

Size Gradients and Shell Polymorphism in Limpets with Consideration of the Role of Predation

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(9 Text figures)

INTRODUCTION

ROCKY SHORES are generally inhabited by a number of different limpet species which have overlapping vertical distributions and which show considerable variation in size and colour or shell pattern. This variation is, however, of an ordered nature. Definite shore-level size gradients have been detected in limpets (VERMEIJ, 1972; 1973; BREEN, 1972). Size gradients have also been found in a variety of other intertidal organisms including other gastropods (EDWARDS, 1969; BERTNESS, 1977; LOUDA, 1979) and bivalves (READING, 1979). Explanations for these size gradients have included vertical migration (FRANK, 1965; BREEN, 1972), differential growth (LOUDA, 1979), physiological stress (WOLCOTT, 1973) and differential mortality (VERMEIJ, 1972). The explanation by Vermeij is based on the idea that gradients in mortality occur and that postlarval prereproductives will generally be found in a zone of minimum mortality. BERTNESS (1977) has questioned this interpretation in his study of carnivorous snails (Thaididae). Size gradients in these snails are regulated by behavioural responses to light and gravity and the selective advantage in the size gradient pattern appears to be related to a similar pattern in their prey, the barnacle. The snails are placed in close proximity to the size classes and species of barnacles which are preferred and most efficiently utilized. The size gradient in the balanoids is presumably developed by a tidally induced gradient of available feeding times.

In the case of limpets, it seems probable that both migration and predation mortality are involved. That migration is an important factor is well brought out by Frank's paper (FRANK, 1965) in which it was shown that fingered limpets, *Collisella digitalis* (RATHKE, 1833) ascended in

the fall and winter and descended to a lesser extent in the spring. Such net upward movements (also detected by BREEN, 1972) result in older and larger individuals occurring at higher levels. Both Frank and Breen suggest that such movements are adaptive and very possibly related to predation pressure.

The action of predators has been considered by PALMER (1977) as the probable force behind shell form and sculpture in *Ceratostoma foliatum* (GMELIN, 1791) and other gastropods (VERMEIJ, 1976; PALMER, 1979) and behind the existence of shell polymorphisms in limpets (GIESEL, 1970). As early as 1945, Test noted the absence of conspicuous forms of limpets on the intertidal and suggested that their resemblance to the substrate was the result of continual selective predation by visual predators like shorebirds. Giesel accepted predation by shorebirds as an explanation for the presence of 2 morphs of *Collisella digitalis*, one form tending to inhabit rock surfaces and the other being associated with the gooseneck barnacle *Pollicipes polymerus* (SOWERBY, 1833). According to Giesel, disruptive selection was the force behind the establishment and maintenance of the polymorphism. Visual predators were also thought to be an important factor in the colour polymorphism detected in *Crepidula convexa* Say, 1822 (HOAGLUND, 1977).

Although predation has been cited as an important process affecting both size and shell pattern of limpets and other forms on the intertidal, evidence for such a role is sadly lacking. This is especially true for avian predators which in a number of studies have been singled out as important. HOAGLUND (1977) made one observation of a gull attacking a snail, *Littorina littorea* (Linnaeus, 1758), with 2 *Crepidula convexa* attached and on this basis suggested that visual predators which detect pigment differ-

ences were important to the colour polymorphism in *Crepidula*. BREEN (1972) did not observe any predation by shorebirds. GIESEL (1970) based his premise partly on the coincidence of the timing of greatest disruption of pattern frequencies in limpets with the seasonal occurrence of high densities of oystercatchers and other shorebirds but had no supporting data on foraging by the birds. The present study was initiated in order to confirm the existence of reported patterns of size and shell colour in *Collisella digitalis*, to extend the study to other limpet species and to examine the influence of Black Oystercatchers *Haematopus bachmani* Audubon on the observed patterns. Previous studies had indicated that these birds utilized many limpets, including *C. digitalis*, in their diet (HARTWICK, 1976).

MATERIALS AND METHODS

The study took place on Cleland Island on the west coast of Vancouver Island, Canada. This is a small island with exposed rocky shores and a considerable population of Black Oystercatchers which utilize these shores for feeding (HARTWICK, 1974). Much of the study took place in 2 shore areas with relatively uniform topography and exposure and well developed zonation. Quadrats (0.093 m^2) were randomly placed along transects and all limpets within the quadrats were removed. Previous observations (HARTWICK, 1976) had indicated that oystercatchers might hunt differently in the different zones occurring on exposed rocky shores. Since these zones were arranged vertically, they were used to stratify sampling. The zones considered were a high intertidal rockweed zone (largely *Fucus* and *Endocladia*), the mussel bed (*Mytilus californianus* Conrad, 1837), groves of sea palms (*Postelsia*) and finally, the lower intertidal, which can be designated as the *Laminaria* zone. Sampling then was carried out within these 4 zones. All limpets were identified to species, measured by vernier calipers (length) and given a colour code. Shell scoring was a modified version of that described by GIESEL (1970). The rim and apex were scored 0 for white, 1 for grey, 2 for brown and 3 for black, while the striping on the general shell surface was scored as 0 for plain white, 1 for light with a single stripe, 2 for mostly light with more than a single dark band, 3 for when dark shades predominate, and striping is heavy, 4 for almost all brown with very little white, 5 for mottled brown-black and 6 for black or dark grey-black. Final score was obtained by adding the 3 scores together for each limpet so that a maximum score of 12 represented a uniformly dark limpet while the lowest

score of 0 represented a light limpet. This scoring scheme worked well and was consistent when different people used it.

Black Oystercatchers feeding in the area were observed and limpets attacked by the birds on the intertidal were carefully collected after observation. Preyed upon limpets were identified, measured and scored for shell patterns.

Limpets of similar size were collected and scored for shell pattern. Light and dark ones were separated and then placed in arrays of 20 in rockweed and open rock areas where Oystercatchers were known to forage. The sequence in which the birds attacked light and dark limpets within these alternating arrays was noted (see HARTWICK, 1978a, for details on the method).

Counts of limpets within the quadrats provided estimates of density. Sampling for limpets was carried out monthly from July 1976 to July 1977, although several winter collections were missed entirely or partly because of heavy sea conditions.

Foraging time spent in each of the zones was recorded for 5 different pairs of birds at various times in their breeding cycle. Observations were made by telescope or binoculars from blinds or from vantage points some distance away.

RESULTS

Trends in Shell Length

Limpet species examined included *Collisella digitalis* (RATHKE, 1833), *C. pelta* (RATHKE, 1833), *Notoacmea persona* (RATHKE, 1833), and *N. scutum* (RATHKE, 1833). The mean lengths for all limpet species combined were significantly different in each of the 4 designated zones ($p < 0.05$). Limpets showed an increasing size gradient from the high intertidal (mean length = $8.63 \pm 2.80 \text{ mm}$) down to the *Postelsia* beds (mean length = $11.30 \pm 3.44 \text{ mm}$) with a slight drop in mean size in the lower intertidal or *Laminaria* zone (Table 1).

The trend in shell length for *Collisella digitalis* was similar to that described for all species combined. Mean shell length peaked in the *Postelsia* bed (Table 1). The species was scarce in the lower intertidal.

Seasonal changes in mean length of all limpets combined were observed in all 4 zones. The data in Table 1 indicate that a pattern of increasing length occurs in the rockweed and mussel bed zones from October to April and then there is an abrupt decrease in April and May. In the *Postelsia* bed mean shell length increases from May to reach a high

Table 1

Shore-level trends in shell length for all limpet species combined and for *Collisella digitalis* alone at various times in the year. Data on *Collisella digitalis* alone are given in brackets. Sample size is also indicated in brackets. A dash indicates data not available.

Time of Sampling	Mean Shell Length $\pm$ SD (n)			
	Rockweed zone	Mussel bed	<i>Postelsia</i> grove	<i>Laminaria</i> zone
July/76	8.14 $\pm$ 1.63 (161) (8.37 $\pm$ 1.54, 135)	7.69 $\pm$ 2.69 (351) (8.57 $\pm$ 2.86, 195)	11.54 $\pm$ 1.51 (110) (10.16 $\pm$ 2.38, 33)	12.34 $\pm$ 5.14 (7) —
Aug.	9.49 $\pm$ 1.98 (166) (9.53 $\pm$ 1.66, 131)	9.47 $\pm$ 2.07 (236) (9.68 $\pm$ 1.82, 204)	11.71 $\pm$ 4.17 (151) (9.63 $\pm$ 2.40, 87)	8.83 $\pm$ 3.67 (3) —
Oct.	8.89 $\pm$ 1.69 (102) (8.89 $\pm$ 1.69, 102)	8.77 $\pm$ 1.99 (160) (8.79 $\pm$ 3.29, 133)	12.35 $\pm$ 3.71 (71) (10.22 $\pm$ 2.43, 34)	— —
Jan./77	8.94 $\pm$ 1.82 (68) (8.94 $\pm$ 1.82, 68)	10.05 $\pm$ 1.48 (29) (10.05 $\pm$ 1.48, 29)	— —	— —
April	10.28 $\pm$ 1.67 (12) (10.28 $\pm$ 1.67, 12)	10.44 $\pm$ 1.72 (19) (10.44 $\pm$ 1.72, 19)	— —	— —
May	8.12 $\pm$ 1.61 (139) (8.16 $\pm$ 1.61, 134)	9.34 $\pm$ 2.29 (189) (9.36 $\pm$ 1.87, 148)	8.05 $\pm$ 3.60 (30) (7.86 $\pm$ 3.13, 11)	9.65 $\pm$ 5.4 (39) (5.00 $\pm$ 0.0, 1)
June	7.93 $\pm$ 1.70 (162) (8.19 $\pm$ 0.79, 130)	8.89 $\pm$ 1.80 (286) (9.42 $\pm$ 1.69, 200)	9.86 $\pm$ 3.20 (62) (9.54 $\pm$ 1.96, 12)	9.19 $\pm$ 3.21 (65) (8.37 $\pm$ 0.90, 3)
July	8.98 $\pm$ 5.67 (161) (9.17 $\pm$ 6.03, 139)	9.38 $\pm$ 1.42 (230) (9.66 $\pm$ 1.31, 189)	11.48 $\pm$ 3.59 (145) (10.78 $\pm$ 1.64, 23)	12.28 $\pm$ 3.40 (33) —
overall means	8.63 $\pm$ 2.80 (971) (8.75 $\pm$ 2.81, 851)	8.86 $\pm$ 2.11 (1500) (9.31 $\pm$ 2.17, 1117)	11.30 $\pm$ 3.44 (564) (9.85 $\pm$ 2.35, 200)	10.15 $\pm$ 4.04 (147) —

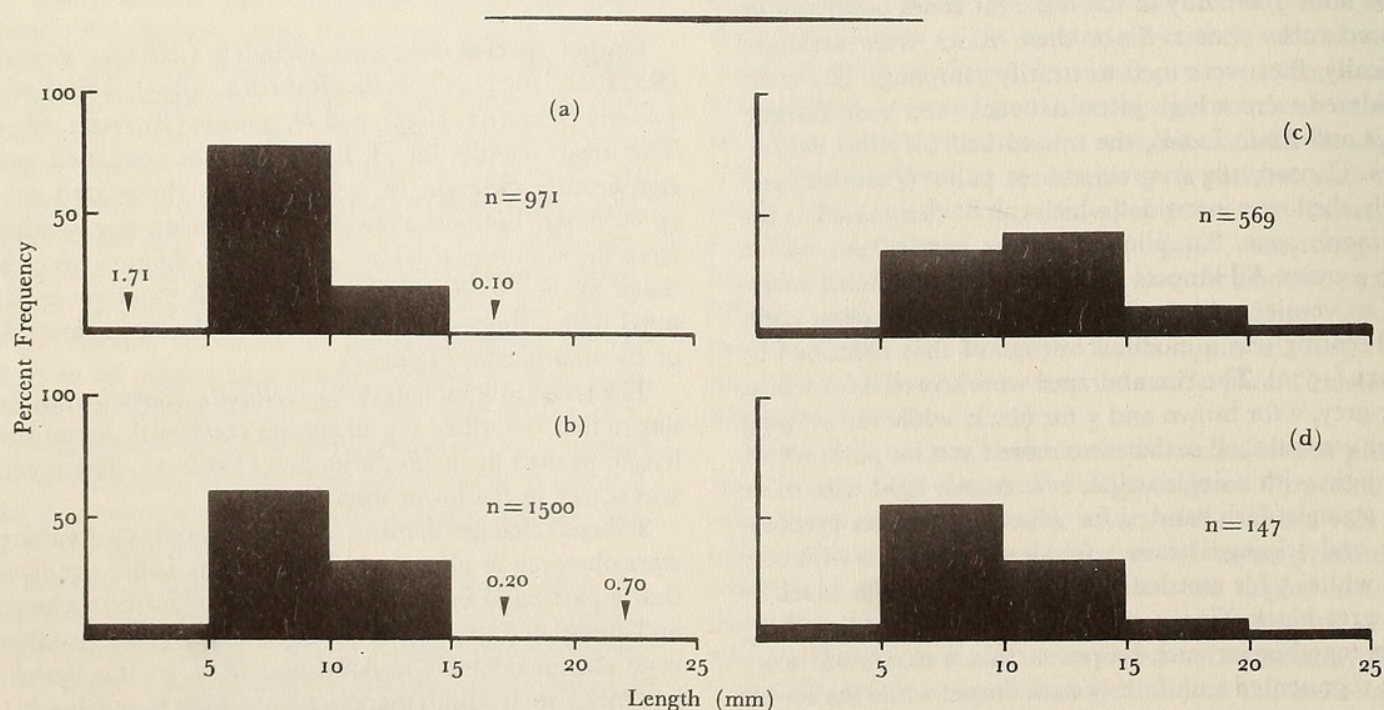


Figure 1

Frequency histograms for shell length of all limpets in each of the designated zones: (a) rockweed; (b) mussel bed; (c) *Postelsia* bed; (d) *Laminaria* zone

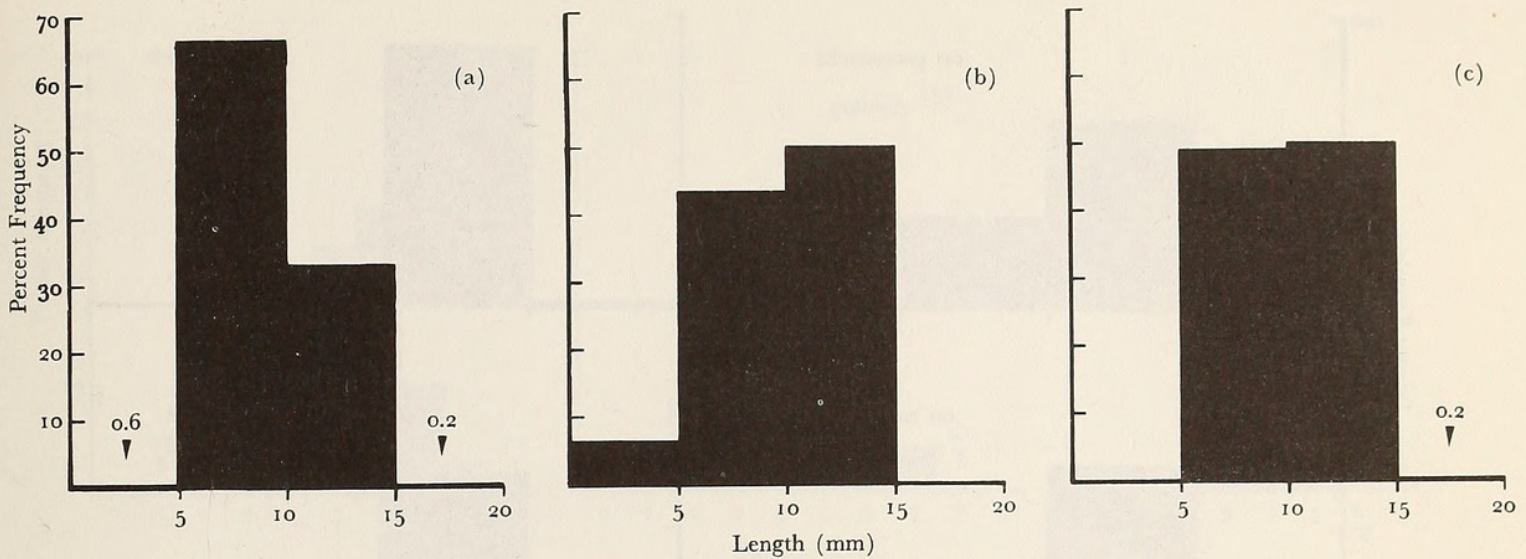


Figure 2

Frequency histograms for shell length of *Collisella digitalis* in each of the designated zones: (a) rockweed; (b) mussel bed; (c) *Postelsia* bed

in October and then drops during the winter. In the *Laminaria* zone limpet length increases over summer from May to July and then decreases abruptly in August at a time when mean length in *Postelsia* is rapidly increasing.

Seasonal fluctuations occurred in mean length of *Collisella digitalis* but trends were difficult to identify.

The shore level size gradients are further illustrated by Figure 1. Proceeding in a down-shore direction there is an increase in the frequency of limpets over 10 mm in length and a decrease in the proportion of limpets under 10 mm. More than 80% of the limpets in the rockweed and mussel bed zones were less than 10 mm in length. The *Postelsia* bed had the highest percentage (59.9%) of limpets over 10 mm in length. Limpets greater than 15 mm were found most frequently in *Postelsia* beds and *Laminaria* zone.

Based on the total sample of 3187 limpets, those with shell lengths greater than 15 mm comprised only 6.9%.

When *Collisella digitalis* is considered by itself, a somewhat similar pattern is detected (Figure 2). A greater percentage of limpets less than 10 mm in length are found in the rockweed area than below it. Fingered limpets in the mussel bed tended to be less than 15 mm in length. Small numbers of large fingered limpets are found in both the rockweed zone or upper intertidal and the *Postelsia* beds.

Attempts to relate fingered limpet size to substrate type provide some significant patterns (Figure 3). The frequency of fingered limpets over 10 mm in length was gen-

erally higher on *Pollicipes* and bare rock than on mussel bed or balanoid barnacles. Almost all of the limpets over 15 mm in length occurred on bare rock. Limpets on barnacles had the highest frequency (91.9%) of limpets with shell length less than 10 mm. Mean shell lengths of *Collisella digitalis* were not statistically different on the 4 substrate types with the exception of those on barnacles which were on average smaller ($p < 0.01$). There are, however, significant differences in mean lengths on particular substrates in the lower part of the mussel bed compared with the upper part. The mean shell length of *C. digitalis* on *Pollicipes*, or *Mytilus* or *Balanus* is greater when these occur in the upper mussel bed than when the same substrates are examined lower down ($p < 0.01$). For example, the mean length of limpets on mussels in the lower mussel bed is 8.48 ± 1.82 mm while those in the upper mussel bed have a mean length of 9.62 ± 1.48 .

There was also a significant increase in mean length of fingered limpets on bare rock surface in the upper mussel bed (8.22 ± 1.20 mm) as compared with those on the same substrate above the mussel bed (10.6 ± 1.95 mm). Thus, shore level size gradients with increasing size in an up-shore direction are detectable when similar substrates are compared. If fingered limpets on the different surfaces are compared within the mussel bed zone only, those on *Pollicipes* tend to be larger than those on the other 3 substrates in the same zone. Similarly, when fingered lim-

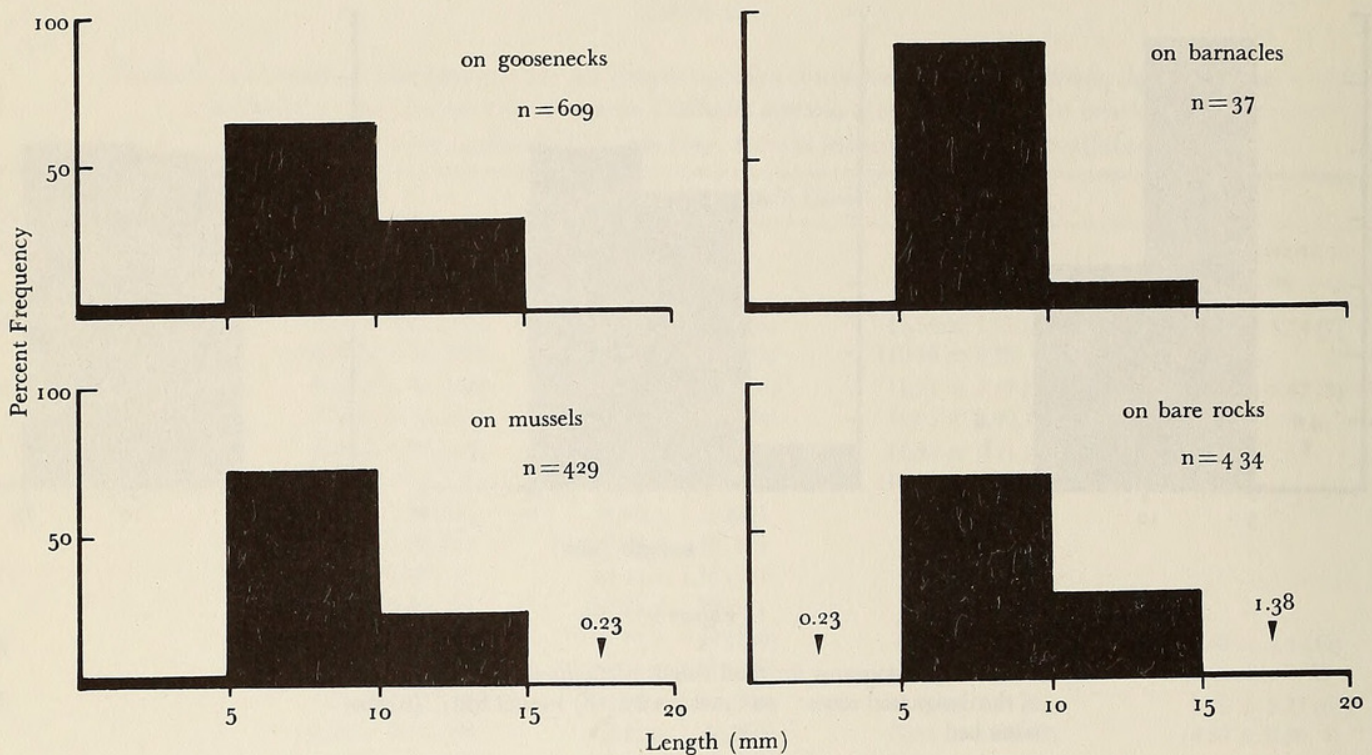


Figure 3

Frequency histograms of shell length of *Collisella digitalis* on various substrates

pets using mussels as a substrate are compared in quadrats containing mussels only and in quadrats containing both mussels and gooseneck barnacles limpet shell length tends to be greater when goosenecks are present than when absent ($p < 0.01$).

Shell Length of Predated Limpets

In an earlier study (HARTWICK, 1976), shell lengths of limpets taken by Black Oystercatchers were shown to be relatively large. In the present study, limpets taken by these birds were again relatively large. In fact, pooling all species, 79% of 222 predated limpets were over 15 mm in length. Many of these were taken in the *Postelsia* beds and *Laminaria* zones. Similarly, *Collisella digitalis* attacked by the birds tended to be large, with 95% over 10 mm and 31% over 15 mm.

The tendency for oystercatchers to select larger limpets was also shown in another study involving arrays of limpets placed on the intertidal (HARTWICK, 1978a).

Trends in Shell Patterns

Considering *Collisella digitalis* by itself first, a unimodal distribution of pattern scores is exhibited in each zone (Figure 4). Fingered limpets inhabiting the rockweed zone had a higher pattern score than those in the mussel and *Postelsia* beds. Thus, 62% of *C. digitalis* in rockweed had pattern scores greater than 4 compared with only 39% and 38% in mussel and *Postelsia* beds, respectively. Comparison of mean pattern scores in the various zones based on collections over the full year indicates that the rockweed zone is inhabited by limpets with higher pattern scores than those on either the mussel or *Postelsia* ($p < 0.01$).

Interestingly, the range in pattern scores decreases in a down-shore direction from the upper intertidal down to *Postelsia* (Figure 4).

If only fingered limpets greater than 10 mm in length are considered for the summer months when predation by oystercatchers is heavy, the shell pattern distribution is unimodal at a score of 4 (Figure 5). A similar pattern dis-

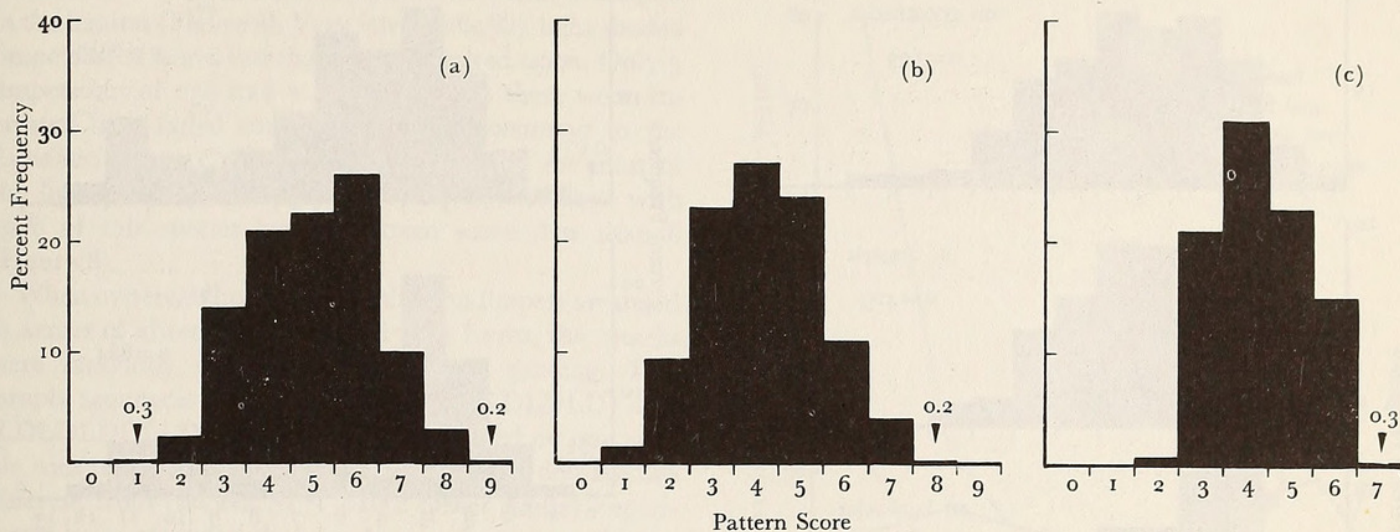


Figure 4

Distribution of shell pattern scores for *Collisella digitalis* in each of the designated zones: (a) rock weed; (b) mussel bed; (c) *Postelsia* bed

tribution arises when all sizes of *Collisella digitalis* are considered in the rockweed and mussel bed combined.

When pattern scores of *Collisella digitalis* are compared on each of the different substrates, again interesting differences arise. Dark limpets with pattern scores greater than 9 have the highest frequency on bare rock (Figure 6). Very

few of these occur on gooseneck barnacles, mussels or other barnacles. Mean scores for limpets on the different substrates are significantly different. Thus, the mean score on rock was 7.99 ± 2.88 ($n = 434$) which was significantly ($p = 0.01$) higher than that on gooseneck barnacles (4.62 ± 2.24 , $n = 609$). The pattern score of limpets on barnacles other than *Pollicipes* was lowest of all (3.57 ± 1.80 , $n = 37$). Pattern scores of limpets on *Mytilus* were similar to those on *Pollicipes*.

If *Collisella digitalis* limpets on the same substrate are compared at different shore levels a significant increase in shell pattern score is detectable in an up-shore direction. Thus, limpets on gooseneck barnacles in the lower mussel bed had mean pattern scores (3.78 ± 1.55 , $n = 209$) less than those in the upper mussel bed in the same area (4.22 ± 1.77 , $n = 70$) which in turn were lighter than those above (5.53 ± 2.09 , $n = 298$). However, the darkest limpets occurred on bare rock above the mussel bed.

Shell patterns were also determined for all limpet species combined for all sizes and for limpets with shell lengths over 10 mm (Figure 7). Most limpets fell in intermediate categories with pattern scores between 3 and 6. There may be a bimodality detectable with modes at 4 and 11. Comparisons of mean pattern scores for all species combined in each of the zones indicates a trend toward higher pattern scores in a down-shore direction at least in mid summer but the pattern is not clear at other times. However,

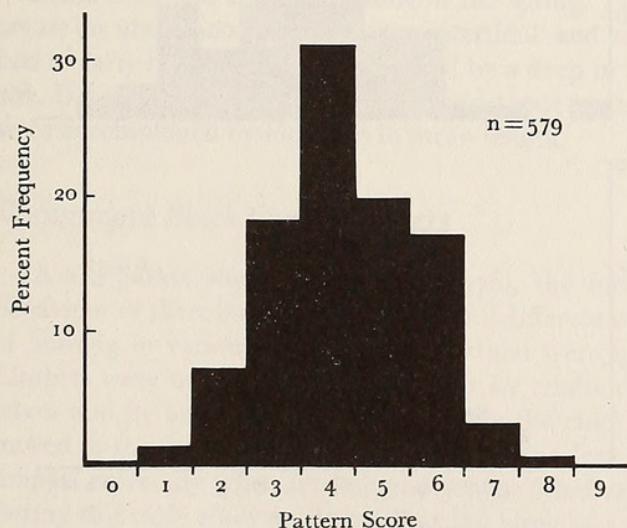


Figure 5

Distribution of shell pattern scores for *Collisella digitalis* over 10 mm in length for all zones combined over the summer months

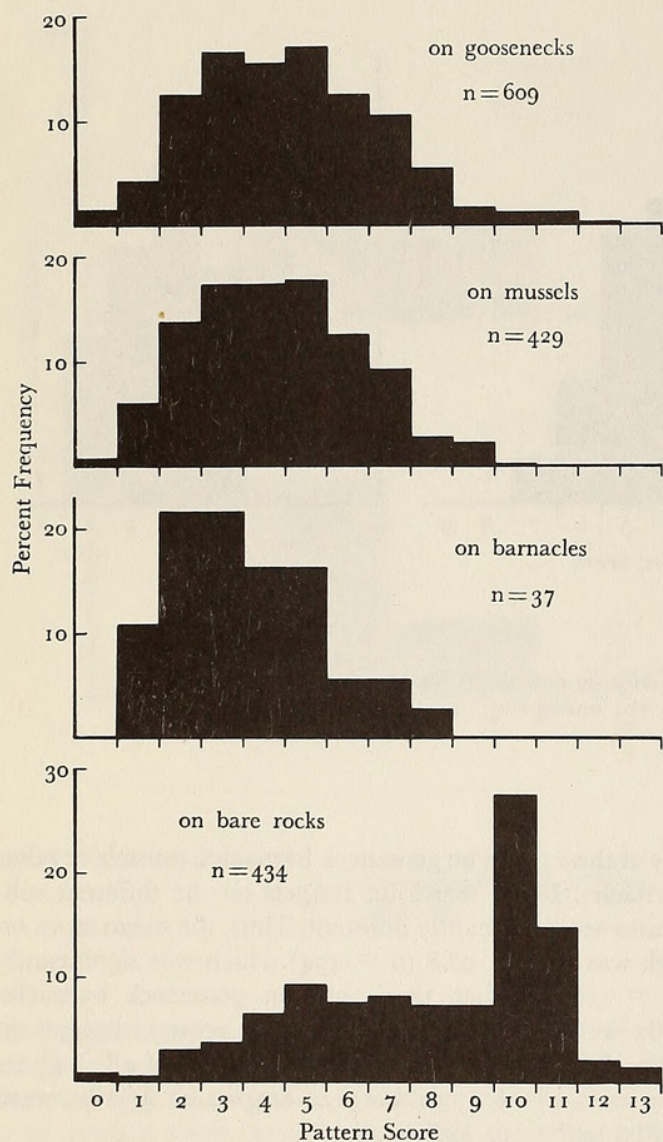


Figure 6

Distribution of shell pattern scores of *Collisella digitalis* on various substrates

limpets inhabiting *Postelsia* and *Laminaria* zones were definitely darker than those at higher levels. Thus, the mean pattern score for all limpets combined in the *Postelsia* bed varied over the year from 6.12 to 7.62 and those in the *Laminaria* zone varied from 5.67 to 9.83. Mean scores in the upper 2 zones tended to be in the range 4.24 to 6.88 with most approximately 5.00.

Pattern Scores of Predated Limpets

When limpets attacked by oystercatchers are scored for shell patterns, the distribution obtained is shifted toward

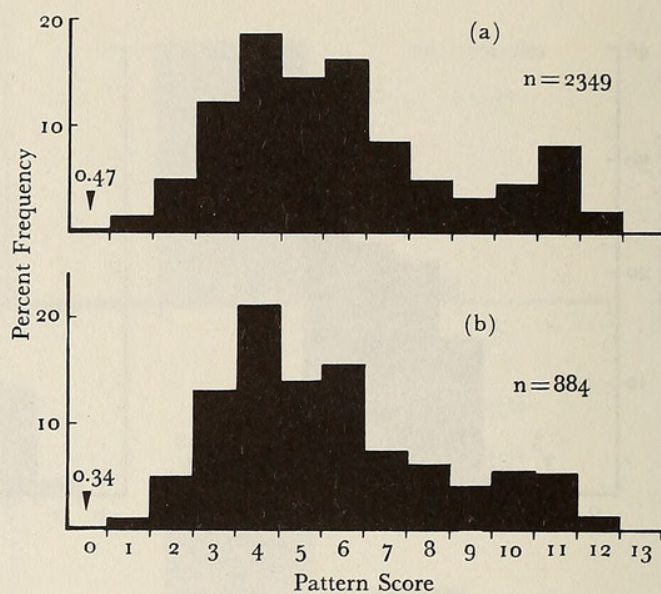


Figure 7

Distribution of shell pattern scores of all limpet species combined for the summer months (June, July, August): (a) all limpets; (b) limpets over 10 mm in length

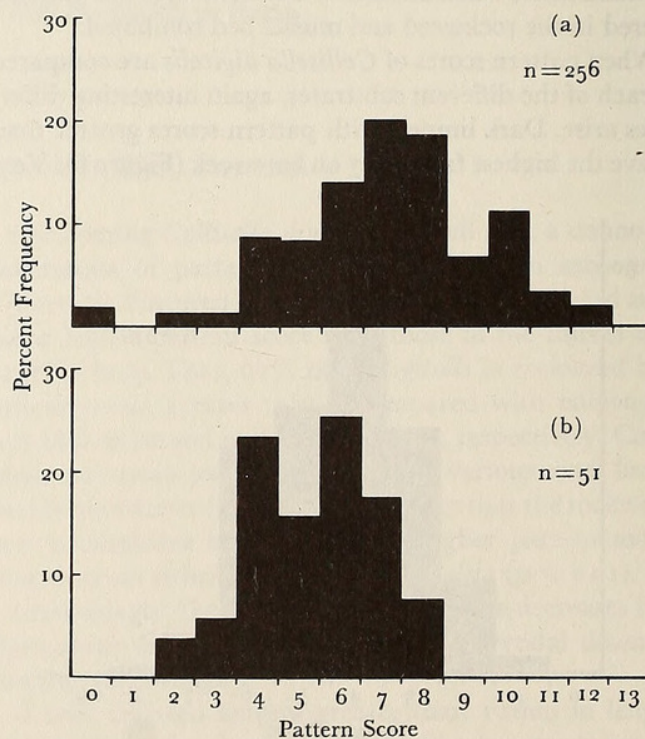


Figure 8

Distribution of shell pattern scores of limpets preyed upon by Black Oystercatchers: (a) all limpets; (b) *Collisella digitalis* only

the darker end of the scale compared with that of limpets in the habitat (Figure 8). Very few (22.64%) light shaded limpets with scores less than 6 were preyed upon. Only 3 limpets out of 256 had a score of 0 and these were encrusted in a faded coralline red algae common to the *Laminaria* zone. *Collisella digitalis* accounts for most of the lighter coloured limpets which were attacked with 49% of this species having pattern scores less than 6 (Figure 8).

When oystercatchers began feeding on limpets arranged in arrays of alternating dark and light forms, the attacks were randomly distributed in terms of shading. Two sample sequences are as follows (LDDLLDLDLD) and (LDLDDLLDLDLDDDDLLDLDL). Based on one sample runs tests, these and other sequences recorded are not different from random ($p < 0.05$). Other similar experiments have suggested that size is more important (HARTWICK, 1979).

Variation in Density of Limpets

The abundance of limpets, based on counts within the quadrats (0.093 m^2), varied over the year. In the rockweed and mussel bed zones the mean number of limpets per quadrat was generally high in the summer months, decreasing to low values over fall and winter (Figure 9). Density of limpets was generally highest in the mussel bed. Trends in the lower zones were difficult to detect but there appears to be a drop in numbers in the *Postelsia* bed in the early fall and a possible increase in numbers in both *Postelsia* beds and *Laminaria* zone in the spring. The increase in abundance in the upper intertidal and mussel bed in early summer was accompanied by a drop in mean size. Decreases in numbers in the *Postelsia* zone in the fall were accompanied by increases in mean length.

Foraging of Black Oystercatchers

In a separate study (HARTWICK, 1976), the foraging behaviour of these birds was described and different modes of hunting in various parts of the intertidal were noted. Limpets were utilized to a large extent by adults themselves and by both adults and chicks once the chicks are moved to the feeding area. The birds tend to select large limpets especially when feeding the young. Observations during this early study indicated that the birds may walk directly and rapidly to an area with large limpets on, for example, an accessible rockface. They may remove one or more of these and carry them to the young. At times, how-

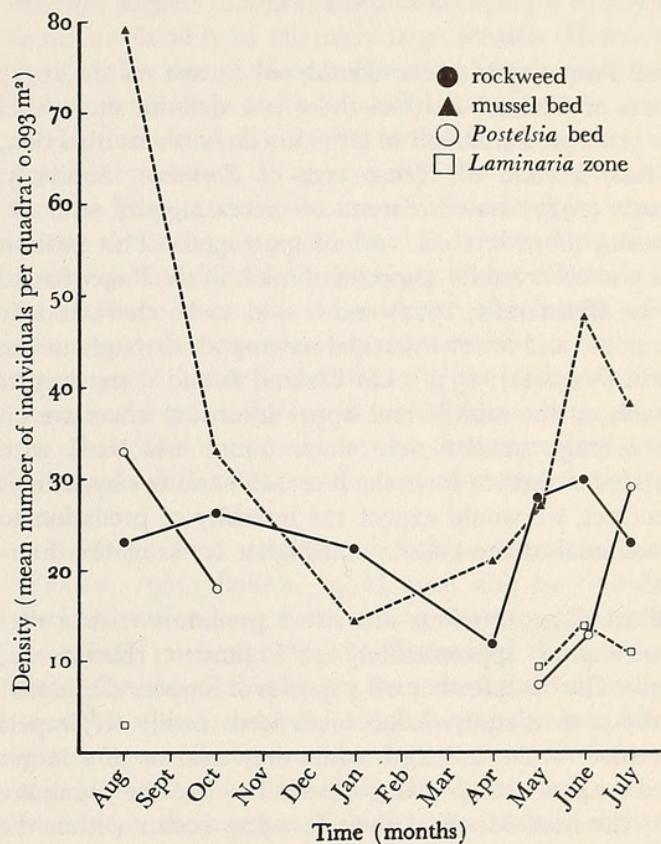


Figure 9

Variation in the density of limpets over time in each of the designated zones

ever, limpets are ignored and mussels or other prey are utilized.

In the present study, records of the foraging time spent by 5 pairs in each of the zones (except for *Postelsia*) indicated that most of the time (57%) was spent in the mussel bed while a lesser and equal time was spent in the rockweed zone and *Laminaria* zone (22% and 21%, respectively). Earlier records (HARTWICK, 1973) suggest that most foraging time is spent in the low to mid mussel bed but that the particular pattern for any pair is affected greatly by the stage in the reproductive cycle. A pair of adults that is involved in mating or has just lost a clutch will often spend almost all of their time feeding on limpets and other small items on the mussel bed. The higher and lower areas may be utilized more and more as the season progresses.

DISCUSSION

If all limpet species are considered as one on the rocky shores of Cleland I., then there is a definite shore-level size gradient from small to large in a down-shore direction, at least beyond the dense beds of *Postelsia*. Similarly, LOUDA (1979) noted a trend of increasing size with decreasing shore level of various gastropods. This pattern was also observed for 4 species of snails in the Puget Sound region (BERTNESS, 1977) and is said to be characteristic of middle and lower intertidal gastropods throughout the world (VERMEIJ, 1972). On Cleland Island then, limpets inhabiting the middle and upper intertidal areas are on the average smaller than those found associated with *Postelsia* or farther down the shore. If Vermeij's hypothesis is correct, we would expect the intensity of predation to be minimal at the middle and higher levels of the intertidal.

Black Oystercatchers are visual predators with a diet consisting of approximately 40% limpets (HARTWICK, 1976). The birds feed on all 4 species of limpets considered in the present study. Adult birds feed readily on limpets less than 1.5 cms in length while they tend to offer larger sized limpets to their young especially when the young are near the nest. Much of their foraging occurs within the mussel bed; and where *Postelsia* occurs, they are apt to forage at times within the *Postelsia* for limpets and other prey items.

There are a number of reasons why oystercatchers may not have a great effect on limpets before or during the early stages of their breeding season (i.e., in the period prior to June). In winter and early spring the birds are often found foraging in protected mudflats rather than at their summer breeding site (HARTWICK & BLAYLOCK, 1979). On arriving at the breeding site the birds spend a considerable time defending their territories and engaging in mating activities. They also make foraging trips away from their territories (HARTWICK, 1978b), so that their impact within the territory may be minimal at this time. As the breeding season progresses chicks make an appearance and the adults search more for larger limpets to carry to the young at the nest. The adults themselves continue to feed on smaller limpets. In late summer and fall, observations on foraging (HARTWICK, 1976) indicate heavy use of small and medium sized limpets by both adults and young in the upper mussel bed and rockweed areas. Usually the young birds are with the adults in the feeding territory at that time. However, the sudden appearance of large limpets

brings a rapid response by foraging adults. The large limpets are quickly taken and usually offered to the chicks. The rapidity of the response suggests that the birds would effectively remove many of the larger limpets in the middle and high intertidal except in places of inaccessibility. The effect would be greatest in territories in which the birds successfully reared a brood. Predation on the large limpets would occur mainly in late summer and early fall.

In the lower intertidal limpets occurring below the mussel bed are often covered by *Laminaria* and other plants. The birds must probe underneath to find the prey. Observations suggest that low, low tides are times of low food availability within some territories (HARTWICK, 1978b). The algal cover and the short exposure time may make the lower zone a suitable refuge from extensive predation by these birds.

In the case of *Collisella digitalis*, there exists considerable evidence for a trend of increasing size with increasing shore-level (FRANK, 1965; BREEN, 1972; VERMEIJ, 1972). This trend was also detected for *C. digitalis* in the present study when similar substrates were compared. Moreover, the largest sizes of this limpet species were found on steep rockfaces often in mid to high intertidal and in places relatively inaccessible to oystercatchers. When all samples of *C. digitalis* are combined though, the gradient in size is similar to that of the other species, increasing in a down-shore direction. It should be noted that when the mussel bed was thick, only limpets within bill depth of Black Oystercatchers were examined (see HARTWICK, 1973 for method). Thus, deep within the mussel bed matrix considerable numbers of very small individuals would shift the size gradient to that postulated (VERMEIJ, 1972) for high intertidal forms. Small fingered limpets were also common on balanoid barnacles in areas which GIESEL (1970) referred to as having background heterogeneity. In the middle intertidal *C. digitalis* on *Pollicipes* tended to be larger in size than those on other substrates in the same zone. According to GIESEL (1970), many *C. digitalis* migrate to *Pollicipes* after initial settlement and these *Pollicipes*-type limpets survive better in late spring and in summer when the risk of desiccation is high and algal productivity is low. However, food intake of these limpets will depend on the amount of time available for foraging on rock surfaces nearby. In early spring and in fall the advantages are shifted toward limpets inhabiting rock surfaces where algal productivity is high at a time when desiccation is less of a risk (GIESEL, 1970). Bird predation is thought to overlie and interact with these two

opposing tendencies. Giesel suggested that bird predation would be greatest in high intertidal areas with long exposure times and low background heterogeneity. Giesel's work dealt mainly with shell polymorphism in *C. digitalis*. In high intertidal areas selection against light coloured conspicuous limpets would be intense and Giesel reported that large light coloured limpets did disappear from rock surfaces. Similarly, large dark coloured limpets disappeared from *Pollicipes* beds. In the present study, the responses of adult birds to arrays of limpets suggest that size of limpet is important but colour pattern is not. The birds may be restricting the larger limpets in the middle and high intertidal to steep rockfaces inaccessible to predation. Their influence on colour pattern frequency is not so clear. GIESEL (1970) found that limpets on *Pollicipes* became lighter as their size increased. That is, average pattern score was a decreasing function of limpet size. Presumably dark animals were being selected against. According to Giesel, the polymorphism in *C. digitalis* first appears in very small sizes. By the time the limpets reach 4-8 mm in June, there is a well established bimodality. Giesel links this with an apparent heavy selection against limpets with intermediate pattern scores in the period February to May. However, this effect may not be attributable to predation by oystercatchers. As noted earlier, the impact of the birds on limpets may be less in that period of time than later on. Moreover, collections of predated shells in this and previous studies on Cleland Island indicate that the birds feed on limpets ranging in size from 5 mm to over 30 mm. The small amount of predation by oystercatchers on limpets near the bottom end of the size range would probably not have the disruptive effect postulated by Giesel. On the other hand, Black Oystercatchers did feed most heavily on *C. digitalis* with pattern scores intermediate between those on bare rock and those on *Pollicipes*. Thus, 82% of predated *C. digitalis* were scored from 4 to 7 while those inhabiting *Pollicipes* and rock surfaces had pattern modes near 4 and 10, respectively. If other shorebirds migrating through the area in early spring take small limpets, then the combined effect of their predation with that of oystercatchers may be significant.

GIESEL (1970) refers to high densities of oystercatchers in the period of February to May but similar observations were not made on Cleland Island. Giesel also suggests that high *Pollicipes* densities may be a strong feeding stimulus with areas of low *Pollicipes* density being less attractive to the avian predators. Foraging studies on Black Oyster-

catchers suggest that at times their foraging is closely tied to the availability of relatively large mussels (HARTWICK, 1976) rather than *Pollicipes*. However, whether this is true when the birds are in flocks is not known.

The data on shell patterns for all limpet species combined is interesting. It appears that the birds are feeding most on limpets with pattern scores intermediate between modes occurring at 4 and 11. When only limpets over 10 mm are considered, the birds are taking relatively dark forms. Since there was no evidence of selection of one colour pattern over another in the experiments the greater frequency of darker limpets taken by the birds must reflect their tendencies to forage in areas where those are most prevalent. It is not possible at this time to explain general patterns of shell colour on the basis of predation by oystercatchers.

Evidence that vertical migrations occur in limpets (FRANK, 1965; BREEN, 1972) must also be considered. Such migrations may occur in all 4 limpet species and will contribute to changes in abundance and mean size over time. The observed increases in mean size of limpets in the mussel bed and rockweed zones during the late fall and winter may reflect net upward movements similar to the migrations described for *Collisella digitalis* by Frank. The increase in the number of small individuals in early summer observed in the present study was consistent with the pattern noted by BREEN in 1972.

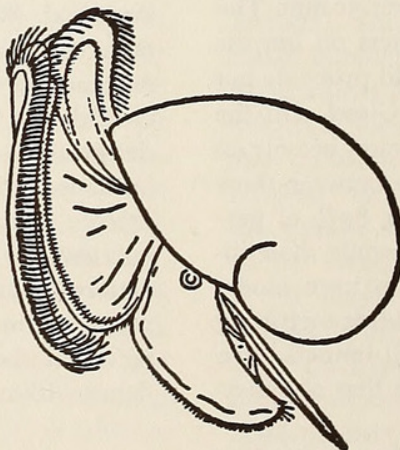
Differential growth, migration and other processes will clearly play a role in determining the final patterns on the intertidal. Both VERMEIJ (1972) and BERTNESS (1977) point out that it may well be naive to look for a universal explanation for intraspecific shore-level size gradients. Considering the sizes of limpets taken by oystercatchers the size gradients observed are such that large limpets end up in the lower intertidal where a partial refuge from oystercatcher predation exists. Higher intertidal forms are often restricted to near vertical rock surfaces inaccessible to oystercatchers. The middle intertidal is a zone of intense predation by oystercatchers but the predation is not directed at the very small sizes which occur in such abundance within the mussel bed.

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