# NICHE DIFFERENCES BETWEEN TWO SYMPATRIC LIMPET SPECIES (GASTROPODA) IN THE HIGH INTERTIDAL OF BRITISH COLUMBIA

by

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# ABSTRACT

In the upper intertidal zones of British Columbia two sympatric limpet species, _Acmaea digitalis_ and _Acmaea persona_, co-exist with few apparent niche differences. The degree of niche separation between the two species was determined by observations and transect studies documenting their distribution and abundance with respect to macro- and micro-habitat categories. Significant habitat differences between the two species were observed, correlated with different shoreline types. Only _A. digitalis_ is found along shoreline in open coast environments and on the seaward ends of shoreline convexities (points, headlands) in more wave protected water. _A. persona_ occurs alone in boulder fields and the inner reaches of shoreline concavities (inlets) both characteristic of semi-exposed to protected wave environments. Regions of co-existence between the two species are intermediate between the previous two categories, and occur on vertical rock surfaces in semi-wave-exposed to protected environments. The spatial distributions of the two species result in a predominantly horizontal separation between them, rather than the more typical vertical separation between other species of _Acmaea_. Environmental factors causing the observed habitat differences between _A. digitalis_ and *A. persona* were studied by laboratory and field experiments. Increased solar radiation (increased desiccation and temperature) in the habitats where *A. digitalis* occurs alone appeared to be the major environmental factor restricting the distribution of *A. persona* from these habitats. *A. persona* is less tolerant to desiccation because of increased rate of water loss caused by its flatter shell shape. Factors causing the absence of *A. digitalis* from the habitats of *A. persona* were less clear. Predation by the crab, *Hemigrapsus nudus* in boulder fields appeared to be significant, since experimentally these crabs prefer *A. digitalis* to *A. persona*. Fresh water run-off may also decrease the survival of *A. digitalis* in the habitats where *A. persona* occurs alone. Active exclusion of one species by another does not seem to occur in the habitats occupied by only one of the species. Exploitive competition for food between *A. digitalis* and *A. persona* appeared likely in areas of niche overlap, but field enclosure experiments testing whether competition occurs were inconclusive. The observed niche differences between the two species are sufficient to explain their co-existence in the intertidal. These niche differences appear to have evolved as independent adaptations by each species to the environment, rather than the result of a history of competitive interaction. But inter-specific competition may act to maintain the observed niche differences between them.

# ACKNOWLEDGEMENTS

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## I. INTRODUCTION

When closely related ecologically similar species are found co-existing in a community, four questions can be asked with respect to the possibility of competitive exclusion (Hutchinson, 1959; Hardin, 1964; Miller, 1967) : (1) are the species' niches partially non-overlapping in any way which allows them to partition the use of necessary environmental resources; (2) are resources limiting in area of niche overlap such that competition occurs between the species for any of them; (3) what are the short term and long term (evolutionary) effects of inter-specific competition, if it occurs, on the niches of these species; and (4) what are the effects of other environmental factors, both physical and biological, on their niches. All of these questions are closely tied both to traditional problems of evolutionary ecology such as adaptive radiation in sympatric species of a genus (Lack, 1947) and to recent theoretical problems of niche theory, competition, and co-evolution of species (MacArthur and Levins, 1964; Levins, 1968; McNaughton and Wolf, 1970; Alaya, 1971), where the common concern is to reveal the underlying factors determining the species composition of communities.

In natural communities, most studies of closely related co-existing species have concentrated mainly on attempting to quantify the degree of niche overlap between species. The literature on this topic is extensive, but some examples from the marine environment are Kohn (1959), Paine (1962), Jeffries (1966), Croker (1967), and Wells (1970) for benthic invertebrates; and Stephen *et al* (1970) for fishes. These studies provide a detailed description of important niche differences for certain species, and may explain their co-existance, indirectly, in terms of the competitive exclusion principle. But the question of whether interspecific competition does occur in areas of niche overlap, and whether these niche differences are caused by competition and are a necessary condition for the persistence of the species, generally remains unanswered. Some studies have demonstrated the process of competition as well as niche differences in the marine environment. These are Harger (1970) for mussels, Connell's (1961) study of barnacles, and Haven's (1966, 1971a) study of limpets. However, few studies have determined niche differences between similar species and compared the respective importance of interspecific competition and other environmental factors, such as predation and physical factors, in causing this niche separation.

The limpet genus, *Acmaea*, lends itself to a study of these questions because it exhibits extensive adaptive radiation resulting in large numbers of sympatric species. There are 17 distinct species of this genus occurring intertidally along the west coast of North America; along the coast of British Columbia, 13 species live sympatrically (Fritchman, 1961).

Although most of these species exhibit prominent niche differences, either by existing on specialized algal substrates or by occupying different intertidal zones or micro-habitats (Test, 1945; Shotwell, 1950; Fritchman, 1961; Haven, 1971a), two species, *A. digitalis* Rathke and *A. persona* Eschscholtz, appear to co-exist in the upper intertidal zones of British Columbia with little niche separation (Fig. 1). Both species share the same vertical intertidal range along inner coast shoreline. The geographic range of *A. persona* (Aleutian Islands, Alaska to central California) lies within that of *A. digitalis* (Aleutian Islands, Alaska to Baja California, Mexico) (Fritchman, 1961). Both species feed indiscriminantly on encrusting micro-algae and diatoms of the rock surface (Test, 1945) and reproduce by means of planktonic larvae.

Most studies of the ecology of *Acmaea* species have taken place in central California, the southern extreme of the geographic range of *A. persona*. Observations by Test (1945, 1946)

Figure 1. _Acmaea persona_ (large smooth limpets) and _A. digitalis_ (small, with heavy ribs) co-existing on a vertical rock surface at Bamfield, Barkley Sound.

and Fritchman (1961) at this latitude indicate major niche differences between *A. persona* and *A. digitalis*. Both describe *A. persona* as stenotopic, restricted to dark, moist environments such as crevices and caves in the highest intertidal zone, and less abundant than *A. digitalis*. Conversely *A. digitalis* is reported to exist abundantly on most regions of rocky shoreline, feeding at high tide and active during the day. No mention is made in any study that the niche of *A. persona* overlaps to any degree the niche of *A. digitalis*. In contrast, general observations in Oregon by Kenny (1969) and in Alaska by Haven (1971b) indicate that both species overlap broadly, and that the relative abundance of *A. persona* increases in wave protected waters. The sympatry between these species and the similarity of their niches in British Columbia raises the question of their apparently stable co-existence in view of the competitive exclusion principle, as well as the question of explaining the differences in the degree of their niche overlap between British Columbia and California.

Much more information has accumulated on the natural history and ecology of *A. digitalis* than *A. persona*. *A. digitalis* attains lengths of 15-25 mm. (Frank, 1965; Giesel, 1969), and lives and feeds mainly on vertical or sloping rocks predominantly in wave exposed areas above zone 2 (Ricketts, *et al*, 1968). Behaviorally, *A. digitalis* shows seasonal migrations vertically, by moving up higher in the intertidal during the winter months (Frank, 1965; Haven, 1966; Breen, 1970). Also this species feeds when submerged at high tides, and at other times is often found in characteristic clusters in depressions and crevices in the rock surface (Millard, 1968). A detailed study of the niche of *A. digitalis* in central California was done by Haven (1971a), and a good understanding of the population dynamics of *A. digitalis* comes from studies by Frank (1965) and Stimson (1968).

On the other hand, little is known about *A. persona*. This species attains larger sizes than *A. digitalis*, reaching lengths up to 40 mm, (Kenny, 1969). The only description of this species' habitat and behavior are found in the previously described observations by Test (1945, 1946) and Fritchman (1961) indicating the stenotopic niche of this species in central California. No detailed study of the niche of *A. persona* has been done in British Columbia, the center of this species' range, where it is abundant, essentially eurytopic, and overlaps broadly with *A. digitalis*.

If competition does occur between *A. digitalis* and *A.*

*persona* some common resource must be in relative shore supply (Birch, 1957). For these limpet species food shortage appears likely. Food shortages at some times appear to be common for most high intertidal grazing gastropods, evidenced by the almost complete removal of algae from the rock surface by the grazers (Southward, 1956, 1964; Jones, 1968; Castenholz, 1961; and Haven, 1966) and by direct evidence of food limitation in high intertidal species of *Acmaea* (Haven, 1966; Sutherland, 1970).

In this study, the niche relationships between *A. persona* and *A. digitalis* are investigated in three ways: (1) quantification of the degree of niche separation between the two species by investigating their distribution and abundance with respect to several macro- and micro- habitat categories; (2) determination of the environmental factors which proximately limit these distributions; and (3) determination of the importance of interspecific competition for food between these two species in areas of niche overlap. I felt that a study encompassing niche differences, the effects of environmental factors, and the dynamics of competition would be fruitful in understanding the mechanisms allowing these species to live sympatrically and the evolutionary processes involved in adaptive radiation in this genus.

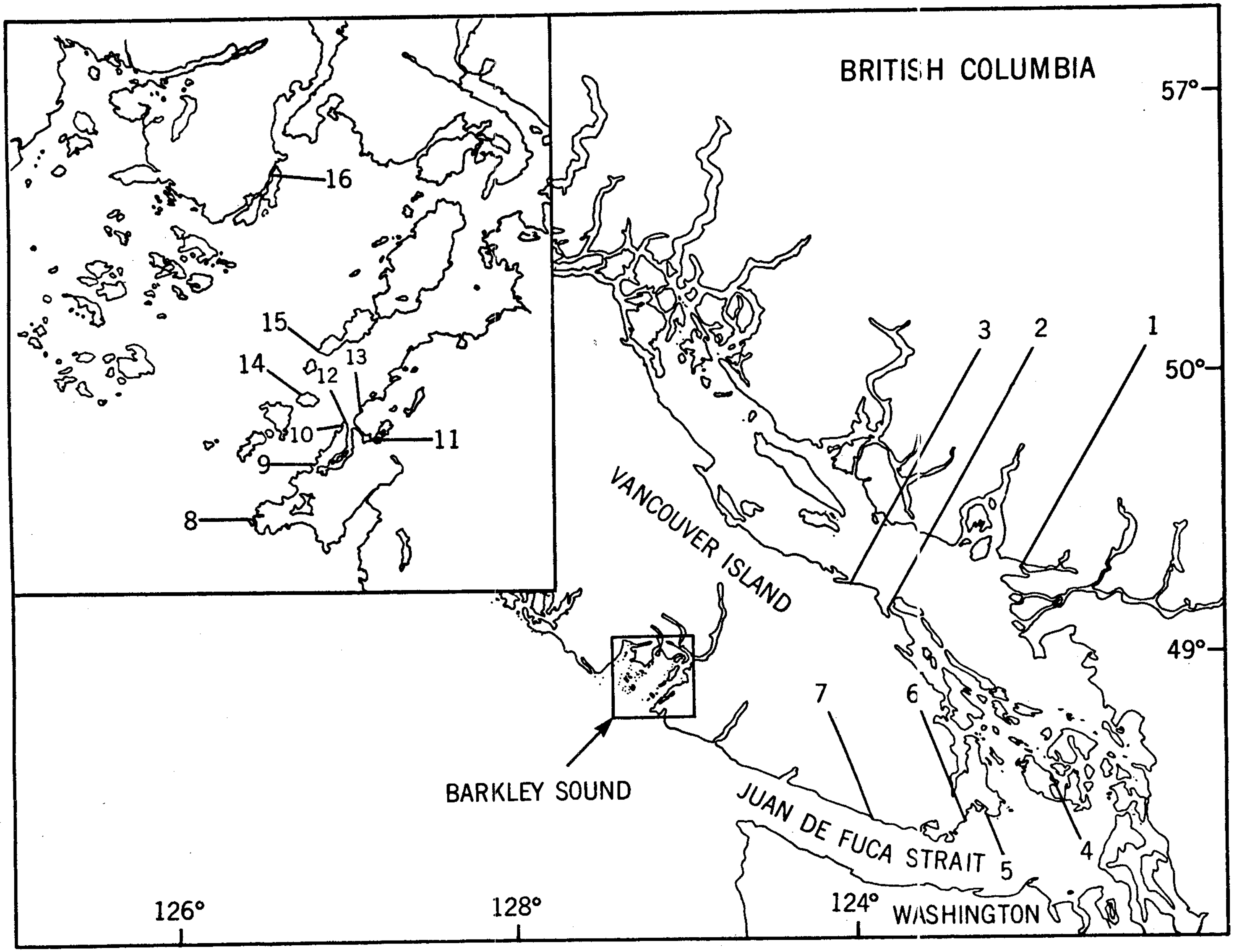
## II. HABITAT DIFFERENCES BETWEEN *A. persona* and *A. digitalis*

The degree of niche separation between *A. persona* and *A. digitalis* was first investigated by determining the macro-habitat differences in their distributions. On the basis of these observations more detailed studies of micro-habitat differences between the two species were carried out by examining the distribution and abundance of each species with respect to the following micro-habitat dimensions: (1) wave exposure; (2) insolation (desiccation, temperature); (3) intertidal height; (4) substrate; (5) food; (6) community associates; (7) fresh water influence.

### METHODS AND STUDY SITES

Macro-habitat differences were investigated by observing populations of *A. persona* and *A. digitalis* in a wide variety of habitats at numerous stations along the coasts of southern British Columbia and northern Washington (Fig. 2). Names of these stations are given in Table 1. At each station, observations were made of the relative abundance of each species, the general characteristics of the rock surfaces they inhabited, and environmental factors associated with these habitats.

Figure 2. Stations where macro-habitat observations were made.


BRITISH COLUMBIA
57°
50°
49°
1
2
3
4
5
6
7
VANCOUVER ISLAND
JUAN DE FUCA STRAIT
WASHINGTON
BARKLEY SOUND
126°
128°
124°
8
9
10
11
12
13
14
15
16

Micro-habitat categories of wave exposure, insolation, and intertidal height, were studied quantitatively by documenting the distribution and abundance of the two species in vertical transects at three study sites. Each study site showed a continuous horizontal gradient of limpet distributions from areas where *A. digitalis* or *A. persona* occurred alone to regions of overlap between them. Each study site was mapped and at intervals transects were taken throughout the vertical range of the species present. Each transect was aligned with a common horizontal baseline set up by the use of a hand eye level and surveyor's pole. In this way the relative vertical height of the species as well as their relative abundance could be assessed. The size of the quadrats in each transect and the intervals between transects varied with each area, and are indicated below in the site descriptions.

For the sake of continuity, methods used to determine distributional differences with respect to substrate, food, community associates, and fresh water will be discussed in the appropriate subsections below.

The three principal sites used in the study of micro-habitat differences were as follows:

*Victoria Breakwater*. The breakwater at Victoria, B. C.

is located at the southern extreme of Vancouver Island and faces the Strait of Juan de Fuca (Fig. 2). The two sides of the breakwater differ greatly in exposure to wave action and sunlight (Figs. 3,9). The wave exposed side of the breakwater consists of tiers of large granite blocks arranged in step-like sequence. Between each of these blocks is a large space from 10-20 cm wide. Both the center and the wave-protected side of the breakwater are composed of poured conrete. Vertical crevices, approximately 6 meters apart, are present on the protected side. These crevices were often broken and fused along part or all of their vertical extent. If the crevice was fused completely a rough vertical indentation remained in the wall. At the base of the protected side are loose irregularly shaped boulders; the exposed side has the granite blocks throughout its vertical range.

During summer observations in morning and late afternoon, the protected side of the breakwater was shaded but the exposed side was not. In mid-afternoon, however, both sides received direct sunlight. Even during periods of direct insolation, the crevices on the protected side remained shaded.

Transect censuses were taken along most crevices on the protected side, and at 60 meters intervals on the exposed side. The transects were composed of quadrats 10 cm. high

Figure 3. Victoria breakwater. Above, exposed and protected sides, looking shoreward. Below, protected side, in shade, looking seaward (June, 1969).

and 15 cm wide. The common horizontal baseline was the top of the concrete wall.

Limpet Point. Limpet Point (unofficial name) is an outcropping of shoreline on the east shore of Barkley Sound approximately 2 miles northeast of Cape Beale (Fig. 4). The area contains very exposed surfaces as well as concavities protected from waves and sun (Fig. 10). The larger concavity has a horizontal shelf at approximately the 3 meter tide level and is therefore submerged only at the highest tides.

Because of the great irregularity of horizontal and vertical surfaces at Limpet Point, transects were not taken throughout the vertical range of the limpets, but were confined to the upper 160 cm of their range. Transects were composed of quadrats 10 cm high and 20 cm wide; the baseline lay near the upper limit of the barnacles.

Mills Cove. The region of shoreline I have called Mills Cove lies just south of Aguilar Pt., Bamfield, in Barkley Sound (Fig. 4). This area consists of a small boulder beach 3-6 meters wide, bordered by two basaltic walls, 2 1/2 -6 meters high. These walls are oriented perpendicular to the beach (Fig.5).

The aspect of both vertical walls was such that one wall faced almost due north, and the other, due south (Fig. 11).

Figure 4. Aerial photograph showing the relationship of two study sites, Limpet Point and Mills Cove, to Bamfield.

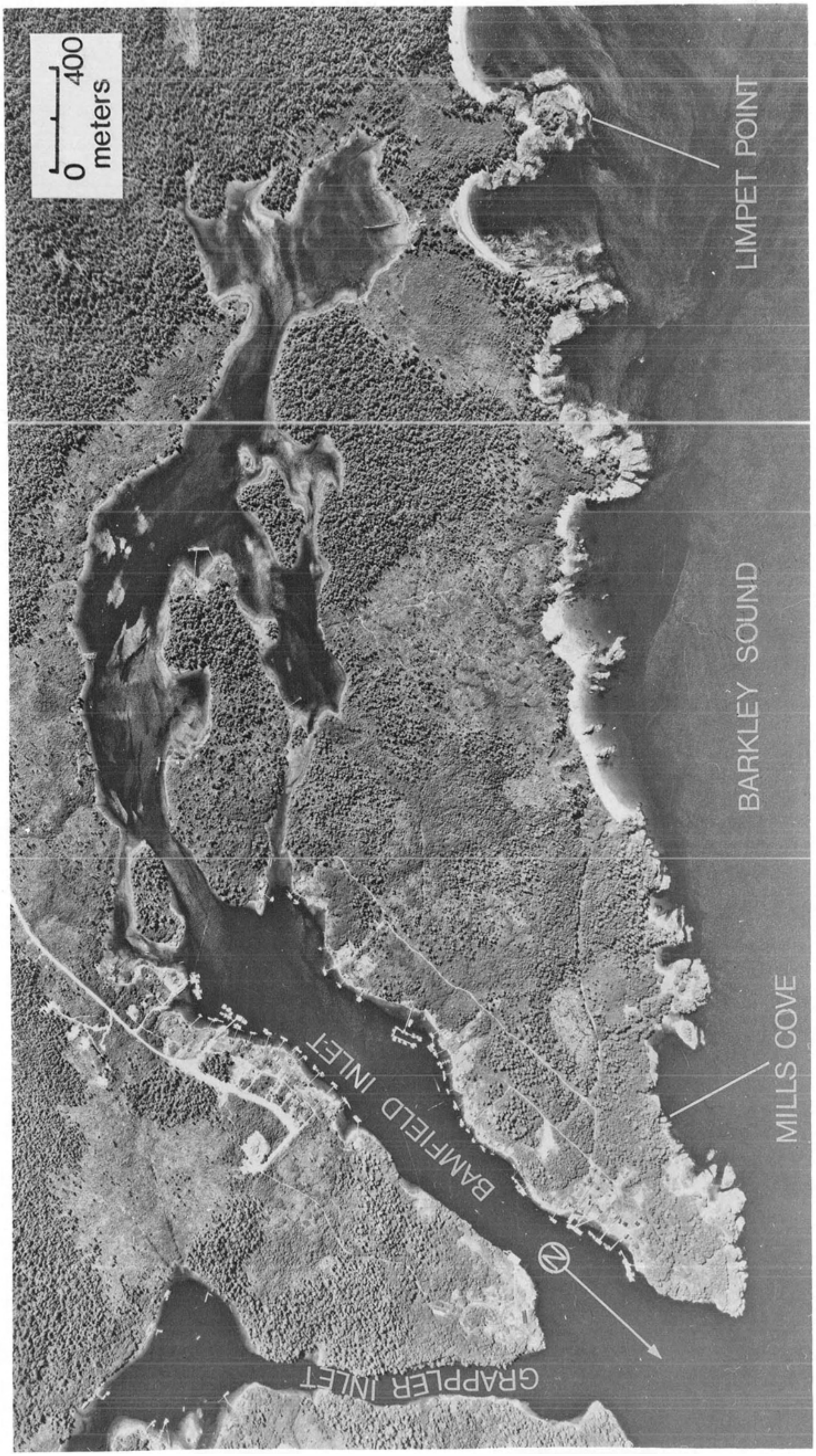
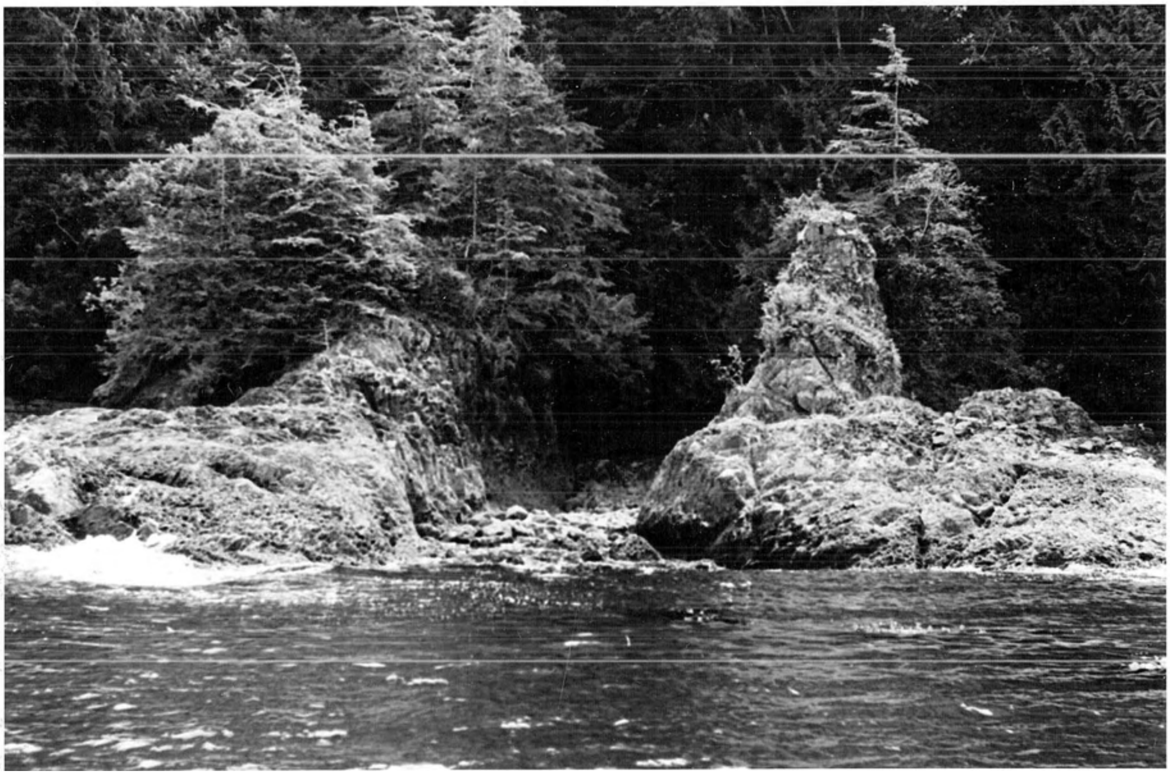

0
400
meters
LIMPET POINT
BARKLEY SOUND
MILLS COVE
BAMFIELD INLET
GRAPPLER INLET
N

Figure 5. Mills Cove. Small boulder beach (center of photograph) lies between the two vertical walls. The seaward ends of these outcropping are typical convexities of the shoreline. The inner reaches represent small shoreline concavities. *A. digitalis* occurs alone on the tips of the outcroppings, while *A. persona* occurs alone at their inner reaches. (August, 1970).



The prevailing swell was consistently parallel to the beach shoreline and thus perpendicular to each wall. Wave action, therefore,appeared to be equal on both walls, and on each wall the wave exposure increased toward the seaward end.

Transects at Mills Cove were composed of quadrats 10 cm high and 30 cm wide, and were taken at 1.6 meter intervals along each vertical wall.

## RESULTS

### Macro-Habitat differences:

In Table 1 the observations from most of the stations visited are summarized. A synthesis of these observations yielded three generalizations characterizing areas where _A_. _digitalis_ occurs alone, where _A_. _persona_ occurs alone, and where the two species co-exist. These generalizations depict the horizontal distribution patterns of the two species along different types of shoreline.

Areas where only _A_. _digitalis_ is found are (1) the rocky shores of wave-exposed outer coast, and (2) convexities, (e.g. points, headlands) in the shoreline of semi-wave-exposed waters (Figs. 5,6). These convexities may be defined as any rocky region of shore in semi-exposed water which juts out to sea when viewed against the prevailing shoreline. Semi-exposed wave conditions are those characteristic of large sounds or straits (e.g. Barkley Sound, Straits of Georgia). This would include some of what Ricketts, _et_ _al_ (1968) term "bays and estuaries", as well as some shore habitats which they list as "protected outer coast". The outer coast environments are generally wave swept shores where such indicators as the alga

TABLE 1

*A. persona* and *A. digitalis* at representative localities

| | Area | Physical Characteristics | *A. digitalis* | *A. persona* |
|---|---|---|---|---|
| 1. | Stanley Park (Vancouver) | Semi-protected, vertical concrete wall | common | common |
| 2. | Duke Point (Nanaimo) | Very protected tidal inlet; tree lined, many oysters | none | common |
| 3. | Lanztville (Vancouver Island) | Semi-exposed, igneous rock outcropping | none | none |
| 4. | Friday Harbor (San Juan Island) | Semi-protected, south-east shore of island | common | common |
| 5. | Victoria breakwater | Exposed to waves; *Pollicipes* present; regular arrangement of crevices & exposed vertical surfaces | abundant; mainly in crevices | none |
| | Victoria breakwater | Wave-protected side (facing harbor); vertical surfaces with regular vertical crevices | abundant on vertical surfaces as well as crevices | abundant in crevices only |

TABLE 1 (con't)

| | Area | Physical Characteristics | *A. digitalis* | *A. persona* |
|---|---|---|---|---|
| 6. | Rocky Point (Victoria) | Protected bay, rocky shore | none | none |
| 7. | Point-No-Point | Semi-exposed; convex, igneous outcropping | abundant | rare - confined to crevices or rocks facing away from waves |
| | Point-No-Point | Semi-exposed; boulder field | none | abundant under boulders |
| 8. | Cape Beale (Barkley Sound) | Wave-exposed; *Pollicipes* present, *Postelsia* present nearby; vertical fused rock surface | very abundant | none |
| 9. | Limpet Point (Barkley Sound) | large point, wave and sun-exposed shoreline common | abundant | un-common (found only in locally occurring shoreline indentations) |

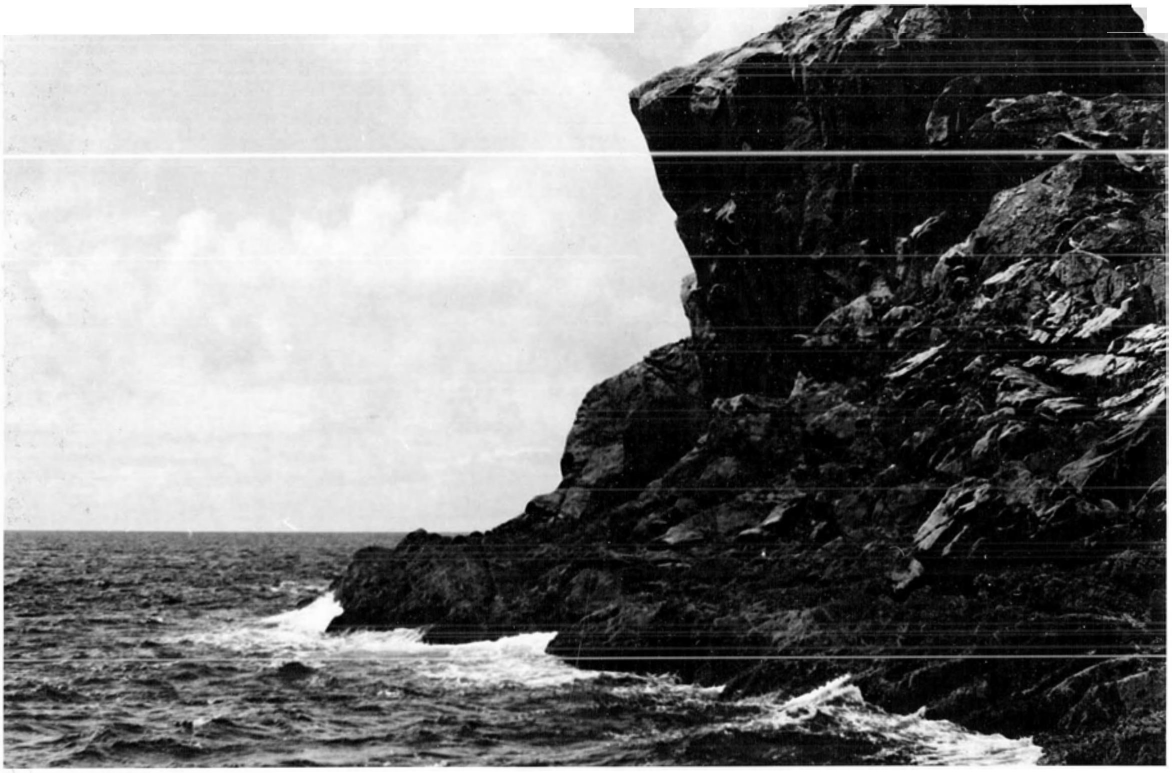
TABLE 1 (con't)

|  | Area | Physical Characteristics | *A. digitalis* | *A. persona* |
|---|---|---|---|---|
| 10. | Caves near **Bamfield Inlet** (Barkley Sound) | Dark caves, moist clumps of *Pollicipes* present inside | none | few |
| 11. | Grappler Inlet (Barkley Sound) | Very protected; tree lined inlet with steep vertical walls | few | common |
| 12. | Aquilar Point (Barkley Sound) | Semi-exposed; convex outcropping of shoreline | abundant | none |
| 13. | Cedar Cove (Barkley Sound) | Semi-wave-protected; *Fucus* present, wide bay, vertical rock surfaces | abundant | abundant |
|  | Cedar Cove | Semi-wave-protected boulder field | rare (only on boulders with barnacles) | abundant |
| 14. | Helby Island (Barkley Sound) | Small inlet, protected from direct wave swell and shaded | common | common |
|  | Helby Island | Small boulder field | none | common |
| 15. | Sanford Island (Barkley Sound) | Semi-exposed; receives direct swell from ocean, small bay examined | abundant throughout bay | confined to inner reaches of bay on vertical surfaces of sharp crevices in rock |

TABLE 1 (con't)

| | Area | Physical Characteristics | *A. digitalis* | *A. persona* |
|---|---|---|---|---|
| 15. | Sanford Island (Barkley Sound) | Very protected from waves; Abundance of *Fucus*; convex outcropping facing south | few | none |
| 16. | Julia Passage (Barkley Sound) | Very protected, large waterfall 30 meters away. Oysters common | none | abundant |

Figure 6. Open coast habitat where only A. digitalis is found. Folger Island, Barkley Sound. (July, 1971).



*Postelsia palmaeformis* and colonies of the stalked barnacle, *Pollicipes polymerus*, are present.

Habitats where *A. persona* is found alone are (1) boulder fields, which are most prevalent in semi-exposed to protected waters, and (2) vertical surfaces at the inner reaches of some concavities in the shoreline. Boulder fields are usually found in small bays among island groups and in sounds and consist of smooth rounded or flattened rocks which average from 0.3 - 0.6 meters in diameter, usually devoid of dense barnacles, (Fig. 7). On sunny days, individuals of *A. persona* are found on the undersides of these boulders. On heavily overcast days, they are found on the tops of the boulders. Extremely large or immobile boulders usually support a growth of barnacles, and individuals of *A. digitalis* may also be present. Concavities in the shoreline where *A. persona* is found alone range from large crevices or cracks in the rocks, through shoreline indentations, to inlets (Fig. 8). Only at the inner reaches of these concavities is *A. persona* sometimes found alone.

In general, the shores where *A. persona* occurs seem to experience less wave action and less direct insolation than areas where *A. digitalis* is found alone. However, there is

Figure 7. Boulder field habitats of <u>A</u>. <u>persona</u> in Barkley Sound. Above, <u>A</u>. <u>persona</u> on boulders at Cedar Cove (May, 1970); below, the small boulder beach at Mills Cove.

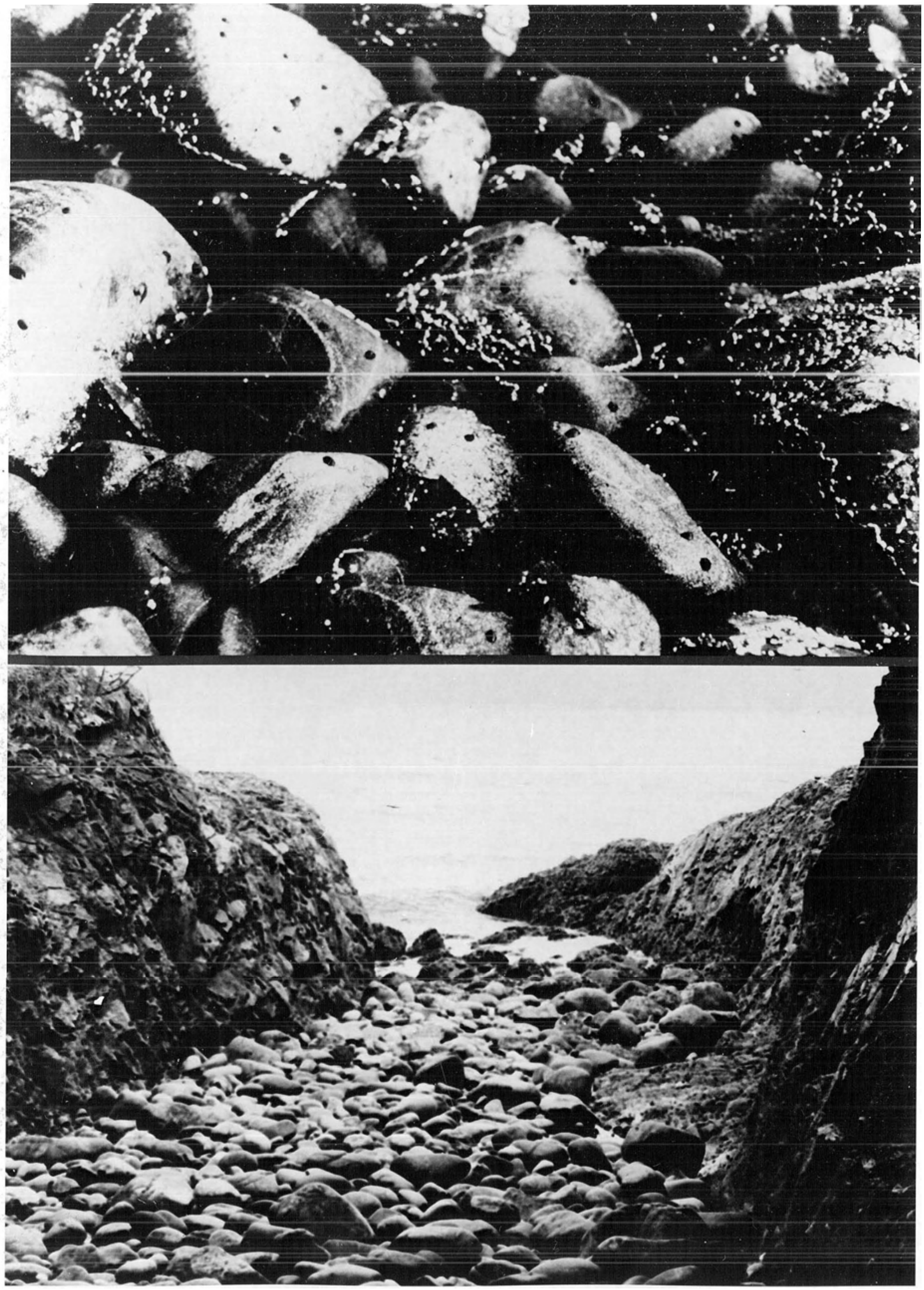
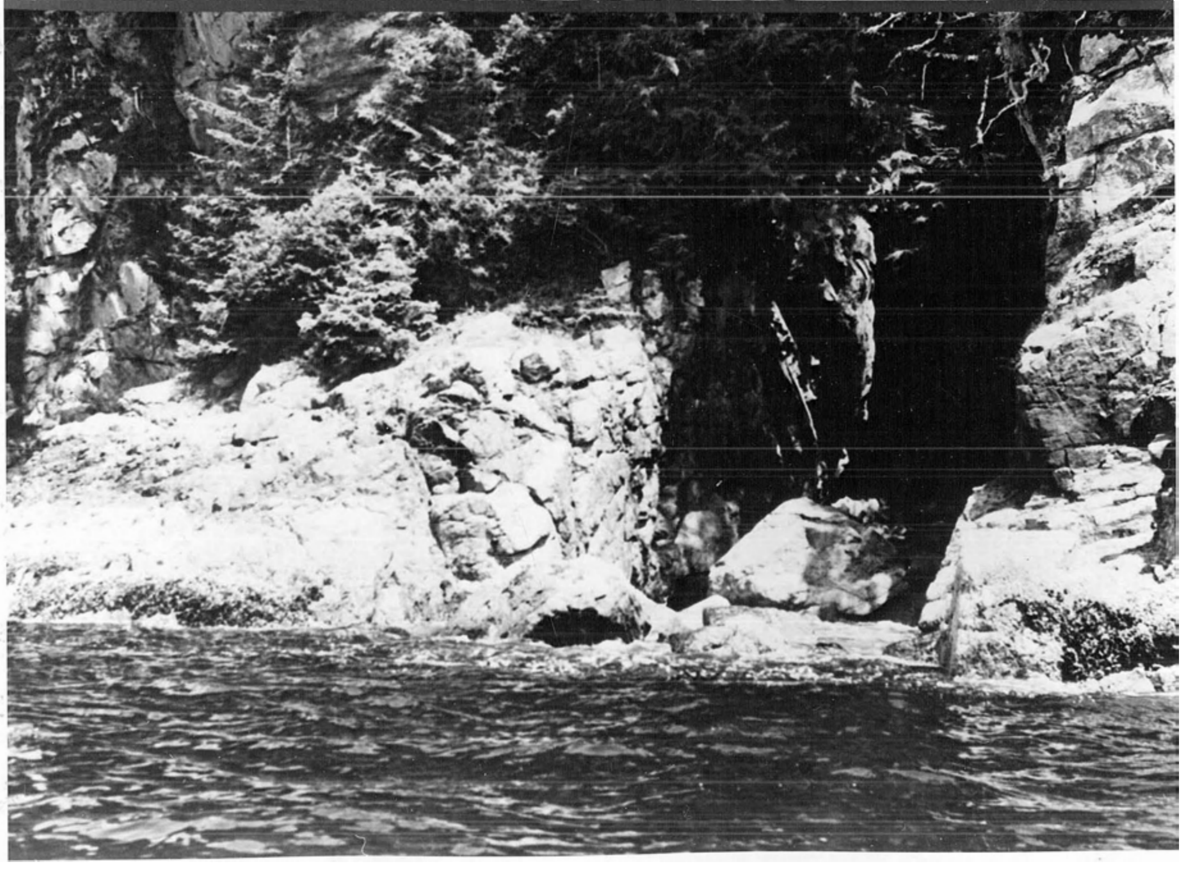


Figure 8. Shoreline concavities where only _A_. _persona_ occurs at the inner reaches. Above, looking towards the mouth of Grappler Inlet, Barkley Sound (July, 1971). Both species occur on the shores visible; _A_. _persona_ occurs alone farther in the inlet. Below, small shoreline indentation near Bamfield, "Boulder Cove", Barkley Sound (July, 1971). (_A_. _digitalis_ occurs on the seaward ends of these indentations.)



difficulty in separating these two factors. Crevices are usually dark, shaded by their sides, and also potentially protected from wave action. Inlets, or deep concavities, are often shaded by overhanging rocks and trees, and usually protected from direct wave swells. Conversely, points or headlands exposed to heavy surf are generally unshaded. Boulder fields offer protection from both waves and insolation where A. persona is often found.

Areas where A. digitalis and A. persona co-exist are difficult to define since they are intermediate between the two previously described categories. These areas are mainly shores in semi-exposed to semi-protected water, characteristic of large sounds, straits, and archipelagos. For example, extensive areas of overlap between the two species were noted throughout Barkley Sound and on San Juan Island (Fig. 1), both areas consisting of a labryinth of islands.

At some stations visited on the south and east coast of Vancouver Island, no limpets of either species were present (Table 1). Reasons for their conspicuous absence were not clear, since the shoreline supported large barnacle populations and appeared to be as habitable as other stations which maintained dense limpet populations.

## Micro-Habitat Differences

*Wave action and insolation*. The absolute and relative abundances of both species in the vertical transects at the three study sites are shown in Figs. 9,10, and 11. These data show prominent differences in the horizontal distributions of *A. persona* and *A. digitalis* along gradients in wave-action and insolation.

At Victoria Breakwater (Fig. 9) both *A. digitalis* and *A. persona* were present on the wave protected side. Individuals of *A. digitalis* were found spread over the concrete surface, as well as in vertical crevices. However, *A. persona* was confined solely to the vertical crevices and was only found in those which retained a distinct opening, as opposed to being fused. On the wave-exposed side of the breakwater only *A. digitalis* was present, and occurred mainly in the crevices.

At Limpet Point (Fig. 10) only *A. digitalis* was present on wave-exposed surfaces, while *A. persona* was confined to the two prominent concavities. The relative abundance of *A. digitalis* decreased towards the inner reaches of concavities where *A. persona* occurred. Only *A. persona* was present at the innermost portion of one concavity.

At Mills Cove (Fig. 11) the same trend is obvious. *A.*

Figure 9. Relative abundance of A. *persona* and A. *digitalis* in vertical transects at Victoria breakwater. (The thickness of the breakwater is not drawn to scale.)

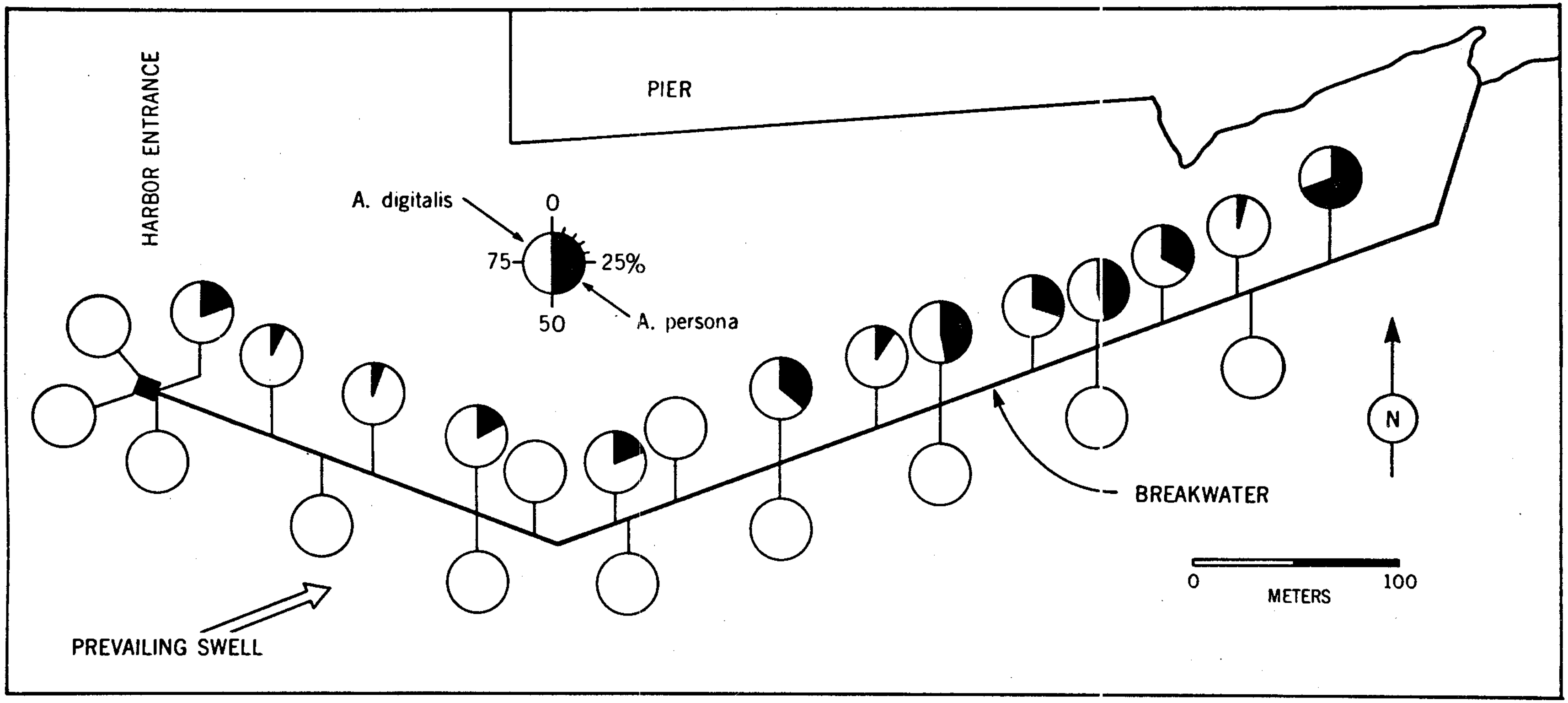

PIER
HARBOR ENTRANCE
A. digitalis
0
75
25%
50
A. persona
BREAKWATER
N
0
METERS
100
PREVAILING SWELL

Figure 10. Limpet populations in relation to shoreline at Limpet Point, Barkley Sound. Shoreline mapped is the profile of vertical surfaces at the transect baseline, roughly mean high water level. Asterisk represents the site of transplant experiments.

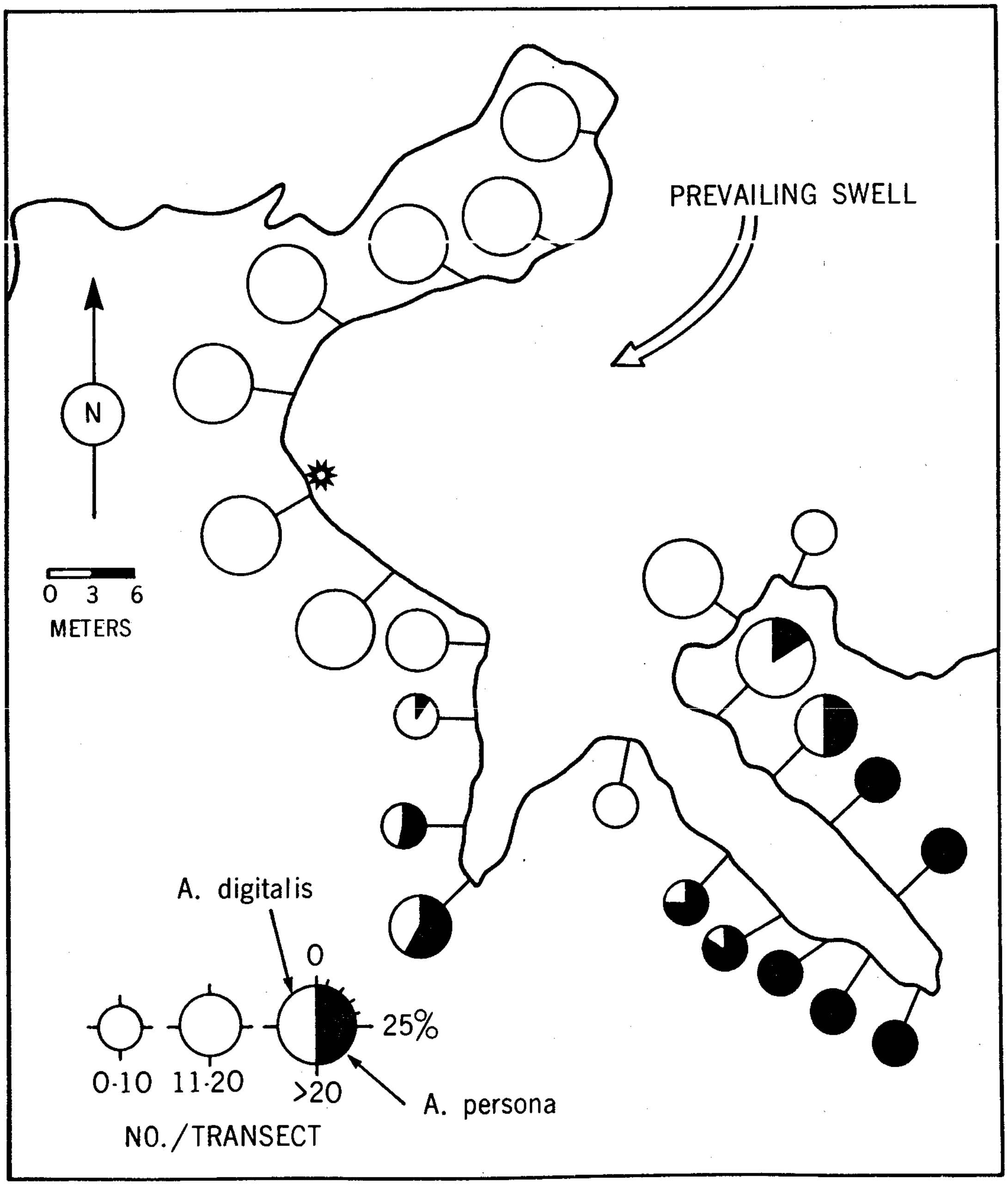
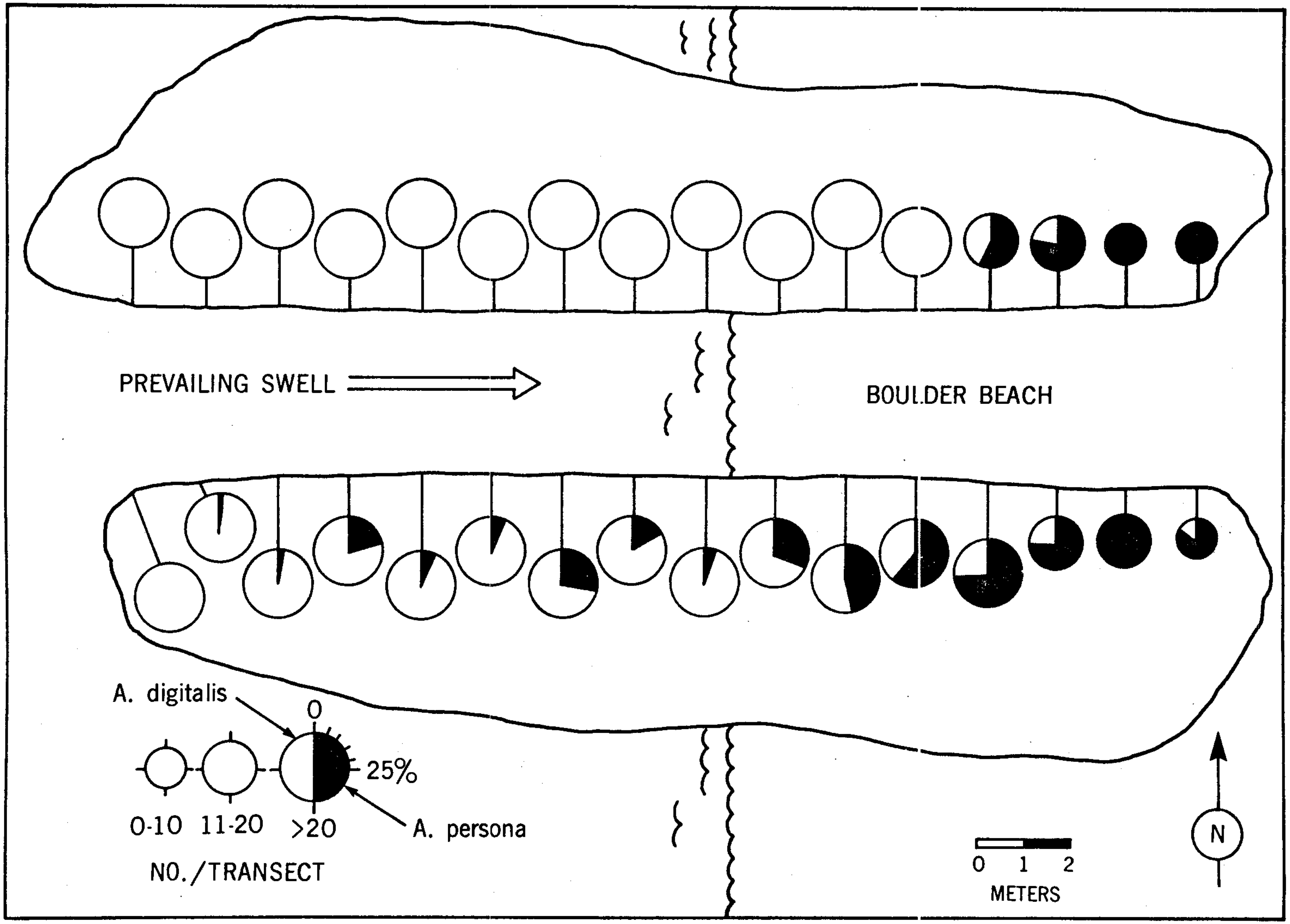

PREVAILING SWELL
N
0 3 6
METERS
A. digitalis
0
25%
0-10
11-20
>20
A. persona
NO./TRANSECT

Figure 11. Limpet populations in relation to shoreline at Mills Cove, Barkley Sound. Shoreline mapped represents vertical surfaces at baseline level.


PREVAILING SWELL
BOULDER BEACH
A. digitalis
A. persona
0
25%
0-10
11-20
>20
NO./TRANSECT
0
1
2
METERS
N

*digitalis* occurred alone at the seaward end of each wall, and its relative abundance gradually decreased towards the inner, or shoreward, end. Conversely, the relative abundance of *A. persona* increased towards the inner end of each wall.

However, at Mills Cove there was a large difference between the distribution of *A. persona* on the south facing and north facing wall, indicating that insolation is more closely correlated with the distribution of *A. persona* than wave action. While the population of *A. persona* extended to almost the seaward extreme of the north facing wall, it did not extend beyond a third of this distance on the south facing wall. In addition, the relative abundance of *A. persona* gradually decreased toward the seaward end of the north facing wall, but dropped off suddenly on the south facing wall. This sudden drop-off roughly corresponded with the limit of trees above the limpets on the north facing wall, the absence of these trees increasing insolation.

Also, at Victoria breakwater, if wave action were more important than insolation, one would expect the occurrence of *A. persona* on surfaces anywhere on the wave-protected side. However, *A. persona* is confined solely to crevices on the protected side. As mentioned earlier, these crevices were shaded, even when both sides of the breakwater were exposed to direct sunlight.

Intertidal height. The results of representitive vertical transects on the protected side of Victoria Breakwater are shown in Fig. 12. Where *A. persona* and *A. digitalis* co-exist in crevices their populations have slightly different vertical positions. The peak population density of *A. digitalis* is at a lower vertical position than *A. persona*. Also, *A. persona* extends higher than *A. digitalis*, and *A. digitalis* extends lower than *A. persona*. The gradual shift upwards in each species towards the seaward end of the breakwater is a result of increasing wave exposure. The vertical range of *A. digitalis* appears to be the same whether or not *A. persona* is also present in the crevice.

At the breakwater, the upper limit of each species was measured in every crevice where both species co-existed. This was done by taking the distance to the highest individual of each species from the top of the concrete wall. These results were plotted as linear regressions (Fig. 13). The slope of these lines again indicates the effect of increasing wave exposure which displaces the populations upward. The different intercepts, however, reflect a consistent difference in the upper limits of both species. A student's t-test was used to

Figure 12. Abundance of both species in vertical transects in crevices where both species occurred and crevices where only A. digitalis occurred at Victoria breakwater. Crevice numbers increase towards the seaward end of the breakwater.

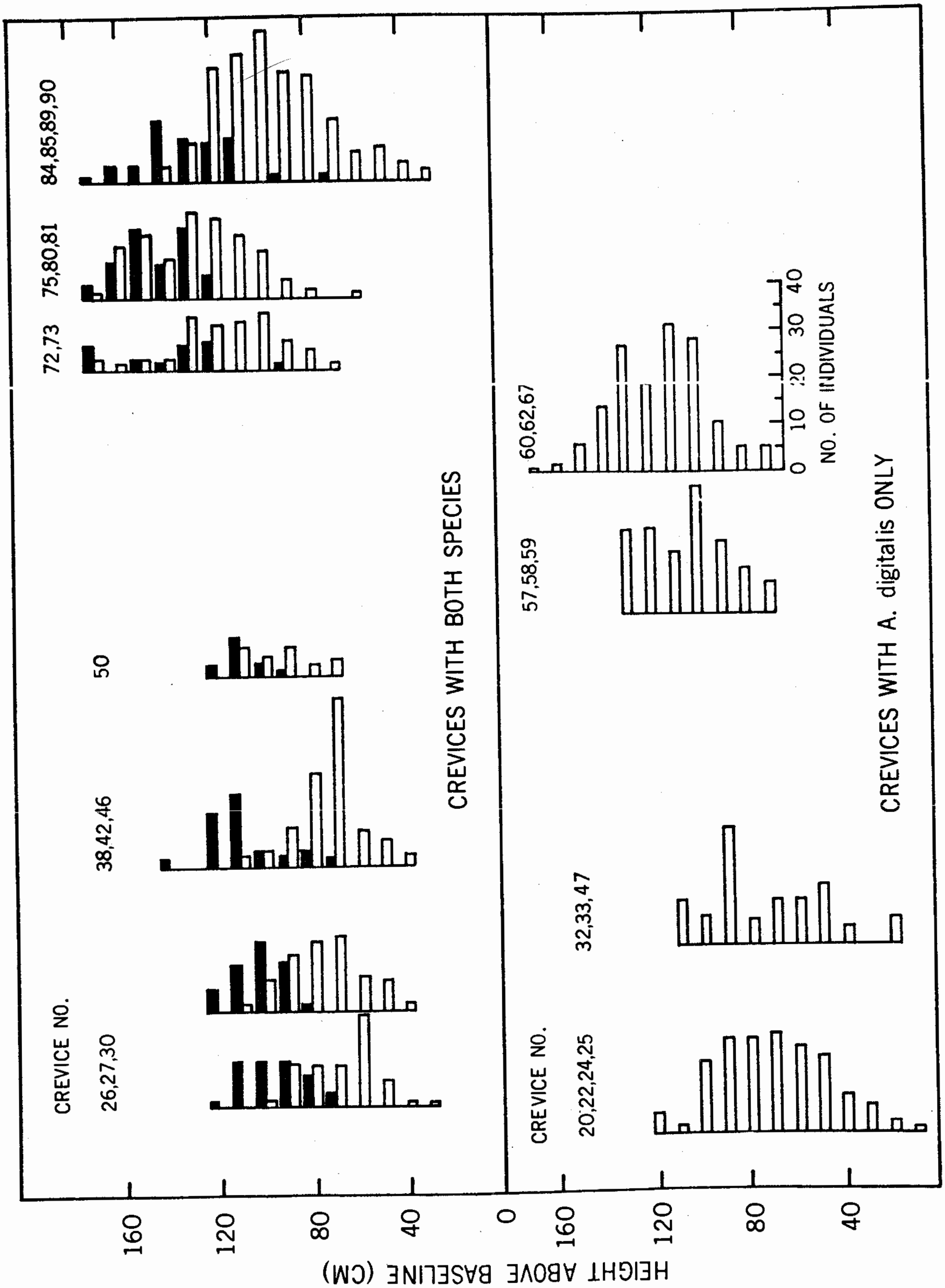
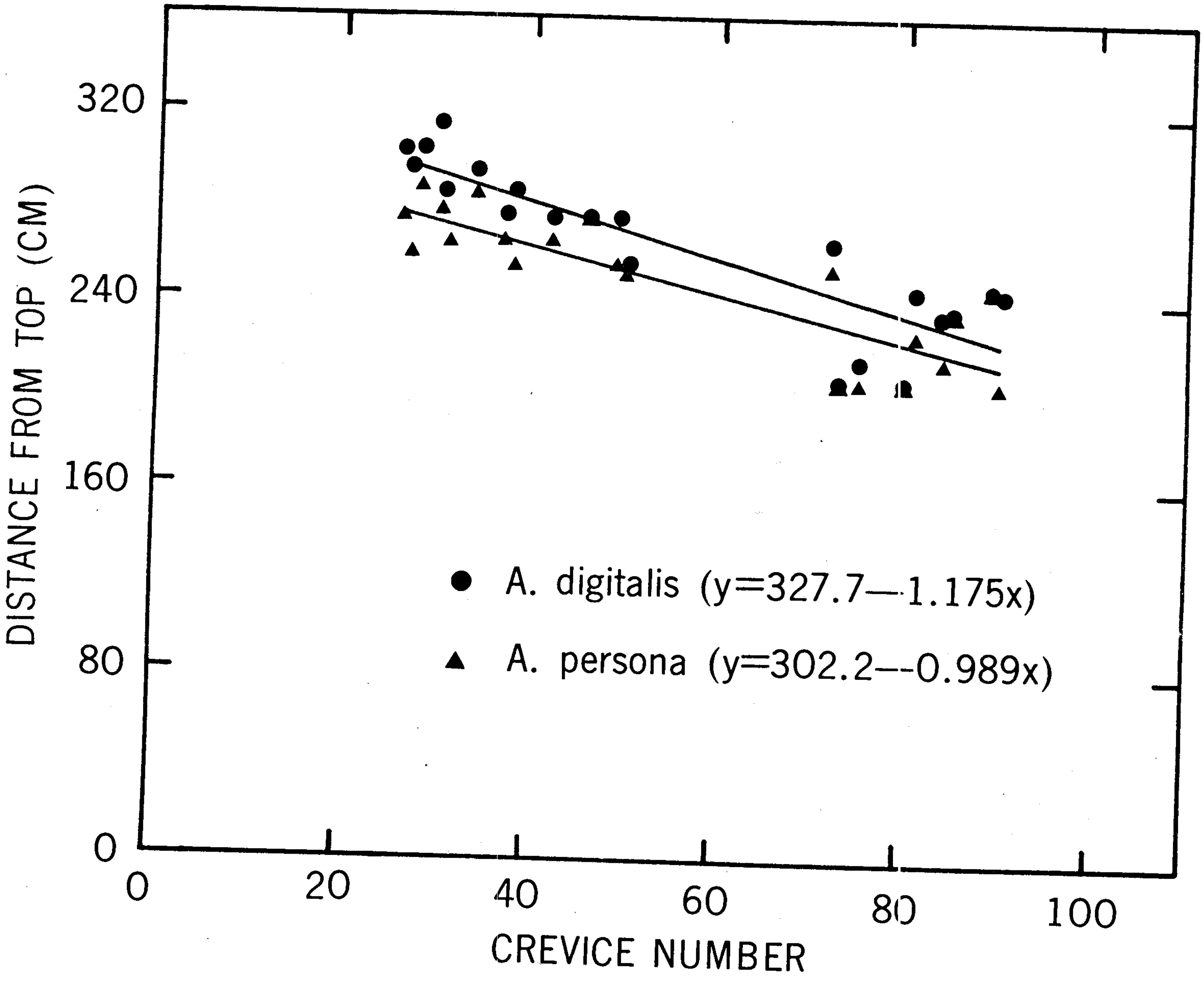

CREVICE NO.
26,27,30
38,42,46
50
72,73
75,80,81
84,85,89,90
CREVICES WITH BOTH SPECIES
CREVICE NO.
20,22,24,25
32,33,47
57,58,59
60,62,67
CREVICES WITH A. digitalis ONLY
0
10
20
30
40
NO. OF INDIVIDUALS
160
120
80
40
0
160
120
80
40
HEIGHT ABOVE BASELINE (CM)

Figure 13. Upper limits of both species at Victoria breakwater. "Distance from top" refers to the distance from the top of the breakwater.


DISTANCE FROM TOP (CM)
320
240
160
80
0
0
20
40
60
80
100
CREVICE NUMBER
● A. digitalis (y=327.7—1.175x)
▲ A. persona (y=302.2—0.989x)

test the difference between the two intercepts after the method of Simpson, et al., (1960). The upper limit of A. persona was significantly higher than A. digitalis ($p < .01$).

Results from transects at Mills Cove (Barkley Sound) are shown in Fig. 14. These results did not reflect the same vertical distributions found at Victoria Breakwater. No difference between the upper limits of the two species was apparent. However, on these vertical surfaces, A. digitalis usually extended lower than A. persona.

Upper and lower limits of both species were also determined at Cedar Cove and Helby Island in Barkley Sound (Fig. 15) using an eye level and surveyor's pole. Where populations of A. persona and A. digitalis co-existed on vertical surfaces there was no significant difference in their upper limits. In the adjacent boulder field at Cedar Cove, however, the upper limit of A. persona was significantly lower than the upper limit of A. persona on the vertical surfaces at these same areas. Lower limits at these areas varied a great deal and were difficult to determine accurately. Nevertheless, populations of A. persona also seemed to extend lower in the boulder fields than on vertical surfaces.

The whole vertical range of A. persona, therefore, appears to be shifted downward in the boulder fields. At Mills Cove

Figure 14. Vertical distribution and population size of A. *persona* (dark) and A. *digitalis* (light) on the north facing wall at Mills Cove.

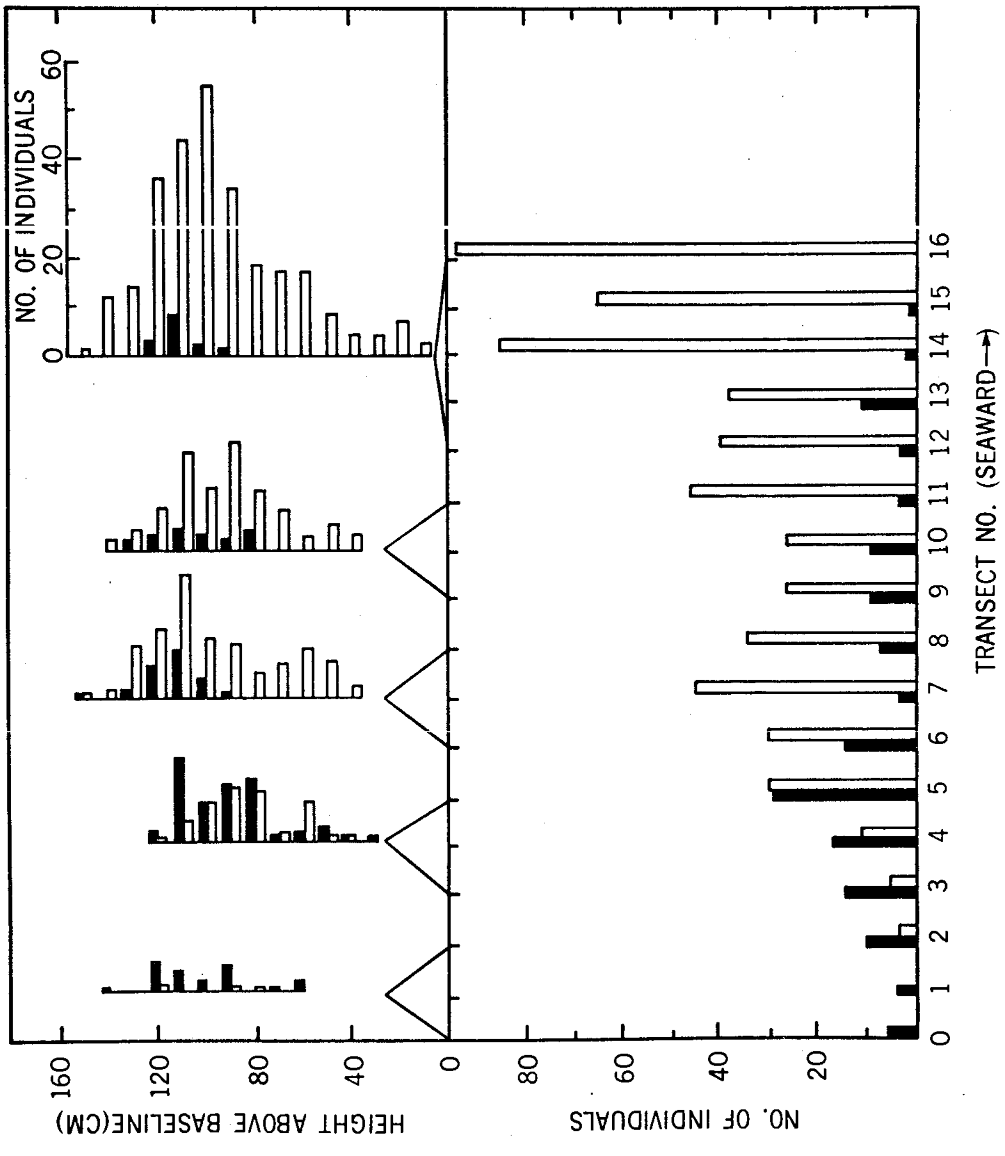
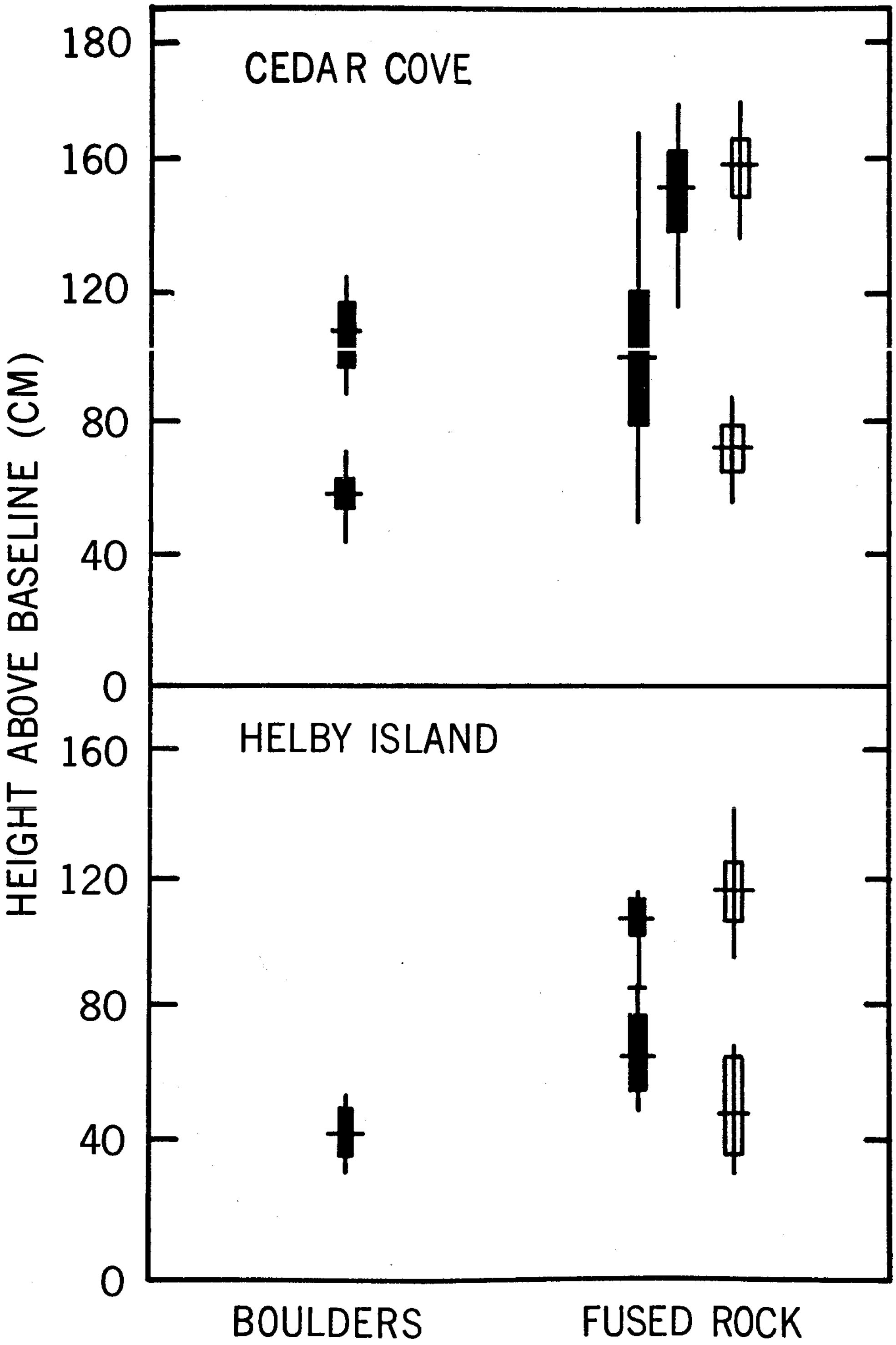

NO. OF INDIVIDUALS
0
20
40
60
HEIGHT ABOVE BASELINE(CM)
160
120
80
40
0
NO. OF INDIVIDUALS
80
60
40
20
TRANSECT NO. (SEAWARD→)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

Figure 15. Upper and lower limits of A. persona (dark) and A. digitalis (light) in boulders and on adjacent fused rocks at Cedar Cove and Helby Island, Barkley Sound. In boulders at Helby Island, only the lower limit of A. persona could be measured.


CEDAR COVE
HELBY ISLAND
HEIGHT ABOVE BASELINE (CM)
180
160
120
80
40
0
160
120
80
40
0
BOULDERS
FUSED ROCK

and Cedar Cove, the incoming tide would begin covering the population of _A_. _persona_ in the boulders well before it reached the population of _A_. _persona_ and _A_. _digitalis_ on the adjacent vertical rocks. In addition, near the lower limit of _A_. _persona_ in boulder fields, individuals of _A_. _persona_ were found mixed with individuals of _A_. _scutum_, a limpet characteristic of the middle intertidal zone (Test, 1945). On vertical surfaces, only _A_. _digitalis_ sometimes extended down to the upper limit of _A_. _scutum_.

The data from Victoria breakwater indicates that in some areas the upper limit of _A_. _persona_ may exceed that of _A_. _digitalis_. This particular instance appeared to be the result of _A_. _persona_ attaining much larger sizes than _A_. _digitalis_, thereby increasing its ability to withstand the desiccation experienced at higher tidal levels (discussed below). Since _A_. _persona_ seems to grow consistently larger than _A_. _digitalis_, vertical distributions similar to those at Victoria breakwater may be common elsewhere.

To summarize, most of the evidence presented above indicates that where both species co-exist on solid rock surfaces, the vertical range of _A_. _persona_ lies within that of _A_. _digitalis_. Both species have the same upper limit, but _A_. _digitalis_ extends lower than _A_. _persona_. In boulder fields, the vertical range of A. persona is lower than on vertical rock surfaces.

Substrate. The possible influence of substrate texture on the distributions of A. persona and A. digitalis was investigated at Victoria breakwater. Here, two distinct substrate types were evident: the smooth surface of concrete, and a rough surface left when the outer layer of concrete had eroded or broken away. When transects were taken in crevices where both species occurred, the kind of surface each limpet was on was noted. Although A. digitalis was found on both kinds of surfaces (25% on smooth), A. persona occurred almost exclusively on the smooth surface (97% on smooth).

Except for the breakwater, where clear substrate types could be distinguished, the effect of substrate texture on limpet distribution was difficult to assess on natural rock surfaces. However, it did not appear to be a factor significantly related to limpet distributions. Most areas where only one species occurred offered a substrate similar to regions where both species were found together.

Another aspect of substrate was the difference between vertical rock surfaces, where both species were found, and boulder fields, where only A. persona occurred. As described earlier, boulder fields differed from vertical rocks in offering an essentially horizontal substrate consisting of smooth rounded or flattened rocks. Since A. persona move under boulders when exposed to sunlight, I felt that the absence of A. digitalis from the boulder habitat might be due to the absence of this behavior, which appeared peculiarly adaptive to this kind of substrate.

To test for this behavior in A. digitalis, 15 limpets of each species, collected from nearby vertical surfaces, were placed on the top side of a large boulder which was moved above the tide and into the sun. Within five hours, all of the limpets of both species had migrated to the underside of the boulder. The ability to move underneath boulders when exposed to the sun is therefore present in both species.

Food. The possibility that A. persona and A. digitalis prefer different algal foods whose distribution might correspond to the distributions of the two limpets was investigated by examining the algal remnants in the feces of A. digitalis and A. persona collected from habitats where only one species occurred, and habitats where they both overlapped (Mills Cove, late August, 1970). The feces were teased apart and examined under a microscope.

A comparison of the fecal material from the three different habitats did not indicate any differences in food preferences between the two species of limpet. The major identifiable constituents of the feces were the silicious casts of diatoms. Although several different kinds were noted, there was large overlap between all of the limpets from each area.

Community Associates. The kinds of animals associated with both species of limpet were noted in many areas of Barkley Sound to determine if there were differences between habitats where *A. digitalis* occurred alone, areas where *A. digitalis* and *A. persona* overlapped, and areas where *A. persona* occurred alone. Only major differences in the presence or absence of species were noted.

Moving from exposed convexities, where only *A. digitalis* occurs, into semi-protected waters, where *A. persona* and *A. digitalis* co-exist, little change occurs in the community associates. The barnacle population becomes thinner in the more protected areas. In Barkley Sound potential bird predators such as gulls, oystercatchers, turnstones, and surf birds seemed to congregate on the exposed, or convex, regions of shore at low tide and on horizontal surfaces.

A large difference in community associates is found between boulder fields where only *A. persona* occurs, and vertical surfaces of solid rock shoreline, where the two species overlap. In boulder fields common animals were the crab, *Hemigrapsus nudus*, *Idothea sp*. and another unidentified isopod, polyclad flatworms, large populations of the herbivorous snail *Tegula funebralis*, and the crab *Petrolisthes sp*. Barnacles were sparse, or absent entirely. Only in one area *Tegula funebralis* co-existed with *A*. *persona* and *A*. *digitalis* on vertical surfaces. Otherwise, none of the above species were found in the fused rock habitats where *A*. *persona* and *A*. *digitalis* both occurred. These large differences indicated that *A*. *persona* in boulder fields live in a kind of intertidal community very different from that on vertical rocks where *A*. *persona* and *A*. *digitalis* occurred.

Some of the animals in the boulder fields may be important as limpet predators. A crab similar to *H*. *nudus*, *Pachygrapsus crassipes*, has been observed eating limpets (Test, 1945; Chapin, 1968; Stimson, 1968). Flatworms have also been observed eating *A*. *digitalis* (Frank, 1965). In addition, mink, bear, and racoon were often seen in boulder fields turning over rocks for food. However, it is not known if they eat limpets.

The large populations of *Tegula funebralis* indicated a potential competitor with limpets for food. This snail, like the limpets, also feeds on microscopic algae (Best, 1964).

It is possible that these different animals in boulder fields compared to solid vertical surfaces may prevent populations of *A. digitalis* from existing in the boulder habitat.

*Fresh Water*. In areas of high rainfall, certain regions of shoreline will receive large amounts of fresh water run-off and in wave protected waters this fresh water may remain as a layer on the surface. The effects of this fresh water on the high intertidal marine community may determine the distribution of some organisms depending on their tolerance to low salinity and their ability to osmoregulate.

Regions of shoreline where only *A. persona* occurs appear to receive a greater amount of fresh water as run-off than shoreline supporting populations of *A. digitalis*. For example, the inner reaches of large inlets, with a tree lined shore and very protected water, often contain permanent streams on the shore (e.g. Grappler Inlet, Julia Passage, Duke Pt.). Also, the inner reaches of some concavities are characterized by fresh water seepage. Boulder fields may also collect more fresh water at low tide because of their horizontal aspect.

Observations during rainstroms in Barkley Sound supported this hypothesis. Many *A. persona* were found directly in run-off streams and pools both in boulder fields and the inner reaches of small concavities, where there were no *A. digitalis*.

In Julia Passage, Barkley Sound, A. persona were found near a large waterfall outlet. There were no A. digitalis present (Table 1).

## III. EXPERIMENTAL STUDIES OF FACTORS CAUSING HABITAT DIFFERENCES BETWEEN A. persona and A. digitalis

The habitat studies (above) revealed significant differences between the horizontal distributions of A. persona and A. digitalis. However, the question of what factors cause the species to maintain these different distributions remains unanswered. Specifically, why is A. persona restricted from the regions of shoreline where only A. digitalis is found; and conversely, why is A. digitalis absent from the habitats exclusive to A. persona. One possibility is that environmental factors associated with the different habitats independently limit each species.

Micro-habitat studies indicated several environmental factors which were correlated with the observed distributions of each species. The main factors correlated with the distribution of A. persona were wave action and insolation. Where both of these factors increased, the relative abundance of A. persona decreased. Environmental factors correlated with the horizontal distribution of A. digitalis were the degree of exposure to fresh water, the presence of the predatory crab Hemigrapsus nudus, and the absence of barnacles. Where the influence of fresh water appeared to increase (shoreline concavities and boulder fields) the relative abundance of A. digitalis decreased

Where barnacles became scarce and the predatory crab, *H. nudus*, was abundant (boulder fields) the relative abundance of *A. digitalis* also decreased.

Field and laboratory experiments were performed to determine which, if any, of these environmental factors are casually related to the observed limpet distributions.

## METHODS

1. Field experiments were performed at Limpet Pt., Barkley Sound, to test independently for the effects of wave-action and insolation (dessication and high temperatures) on the survival of _A_. _persona_. The experimental procedure consisted of transplanting young _A_. _persona_ (5-7 mm) into areas where only _A_. _digitalis_ was present. Their survival under conditions where wave action and insolation remained unaltered was then compared with their survival under conditions where the effects of wave exposure and/or insolation were artificially eliminated.

On a small region of shoreline, which was vertical and of uniform aspect (Fig. 10), rectangular enclosures were constructed within which the young _A_. _persona_ could be transplanted. Enclosures were made of strips of underwater epoxy "sea-goin poxy-putty"; Permalite Plastics, California) which were glued directly to the rock surface. After the epoxy strips dried, they were painted with a thick coat of copper "anti-fouling" paint. Three large enclosures, 30 x 20 cm, were constructed in the upper half of the vertical range of _A_. _digitalis_. In addition, two small square enclosures, 10 x 10 cm, were constructed: one at the level of the three large grids, and one at the lower limit of _A_. _digitalis_. All _A_. _digitalis_ in each grid were removed.

The effects of insolation on transplanted limpets were eliminated in two ways. One was to place a sea-water reservoir, consisting of four 16 gallon plastic containers, above the grids. This sea water was then dripped slowly over one of the grids to keep it wet during low tide exposure (Fig. 16). The reservoir was filled daily with fresh seawater using a gasoline powered water pump.

The other method was to place a plywood barrier over an enclosure to provide shade. As well as keeping the area underneath in constant shade, this also served as a protection from wave action (Fig. 17). The plywood was 1/4 inch thick, painted black on its underside, and was applied to within 2 cm of the rock surface. It was attached using 3/8 inch bolts were embedded in the rock using masonry bolt anchors and epoxy cement.

The effects of wave action were separated from those of insolation by using both the plywood barrier and transparent plexiglass barrier, 1/2 inch thick (Fig. 17). The plexiglass barrier was attached in the same manner as the board, and bolts which supported these barriers were placed on two of the three large grids, such that the plywood and plexiglass barriers could be interchanged between them to control for a grid effect.

Figure 16. Diagram of sea water apparatus used in transplant experiments at Limpet Point.

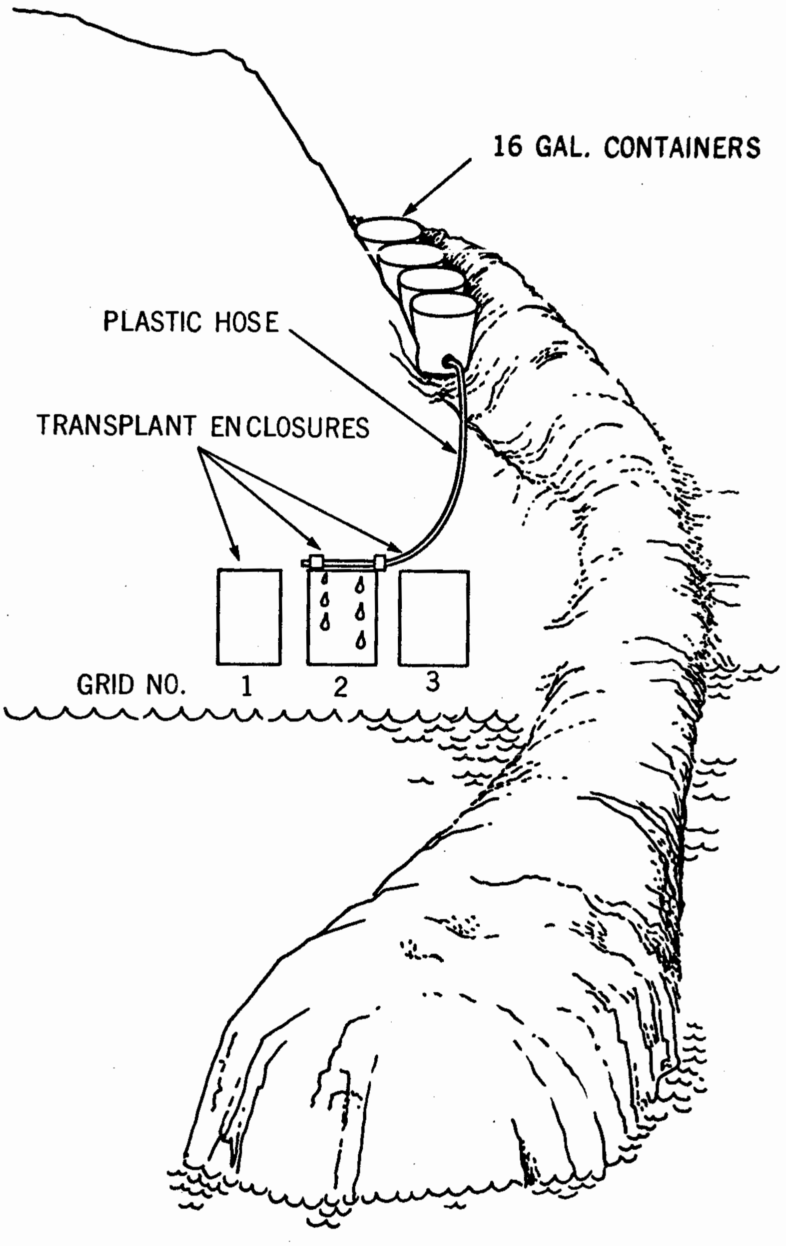
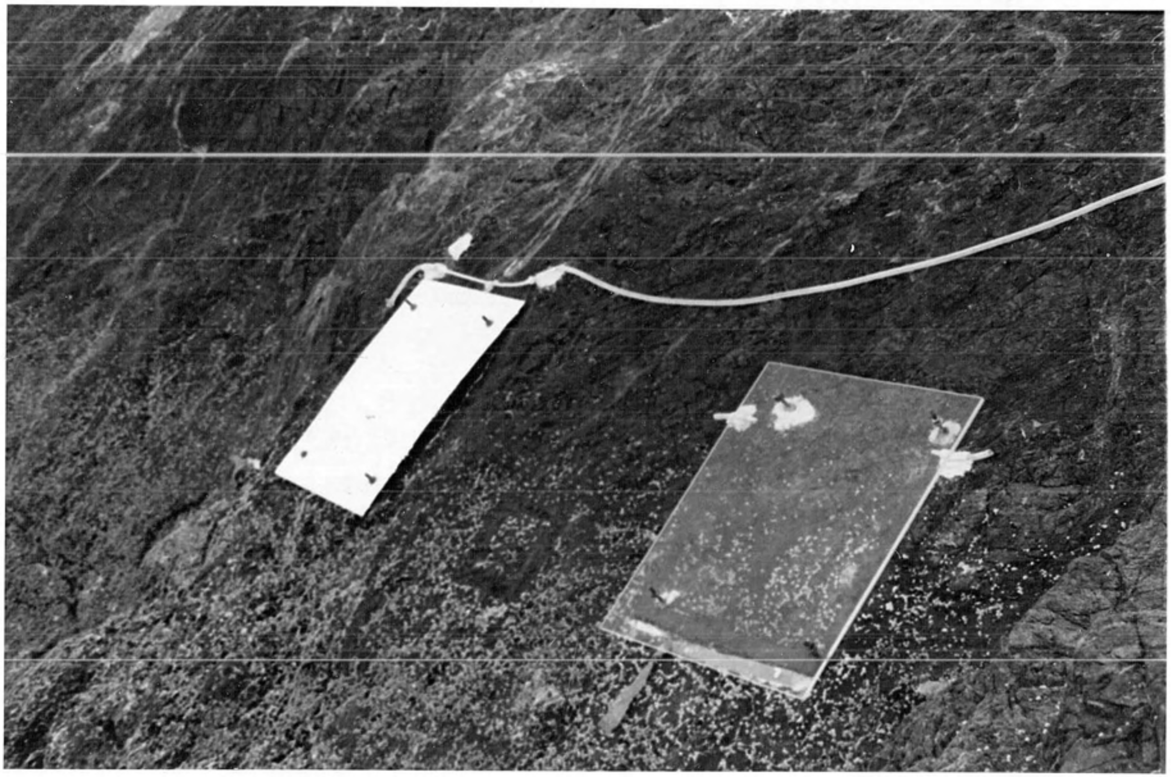

16 GAL. CONTAINERS
PLASTIC HOSE
TRANSPLANT ENCLOSURES
GRID NO.
1
2
3

Figure 17. Opaque and transparent wave barriers used in transplant experiments at Limpet Point.



2. Interspecific differences in the ability to withstand desiccation were investigated in the laboratory by determining the rates of water loss in the two species and the water retaining capacity of their shells. The latter involved a comparison of (1) the relative height of each species (i.e. a flat relative to a tall spire), (2) their shell thickness, and (3) their capacity for storing extra-visceral water (i.e. water stored in the mantle cavity and between the mantle and shell).

Rates of water loss were determined by simple weight-change experiments. Both species of limpet, <1.3 cm, were collected from Mill's Cove, Barkley Sound, and brought back to the laboratory aquarium. After approximately 48 hours in the aquarium limpets were placed in plastic petri dishes and allowed to adhere. The excess sea water was then removed from the dish and from the limpet shells. Each dish was weighed and placed in one of several large glass desiccators containing a silica-gel desiccant. Every dish was subsequently weighed at hourly intervals.

After the experiment, the shell volume of each limpet was determined (see below) and the water lost at each weighing interval was expressed as the percentage of the total water in each limpet.

To assess the water retaining capacity of shells, large samples of limpets collected from Barkley Sound, including limpets from the desiccation experiment, were measured for body weight, shell volume, shell weight, shell length, and shell height.

All linear measurements were made with a micrometer accurate to 0.01 mm. Shell volume was measured after the method of Segal (1956) by filling inverted shells with benzene from a small syringe (accurage to 0.01 cc). The dry weight of each limpet was used as the index of body size, and this measurement, as well as shell weight, was made on a Mettler analytical balance.

3. Survival of *A. digitalis* in the habitats of *A. persona* was tested by field transplant experiments in which *A. digitalis* was transplanted into the two kinds of habitat where only *A. persona* occurs (boulder fields and the inner reaches of shoreline concavities). Groups of *A. digitalis* were transplanted onto boulders at Mills Cove (Fig. 7) and into a large shoreline concavity at Limpet Point.

In boulders, two kinds of experiment were performed. In one, the survival of *A. digitalis* in the presence of *A. persona* was compared to its survival in the absence of *A. persona*. In the other, the survival of *A. digitalis* transplanted onto bolders with barnacles was compared to their survival on smooth boulders. At Limpet Point, only one experiment was performed comparing the survival of *A. digitalis* in the presence and absence of *A. persona*. Two kinds of controls were used in each area. One was an adjacent population of *A. persona* left undisturbed; the other, a group of *A. digitalis* transplanted within their own habitat.

Enclosing populations of transplanted *A. digitalis* in boulder fields was a problem. Initially, plastic window screen was made into bags, which could be opened at one end, into which the boulders containing the transplanted limpets were placed. However, the screen proved too fragile and was usually ripped from the rocks by wave action. Also, the extra handling required to remove the boulder in order to count the limpets remaining each day causing some of the limpets to drop off and crushed others.

A better method was to place the boulder containing the transplanted *A. digitalis* onto a large sheet of plastic screen (Fig. 18). This appeared to be effective in preventing limpets from migrating to or from the boulder and allowed other animals in the community access to the transplanted population. However, the plastic screen was often ripped by the abrasive action

Figure 18. Screen enclosures used in transplants at Mills Cove. (Boulder at left center contains transplanted limpets.)

of the rocks and waves. In later experiments, stainless steel screen was cut into large squares and substituted for the plastic screen.

The enclosures for limpets transplanted to Limpet Point as well as control enclosures for transplanting _A_. _digitalis_ within their own habitat, were constructed of epoxy and copper paint (see above).

4. To compare the tolerance of _A_. _persona_ and _A_. _digitalis_ to fresh water, large numbers of both limpet species were collected from Mills Cove, Bamfield and submerged for 24 hours in a bucket of sea water. All limpets were between 10 and 15 cm. The limpets were placed upside down in preparation dishes which were filled with freshly collected rain water (8°C). After 10 hours had elapsed, 15 limpets of each species were returned to sea water at hourly intervals until 15 hours had elapsed. The percentage recovery in each of these groups was then determined after 12 hours in sea water. The maximum time of 15 hours was chosen because no limpets survived beyond this time in a pilot experiment performed previously.

Since Bamfield was experiencing a prolonged rainstorm when the experiment was carried out, observations were also made in the field of limpets experiencing fresh water run-off in streams and pools.

5. Experiments were performed to test whether the crab, *H. nudus*, will eat limpets on smooth boulders and whether they show a preference between *A. digitalis* and *A. persona*. Three small smooth boulders were placed in a plastic pan filled approximately one inch deep with sea water. Several small individuals of *A. persona* and *A. digitalis* (approx. 5 mm) were then placed on these boulders and allowed to adhere. Three crabs, measuring approximately 23 mm across the carapace, were then placed in the tray and left undisturbed for 24 hours. This experiment was repeated three times, replacing eaten limpets, but using the same crabs each day.

# RESULTS

## Field Experiments: Effects of Wave-Action and Insolation on A. persona

Effects of transplanting procedure. To determine the initial mortality caused by the transplanting method, three groups of 20 A. persona were marked with paint and moved from their boulder habitat at Mills Cove to an adjacent vertical surface where other A. persona were present. Their survival was assessed daily for a period of four days.

Results indicated that the transplanting procedure accounted for up to 30% of the initial losses (Fig. 19). These data served as a control to compare with the transplants at Limpet Point.

Survival in wet and dry enclosures. Into each of three large enclosures at Limpet Point, 20 A. persona were transplanted. Enclosure 2 (grid numbers identified in Fig. 16) was kept wet by dripping sea water, while enclosures 1 and 3 remained unaltered.

It is clear that limpets survived better in the wet grid than in the two unaltered enclosures (Fig. 20A). Survival of limpets in the wet enclosure was slightly higher than the

Figure 19. Survival of control transplants of *A. persona* moved from boulders at Mills Cove to an adjacent vertical surface where other *A. persona* existed. Each point represents the average survival for three groups of 20 individuals; vertical bar represents range.

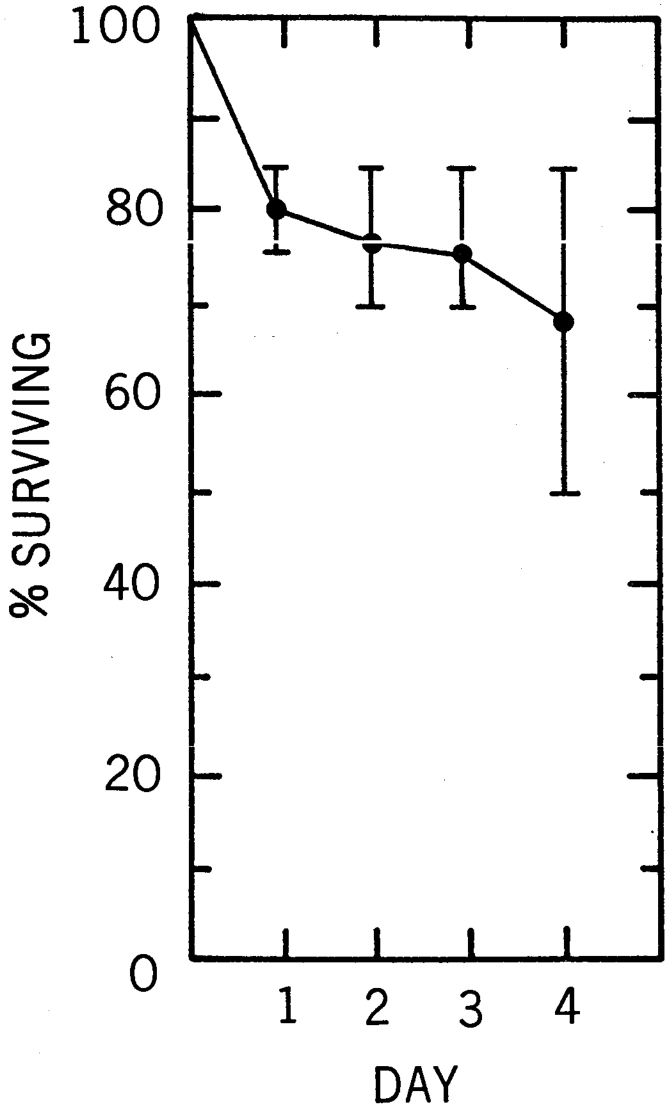
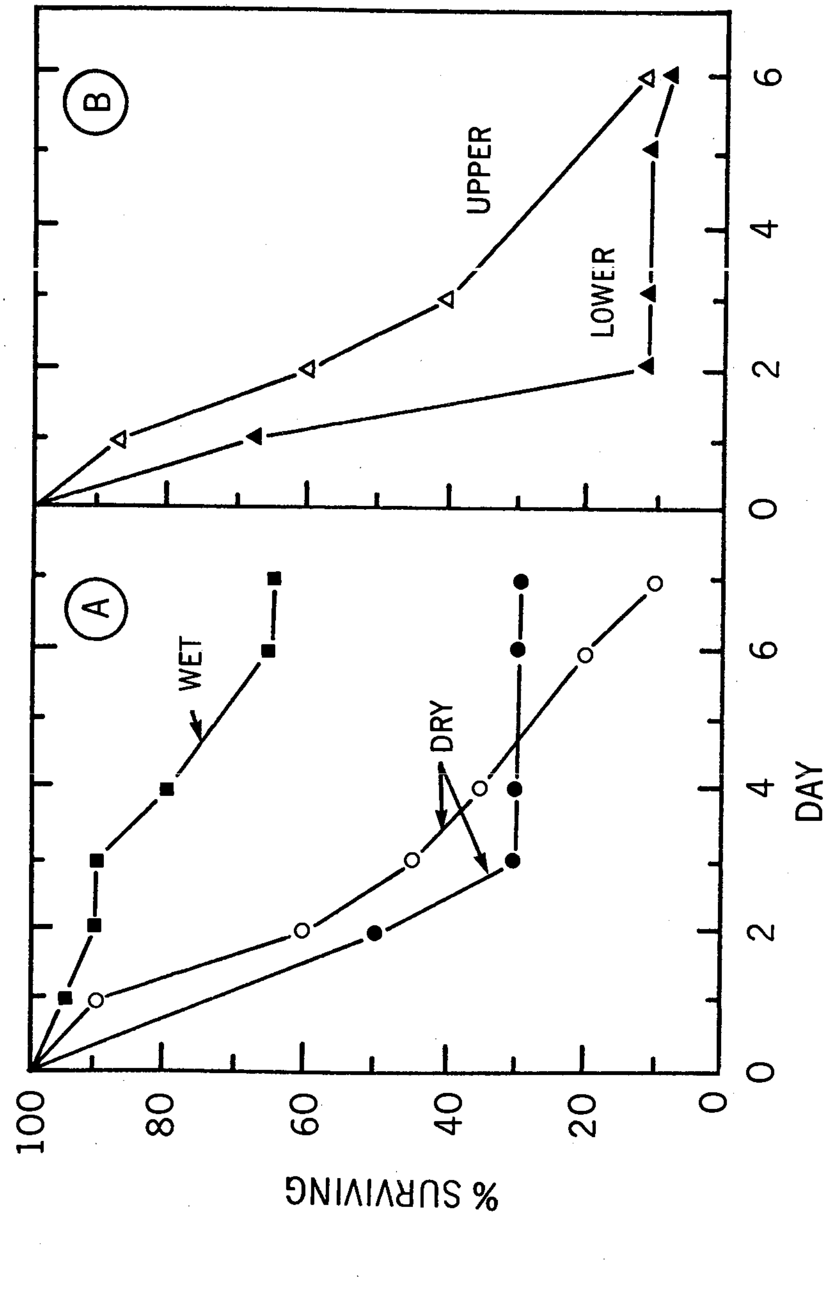

100
80
60
40
20
0
% SURVIVING
1
2
3
4
DAY

Figure 20A Survival of transplanted *A. persona* in upper grids at Limpet Point when enclosure 2 was kept wet at low tide daily, and 1 and 3 were left unaltered.

Figure 20B Survival of *A. persona* when transplanted into upper and lower enclosures at Limpet Point.


A
WET
DRY
B
UPPER
LOWER
% SURVIVING
100
80
60
40
20
0
DAY
0
2
4
6
0
2
4
6

control experiment (Fig. 19); survival in the other enclosures was lower.

To test whether the high mortality in the unaltered enclosures was a result of transplanting limpets too high in the intertidal, two groups of limpets were transplanted into the upper small square enclosure and the lower enclosure respectively. This experiment was simultaneous with the previous one in the large enclosures.

Results indicated that survival in the lower enclosure was similar to the upper enclosure and to the large unaltered enclosures (Fig. 20).

Survival in shaded and non-shaded enclosures. In experiments separating the effects of wave action and insolation, the plywood barrier providing shade plus wave protection and the transparent plexiglass barrier providing wave protection but no shade were attached to enclosures 2 and 3 respectively. Enclosure 1 remained unaltered. Again, 20 *A. persona* were transplanted into each grid. This experiment was repeated four times, interchanging the plywood and plexiglass barriers after the second repetition.

The results of these experiments are shown in Fig. 21 and 22. The limpets under the board survived consistently better

Figure 21. Survival of _A_. _persona_ under the shaded board (●), transparent plexiglass (○), and in the unaltered enclosure (▲) at Limpet Point. Opaque board and plexi-glass barriers could be interchanged to control for a grid effect.

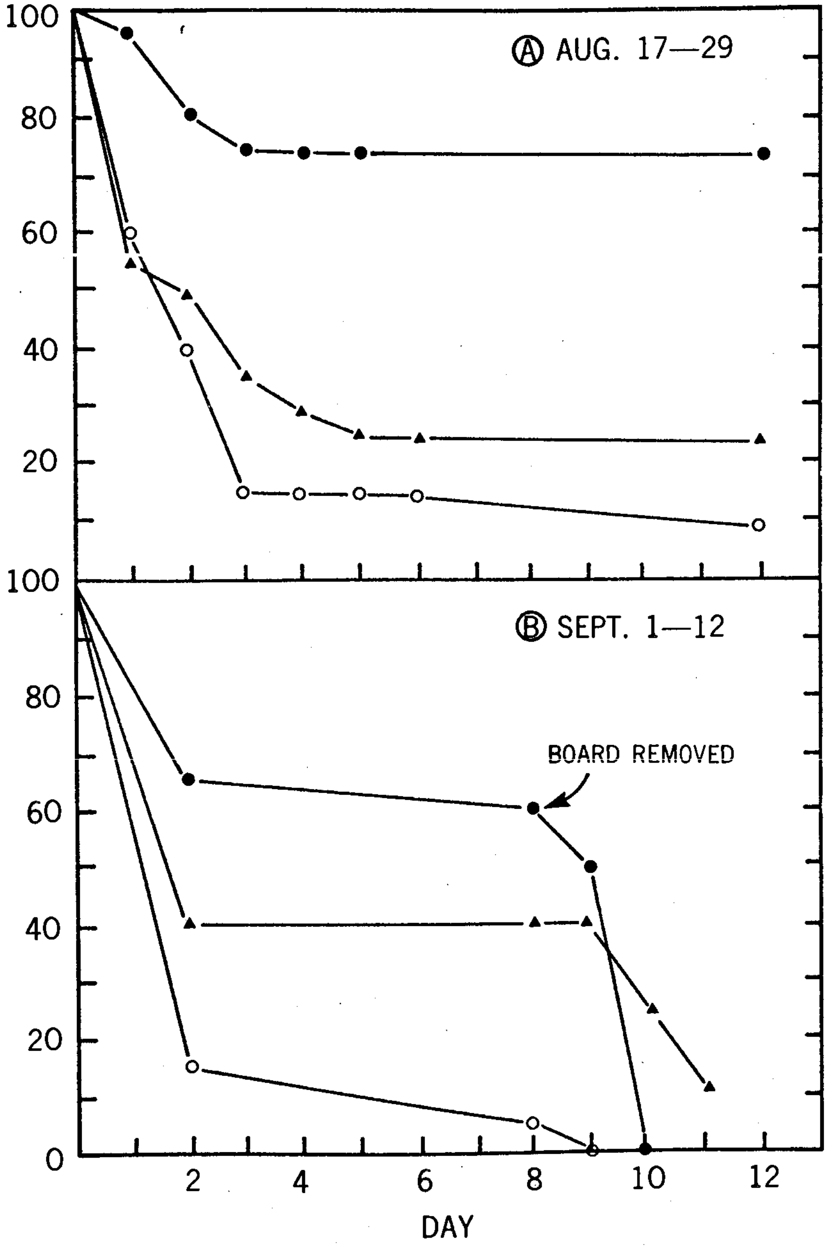
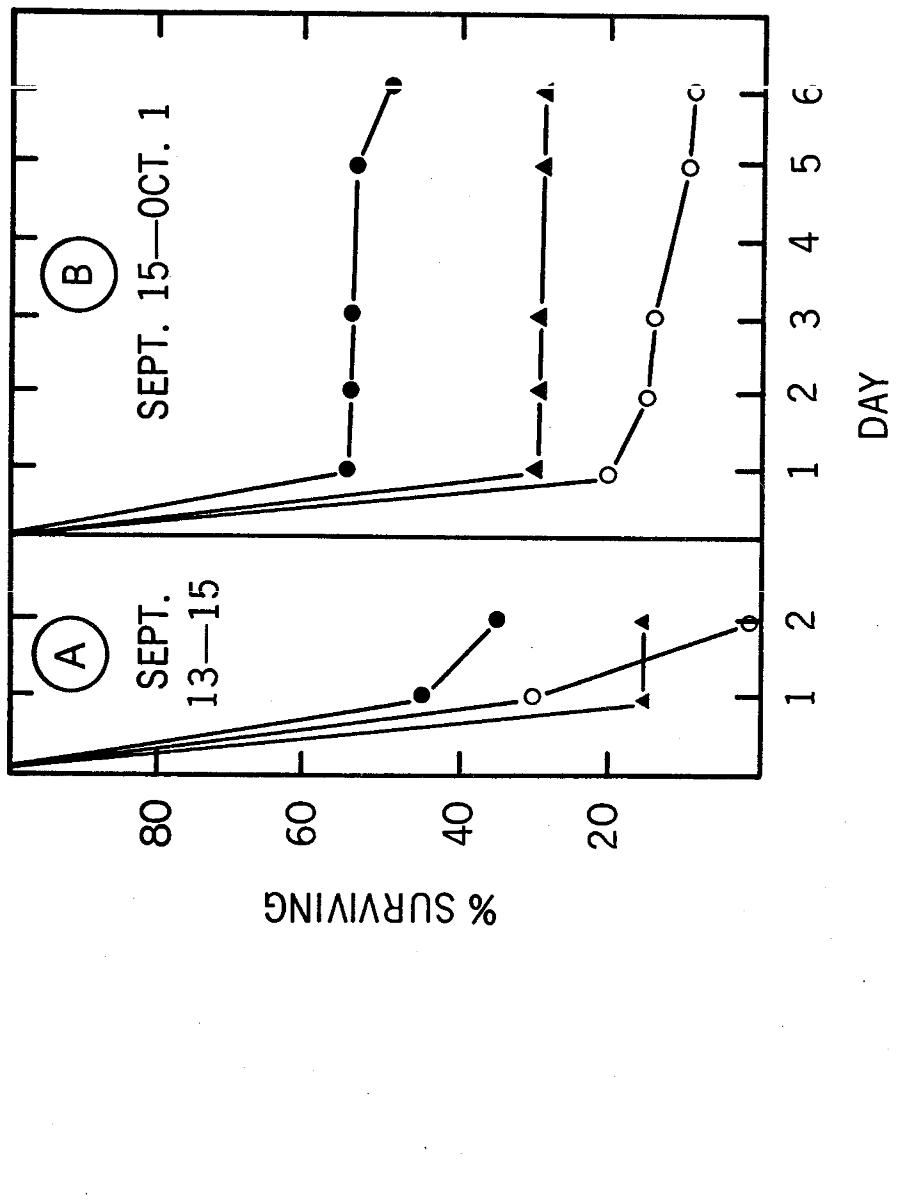

Ⓐ AUG. 17—29
Ⓑ SEPT. 1—12
BOARD REMOVED
100
80
60
40
20
0
2
4
6
8
10
12
DAY

Figure 22. Same as Figure 21, except that the positions of the plywood board and the plexiglass were inter-changed.


A
SEPT.
13—15
B
SEPT. 15—OCT. 1
% SURVIVING
80
60
40
20
DAY
1
2
1
2
3
4
5
6

than limpets in the other enclosures, indicating that shade improved the survival of A. persona more than the elimination of wave action.

The continued survival of small numbers of limpets in the unshaded enclosures was probably the result of micro-habitats within each enclosure, such as small crevices and moist depressions among barnacles, where a few limpets maintained themselves.

## Tolerance of Both Species to Desiccation

Rate of water loss. Results from the desiccation experiments were plotted as percent water loss against time for each limpet (Fig. 23). Except for the earliest and latest portions, the curves for individual limpets were linear, and the slope of the line represented the rate of water loss. Therefore, the slope of this line was calculated for every limpet and multiplied by the appropriate factor to give the percent water lost per hour. These data were plotted against shell volume, and regression lines were fitted by the least squares method (Fig. 24).

The correlation coefficients for both lines are small because of variability inherent in the limpet population (discussed below), and because of large sources of experimental

Figure 23. Per cent water lost at each weighing interval for 4 typical individuals of *A. persona* (●) and *A. digitalis* (○) in the desiccation experiments. (number in brackets is the shell volume of each individual)

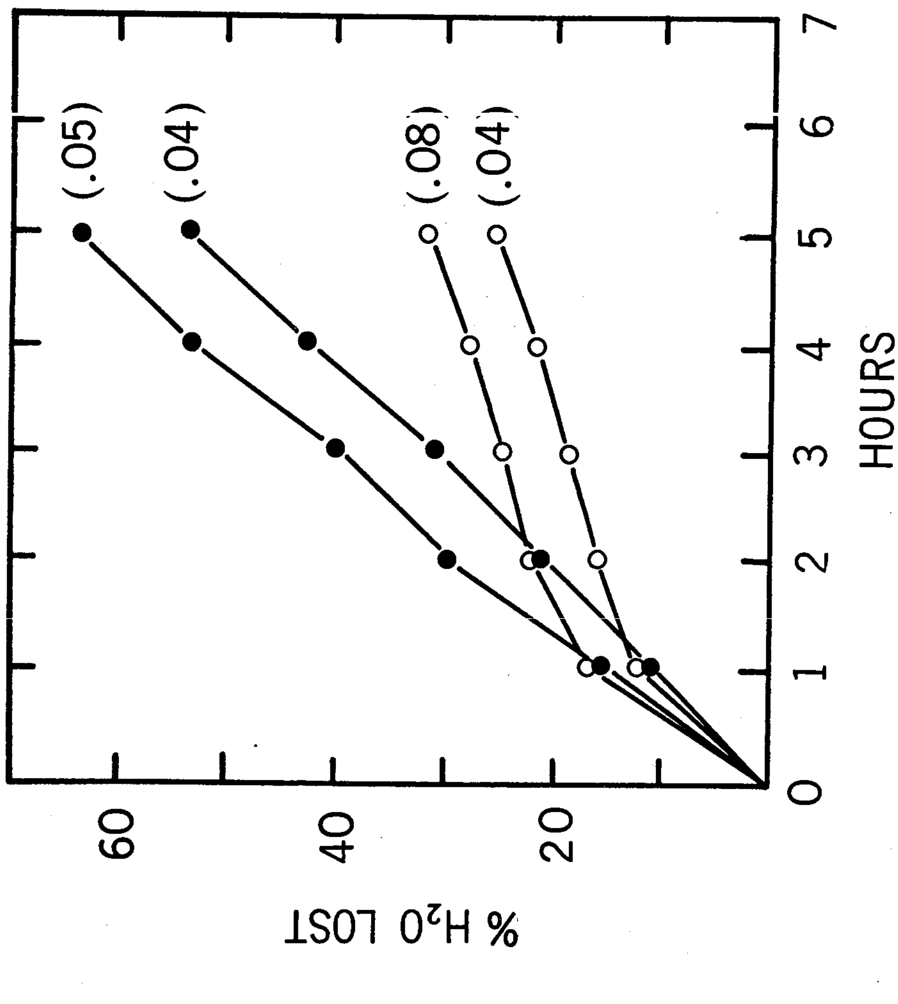
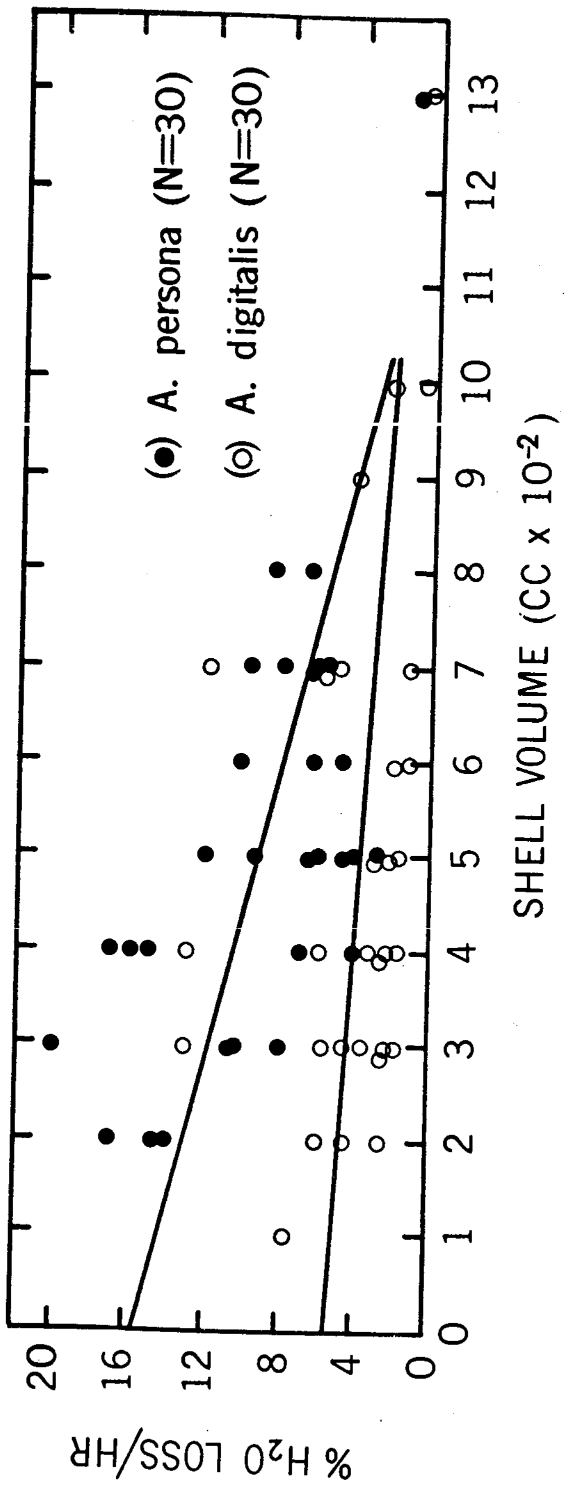

% $H_2O$ LOST
60
40
20
0
1
2
3
4
5
6
7
HOURS
(.05)
(.04)
(.08)
(.04)

Figure 24. Regressions of rate of water loss on shell volume for the two species. (*A. persona*, y = 1.252x + 15.49; *A. digitalis*, y = 0.315x + 5.68)


(●) A. persona (N=30)
(○) A. digitalis (N=30)
% $H_2O$ LOSS/HR
0
4
8
12
16
20
SHELL VOLUME (CC x $10^{-2}$)
0
1
2
3
4
5
6
7
8
9
10
11
12
13

variability. For example, some limpets had air trapped beneath their shell, thereby reducing the amount of water stored.

Despite the great variability, the results indicated that small A. persona lose water significantly faster than A. digitalis of comparable size. Using a student's t-test (Simpson, et al, 1960), the difference between the intercepts of the two regressions was significant ($p<001$).

Shell Height. The relative heights of the shells of the two species were compared by plotting the length to height ratio of every limpet against its shell volume (Fig. 25). For any shell volume, the higher the ratio, the flatter the limpet. Since limpets are essentially conical, the ratio therefore reflects the relative size of the shell perimeter, through which water is lost during desiccation, to the shell volume.

From Fig. 25 it is clear that for all sizes, A. persona is relatively flatter than A. digitalis. But because the ratio rapidly increases in small A. persona (<0.1 cc) the difference is especially great among small limpets. Small A. digitalis are only slightly flatter than large A. digitalis.

Shell thickness. Interspecific differences in shell thickness were determined by comparing regressions of shell weight on shell volume for the two species (Fig. 26). The

Figure 25. Relative shell height of *A. persona* and *A. digitalis*. Curves fitted by eye.

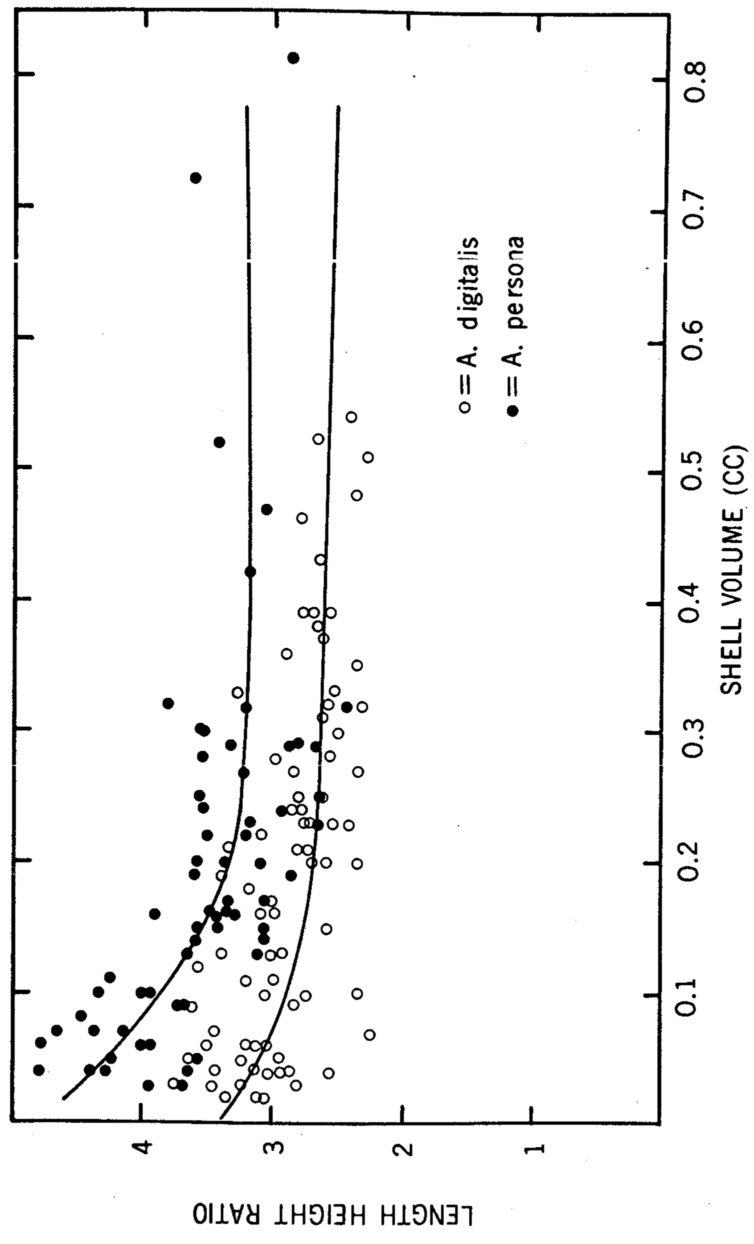

LENGTH HEIGHT RATIO
1
2
3
4
SHELL VOLUME (CC)
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
○ = A. digitalis
● = A. persona

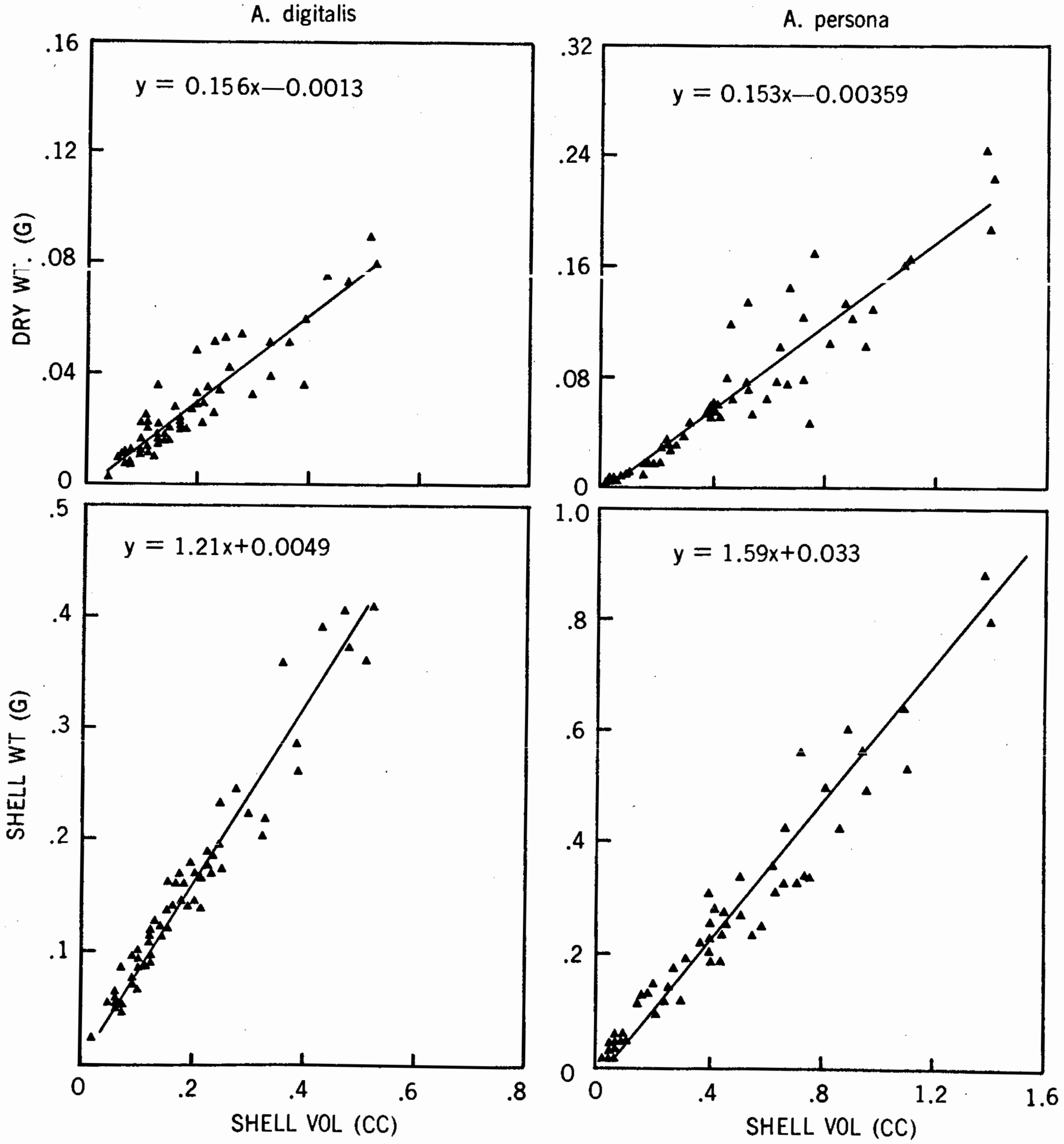
Figure 26. Regressions of shell weight on shell volume (lower graphs) indicate the differences in shell thickness between the 2 species. Regressions of dry weight on shell volume (upper graphs) indicate the differences in extra-visceral water holding capacity.

<u>Erratum</u>:

Equations for the two bottom graphs should read as follows:

Bottom left, $Y = 0.78x + 0.0049$

Bottom right, $Y = 0.60x - 0.0074$


A. digitalis
A. persona
y = 0.156x—0.0013
y = 0.153x—0.00359
y = 1.21x+0.0049
y = 1.59x+0.033
DRY WT. (G)
SHELL WT (G)
SHELL VOL (CC)
SHELL VOL (CC)
.16
.12
.08
.04
0
.32
.24
.16
.08
0
.5
.4
.3
.2
.1
1.0
.8
.6
.4
.2
0
0
.2
.4
.6
.8
0
.4
.8
1.2
1.6

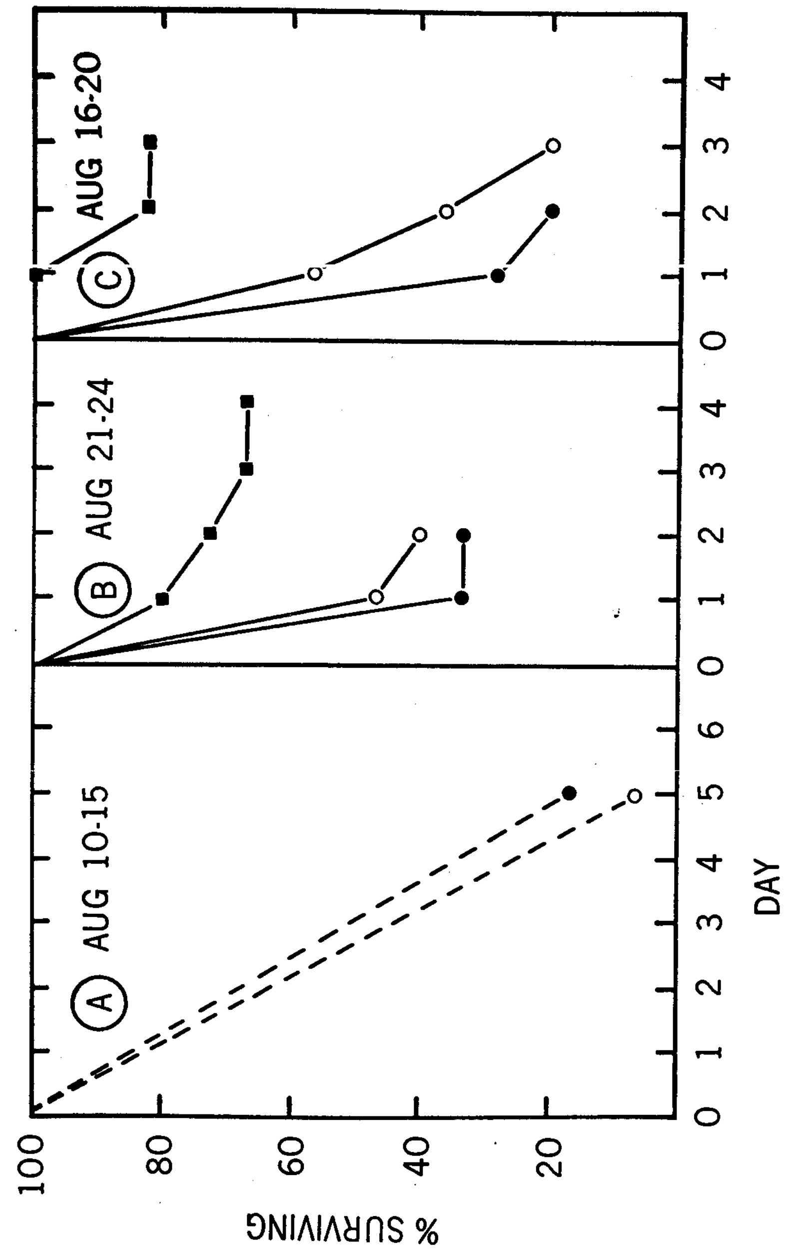
slopes of these lines were not significantly different ($p>.05$), indicating no difference in shell thickness between the two species.

Extra-visceral water. When the internal volume of the limpet shells was plotted against the dry weight of soft parts (body size), no significant difference was found between the two species (Fig. 26). Therefore, individuals of *A. persona* and *A. digitalis* of the same body size appear to have the same capacity for storing extra-visceral water. However, from the sample of *A. digitalis* measured, many were eliminated because their gonads were well developed, which would give disproportionately larger values for body size. Since it is not always clear when gonads are developing, the results may show a greater slope than results from a population with completely regressed gonads.

### Survival of *A. digitalis* in the habitats of *A. persona*

Boulder field transplants. In the boulder fields, mortality of *A. digitalis* was rapid compared to controls on both the boulder with *A. persona* and without, and there was little difference between the two (Fig. 27). Surviving *A. digitalis* sought refuge in small depressions and among small groups of barnacles on each boulder. Causes of the rapid mortality were

Figure 27. Experimental transplants of *A. digitalis* onto smooth boulders at Mills Cove. Each experiment terminated because the screen was torn off by wave action in at least one of the enclosures. *A. digitalis* controls (■), *A. digitalis* with *A. persona* (●), *A. digitalis* alone (○). (A, 30 individuals transplanted per enclosure; B & C, 15 individuals per enclosure)


% SURVIVING
100
80
60
40
20
DAY
0
1
2
3
4
5
6
Ⓐ AUG 10-15
Ⓑ AUG 21-24
Ⓒ AUG 16-20

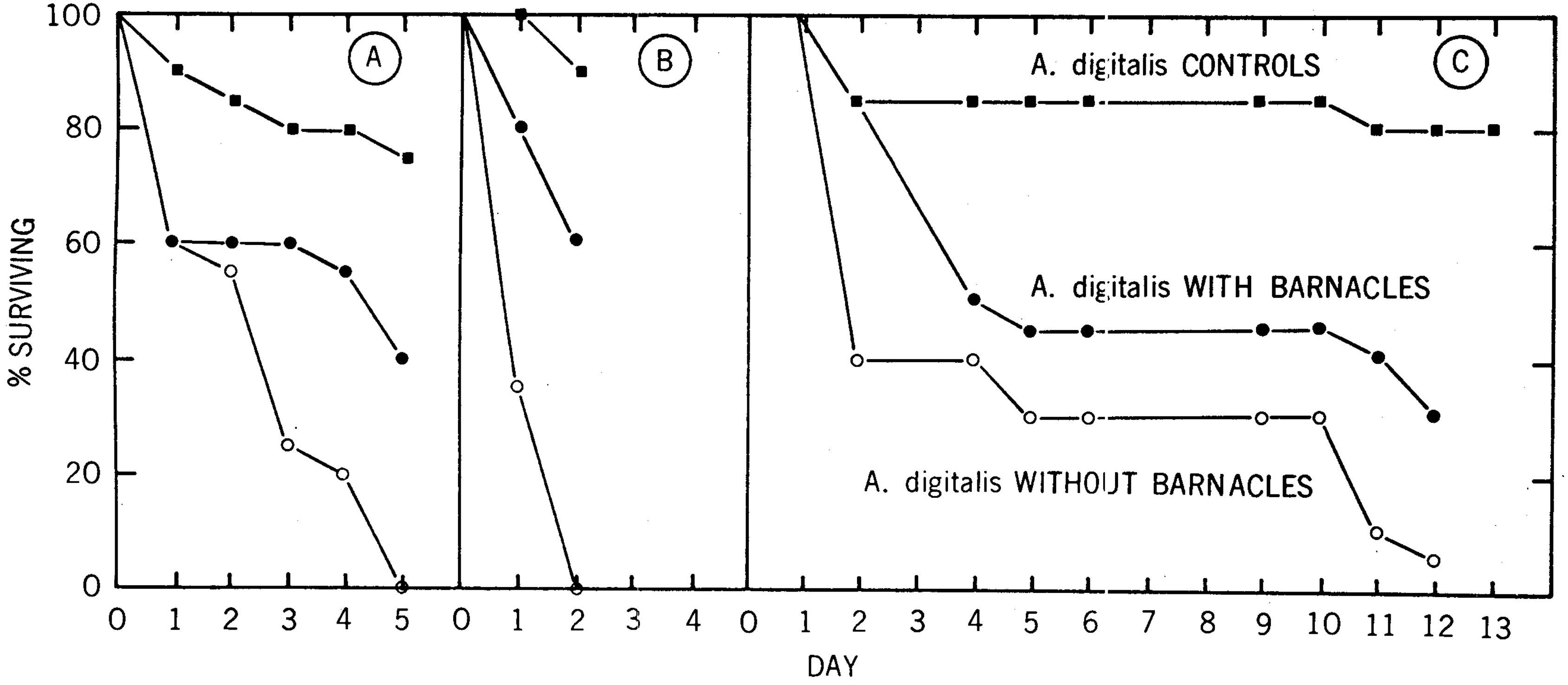
obscure, but in several experiments, the boulders with transplanted limpets were overturned by wave action while the control boulder with A. persona remained stationary.

Since transplanted limpets sought refuge among barnacle clumps and were found naturally occurring on some barnacle covered boulders, experiments were performed comparing the survivial of transplanted A. digitalis on boulders with barnacles and boulders without barnacles. These were compared with a control transplant nearby on a fused rock surface.

In all three experiments limpets survived consistently better on the barnacle covered boulders than on smooth boulders (Fig. 28). However, the difference was not great between the two, and mortality was greater in both populations than the controls.

Limpet Point transplants. In a shoreline concavity at Limpet Point, where only A. persona occurs, A. digitalis survived well in the presence and absence of A. persona. After one month there was a 30% mortality of A. digitalis in the enclosure with A. persona, and 10% mortality in the enclosure without A. persona. Although mortality of A. digitalis was slightly higher in the enclosure with A. persona, the presence of A. persona did not seem to have an effect of the survival of A. digitalis. The observed mortality was probably caused

Figure 28. Experiments testing the effect of barnacles on the survival of _A_. _digitalis_. (A, Sept. 14-19; B, Sept. 29-Oct. 1; C, Oct. 1-12)


100
80
60
40
20
0
% SURVIVING
A
B
C
A. digitalis CONTROLS
A. digitalis WITH BARNACLES
A. digitalis WITHOUT BARNACLES
0 1 2 3 4 5
0 1 2 3 4
0 1 2 3 4 5 6 7 8 9 10 11 12 13
DAY

by desiccation stress, resulting from a long period of emergence and sunny weather.

## Tolerance of Both Species to Fresh Water

The results of the fresh water experiment were inconclusive. After 15 hours of continuous submersion in fresh water the survival of either species did not drop below 90%. This great discrepency with the laboratory population in the pilot experiment, where no individuals survived for 15 hours, may be due to a lower tolerance in the laboratory population. This may have been due to an initially lower salinity of the body fluid, caused by lower salinity in the aquarium water.

In the field limpets of both species do not move away from fresh water, but instead, clamp down their shells tightly to the rock surface, minimizing the penetration of fresh water into their tissues. This contrasts with their behavior on sunny days when limpets usually maintain a space between the shell and the rock to allow for evaporative cooling (Segal and Dehnel, 1962).

Field observations were consistent with the hypothesis that where _A. persona_ occurs alone there is more fresh water run-off. Many _A. persona_ were found directly in run-off streams and pools both in boulder habitats and the inner reaches of small concavities. When limpets were removed from these pools and streams it was noted that their tissue, although swollen compared to limpets out of pools, was not swollen to the degree that the experimental animals manifested after only a few hours in the same water. Since it had already been raining for several days, this observation indicated that the "clamping down" behavior is very effective in preventing the invasion of fresh water and may enable limpets to withstand very considerable lengths of time in fresh water (e.g. one week's exposure to fresh water under natural conditions may equal the effect of 15 hours submersion on experimental animals). Another important question, then, is whether the habitats of A. persona experience prolonged enough exposure to fresh water to have any effect on limpet survival in either species.

## Crab Predation Experiments

The results of the three predation experiments are shown in Table 2; a chi square test was applied to the total numbers of each species eaten in all three experiments, with the null hypothesis that either species had an equal probability of being eaten. The crabs ate a significantly greater number of A. digitalis than A. persona, consuming 72% of the A. digitalis and 11% of the *A. persona*.

There are several reasons why the crabs may prefer *A. digitalis*. Firstly, on smooth dark colored boulders, cream-colored *A. digitalis* are conspicuous compared to the dark green *A. persona*. On boulders with acorn barnacles *A. digitalis* is probably less conspicuous. Secondly, crabs appear to grasp rough shelled, high apexed limpets like *A. digitalis* more easily than the smooth low spired *A. persona* (Stimpson, 1968). Predation by these crabs, therefore, may partly account for the absence of *A. digitalis* from smooth boulders.

## TABLE 2

Numbers of *A. persona* and *A. digitalis* consumed by *H. nudus* in predation experiments.

| Exp. | # *A. dig.* eaten | # *A. dig.* present | # *A. pers.* eaten | # *A. pers.* present |
|---|---|---|---|---|
| I | 5 | 9 | 0 | 6 |
| II | 6 | 10 | 1 | 11 |
| III | 10 | 10 | 2 | 10 |
| total | 21 | 29 | 3 | 27 |

$$\lambda^2 = \frac{(21-12.4)^2}{12.4} + \frac{(3-11.6)^2}{11.6} = 12.33$$

d.f. = 1: $p<0.001$

## IV. COMPETITION FOR FOOD BETWEEN *A. persona* and *A. digitalis*

Field experiments similar to those of Haven (1966) were performed to determine if competition for food occurs between the two species in areas where they co-exist.

### METHODS

On vertical surfaces where both *A. persona* and *A. digitalis* co-existed and were abundant, four rectangular enclosures similar to those described in section III were constructed adjacent to one another. In one enclosure, all of the limpets present were removed. This was termed the grazer-free enclosure. Its purpose was to assess the effect that the limpets had on the algal growth. In another enclosure, all of the *A. digitalis* present were individually marked, and their length was measured to the nearest millimeter using compass dividers. All of the *A. persona* present were removed. This process was repeated, in a third enclosure, marking the *A. persona* instead and removing the *A. digitalis*. In the fourth enclosure, all of the limpets of both species were individually marked and measured. The first and fourth enclosures were controls.

Every month, the length of each marked limpet was measured and recorded. Also, the grazer-free plot and the other plots were examined for algal growth and photographed. In this way, the growth of each species when together could be compared with their growth in the absence of the other species, and the effect of limpets upon algal growth could be determined.

Two experiments were set up, one in February, 1970 at Cedar Cove, Bamfield (Fig. 2), the second in June, 1970 at Boulder Cove, Bamfield (Fig. 8). The dimensions of the enclosures and the average initial densities of limpets are given in Figs. 29 and 30.

RESULTS

Limpet growth in both experiments is shown in Figs. 29 and 30. Both experiments terminated after only four months because of exceptionally high mortality from unknown causes which removed all of the limpets in one of the four enclosures. At Cedar Cove all of 19 *A. digitalis* disappeared from an enclosure in June, and at Boulder Cove all of 8 *A. persona* were gone from an enclosure in October. The two experiments taken together indicate that no growth took place in either species from February to September.

The grazer-free plots in each experiment did not yield any conclusive results. At Cedar Cove, no algal upgrowth appeared in the Spring. This did not appear to be due to grazers

Figure 29. Growth of limpets in competition grids at Cedar Cove. Solid line represents the growth of the species when alone; broken line represents growth in the presence of the other species. For each point, the horizontal bar is the mean length of all limpets of a species in the enclosure; the vertical bar is the 95% confidence interval. Enclosures were 60 x 30 cm; the average numbers of <u>A</u>. <u>persona</u> and <u>A</u>. <u>digitalis</u> per enclosure at the beginning of the experiment were 19 and 108 respectively.

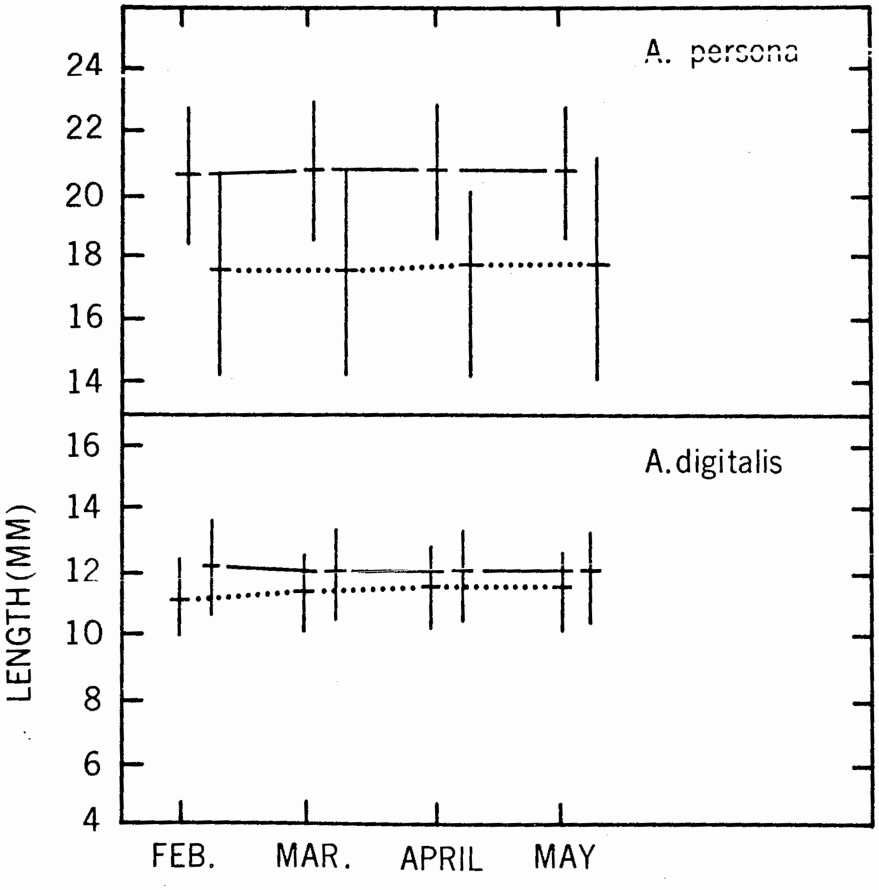
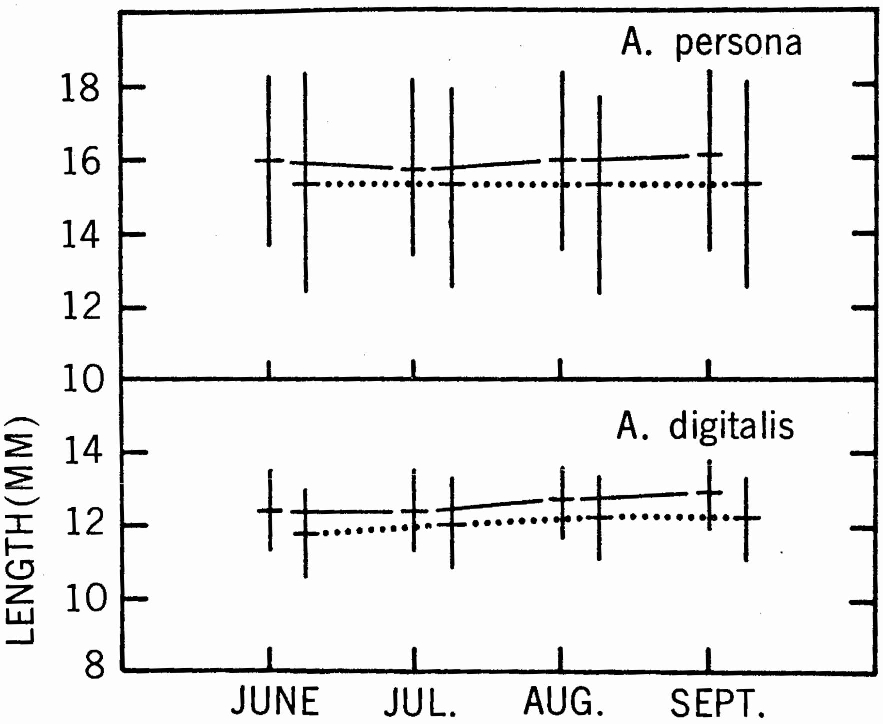

A. persona
A.digitalis
LENGTH(MM)
24
22
20
18
16
14
16
14
12
10
8
6
4
FEB.
MAR.
APRIL
MAY

Figure 30. Growth of limpets in competition grids at Boulder Cove. See Figure 29 for explanation. Enclosures were 60 x 30 cm; the average initial numbers of *A. persona* and *A. digitalis* were 11 and 13 respectively.


A. persona
A. digitalis
LENGTH (MM)
18
16
14
12
10
14
12
10
8
JUNE
JUL.
AUG.
SEPT.

entering the enclosure, since none were ever found inside it at each month's census, although some may have entered and left at high tide. At Boulder Cove, also, no algae appeared in the grazer-free plot. However, in this area, the enclosure was definitely not effective in preventing grazer immigration. Every month one to three *Tegula funegralis* were found in the enclosure and removed. Only three limpets were found in this grazer-free enclosure throughout the four months. The ineffectiveness of this enclosure in preventing grazer immigration, precluded any statement about the effects of the limpets on the available food.

However, in early October all of the *A. persona* and *A. digitalis* were removed from an enclosure at Mills Cove which was used previously for another experiment. In one month, a significantly greater growth of algae was coating this grid, compared with the surrounding rocks. Also, in the enclosures at Limpet Point (see Section III), growths of algae in the absence of limpets were observed by October when the surrounding rocks were still bare.

## V. DISCUSSION

### Niche differences

The results of this study indicate that despite the extensive co-existence of A. persona and A. digitalis in the high intertidal community in British Columbia, there are significant habitat differences between the two species. The most prominent differences observed were the macro-habitat differences related to shoreline type. Briefly summarizing, A. digitalis occurs alone on wave and sun exposed shoreline, typical of outer coast shores and the tips of shoreline convexities in more wave-protected waters. Extensive co-existence between the species is evident along shoreline generally protected from direct or prolonged wave and sun exposure. In boulder fields and the innermost reaches of the shoreline concavities (shoreline indentations and inlets), characteristic of large sounds and straits, only A. persona occurs. These results are predominantly horizontal differences between the two species' distributions, rather than the more typical vertical separation between sympatric intertidal animals, including most species of Acmaea (Test, 1945).

These habitat differences between the species appeared to be the most significant dimension of niche-separation between them, and along this dimension, the two species have partially non-overlapping niches. This spatial separation results in the partitioning of food resources by the two species, since portions of each species' population will consistently graze in different areas. Therefore, with respect to the classical model of competitive exclusion (Hardin, 1960), these niche differences alone may be sufficient to enable both species' to persist in what appears to be a stably co-existing relationship.

Ecological separation between the species may also occur along niche dimensions not examined in this study. For example, behavior patterns such as periods of activity may differ for the two species allowing them to partition the use of their food supply temporally, and share this resource by decreasing the total grazing pressure at any time. Observations of both species in California indicated that _A. digitalis_ feeds at high tide during the day (Millard, 1968), while _A. persona_ is nocturnal (Test, 1945). However, these differences are probably not as great in British Columbia, where cloudy cool weather is more prevalent. I observed _A. persona_ actively feeding on overcast dim days. Also, seasonal and tidal movements of the two species may differ serving to separate them vertically in the intertidal during some seasons. Nothing is known about seasonal or tidal movements in A. persona, but A. digitalis does show prominent seasonal migrations by moving higher intertidally in the winter (Frank, 1965; Breen, 1970; and Haven, 1971a). In this study, little difference was found between the vertical ranges of the two species, but all of the transects were done at low tide during the summer. Winter observations at Bamfield, however, did indicate that seasonal changes are significant. At Mills Cove, the vertical distributions of both species were noticeably higher than in summer, and A. persona appeared to be consistently higher than A. digitalis.

predation > in summer

In general the habitat descriptions of A. digitalis in this study are in close agreement with previous studies of A. digitalis in central California (especially Haven, 1970; also Test, 1946; and Fritchman, 1961). That is, the primary habitat of A. digitalis (habitats where it is most abundant) are the vertical surfaces of wave-exposed shoreline.

Habitat descriptions of A. persona, however, expand upon previously published information which was based mainly on observational evidence. Test (1945) and Fritchman (1961) along the central California coast described A. persona's niche as stenotopic, confined solely to dark crevices and the roofs of caves. The information presented in this study, however, clearly indicates that along some regions of shore, in the waters of southern B. C., A. persona is more widely distributed and abundant, occurring extensively in boulder fields, a habitat not previously noted for this species, and co-existing with A. digitalis on open rock surfaces. Haven (1971b) also observed the widespread and generally abundant distribution of A. persona in Prince William Sound, Alaska. He noted that towards wave-exposed shoreline A. persona became much less abundant than A. digitalis, but in more protected waters A. persona was the dominant high intertidal limpet.

Since central California is near the southern most limit of the geographic range of A. persona (Fritchman, 1961), the restricted habitat described for the species may reflect the effects of a generally less optimal environment. But it may also be an effect of broad differences in shoreline characteristics between the coastline south of Juan de Fuca strait (Washington, Oregon, California) and north of it (British Columbia, Alaska). South of the strait, the coastline is relatively unbroken, lacking the fjords, inlets, sounds, and archipelagos which characterize the north-west coastline above the strait. As noted earlier, shoreline type has a significant effect on the distribution of A. persona; the shorelines of straits, sounds, etc., provide ample habitats in the form of boulder fields and shore concavities. Specifically, A. persona may be less common south of the Juan de Fuca strait because its preferred habitat is less common.

Another factor which would likely contribute to broadening the niche of northern populations of A. persona is the increased frequency of cloudy and rainy days along the north-west coast, and the fact that towards northern latitudes the intensity of solar radiation decreases. This may help reduce desiccation stress or reduce the tendency of A. persona to avoid light.

From both of these factors, it seems reasonable to conclude that A. persona, as a species, is primarily adapted to the environment uniquely characteristic of the north-west coastline (Alaska, B. C.), where cloudy cool weather and broken (wave-protected) shoreline are common. In this environment, A. persona is widespread and abundant (essentially eurytopic), and therefore it seems likely that this region is where A. persona evolved. The niche of A. persona in California appears stenotopic probably because there is a general lack of suitable habitat, this being a function of the interaction of shoreline type and weather, rather than any difference in the species, itself, in these southern regions. Fritchman (1961) referred to the number of niches available to species of _Acmaea_ as being a function of tidal action rather than latitude. The foregoing discussion, however, indicates that latitude as well can affect the number and size of available niches.

The primary habitat to which _A. digitalis_ is adapted, vertical surfaces of wave-exposed shoreline, is abundant throughout the geographic range of the species. Thus, north of California, the niche breadth of this species does not reflect any specific latitudinal changes like those mentioned above for _A. persona_.

The extensive occurrence of _A. persona_ in boulder fields has not previously been reported. _A. persona_ is the only limpet species occurring in the middle to high zones (Ricketts-Calvin's zone 1 and 2) of this habitat. Conversely, adjacent fused rock surfaces from mid to high tidal levels contain individuals of _A. persona_, _A. digitalis_, _A. pelta_, and _A. paradigitalis_. The causes for this difference in limpet diversity between adjacent habitats are unclear. Also, transect studies indicated that the vertical distribution of _A. persona_ is different for boulders than for adjacent vertical surfaces. While _A. persona_ does not extend as high on the boulders as it does on fused rock surfaces, it does extend much lower in boulders. This lower vertical limit in boulders could possibly result from the absence of the other species mentioned above allowing A. persona to utilize this otherwise "empty" niche. This would imply that the presence of the other species on vertical surfaces restricts the lower limit of A. persona there, perhaps by interference competition for space as demonstrated in other limpets (Stimson, 1968; Sutherland, 1970). This hypothesis could be tested by field experiments. In general, the relationship of A. persona to these two qualitatively different habitats, boulder fields and fused rock surfaces, is an interesting problem for further study.

## Effects of environment on the niches of both species

When the niche differences between A. persona and A. digitalis are viewed from a community evolutionary perspective, two important questions remain to be answered: (1) what selective factors have caused and continue to cause the species to possess the distinct niches which they have, and (2) are these niche differences a necessary condition for the continued presence of both species in the intertidal. Here, competition as a causative selective factor becomes important, for one basic school of community evolutionary thought states that competition between similar species may present selective pressures which cause their niches to diverge or may act to maintain niche separation between them (Miller, 1967; Futuyma, 1970). Therefore, although the niche differences between A. persona and A. digitalis are clear, the important question of whether their differences are the result of competitive interaction or the result of other selective factors remains unanswered.

This problem can be approached by first analyzing the degree to which the observed niches of both species reflect independent effects of environmental factors, other than competition, on these species and subsequently analysing the possibility of competitive interaction between them.

Experimental evidence indicates that the observed horizontal distribution of A. persona is partially accounted for by the vulnerability of young individuals of this species to desiccation, and possibly temperature, stresses.

The results of field transplant experiments at Limpet Point indicated that when the effects of insolation were eliminated by artificially providing moisture or shade, A. persona could survive in the convex, exposed areas where only A. digitalis naturally occurs. Protecting the transplanted animals from wave force, alone, did not improve their survival. However, because wave action is noticeably less severe in the summer and fall, when these experiments were performed, than in the winter, the effects of wave action could not adequately be tested. Conversely, the effects of insolation are much less severe during the winter when temperatures are lower and rocks remain wet. Both of these physical factors are therefore dominant during different seasons and may both affect the survival of _A. persona_.

The rapid mortality of _A. persona_ in unshaded enclosures indicated that perhaps desiccation was only an indirect cause of limpet deaths. For example, transplanting limpets from a shaded habitat into a sun exposed habitat may alter their behavior, either causing them to move when they should conserve water or by affecting their hold on the rock. Even stationary limpets might lose sufficient water to be removed by mild wave swell before the lethal limit of water loss is reached, since the limpet's hold on the rock is weakened when the animal is severely desiccated. From data on rates of water loss, it seemed plausible that most of the limpets did lose sufficient water either to cause death or removal by waves within the first 24-48 hours. With an average exposure of 8 hours between each tide, and a rate of 8% water loss per hour this would amount to approximately 64% water loss at each emergence during the day. Davies (1970) reports a lethal water loss of about 50% for *Patella vulgata*, a high intertidal European limpet.

Temperature stress, also, may be a complementary effect of insolation affecting the survival of *A. persona*. Higher aerial temperatures and heated rock surfaces may directly affect the physiology of the limpet. Or indirectly, the loss of water by increased desiccation stress might decrease the ability of the limpet to withstand temperature stress, since limpet water (both extra-visceral and internal) may act as a temperature buffer. Segal and Dehnel (1962) have shown that the extra visceral water in *Acmaea limatula* functions as a temperature buffer.

The greater rate of water loss observed in *A. persona* is also consistent with the hypothesis that desiccation stress limits the horizontal distribution of *A. persona*, preventing its establishment in sun exposed areas where only *A. digitalis* is found.

Assuming that water evaporates equally fast from the tissue of both species, it seems probable that the greater rate of water loss in small *A. persona* is the result of its low spire compared to *A. digitalis* and large *A. persona*, increasing the relative size of the shell perimeter where water is lost. The connection between shell height and rate of water loss has been observed by Davies (1970) and others (see Segal, 1958) for the European limpet, *Patella*. However, previous studies have almost exclusively compared the ability to withstand desiccation between individuals living high in the intertidal and individuals living low in the intertidal. It has not previously been noted that the same criteria appear to explain differences in the horizontal distributions between different limpet species. Segal (1956) observed that in *A. limatula*, a southern species, high intertidal individuals had a thicker shell and also stored more extra-visceral water (i.e. water in the mantle cavity) than low intertidal individuals, and Segal and Dehnel (1962) demonstrated that these differences were probably an adaptation by the higher form to desiccation and temperature stresses. Although a comparison of shell thickness and extra-visceral water holding capacity between *A. persona* and *A. digitalis* did not yield statistically significant differences between the species, it was pointed out earlier that these experiments were not conclusive, because of larger gonads in individuals of *A. digitalis* (which would affect measurement of extra visceral water) and because there was an observable trend indicating that *A. persona* does have a thinner shell than *A. digitalis*.

Although data on the rates of water loss were based on a narrow range of limpet sizes, sampling a wider range of sizes would probably yield similar differences between the two species, since large *A. persona* are also relatively flatter than comparably sized *A. digitalis*. However, especially in large sized limpets, the ability to withstand desiccation is not solely dependent on the rate of water loss. If a limpet simply becomes large enough, it may be able to store more than enough water to carry it through long periods of desiccation. Since *A. persona* attains larger sizes than *A. digitalis*, its ability to withstand desiccation, when large enough, may be greater than *A. digitalis*, despite its higher rate of water loss. This possibly may explain the existence of some *A. persona* particularly large individuals, higher in the intertidal than *A. digitalis*.

Since the young individuals of *A. persona* are much more vulnerable to desiccation than young *A. digitalis*, they require a habitat which offers a distinct refuge from solar radiation (i.e. shade and/or moisture). Sun-exposed shoreline, the typical habitat of *A. digitalis*, provides few refuges for young *A. persona*. Individuals of *A. persona* are therefore confined to locally occurring crevices or caves. Conversely, boulder fields and some shoreline concavities characteristic of large bodies of semi-exposed to protected water provide abundant refuges from direct insolation for the young limpets. This one physical factor, solar radiation, therefore, appears to account significantly for the horizontal distribution of *A. persona*.

Factors which determine the horizontal distribution pattern of *A. digitalis* remain obscure. Why should *A. digitalis* be entirely absent from smooth boulders and shaded, wave-protected concavities? Haven (1971) in a detailed study of *A. digitalis* in central California concluded that desiccation or temperature stress caused both the decrease in abundance of *A. digitalis* in wave-protected habitats and its general absence from horizontal substrates. This explanation, however, does not apply to the observed horizontal distributions of *A. digitalis* in this study. In California the sites protected from wave action had greater desiccation stress (i.e. greater sun exposure and less cooling spray), whereas in British Columbia they had less desiccation stress because of shade.

Field experiments, although inconclusive, seemed to indicate that mortality of *A. digitalis* in boulder fields was rapid, and the presence of *A. persona* had no effect on the survival of *A. digitalis*. On the other hand, crab predation experiments indicated that the crab, *Hemigrapsus nudus*, ate significantly more *A. digitalis* than *A. persona*. Stimson (1968) also experimentally demonstrated that a similar grapsoid crab, *Pachygrapsus crassipes*, which occurs south of Juan de Fuca strait, prefers small, rough shelled limpets (*A. digitalis*) to small smooth shelled limpets (*A. fenestrata*). The preference by crabs for rough shells appears to be related the ease with which they can be grasped by the crabs chelae (Stimpson, op. cit.). The smooth shelled species, *A. fenestrata*, is a close relative of *A. persona* (Test, 1946) and occurs on smooth boulders set in sand. The crab, *H. nudus* is almost always abundant in the boulder habitat of *A. persona*, but is uncommon or absent on steep fused rock surfaces.

The better survival of *A. digitalis* on boulders with barnacles compared with survival on smooth boulders, as well as the natural occurrance of *A. digitalis* on barnacle covered boulders, suggested that the association between *A. digitalis* and barnacles conveys survival advantage to *A. digitalis*. Haven's (1971a) hypothesis that barnacles offer a refuse from desiccation does not seem applicable to this situation, since these boulder fields do offer an adequate refuge without barnacles (see above). In the field it was sujectively noted that A. digitalis is cryptic when associated with barnacles, because of its pale color and corregated shell, and in this way , A. digitalis may escape predation on boulders. In contrast, dark smooth A. persona are generally inconspicuous, even on smooth boulders without barnacles. Giesel (1970) has already demonstrated crypsis in A. digitalis with respect to shell color pattern, barnacles, and bird predation. He found evidence that bird predation is a significant selective factor responsible for two distinct and cryptic polymorphisms of A. digitalis on wave exposed coast. One is the dark color pattern of limpets on the rock face substrate; the other, light shelled forms on goose-neck barnacle (Pollicipes) shells. He did not mention, however, the possibility of A. digitalis mimicking the color and texture of acorn barnacles as well, which they appear to do. In boulders, other predators than crabs, such as birds, may also be common and more efficient since they seem to prefer horizontal substrates. Although it would seem unlikely that predation would be responsible for the almost complete absence of A. digitalis from boulders, Connell (1970) and Paine (1966) have documented the virtually complete elimination of some other prey species from certain regions of the intertidal. Thus there is some support for the hypothesis that A. digitalis is absent from boulders because small A. digitalis on smooth boulders are conspicuous and are the preferred prey for the crab, Hemigrapsus nudus and perhaps other predators. Instances of differential predation directly causing niche differences between similar species have not been reported.

The inability of A. digitalis to exist in the inner reaches of shoreline concavities also remains unexplained. Predation does not seem likely, since these are largely vertical surfaces and no crabs or birds appear to feed here. One possibility, which needs to be studied in more detail, is the effect of fresh water on A. digitalis. This factor appears to be significant because, in general, the habitats where A. digitalis becomes less abundant or absent seemed to correlate with an increase in fresh water run-off over the rock surfaces or lower salinity surface water. Also, Frank (1965) observed that mortality was higher in a group of A. digitalis which was exposed to fresh water run-off, compared to mortality of an adjacent group not directly exposed to fresh water. My experiments testing the tolerance of both species to fresh water were inconclusive but both species appeared to be able to withstand prolonged periods of exposure to fresh water by clamping their shells tightly to the rock surface.

Another possible factor is elimination of *A. digitalis* from the inner reaches of some concavitites by direct interference with *A. persona*. This, however, does not seem likely because individuals of both species are found adjacent to one another in the regions of co-existence, and competition for favorable micro-habitat spots does not appear to occur.

It is not known how much of the observed distributions of both species is the result of active habitat selection, such as the movement of limpets or behavior of settling larvae, and how much is determined by mortality of limpets in unfavorable habitats. Frank (1965) and Stimson (1968) cite evidence that mortality of *A. digitalis* is greater outside of its optimum vertical range. It is unknown whether this also applies to individuals in habitats outside of the species' horizontal range. It would seem unlikely that these species have not evolved some means of behaviorly detecting suitable habitats, since selection would act continously. There is evidence by Frank (1965) and Haven (1970) that for *A. digitalis* behavioral choice plays a significant role in determining where individuals are found. This species shows pronounced seasonal movements (vertically) and also actively selects suitable micro-habitats (vertically and laterally). For *A. persona*, as well, behavior is probably significant in determining their distributions, since my own observations of movement in a group of *A. persona* (not reported in this study) indicated that the species definitely does not show specific homing behavior characteristic of some other *Acmaea* species, such as *A. scabra* (Haven, 1970). In addition, Test (1946) observed the species as negatively phototropic, causing it to seek "the most dimly lighted locations available". My own observations generally confirm Test's conclusion. However, where *A. persona* co-exists with *A. digitalis*, it often occurs on open rock surfaces, and on overcast days in boulder fields, individuals of *A. persona* are found extensively on the tops of boulders, rather than their more shaded undersides. Therefore, it appears that at least in British Columbia, *A. persona* will tolerate a certain amount of light and is not strictly confined to the darkest available habitats.

The significance of larval settling behavior in determining limpet distributions remains a mystery for all species of *Acmaea*, and represents a large gap in the knowledge of limpet ecology. It is certainly possible that larvae could be genetically "programmed" to select certain environmental indicators, such as substrate texture, light, or rock angle, which would either directly or indirectly represent a likely habitat for continued survival. However, Connell (1961, 1970) demonstrated that in several species of barnacle, the larvae consistently settle and begin to grow in intertidal regions where their probability of survival is consistently poor. He demonstrates that because the young barnacles are usually eliminated by biological factors (competition or predation) the large spread of larvae is a kind of "opportunism" which allows survival of barnacles in regions where the biological factor is sometimes absent. This kind of "opportunism" may also occur in these limpets. However it would seem unlikely that A. persona would exhibit this trait, since the distribution of this species appears to be controlled by a physical factor which would continuously select against young limpets in unfavorable habitats, i.e. the effects of this factor would rarely be absent. If the distribution of A. digitalis is predominantly determined by biological factors, e.g. predation, opportunism by larval settlement may occur.

## Competition and niche evolution

From the foregoing discussion, the observed niche differences between *A. persona* and *A. digitalis* may be viewed as independent adaptations by each species to the physical or biological environment exclusive of the other species. Populations of *A. persona* appear to be largely restricted to shaded regions of shore, because the young individuals cannot tolerate the desiccation or temperature stresses of sun exposed shore. Similarly, *A. digitalis* appears to be ill adapted to the boulder fields or shoreline concavities where *A. persona* is found. The regions of co-existence between the species may then represent intermediate habitats to which both species are adapted. It does not seem likely that active exclusion of one species by another occurs in the habitats occupied by only one of the species, since individuals of both species are found adjacent to one another in the regions of co-existence, ruling out extensive "interference" competition, and in general, favorable micro-habitats do not appear to be limiting.

There is some suggestive evidence that competitive displacement upwards of *A. persona* by *A. digitalis* and other species may occur in some habitats. At Victoria breakwater, where *A. persona* extended higher than *A. digitalis*, available micro-habitat space for *A. persona* (crevices) may be more limiting than at Mills Cove, where there were no differences in the upper limits of the two species. Even at Mills Cove the lower limit of *A. persona* became higher as the relative abundance of *A.*

*digitalis* increased. Also, the lower vertical range of *A. persona* in boulder fields (above), where no *A. digitalis* occurs, suggest that interference competition for space may occur, in some habitats, resulting in the higher vertical range of *A. persona* in the presence of *A. digitalis*. Interference competition has been demonstrated in other limpet species (Stimson, 1968; Sutherland, 1969).

Aside from the possibility of "interference" competition affecting their vertical distributions, removing one species would not result in increasing the niche of the remaining species in any short term sense. With respect to Hutchinson's (1957) terminology, the realized niche and the fundamental niche of each species with respect to the possible influence of either species, is the same. However, from a community evolutionary perspective, the adaptive differences between the species, represented mainly by their different horizontal distributions, may still reflect competitive interaction between them. This problem can be broken down into two related questions: (1) does it appear that inter-specific competition has played any historical role in diverging the niches of the two species, and (2) is competition an active process maintaining niche separation between the species? Both of these questions are really corollaries of the competitive exclusion principle (Hardin, 1960; Miller, 1967; Futuyama, 1970).

Although conclusive evidence on the occurrence or absence of competition is lacking, it can be argued that inter-specific competition has played little historical role in diversifying the niches of the two species. This is largely because it seems likely that during the adaptive radiation of the genus *Acmaea*, these two species evolved via two different pathways into the higher intertidal zones.

The ancestral species of *A. persona* is probably *A. scutum* (Test, 1946). This limpet is characteristic of middle to low intertidal zones, possessing a large round aperture and very flat shell. Conversely, *A. digitalis* represents the ancestral form of another sub-genus in which all of the species have a relatively high apexed shell which is ribbed or scalloped (Test, 1946). These differences are significant, because they explain why the young of *A. persona*, which are so suseptible to desiccation, develop as very round and flat limpets relative to adults. Young *A. persona* are superficially indistinquishable from *A. scutum*. Only after the limpets have reached lengths of over one centimeter do they manifest the higher apex characteristic of *A. persona*. Therefore, although the evolutionary strategy of *A. persona* in invading the higher intertidal zone was to raise its shell apex in order to resist the increased desiccation stress (Test, 1946; Segal, 1956; Davies, 1969), it has always been restricted to habitats which would provide a refuge for the developing small _scutum_-like limpets, i.e. primarily boulder fields and shaded crevices and concavities. On the other hand, _A_. _digitalis_ has never required such a refuge; the young individuals of this species already manifest a relatively high apexed shell and narrow aperture. These firmly based ancestral (genetic) differences between the species indicate that the species probably evolved along qualititively different kinds of shoreline, and therefore the observed niche differences with respect to their horizontal distributions do not appear to be the result of a past history of inter-specific competition. In other words, spatial overlap when the two species became sympatric was probably little different than it is at present. This idea is also indirectly supported by the fact that only _A_. _persona_ occurs in the boulder habitat, and it is only in this habitat where individuals of _A_. _persona_ overlap slightly the distribution of _A_. _scutum_, its close relative and probable ancestor (Test, 1946). Thus, boulder fields may be the primary habitat to which _A_. _persona_ evolved, while wave-exposed outer coast is probably the primary habitat of _A_. _digitalis_ (Haven, 1971a).

This provides an interesting comparison to the niche relationships between _A. scabra_ and _A. digitalis_ studied by Haven (1971a) in central California. Both of these species are closely related, belonging to the same sub-genus (Test, 1946), and both occupy similar habitats on outer coast shoreline. For example there are no macro-habitat categories which serve to separate these species. In this instance, competition for food does occur where their niches overlap and appears to have had a significant effect on the evolution of their niche differences (Haven, 1966).

Field experiments in this study testing whether competition occurs between _A. digitalis_ and _A. persona_ were inconclusive and did not rule out the possibility of its occurrance in regions of overlap between the species. Food limitation for these species did appear likely, because of the upgrowth of algae I observed in some grazer-free plots during the fall in Barkley Sound. Also, food shortages at some times appear to be common for most high intertidal grazing gastropods, evidenced by the almost complete removal of algae from the rock surface by the grazers (Jones, 1948; Southward, 1956; Castenholz, 1961; and Haven, 1966) and by direct evidence of food limitation in high intertidal species of _Acmaea_ (Haven, 1966; Sutherland, 1970).

I found no evidence for food preferences in *A. digitalis* and *A. persona*, and food preferences in other benthic grazers seem to be limited to species in lower zones and involve preferences among macro-scopic algae (Dahl, 1964; Best, 1964; Craig, 1968; Eaton, 1968).

The lack of any algal upgrowth in grazer-free plots during the spring (Feb.-June) at Cedar Cove does not agree with the results of Haven (1966) and Castenholz (1962) who demonstrated significant algal growth, in the absence of grazers, during this season. Perhaps the enclosures were in a unique micro-habitat which could not maintain a heavy algal population. The absence of growth in limpets during this period may have been caused by this lack of algae. Frank (1965) and Haven (1966) did record significant growth of *A. digitalis* during the spring in Oregon and California respectively. Another possible reason that no growth was recorded in my experiments is that in British Columbia, the limpets may put all of their energy into reproduction in spring rather than growth.

If competition does occur between the species in regions of niche overlap it may selectively favor niche divergence between them or may act to maintain their niche differences. For example, if one species were completly removed from all of its habitats, eliminating competition, the other species might evolve means to expand into the niche of the removed species. The question of whether either species could evolve in this way is academic, but would depend on the genetic variability or plasticity in the species and the degree of difference between their habitats.

## SUMMARY

1. In the upper intertidal zones of British Columbia two sympatric limpet species, <u>Acmaea</u> <u>digitalis</u> and <u>Acmaea</u> <u>persona</u>, co-exist with few apparent niche differences. The degree of niche separation between the two species was determined by observations and transect studies documenting their distribution and abundance with respect to macro- and micro-habitat categories.

2. Observations revealed significant habitat differences between both species, correlated with shoreline type. Only <u>A</u>. <u>digitalis</u> is found along shoreline in open coast environments and on the seaward ends of shoreline convexities (points, headlands) in more wave protected waters. <u>A</u>. <u>persona</u> occurs alone in boulder fields and the inner reaches of shoreline concavities (inlets), both characteristic of semi-exposed to protected wave environments. Regions of co-existence between the two species are intermediate between the previous two categories, and occur on vertical rock surfaces in semi-wave-exposed to protected environments.

3. Quantitative micro-habitat studies correlated the

distribution and abundance of each species with environmental factors. Wave-action and insolation were most closely correlated with the distribution of *A. persona*. Where both of these factors increased, the relative abundance of *A. persona* decreased. The degree of fresh water run-off and the abundance of limpet predators (along with the absence of barnacles) were correlated with the distribution of *A. digitalis*. Greater fresh water run-off occurred both in boulder fields and shoreline concavities where *A. persona* predominanted. Predators were abundant and barnacles absent from boulder fields only.

4. Field and laboratory experiments tested the effects of wave action and insolation on the survival of *A. persona*. Results from field transplant experiments indicated that increased solar radiation (increased desiccation and temperature) in the habitats where *A. digitalis* occurs alone appeared to be the major environmental factor restricting the distribution of *A. persona* from these habitats. Desiccation experiments and shell measurements indicated that *A. persona* is less tolerant than *A. digitalis* to desiccation (and temperature) because of increased rate of water loss caused by its flatter shell shape.

5. Experiments tested whether the fresh water tolerance of the two species differed. Results were inconclusive, but indicated that both species could withstand prolonged periods of fresh water exposure. Predation experiments indicated that the crab, *Hemigrapsus nudus*, which is abundant in boulder fields, will eat limpets and prefers *A. digitalis* to *A. persona* probably because *A. digitalis* is more conspicuous, has a higher shell apex, and is rough textured. Both fresh water influence and predation may restrict the distribution of *A. digitalis*, preventing this species from existing in the habitats occupied exclusively by *A. persona*.

6. Field enclosure experiments testing whether interspecific competition for food occurs between the two species were inconclusive because of high mortality and no observed growth in the limpets.

7. The observed niche differences between the two species appeared to be sufficient to explain their apparent co-existence in the intertidal. Experimental evidence indicates that the niche differences between the species, at least with respect to habitat, are determined proximately by independent environmental effects on each species (physical

factors, predation). The two species have probably evolved from different ancesters, in two qualitatively different habitats, vertical surfaces on the open coast (A. digitalis) as opposed to boulder fields and inlets in regions of semi-exposed to protected water (A. persona). Thus the two species appear to have evolved into the higher intertidal zones via different ecological pathways, indicating that their niche differences have evolved as independent adaptations by each species to the environment, rather than the result of a history of competitive interaction. But interspecific competition may act to maintain the observed niche differences between them.

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