shore is altered. Limpets are potential 'leverage species' in that their removal, or alterations of behaviour in response to climate change may have fundamental consequences on the ecosystem (Harley et al. 2006). Limpets are frequently considered as homing animals in that many species return to the same location after foraging, and these patterns have strong temporal consistency (Branch 1981, Coleman 2007). In some species of limpet, however, individuals may not return to the same sites after foraging. *Cellana tramoserica* (Holten 1802), for example, has been described as an intermittently homing species, as the frequency of homing in the population can fluctuate with food abundance (Underwood 1977). In these cases, the places where limpets wait out emersion are best referred to as resting sites. On rocky shores in New South Wales, Australia, *C. tramoserica* is one of the most abundant limpets (Edgar 2000). They feed during high tide (Underwood 1975, Mackay & Underwood 1977) and are inactive during emersion. Where topography is relatively uniform, *C. tramoserica* are not aggregated and are often dispersed more uniformly than if by chance (Underwood 1976).

Previous work on other species of patellid limpets has noted, often anecdotally, that there appears to be a bias in the direction individuals orientate during low tide. These biases were in either an upward (e.g. Iwasaki 1993) or downward (e.g. Gallien 1985, Williams et al. 1999) direction. Differences in orientation have been noted between aggregated and solitary *Colisella digitalis*, such that aggregated limpets were positioned at a 90° angle as opposed to an observed downwards orientation of solitary limpets (Gallien 1985). Unfortunately, Gallien (1985) scored a limpet's orientation according to an 8-point system, which oversimplifies possible patterns of orientation and ignores the circular nature of the data (see next paragraph). Orientation was also only measured at one point in time. In several other species of limpet, individuals have also been anecdotally observed to orientate in a similar direction each low tide (e.g. Hewatt 1940), but an extensive search of literature has found no evidence of this having been formally tested.

Linear statistics are inadequate for testing hypotheses dealing with circular data as they ignore the finite and circular nature of the data (Batschelet 1981, Fisher 1993). For example, though 10° and 350° are numerically very different, in terms of circularity they are instead quite similar and thus should be dealt with in an appropriate manner. The use of circular statistics, though mathematically complex, overcomes these problems by transforming all data points into vectors,

which creates a finite looped data set (Fisher 1993). Techniques have also been developed to compare mean directions between more than one sample of circular data (Batschelet 1981, Fisher 1993), but these are under-used, and instead samples are compared subjectively (for review see Chapman & Underwood 1992). Statistical tests specifically developed to deal with circular data are the appropriate methods for examining patterns of limpet orientation, as opposed to adapting linear statistical frequency tests, and therefore were used to examine limpet orientation in the present study.

The present study aimed to, firstly, determine if a bias in limpet head orientation existed and if the mean orientation differed between aggregated and solitary limpets. Secondly, the model that the observed biases in orientation were a result of individual limpets consistently orientating in the same direction was tested. Finally the model that a limpet's orientation was dependent on its previous orientation was tested. We also examined whether consistency of orientation was dependent on the limpets returning to their original resting site.

## MATERIALS AND METHODS

**Site description.** The present study was carried out at a number of sites within the intertidal region of Cape Banks Scientific Reserve, Sydney, Australia (34° 99' S, 151° 25' E). The study sites consisted of a series of steeply sloped rock surfaces and/or large boulders and varied in size (minimum size: 2 m<sup>2</sup>). Steeply sloped surfaces were defined as having a slope of  $\geq 60^\circ$ , excluding overhangs; this angle was chosen because previous observations on limpet orientation were made on surfaces with slopes between 60 and 95° from the vertical (Williams et al. 1999). The weather was not atypical for the study periods (Australian Bureau of Meteorology, www.bom.gov.au), and as no hypotheses on a possible relationship between weather conditions and limpet head orientation had been proposed, there was no need to test for this.

**Calibration.** To determine the precision of the measurements of limpet orientation, a calibration study was done. This was important so that we could determine whether a measured difference was due to a real difference in orientation or a lack of precision. Twenty limpets resting on a steeply sloped rock were selected and each individual limpet was measured 10 times, in a random non-sequential order to avoid bias in measuring. To quantify the anterior-posterior orientation of a limpet, a spirit-level protractor (magnetic POLY-CAST) was aligned along a limpet's axis from head to tail. In *Cellana tramoserica*, as with most patellid lim-

pets, the profile of the shell is asymmetric, with the peak being at the anterior end. For each limpet, a 95 % confidence interval (CI) was obtained and then an overall 95 % CI for the sample was calculated. As the range of orientations for each limpet was very small, linear CIs are valid for this situation.

**Is there a bias in limpet orientation?** Orientation of *Cellana tramoserica* on steeply sloped surfaces at low tide was studied in October and November 2009 and again in May 2010. Six different sites were studied, 3 during October and November and 3 in May. This temporal replication here and in subsequent experiments reduced the effect of random environmental and spatial variation (Underwood 1997). The anterior-posterior orientation of 100 limpets was measured at each site on 3 separate occasions, at least 1 wk apart. During the first sampling period, limpets were classed as either aggregated ( $\leq 2$  cm from another limpet) or solitary ( $> 2$  cm from another adjacent limpet) in order to compare the mean orientation of these 2 groupings. Previous experiments on the orientation of aggregated limpets did not specify what was defined as an aggregated individual (Gallien 1985), and so preliminary observations were done to determine these 2 classes. For all experiments, we examined adult limpets between 16 and 35 mm in length.

The null hypothesis of there being no difference in the distribution of orientations compared with a uniform distribution was tested using Rayleigh's test (Fisher 1993). Rayleigh's test was also used to determine if the distribution was unimodal, and if it was, then the mean direction and 95 % CI were also calculated. In circular statistics, a uniform distribution is defined as having an undefined mean, a mean resultant length of zero and the circular dispersion being infinite (Fisher 1993). If the distribution is unimodal, this means that there is a bias in the orientation of limpets. Watson's Y-test (Fisher 1993) was used to test for a common mean between samples. Multifactorial tests of directionality could not be used as the condition of a mean resultant length of  $> 0.45$  was not fulfilled (Underwood & Chapman 1985). To test if there was a significant difference in orientation between solitary limpets and aggregated limpets, a  $\chi^2$  goodness-of-fit test was used. The frequency of occurrence of events when the difference between the mean orientation of the solitary limpets and 180° was smaller than the difference between the mean orientation of the aggregated limpets and 180° was compared. For this and subsequent tests,  $\alpha$  was 0.05.

**Do limpets return to the same orientation?** During November 2009 and May 2010, 18 sites were selected and 3 sites were measured on each paired set of days. To ensure that each limpet was most likely to be independent of other measurements and animals, each

target limpet was the second limpet from a randomly chosen spot. Limpets ( $n = 20 \text{ site}^{-1}$ ) were labelled *in situ* with shellfish tags, and a stripe of nail varnish was painted across both the limpet and adjacent rock; this was used to detect if limpets had moved away from their resting site. The orientation of individual limpets was measured over consecutive days and the difference in orientation was calculated. In order to be considered to have returned to their original orientation, a limpet must have been within  $10^\circ$  of their starting orientation. The mean 95 % CI (calculated from the calibration) indicated that it was possible to precisely measure a limpet's orientation to within  $\pm 3.5^\circ$ . When comparing 2 different limpet orientations, a difference of  $\pm 10^\circ$  was the minimum difference that could be detected as a true difference, rather than imprecise measuring.

As not all limpets depart their resting site to forage during high tide, the expected number of limpets in the same orientation on consecutive days would be greater than if all limpets left their resting sites. Previous work has suggested that approximately 16 % of *Cellana tramoserica* at Cape Banks do not forage during high tide (R. A. Coleman unpubl. data). This estimate was used, in addition to the number expected by chance, to calculate an expected value of limpets returning to the same orientation for the analysis. The number of limpets returning to the same orientation expected by chance alone is calculated to be 1/18 of the total number of limpets, as the range which has been defined as being the same orientation is equal to 1/18 of all possible orientations. The sum of the number expected by chance and the number predicted to not forage was used as the expected value for the analysis. The total value was found to be approximately 22 % of the total number of individuals. To test the null hypothesis that there was no difference in the number of limpets returning to their original orientation than would be expected (using the same expected values as calculated for the previous experiment), a replicated goodness-of-fit test (Sokal & Rohlf 1995) was done. When testing such a hypothesis, it is important to first test for homogeneity of samples;  $G_H$  is the test statistic used for the heterogeneity  $G$ -statistic, whereas  $G_P$  is used to annotate the pooled  $G$ -statistic.

**Are limpet orientations dependent on their previous orientations?** To test the prediction that the orientation of *Cellana tramoserica* during low tide was either related to their previous orientation or that there were 'downward facing' or 'upward facing' limpets, experiments were done in mid-December 2009 and repeated during May 2010. The day before manipulation, approximately 90 individuals were labelled per site as above. The next day, each individual's orientation was measured as before. Each limpet was then rotated depending on their treatment (Table 1) and their position on the rock marked with nail varnish. Limpets were removed from the rock using a palette knife, the resting site was made wet again with seawater, and the limpet rotated, before replacing them on their original resting site. *C. tramoserica* will quickly re-attach when replaced back on the rock if the surface is sufficiently wet (Underwood 1978). On the second day, each individual's final orientation was measured. The null hypothesis of there being no difference between treatments in the number of limpets returning to their original orientation was tested using a 2-way ANOVA, with 1 fixed factor (4 levels: 3 procedural controls and treatment) and 1 random factor (2 levels: time). Heteroscedasticity was tested using Cochran's  $C$ -test. A goodness-of-fit test was used to test the null hypothesis that the number of limpets that returned to their original orientation was not dependent on whether they return to the same resting site (expected value: 0.5).

## RESULTS

**Calibration.** The mean 95 % CI was approximately  $3.5^\circ$ .

**Is there a bias in limpet orientation?** There was no significant difference between the mean orientation of solitary limpets and that of aggregated limpets ( $\chi^2_1 = 0.1$ , ns.). The frequency of occurrence of events where the difference between the mean orientation of the solitary limpets and  $180^\circ$  was smaller than the difference between the mean orientation of aggregated limpets and  $180^\circ$  was 3 of a possible 7 times. As a result of this, the aggregated and solitary data sets were

Table 1. *Cellana tramoserica*. Experimental treatments used to test if limpet orientations are dependent on their previous orientations

Treatment	What was done to limpet	Why
A	Untouched	Control
B	Removed from rock and replaced in same orientation	Procedural control for removal from rock
C	Removed from rock and rotated $360^\circ$ before replacing in same orientation	Procedural control for rotating limpet
D	Removed from rock, rotated $180^\circ$ and placed in new orientation	To test if an individual's orientation is dependent on its starting orientation

combined into 1 data set of 100 limpets for each site. The distribution of 17 of the 18 data sets (3 sites on each of 6 d) were each significantly different from a uniform distribution and instead had a unimodal distribution. Rayleigh's test showed that the distribution of limpet orientation on Day 4 at Site 4 was uniform ( $Z = 2.26$ ,  $p = \text{ns}$ ). This data set was excluded as it could not be analysed further since it does not have a true mean to compare with other data sets. The individual mean orientation of all samples lay between  $140$  and  $220^\circ$  from the vertical, i.e. downwards. There was no significant difference in mean orientation between samples ( $Y_{16} = 20.49$ ,  $p = \text{ns}$ ), so all 17 samples were combined together and tested again for uniformity. The distribution of the combined samples was also significantly different from a uniform distribution ( $Z = 165.71$ ,  $p < 0.05$ ) and had a mean orientation of  $180.04$  (Fig. 1). It should be noted that though the distribution of orientations was unimodal, the variance ( $V = 0.69$ ), standard deviation ( $v = 1.01$ ) and circular dispersion ( $\delta = 5.29$ ) were all still quite high, indicating that the data were highly dispersed. Of these measurements, circular dispersion is the most useful as there can be problems with the interpretation of circular variance, as a value of 1 does not always equate to a maximal spread of data points (Fisher 1993).

**Do limpets return to the same orientation each low tide?** There were no differences among sites in the pro-

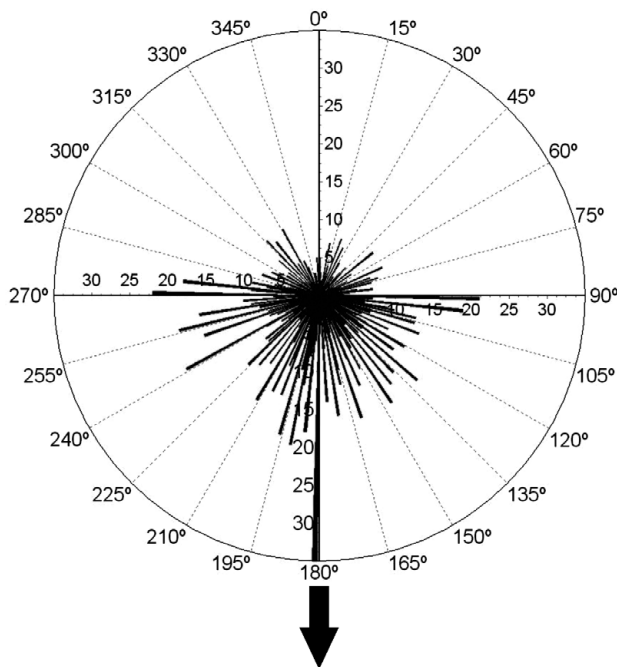


Fig. 1. *Cellana tramoserica*. Frequency distribution (no. of ind.) representing different limpet orientations ( $Z = 165.71$ ,  $p < 0.05$ ). The different axes represent the frequency of limpets orientating in that direction.  $180^\circ$  = vertically downwards. Arrows indicate mean direction of orientation

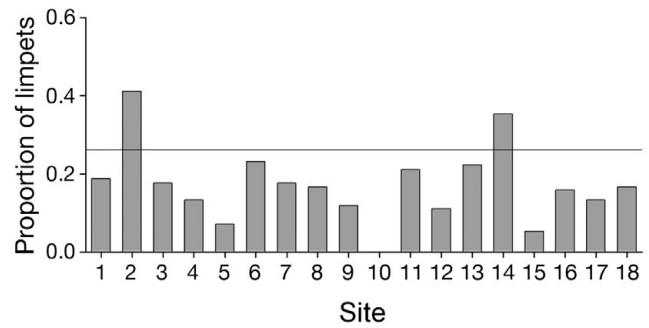


Fig. 2. *Cellana tramoserica*. Proportion of limpets returning to their original orientation after 2 tidal cycles. Horizontal line indicates expected proportion. See Table 2 for further details

Table 2. *Cellana tramoserica*. Replicated goodness-of-fit ( $G$ ) test of the frequency of limpets with a consistent orientation. See Fig. 2

Tests	df	$G$	$p$
Pooled ( $G_p$ )	1	0.22	$>0.63$
Heterogeneity ( $G_H$ )	17	21.54	$>0.20$
Total	18	21.76	$>0.24$

portion of limpets that returned to their original orientation after foraging ( $G_{H(17)} = 21.54$ ,  $p = \text{ns}$ ), and at all 18 sites the number of limpets that returned to their original orientation did not differ from what was expected ( $G_{P(1)} = 0.22$ ,  $p = \text{ns}$ ; Fig. 2, Table 2). Individuals that, at the following low tide, had settled on a surface with a slope of  $<60^\circ$  or  $>90^\circ$  were excluded as they were in a location that did not satisfy the original criteria.

**Are limpet orientations dependent on their previous orientations?** There were no significant levels of heteroscedasticity ( $C = 0.34$ ,  $p = \text{ns}$ ), and there was no significant difference in the mean number of limpets returning to the same orientation between treatments, and this was consistent between times (Fig. 3, Table 3).

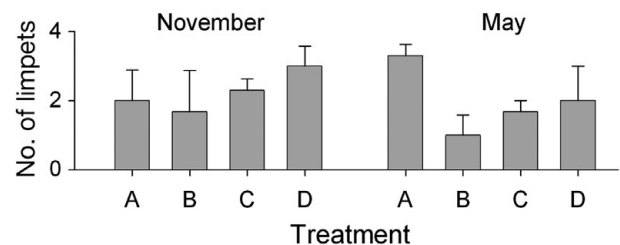


Fig. 3. *Cellana tramoserica*. Mean (+SE) number of limpets returning to their original orientation after 2 tidal cycles. See Table 1 for description of Treatments A to D. See Table 3 for ANOVA



Table 3. *Cellana tramoserica*. 2-way ANOVA of the number of limpets that returned to the same orientation between treatments. See Fig. 3

Source	df	MS	F	p
Treatment	3	1.60	0.55	>0.68
Month	1	>0.01	0.03	>0.87
Month $\times$ Treatment	3	2.93	1.85	>0.18
Residual	16	1.58		

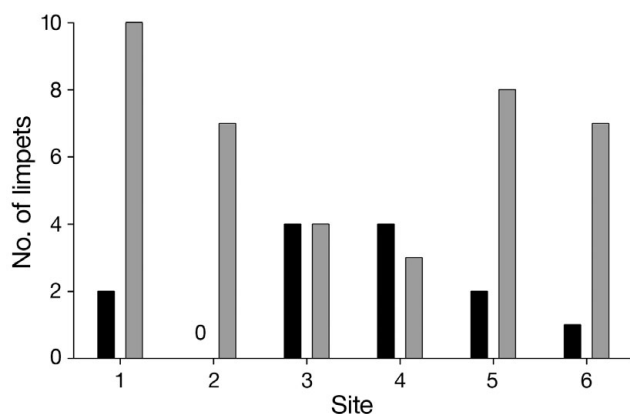


Fig. 4. *Cellana tramoserica*. Number of limpets, found in a new resting site (black bar) and found in their original resting site (grey bar), that return to their original orientation

The number of limpets that returned to their original orientation was dependent on whether they returned to the same resting spot ( $G_{P(1)} = 13.61$ ,  $p < 0.05$ ; Fig. 4). The number of limpets that returned to their original orientation in each treatment was not significantly different from what was expected ( $G_{P(1)} = 1.55$ ,  $p = \text{ns}$ ).

## DISCUSSION

Within the population of limpets studied at Cape Banks there was a downward bias in limpet orientation, as the frequency distribution of limpet orientations on steeply sloped surfaces was unimodal. This pattern was consistent in time and space. It appears as if populations of *Cellana tramoserica* orientate downwards, similar to solitary *Collisella digitalis* (Gallien 1985) but different from the congener *Cellana toreuma*, which were found to face predominantly upwards (Iwasaki 1993). Unfortunately these studies were done at different spatial scales and periods of time from each other and from the present study, so it is impossible to come to any definitive conclusions about similarities between them.

No difference in orientation was found between solitary and aggregated limpets, contrary to that previously observed in *Collisella digitalis* (Gallien 1985). It was suggested that solitary limpets compensate for the benefits they would otherwise receive from being in a group by altering their orientation with respect to the vertical plane (Gallien 1985), and that a downward orientation would allow the limpet's head to stay wet for a longer period of time, and thus place the limpet under less desiccation stress (Gallien 1985). Gallien (1985) concluded that aggregated limpets were already decreasing their desiccation stress by means of being within a group and therefore did not need the benefit that a downward orientation would confer, though more recent work has shown that limpets in groups are under no less desiccation stress than those that are solitary (Coleman 2010). If orientating the head downwards confers benefits, it must be expected that there are also costs for doing so, for if there were no costs, the majority of limpets should be so orientated. In the published accounts of limpet orientation there are no reported tests of hypotheses related to costs of patterns of orientation (Gallien 1985, Iwasaki 1993, Williams et al. 1999). As there were no differences in orientation between solitary and aggregated limpets, this suggests that the possible benefits and costs of a specific orientation are not dependent on an individual's group status.

There was no evidence to suggest that the observed pattern of head orientation was maintained by limpets consistently returning to the same orientation, as the number of both unmanipulated and manipulated limpets that returned to their original orientation was no greater than the calculated expected value. Much work on animal orientation, with some exceptions, has focused on finding a relationship between an individual's orientation and possible survival benefits as opposed to examining whether observed patterns are a result of individuals consistently orientating in the same direction, as has been done in the present study. This means that it is difficult to compare the present results with previous findings. One exception is from work done on the amphipod *Talitrus saltator*, which in laboratory trials appeared to consistently orientate in the same direction (Scapini et al. 1999). Previous experiments had, however, noted variation in the orientation of individuals depending on if they were observed under natural or controlled conditions (Borgioli et al. 1999) and so the results of Scapini et al. (1999) may not be representative of what occurs in the amphipods' natural environment. Consistency of orientation has also been examined in orb-weaving spiders but only for unmanipulated individuals (Zschokke & Nakata 2010), and it has been noted that such experiments nearly always inherently confound observed results with spatial and temporal variation (Coleman 2010).

As the mean number of limpets returning to their original orientation did not differ between treatments, with limpets whose orientation had been flipped neither returning more often than expected to their original nor flipped orientation the following day, it can be concluded that an individual's orientation is independent of their starting orientation. This means there is no relationship between where a limpet starts in terms of their orientation and their final orientation.

Though there was a definite bias in head orientation during low tide, the circular dispersion of the orientations indicates that orientation is highly variable within the limpet population. This either suggests that there could be certain individuals who are 'downward-facing' limpets and certain individuals who are 'upward-facing' limpets, or that orientation is dependent on where a limpet rests during low tide. As limpets do not consistently return to the same orientation each low tide, this suggests that the first option is not the case and that instead orientation may be dependent on their resting site during low tide.

In order to test whether an individual's orientation is dependent on their resting site during low tide, the orientation of limpets in specific resting sites would have to be monitored and the orientation of occupants of the same resting site at different points in time compared. An extension of this would be to also examine whether limpets are responding to intrinsic resting-site properties, such as rock topography or algal cover, or if they are instead aligning themselves against the mucous pad of the previous resting-site occupant.

Before questions can be asked about the processes behind observed patterns, it is important to first quantitatively establish if the observed pattern is actually occurring (Underwood et al. 2000). In the present study we have only attempted to determine if previously observed patterns of orientation occur, and have left the question of the processes behind this pattern for future studies. So why might *Cellana tramoserica* orientate in a downward manner during low tide? Various models to explain biases in limpet head orientation have been suggested but nothing has been done to formally test these. Thermoregulation has been most frequently described as the causal explanation for observed biases in orientation (e.g. Bartholomew 1966, DeWitt et al. 1967, Lustick et al. 1978, Brodsky & Weatherhead 1984, Fortin et al. 2000). In addition to models around thermoregulation, another proposed explanation is that a downward orientation decreases desiccation stress or allows for a greater capacity for water storage, as the head area is wet for a longer period of time (Gallien 1985, Williams et al. 1999). Alternatively, a downward head orientation may allow for greater flushing of the nuchal cavity to remove waste products such as faecal matter and CO<sub>2</sub> (Williams et al. 1999). The flush-

ing of the nuchal cavity is important, as the anus and both the right and left renal openings open into this cavity (Fretter & Graham 1994). Alternatively, an individual limpet may orientate in a specific direction in order to obtain the best fit to the substratum, and not because of any specific benefit orientating in that direction may confer. In this case, on topographically smooth surfaces it would be predicted that the distribution of limpet orientations would be uniform.

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