CALIFORNIA STATE UNIVERSITY, NORTHRIDGE

ACTIVITY PATTERN AS A MECHANISM OF PREDATOR AVOIDANCE

IN TWO SPECIES OF ACMAEID LIMPET

A thesis submitted in partial satisfaction of the
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DEDICATION

Without the love and support of four special people, this thesis would never have been completed. Joyce Wells has always encouraged me to pursue my interests, while enduring the difficulties this has imposed on her. My son, Aaron Wells, has put up with my absences - both mental and physical - and shared in my adventures. My parents, Clyde Wells and Wilma Wells, have supported me in the pursuit of my goals, and provided caring and comfort when I have stumbled along the way. I am very fortunate to know these people, and this thesis is dedicated to them.

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ABSTRACT

ACTIVITY PATTERN AS A MECHANISM OF PREDATOR AVOIDANCE IN TWO SPECIES OF ACMAEID LIMPET

by

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Activity patterns in the foraging activity of two species of acmaeid limpet, Collisella limatula (Carpenter, 1864) and Collisella scabra (Gould, 1846) were documented over the entire tidal cycle. Collisella limatula was found to be active only while awash by the tide and during nighttime emergence; periods of inactivity were spent in crevices and on the undersides of boulders. Collisella scabra, which homes to a scar on the upper surfaces of rocks, foraged only while awash in daylight. In laboratory experiments both species of limpet were shown to orient their movement relative to light and gravity stimuli, while turbulence was necessary to elicit a response in C. scabra and produced an increased intensity of response in C. limatula. The activity pattern of C. limatula was demonstrated to be an effective mechanism for avoiding predation by Octopus sp., a

major visual predators of limpets, in both laboratory and field experiments. The homing habit of C. scabra was also shown to reduce the rate of predation in the laboratory. Fishes and birds, other visual predators, were also found to prey on limpets during the submerged and emerged portions of the tidal cycle respectively. It is suggested that the observed activity patterns have evolved in response to predation pressure from swift-moving predators which locate their prey visually.

INTRODUCTION

Observations of the intertidal region have been largely confined to periods of low tide emergence. As a result our understanding of biological interactions, especially predation, is based upon events observable during low tide emergence and upon deduction of events occurring during submergence periods (Paine, 1971, 1975).

Numerous predators of limpets have been reported on the California coast as well as in Britian and South Africa. The list of predators includes birds, rodents, crabs, gastropods, sea stars and fishes (see Branch, 1978 for review).

The primary mechanism demonstrated in limpets for avoiding invertebrate predators is a behavioral escape response elicited by certain gastropods and asteroids. It genreally consists of lifting the shell margin high off the substrate, a so-called "mushrooming", followed by accelerated movement or "running" (Bullock, 1953; Feder, 1959, 1963; Margolin, 1964; Yensen, 1973). A second type of response to invertebrate predators is an aggressive maneuver. The limpet's shell is elevated and then clamped down on the foot of the gastropod or tube feet of the asteroid. This generally results in the escape of the limpet (Stimson, 1970; Branch, 1979).

Such escape responses may be effective in nature for avoiding slow-moving, non-visual predators, but there is little to suggest whether and how limpets avoid predation by swift-moving visual predators. Bakus (1964) has advanced the idea that the cryptic habit of invertebrates in coral reef communities has evolved to this end.

In this investigation the foraging activity of two species of acmaeid limpets, Collisella limatula (Carpenter, 1864) and Collisella scabra (Gould, 1846) was observed over the diel cycle during both emergence and submergence of the intertidal zone. The adaptive significance of the observed activity patterns of these two species as a mechanism of predator avoidance was experimentally evaluated.

MATERIALS AND METHODS

Study site.

This study was conducted on the leeward side of Santa Catalina Island, California, U.S.A., in the rocky intertidal of Big Fisherman's Cove (latitude= $33^{\circ} 25.4' N$, longitude= $118^{\circ} 30.8' W$). This shore receives little wave action except from infrequent northwesterly storms occurring from December through April. Due to the lack of wave action, during most of the year turbulent water movement usually only occurs along a band approximately 0.5m in height at the edge of the tide. The lack of wave wave-shock makes it possible to observe the intertidal during submergence using snorkel and SCUBA. Water temperatures range from $13^{\circ}C$ in the winter to $24^{\circ}C$ in the fall.

The intertidal substratum consists of loose cobble with a few boulders. Rock types are sandstone, granite and rugose igneous rock. The seaward extent of the intertidal region is roughly 18m at a slope of approximately 15° . Low in the intertidal some rocks are stabilized by the calcareous tubes of the gastropod Serpulorbis squamigerous. Subtidally the substratum is largely a sand/mud mixture.

Measurement of intertidal height.

The tops of two boulders, one high and one low in the intertidal, were used as reference points for the measurement of intertidal height. The height of each rock was estimated by comparing the time of its submergence with plots of tidal flux from U.S. Coast and Geodetic Tide Tables, 1975. The intertidal height of other points was estimated using a line level with a sliding mount on a meter stick.

Vertical distribution.

The vertical distribution of Collisella limatula and C. scabra was examined in ten randomly located transects run perpendicular to the shoreline from the highest reach of the intertidal to zero datum. The number and length of all limpets found in 0.5m by 0.5m quadrats spaced at one meter intervals were recorded. Each quadrat was thoroughly searched and all movable rocks overturned.

Distribution and substratum type.

The numbers of Collisella limatula and C. scabra, relative to the type of substratum, were recorded in three 8.0m transects. 0.25m in width, run parallel to the shoreline through the mid-intertidal. Substrata were qualitatively classified as highly rugose (+++), smooth with cracks or pits (++) , and smooth (+).

Tagging.

Individual limpets were marked for identification in situ by the following procedure. Plastic lettering tape (Dymo Tape R) with a single letter or digit was cut into pieces approximately 4mm by 4mm. During low tide the shell was dried and an area the size of the tag

was filed flat. The tags were then glued to the shell using technical cement (Dekaphane R). Tags of this type remained attached up to six months.

Activity patterns.

Observation of the movements of *Collisella limatula* were made over 24 hours in ten permanently marked 1.0 m^2 quadrats located between +0.31m and +0.92m intertidal height. The number of limpets visible without overturning rocks, as well as light and tidal conditions, were recorded at one hour intervals. Limpets observed on the sides and tops of rocks were considered to be "active". This criterion for activity is justified because visible individuals were actively foraging while those on the undersides of rocks did not move; grazing marks from radulae were observed only on the tops and sides of rocks. The number of active limpets from all ten quadrats was pooled for each hourly observation and mean values were computed.

A different approach was necessary for *Collisella scabra* due the homing habit and shortness of activity period in this species. Preliminary investigation revealed that individuals of *C. scabra* moved from their home scars only during the awash period (i.e. the time interval during which the zone of turbulence accompanying the tide is present at a particular tidal height). Therefore, the interval between observations was shortened to 15 minutes beginning one hour before the sites were awash and continuing for one hour afterwards. Individuals not on their home scars were considered to be active.

Three relatively flat rocks, each rising 0.5m to 0.8m above the

surrounding substratum, were chosen for observation of the activity of *Collisella scabra*. The three sites were at intertidal heights of +0.92m (B), +0.62m (A), and +0.31m (E). By choosing sites at different heights tidal condition could be separated from time. Because the density of limpets differed between sites the number of active limpets was converted to a percentage of the population of each site. In addition, on several occasions the number of *C. scabra* active and inactive was recorded at different light and tidal conditions.

Foraging range.

The foraging ranges of *Collisella limatula* and *C. scabra* were determined by observing their movements during several periods of activity. Tagged individuals of *C. scabra* were followed on sites A and B. A cumulative map of the points of furthest displacement from the home scar during each activity period was plotted for each individual. Foraging range was taken as the greatest distance obtained by connecting points with a straight line passing through the home scar.

Estimation of the foraging range of *Collisella limatula* was complicated in that they live on cobble and move over a relatively large area. To avoid these problems and still provide some measure of the distance over which this species forages, foraging range was estimated on a large rock which had five individuals of *C. limatula* in a crevice at the base. Hash-marks were painted on the rock with marine enamel at 4.0cm intervals in four vertical and four horizontal rows forming a grid. To estimate distance of movement the position of each individual was recorded at ten minute intervals on site maps drawn on plastic

slates. In addition, 20 individuals of C. limatula, located in permanent quadrats in the cobble, were tagged and their movements observed. Due to the irregular nature of the cobble substratum the distance moved could not be accurately measured. Therefore their approximate position relative to the quadrat in which they were originally marked was noted.

Response to light, gravity, turbulence and tidal condition.

An acrylic plastic (Plexiglas R) aquarium (dimensions 88cm by 60cm by 30cm) with running seawater was fitted with a hood 60cm high and was used as a behavioral arena (Figure 1). The entire apparatus was made light-proof with black polyethylene film. A stage was constructed of 0.95cm thickness acrylic sheet measuring 80cm by 40cm. A 4.0cm by 4.0cm grid was scored on one side and filled with light colored paint. A coat of black epoxy paint was then applied over the light colored paint resulting in a light colored grid superimposed on a black background. The unpainted side was roughened with sandpaper to reduce light reflection. The stage could be positioned vertically or horizontally in the arena. A 100 watt tungsten light source with a reflecting shield was secured 50cm above and 16cm from one end of the horizontally positioned stage. The placement of the light source produced a gradient of light intensity on the stage surface. When the stage was vertically oriented the light source was directly over the middle and 50cm above the longitudinal mid-line. Water depth was maintained 20cm above the surface of the horizontal stage and the longitudinal mid-line of the vertical stage. Turbulence, simulating conditions

during the awash period of the tidal cycle, was provided by aeration with air-stones and by directing jets of water at the stage from above (Figure 1).

Limpets were collected at low tide emergence of the study site, placed in nylon mesh bags, and transported to the nearby laboratory where they were maintained in running sea water aquaria. All experiments were performed within 24 hours of collection and were run at the same time each evening. Thirty different individuals were used in three separate trials of ten each in for each experimental treatment. In each trial individuals were originally oriented perpendicular to the light intensity gradient in the middle of the stage with equal numbers facing oppositely. The arena was sealed at the start of each trial. After 30 minutes the arena was opened and the position of each individual with respect to the grid system was recorded. Thus, net displacement, rather than total distance of movement, was observed. Positions were recorded as -, indicating movement away from light; +, movement towards light; and 0, indicating no net displacement. It was arbitrarily decided that to receive a non-zero score it was necessary for an individual to be displaced more than two shell lengths from its original position. Response to light, gravity, submergence/emergence, and turbulence was tested under 12 different combinations of these factors. The results were expressed as presence or absence of movement and the direction of the movement. The data were analyzed using a chi-square goodness-of-fit test. The null hypotheses were no difference in the proportion of individuals moving or not moving and no directionality of movement.

Predator avoidance in the laboratory.

Octopus bimaculatus and/or O. bimaculoides were observed preying on Collisella limatula in the field, and holes drilled by these species were found in empty limpet shells. An experiment was performed in the laboratory to test whether the tendency of C. limatula to remain on the undersides of rocks during submergence by the tide is effective in avoiding predation by octopuses.

A pile of stones simulating the cobble found at Big Fisherman's Cove was placed in an aquarium. Twenty limpets were allowed to attach to the undersides of the stones. Another aquarium with 20 limpets but no stones served as a control. One octopus, collected 24 to 48 hours prior to the experiment from an area adjacent to the study site, was placed in each tank. A clump of algae was provided as shelter. The experiments were performed in an empty laboratory to avoid disturbance. The number of limpets consumed by the octopuses was recorded at 12 hour intervals and the experiment was repeated twice using different octopuses.

The effectiveness of homing to scars on the upper surfaces of rocks as a means of avoiding octopus predation was tested in Collisella scabra. Rocks with homed individuals were removed from the intertidal and placed in aquaria. Limpets placed on rocks lacking their home scars served as controls. The homed limpets were also removed from their home scars and replaced. The number of limpets consumed was recorded at six hour intervals. The rest of the procedure was the same as for the experiments with C. limatula.

Predator avoidance in the field.

The following experiment was performed to determine the effectiveness of the activity pattern of Collisella limatula in avoiding predators in the field. Fence enclosures or complete cages of galvanized hardware fabric (1.8cm mesh) measuring 25cm by 25cm were attached to boulders in the field using plastic screw anchors and stainless steel screws. There were three treatments: (1) fenced area on top of boulders; (2) fenced area on the undersides of boulders; and (3) caged area on top of boulders. There were three replicates of the fenced treatments and two of the cage treatments. Five individuals of C. limatula were placed in each enclosure. After 48 hours the number of limpets missing from each replicate was recorded. Five trials of the experiment were run over a 44 day period.

Predators.

The gut contents of five juvenile opaleye (Girella nigricans) and seven wooly sculpins (Clinocottus analis) observed feeding in the study site were examined. In addition, a list of actual and suspected predators of limpets was compiled.

RESULTS

Vertical distribution.

The distribution of both species of limpets with respect to intertidal height is presented in Figure 2. The highest extent of occurrence of both Collisella limatula and C. scabra was 1.3m above zero datum. Both species were relatively abundant in the lowest quadrat

censused. The vertical distributions of the two species did not differ significantly (Kolmogorov-Smirnov 2-sample test, $p = 0.05$, Tate & Clelland, 1957).

Distribution and substratum type.

The distribution of each species with respect to substratum type was significantly different when compared with a chi-square goodness-of-fit test (H_0 : no difference, $p = 0.05$). Collisella scabra was found primarily on the upper surface of highly rugose rocks and in cracks and pits on smoother rocks while C. limatula was found on the undersides of all rock types, but was more abundant on smooth rocks (Table I). There was a tendency for the bottoms of all rocks to be smoother than the upper surfaces, probably due to scouring by sand.

Foraging range.

The mean foraging range of Collisella scabra was 12.8cm (computed from a total of 145 forays by 33 individuals over 3 to 7 activity periods, S.E.=6.5). The foraging range of C. limatula was 50.7cm (12 forays, 5 individuals, 5 activity periods, S.E.=18.8). Tagged individuals of C. limatula were observed to move distances of up to 1.0m during nighttime low tide. The mean foraging distances of C. limatula and C. scabra differed significantly ($t=10.2$, d.f.=43, $p = 0.05$).

Activity patterns.

The average number of individuals of Collisella limatula observed to be active over six to seven 24-hour periods is presented in Figure 3. Individuals of C. limatula, when not active, were found in crevices

or on the undersides of rocks. Activity during the daytime was restricted to the awash period. No activity was observed during daytime low tide and only a small amount during the hour of submersion preceding the awash period (Figure 3). Nighttime activity commenced the hour before the awash period preceding low tide, peaked during emergence, decreased through the awash period following low tide, and ceased with submergence by the incoming tide. Activity was greater during the nighttime than during the daytime. There was a great deal of variability in the number of limpets active on any one occasion.

Figures 4a - c represent the activity of Collisella scabra over three separate 24-hour periods at each site. Individuals of C. scabra were found off their home scars only during the day and only while rocks were washed by the ebbing tide; none were found off their scars while submerged. In over two years of observations at all tidal and light conditions C. scabra was found to be completely faithful to this pattern.

Comparison among sites at different tidal heights on the same date shows activity to correspond to awash periods. Activity at the lowest site (E) occurred earlier on incoming and later on outgoing tides than at the higher sites (A and B). The duration of the awash periods was shorter on spring tides (maximum tidal excursion) resulting in generally less activity compared to neap tides (minimum tidal excursion). Site E was often exposed only once daily or not at all on neap tides.

Response to light, gravity, turbulence and tidal condition.

Collisella limatula and C. scabra both exhibit responses to light

and gravity although the magnitude of response and the conditions under which they are elicited are different for each species (Table II).

Collisella limatula was more responsive than C. scabra, demonstrating strong negative phototaxis and both negative and positive geotaxis under different conditions.

Individuals of Collisella limatula were negatively phototactic in the laboratory; a strong directional response was demonstrated under all experimental conditions (Table II). In the absence of light limpets submerged on the vertically positioned stage moved upwards until out of water showing negative geotaxis. However, when a light was shown from above the limpets moved downwards. Individuals of this species crawled downwards on the emerged vertical stage regardless of light conditions. On the horizontal stage there was no significant movement in the absence of light, however, the introduction of turbulence resulted in significant movement but in no particular direction.

Collisella scabra did not move except when submerged on the vertical stage and subjected to turbulence (Table II). With the light off there was a significant negative geotactic response; with the light on there was no statistically significant directional response.

Predators.

Evidence from collections of limpet shells, field experiments, and over 60 hours of direct underwater observation suggests that Collisella limatula is subject to considerable predation by octopuses. Three octopuses with lairs in the study site were frequently observed. On five separate occasions these individuals were found actively feed-

ing on C. limatula.

A total of 125 shells of Collisella limatula were collected from the study site, 53 (42%) of which could be identified by holes drilled in their shells as having been victims of octopus predation (Wodinsky, 1960). The actual number of individuals consumed by octopuses is likely to be higher since Octopus also captures limpets by prying them from the substratum with their beaks (personal observation). Damage to shell margins resembling that found in shells of limpets eaten by Octopus bimaculatus in the laboratory was present in 82% of the shells collected.

Several other actual and suspected predators of limpets occurred in the study site (Table III). The most common of these were the fishes Clinocottus analis, Girella nigricans, and Hypsoblennius sp. The gut contents of the juvenile G. nigricans (std. length= 69 - 125mm) were filled almost exclusively with plant material and an occasional mysid or amphipod. The guts of the adult Clinocottus analis were found to contain one Collisella limatula (length=3mm), one Collisella strigatella (length=5mm) and four chitons in a partially digested state (3 - 6mm). Hypsoblennius were not collected because they occurred in small numbers. Other species of fish known to prey on molluscs (Pimelometopon pulchrum, Embiotica jacksoni, and Gibbonsia elegans) were also present. The sea stars Astrometris sertulifera and Pisaster giganteus, which readily fed on limpets in the laboratory, were also found in the study site. No species of predatory gastropods were present. The gulls Larus sp. and Arenaria sp. were frequently observed preying on limpets at low tide, after which freshly broken

shells with adhering flesh were collected.

Predator avoidance in the laboratory and field.

Individuals of Collisella limatula which remained on the undersides of rocks effectively avoided predation by octopuses for 72 hours. Only three of 40 limpets were consumed in the experimental treatment in contrast to 39 of 40 in the controls (Table IV). Homed individuals of C. scabra were eaten more slowly than non-homed controls; twice as much time (24 hours) was required to consume all of the experimental animals compared to the controls (12 hours).

In the field experiments significantly greater numbers of Collisella limatula were missing from enclosures on the upper surfaces of rocks than from underneath (Table V, $p < 0.05$, Mann-Whitney U-test). Throughout the trials all but three individuals in the total enclosure treatment survived. The shells of the non-survivors were too large to be removed through the mesh and bore drilled holes identifying octopuses as the predators.

DISCUSSION

Light and gravity have been repeatedly demonstrated to be cues for the orientation of animals (Fraenkel & Gunn, 1961). Response to light and gravity in other intertidal invertebrates, including reversals in taxes mediated by tidal conditions (Bock & Johnson, 1967), have been shown to be factors in orientation relative to the shore (see Segal, 1970 for review). For Collisella limatula and C. scabra it appears that turbulence is an important external cue in initiating movement

both in nature and in the laboratory.

The intensity and combinations of the factors of light, gravity, turbulence, and emergence/submergence necessary to elicit responses in the laboratory probably reflect the respective adaptive responses of these two species in nature. Over the course of the tidal cycle Collisella limatula undergoes a migration from the undersides of rocks to the upper surfaces and back to the undersides again, changing its orientation to light and gravity in the presence of turbulence accompanying the awash period. The laboratory experiments demonstrate that both C. limatula and C. scabra move in response to light and gravity stimuli and that upward movement in darkness (negative geotaxis) is reversed or ceases when light is introduced from above. Movements in the field may be interpreted as an interplay of these taxes in which reversals of responses or changes in a hierarchy of response strengths may occur. C. limatula migrates to the tops of rocks during the advancing awash period in light or in darkness and remains on top through the nighttime emergence period. With approaching daylight this species migrates back to the undersides of rocks during the advancing awash period in what may be termed positive geotaxis and/or negative photaxis. During the daytime C. limatula migrates upwards on the advancing and retreating awash periods, and returns to the undersides of rocks by the time the area is submerged or emerged. This may be explained as a change in response from positive phototaxis and/or negative geotaxis to negative phototaxis and/or positive geotaxis. Another equally likely possibility exists that only two directional responses exist, such as negative geotaxis and negative phototaxis,

but that the direction of movement is determined by domination of one response by the other, the hierarchy of which is mediated by an external cue or intrinsic rhythm. Because the responses or taxes are defined relative to stimuli which cannot be manipulated independently in the field, it is not possible to distinguish between these mechanisms. Some support for both mechanisms is present in the result of the laboratory experiments with C. scabra, in which movement occurred only when turbulence was introduced. With this external stimulus C. scabra moved in the presence of light but with no apparent photaxis, but in darkness was negatively geotactic. In this case it appears that in light the geotactic response ceases and that geotaxis is only expressed when turbulence is present. Collisella limatula also responded with a significant amount of movement in the presence of turbulence but lacked directionality in the absence of light and gravitational stimuli. The conditions under which C. scabra responds in the laboratory partially reflects its natural habits. This species is found on the relatively horizontal upper lighted surfaces of rocks, and may not use light for orientation of movement to the degree that C. limatula does; movement occurs only during the daytime awash periods. The reason for movement and geotaxis in darkness in the laboratory in the context of this species natural behavior is not aparent. It is possible that geotaxis is a part of the repertoire of response of limpets but is not expressed in an obvious manner in all species.

The failure to produce reversals of taxes in the laboratory such that the entire activity pattern of these species can be reproduced may be due to handling effects, the disturbance of a biological

rhythm, or other extrinsic factors, such as depth, not examined in this study. The strong possibility also exists that the behavior of limpets is too complex to be interpreted simply in terms of an interplay or hierarchy of taxes.

The observed activity pattern of Collisella limatula was, in some respects, similar to that observed by Eaton (1968), however, in his study activity was lowest during nighttime emergence. Brant (1950) found C. scabra to be also be active at night, although to a lesser extent than during the daytime. These differences may be a function of topography and/or other physical conditions. Both investigators worked in sites exposed to considerable wave action, while Eaton's (1968) population was located on a flat vertical granite face.

The results of this investigation suggest that intertidal limpets are subject to a considerable amount of predation from swift-moving visual predators and that the activity patterns of Collisella limatula and C. scabra are effective mechanisms for reducing predation. Both species use physical refuges and are inactive during periods when their predators are most active; foraging takes place only when predators are absent or less active due to wave action. The forms of refuge differ between the species; C. limatula stays out of sight while C. scabra remains visible but returns to a home scar from which removal by a predator would be difficult.

Results of the laboratory experiments with octopuses, which are primarily visual predators (Young, 1964), are assumed to be representative of those which would be obtained using other visual predators such as fish and birds. In the field experiments predators are pre-

sumed to be responsible for the disappearance of limpets. Support for this hypothesis is lent by the results of the total enclosure treatment in which octopuses were positively identified as the predators. These results do not preclude the possibility that other species of predators may have contributed to the loss of limpets from the fenced treatments. Hypsoblennius as well as Clinocottus analis are both reported to prey on limpets (Mitchell, 1953; Stephens, et al, 1970) (Table III). Juvenile Girella nigricans are suggested to be carnivorous (Williams & Williams, 1957), appeared in this case to ingest animals only incidental to feeding on algae. Birds are also confirmed as including limpets in their diets at other localities (Giesel, 1970; Branch, 1978). An indication of the desirability of limpets as prey items for octopuses come from observations of octopuses crawling out of the water to feed on limpets foraging at night.

Results of this and other studies support the general hypothesis that the activity patterns of many marine invertebrates have evolved as predator avoidance mechanisms due to selective pressure from swift-moving predators which locate their prey visually. Slower moving predators allow prey the opportunity to escape by response to individual encounters. Escape from faster moving predators is best effected if safe-refuge is accomplished prior to the predator's presence.

Ebling et al (1966) have presented experimental evidence which supports a model of predator mediated diurnal migration in the intertidal region of Lough Ine, Ireland. Invertebrates, representing two levels in a food chain, migrate between the tops and bottoms of boulders such that the activity of individuals on one level occurs when

members of the higher level are scarce or absent. In this system periodicity is set by swift-moving visual predators (birds) which prey on crabs (Cancer, Portunus, and Carcinus) which in turn prey on urchins (Paracentrotus) and snails (Gibbula).

Several authors have suggested that the activity patterns of subtidal echinoids are a response to fish predation (Lawrence, 1975). Experimental evidence has been provided by two recent investigations. Glynn et al (1979) observed that the urchin Eucaridaris thouarsii is smaller, less abundant, and has more cryptic habits in Ecuador and Panama, where it forages nocturnally on reefs, than in the Galapagos Islands where it forages during the daytime. Experimentally they demonstrated that more intense fish predation in Panama and Ecuador may account for these differences. In southern California, Nelson and Vance (1979) have shown that the diademid urchin, Centrostephanus coronatus, avoids a strictly diurnal predatory fish, Pimelometopon pulchrum, by feeding at night and maintaining a protected position in crevices during daylight hours.

Examination of predator-prey relations in the intertidal zone during submergence will no doubt yield other examples of predator influenced invertebrate activity patterns. However, in the case of intertidal organisms, the physical factors of radiant heating and desiccation present an alternative hypothesis to explain the emergence portion of the observed activity patterns.

It has long been assumed that resistance to high temperatures and/or desiccation is limiting the intertidal distribution of limpets and other invertebrates (see Newell, 1970 for review). However,

Wolcott (1973) presents evidence that limpets may behaviorally avoid physically stressful conditions. Based on three years monitoring of the microhabitat conditions of five species of Collisella, he reported that temperatures never reached the physiological limits determined in laboratory stress experiments and that desiccation only limits those species that occur high on the shore. He therefore concluded that by selecting suitable microhabitats limpets behaviorally avoid conditions approaching their tolerance limits. This conclusion is open to the criticism that rare events, during which physical conditions exceed tolerance limits, may occur less frequently than every three years. It does, however, provide evidence of behavior being influenced by physical conditions during emergence. I have observed individuals of C. limatula, when placed on a warm rock, to respond by crawling downwards until reaching a shaded vertical surface, as has also been reported by Segal (1956). A response of raising the shell off the substratum and crawling downward during radiant heating was also seen by Segal & Dehnel (1962). Whether or not the observed activity patterns are ultimately in response to physical stress has not been shown since physical factors could also function as cues as for avoidance of predators.

Homing has been suggested as a mechanism to reduce the desiccation rate of Collisella scabra because the shell margins conform closely to the surface of the home scar (Collins, 1976). Collisella digitalis, a smaller species which sometimes homes (Galbraith, 1965; Villet & Groody, 1940), has been shown to produce a mucous barrier between the shell and substratum effective in slowing desiccation

(Wolcott, 1973). Seeking refuge from thermal stress by returning to a home scar or crawling to the underside of a rock prior to emergence may both be selected for as a result of physical factors.

An attractive hypothesis would hold that both physical factors and biological interactions are acting in concert to select for the activity patterns of these two species. While an hypothesis of selective pressure from predation seems sufficient to explain the submergence portion of the limpets activity pattern, obviously physical factors are also important during emergence of the intertidal zone and must be included in the hypothesis until proven otherwise.

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APPENDIX A

TABLES

Table I

The distribution of Collisella limatula and C. scabra with respect to substratum type in Big Fisherman's Cove. Three 8.0 m transects were run horizontally through the mid-intertidal zone. Substratum was classified as highly rugose (+++), smooth with cracks and pits (++) , and smooth (+). The distribution of both species with respect to substratum differed significantly ($p < 0.05$, Chi-square test).

	Substratum		
	<u>+++</u>	<u>++</u>	<u>+</u>
No. <u>Collisella scabra</u>	149	80	0
No. <u>Collisella limatula</u>	14	74	37

Table II

Summary of the responses of Collisella limatula and C. scabra to various combinations of light, gravity, submergence, emergence, and turbulence. L= light, D= dark, V= vertical stage, H= horizontal stage, + = turbulence, - = no turbulence. Chi-square test, H_0 : no difference between numbers moving or not moving (movement) and no directionality of movement (phototaxis, geotaxis).

Collisella limatula

CONDITIONS	MOVEMENT	p<	GEOTAXIS	PHOTOTAXIS	p<
S-HL	yes	0.001	-	neg.	0.001
S-HD	no	n.s.	-	-	-
S-VL	yes	0.001	pos.	neg.	0.001
S-VD	yes	0.001	neg.	-	0.001
S+HL	yes	0.001	-	neg.	0.001
S+HD	yes	0.025	-	-	-
S+VL	yes	0.001	pos.	neg.	0.001
S+VD	yes	0.001	neg.	-	0.001
E-HL	yes	0.005	-	neg.	0.001
E-HD	no	n.s.	-	-	-
E-VL	yes	0.001	pos.	neg.	0.001
E-VD	yes	0.005	pos.	-	0.001

Table II (continued)

Collisella scabra

CONDITIONS	MOVEMENT	p<	GEOTAXIS	PHOTOTAXIS	p<
S-HL	no	0.001	-	-	-
S-HD	no	0.001	-	-	-
S-VL	no	0.001	-	-	-
S-VD	no	0.01	-	-	-
S+HL	no	0.001	-	-	-
S+HD	no	0.001	-	-	-
S+VL	yes	0.025	-	n.s.	0.10
S+VD	yes	0.001	neg.	-	0.05
E-HL	no	0.001	-	-	-
E-HD	no	0.001	-	-	-
E-VL	no	0.001	-	-	-
E-VD	no	0.001	-	-	-

Table III

Predators of limpets. Species observed in the study site in Big Fisherman's Cove which are reported to prey on limpets,

Species

Invertebrates

<u>Octopus</u> spp.	this study
<u>Pisaster</u> <u>ochraceus</u>	Bullock (1953); Feder (1959); Margolin (1964)
<u>Astrometris</u> <u>sertulifera</u>	this study
<u>Pachygrapsus</u> <u>crassipes</u>	Chapin (1968)
<u>Panulirus</u> <u>interruptus</u>	Engle (1979)

Vertebrates

<u>Clinocottus</u> <u> analis</u>	this study
<u>Embiotica</u> <u>jacksoni</u>	Coyer (pers. comm.)
<u>Gibbonsia</u> <u>elegans</u>	Mitchell (1953)
<u>Girella</u> <u>nigricans</u>	Williams & Williams (1957)
<u>Hypsoblennius</u> spp.	Stephens <u>et al</u>
<u>Larus</u> spp.	Giesel (1970); this study
<u>Arenaria</u> sp.	Branch (1878); this study

Table IV

Laboratory predation experiments. The number of limpets consumed by Octopus over time is indicated. Collisella limatula were attached to the undersides of rocks and C. scabra were homed to scars on the tops of rocks. Controls lacked rocks or rocks with home scars respectively. One octopus and 20 limpets were used in each treatment and no individual was used more than once.

Collisella limatula

Treatment	Elapsed Time in Hours					
	<u>12</u>	<u>24</u>	<u>36</u>	<u>48</u>	<u>60</u>	<u>72</u>
A Experimental	0	1	0	0	0	0
A Control	7	12	0	1	-	-
B Experimental	0	0	2	0	0	0
B Control	12	8	-	-	-	-

Collisella scabra

Treatment	<u>6</u>	<u>12</u>	<u>18</u>	<u>24</u>	<u>30</u>	<u>36</u>
A Experimental	11	5	2	2	-	-
A Control	20	-	-	-	-	-
B Experimental	5	7	6	1	0	1
B Control	14	4	0	0	0	0

Table V

The number of individuals of Collisella limatula missing from an initial number of five per replicate. Dashes are missing replicates. Treatments are fence enclosures attached to the tops and bottoms of boulders in Big Fisherman's Cove. Significantly greater numbers were missing from the top treatment (Mann-Whitney U-test, $p < 0.05$).

Date	Treatment	
	<u>Top</u>	<u>Bottom</u>
10 March 1979	3	0
	5	3
	2	-
14 March 1979	2	0
	1	0
	5	-
20 March 1979	0	0
	1	0
	5	-
19 April 1979	2	0
	2	0
	1	2
22 April 1979	2	0
	2	0
	1	3

APPENDIX B

FIGURES

Figure 1. Behavioral arena. An aquarium with running seawater made light-proof with a black plastic hood. The light source is positioned above and water turbulence is provided by aeration with air-stones and jets of water directed downwards. The stage can be positioned either vertically or horizontally.

Figure 2. The vertical distributions of Collisella limatula and C. scabra in the intertidal region of Big Fisherman's Cove, Santa Catalina Island. Bars represent the percentage of individuals of each species in ten 0.25 m² quadrats at different intertidal heights.

Figure 3. The activity pattern of Collisella limatula in Big Fisherman's Cove. Points represent the combined number of individuals active in 20 permanent 1.0 m² quadrats between +0.31 and +0.92 m intertidal height over six to seven 24 hr periods. Hours preceding and following emergence are indicated. S= submergence, E= emergence, A= awash period. Bars indicate the standard error of the mean.

Figures 4a-c. The activity pattern of Collisella scabra at three sites in the intertidal region of Big Fisherman's Cove over three separate 24 hr. periods. Intertidal heights of sites: B= +0.92m; A= +0.62m; E= +0.31m. Bars represent the percentage of the population active or off home scars. Light conditions are indicated by light and dark bars. See Figure 3 for an explanation of symbols.

Collisella scabra