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William G. Wright

James W. Nybakken

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EFFECT OF WAVE ACTION ON MOVEMENT IN THE OWL LIMPET, *LOTTIA GIGANTEA*, IN SANTA CRUZ, CALIFORNIA

William G. Wright and James W. Nybakken

ABSTRACT

The critical role of wave energy in the ecology of nearshore organisms is widely accepted, based primarily on biotic correlations over large scales of time and space. Much less is known about how large waves impact the behavioral ecology of individual organisms. Theoretical considerations and measurements of tenacity predict that intertidal gastropods should minimize the chances of dislodgement during periods of high waves by remaining stationary. We tested this prediction by observing a population of the owl limpet, *Lottia gigantea* G. B. Sowerby I, 1834, in a range of sea conditions. We found the proportion of the population moving during high tide was reduced when maximum wave height exceeded 1 m. This relatively low threshold suggests that ambient sea state has a consistent influence on foraging strategy of intertidal limpets.

Extreme environments have long been recognized as fertile testing grounds for adaptive hypotheses (Wharton, 2002). One such environment is the intertidal zone of the world's oceans (Lewis, 1964; Stephenson and Stephenson, 1971; Ricketts et al., 1992). In addition to wide fluctuations in temperature and salinity, intertidal organisms of outer-coast intertidal zones are also exposed to damage and dislodgment due to high fluid velocities generated by ocean swells as they collide with the shoreline (Denny 1985, 1988). Swell-induced wave energy is thought to have profound effects on intertidal community structure (e.g., Dayton, 1971; Paine and Levin, 1981; McQuaid and Branch, 1985), as well as the biology of individual species, both sessile (Denny et al., 1985; Holbrook et al., 1991; Blanchette, 1997; Denny and Gaylord, 2002) and mobile (Denny 1985, 1988). Intertidal limpets have been widely utilized for research into the ecological effects of wave energy on mobile species (Denny, 1985, 1988; Brown and Quinn, 1987; Judge, 1988; Denny and Blanchette, 2000; Jenkins and Hartnoll, 2001; Jonsson et al., 2006), and the overwhelming consensus is that wave energy can exert strong selection on the ecology of these organisms. Nevertheless, the evidence for such selection is mainly indirect, resting on experiments and correlations across relatively large scales of space and time (e.g., Dayton, 1971; Paine and Levin, 1981; McQuaid and Branch, 1985).

Additional independent tests of the adaptive hypothesis that wave energy constrains the biology of mobile intertidal invertebrates may be realized by behavioral observations. For example, brooding starfish have been shown to allocate a greater proportion of their arm length to adhering to the substratum in sites of high wave energy compared to sites of low wave energy (Menge, 1974). Similarly, when drag-inducing flanges are attached to the shell of exposed limpets, movement is inhibited, relative to unmanipulated control limpets (Judge, 1988). Although these observations provide indirect evidence that high wave-energy constrains movement of intertidal organisms, there are no direct observations of the influence of large waves on the decision to move. Early studies (Miller, 1974; Denny, 1985; W.G.W., pers. obs.) and recent work on the properties of mucous in gastropods (Smith et al., 1999; Smith, 2002), indicate that moving limpets are more vulnerable to dislodgement than are
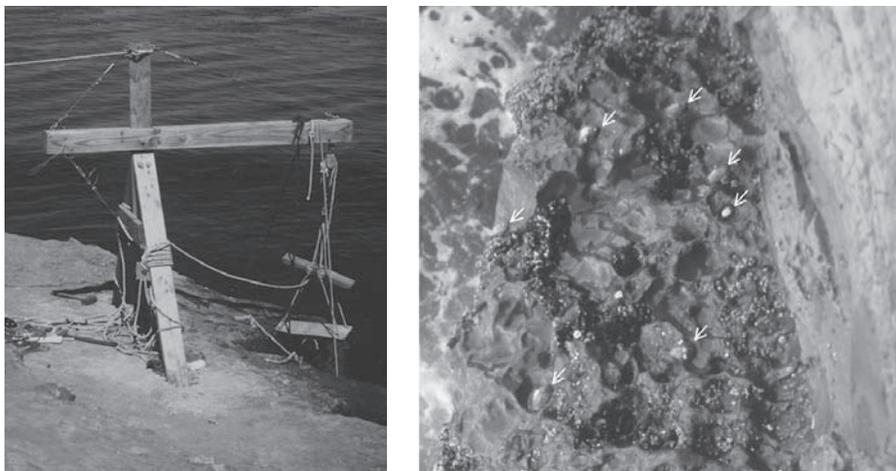
Figure 1. (A) A block and tackle suspended from a wooden frame allowed the observer to make precise measurement of the half-hourly positions of 9–13 limpets during all levels of tide and sea state. (B) Photograph showing some of the marked limpets (arrows). This photo was traced in order to make copies on which to accurately place the location of each limpet at successive half-hour intervals during each study.

stationary ones. Thus, an adaptive limpet would be expected to curtail movement during periods of high wave energy. The present paper tests this prediction, and reports, for the first time, that natural variation in wave energy is correlated with the decision to move: movement in the owl limpet *Lottia gigantea* G. B. Sowerby I, 1834 is inhibited at high tide during periods of relatively larger waves. Some of the results of this research have been reported in abstract form (Wright, 1978)

Materials and Methods

We took advantage of an accessible sandstone cliff in Santa Cruz, California, to observe the movement of 9–13 marked limpets during 14 study periods from April, 1977 through March, 1978. The observer used a wooden A-frame (Fig. 1A) with a block and tackle to lower himself to a position over the limpets, in order to map their position and orientation every 0.5 hrs for the duration of each study period (8–30 hrs). The map was made from photographs of the area (Fig. 1B), and allowed a precise estimate (ca nearest 1 cm) of the position of each limpet.

We subjectively estimated maximum swell height before each study by comparing the size of the waves at a nearby surfing area ("Stockton Avenue") to the surfers riding them. Head-high wave-faces were considered 1.25 m, double overhead waves were considered 2.5 m, etc. These estimates ranged from 0.5 to 2.5 m and were used to rank each of the 14 study periods.

During one study with particularly large waves (10 June, 1977, Fig. 2), which showed clear evidence that limpet movement was inhibited at high tide, we began counting the number of waves washing the area over a 5 min period. We continued these assessments of wave wash in all subsequent studies. This number gave an independent estimate of wave energy, thus allowing evaluation of our more subjective wave-height estimate (see Results). Tidal height data were obtained from the program XTide (David Flater) <http://www.flaterco.com/xtide/>.

We performed a two-way repeated measures ANOVA (SPSS, mixed linear model) on the entire data set, after first arcsin transforming the proportion moving data. This allowed us to test the main effect of waves (low swell vs high swell; between group effect), time (relative to higher high tide; within group effect), and their interaction. We also performed non-parametric Mann Whitney U tests to compare specific low- and high-swell data.
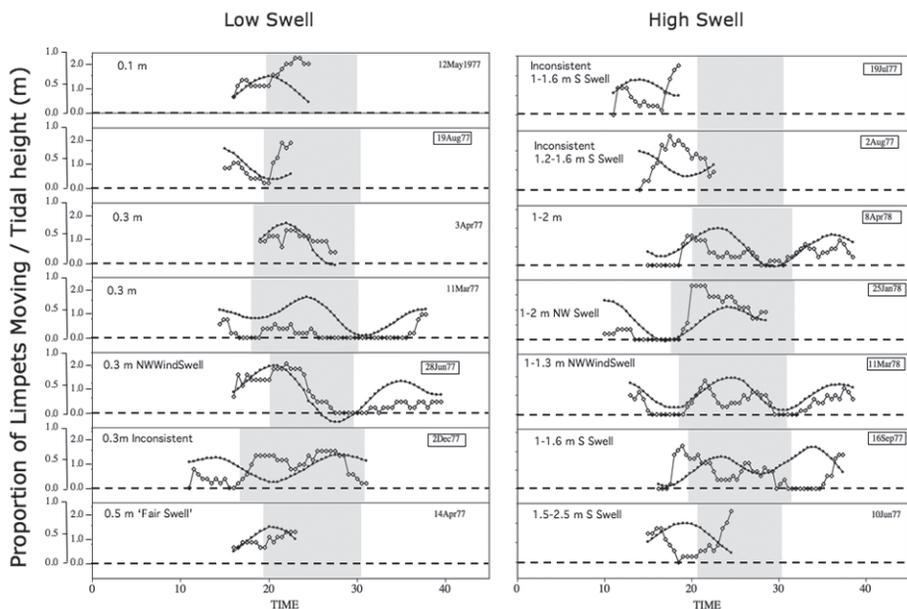
Figure 2. Proportion of limpets moving was quite variable, but appeared to be reduced during high-tide during the observations made during the largest waves. All fourteen observation periods were ordered according to subjective estimate of maximum swell height: low wave energy studies on left, high wave energy studies on right. Tidal height (right vertical scale, closed circles) and proportion of limpets moving (left vertical scale, open diamonds) are shown across time. Darkness indicated by shading. Dates enclosed in boxes indicate observation periods in which the number of waves washing the limpets (see Figs. 5, 6) was measured.

Results

Because *L. gigantea* lives relatively high in the intertidal zone in central California, and because of the advantageous geometry afforded us by our "cliff-hanger" (Fig. 1), we were able to observe individually tagged limpets at all times of the day and across all tides. Furthermore, we found we could observe them over a wide range of sea states, from virtually no waves (Fig. 2, upper left panel) to conditions with maximum swell heights of > 2 m (Fig. 2, lower right panel).

We observed limpet movement during 14 separate study periods from June 1977 through April, 1978 (our planned May, 1978, study was aborted when every limpet was removed, most likely by a local fisherman). As a general rule, limpets only moved when washed by the sea. As the tide subsided toward ca 0.0 ft, movement generally ceased (e.g., 11 Mar 1977, 28 Jun 1977, 8 April 1978). Within this general rule, we observed a good deal of variation. First, limpets moved more at night, even when the tide was relatively low (e.g., Fig. 2; 28 Jun 1977, 2 Dec 1977). Second, during times of high swell, limpets appeared to be inhibited from moving. Whereas observations made during the lowest swells (Fig. 2, left panels) generally showed more limpet movement during high tides, observations made during the highest swells (Fig. 2, right panels) showed an inhibition of movement during the peak high tides (especially the bottom three traces, 11 Mar 1978, 16 Sep 1977, 10 Jun 1977). This inhibition of movement was apparent during both day and night-time high tides.

We next grouped the low-swell observations to compare to the grouped high-swell observations. Because every study included one higher high tide, we aligned each ob-
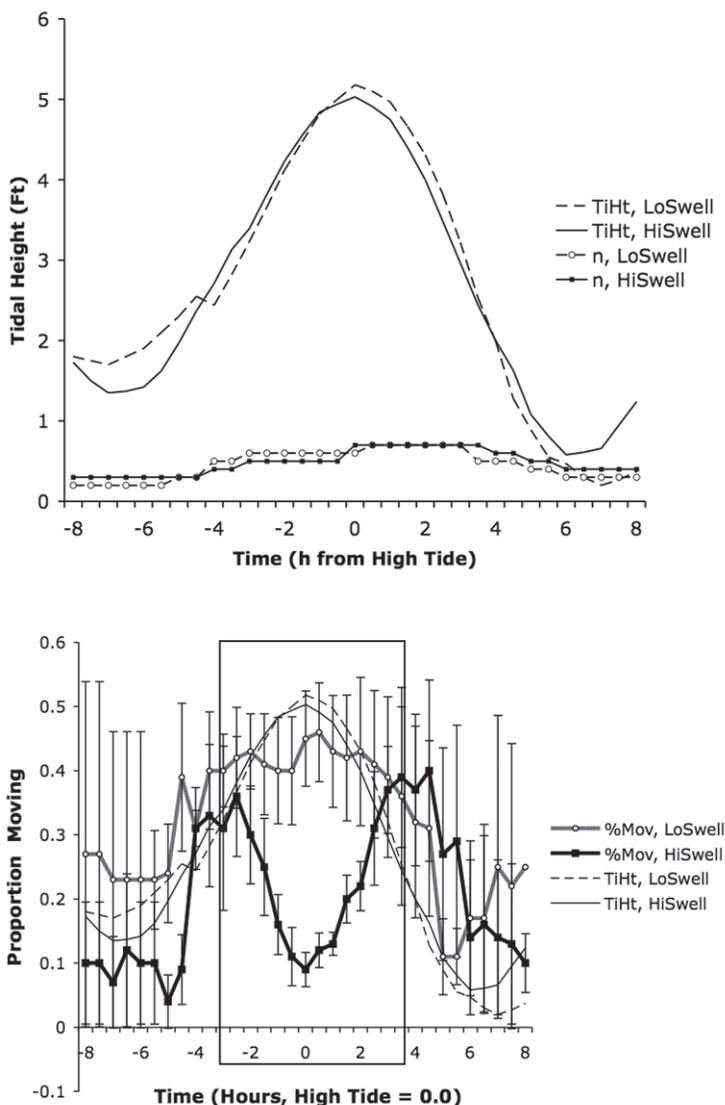
Figure 3. Observations made during higher high-tide. All 14 observation periods of Figure 2 were aligned by the time of higher high water in each study. (A) Tidal height for low-swell observations was very similar to that of high-swell studies. Shown is the average tidal height (ft) for the low-swell observations (dashed line) separate from the high-swell observations (solid line). Also shown are the number of observation periods (ranging from minimum of 2 to maximum of 7) represented at each time point for low-swell (open circles) and high-swell (closed squares) observations. (B) Proportion of limpets moving was relatively constant throughout the higher high tide for low-swell observations, but showed a marked decline at the peak tide during the high-swell observations. Shown (in addition to the tidal height from part A) at each time, is the average (± SE) proportion moving for low-wave (open circles) and high-wave (solid squares) observations. Observations within vertical rectangle comprised the data for the statistical analysis (Fig. 4).
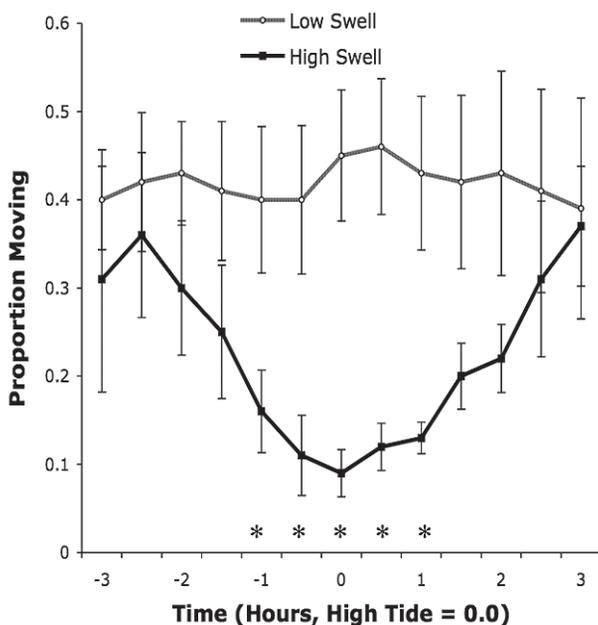
Figure 4. During the 6 hrs of higher high tide, the proportion of limpets moving during high-swell observations was significantly lower than during low-swell observations. Shown are the average (± SE) proportion of limpets moving for high-wave (black squares) and low-wave (open circles) observations. These observations comprise a 6-hr subset of those shown in the rectangle in Figure 3. Asterisks indicate significant differences (Mann-Whitney U test: $P < 0.05$) between low- and high-swell observations.

servation period by centering the data set on the half-hour interval that included the higher high tide. When aligned in this way, the average observed tidal height of the low-swell observations matched very closely the average tidal height of the high-swell observations (Fig. 3A). By contrast, when we superimposed the average proportion moving on the same figure (Fig. 3B), a clear difference emerged between the low- and high-swell observations. In both sets of observations, as the tide flooded from −6 to −3 hrs (6−3 hrs before high tide) limpet movement also increased. However, during the next 6 hrs, the proportion moving changed in very different ways (Fig. 4). The proportion moving during the low-swell observations remained fairly constant at ca 0.4. By contrast, the proportion moving during the high-swell observations dropped dramatically as high tide approached, to a minimum of ca 0.1, increasing again to 0.4 as the tide ebbed. After arcsin transforming our proportion moving data, we performed a repeated measures analysis of variance using a within group treatment of time (−3 to +3 hrs) and a between group treatment of waves (low swell, high swell) applied to the period 3 hrs before and after the high tide (box, Fig. 3B). This was the only period that had a large enough sample size (> 5 observations) to allow meaningful statistical comparison. The repeated measures ANOVA revealed that during the high-swell observations, a significantly lower proportion of limpets was moving than during the low-swell observations ($F_{1, 12} = 5.1$; $P = 0.04$). Furthermore, there was a significant interaction across time ($F_{12, 125} = 1.9$; $P = 0.04$). Because these were frequency data, we also performed a non-parametric Mann-Whitney test of these data, which revealed a significant difference between low- and high-swell periods ($P < 0.05$; asterisks, Fig. 4) throughout the period extending from 1 hr before until
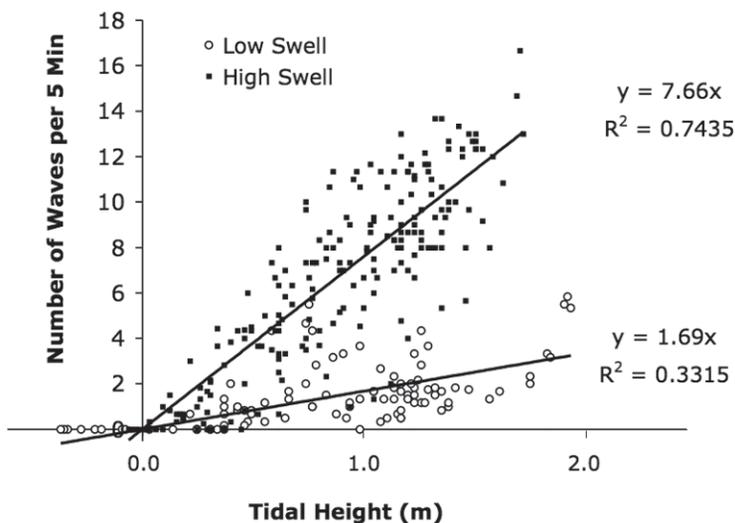
Figure 5. Number of waves washing limpets per 5 min increased with tidal height, and the slope of this relationship was much greater during the high-wave observations than during low-wave observations. Shown are number of waves washing limpets for each half hour of the observations shaded in Figure 2, as a function of tidal height. The slope of the high-wave observations (solid squares; b = 2.33) was significantly steeper (P < 0.001) than that (b = 0.52) of low-wave observations (open circles). This distinct difference in slope validates the subjective assignment into low- vs high-wave categories (Figs. 2–4).
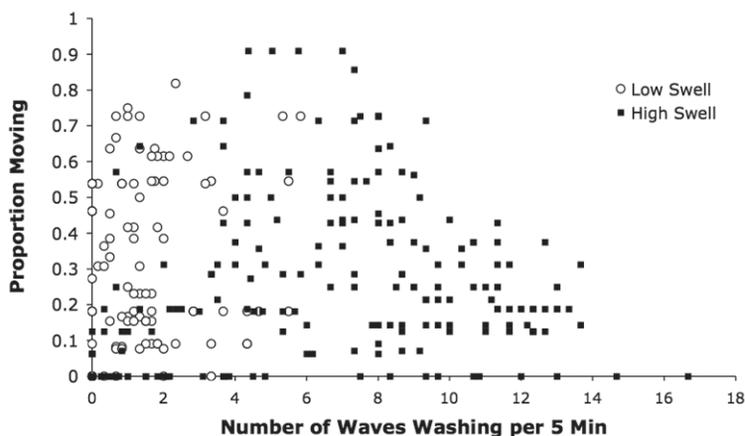
Figure 6. Limpet movement was inhibited during times of high waves. The proportion of limpets moving vs number of waves washing them per 5 min is shown separately for low-wave (open circles) as well as high-wave (solid squares) observations. Each symbol represents the proportion of limpets moving during one time-point of 9 of the 14 studies. A reduction in the range of observed proportions is evident as the number of waves per 5 min rises above 8.

1 hr after the maximum tide. These data clearly indicate that limpet movement was inhibited during high tide during high-swell periods relative to movement during the low-swell periods.

The assignment of relative swell height in each of the observation periods in the above analysis was based on a subjective assessment of maximum swell height (see Methods). In order to gain a more objective measure of swell energy, we counted the number of waves in a 5-min period that were big enough to wash the limpets. Not surprisingly, this number increased with increasing tidal height, but the functional relationship differed during the different observations periods, in a way that was consistent with our subjective assessment of swell height. In particular, we found that during the high-swell observations, there was a steeper relationship (slope = 7.66) between the number of waves washing the limpets and tidal height than during low-swell observations (t = 11.7, n = 98, 205; P << 0.01; Fig. 5).

We used the number of waves washing in a 5-min period as a surrogate measure of relative wave action, and plotted the proportion of limpets moving as a function of that wave action. Because we only assessed the number of waves washing for 9 of the 14 observation periods (Fig. 2, dates enclosed in boxes), we were only able to analyze this restricted data set (Fig. 6). Nevertheless, this scattergram confirmed that (1) the wave energy in the "low swell" studies was on average less than that in the "high swell" studies, and (2) that limpet movement was inhibited during periods of high wave wash. When the number of waves washing the limpets was intermediate, between 4 and 9 waves per 5 min, the proportion of limpets moving ranged up to 0.8–0.9. However, when more than 9 waves washed the area per 5 min, limpet movement was rarely over 0.5, and in the highest wave wash (12–14 per 5 min) periods, even fewer limpets moved.

Discussion

These results support the idea that movement of an intertidal organism can be limited by large waves. It appears that in the owl limpet, *L. gigantea*, the decision to move or remain stationary includes an assessment of the risk of dislodgement by wave action. During days with relatively small swells, limpets tended to move throughout the high tide, whereas high-tide movement during days with larger swells was sharply reduced. This is the first direct observation to our knowledge of the inhibitory effects of larger waves on the probability of movement in any species, although Judge (1988) observed a reduction in movement when wave-induced drag was artificially enhanced with flanges attached to the shells of limpets.

The idea that gastropods might cease movement to increase their tenacity was first proposed by Miller (1974), who observed that gastropods were more easily dislodged when moving. This observation was repeated by Denny (1985), who compared the force required to dislodge moving and stationary limpets with the forces likely to threaten them in the intertidal. Denny found that the wave-induced forces commonly observed during periods of high swells in the outer-coast intertidal were fully capable of dislodging a moving limpet, and predicted that movement would be curtailed during periods of high swell.

Although Denny's (Denny and Blanchette, 2000) theoretical considerations predicted a reduction of movement during large swells, the present study revealed that such reduction is observed even in relatively modest swells. In particular, the maxi-

mum swell height of our "large swell" studies never exceeded 3 m, whereas the maximum swell height observed by Denny (1985) was larger (2–4 m). Indeed, inspection of Figure 2 suggests that even swells in the 1–2 m range can inhibit movement at high tide. Such swells are relatively common in Monterey Bay, suggesting that wave energy is an almost daily determinant of limpet foraging. Thus, far from being a "last resort" strategy to avoid dislodgement during rare periods of very high swells, it appears that wave-induced inhibition of movement may be a relatively routine determinant of foraging. Furthermore, the many relatively complex factors of the behavioral ecology of *L. gigantea*, including agonistic encounters (Wright, 1982), reproductive biology (Wright, 1989), and risk of predation (Lindberg et al., 1987), are quite likely to interact with the risk of dislodgement by waves in ways we cannot yet foresee.

Recent research on gastropods raises some mechanistic hypotheses to account for the large differences in tenacity between stationary and moving limpets. Differences in the protein composition of the mucous of stationary versus moving gastropods may account for the differences. Additionally, "clamping behavior" (Ellem et al., 2002) may reduce danger from shear forces in stationary limpets below that predicted by the work of Denny and colleagues (Denny, 1985; Denny et al., 1985; Denny and Blanchette, 2000). Finally, interaction of clamping behavior and mucous protein content with the homing habit of many limpets to a specific home scar (e.g., Garrity and Levings, 2004) may confer even more tenacity to stationary limpets resting on their home scars.

These results raise many ecological questions about the role of wave action in the ecology of intertidal limpets. At the very least, they suggest that wave-action represents a routine physical challenge requiring an effective behavioral strategy. Ecological trade-offs between the benefits of foraging (e.g., territory maintenance, feeding) and the risks of dislodgement while moving during periods of even moderate wave action, appear to be evaluated almost daily in the lives of these limpets. It is tempting to hypothesize that wave action may put limits on limpet foraging, for example, during winter months when waves can exceed 2 m for weeks. However, it is not clear whether total available foraging time is, in fact, limited by such stormy weather. Limpets could very well confine their foraging to times of lower tides, when water velocities would be lower; times which would otherwise be dry in low-swell conditions. Interestingly, a cursory look at Figure 3B suggests that the overall percentage of limpets moving integrated over this 6-hr time interval is somewhat lower during high-swell periods than during low-swell periods. However, because the number of observations made outside of the 6-hr window is low, this hypothesis requires further observations. In any case, it seems unlikely to us that winter months pose an energetic challenge to *L. gigantea*. Indeed, most population studies (e.g., Daly, 1975; Shanks and Wright, 1986; Wright, 1989) show maximal growth during winter months, inconsistent with such an energetic challenge. Nevertheless, it is at least possible that some particularly exposed microhabitats with high flow rates may be uninhabitable, not because limpets are washed off the rock, but because the water flow prevents them the opportunity to forage.

numerous to list. We would also like to acknowledge the seminal role of John Pearse, who originally introduced the authors, and encouraged their research. Dr. Pearse's role as "middle man" among scientists is one of his less publicized, yet exceedingly significant, traits. Thank you.

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Addresses: (W.G.W.) *Biological Sciences, Chapman University, One University Drive, Orange, California 92866.* (J.W.N.) *Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, California 95039.* Corresponding Author: (W.G.W.) *E-mail: <wwright@ chapman.edu>.*

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