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A CRITICAL REVIEW OF HOMING AND FORAGING BEHAVIOR IN LIMPETS
(MOLLUSCA; GASTROPODA): A CENTURY OF OBSERVATIONS, EXPERIMENTS,
AND CONTROVERSIES (1894 TO 2001)

by

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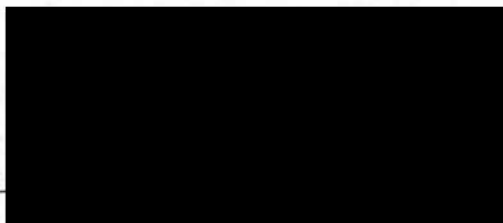


TABLE OF CONTENTS

Chapter	Page
I. INTRODUCTION	1
II. NATURE AND ORIENTATION OF LIMPET CLUSTERS	5
III. FACTORS INITIATING LIMPET MOVEMENTS	14
IV. NATURE OF OUTWARD AND RETURN MOVEMENTS	21
V. CONTROVERSIES REGARDING HOMING MECHANISMS	37
VI. ABIOTIC AND BIOTIC FACTORS AFFECTING FORAGING	45
VII. RECENT METHODOLOGICAL ADVANCES	61
VIII. CONCLUSIONS AND PROPOSAL	74
BIBLIOGRAPHY	90

List of Tables

Table	Page
1. Summary of records of homing behaviour in various limpets	6
2. Summary of activity rhythms in limpets15
3. Travel distance summary in various homing limpets. . .	.34
4. Summary of travel speeds in various homing limpets . .	.35

List of Figures

Figure	Page
1a. Examples of consecutive foraging excursions of two <i>Patella vulgata</i> on a vertical wall at Menai Bridge (Anglesey)	21
1b. Representative sample of foraging excursions undertaken by <i>Siphonaria pectinata</i> at Gibraltar	22
2. The tracks of all limpets on a single plot on a single night between 03.30 and 05.00 BST	25
3. Different excursions (A-C) performed by the same limpet on three different nights.	26
4. Foraging directions shown by <i>Patella vulgata</i> at a) Menai Bridge and b) Porthoustock	26
5. Individual mean directions (circles) and pooled frequency distribution (solid line, scale on the horizontal axis) relative to the directions taken by the limpets on leaving the home scar	27
6. Return track obtained by triangulation between 02.10 and 05.52 BST showing that a limpet need not necessarily follow its outward trail in order to home	38

7.	Frequency-distribution of Total Length (TL) and Total Duration (TD) at spring and neap tides50
8.	<i>Patella vulgata</i> at 2 shores. Level of gonad development and grazing activity in mid-shore populations on the Isle of Man	60
9.	Arrangement of the equipment used to record the 'home-away' status of limpets63
10.	Cross-section of plastic screw cover showing (a) technique for filling with wax, (b) cross-section of disc assembly, and matching recess in the bedrock on the shore68
11a.	Mean chlorophyll a concentrations on rock chips from 2 exposed rocky shores at each of 3 locations over 15 mo	71
11b.	Mean chlorophyll a concentrations on rock chips at 3 locations for each of 2 seasons, summer and winter72
12a,b	Chlorophyll a density at various distances from the cluster center of <i>L. digitalis</i>	81
13a,b,c	Chlorophyll a density at various distances from the cluster center of <i>L. digitalis</i>83
14.	Configuration of cores and/or wax disks in the field, where disks are 12 mm in diameter and 3 cm apart	84
15a-f	Chlorophyll a density at various distances from the cluster center of <i>L. digitalis</i>88-89

Chapter I

Introduction

Homing limpets are characterized by their predictable stationary resting behavior in their home territory during periods of inactivity, followed by active feeding excursions ranging up to a few meters away from home. They almost always return to their previous resting spot (home scar) during a tidal cycle. Limpets are grazers that use their radula to scrape and feed upon microalgae, macroalgal settlers, bacteria, cyanobacteria, diatoms and other phytoplankton, and animal larva that settle inside their grazing grounds, called the feeding arena.

Home scars lie within the feeding arena and vary according to species. Most limpets live on rock, some live on macroalgal fronds, and some even live on the shells of other gastropods. Some home scars are visible as a chiseled indentation in rock that fits the shape of the limpet's shell perfectly. This depression is caused by the repeated scraping of the returning limpet's shell at the home scar. Other homing limpets do not make a strict scar, rather, they home to a region rather than a spot. Certain homing limpets will join clusters of conspecifics, returning to roughly the same position within the cluster from day to day.

The habitat of homing limpet species ranges from tide pools in the lower intertidal, to the high intertidal where only tidal splashing occurs. Homing species exhibit a wide range of foraging behaviors. Some feed only during the day or night, or both, while some feed during high or low tide only, or during both. It is not known why limpets exhibit homing and clustering behaviors, though it has been speculated it is due to avoidance of high temperatures, salinity fluctuations, desiccation risk, predation avoidance, or possibly a combination of these factors. In high intertidal zones, limpets are physiologically challenged by desiccation, thermal fluctuations, sudden salinity changes (rain and evaporation), and also encounter predatory organisms such as oyster catchers and other birds. In lower intertidal zones, limpets are confronted with predation risk, from crabs, starfish, whelks, and fish. Perhaps the alteration of feeding with homing/resting behaviors is the evolutionary result of limpets attempting to avoid mortality pressures. The mechanism by which they find their way home is also not clear, and will be discussed in detail here.

Homing limpets play important roles in structuring communities in the rocky intertidal. As grazers, they crop microalgae and maintain a short biofilm within their territories. Settling larvae are eaten or pushed off the territory. Farrell (1988) has experimentally demonstrated that

in the absence of grazing limpets, there is a rapid increase in the density of macroalgae, barnacles, and sessile organisms. Branch (1981) and Hawkins and Hartnoll (1983) wrote more detailed descriptions of the effects of limpets in structuring communities, in which green algae blooms first in the absence of limpets, followed by *Fucus*, which eventually thickens into dense clumps. *Fucus* spp. are of special interest in relation to limpet grazing. It was found that in the absence of limpets, *Fucus* can grow and exist higher in the intertidal zone. Southward and Southward (1978) even proposed a cyclic relationship between limpets and *Fucus*, in which *Fucus* promotes limpet settlement and growth, followed by a reduction of *Fucus* over time as limpets grow and graze upon the holdfasts, thus opening up more room for *Fucus* settlement and growth.

Geographically, different limpet species have varying effects on algal growth so one cannot over generalize their roles in structuring intertidal communities. Limpet species on a geographic scale exhibit varying methods of grazing, and are spread over a wide tidal range, so their grazing effects on algae settlement and growth will certainly not be identical from one place to the next. For example, *Cellana tamoserica* is able to suppress macroalgal development, but *Siphonaria* (a pulmonate limpet) species cannot do so successfully due to different feeding techniques and shore height dynamics of algae growth

(fast growth rates on low shore, slow growth rates at high shore). In low intertidal zones, feeding rates of limpets may not always exceed algal growth rates (Branch 1981). Limpets can affect microalgae growth and density on shores too, as Castenholz (1961) determined in caging experiments of *Acmaea digitalis* (= *Lottia digitalis*, all *Acmaea* now are *Lottia*) at high and low intertidal levels, in which *L. digitalis* was able to keep upper intertidal caged areas diatom-free.

Interestingly, while limpet grazing may set the upper limit of algae zonation for some species, algae may determine the lower limit of limpet zonation for some limpets. Creese (1978), for example, found that if the limpet *Patella lastistrigata* is placed in cleared patches in the lower intertidal, it will soon be outcompeted by fast growing *Ulva*. Other studies which discuss limpet roles in structuring communities include Branch (1985), Branch and Barkai (1988), and Liu (1993).

In this paper I will review the literature on limpet homing behavior from the 1960s to present. This will include summaries of experiments studying clustering and hypothesized homing mechanisms as well as many observational and manipulative studies of homing behaviors from a variety of limpet species around the world. There will be a slight emphasis on recent techniques for studying homing limpets.

Chapter II

Nature and Orientation of Limpet Clusters

Homing limpets return to their home scar and/or cluster of conspecifics (clusters defined as three or more limpets resting in contact with one another), usually as the tide ebbs. The percentage of limpets that home with each tide varies between studies, resulting in ambiguity as to whether or not a certain limpet species homes. For example, Miller (1968) and Willoughby (1972) found that *L. digitalis* homes 25% of the time while Gailbraith (1965) found that *L. digitalis* homes 54% of the time. Millard (1968) observed clusters of *L. digitalis* daily, and found that only half the original tagged limpets remained with the cluster after 1 month. Frank (1964) argues that *L. digitalis* does not exactly home, but rather, has a home range; an idea that is also supported by Breen (1971) and Connor (1986). Such differences in observations could be due to the short duration of most studies, or local effects. See Table 1 below for a summary of homing frequencies in various homing limpet species (From Branch 1981).

Table I Summary of records of homing behaviour in various limpets

Species	Zonation	Author	Result
<i>Patella depressa</i>	Low to mid	Cook <i>et al.</i> , 1969	Rigid homing
<i>P. aspera</i>			
<i>P. vulgata</i>	Mid to high	Morgan, 1894 Russell, 1907 Loppens, 1922 Orton, 1929 Bree, 1959 Cook <i>et al.</i> , 1969	Rigid homing Small animals often do not home Changes scar if food short or rock crumbles Smooth or wet substratum reduces homing Rigid homing Rigid homing and tidal rhythms of movement
<i>P. granularis</i>	Mid to high	Stephenson, 1936 Branch, 1971	Homing occurs Homing most rigid in high shore
<i>P. granatina</i>	Mid	Branch, 1971	Has homing behavior
<i>P. oculus</i>	Mid	Branch, 1971	Larger animals have a home scar
<i>P. longicosta</i>	Low	Branch, 1971, 1975c	Rigid homing: territorial behaviour
<i>P. tabularis</i>	Subtidal	Stephenson, 1936	
<i>P. cochlear</i>	Very low	Branch, 1971, 1975b,c	Very rigid homing. Adults territorial and rotate on scar to feed
<i>P. argenvillei</i>	Low	Branch, 1971	Well-developed scar
<i>P. barbara</i>	Low to subtidal	Branch, 1971	Poorly defined scar often random orientation on scar
<i>P. miniata</i>	Subtidal	Branch, 1971	Scar poorly defined and only in adults
<i>P. compressa</i>	Subtidal	Branch, 1971, 1975c	Homing well developed in adults on kelp stipes
<i>Notoacmea persona</i>	Low to mid	Richardson, 1934; Villem & Groody, 1940	No homing
<i>Collisella testudinalis</i>	Low	Wells, 1917	Indefinite results
<i>C. scabra</i>	High	Villem & Groody, 1940 Hewatt 1940 Wells, 1917 Jessee 1968	Large animals home rigidly Rigid homing. Animals <6 mm do not home Indefinite results 95% homed rigidly
<i>C. digitalis</i>	High	Gailbraith, 1965 Frank, 1964 Villem & Groody, 1940	54% homing No homing to a scar, but a 'homing range' No definite homing
<i>C. pelta</i>	Low-mid	Villem & Groody, 1940	No homing
<i>Notoacmea scutum</i>			
<i>N. petterdi</i>	Very high	Creese, 1980c	Very rigid homing.
<i>Lottia gigantea</i>	Mid-high	Richardson, 1934 Gailbraith, 1965 Stimson, 1970	No homing 75% home rigidly Large animals territorial, home rigidly
<i>Cellana tramoserica</i>	Low-high	Underwood, 1977 Mackay & Underwood 1977	Both homers & non-homers in the population Proportion homing related to food availability
<i>C. exarata</i>	Mid-high	Kay & Magruder, 1977	High-shore animals home; low-shore do not
<i>C. nigrolineata</i>	Mid-high	Hirano, 1979a	Homing more rigid on exposed rocks than in crevices
<i>C. toreuma</i>	Mid	Hirano, 1979b	No home scar
<i>C. ornata</i>	High	Beckett, 1968	Animals > 12 mm home to scar
<i>C. radians</i>	Low-mid	Beckett, 1968	No homing
<i>Nacella concinna</i>	Subtidal-low	Walker, 1972	No homing

Many studies have involved tagging and then recording limpet resting positions during low tide. Willoughby (1972) found that *L. digitalis* sometimes shuffle positions in the cluster on different days, as did Villee and Groody (1940). Willoughby (1972) found that 20% of marked *L. digitalis* returned to their original cluster. The clusters' memberships were remarkably stable during the study. Furthermore, while clustering, limpets had a slight tendency to orient with heads pointing downwards; 85% of these *L. digitalis* clustered in contact with other limpets (Willoughby 1972).

Millard (1968) and Willoughby (1972) also noted that *L. digitalis* oriented with anterior portions downward and to the right while resting in clusters. Millard (1968) studied this phenomenon by marking grids on rocks and following the positions of *L. digitalis* at low tides (she tried observing at high tide, but the water was too rough) daily for a week, then at intervals of one to seven days for an additional 32 day period. She found that a cluster of *L. digitalis* shifted its position daily, but the position of the cluster overlapped the position occupied the previous day. Membership of the clusters varied daily, and she concluded that the clusters of *L. digitalis* remained constant but membership within the cluster changed slightly over time (Millard 1968).

Similarly, Miller (1968) also observed clustering behavior of *L. digitalis* at low tides and paid special attention to orientation direction while at rest. Over a three day observation period during low tides, there was a clear tendency for *L. digitalis* to orient with its head downwards (from four to seven o'clock positions). This is therefore a common observation for this species, though no one has yet determined why this orientation behavior occurs.

Another common observation is that limpets will not always home precisely back to their starting point. Craig (1968) found that over a four day period, only four out of 16 *L. digitalis* returned home. Eaton (1968) observed 13 *Lottia limatula* for 45 hours straight, recording positions once every 1.5 hours. Nine of thirteen *L. limatula* homed in one location while one of 13 homed in another. Villee and Groody (1940) watched homing of different *Lottia* species, and only 29 of 102 homed. Hewatt (1940) reported that *Lottia scabra* (= *Macclintockia scabra*) homes regularly. Earlier, Russell (1907) recorded homing consistency of *Patella* in Britain, and Stephenson (1936) recorded homing of *Patella granularis* in Africa, both of which consistently homed. In most homing limpet species, homing has been well studied over short periods, but not over long term periods (> 6 months to years); In fact, there are no homing studies yet which were carried out continuously for more than 15 months.

There are few descriptions of circumstances in which normally homing limpet species do not home. Orton (1929) (in Santina *et al.* 1994), for example, found that *P. vulgata* do not home on smooth, wet rock surfaces during low tide. Lewis (1954) found no homing of another homing species on a smooth concrete breakwater, suggesting that homing is normal in most circumstances, but not on places where the limpet's shell fits anywhere. This observation agrees with the hypothesis that homing avoids desiccation and displacement on uneven substrates (Cook *et al.* 1969). Breen (1971) states that such instances of non-homing and other discrepancies in the descriptions of homing behavior could be due to differences in study methodologies. Studies performed with limpets on different types of substrate may yield different behaviors. Other factors that could be affecting homing include animal size, time of tide, duration of observations, tidal elevation, population density, and angle of substrate (Collins 1977). Food density is a seldomly mentioned factor that may affect homing behavior.

Willoughby (1972) states that there have not been any previous studies describing contact behavior in clustering limpets. Often, clustering limpets will make physical contact (using their tentacles) with other conspecifics before moving into a clamped, stationary position within their cluster. To separate chemical cues from physical cues as having roles in

facilitating clustering behavior, Willoughby (1972) created dummy clusters of empty *L. digitalis* shells (boiled to remove all traces of tissue), some with and without plaster of Paris filling. These false clusters were placed in close proximity to other real limpet clusters and observed for ten days. No limpets clustered with the false clusters. He also noted that no one specific part of the animal or shell appeared to be preferentially in contact with the shells of other limpets. He suggested that rock topography, and contact with other limpets within the cluster determine resting orientation.

Willoughby's (1972) results seem inconclusive, however, because 10 days is much too short a period to wait for new limpet immigrants. No other studies since then have addressed the nature and importance of physical contact or chemical cues to clustering. It is not clear whether limpet chemical cues, or physical contact with conspecifics (or both) determine resting position of limpets while at rest in a cluster.

Reasons for homing

The reasons for homing remain unclear, though many hypotheses exist. It is likely that different species may home for different reasons. Cook (1969) suggests that homing is a likely response to desiccation, while Wells (1980) suggests

predation, MacKay and Underwood (1972) propose food availability, Creese and Underwood (1982) suggest competition, and Cook (1976) suggests wave action and sand scour influence homing (in Branch and Cherry 1985).

It is unlikely that homing has evolved as an escape mechanism from predation, but may rather be a response to desiccation and avoiding wave action. Branch and Cherry (1985) studied *Siphonaria capensis* in South Africa. This homing limpet lives in intertidal pools and is active during day and night low tides. Some also live higher in the intertidal, and when they are exposed to air, are only active during nocturnal or late evening low tides. Experimentation demonstrated that desiccation avoidance drives the higher limpets to move only during darkness, while limpets in lower pools return home regularly in order to avoid osmotic stress when pools evaporate in the day or when rain falls. If too much fresh water floods into a pool, the limpet's foot will become turgid and swollen, causing the limpet to lose its grip from a rock (Branch and Cherry 1985). If the limpet has homed and clamped tightly onto a rock, thus creating a seal, then freshwater cannot surround the limpet's foot and produce osmotic stress. Osmotic stress may therefore encourage homing behavior in this species in the lower intertidal. This demonstrates that desiccation is not the sole reason for homing in all limpet species, otherwise limpets which

live in tide pools would have no reason to home, yet, *S. capensis* in pools do home. Also, the fact that some limpets are active at low tide also eliminates desiccation as the main reason for homing in some homing limpet species (Branch and Cherry 1985).

Most limpets are prosobranchs, which contain gills and breathe dissolved oxygen in water. However, some limpets, such as *Siphonaria spp.*, are known as pulmonate (or false) limpets. These limpets do not possess gills, but rather breathe air, though some have secondary gills that allow them to remain submerged for certain periods. Some can also trap air in the mantle cavity to breathe when later submerged. Some *Siphonaria* live in pools and are submerged the majority of the time, while other individuals live higher upshore in the intertidal on rocks and are exposed to air at low tide (Branch and Cherry 1985). Due to the differences in respiratory anatomy between Prosobranchs and Pulmonates, these limpets may behave differently. For example, *Siphonaria* is often most active when exposed to air at low tide, since this is when they can breathe, where as gill-breathing Prosobranchs are usually active at high tide when submerged. These behavioral differences will be taken into consideration when comparing Pulmonate feeding and homing behaviors to Prosobranch behaviors.

Branch and Cherry (1985) state that *S. capensis* is poorly attached to the rock, and is vulnerable to being swept away by waves while it is moving. This is probably another reason why these pulmonate limpets only move when exposed at low tide. Furthermore, it is unlikely that predation has influenced evolution of homing behavior in all homing limpet species, since *S. capensis* excretes a mucous that repels its terrestrial and marine predators (oystercatchers and clingfish), thus minimizing predation stress; yet it still homes.

The research of Verderber et al. (1983) as well as many others support the idea that desiccation is an important factor influencing homing behavior. In their study, *S. alternata* were deprived of their home scar, and lost 60% of their body water in five hours. In contrast, limpets that were allowed to home to their scar only lost 47% of their body water in 5 hours. By creating a seal on the home scar, limpets effectively reduce water loss.

Chapter III

Factors Initiating Limpet Movements

Observations of movement

Many researchers have made field observations to determine the timing of movement and the cues that may initiate movement of limpets. The incoming tides seem to play a major role in initiating movement. Gailbraith (1965) observed that *L. digitalis* and *L. gigantea* remained stationary at times of high tide, and only began to move when splashed by waves of the incoming tide. Miller (1968), Millard (1968), and Willoughby (1972) also noted that *L. digitalis* is stimulated to move by tidal splashing. Cook (1969) observed a similar pattern for the homing pulmonate limpet *Siphonaria normalis* in Hawaii. Iwasaki (1999) noted that the limpet *Patella flexuosa* in Japan also begins movement when splashed. Craig (1968) recorded that *Lottia pelta* is stationary while out of water, and will not move until it is submerged. Eaton (1968) observed that *Lottia limulata* only moves when splashed or submerged, although they do not move immediately when first splashed. The following homing South African limpets move when splashed by the incoming tide: *Patella cochlear* (feeds only when splashed strongly), *Patella argenvillei*, *Patella granularis*, and *Patella oculus* (Branch

1971). Studies of the timing of limpet movement are summarized in Table 2 (From Branch 1981).

Table 2 Summary of activity rhythms in limpets

Species	Reference
A. Movement while awash, usually day and night	
<i>Cellana toreuma</i>	Hirano, 1979b
<i>Siphonaria alternata</i>	Cook, 1976
<i>S. normalis</i>	Cook, 1976
<i>S. pectinata</i>	Thomas, 1973
<i>Patelloida saccharina</i>	Ohgunshi, 1954
<i>Notoacmea scutum</i>	Rogers, 1968
<i>Collisella limatula</i>	Wells, 1980
<i>C. scabra</i>	Wells, 1980
B. Movement when submerged, day and night	
<i>Patella cochlear</i>	Branch, 1971
<i>P. vulgata</i>	Punt, 1968
<i>Cellana ornata</i>	Beckett, 1968
<i>C. exarata</i>	Kay & Magruder, 1977
<i>C. radians</i>	Beckett, 1968
<i>C. radiata</i>	Balaparameswara Rao & Ganapati, 1971a
<i>Collisella limatula</i>	Connor, 1975; Eaton, 1968
<i>C. pelta</i>	Craig, 1968
C. Movement when exposed at low tide, and only at night	
<i>Collisella pelta</i>	Connor, 1975
<i>Patella vulgata</i> : low shore	Cook <i>et al.</i> , 1969
<i>P. depressa</i> : low shore	Cook <i>et al.</i> , 1969
<i>P. vulgata</i>	Dearnaley, <i>et al.</i> , 1969; Funke, 1968
<i>P. granularis</i>	Stephenson, in Thorpe, 1962
<i>Siphonaria aspersa</i>	Branch (unpubl.)
D. Movement mainly when submerged, and mainly at night	
<i>Patella vulgata</i> : (only moves during day)	Hartnoll & Wright, 1977
<i>Patella vulgata</i> : high shore (only at night)	Cook <i>et al.</i> , 1969
<i>P. depressa</i> : high shore	Cook <i>et al.</i> , 1969
<i>P. coerulea</i>	Funke, 1968
<i>Cellana nigrolineata</i>	Hirano, 1979a
<i>Collisella testudinalis</i>	Steneck (in prep)
<i>Acmaea dorsuosa</i>	Abe, 1931
<i>Patelloida virginea</i>	Clokie & Norton, 1974
E. Movement when exposed at low tide, day and night	
<i>Siphonaria capensis</i>	Branch (unpubl.)

Endogenous Rhythms

There is sufficient evidence that endogenous rhythms play an integral role in initiating limpet movement. However, endogenous rhythms have been difficult to study due to confounding factors of wave/tidal oscillations and light cues. Santina and Naylor (1993) studied endogenous rhythms in homing behavior of *P. vulgata*. Up until this study, no rigorous scientific experiments had investigated endogenous rhythms in homing limpets, though much speculation had been put forth. Santina and Naylor (1993) found both circatidal and circadian components to *P. vulgata* movements. In one experiment, they exposed nine *P. vulgata* to moist (due to salt water sprayers) air for four consecutive days in the laboratory under constant temperature and darkness. Limpets were active during the times of low tides over those four days, providing support for the presence of endogenous rhythms.

In the second experiment, Santina and Naylor (1993) immersed eight *P. vulgata* in seawater after two days of recording their movement in moist air (all under constant temperature and darkness). The flooding of seawater was timed to correspond with the natural incoming tide. While in the moist air (without an external cue), the limpets were active during the times of naturally occurring ebbing tides, as would

have occurred in the wild. However, once the tanks were flooded in correspondence with the time of an incoming tide after two days, activity was mostly suppressed; limpets moved very little. This suggests that ebbing water itself may not be the movement/feeding trigger, but rather, time of the ebbing water is the mechanism to initiate activity.

Santina and Naylor (1993) confirmed this by reversing experiment two; this time, they submerged limpets for two days in constant darkness and temperature. Then, they drained the tank at the time of ebb tide. While submerged, limpets showed very little activity. But when exposed to air, in an apparent free-running endogenous circatidal rhythm, they displayed major foraging activity peaks during the expected times of low tide.

In the final experiment, Santina and Naylor (1993) again immersed nine *P. vulgata* for two days in tanks under constant light and temperature conditions. They then drained the tanks during the time when the natural tide was rising. The limpets became active soon after they were exposed to air. Interestingly, in these experiments there was a slight phase advance in activity times that corresponded with the expected delay of the low tides, meaning movement occurred almost an hour later each day, corresponding with low tides.

Chelazzi *et al.* (1993) could not distinguish between tidal and diel components in activity of *P. rustica* in Italy. This

homing limpet lives high in the intertidal zone. It was found that its activity did not depend on wave height, splashing, or submersion; rather, the limpets became active on a periodicity that was slightly longer than 12 hours. Chelazzi et al. (1993) suggested a double mechanism controls activity for this species: 1) an external, often unpredictable signal to trigger activity (wave splashing), and 2) a short term (probably instinctive) clock to trigger the actual beginning and ending of activity. It appears that a combination of physical stimuli and instinctive behavior cause limpet movement, though more studies are needed which run for a longer period and use other limpet species besides *P. vulgata*.

Other factors initiating movement

Other factors besides rising tides and endogenous rhythms may also be responsible for encouraging movement off the home scar. Some limpets will only feed at night, suggesting daylight as a movement/feeding inhibitor, and darkness as a movement/feeding stimulus. Serra et al. (2001) observed that the key hole limpet, *Fissurella crassa*, of Chile only moves during nocturnal low tides, suggesting that emersion (since it is an air breather) as well as darkness may trigger movement.

Eaton (1968) performed indoor experiments to simulate day and night time rising tides. He maintained *L. limatula* on marble slabs in aquaria. To simulate the rising tide, seawater was allowed to rise two inches every 15 min and air bubbles were added to simulate splash. The only variable was light, as he completed the study in a darkroom or in daylight. Eaton (1968) confirmed the tendency of this species to move downwards during incoming tides in daylight, and upwards during incoming tides at night. It would have been interesting if Eaton could have teased apart the effects of splash stimulation, light level, and circadian rhythm on the limpet's initiation of movement behavior.

In some homing limpet species, movements do not appear to be triggered by any cues. For example, *Patella barbara* moves and feeds at any time of the tide cycle. This South African homing limpet species is located low in the infratidal to lower balanoid zone and maintains a rough home scar on the calcareous algae, *Lithothamnion* (Branch 1971). Since it is so low in the intertidal zone and desiccation is less of a threat, the limpet is able to forage at anytime. Another South African species, *Patella miniata*, is found from the lower balanoid to 11 meters below spring tide. This homing species also makes a home scar on *Lithothamnion*, or sometimes owns no scar at all (not all individuals home to the same place all the time). Like *P.*

barbara, *P. miniata* appears to move randomly, day or night, and at any time of the tidal cycle (Branch 1971). The stimulus triggering movement remains unclear.

Chapter IV

Nature of Outward and Return Movements

Shapes of foraging paths

It wasn't until the 1990s that the exact nature of foraging excursions could be documented continuously and accurately using automated cameras. Earlier photographic techniques documenting the movement of limpets relied on triangulation methods, which were not as accurate as modern automated photography coupled with computer recording devices. Most homing limpets perform a looped excursion away from and back towards their home scar. (See Figures 1a and 1b for looped and other examples of excursion shapes).

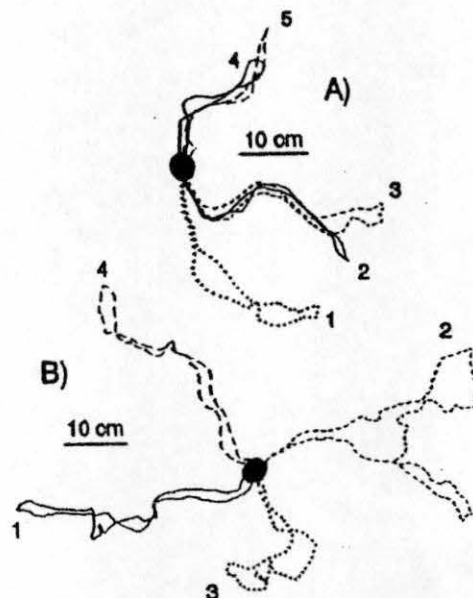


FIGURE 1a Examples of consecutive foraging excursions of two *Patella vulgata* on a vertical wall at Menai Bridge (Anglesey). The five excursions of limpet (A) were recorded in November 1992; the four excursions of limpet (B) were recorded in April 1992. Black ovals, home scars.

(From Chelazzi *et al.* 1998)

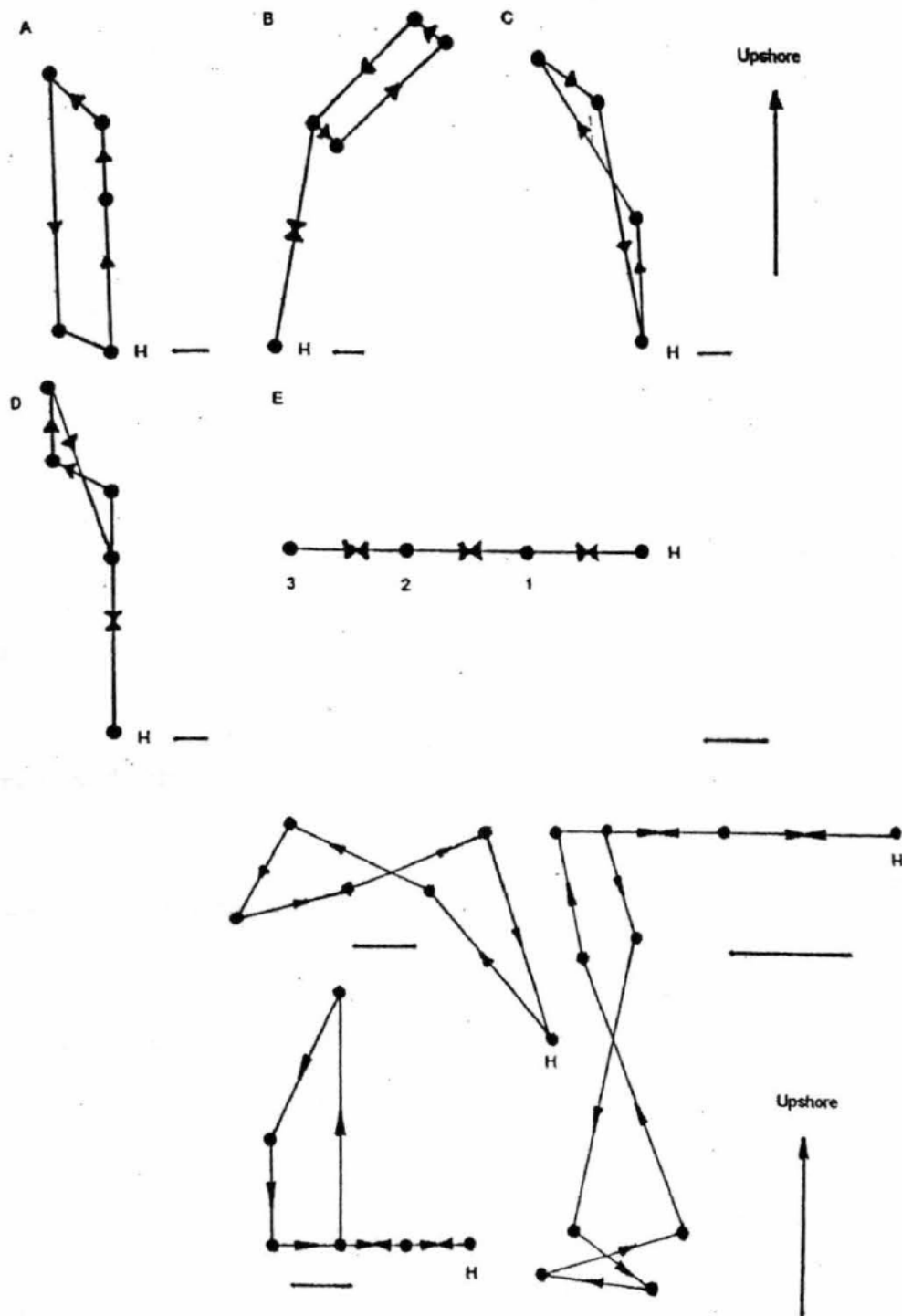


FIGURE 1b Representative sample of foraging excursions undertaken by *Siphonaria pectinata* at Gibraltar. Points/numbers represent the position of the limpet at 10 minute intervals. H denotes the position of the home scar.

(From Ocana and Emson 1999)

Chelazzi *et al.* (1998), for example, recorded 174 complete excursion routes of *P. vulgata*, and frequently observed looped trails (Chelazzi *et al.* 1998). Limpets usually perform only one foraging trip per tide, but sometimes they will make two (Cook and Cook 1981); *S. normalis* will not travel in the same direction of their first feeding excursion during the same tide. Chelazzi *et al.* (1983) found interindividual variability in foraging loops, in which short outward trails were shaped like straight lines, (which they followed back home), but longer paths were more complex with double or multiple loops. Limpet trails therefore vary greatly in terms of shape.

Temporal and spatial feeding continuity

Homing limpets feed by rasping algae with their radula while moving. Feeding is usually, but not always continuous while the limpet is in motion, and rasping rates may vary at different times and places along an excursion. Craig (1968) observed that *L. pelta's* feeding was not continuous during an excursion, and that *L. pelta* did not feed during every tide cycle. Chelazzi *et al.* (1994b) showed that the travel speed of *P. vulgata* can vary with each foraging excursion, perhaps due to variation in the rock surface, algal density, etc., while radula movement remained constant the whole time it was away from its

scar. Similarly, Parpagnoli and Chelazzi (1995) showed that the Mediterranean limpet, *P. caerulea* also exhibited continuous grazing activity throughout the foraging excursion. Ocana and Emson (1999) found that the pulmonate limpet *Siphonaria pectinata* at Gibraltar foraged continuously or intermittently when in air, when humidity at the rock surface was > 75%. Paths of *S. pectinata* were single or compound loops beginning and ending at the home scar. Feeding is therefore continuous in some limpet species but not others. Since most other homing studies observed limpets at rest, feeding continuity is not known for other limpets.

Route selection outward

What route do limpets select when moving away from the home scar? Since most homing limpets move when submerged, it has been extremely difficult for scientists to follow their exact paths through the entire tidal cycle in the field. The earliest studies simply studied homing behavior via tagging limpets and noting their positions spatially and temporally at low tides. A few studies involved scuba diving in order to make observations, while more recent studies employed automated cameras or other such technology.

Cook *et al.* (1969) found that *P. vulgata* did not necessarily follow the same feeding path on different excursions; of 39 limpets, only five followed the same path on different days (Figure 2).

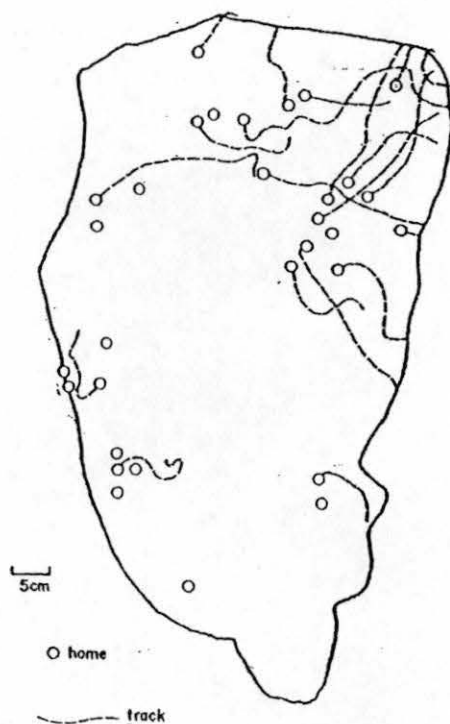


FIGURE 2 The tracks of all limpets on a single plot of a single night between 03.30 and 05.00 BST showing paths crossing and the lack of a common direction.

(From Cook *et al.* 1969)

It was also noted that the limpets did not begin movement at the same time when splashed, nor did they all move in the same direction. Chelazzi *et al.* (1994a) found that *P. vulgata* had a weak avoidance of the last foraging excursion (Figure 3). Cook and Cook (1985) noted the same phenomenon of previous path avoidance with *Siphonaria normalis* and *S. alternata*. The literature lacks more studies which have determined whether

other species avoid the previous path while embarking on a new excursion.

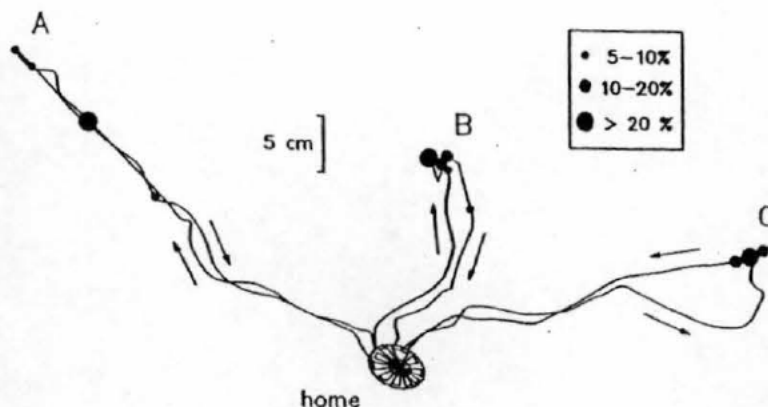


FIGURE 3 Different excursions (A-C) performed by the same limpet on three different nights. Black circles indicate local density of foraging (legend) expressed as percentage of the total number of rasps performed during the whole excursion. Arrows indicate direction of movement.

(From Chelazzi et al. 1994b)

The direction of trails has been documented more often than trail avoidance. Gray and Naylor (1996) observed that 20 *P. vulgata* (observed at two sites over two different time periods of three alternating days each) moved in all directions, when uncovered by the tide, but there was a mean direction vector downwards (Figure 4).

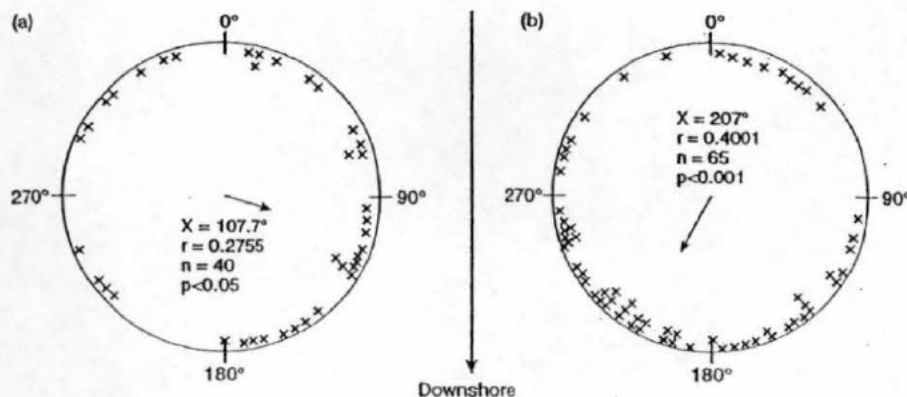


FIGURE 4 Foraging directions shown by *Patella vulgata* at a) Menai Bridge and b) Porthoustock. Results obtained over the 3 days have been pooled. Each cross represents one excursion. n-number of excursions observed and plotted, r-an estimate of the non-uniformity of the circular distributions given as mean vector lengths by the Rayleigh test.

(From Gray and Naylor 1996)

Other studies have observed a net movement upwards. Little *et al.* (1988) found that *P. vulgata* at high intertidal zones moved upwards, while mid-tide limpets exhibited no preferential direction of movement, and the lower intertidal limpets moved horizontally.

Chelazzi *et al.* (1998) studied route selection in *Patella vulgata* for five days using LED (light emitting diode) tracking, a technique which will be discussed later. They were able to calculate the leaving angle, and found that *P. vulgata* varied the leaving angle during different foraging excursions (Figure 5).

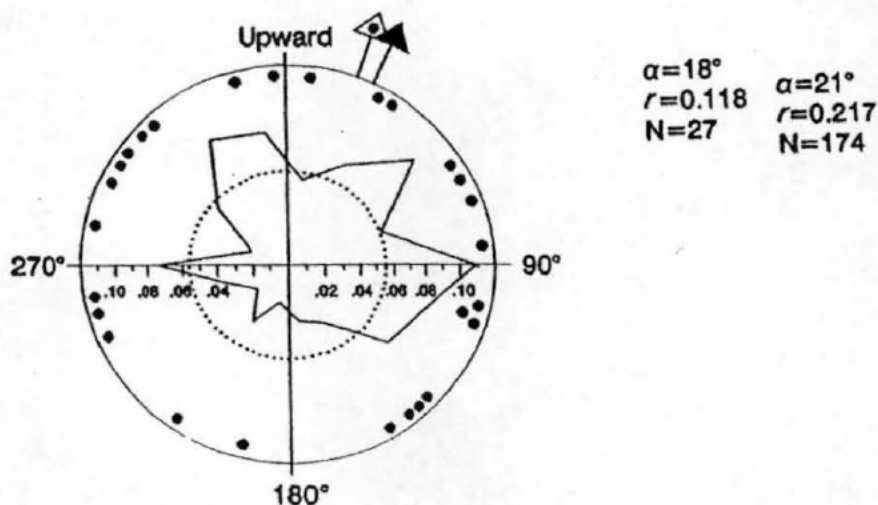


FIGURE 5 Individual mean directions (circles) and pooled frequency distribution (solid line, scale on the horizontal axis) relative to the directions taken by the limpets on leaving the home scar. Dotted circle, uniform distribution. External arrows and values: resultant directions of the pooled distribution (black arrow) and of individual means (arrow with circle); alpha, resultant direction; r, vector length. Mean individual directions are indicated only for limpets with more than three excursions.

(From Chelazzi *et al.* 1998)

They noticed a very slight tendency for limpets to leave the home scar moving upwards, but claim this may be due to geometry of the rock at that location. There was no significant

preferential direction of foraging at the population level, and there was high individual variability of leaving angle. Over two consecutive nights, in 35 of 84 cases, the leaving angle of the second night differed < than 20° with respect to the previous night's excursion (Chelazzi *et al.* 1998). Chelazzi *et al.* (1998) concluded that the main direction of movement was determined early during each excursion. Unlike the previously seen trail avoidance behavior, they noted that there was a large overlap between the outward excursion of one night with the homing excursion of the previous night. So in a sense, limpets are exhibiting trail following since they follow the return trail of the previous night during their next foraging excursion. Perhaps directional decisions may be trail-following based for *P. vulgata*.

Ocana and Emson (1999) failed to mention in which direction *S. pectinata* moved at Gibraltar, but did mention that outward and inward paths were independent, so it appears no trail following was occurring. Serra *et al.* (2001) also failed to mention direction of movement for *F. crassa*. Miller (1968) noted that with *L. digitalis*, as the tide came in, movement increased and orientation became more random, and they moved up or down. But at the high water mark, Miller (1968) saw a tendency for these limpets to move upward. In Miller's (1968) study, 50% of *L. digitalis* splashed by waves oriented their

heads upward, then moved upward in the first hour of the excursion, during day or night tides. Frank (1964) found net vertical movements by *L. digitalis* more often than horizontal movements during excursions. Limpets often exhibited a local net displacement upward at night due to HHW, and downward vertical displacement during LHW, suggesting day vs. night differences in displacement may be due to water levels, not light levels.

Santina *et al.* (1995) found at Menai Bridge (Wales) that *P. vulgata* forage at night. Using LED tracking, they noted that limpets usually followed a single path outward then followed it back home. These limpets seldom made two foraging loops in one night. Paths were rarely straight, and limpets followed the paths home. Often the homeward path overlapped the outward trail. Outward trails therefore do not seem to follow a strict pattern in homing limpets.

Triphasic foraging excursions

Many authors have described the foraging excursions as being tri-phasic, in which the outward excursion is rapid, the middle foraging phase is much slower, followed by a rapid homeward journey. The middle foraging phase often occurs at the top of the excursion loop, or at the furthest point away from

the home scar. Gray and Hodgeson (1998) found that excursions made by *Helcion pectinulus* were tri-phasic. Little *et al.* (1988), Hartnoll and Wright (1977), Santini *et al.* (1991) and Evans and Williams (1991) found that excursions made by *P. vulgata* were tri-phasic. Though additional foraging limpet species also seem to forage in this manner, authors of these studies have not adopted this terminology.

Return movements

The characteristic return home varies with limpet species. Most limpets continue feeding during the return journey. The mechanisms by which they find their way home will be discussed in the next chapter.

Feeding-Rasping

Feeding has not been studied in all homing limpet species. The limited number of studies is probably because it requires sound equipment and expensive electronics, and is logistically difficult to study. It is therefore not known for most homing limpet species when they rasp, whether they continuously rasp or not, or if they spatially or temporally concentrate rasping in any areas of the feeding excursion. Rasping is the scraping of

the limpet's radula against a surface while feeding, and this noise can be recorded to gain a record of when a limpet feeds. Chelazzi *et al.* (1994b) found that rasping began one to two hours before *P. vulgata* left their home scar when the limpets were still exposed to air at ebb tide. Rasping was variable in rate, with non-rhythmic bouts separated by resting phases. No significant correlation was observed between rasping rate and travel speed during different parts of the excursion. Rasping occurred during most of the excursion, but was not continuous. There is evidence that the limpets concentrate foraging effort in the central part of each looped path (max distance from home scar), though the algae around the home scar was also intensely grazed and relatively devoid of algal film. The main finding was that the spatial organization of foraging activity in *P. vulgata* is not due to temporal modulation of the rasping rate, but only to the changing travel speed along the path. This suggests that foraging intensity varies with changes in travel speed which in turn varies according to food density (Chelazzi *et al.* 1994b).

Kitting (1979) found that *L. scutum* and *L. limulata* in California fed almost continuously for up to an hour, interspersed with pauses lasting several hours (in Chelazzi *et al.* 1994). Little and Stirling (1985) concluded *P. vulgata* fed for almost the entire time while active (in Chelazzi *et al.*

1994b). More studies are needed which study rasping rates spatially and temporally in the field.

Home and feed every day?

Homing limpets do not necessarily leave the home scar and feed during each tide cycle. It is not clear whether this is because their stomachs are full from the previous excursion, or they are avoiding the risks of predation or being washed away by waves while moving, or all of the above. Branch (1971) notes that about 60% of *P. cochlear* may remain on their home scar during a tide. Willoughby (1972) found that the maximum period of inactivity for *L. digitalis* was nine days. The largest number of consecutive days for a limpet to move and to forage was seven days. Limpets rested an average of 6.3 days out of 10, and moved an average of 3.5 days out of 10 (n = 30 limpets). Rest periods often lasted longer than one day (Willoughby 1972). Craig (1968) found that in *L. pelta*, if it did not move during one tide, it would usually move during the next tide. Craig (1968) also observed that feeding of *L. pelta* was not continuous while limpets were moving, and animals did not feed during every tide cycle. It is therefore evident that limpets do not necessarily feed every day, probably due to a stomach or the need to conserve energy.

Length and duration of movement

Length and duration of movement vary considerably between and often within homing limpet species. Serra *et al.* (2001) found that total length and duration of *Fissurella crassa* varied among 36 limpets. See Table 3 on the next page for a summary of limpet travel distances. Gray and Naylor (1996) found that at Porthoustock, Cornwall, England, *P. vulgata* moved an average distance of 39 cm, while at Menai Bridge (Wales) they moved 18 cm. It was speculated that the difference was due to the abundant barnacle cover at Cornwall, forcing limpets to move further to find suitable food to graze. Furthermore, at Cornwall, there was a significant difference in average travel length from day to day, but average travel length was not significantly different day to day at Menai Bridge. Gray's and Naylor's (1996) observations were only made over three day periods at each site.

Also note that intraspecific differences in travel lengths exist. For example, Craig (1968) saw that one *L. palata* moved two inches (5.08 cm) during any one high tide over four days, while another *L. pelta* moved six feet (182 cm) during a single high tide period, so movements between individuals of the same species can be highly variable.

Table 3 Travel distance summary in various homing limpets

Species	Round trip average excursion distance (cm)	One-way (outward) average excursion distance (cm)	Maximum travel distance from home (cm)	Average excursion duration (min)	Source
<i>F. crassa</i>	ND	308.6 ± 116.8 (spring tide)	60.3 ± 30.1 (spring tide)	227.7 ± 83.2 (spring tide)	Serra <i>et al.</i> (2001)
	ND	257.4 ± 94.4 (neap tide)	48.8 ± 24.5 (neap tide)	228.2 ± 104.8 (neap tide)	
<i>S. pectinata</i>	ND	15	75	ND	Thomas (1973)
<i>M. scabra</i>	19	ND	40	ND	Hewatt (1940)
<i>L. digitalis</i>	30.9	12.98	ND	ND	Gailbraith (1965)
<i>L. gigantea</i>	8.9	7.89	ND	ND	
<i>L. digitalis</i>	183	ND	ND	ND	Millard (1968)
<i>P. flexuosa</i>	15.4 (spring tide)	6.7	ND	ND	Iwasaki (1999)
	13.9 (neap tide)	5.5	ND	ND	
<i>P. vulgata</i>	ND	40	ND	ND	Hartnoll and Wright (1977)
<i>P. vulgata</i>	70.3	23	23.07	247	Santina <i>et al.</i> (1995)
<i>P. vulgata</i>	ND	39 (Cornwall)	ND	ND	Gray and Naylor (1996)
	ND	8.9 (Menai Bridge)	ND	ND	
<i>P. argenvillei</i>	60	ND	ND	ND	Branch (1971)
<i>P. granatina</i>	75	ND	ND	ND	
<i>P. longicosta</i>	200	ND	ND	ND	
<i>P. oculus</i>	150	ND	ND	ND	

Speed of movement

Limpet crawling speed also varies considerably between species and on an interindividual basis. A few speeds will be mentioned here, see Hartnoll (1986) for more information regarding limpet travel speeds. Table 4 shows a summary of limpet crawling speeds.

Table 4 Summary of travel speeds in various homing limpet species

Species	Average travel speed (cm min ⁻¹)	Maximum travel speed (cm min ⁻¹)	Source
<i>F. crassa</i>	0.8 ± 0.03	ND	Serra <i>et al.</i> (2001)
	0.7 ± 0.3	ND	
<i>S. pectinata</i>	ND	1.36	Ocana and Emson (1999)
<i>S. pectinata</i>	ND	3.36	Hartnoll and Wright (1977)
<i>P. vulgata</i>	ND	1.13	
<i>P. vulgata</i>	0.29	ND	Santina <i>et al.</i> (1995)
<i>P. vulgata</i>	0.2 to 0.9	1.3	Little <i>et al.</i> (1988)
<i>P. vulgata</i>	ND	1.5	Cook <i>et al.</i> (1969)
<i>L. digitalis</i>	0.5 to 0.8	1.3	Miller (1968)

Serra *et al.* (2001) found that the keyhole limpet (*Fissurella crassa*) moved faster away from the home scar than towards it. Perhaps stomach satiation can influence limpet crawling speed. Ocana and Emson (1999) recorded crawling speeds

of *Siphonaria pectinata* to be up to 1.36 cm min^{-1} but found they exhibited a range of crawling speeds when moving. This could be due to grazing intensities.

Santina *et al.* (1995) recorded the average speed of *P. vulgata*, which was $.29 \text{ cm min}^{-1}$. Cook *et al.* (1969) recorded a maximum speed for *P. vulgata*, which was 1.5 cm min^{-1} . Hartnoll and Wright (1977) recorded max speed of *P. vulgata* as 1.13 cm min^{-1} , (with mean outward speed of 0.60 cm min^{-1} , and intermediate browsing speed of 0.08 cm min^{-1}), while Little *et al.* (1988) recorded it to be 1.3 cm min^{-1} , with an average speed of 0.2 to 0.9 cm min^{-1} . The speed values for *P. vulgata* in these studies all seem in accordance with one another. Little *et al.* (1988) states that speeds vary with limpet size, so such data is not particularly useful. If speeds for other homing limpet species have been recorded, they are not mentioned in the homing literature.

Chapter V

Controversies Regarding Homing Mechanisms

Mucus trails

Homing is a behavior in which limpets return to their previous resting spot after a feeding excursion. Many hypotheses exist which explain how limpets manage to find their way back to the home scar. Since limpets cannot see their environments, they must rely on other senses, such as touch or taste. Possible homing mechanisms include mucus trail following, dead reckoning, recognition of topography, chemical gradients, gravity, sunlight cues, etc. Many studies tested these hypotheses, many of which yielded conflicting results with other studies.

Limpets may find their way home by following their mucous trail laid down during the outward journey. The role of mucous trails in guiding homing has been examined for decades, and has yielded conflicting results. Serra et al. (2001) found evidence that *Fissurella crassa* in Chile uses trail following to find its way home. Cook et al. (1969) did not find evidence that *P. vulgata* follow their outward trails back home (Figure 6). While limpets returning to their home scar may sometimes cross their outward path, they do not always appear to follow it home.

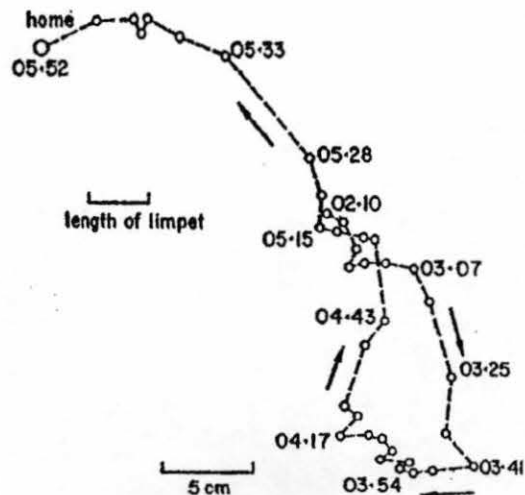


FIGURE 6 Return track obtained by triangulation between 02.10 and 05.52 BST showing that a limpet need not necessarily follow its outward trail in order to home.

(From Cook *et al.* 1969)

Similarly, Ocana and Emson (1999) found little evidence of trail following for the pulmonate limpet *S. pectinata* at Gibraltar. Contrastingly, Thomas (1973) found that *S. pectinata* moved outward and returned in a straight line, perhaps to avoid pregrazed areas; *S. pectinata* therefore did appear to follow their trail back home. More long term studies are needed to clarify such contradictions in *S. pectinata*'s as well as other species' behavior.

Perhaps trail following is used in choosing outward paths rather than for selecting return journeys home. This may help the limpets avoid grazing the same area consecutively, which would result in exhaustion of algal resources. Chelazzi *et al.* (1998) calculated return angles at which *P. vulgata* returned to the home scar. They found that in 21 of 84 excursions, the leaving direction of the next excursion was closer to the return

path than the leaving path of the last excursion. In 30 or 84 excursions, pairs, the angular difference in leaving direction with return direction was greater than ten degrees. This suggests that when homing, limpets may leave some info along the homing branch of foraging excursions, which can be used to relocate the foraging area during the next excursion, perhaps to avoid it directly. Trail following studies have yielded many contradictory results in limpets, and today it remains unclear as to whether or not it is used for homing. There is a need to search for trail following in other homing limpet species besides the above mentioned species.

In the 1980s, following a string of contradictory studies, emphasis on mucous trails was redirected from its role in homing to its possible role in trapping microalgae and enhancing its growth. From 7-26% of a snail's energy budget goes to mucous production (Calow 1974, and Denny 1980b) (in Conner 1986). If mucous can trap and enhance algal growth, then the energy invested in mucous production may be repaid by enhanced resource abundance.

Connor (1986) examined the ability of mucous trails of *L. gigantia*, *M. scabra*, and *L. digitalis* to trap and grow microalgae. The first two limpets' mucous did stimulate algae growth significantly, while *L. digitalis*'s mucous did not. In the lab, mucous of *L. gigantea*, *M. scabra*, and *Nucella* did not

significantly vary from one another in terms of ability to have microalgae stick to it. However, all three species' mucous were significantly more sticky in trapping algae than that of *L. digitalis*. Furthermore, mucous of *L. gigantea* and *M. scabra* grew more microalgae in the lab than mucous of *Nucella* and *L. digitalis* (Connor 1986). Of course duration of the mucous in the field is a major factor in determining the success of the mucous at trapping growing microalgae, as Connor (1986) found that local wind and wave conditions may significantly reduce mucous persistence at some sites more than others. More studies are needed which measure mucous persistence and algal growth on mucous in the field.

Dead Reckoning

Limpets may utilize a form of dead reckoning to find their way home. In dead reckoning a limpet would remember its outward course relative to home and would use this memory to guide them to their home scar. Cook (1969) evaluated dead reckoning in *P. vulgata* as a homing mechanism. She removed limpets from their outbound trails, and placed them back on rocks at a distance away from this outbound trail. Fifteen were placed two to eight cm from home on areas in which they had previously traveled. All 15 limpets returned home within five to 20 minutes, all of which

went directly home. Four were placed two to eight cm away from home in areas which they had not been observed moving previously. The four limpets did not return home, but went in one direction, turned around, then returned to positions where they were transplanted. As soon as the four were placed in areas in which they had previously been, they went directly home.

In all displacements, limpets returned home along routes other than their outward trail. This study yielded evidence that trail following is not necessarily essential, but that prior experience is needed in an area in order to home; perhaps remnants of old mucous trails helped guide the limpets home. Dead reckoning is not the method used to home either (Cook 1969). It is possible though that if chemical gradients exist in the mucous, the limpets could have been using this to know how close they were to home.

Chiseling/scrubbing experiments

Another common experiment in the literature involves chipping away rock around the home scar to determine if microgeography or chemical cues are mechanisms of homing. Chipping experiments are reported as far back as Bohn (1909), Pieron (1909) and Hewatt (1940). More recently, Cook *et al.*

(1969) chiseled the area between 12 feeding *P. vulgata* and their home scar. Only one of twelve failed to home successfully. In another experiment, Cook *et al.* (1969) scrubbed the paths of four away from home limpets with detergent, and all four *P. vulgata* still successfully homed. When using oven cleaner, some homed and some did not. Cook *et al.* (1969) concluded that trail following is not necessary for homing in *P. vulgata*.

Furthermore, Cook *et al.* (1969) observed that while *P. vulgata* home, they may not necessarily follow their outward trail back home, lending further evidence against chemical trail following.

Cook *et al.* (1969) also tried obstructing paths with small globs of plaster of Paris, but the limpets still homed successfully around them. Cook *et al.* (1969) also believes topographical memory as well as chemical trail following cannot completely explain homing. Their displacement experiments ruled against use of a kinaesthetic memory (remembering topography) in homing. Cook *et al.* (1969) concluded that information available to guide homing is restricted to the rock surface and the limpet's past movements. They propose that limpets can find their way home along any of its previous excursion trails, perhaps due to concentration gradients of a chemical found in the mucous.

Gailbraith (1965) also attempted rock scrubbing and chiseling experiments to test topographic and chemical cues as

guides for homing. He chiseled and scrubbed around the home scar while the limpets were at home (unlike Cook et al. 1969) and away from home for *L. digitalis* and *L. gigantea*. The rock was scrubbed with a wire brush, on a five cm area around the home, then rinsed with seawater. No chemicals were used in scrubbing while limpets were away. For chiseling, a two cm wide by 0.3 cm deep area around the home was chiseled. In controls, 54% of *L. digitalis* homed, as did 76% *L. gigantea*.

All the *L. digitalis* (n=14) crossed a scrubbed area to leave home. In the away from home experiments, 50% of the *L. digitalis* crossed scrubbed areas to return home. In chiseling, 21 of 27 *L. digitalis* (78%) crossed a chiseled area to leave home. Three of 26 *L. digitalis* crossed a chiseled area to return home, which is significant, thereby supporting rock topography use in homing (Gailbraith 1965); this is contradictory to the findings of Cook et al. (1969), in which rock topography did not appear to guide homing.

Scrubbing experiments were also performed using *L. gigantea*. Ten of 33 (30%) limpets crossed a scrubbed rock area to leave home, while 15 of 34 (44%) crossed a scrubbed area to return home. The results involving *L. gigantea* were not open to clear interpretation because it was difficult to separate general inhibition of movement vs. a disturbance in homing mechanisms in governing the homing behavior. Three of 26

returning home successfully suggests that tactile memory is involved, though again, it is difficult to interpret (Gailbraith 1965).

Jessee (1968) found that *M. scabra* continued to home after its territory was scrubbed, but did not home when the territory was chiseled. There are therefore conflicting results involving topographical memory.

Chapter VI

Abiotic and Biotic Factors Affecting Foraging

Day vs. night effects

Homing limpets vary in the time of day in which they are actively moving and grazing according to species; though there is sometimes interspecific variation according to location. Some homing species are active exclusively during the day, others only at night, and a few during both. Often a combination of illumination and tide cycle will determine when a limpet becomes active, and direction of movement may be governed by whether or not it is day or night, high tide or low tide. Eaton (1968), for example, states that like *M. scabra*, *L. limatula* forages day and night during high tide. *L. limatula* exhibits an upward displacement at night, then when the tide returns during the day, they travel downwards, thus exhibiting an interaction between daylight and tide cycle in initiating directional movement. *M. scabra* moves upwards with a rising tide and down with falling tide day or night, but the upward displacement during the day high tides are smaller than the upward displacement during night tides.

Cook *et al.* (1969) saw that *P. vulgata* moves and homes day and night, even at all states of the tide (though no observations were made during nighttime high tide) over 14 days. Little *et al.* (1988) saw that *P. vulgata* (at Lough Hyne, Ireland), when high in the intertidal, moved only at night during low tide. This is also the case with *P. vulgata* at some other locations such as at Menai Bridge (Wales) in Chelazzi *et al.* (1998). Miller (1968) studied day vs. night movements of *L. digitalis*, and there was no significant difference in movement rates day or night. *F. crassa* on the other hand is inactive during the day, lying in crevices probably to avoid desiccation (Serra *et al.* 2001). Craig (1968) found that most feeding of *L. pelta* occurs while the animal is submerged at ebb tide. At night, they move upwards at rising tides, and down with falling tides (Craig 1968). Daylight and darkness are therefore obviously two important factors in influencing homing limpet movements.

Gray and Hodgeson (1998) studied the behavior of the South African high shore limpet, *Helcion pectinulus*. They found that activity rhythm of *H. pectinulus* varies due to differences in directional orientation. Limpets facing east and west on rock surfaces were both active at nocturnal low tides, while only the west facing limpets were active during daytime low tides while in the shade. This is an example of intraspecific variation in

behavior due to location and orientation. Adequate shade lengthens movement and foraging time for limpets facing west, perhaps by reducing desiccation.

Low vs. high shore

Intertidal elevation can also influence homing behavior. Limpets inhabiting the high shore levels must wait longer for rising tides to submerge them, and also become exposed more quickly than lower shore limpets as the tide ebbs. This means they may experience less feeding time if they only feed when splashed or submerged. They are also more vulnerable to desiccation and predation by birds and terrestrial animals. Perhaps this is why high shore limpets often travel shorter distances and remain on the home for longer periods than lower shore limpets.

Santina *et al.* (1995) saw low vs. high shore differences in locomotion in *P. vulgata*; however, these differences were not significant when statistically tested. Low shore limpets appeared to move faster and greater distances than high shore limpets. This could be due to increased intraspecific competition on low shores, where limpets would move faster and further to avoid crowding with other conspecifics while feeding. There were greater limpet densities on low shore, and more

abundant food; one would expect shorter movement distances for less duration, but that was not the case. Santina *et al.* (1995) therefore did not find significant differences in travel distances and speeds between low and high shore limpets.

Little *et al.* (1988) studied *P. vulgata* on vertical rock faces at Lough Hyne, Ireland. The limpets highest on the rock were active only at night at low water, and moved vertically up the rock to feed near lichens. The mid level limpets moved in random directions, with no choice of feeding area, probably because of the local high barnacle density. The limpets lowest in the intertidal were active near times of low tide day and night, moved horizontally, and chose areas of low barnacle density in which to feed. The times of activity and movement patterns therefore vary for limpets at different shore heights.

Little *et al.* (1990), in contrast to Santina *et al.* (1995), found there were significant differences between low vs. high shore dwelling *P. vulgata*. Little *et al.* (1990) studied *P. vulgata* at Lough Hyne, Ireland and noted abiotic factors affecting feeding behavior. Limpets were more active lower on shore where more wave action occurred, and low humidity levels were found to reduce activity. There is more algal food lower on shore, and the guts of these lower limpets contained more diatoms. Lower shore limpets also ingested less mineral fragments, revealing they are eating surface of rock. Higher

shore limpets possessed more rock in their gut (but there may be a difference in rock type high vs. low), and there were more cyanobacteria up high in the intertidal. The energetics of the 2 feeding strategies may therefore be different (Little et al. 1990). An interesting question for future studies would be to investigate the amount of rock ingested and its effects on energetics and movement, since such data is lacking in the literature.

Spring vs. neap tide

It is possible that spring and neap tides may affect duration and length of feeding movements. During spring tides, tide levels reach higher up shore, and the longer submersion time may allow longer feeding excursions. During neap tides, tidal levels do not reach as far upshore, and this could possibly lead to shortened foraging excursions and a reduction in feeding. Little et al. (1990) found that limpet foraging behavior varied significantly between spring and neap tide in *P. vulgata*. In Little et al. (1988), feeding excursions were prolonged during spring tides.

Serra et al. (2001) also found significant differences in limpet foraging behavior of *Fissurella crassa* during spring and neap tide cycles (Figure 7).

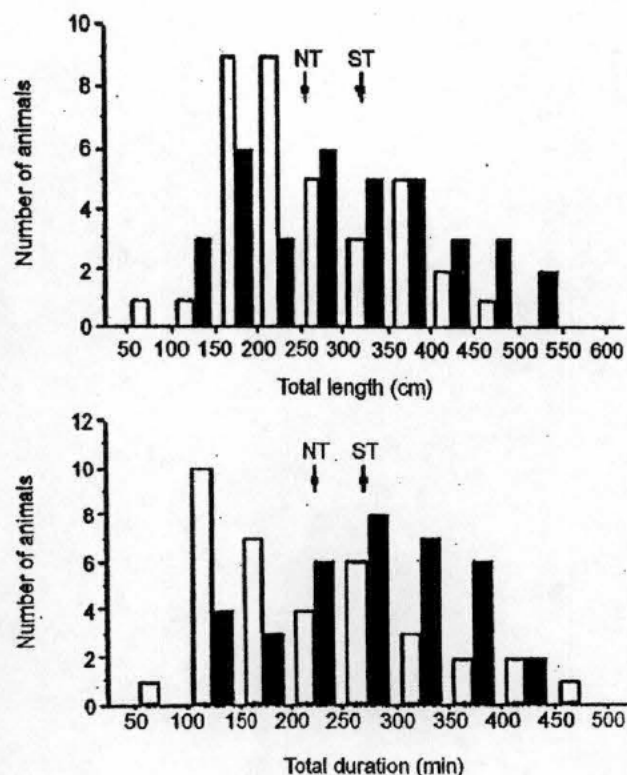


FIGURE 7 Frequency-distribution of Total Length (TL) and Total Duration (TD) at spring and neap tides. N=36; black bars, spring tides (ST=mean); white bars, neap tides (NT=mean).

(From Serra *et al.* 2001)

Inter individual variability of time of departure from home was higher during neap tide than spring tide in *F. crassa*. Homing precision did not differ significantly between spring and neap tides (homing precision was not defined in the study). Trail overlap varied from spring and neap tide, but not significantly. Direction angle of the excursions did not vary during both spring and neap tides, and the majority of limpets headed downwards to feed (Serra *et al.* 2001). *F. crassa* exhibited a higher total length of maximum distance of excursion during spring tide than neap. Total duration of excursion and

average speed did not vary between spring and neap tides. However, the lowest point in the intertidal zone reached by a limpet occurred during a spring low tide. Few other studies have addressed the influences of spring and neap tides on other species of homing limpets, yet another factor that has received little attention in the study of limpet homing behavior.

Winter vs. summer

Gray and Hodgeson (1998) found that the high shore limpet *Helcion pectinulus* of South Africa traveled further in winter (average 85.53 cm) than in spring (average 55.7 cm) or summer (average 48.8 cm). Since most studies of homing limpets are short term from a few days to a month, there is a lack of data regarding seasonal variation in limpet homing behavior.

Microclimate

The microclimate in the habitats in which homing limpets dwell has been largely neglected in the literature. Rock dampness is one such factor which needs further investigation. Some homing limpet species will forage on damp rocks when not submerged. The degrees of dampness necessary, as well as salinity tolerances and temperature ranges in which limpets will

move and forage upon these damp rocks have not been determined. Ocana and Emson (1999) state that there have been few studies of the microclimate experienced by intertidal limpets.

One exception is the work of Verdeber *et al.* (1983), in which they correlated level of rock wetness with foraging activity of *Siphonaria alternata* (foraging occurred only when the home scar was covered by water, not when the rocks were just damp). Little *et al.* (1990) found that foraging activity of limpets was suppressed during heavy rainfall; few other studies have mentioned the effects of rainfall on homing. Little *et al.* (1990) states that rock dampness needs to be assessed more thoroughly in the future, and should be separated from the confounding effects of temperature.

Substrate angle

Substrate angle has been clearly shown to affect limpet foraging behavior. Williams *et al.* (1999) studied *P. vulgata* at Lough Hyne, Ireland, and found behavioral differences between limpets on vertical or horizontal surfaces. *P. vulgata* on steep slopes were active at night when emersed, while those on horizontal rocks were active during the day while submerged. Previous studies of slope were confounded by geographic differences in tidal range (ie, tide height differed along

latitudes), and have been done over short periods. No clear evidence was found for the cause of *P. vulgata*'s behavior, though perhaps it is to avoid predatory crabs (which are abundant at night) or to avoid daytime predators during low tide (Williams *et al.* 1999).

Collins (1977) studied the effect of substrate angle on the movement and orientation of *L. digitalis* and *M. scabra* in the field. Few studies have manipulated substrate angle, this one did not; rather, observations were made on rocks with naturally varying angles in the field. The amount of movement by *L. digitalis* increased with increasing angle, while for *M. scabra*, movement decreased with increasing angle. *L. digitalis* moves more than *M. scabra* at substrate angles of 35 to 60 degrees, and 65 to 90 degrees. Clock position of orientation was also measured, and revealed that over 10 days, neither species oriented evenly in any direction on rocks at low tide.

Cook *et al.* (1969) also studied substrate angle, and this was one rare study in which substrate angle was directly manipulated in the field. Rocks containing home scars and homing *L. digitalis* were turned 180 degrees on a horizontal axis while limpets were away from home at low tide. Eight rocks containing 23 limpets total were turned in this manner, and eight limpets homed successfully, three took up new positions, while two took up new homes before the rock was moved. The rest

did not home, but moved, which was attributed to the normal mobility of the limpets at this place and time. This was also carried out once before at another location, in which four limpets on a rock were turned 180 degrees on horizontal axis when they were not at home. They homed regularly (one got crushed though) (Cook *et al.* 1969).

In another study, Cook (1969) rotated rocks 90 degrees on a horizontal plane while 53 limpets (*Siphonaria japonica*) were away from home. Fifty-two of 53 returned home, while the one limpet that could not return home had its scar blocked by another limpet. Gravity as a homing mechanism was also investigated, by rotating rocks 180 degrees in a vertical plane while away from home. All 14 limpets returned home; gravity is therefore evidently not a homing mechanism. This study also ruled out polarized light, sun compass clues, position of neighboring objects, and all other external clues as potential homing mechanisms (Cook 1969).

Obstructions: mussel barriers

Not many studies have mentioned obstructions in or around the territory of homing limpets, and how such things may affect homing behavior. Such obstructions include barnacles, crevices, rock outcroppings, and mussel beds, which all may affect

foraging behaviors via restriction of territory size and inhibition of limpet excursion length or migration/emigration. Iwasaki (1999) observed marked limpets (*Patella flexuosa*) in the lower intertidal for 12 months to see if they migrate over mussel patches to reach new territory. After 12 months, 10% of marked limpets were found in new gaps, meaning they did crawl over mussel beds. Furthermore, 80% of those migratory limpets had moved to gaps with lower limpet densities. The shell lengths of emigrants were smaller than nonimmigrants, and they emigrated more in summer and autumn than winter and spring. Iwasaki (1999) also noted that activity pattern, short term site fidelity, and foraging behavior have been studied intensely on open rock surfaces, but no long- or short-term reports regarding movement of limpets within and among patchy intertidal habitats have been made.

More studies are needed which investigate patchy vs. nonpatchy environments (in terms of barnacle obstructions especially) at least on the Oregon coast, where many homing limpets live in oases of microalgae surrounded by dense barnacle mats, on vertical surfaces of cliffs and large boulders (personal observation). The dynamics of barnacle settlement and encroachment in homing limpet feeding arenas has yet to be described in a long term study. Furthermore, I have not seen any studies regarding behavioral differences on boulders vs. cliff

walls, if any such differences exist. Obviously factors such as emigration may be more complicated in a boulder field, where limpets would have to cross boulders or even sand patches and other obstructions to find new territory and clusters.

Limpet size effect on foraging

Limpet size effects on foraging behavior has been directly studied in a few homing species, but not mentioned at all in others; the current data is still inadequate and still does not address all homing species. Many homing studies (which do not focus on limpet size) passively mention the sizes of the limpets used in the study, but ignore possible size effects on feeding behavior outcomes and fail to discuss this in the conclusions of the literature. This is an important oversight, because some studies have found significant size effects of limpets on foraging behaviors. Factors such as excursion length, excursion duration, amount of food ingested, rasping rate, and travel speed may or may not vary among limpets of varying sizes in different species. Furthermore, limpet size may directly affect feeding territory; for example, Stimson (1970) (in Little *et al.* 1988) states that feeding areas of *L. gigantea* increase with limpet size.

Ocana and Emson (1999) found that there was no correlation between size of *Siphonaria pectinata* and duration of excursion. Cook and Cook (1981) found that in *S. normalis* located in Bermuda, larger limpets moved further than smaller ones at one site, while at Enewetak Atoll, there was no significant relationship between limpet size and distance moved. Thomas (1973) found that in *S. pectinata*, larger individuals traveled further away from their home scar than smaller individuals, though there was always considerable variation. Iwasaki (1999) found no significant correlation between shell length and total distance moved in one excursion in *P. fluxuosa*.

Santina *et al.* (1995) found differences in *P. vulgata* size with behavior, revealing a linear increase of shell length with total duration of excursion, and found that larger limpets moved further distances. Little *et al.* (1988) also found a similar relationship in which distance moved and speed of movement were linked to limpet size. More data is needed regarding size effects of homing limpets in the field.

Density manipulation

More studies exist that have investigated the effects of density manipulation on foraging behavior of limpets. A primary example is that of Breen (1971), who increased the densities of

L. digitalis in enclosures to test if homing was a response to unfavorable conditions. He found that new limpets added to clusters displayed higher emigration rates than original cluster members. There was no significant correlation between density and migration rate though. However, he speculated that since this study was performed during the summer, a time when limpets restrict their movements, there was less emigration occurring.

In the same study, Breen (1971) also decreased food and space to make conditions less desirable to see if clusters would disband. He removed algae within 60 cm from the cluster with a wire brush. The majority of limpets did not emigrate. He also tried decreasing space available by adding limpets to a clump. This did not work, however, because in the control group, a high proportion of moved limpets left their home. Removal can be traumatic enough to destroy homing behavior in *L. digitalis* anyway.

In fact, Cook *et al.* (1969) knocked 10 limpets off their home scar with wood (not to study density, but to study homing), then displaced them five to seven cm from home, and eight made it home within two hours, two of which made it home after one tide. Six control limpets were removed in the same manner and replaced back on home, and it seemed that the violent removal had no effect on homing. This contrasts to Breen (1971), who found that removal of *L. digitalis* was traumatic and disturbed

normal homing behavior. Experiments involving limpet removal are therefore not desirable to studying true limpet behaviors, and are often harmful to limpets.

While some studies have investigated the effects of limpet density, few homing studies take into consideration the effects of territory size on homing limpet feeding. Limpet density studies are incomplete until they are coupled with data regarding territory size interactions with limpet densities. Increasing limpet density may not necessarily have the same behavioral effects as decreasing feeding arena size; such things need to be investigated in future studies.

Gonad ripeness

Santina *et al.* (1995) state that *P. vulgata's* gonad development occurs in November and inhibits movement and foraging, though seasonal variation in algal density could also be inhibiting the movement. Seasonal variations were evident in the behavior of *P. vulgata*, in which they had longer excursions in April through November (seasonal variations had never been described in *P. vulgata* until this study). In April, total excursion distances and temporal durations were longer than in November. The maximum distance from the home scar was greater in April than November in low shore limpets. The total

excursion time was greater in April than November in high shore limpets (Figure 8). The literature lacks other studies investigating effect of gonad development on homing limpet foraging behavior.

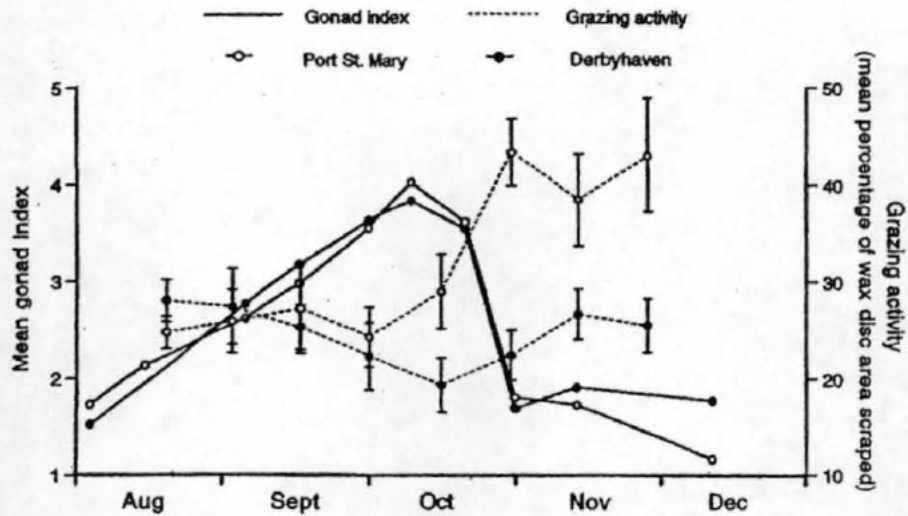


FIGURE 8 *Patella vulgata* at 2 shores. Level of gonad development and grazing activity in mid-shore populations on the Isle of Man. Mean gonad index was calculated for individuals with shell length of 30 to 50 mm. Each estimate of grazing activity is plotted at the end of the 2 wk period to which it applies. Error bars = ± 1 SE.

(From Jenkins *et al.* 2001)

Chapter VII

Recent Methodological Advances

Techniques

A variety of new technologies have allowed scientists to record images and rasping sounds of moving/feeding limpets. Recordings of radula noise were first made in 1965 (Carriker and Martin), then later by Boyden and Zeldis (1979), Kitting (1979), Little and Stirling (1985), Horn (1986), Petraitis and Sayigh (1987) and Petraitis (1992). Despite the advances made through the recordings, early methods of recording limpet activity lacked automatic devices that could be used spatially and temporally, and were often labor intensive. Hartnoll (1986) reviewed these different methods of studying limpets, and concluded that more field techniques were needed to gather quality data on homing, timing of activity, and morphology of feeding paths.

More recently, Chelazzi *et al.* (1994b) and Parpagnoli and Chelazzi (1995) used piezoelectric transducers, small amplifiers, and microlighters (all glued to limpets shells) to track and monitor feeding behavior of *P. vulgata* at Menai Bridge. A remote sound filter, sound amplifier, and recorder continuously recorded rasping noises through nocturnal low tide,

and an automated camera tracked movement. The advances made here were that they could differentiate between other noises like scraping shells on rock, and they could record activity over different time scales, milliseconds to days, automatically on a computer.

While sound technology was evolving, photography was used sparsely in the 1960s to monitor limpet movements and to estimate foraging routes. Automated time lapse photography was used by Chelazzi *et al.* (1990) to determine the total lengths and duration of excursions, as well as homing accuracy, and trail following. However, direct foraging estimates were difficult to assess with this method, as one cannot tell from photographs when and where in the excursion the limpets were feeding. Chelazzi *et al.* (1994b) then made another advancement by combining monographic and sonographic techniques in the field to find rates and times of rasping behavior, and to relate it to travel speeds and precise position during an excursion.

Chelazzi *et al.* (1990) also pioneered other methodologies, and recorded temporal and spatial parameters of limpet activity using reed switches (Figure 9) activated by a magnet glued to the shell apex. This allowed them to record the "at home" or "away" status continuously for one month with the help of a computer. They coupled this with LED tracking with an automated camera, that recorded positions once every ten minutes.

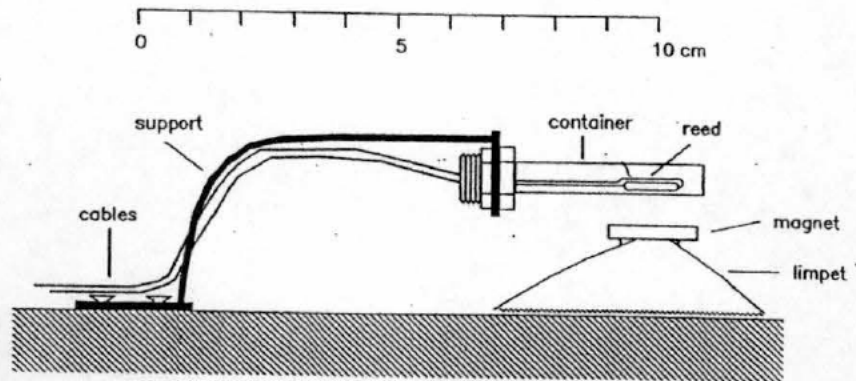


FIGURE 9 Arrangement of the equipment used to record the 'home-away' status of limpets.

(From Chelazzi *et al.* 1990)

A drawback with reed switches is that they only work for limpets possessing a permanent home scar. The magnetic shell attachments alter the thermal and hydrodynamics, and the magnetic field may also influence homing behavior. Tracking limpets with photography and LED is preferred over reed switches (Chelazzi *et al.* 1990).

LED was first introduced by Wolcott (1977, 1980) (in Chelazzi *et al.* 1983) for use in tracking ghost crab behavior. LED was first used on gastropods by Chelazzi *et al.* (1983) on *Nerita textilis*. LED (light emitting diode) contains a 1.5 volt battery continuously emitting tiny red lamps three mm in diameter, that is encased in dental acrylic, weighing only 1.2 grams. Lights are glued to the gastropod's back, and during the night, an automated camera can photograph the light's locations as the limpet moves. So far LED has been used on limpets emersed at low tide. No one has continuously recorded limpet

foraging in the intertidal while limpets were fully submerged in a long term study. Automated, durable waterproof cameras could reveal much about the foraging movements of submerged limpets, though debris in the water, as well as rough wave conditions have inhibited this from occurring successfully.

Modeling of Energetics and Feeding

More recent studies have attempted to model the foraging behavior of homing limpets. Santini and Chelazzi (1996) modeled two feeding strategies of *P. vulgata*. One hypothesis was that feeding excursions maximize energy gain; this predicts that limpets would forage for the entire duration of their potential activity phase (nocturnal low tides), and that the duration of grazing is predicted to be independent of limpet size. The second hypothesis was that limpets should minimize the time spent away from the home scar. This hypothesis predicts that there is less predation risk and less desiccation, and that limpets would only spend the time away from home necessary to balance energy expenditures. Hypothesis two also predicts a positive correlation time of grazing with size.

Comparison of empirical data with model outputs determined that neither hypothesis explained limpet foraging accurately for *P. vulgata*, but rather, *P. vulgata* follows a combination of the

two hypotheses at that site. In this study though, *P. vulgata* fed continuously at Menai Bridge (Wales) throughout the excursion, but in other studies and locations, such as in Evans and Williams (1991) at Lough Hyne, *P. vulgata* feeds triphysically. Santini and Chelazzi (1996) state that empirical evidence for continuous/noncontinuous feeding is still poor and needs further investigation, especially since *P. vulgata* exhibit different feeding patterns at different locations.

A similar modeling study was performed earlier by Evans and Williams (1991). They tested three hypotheses describing *P. vulgata*'s feeding behavior. The hypotheses were as follows: 1) foraging excursion would maximize net energy gain, 2) minimize energy costs, and 3) minimize the time spent away from the home scar. It was concluded using empirical evidence of *P. vulgata* at Lough Hyne, Ireland (which move only at night at high zones while lower intertidal limpets moved day and night, both of which foraged during the entire triphasic excursion) that *P. vulgata* adopts a time minimization strategy. Also discussed in the study were environmental constraints (such as desiccation) which could influence limpet foraging trips, and how these constraints change as one moves upshore. Desiccation risk for example, increase from low to high shore, and may force limpets at higher shore levels to shorten their excursions so they would not become dehydrated.

The first hypothesis presented by Evans and Williams (1991) was rejected because it would only be appropriate if they had a fixed amount of time in which to forage and an uncertain time before it would feed again, or if it was selected to maximize its growth rate. *P. vulgata* has a very predictable feeding time between tides so this hypothesis does not apply. Also, the limpets do not forage every tide. The second hypothesis was rejected because it would only work if limpets were under no pressure to achieve high growth rates, and experience few periods of resource stress, which did not occur for *P. vulgata* at Lough Hyne. The limpets may be minimizing the time away from the home scar, since they do not always feed during every tide. Both studies, however, assumed that the standing crop of microalgae was uniform in the study areas (Evans and Williams 1991).

Such modeling requires more experimentation, because different patterns of grazing activity can strongly influence the rate of energy intake, which in turn can affect energy balance within the functional cycle. Empirical evidence gathered at one location to test the model cannot be used to generalize behaviors for the same limpet species at other locations, due to variations in feeding behaviors. Foraging behavior of *P. vulgata* varies around Great Britain, which could be due to combinations of predation and desiccation risks among

other factors. Little *et al.* (1988) notes that limpets on low shore are smaller than limpets at high shore; limpet size can drastically influence behaviors too, a factor which modeling could overlook. Modeling also needs to consider the amount of rock ingested, mucous production, and respiration, because such factors can affect modeling outcomes.

Santini *et al.* (1995) investigated the energetic constraints (respiration, mucous production, and food ingestion) on the behavior of *P. vulgata*. They were able to determine the minimum acceptable energy content per unit area that an algal pasture should have in order to be profitably exploited by a limpet of a given size. They also modeled linear excursions, in areas in which the energy content per unit area linearly increased with distance from a limpets resting site. This model predicts that larger limpets will have a lower net rate of energy intake over a whole excursion than smaller ones. This agrees with the observations of Santina *et al.* (1995) in which although distance reached from home was not significantly related to individual limpet size, the individual duration and total length of excursions was positively related to shell length. The model was successful in reproducing size related constraints on foraging, and the predicted differences agreed with field observations. Models like this still need to take into affect the amount of mucous ingested on the way home

though, because this can reduce the net energy loss of foraging limpets.

Wax disks

Wax disks are a recently developed method to study homing behavior of limpets. This promising method involves pouring melted dental wax into a series of drilled holes (usually about 12 mm diameter) in rock in the field, until the wax is flush with the rock surface (Figure 10).

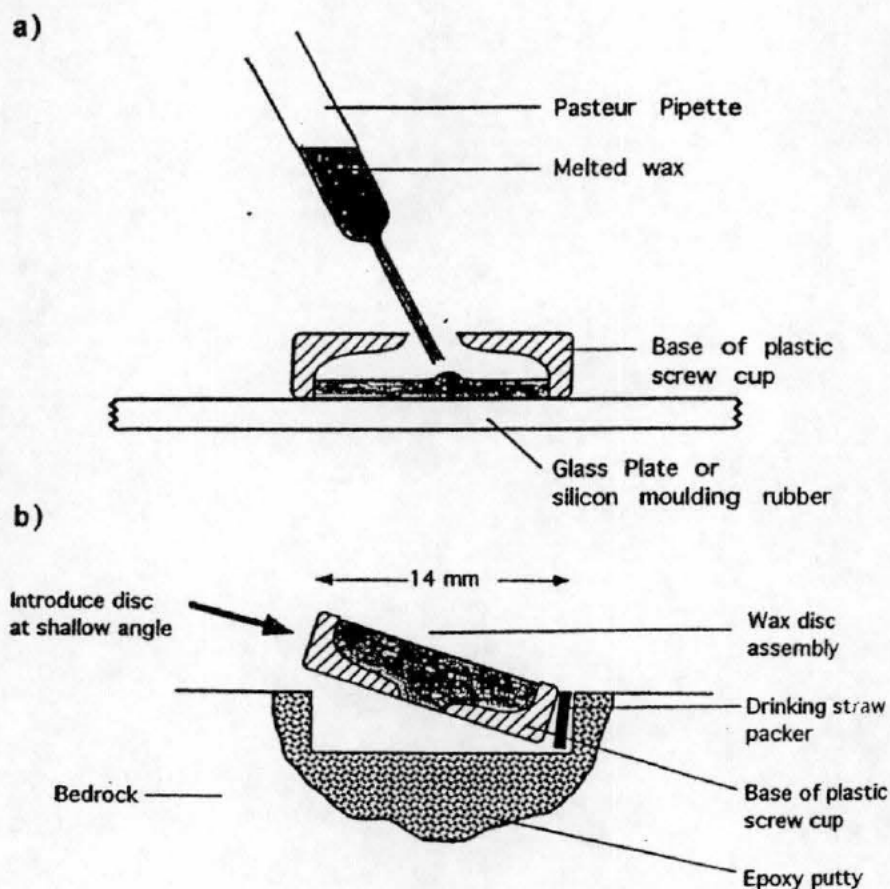


FIGURE 10 Cross-section of plastic screw cover showing (a) technique for filling with wax, (b) cross-section of disc assembly, and matching recess in the bedrock on the shore.

(From Thompson 1997)

When the wax hardens, it will be colonized by microalgae within a few weeks. Limpets will graze the microalgae on the disks, leaving permanent imprints of their radula marks. From this information, one can identify the species of gastropod which grazed the disk, determine how far limpets grazed from their home scar, determine a grazing intensity index, among other such useful data (see Hickman and Morris 1985).

While wax disks have proven to be a viable technique, they have limitations. The greater number of disks deployed, the more get grazed, so one must carefully plan how many days to leave out disks. Since grazer density affects how many disks get grazed, Thompson *et al.* (1997) recommends to leave wax disks in the field for no more than 14 days, otherwise disks get regrazed. Using the wax disk method, one can only obtain an index of grazing intensity, not absolute value, since it cannot be determined if disks are scraped in the same proportion as surrounding natural rock surface (Thompson *et al.* 1997).

Thompson *et al.* (1997) placed dental wax disks of 150 mm² into holes in rock to gauge spatial and temporal grazing intensity of gastropods. They found that grazing intensity increased through late winter and spring at the Isle of Man. This contrasts to the findings of Jenkins *et al.* (2001), in which limpet grazing was highest in the winter months, though no speculations for this feeding observation are found in

Thompson's study. The radula mark shapes could be used to some extent to determine what species grazed on it. In this study, for example, radula marks of *P. vulgata*, *P. gibbular*, and *Littorina obtusata* marks all looked different.

Biofilm

The biofilm on which homing limpets feed also has not received adequate attention until recently. Jenkins *et al.* 2001 measured chlorophyll a on rocks to gauge microalgal abundance. Raffaelli and Hawkins (1996) reviewed the importance of biofilm in community dynamics of rocky shores. Aside from these two writings along with a few others, biofilm in relation to limpet feeding dynamics has received little attention, probably due to difficulty in sampling and quantification of biofilms. In fact, it is difficult to identify the components of epilithic microbial communities since there are limited studies dealing with its taxonomy.

The role of limpets in structuring microalgal communities is somewhat documented, but the relationship between limpets and their food supply is less well studied (see Branch and Branch 1980, Creese and Underwood 1982, and Underwood 1984). Seasonal and spatial variation in food resources can affect life history strategies of gastropods (Bosman and Hockey 1988). Thompson *et*

al. (1997) saw a clear seasonal cycle of foraging effort in *P. vulgata* and microalgal abundance was demonstrated, but no other relationship between the two was apparent. Thompson *et al.* (1997) also states that grazers may help mediate spatial and temporal variation in biofilm.

Jenkins *et al.* (2001) determined how microalgal standing stock and level of grazing intensity on exposed rocky shores changes over a latitudinal gradient on the Isle of Man, southwest England, northern Spain, and SW Portugal. They chiseled samples of rock, and determined chlorophyll a absorbance at 665 and 750 nm. Figures 11a and 11b show chlorophyll a concentrations in three countries.

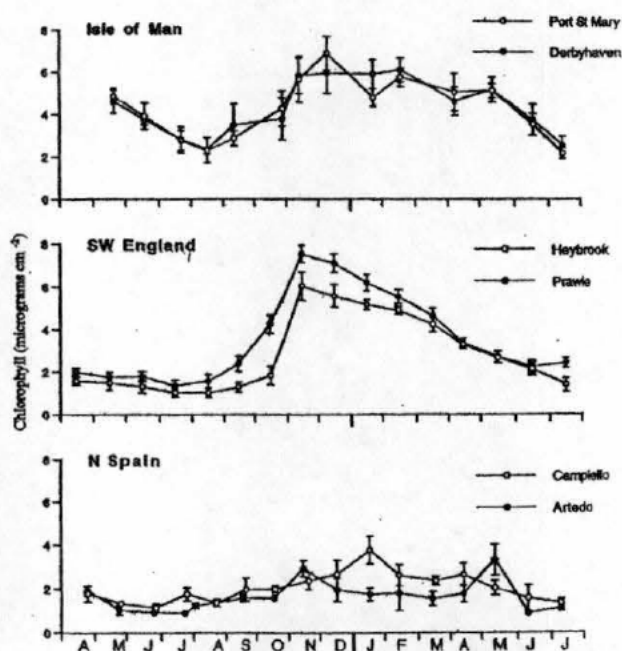


FIGURE 11a Mean chlorophyll a concentrations on rock chips from 2 exposed rocky shores at each of 3 locations over 15 mo. Error bars = ± 1 SE.

(From Jenkins *et al.* 2001)

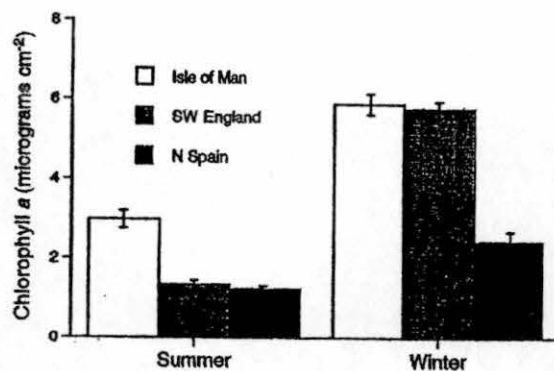


FIGURE 11b Mean chlorophyll a concentrations on rock chips at 3 locations for each of 2 seasons, summer and winter. Error bars = \pm 1SE.

(From Jenkins *et al.* 2001)

Microalgal densities declined with decreasing latitude, and varied seasonally. Limpet density and limpet grazing activity increased with decreasing latitude (except for Spain). No pattern of grazing was revealed by the wax disks in terms of limpet density in any of the four locations. There was, however, seasonal variation on wax disk grazing. Limpets grazed lowest in January and February in England, and peaked in early summer. A more ambiguous pattern emerged in Portugal, but it was similar to patterns seen in England. Northern Spain's two sites showed no consistent pattern. Marks made by crabs and topshells, however, hindered disk sampling in northern Spain. There is not much worry as to whether the limpets could alter behavior on wax disks, because in tests in this study, less than 15% of limpets changed speed or direction when encountering a disk. Finally, there was a significant relationship between mean sea temperature and grazing activity in England and the

Isle of Man. Limpet density and grazing activity therefore varies according to latitude in Europe, while microalgae abundance varies seasonally on rock in the intertidal zone, being highest during winter months (Jenkins et al. 2001).

Jenkins and Hartnoll (2001) studied grazing activity of *P. vulgata* on exposed and sheltered shores. They state that the abundance of microalgae across the wave exposure gradient is undescribed, and that little is known about the effects of wave action on foraging limpets. Chlorophyll a was measured over one year on exposed and sheltered shores in Great Britain, and was found to be more abundant in the winter months compared to summer. Sheltered shores exhibited higher levels of microalgae than exposed shores, which affected limpet grazing rates. At sheltered shores grazing activity was lesser since there was abundant microalgae, while at exposed shores, grazing rates were higher.

Chapter VIII

Conclusions and Proposal

Summary

Limpet homing behavior has been studied numerous times since the late 1800s. However, much still remains unknown about specific foraging patterns of homing limpets, such as when and where radula movements occur during feeding excursions on feeding loops for all homing species. In fact, most homing limpets have been poorly studied; *Patella vulgata* is by far the most observed homing limpet, followed by homing limpets of the west coast United States such as *Lottia digitalis*. Other homing species such as *Fissurella crassa* of Chile have been studied very seldomly; there is a need to study additional homing species so that general behavioral comparisons can be made between the better studied species.

The majority of homing studies occurred from the mid-1960s to the present. Most of these studies focused on gathering data on homing and clustering during low tide when limpets are at rest. Due to the difficulties of direct observation of limpets in rough surf or while submerged for long periods by divers, there is a severe lack of data on behaviors of homing limpets while they are moving and feeding, especially in the earliest

studies. Furthermore, many homing limpets behave erratically in laboratory settings (removal from habitat or moving them in laboratory tanks is traumatic and can alter or destroy homing behavior), rendering captivity a poor, often unsuccessful way to study natural homing tendencies.

Few techniques in the 1990s have overcome these difficulties. Many techniques are expensive and have been performed only by a small handful of scientists investigating just a few limpet species, with emphasis on *Patella vulgata*. LED tracking is one such recent ground breaking technology. It is perhaps one of the most useful, though expensive techniques, and has revealed much about limpet movements spatially and temporally, especially trail patterns and excursion times/durations.

The other two promising methodologies include wax disk placement within limpet feeding arenas in rocks in the field and, along with rock core sampling to reveal information regarding actual grazing data and biofilm biomass. Specific time, location, duration, and intensity of radula activity is largely unrecorded for homing limpets in the field in the literature. Wax disk use would be useful in gaining such knowledge.

Few studies have also investigated the importance and role of biofilm on limpet clusters. The amount and productivity of

the biofilm is undoubtedly very important to the formation and maintenance of clusters. If wax disk methodologies could be combined with chlorophyll sampling in the field, and perhaps with other techniques such as devices to record radula grazing noises, this would be a cost efficient means of investigating the relationships between biomass, grazing effort, and limpet growth inside homing limpet territories. Finally, more studies are needed which attempt to discover how and why limpets home at all, since many studies in the literature were short term, employed small samples, and often yielded contradictory results with other homing limpet studies.

There are only a handful of studies that have investigated the biofilm diet of homing limpets. The role of biofilm and its seasonal dynamics on limpet foraging has been largely overlooked in the literature. More studies are needed which study the variation in biofilm levels different distances from the home scar. Such studies can lead to insights such as shape and size of feeding arena, and how variables such as limpet size and density affect biofilms.

Proposal

Hamilton *et al.* (1966) studied the dispersal patterns of aggregating roosting starlings (*Sturnus vulgaris*) in an attempt

to identify the mechanism controlling movement to and from roosts. California starlings roost in large aggregations during the winter, and make daily foraging excursions away from the roost up to 50 miles away. Large numbers of individuals feeding near the roost cause over-exploitation of local food resources, leading to intraspecific competition. As a result, individuals will disperse, some of which travel greater distances to forage, thereby alleviating competition. Individuals adjust their feeding strategies in an effort to maximize energy gain while minimizing energy expenditure (Hamilton and Watt 1970). Members near the roost conserve energy by feeding near home, but food may be scarce due to exploitation. In contrast, individuals dispersing greater distances may have greater energy expenditure, but are compensated by access to higher food densities. Hamilton *et al.* (1966) stated that this model of balancing energy gain with dispersal time in starlings may form a basis for studying other aggregating animal species.

Starling dispersal is difficult to study since the birds travel vast distances every day, and one cannot easily determine how much prey it gathers in its journey and at what times and locations this occurs. The net energy gained and lost during the trips would also be difficult to measure in terms of caloric intake and loss. Seasonal factors such as temperature and adverse weather (wind) can also make the energetics of starling

dispersal difficult to study by increasing metabolism and creating greater energy demands. Interspecific competition in the territory for food with other birds also complicates the study of starling dispersal and foraging, sometimes forcing starlings to disperse further to find food. Furthermore, insects and seeds are patchy throughout the territory, which further complicates dispersal patterns.

I wish to apply Hamilton's *et al.* (1966) hypotheses to the limpet *Lottia digitalis*, a refuging limpet found in the mid- to high-intertidal zone of the Oregon coast. These semi-homing limpets often cluster in groups of two or more on rocks in the high intertidal while at rest during low tide, then disperse and feed on microalgae during high tide. Since *L. digitalis* lives in such a small territory (unlike starlings), they are an ideal organism for testing Hamilton's assumptions. Unlike Hamilton's *et al.* (1966) starling study, interspecific competition can be eliminated in the field, and microalgal food can be grown uniformly on rocks in the field to avoid patchiness. Seasonal conditions and weather phenomena like wind and temperature can also be controlled in the small environment of limpet arenas. While intraspecific competition between limpets for algal food resources is difficult if not impossible to measure, the impact of the dispersing limpets on algal resources can still be measured fairly easily.

Hypothesis 1: There is not a sharp variation in chlorophyll a at some distance from the cluster center.

Methodology: A series of rock cores around the clusters of *Lottia digitalis* will be collected. Rock corers 12 mm in diameter with diamond tipped rims will be used with a cordless Makita drill to collect cores from sandstone rock in the study area. Cores will be taken about 5 mm deep (algae and cyanobacteria do not exist deeper in rock) and placed into individual aluminum packets and frozen until analysis. Cores are removed from the rock easily as solid cylinders. Cores will be taken every 3 cm beginning inside the limpet cluster center (gently removing a limpet if needed) and radiate in straight lines (6 lines, 60 degrees apart to adequately cover all directions) as far from the cluster as the boulder or cliff will allow, or until two meters (limpets probably do not feed more than two meters away from the limpet cluster) (personal observation). Power analysis will be used to determine how many clusters are necessary to test.

Only isolated limpet clusters will be sampled, meaning clusters are far enough away from one another so that feeding arenas do not overlap. Two meters is sufficient, or clusters

which are surrounded by thick mats of algae like *Enteromorpha* are sufficiently isolated from surrounding grazers.

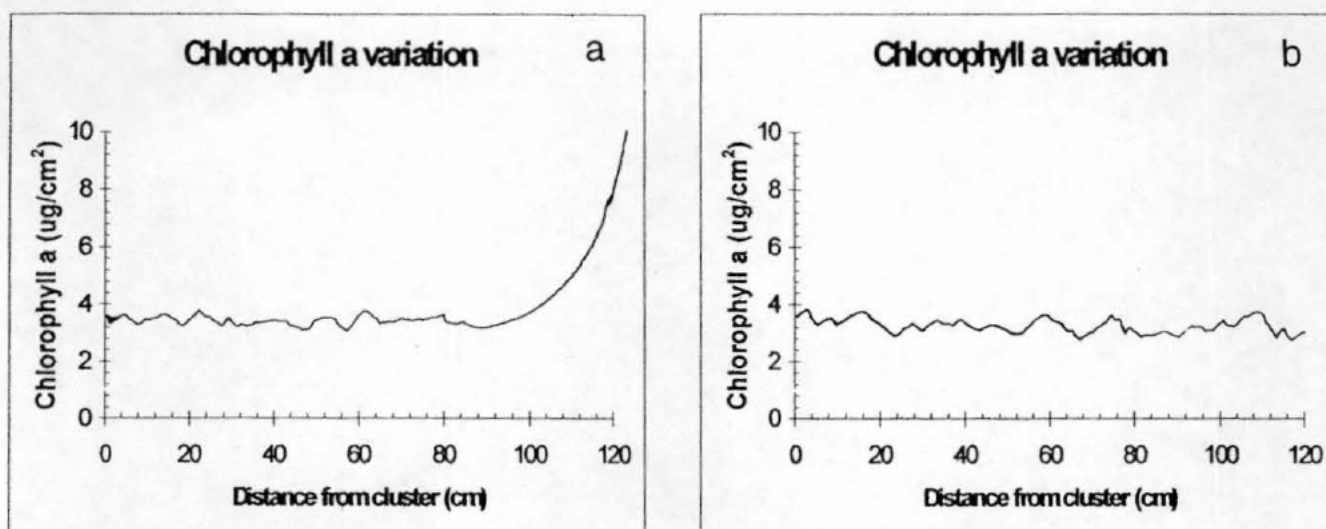
Chlorophyll a levels in the cores will be measured in a fluorometer using the technique of Thompson *et al.* (1997). The samples will be ground up individually using a mortar and pestle. Then 9 mL of methanol is added to the samples in centrifuge tubes, the tubes will then be shaken, then chilled overnight in the refrigerator to extract chlorophyll a. The next day, samples are warmed to room temperature for a half hour, then centrifuged on high for 10 min. The liquid is then decanted and read in a fluorometer

Expected results:

If hypothesis 1 is rejected, then there is a distinct algal front surrounding the limpet cluster (Figure 12a). In Hamilton's *et al.* (1966) model, the range of dispersal will be abrupt, and intraspecific competition is predicted to decline to zero (or close to zero) such that further dispersal beyond the front is not advantageous. This front is the outermost edge of the feeding arena. At some distance from the cluster, it is therefore unprofitable to feed any further away, since energy will be wasted in dispersal. Also, limpets must complete their feeding excursion during a low tide. Given their slow travel speed, they do not have the time to journey far distances away

from the cluster center and return back again. Therefore, one would expect to find an algal front that is significantly higher in chlorophyll a than in the feeding arena.

If hypothesis 1 is not rejected, then there is not a distinct increase in chlorophyll a at a given distance from the cluster center (Figure 12b). The algae in the feeding arena will be grazed about the same intensity as any surrounding algae. This would suggest that the limpets are not restricted to a feeding arena and travel any distance and direction from the cluster center to forage.



FIGURES 12a,b Chlorophyll a density at various distances from the cluster center of *L. digitalis*.

Hypothesis 2: Chlorophyll a levels do not rise sharply within the cluster itself as compared to the surrounding feeding arena.

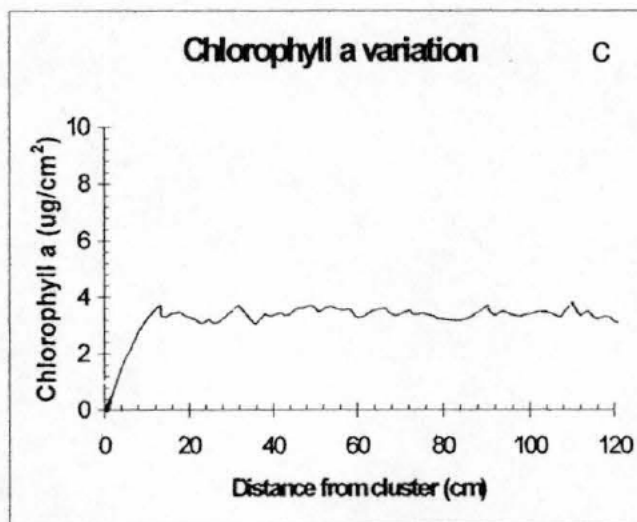
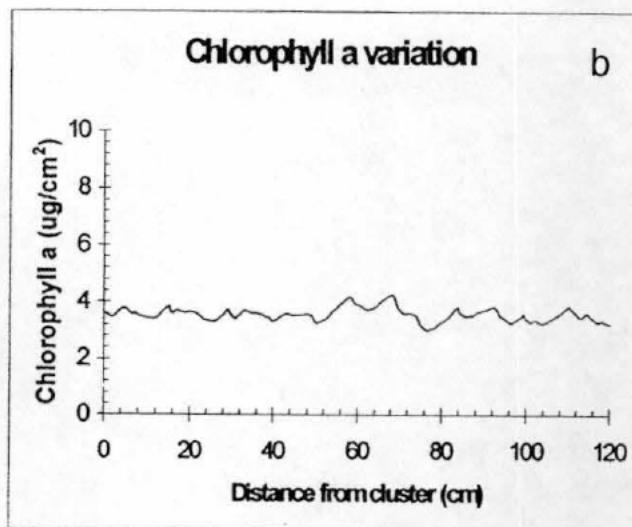
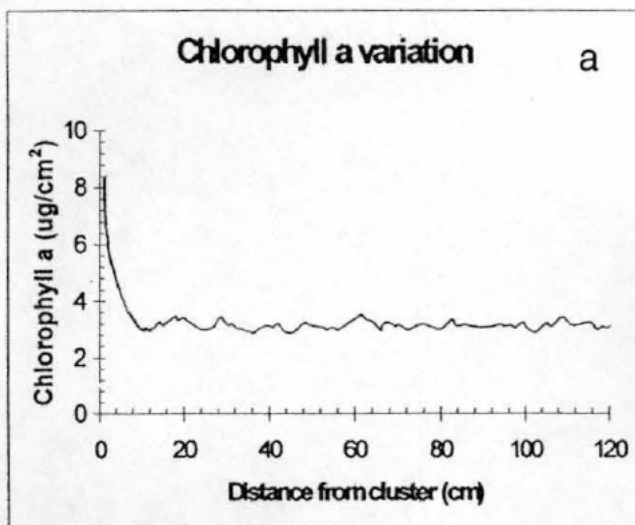
Methodology: Same as above

Expected results:

If hypothesis 2 is rejected, then chlorophyll a levels rise sharply in the cluster center (Figure 13a). It seems probable that in the cluster center, chlorophyll a density would be low due to trampling and feeding by limpets there. However, my pilot study revealed that chlorophyll a levels were higher in the cluster center than in the feeding arena. This could be due to mucus's ability to trap and grow microalgae.

If hypothesis 2 is not rejected, then chlorophyll a levels do not sharply rise in the cluster center. Two results may occur: 1) the chlorophyll a density in the cluster center is similar to chlorophyll a density in the surrounding feeding arena (Figure 13b), or 2) the chlorophyll a density in the cluster center is lower than in the surrounding feeding arena (Figure 13c). In the case of result 1, this suggests limpets are not overtrampling or heavily grazing the algae in the cluster center. In the case of result 2, the limpets are heavily trampling and/or grazing algae in the cluster center,

which might explain why chlorophyll a is lower there than in surrounding regions.



FIGURES 13a,b,c Chlorophyll a density at various distances from the cluster center of *L. digitalis*.

Hypothesis 3: Limpets do not feed throughout the feeding arena.

Methodology: Wax disks 12 mm in diameter will be placed into the holes in rocks previously cored above (Figure 14) for chlorophyll a samples (in the manner of Thompson *et al.* 1997) to gauge feeding patterns. Cores will be left out for a set number of weeks (as will be determined by pilot studies). Disks cannot be left in the field for too long otherwise disks will be grazed over several times, making them unreadable. Cavex hard dental wax will be used, which is melted and poured into plastic cups which are secured in the core holes using sliced plastic straws as springs (See Thompson *et al.* 1997). After exposure, disks will be carefully removed and photographed in the laboratory. Radula marks will be counted and identified to species.

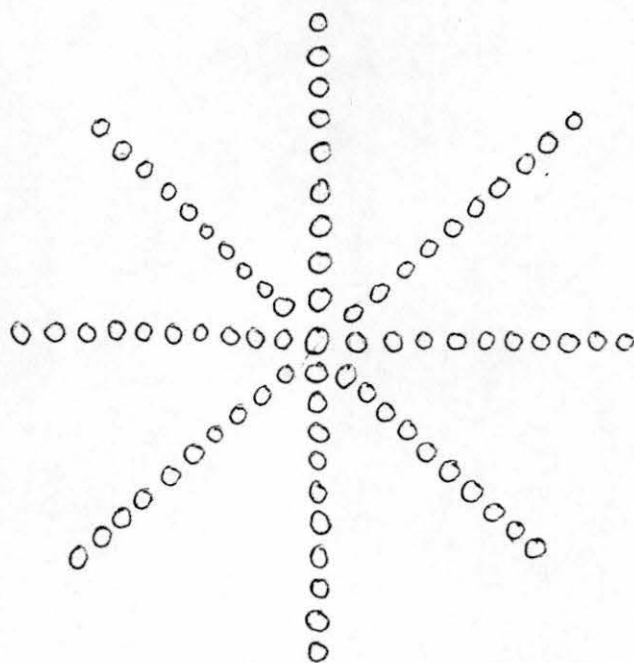


FIGURE 14 Configuration of cores and/or wax disks in the field, where disks are 12 mm in diameter and 3 cm apart.

Expected results:

If hypothesis 3 is rejected, then the limpets are feeding throughout the entire feeding arena (not including site of rest). This would be shown by radula marks on wax disks throughout the feeding arena. It is energetically efficient to feed throughout the territory to reduce interspecific competition for food and space, and to avoid overgrazing of algae in any one region of the arena.

If hypothesis 3 is not rejected, then limpets are not feeding throughout the entire feeding arena. This is apparent if not all the disks were grazed equally in the arena. This would suggest limpets are not being energetically efficient, since they may be favoring and feeding on one side of the arena while feeding, thus competing for algae and space.

Hypothesis 4: The density of *L. digitalis* per unit area decreases away from the limpet cluster.

Methodology: During high tide, limpets must be observed by scuba diving (or automated camera if funding permits) to record their dispersal movements. The number of limpets per cm^2 will be counted and mapped in all regions of the feeding arena throughout the high tide so that average limpet densities at any

given distance away from the resting cluster can be determined at any time. As many limpet clusters as possible at one site will be studied in this manner on as many occasions as is necessary (determined by statistical testing). Also, clusters must contain 10 limpets or greater in order to exhibit ideal dispersal.

Expected Results: Hypothesis 4 is one of Hamilton's *et al.* (1966) predictions regarding clustering animals. According to Hamilton *et al.* (1966), such a dispersal pattern would result in two advantages; 1) a reduction in intraspecific competition for algal resources, and 2) such dispersal compensates further ranging individuals with more available food. If hypothesis 4 is rejected, then we would see that the number of limpets per unit area does not decrease with distance away from the limpet cluster's resting area. There could either be 1) a uniform limpet distribution per unit area throughout the feeding arena, or 2) there could be more limpets per unit area with increasing distance from the cluster center.

If we fail to reject hypothesis 4, then the number of limpets per unit area decreases with distance away from the resting cluster. This is the expected result, since it reduces competition for algae via dispersal. It is more energetically

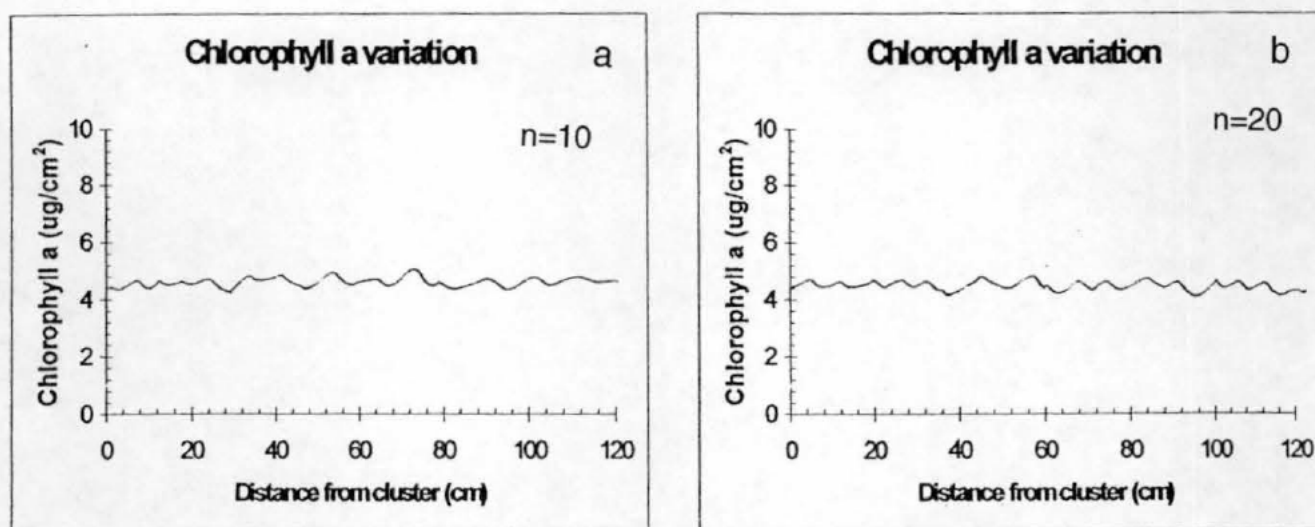
efficient for the disperser since the limpet does not have to graze over areas that were just grazed by other nearby limpets.

Hypothesis 5: Smaller clusters of *L. digitalis* have a lesser impact upon algal resources close to the cluster center than do larger clusters.

Methodology: Small limpet clusters will be defined as 10 *L. digitalis*, while large limpet clusters will be defined at 20 individuals. In the field, areas of vertical rock in the upper intertidal will be cleared of animals and algae so that *L. digitalis* may be contained there. Microalgae will be allowed to grow there first for a month. Replicates (the number of which must first be determined using power analysis) of small and large clusters will each have their independent feeding arenas, surrounded by a circle of copper paint to keep them in and to keep out other grazers. Caging is to be avoided due to its shading effects on algae growth. Limpets will be allowed to graze for one month during the summer, then the chlorophyll a in the feeding arena will be sampled according to the methodology described above.

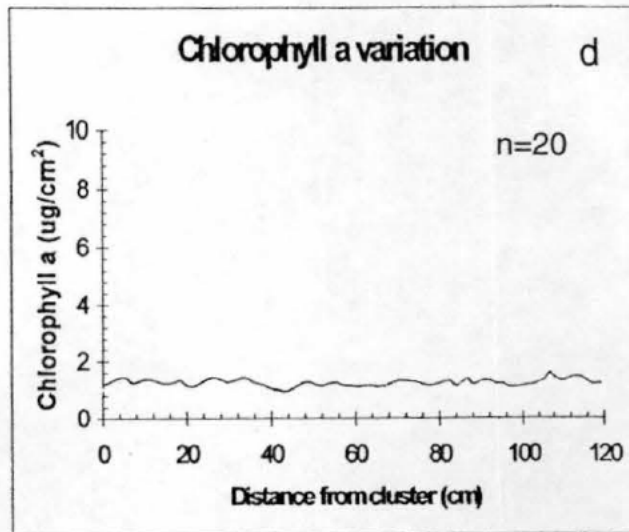
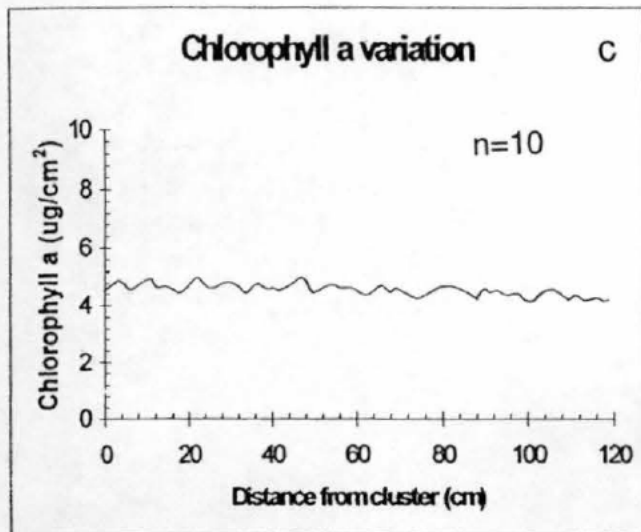
Expected Results: Hypothesis 5 is another one of Hamilton's et al. (1966) predictions regarding numbers of dispersing animals.

If hypothesis 5 is rejected, then the algal resources, as shown by chlorophyll a density, will not be greater near the vicinity of the smaller limpet cluster than near the larger limpet cluster (Figures 15a, 15b). Algal resources will either be equal or greater in the vicinity of the small vs. large limpet clusters.

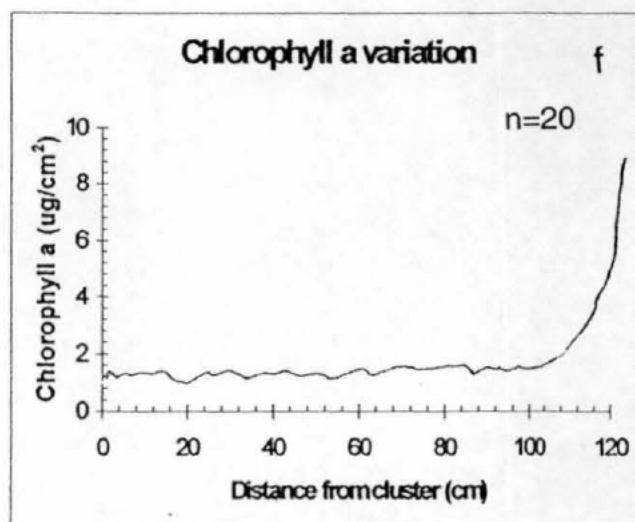
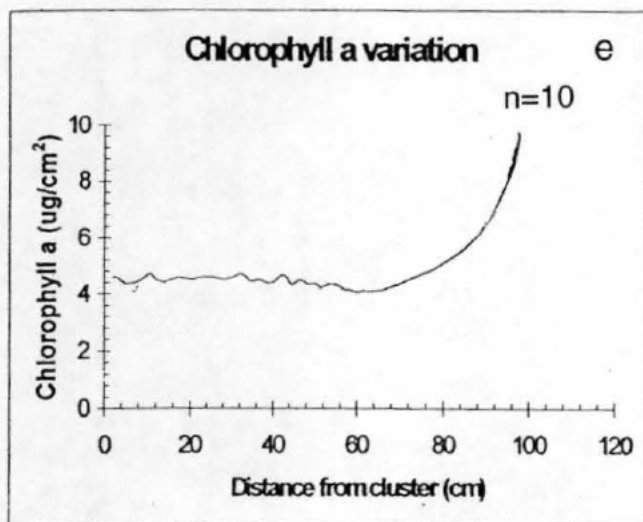


FIGURES 15a-f Chlorophyll a density at various distances from the cluster center of *L. digitalis*. Small clusters are defined as n=10 limpets, large clusters as n=20 limpets.

If hypothesis 5 is not rejected, then we expect the algal density to be higher in the vicinity of the small limpet cluster (Figure 15c) than the large limpet cluster (Figure 15d). This is what is expected, since the more limpets present, the greater amount of algae would be consumed.



Also, we expect that if an algal front is present, it would occur closer to the cluster center in the small cluster (Figure 15e) than large cluster (Figure 15f).



Literature Cited

- Boyden CR, Zeldis JR (1979) Preliminary observations using an attached microphonic sensor to study feeding behavior of an intertidal limpet. *Estuarine and Coastal Marine Science* 9: 759-769
- Bosman AL, Hockey PAR (1988) Life-history patterns of populations of the limpet *Patella granularis*: The dominant roles of food supply and mortality rate. *Oecologia* 75: 412-419
- Branch GM (1971) The ecology of *Patella Linnaeus* from the Cape Peninsula, South Africa I. Zonation, movements, and feeding. *Zoologica Africana* 6: 1-38
- Branch GM (1981) The biology of limpets: physical factors, energy flow, and ecological interactions. *Mar Biol Ann Rev* 19: 235-380
- Branch GM (1985) Limpets: their role in littoral and sublittoral community dynamics. In: Moore PG, Seed R (eds) *The ecology of rocky coasts*. Hodder and Stroughton, Kent
- Branch GM, Barkai A (1988) Interspecific behavior and its reciprocal interaction with evolution, population dynamics and community structure. In: Chelazzi G, Vannini M (eds) *Behavioural adaptations to intertidal life*. NATO ASI series, Vol. 151. Plenum Press, New York
- Branch GM, Branch ML (1980) Competition between *Cellana tramoserica* (Sowerby) (Gastropoda) and *Patiriella exigua* (Lamarck) (Asteroidea), and their influence on algal standing stocks. *J Exp Mar Biol Ecol* 48: 35-49
- Branch GM, Cherry MI (1985) Activity rhythms of the pulmonate limpet *Siphonaria capensis* Q. & G. as an adaptation to osmotic stress, predation, and wave action. *J Exp Mar Biol Ecol* 87: 153-168
- Bohn G (1909) De l'orientation chez les patelles. *C R Acad Sci* 148: 868-870

- Breen PA (1971) Homing behaviour and population regulation in the limpet *Acmaea (Collisella) digitalis*. *Veliger* 14: 177-183
- Carriker MR, Martin B (1965) Analysis of shell boring behavior of muricid gastropod *Urosalpinx Cinerea* (Say) by means of colour motion picture and microhydrophone recording of radula sounds (Abstract). *American Zoologist* 5: 645
- Castenholz RW (1961) The effect of grazing on marine littoral diatom populations. *Ecology* 42: 783-794
- Chelazzi G, Innocenti R, Santina PD (1983) Zonal migration and trail-following of an intertidal gastropod analyzed by LED tracking in the field. *Mar Behav Physiol* 10: 121-136
- Chelazzi G, Santina PD, Santini G (1994a) Rhythmical timing and spatial scattering of foraging in a homer limpet (*Patella rustica*). *Behavioral Ecology* 87: 288-292
- Chelazzi G, Santini G, Parpagnoli D, Santina PD (1994b) Coupling motographic and sonographic recording to assess foraging behaviour of *Patella vulgata*. *J Moll Stud* 60: 123-128
- Chelazzi G, Santini G, Santina PD (1998) Route selection in the foraging of *Patella vulgata* (Mollusca: Gastropoda). *J Mar Biol Ass U.K.* 78: 1223-1232
- Chelazzi G, Terranova G, Santina PD (1990) A field technique for recording the activity of limpets. *J Moll Stud* 56: 595-600
- Collins LS (1977) Substrate angle, movement and orientation of two sympatric species of limpets, *Collisella digitalis* and *Collisella scabra*. *Veliger* 20: 43-48
- Connor VM (1986) The use of mucous trails by intertidal limpets to enhance food resources. *Biol Bull* 171: 548-564
- Cook A, Bamford OS, Freeman JDB, Teideman DJ (1969) A study of the homing habit of the limpet. *Animal Behaviour* 17: 330-339
- Cook SB (1969) Experiments on homing in the limpet *Siphonaria normalis*. *Anim Behav* 17: 679-682

- Cook SB, Cook CB (1975) Directionality in the trail-following response of the pulmonate limpet *Siphonaria alternata*. *Mar Behav Physiol* 3: 147-155
- Cook SB, Cook CB (1981) Activity patterns in *Siphonaria* populations: heading choice and the effects of size and grazing interval. *J Exp Mar Biol Ecol* 49: 69-79
- Craig PC (1968) The activity pattern and food habits of the limpet *Acmaea pelta*. *Veliger* (Supplement) 11: 13-19
- Creese RG, Underwood AJ (1982) Analysis of inter- and intra-specific competition amongst intertidal limpets with different methods of feeding. *Oecologia* 53: 337-346
- Creese RG (1982) Distribution and abundance of the Acmaeid limpet, *Patelloida latistrigata*, and its interaction with barnacles. *Oecologia* 52: 85-96
- Eaton CM (1968) The activity and food of the file limpet *Acmaea limatula*. *Veliger* (Supplement) 11: 5-12
- Evans MR, Williams GA (1991) Time partitioning of foraging in the limpet *Patella vulgata*. *Journal of Animal Ecology* 60: 563-575
- Farrell TM (1988) Community stability: effects of limpet removal and reintroduction in a rocky intertidal community. *Oecologia* (Berlin) 75: 190-197
- Forrest RE, Chapman MG, Underwood AJ (2001) Quantification of radular marks as a method for estimating grazing of intertidal gastropods on rocky shores. *J Exp Mar Biol Ecol* 258: 155-171
- Frank PW (1964) On home range of limpets. *American Naturalist* 98: 99-104
- Frank PW (1965) The biodemography of an intertidal snail population. *Ecology* 46: 831-844
- Gailbraith RT (1965) Homing behavior in the limpets *Acmaea digitalis* and *Lottia gigantea*. *The American Midland Naturalist*. 74: 245-246

- Gray DR, Hodgson AN (1998) Foraging and homing behaviour in the high-shore, crevice-dwelling limpet *Helcion pectunculus* (Prosobranchia: Patellidae). *Marine Biology* 132: 283-294
- Gray DR, Naylor E (1996) Foraging and homing behaviour of the limpet, *Patella vulgata*: a geographical comparison. *J Moll Stud* 62: 121-124
- Hartnoll RG (1986) The monitoring of limpet movement: a review. *Progress in Underwater Sciences* 11: 137-146
- Hartnoll RG, Wright JR (1977) Foraging movements and homing in the limpet *Patella vulgata* L. *Animal Behavior* 25: 806-810
- Hawkins SJ, Hartnoll RG (1983) Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology Annual Review* 21: 195-282
- Hewatt WG (1940) Observations on the homing limpet, *Acmaea digitalis* and *Lottia gigantea*. *American Midland Naturalist* 24: 205-208
- Hickman CS, Morris TE (1985) Gastropod feeding tracks as a source of data in analysis of the functional morphology of radulae. *Veliger* 27: 357-365
- Horn PL (1986) Energetics of *Chiton pelliserpentis* (Quoy and Gaimard, 1835) Mollusca: Polyplacophora) and the importance of mucus in its energy budget. *J Exp Mar Biol Ecol* 101: 119-141
- Iwasaki K (1999) Short- and long-term movements of the patellid limpet *Patella flexuosa* within gaps in intertidal mussel beds. *J Moll Stud* 65: 295-301
- Jenkins SR, Hartnoll RG (2001) Food supply, grazing activity and growth rate in the limpet *Patella vulgata* L.: a comparison between exposed and sheltered shores. *J Exp Mar Biol Ecol* 258: 123-139
- Jenkins SR, Arenas F, Arrontes J, Bussell J, Castro J, Coleman RA, Hawkins SJ, Kay S, Martinez B, Okiveros J, Roberts MF, Sousa S, Thompson RC, Hartnoll RG (2001) European-scale analysis of seasonal variability in limpet grazing activity and microalgal abundance. *Marine Ecology Progress Series*

211: 193-203

- Jessee WF (1968) Studies of homing behavior in the limpet *Acmaea scabra*. *Veliger* 11 (Supplement): 52-55
- Kacelnik A, Houston AI (1984) Some effects of energy costs on foraging strategies. *Animal Behaviour* 32: 609-614
- Kitting CL (1979) The use of feeding noises to determine the algal foods being consumed by individual intertidal molluscs. *Oecologia* 40: 1-17
- Lewis JR (1954) Observations on a high-level population of limpets. *J Anim Ecol* 23: 85-100
- Lindberg DR (1986) Name changes in the "Acmaeidae." *Veliger* 29: 142-148
- Little C, Morrill D, Paterson DM, Stirling P, Williams GA (1990) Preliminary observations on factors affecting foraging activity in the limpet *Patella vulgata*. *Mar Biol Ass U.K.* 70: 181-195
- Little C, Stirling P (1985) Patterns of foraging activity in the limpet *Patella vulgata* L.-a preliminary study. *J Exp Mar Biol Ecol* 89: 283-296
- Little C, Williams GA, Morrill D, Perrins JM, Stirling P (1988) Foraging behaviour of *Patella vulgata* L. in an Irish sea-lough. *J Exp Mar Biol Ecol* 120: 1-21
- Liu JH (1993) Activity rhythms and "homing" behaviour by two pairs of high- and low-zoned intertidal limpets in Hong Kong. In: Morton B (ed) *The Marine Biology of the South China Sea*. Hong Kong University Press, Hong Kong.
- McFarlane ID (1980) Trail-following and trail-searching behaviour in homing of the intertidal gastropod mollusc, *Onchidium verruculatum*. *Mar Behav Physiol* 7: 95-108
- Millard CS (1968) The clustering behavior of *Acmaea digitalis*. *Veliger* (Supplement) 11: 45-51
- Miller AC (1968) Orientation and movement of the limpet *Acmaea digitalis* on vertical rock surfaces. *Veliger* (Supplement) 11: 30-44

- Morgan CL (1894) The homing of limpets. *Nature* 51: 127
- Ocana TMJ, Emson RH (1999) Preliminary observations on the timing and geometry of foraging activity in the intertidal pulmonate limpet *Siphonaria pectinata*. *J Mar Biol Ass U.K.* 79: 459-465
- Parpagnoli D, Chelazzi G (1995) An automatic technique for recording grazing activity of limpets. *J Moll Stud* 61: 339-346
- Petraltis PS (1992) Effects of body size and water temperature on grazing rates of four intertidal gastropods. *Australian Journal of Ecology* 17: 409-414
- Petraltis PS and Sayigh L (1987) In situ measurement of radular movements of three species of *Littorina* (Gastropoda: Littorinidae). *Veliger* 29: 384-387
- Pieron H (1909) Contribution a la biologie de la patelle et de la calyptree. Lesens de retour et la memoire topographique. *Arch Zool Exp Gen Se Ser* 1: 18-29
- Raffaelli D, Hawkins SJ (1996) Intertidal ecology. Chapman and Hall, London.
- Ross TL (1968) Light responses in the limpet *Acmaea limatula*. *Veliger* (Supplement) 11: 25-29
- Russell ES (1907) Environmental studies on the limpet. *Proc Zool Soc Lond* 2: 856-870
- Santina PD, Naylor E, Chelazzi G (1994) Long term field actography to assess the timing of foraging excursions in the limpet *Patella vulgata* L. *J Exp Mar Biol Ecol* 178: 193-203
- Santina PD, Santini G, Chelazzi G (1995) Factors affecting variability of foraging excursions in a population of the limpet *Patella vulgata* (Mollusca, Gastropoda). *Marine Biology* 122: 265-270
- Santina PD, Naylor E (1993) Endogenous rhythms in the homing behaviour of the limpet *Patella vulgata* Linnaeus. *J Moll Stud.* 59: 87-91
- Santini G, Chelazzi G (1996) Energy maximization vs. time

- minimization in the foraging of the limpet *Patella vulgata*.
Journal of Animal Ecology 65: 599-605
- Santini G, Chelazzi G, Santina P (1995) Size-related functional and energetic constraints in the foraging of the limpet *Patella vulgata* (Mollusca, Gastropoda). *Functional Ecology* 9: 551-558
- Santini G, Santina P, Chelazzi G (1991) A motographic analysis of foraging behavior in intertidal chitons (*Acanthopleura* spp) *J Mar Biol Ass U.K.* 71: 759-769
- Serra G, Chelazzi G, Castilla JC (2001) Temporal and spatial activity of the key-hole limpet *Fissurella crassa* (Mollusca: Gastropoda) in the eastern Pacific. *J Mar Biol Ass U.K.* 81: 485-490
- Southward AJ, Southward EC (1978) Recolonization of rocky shores in Cornwall after use of toxic dispersion to clean up the Torrey Canyon Spill. *J Fish Res Board Can* 35: 682-706
- Stephenson TA (1936) The marine ecology of the South African Coast, with special reference to the habits of limpets. *Proc Linn Soc Lond* 148: 74-79
- Thomas RF (1973) Homing behavior and movement rhythms in the pulmonate limpet, *Siphonaria pectinata* Linnaeus. *Proc. Malac. Soc. Lond.* 40: 303-311
- Thompson RC, Johnson LE, Hawkins SJ (1997) A method for spatial and temporal assessment of gastropod grazing intensity in the field: the use of radula scrapes on wax surfaces. *Journal of Experimental Marine Biology and Ecology* 218: 63-76
- Underwood AJ (1984) Vertical and seasonal patterns in competition for microalgae between intertidal gastropods. *Oecologia* 64: 211-222
- Verderber GW, Cook SB, Cook CB (1983) The role of the home scar in reducing water loss during aerial exposure of the pulmonate limpet *Siphonaria alternata* (Say). *Veliger* 25: 235-243
- Villee CA, Groody TC (1940) The behavior of limpets with reference to their homing instinct. *American Midland Naturalist* 24: 190-204

Williams GA, Little C, Morritt D, Stirling P, Teagle L, Miles A, Pilling G, Consalvey M (1999) Foraging in the limpet *Patella vulgata*: the influence of rock slope on the timing of activity. Mar Biol Ass U.K. 79: 881-889

Willoughby JW (1972) A field study on the clustering and movement behavior of the limpet *Acmaea digitalis*. The Veliger 15: 223-230