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FISHERIES RESEARCH BOARD OF CANADA

MANUSCRIPT REPORT SERIES

No. 1213

Some Aspects of the Littoral Ecology of British Columbia

by

J. R. Lewis¹ and D. B. Quayle

**¹Director, Wellcome Marine Laboratory, Robin Hood's Bay,
Yorkshire, England.**

Pacific Biological Station, Nanaimo, B.C.

October 1972

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INTRODUCTION

During the summer of 1968 the Fisheries Research Board of Canada invited the senior author to work at its Nanaimo Laboratory in conjunction with the staff of the Marine Invertebrate section. Surveys of rocky shore populations were made in the following areas: the Nanaimo District generally (including offshore islands), Ladysmith Harbour, Sooke Harbour, and various accessible points westwards along the Strait of Juan de Fuca to Jordan River, the islands in Barkley Sound, the Ucluelet-Tofino area, Pendrell Sound, and a series of semi-exposed and sheltered island sites in the archipelago between Queen Charlotte Sound and Prince Rupert.

Initially a general account is given of what appear to be the principal biological characters of different types of habitats, fusing data from many similar short stretches of shoreline, in an attempt to ascertain recurrent spatial patterns. Such patterns exist in response to environmental gradients, and that associated with the change from wave-swept to sheltered shores has been selected to provide much of the descriptive framework. However, it is clear from previous literature (especially that of Scagel 1961 and Widdowson 1965) that oceanographic differences between the open Pacific coasts and the Strait of Georgia have an important bearing upon distribution. Accordingly, the Nanaimo, Ladysmith, and Pendrell Sound shores are treated separately in a Strait of Georgia section, and the remainder are classed as "outer Pacific shores."

In the absence of any simple quantitative way of assessing the degree of "exposure" or "shelter," one must rely largely upon subjective impressions and experience, although familiarity with a region may permit the use of biological criteria (Lewis 1968). In this instance assessments were based upon such features as orientation to open seas and swell, depth of offshore water, low-tide reefs, and local configuration of the shore. It must be stressed that the lee of a large rocky mass, a narrow channel between islets and so forth can produce pockets of considerable shelter even on an otherwise very expose coast, and it is upon observations of such local variations and the population changes that this account is based. Accepting that much distribution is controlled by exposure, the sudden disappearance or appearance of a conspicuous zone-forming species can lead to the postulation of a considerable number of arbitrary stages along the gradient. Such a procedure, however, ideally necessitates long-term studies on spatial fluctuations induced by factors other than exposure. Accordingly, this account recognizes simply three broad categories: "exposed," "semi-exposed" and "sheltered" and makes appropriate comments on local variation related to slope, aspect, and substratum.

*No see
Harger
1970.*

OUTER PACIFIC SHORES

Littoral Fringe

In all sites the typical high-level "black zone" of lichens (Verrucaria)

or microphytes was recognizable but was frequently patchy and ill-defined except locally in shelter where lack of wave action compressed it into a more prominent belt 2-3 ft in depth. Littorinid snails (see p. 18) were present but not abundant except in crevices in upshore extension of the lower levels. In backshore areas, under shaded overhangs, there was an upshore extension of Collisella persona from the zone below. On very exposed slopes residual growths of Porphyra sp. and filamentous green and red algae (probably of the Ulothrix and Bangia types) suggested greater abundance earlier in the year. Unidentified dark patches may have been Ralfsia which Rigg and Miller (1949) reported prominent at this level.

Because of the comparative bareness and uniformity, this level of the shore will receive no further mention.

Eulittoral Zone-Exposed Situations

The main littoral populations were divisible into the following belts, in succession downshore: (a) high-level acorn barnacles; (b) Mytilus and Polycipes; (c) as (b) or red algae/Phyllospadix/Pisaster; (d) Lessoniopsis.

(a) High-level barnacle belt

This begins with a thin covering of Chthamalus dalli, that is rapidly joined by abundant Balanus glandula and in its lowest levels by the larger B. cariosus, the latter assuming a columnar form where closely packed. Subordinate species are Littorina scutulata and Collisella digitalis, many of the latter occurring on the shells of B. cariosus and B. glandula. Macroscopic algae are virtually absent, apart from occasional small tufts or patches of Porphyra.

(b) Midshore Mytilus/Polycipes belt

Mytilus californianus and the stalked barnacle Polycipes polymerus predominate together with Balanus glandula and B. cariosus but the contribution that each makes varies very locally and probably reflects different phases in a process of settlement and overgrowth in a highly competitive community. Mytilus usually achieves a 100% cover of small (possibly slow growing) individuals in the upper part of the belt and may then continue downshore in this manner with progressively larger animals providing the main substratum for the three barnacles. Elsewhere gaps in the mussel cover are occupied by dense stands of elongate B. cariosus and Polycipes, or by patches of small B. cariosus, B. glandula and even Chthamalus dalli, presumably in situations that have recently been denuded. Polycipes appears to be slightly more tolerant of desiccation than Mytilus and may therefore, form an upper fringe, but otherwise it is distributed throughout the zone mostly in dense clumps but sometimes more thinly.

Collisella digitalis is common in the upper region, C. pelta elsewhere, and both are frequently to be found on the shells of Mytilus and B. cariosus. This pressure for space is also reflected by elongate B. cariosus, 1-1/2 to 2-1/2 inches long, supporting not only Acmaea and small Polycipes but what appeared from their size range to be 5-6 later generations of Balanus. Additional species in this zone include Mytilus edulis (occasionally among the

uppermost M. californianus), Thais emarginata (usually well-hidden during the ebb period in the interstices between barnacles and mussels) and limited tufts of Porphyra sp. Gigartina sp. and Endocladia muricata.

(c) Red algal/Phyllospadix belt

At the third level are two distinct alternatives. On the most seaward masses and steep slopes the Mytilus/Polycipes population continues unbroken down to the kelp zone with less B. cariosus, but with the highly distinctive addition of Postelsia palmaeformis. This alga occurs in compact curiously patchy stands always on very wave-beaten situations. It can occur on steep slopes but favours shoulders and platforms, always well above the kelp zone.

The second alternative is the predominant type of lower-shore population over all exposed sites visited. The dense cover of Mytilus/Polycipes terminates abruptly, and although neither species is completely absent at the lower levels there is a dramatic change to red algae and sea grass (Phyllospadix scouleri). Among the great diversity of red algae the following were widely occurring and conspicuous: Corallina vancouveriensis, Bossiella plumosa, Microcladia borealis, Erythrophyllum delesserioides, Plocamium pacificum, Callithamnion pikeanum and the genera Callophyllis, Gigartina and Iridea. Often the coralline turf and Phyllospadix formed a blanketing layer excluding all else, but locally there was a more open community with Lithothamnia and other encrusting forms. Patches of Postelsia occasionally occurred in the upper part of this belt, but were more common in continuous Mytilus cover. Relatively inconspicuous among the mass of vegetation were large chitons, especially Katharina tunicata and occasionally Cryptochiton stelleri, isolated Balanus nubilis, Acmaea mitra as well as many small C. pelta. By contrast the sea star Pisaster ochraceus is most conspicuous whether it occurs singly or in aggregations of several dozen, on the open rock, in clefts or in shallow pools. (Its role in this community is discussed on p. 14)

At this level all pools, clefts and overhanging surfaces support an extremely rich fauna. The green or yellowish sponge (Halichondria panicea) may cover areas of several square feet and partially imbedded in it may be the fissurellid Megatebennus bimaculatus. The bryozoans Phidolopora and Bugula form a prominent part of the fauna here. Imbedded in a variety of compound tunicates are occasional bottle shells Mytilimeria nuttalli. The simple tunicates Boltenia and Styella are common and the lined chiton Tonicella lineata is well masked among the red coralline algae as is the rarer hooded chiton Placiphorella velata. Another fissurellid Diodora aspera and several species of Calliostoma frequent this habitat. Among the most conspicuous species are the large green anemones (Anthopleura xanthogrammica), the purple urchin Strongylocentrotus purpuratus and the tunicate Synoicum par-fustis. The purple-hinged rock scallop (Hinnites multirugosus), the tube forming polychaete Dodecacaria and the bright red sea star Henricia may also occur, as well as a number of compound tunicates.

(d) The kelp zone

On these exposed shores this zone is dominated by Lessoniopsis littoralis, with some Alaria nana overlying the lower extensions of the

coralline/Phyllospadix or the Mytilus belts. Surf and steep rocks make examination difficult. Nereocystis lutkeana lies at greater depth offshore.

Semi-exposed Situations

The transition to less turbulent conditions is marked initially by an increase in species sparse in exposure or by the appearance of new species. Apart from Postelsia which was erratic in occurrence even when abundant, the decline of other exposed coast forms is relatively slow. Thus there are extensive transitional areas in which the new or more abundant species and communities are superimposed upon those previously described, and as the majority of new species are algae, often of limited vertical extent, more complex zonation patterns develop.

The high level barnacle belt gains small patches and tufts of Pelvetiopsis limitata, and the midshore area of Mytilus/Polycipes/B. cariosus supports increased quantities of Endocladia muricata, Porphyra sp., short Gigartina sp. and the first growth of Fucus. Overlapping the upper part of the red algae/Phyllospadix belt is Halosaccion glandiforme while Hedophyllum sessile appears at slightly lower levels but still above an unchanged kelp zone of Lessoniopsis and Alaria. The exact sequence with which these developments occur from maximum to less exposure is variable and clearly influenced by the profile and topography of the shore. Water action on flatter surfaces is generally less turbulent and the chance variation of slope at different levels brings in patches of appropriate species.

Fuller development of semi-exposed facies necessitates some decline in the attached fauna. Although B. cariosus can act as a substratum for Endocladia and other small algae, Polycipes never does so and M. californianus only rarely. Thus greater growths of Endocladia, Porphyra, Halosaccion and Fucus are usually associated with a decline in Mytilus/Polycipes and more bare rock or B. cariosus. Even under moderate exposure this trend can lead to midshores dominated by Porphyra and Fucus superimposed on or alternating with B. cariosus. At the lower levels Hedophyllum increasingly overshadows Phyllospadix, and may locally be joined by Codium fragile, while Lessoniopsis gives way to a more variable kelp belt in which Laminaria setchellii, Egregia menziesii and Alaria sp. are prominent with Costaria costata, Cymathere triplicata, Pleurophycus gardneri and Pterygophora californica more local or thinly scattered. (Changes among the abundant red algae were not noted.)

Apart from the decrease in Mytilus/Polycipes and loss of Balanus nubilis other faunal changes are rather slight and matters of detail: e.g., B. glandula and Chthamalus dalli common locally in midtide levels; B. cariosus showing more clearly here a division into stable, cumulative populations upshore and a more transient cover at lower levels; Collisella pelta less abundant but the individuals larger; Notoacmaea persona making an occasional appearance in high level clefts or on overhangs; Thais emarginata, T. lima and Searlesia dira becoming more prominent and clearly having a destructive influence upon B. cariosus. Locally, however, there is a dramatic change in the character of the fauna and indeed of the general zonation pattern. The small green anemone Anthopleura elegantissima which is widely distributed, especially in pools and

damp runnels, may locally form extensive patches or even a continuous belt on vertical faces for a height 2-4 ft above the kelp zone and completely replace the Hedophyllum/Phyllospadix/red algae belt. The only feature common to these two different communities is the presence of Pisaster ochraceus.

Sheltered Situations

The physical criteria for classing shores as "sheltered" are either orientation within a bay or channel considerably protected from oceanic waves or swell, or the presence of shingle and small stones with sufficient stability to support more than ephemeral algae.

In such situations not only have species that were declining on the semi-exposed coasts disappeared completely, e.g., Collisella digitalis, A. mitra, Thais emarginata, Polycipes polymerus, Mytilus californianus, (but see p. 12), Katharina tunicata, Phyllospadix scouleri, Alaria nana, but others that first appeared or flourished most under intermediate conditions are also scarce or absent, e.g., Pelvetiopsis limitata, Laminaria setchellii, Egregia menziesii, Endocladia muricata, Thais lima.

Joining the fauna for the first time are the topshell Tegula funebris and the crabs Hemigrapsus nudus and H. oregonensis, while Thais lamellosa becomes locally more abundant than before.

Additions to the flora are more conspicuous for the kelp zone is joined by Sargassum muticum, Macrocystis integrifolia and Alaria tenuifolia.

The distribution patterns in shelter are perhaps the most variable, for as exposure ceases to be the over-riding physical factor more local influences come into play. On North Atlantic coasts the most important of these are the topography and the type of substratum, i.e., rock, boulders or shingle. Growths of fucoid algae there are usually heaviest on gentle slopes, broken irregular masses of rock or stable boulders, becoming patchy or even absent with increasing steepness, and comprising only small plants on the less stable stones. In the two latter cases animals reappear more conspicuously, with barnacle/mussel/limpet communities dominating the former, and gastropods the latter.

In the sheltered sites of British Columbia this type of difference recurs but is less striking because not only are the local fucoids smaller than in Europe and therefore, less physically dominating, but they are often patchy or thinly distributed, even on the flatter surfaces. In general they appear more as a superimposition upon the underlying barnacles than as successful displacers and principal occupiers of sheltered sites. The barnacle populations continue to comprise B. glandula, B. cariosus and Chthamalus dalli, with the latter two varying locally from extreme scarcity to great abundance (e.g., Chthamalus in Sooke Harbour, B. cariosus at Prescott Pass). Although other local factors may cause absence, their ability to live in extreme shelter cannot be doubted. They are accompanied by Notoacmaea persona and N. scutum; Littorina scutulata and less regularly L. sitkana; Thais lamellosa, T. canaliculata, Searlesia dira and Tegula funebris, the latter abundant in backwaters and clefts among algal debris. Mytilus edulis is more common here than on open coasts while at lower levels the

intermittent belt of Anthopleura elegantissima may recur, especially on verticals standing out of deep water. On stable midshore shingle barnacles persist to some extent but limpets and littorinids predominate with Hemigrapsus. Where the subtidal levels are of rock Pisaster ochraceus persists in the lower third of the shore.

On steep rocks little may interfere with the barnacle cover apart from occasional patches of Fucus but on gentler slopes the barnacles and/or Fucus are joined in midshore levels by short algae that may locally displace B. cariosus completely. The following species or genera were noted frequently: Ulva, Leathesia difformis, Scytosiphon, Gigartina, Halosaccion glandiforme, Rhodomela larix, and Cryptosiphonia woodii.

Approaching the kelp zone, the algal populations become more variable. Steep areas may be rather bare with a thin cover of fine filaments, but tumbled rocks and gentler slopes have a denser cover of predominantly red algae (e.g., Halosaccion, Gigartina, Iridea, Prionotis lyallii and P. lanceolata, Gastrodonium coulteri, Rhodoglossum affini, Plocamium pacificum, Microcladia coulteri, Ceramium pacificum) together with Ulva and occasional Codium fragile. The most luxuriant growths however were encountered on boulder/stone/mud flats where Hedophyllum sessile reappeared to dominate tangled masses of soft, flaccid pebble-attached vegetation in which Ulva, Halosaccion, Desmarestia and Cumagloia were conspicuous among many smaller forms and patches of Zostera.

As these populations merge into the kelp zone there is again local variation. Sheltered sites close to open water frequently have Egregia, but the most widely occurring large Phaeophyceae appear to be Sargassum muticum, Costaria costata, Cymathere triplicata, Alaria tenuifolia, Macrocystis integrifolia, and an unidentified Laminaria, with Nereocystis persisting, as always, in the deeper offshore water.

STRAIT OF GEORGIA

Oceanic swell is lacking in these waters but at times many of the more open situations experience as much water movement as the semi-exposed sites of the Pacific coast. To this extent communities of the Strait of Georgia were similar to the semi-exposed and sheltered communities just described. However, as indicated on p. 6 and will be more fully discussed later, many species that figured largely in that account are absent from the Strait of Georgia and consequently the most characteristic feature of shores in the latter is a high degree of uniformity compared with the outer coasts.

However, one new source of variation is the local presence of Crassostrea gigas, the Japanese oyster, whose spread has been documented by Quayle (1964) and which was not very abundant at the time the Nanaimo area was described by Stephenson and Stephenson (1961).

Their account was found to still hold for most areas lacking

Crassostrea. There is a high level belt of Chthamalus dalli and Littorina scutulata to which are rapidly added B. glandula and, less abundantly than on outer coasts, B. cariosus. Mid levels then comprise these same barnacles, or Mytilus edulis, or Fucus or various combinations of all three. Mytilus is much more common in certain areas in the Strait of Georgia than on Pacific shores, presumably because it no longer has to compete with M. californianus. Except on verticals barnacles and mussels give way below midtide level to an increasing variety of red and green algae that mingle with Fucus or replace it. Among these "small algae" are much Ulva and Gigartina and encrustations of the Ralfsia/Hildenbrandia types, but on many open unshaded slopes this population develops downshore into a compact turf dominated by Leathesia difformis, corallines and Sargassum muticum, the latter consisting mostly of short primary branches at this level. This "turf" is best developed in wave-splashed areas (e.g., Snake Island) or where wash from ferry boats is strong and constant during the summer (e.g., the southeast side of Jessie Island in Departure Bay). Here it forms a prominent zone 3-4 ft deep and provides a marked contrast with the much barer "beard zone" described by the Stephensons on Brandon Island and still present there. This low-level algal belt, as on the outer Pacific coasts, was dotted throughout with sea stars, again mostly Pisaster ochraceus.

The "kelp zone" consists generally of a continuation of this turf with many additional red algae, and larger, fruiting plants of Sargassum but few other large Phaeophyceae. Apart from Nereocystis in the offshore positions the only kelps found were limited amounts of Laminaria sp. and Costaria costata. This intertidal poverty of kelps is a major contrast with the outer coast. Largely it stems from the absence of many species from the Strait of Georgia, but it may also reflect a depression of the upper limits of what species are present by the greater desiccation experienced in the Straits where the lowest tides are near to midday, i.e., several hours later than on the open Pacific coasts, in addition to less cloud cover and summer fog.

For more details of the Nanaimo area the papers by Stephenson and Stephenson (1961) should be consulted.

Among areas in which Crassostrea can repopulate naturally are the Nanaimo District, Ladysmith Harbour and Pendrell Sound, but the frequency with which this occurs is least in the first of these. The south slope of Brandon Island which had few oysters in 1947, experienced heavy settlements in 1958 and 1961 (Quayle 1964) and possibly slight settlements subsequently, and by 1968 showed the effects of this intermittent recruitment of this potentially long-lived species upon the indigenous population. Small but old oysters occurred among the topmost mussels and Fucus, and clearly represented the stable, slow-growing survivors of an old settlement (probably 1958 or 1961). Very large specimens probably of the same age, formed a few conspicuous patches in the lower levels but elsewhere throughout the mid and lower shore the slope presented a mosaic or mixture of oysters, mussels, barnacles and Fucus without any discernible pattern of local or vertical distribution. Closer examination showed only a few patches with any of these animals more than 3-4 years old, although some individual mussels and barnacles of greater age were found among and on the very large oysters. Clearly such an area is in a state of continuous flux.

In Pendrell Sound (and Ladysmith Harbour to a lesser extent) the situation is different. Annual population as a result of special hydrographic conditions (Quayle 1969) has led to such a build-up of Crassostrea that it now completely dominates the intertidal zone to within 1-2 ft of the topmost Chthamalus and B. glandula. With no obvious predators except Pisaster ochraceus and occasionally Evasterias at lower tidal levels, smaller barnacles and mussels are apparently unable to displace it naturally and indeed the associated fauna (barnacles, limpets and littorinids) is found on oyster shells as often as on natural rock. Barring an improbable change of hydrographic conditions this Crassostrea-dominated community recently new to British Columbia, appears likely to persist indefinitely in Pendrell Sound and similar situations. Herein lies the major contrast with Brandon Island where intermittent reproduction of oysters gives other species a chance to establish and where predation (by Pisaster ochraceus, see p. 14) is constantly denuding the middle and lower shore.

PROBLEMS OF LOCAL DISTRIBUTION

The description of these shores in terms of the exposure/shelter gradient is an acknowledgment of a universal phenomenon, i.e., the marked correlations between distribution and exposure. However, to recognize correlations and thus specify exact limiting factors are different matters, for the terms "exposure" and "shelter" are but shorthand, omnibus expressions to cover a wide range of known or suspected physical and biological influences. This has been discussed elsewhere (Lewis 1968) as it applies to European waters, and it will suffice to summarize here what are probably the main considerations involved along the exposure/shelter gradient. These are:

- (1) direct physical effects of strong water movement on settlement, dislodgement, tearing of fronds, movement, filter-feeding mechanisms, etc.;
- (2) physico/chemical differences between oceanic and enclosed waters and shorelines, e.g., turbidity, sedimentation, salinity, temperature, oxygen, organic matter in suspension, nutrients and wastes in solution;
- (3) transportation of reproductive stages from one habitat to another;
- (4) the ability of species from one habitat to compete successfully with typical species of another habitat or to make a successful attachment in the first place;
- (5) the influence of any of the above upon predators or grazers.

The direct physical effects of violent water movement, or its lack, tend to be taken for granted and because several of the above aspects are difficult to investigate, it is the differences in hydrographic conditions that have been most studied. The coasts of Scandinavia and British Columbia are similar physically and in both areas biologists have stressed the relationship of salinity and temperature changes either spatially or seasonally to littoral distribution

patterns, particularly to the elimination of species associated only or mostly with open coasts (Brattegard 1966, Jorde and Klavestad 1963, Scagel 1961, Widdowson 1965). The emphasis upon the hydrographic approach in British Columbia stems logically from two major facts: firstly, the most accessible area, the Strait of Georgia, is essentially an inland sea that presents on a large scale the type of "sheltered water" conditions of low or fluctuating salinities and wide seasonal temperature range that are much more limited in occurrence around other coastal areas of the world (Waldichuk 1957, Tully and Dodimead 1957); secondly, the major differences that so obviously exist between littoral populations of the Strait of Georgia and the open Pacific. In recognizing the validity of these correlations there also appear to be other facets of the problems of local distribution that warrant comment.

It is necessary to consider the distribution of some of the species dealt with in the earlier part of this paper - and others to which no reference was made - in relation to exposure and shelter and to their presence on Pacific and Strait of Georgia shores. Recording an "absence" from a particular habitat or list when one has only limited time in the area or the species is small and easily overlooked will inevitably involve some degree of error, but there are believed to be enough "firm" records in each list to validate the discussion and conclusions drawn. (Apart from personal observations additional data have been obtained from Scagel 1961, Widdowson 1965, Stephenson and Stephenson 1961.)

Ignoring species that are found only in the Strait of Georgia five principal categories may be recognized:

- A1. Ubiquitous species, occurring wherever local conditions permit on exposed or sheltered situations on Pacific or Strait of Georgia shores. Among a considerable number are included the commoner species such as:

<u>Balanus glandula</u>	<u>Hemigrapsus nudus</u>
<u>Balanus cariosus</u>	<u>Mytilus edulis</u>
<u>Balanus nubilus</u> ¹	<u>Pycnopodia heliantheides</u>
<u>Chthamalus dalli</u>	<u>Pisaster ochraceus</u>
<u>Littorina scutulata</u>	<u>Dermasterias imbricata</u>
<u>Littorina sitkana</u>	<u>Anthopleura elegantissima</u>
<u>Collisella pelta</u>	<u>Katharina tunicata</u> ¹
<u>Notoacmaea scutum</u>	<u>Nereocystis luetkeana</u>
<u>Acmea mitra</u>	<u>Fucus sp.</u>

¹Localized in tidal passages in the Strait of Georgia.

- A2. Species found on semi-exposed and, or only, sheltered Pacific shores. Present in Strait of Georgia:

Thais lamellosa

Searlesia dira

Notoacmaea persona

Ceratostoma foliata

Tonicella lineata

Anthopleura elegantissima

Metridium senile

Hinnites giganteus

Epiactis prolifera

Ophiopholis aculeata

Pododesmus macroschisma

Cucumaria miniata

Leathesia difformis

Rhodomela larix

Prionitis lyallii

Cryptosiphonia woodii

Odonthalia floccosa

Desmarestia intermedia

Costaria costata

Codium fragile

- B1. Species found only or mostly on exposed Pacific coasts. Absent from the Strait of Georgia:

Mytilus californianus

Polycipes polymerus

Thais emarginata

Collisella digitalis

Strongylocentrotus purpuratus

Placiphorella velata

Megatebennus bimaculatus

Mytilimera nuttallii

Rostanga pulchra

Petrolisthes cinctipes

Cryptolithodes sitchensis

Gersemia rubiformis

Lessoniopsis littoralis

Callithamnion pikeanum

Erythrophyllum delesseoides

Phyllospadix scouleri

- B2. Species found on semi-exposed Pacific coasts and also usually absent from shelter. Absent from Strait of Georgia:

Thais lima

Thais canaliculata

Tegula pulligo

Crepidula adunca

Astraea gibberosa

Tealia lofotensis

Glans carpenteri

Patiria miniata

Kaburakia excelsa

Pelvetiopsis limitata

Egregia menziesii

Pleurophycus gardneri

Laminaria setchellii

Endocladia muricata²

²Recorded at Nanaimo by Stephenson and Stephenson (1961) but not found there during this survey and classed as absent by Widdowson (1965).

C. Species found on semi-exposed and, or only, sheltered Pacific shores:

<u>Anthopleura xanthogrammica</u>	<u>Cymathere triplicata</u>
<u>Tegula funebris</u>	<u>Desmarestia munda</u>
<u>Notoacmaea fenestrata</u>	<u>Halosaccion glandiforme</u>
<u>Tealia crassicornis</u>	<u>Microcladia borealis</u>
<u>Vermetus compactus</u>	<u>Plocamium pacificum</u>
<u>Calliostoma ligatum</u>	<u>Heterochorda abietina</u>
<u>Hedophyllum sessile</u>	<u>Prionotis lanceolata</u>
<u>Macrocystis integrifolia</u>	

Attempting to classify species in this way raises difficulties. For example, Littorina sitkana because of its scarcity on exposed shores should perhaps be in category A2, and Acmaea mitra appears to favour clean water conditions only, but irrespective of whether these are on exposed Pacific or sheltered Strait of Georgia shores.

Of these five categories, A1 needs no further discussion, while species in category A2 appear to have as their prime requirement the avoidance of some attribute of "exposure," and their ubiquity otherwise indicates considerable tolerance to other hydrographic conditions. Similar avoidance of exposure characterizes group C, but in this case the tolerance of other "enclosed water" conditions appears less for they are absent from the Strait of Georgia. The existence of these two different groups of sheltered shore species (i.e. A2 and C) suggests that although small, sheltered bays on the Pacific coast must experience greater variation in hydrographic conditions than the adjacent open coast, the values are generally less extreme than those in the Strait of Georgia. If the distributional limits of group C are indeed controlled by such physico/chemical conditions it would seem likely that these species would be absent from some of the longer, more enclosed inlets that open direct to the Pacific or Queen Charlotte Sound and where the temperature-salinity regimes might approach those in the Strait of Georgia. This is indeed the situation.

Categories B1 and B2 can be considered together for they differ only in their exposure tolerance or requirements. Both are absent from the Strait of Georgia and also from or scarce in other sheltered and enclosed situations. This last point is most significant. It appears highly unlikely that the physico/chemical gradients that extend along the Strait of Juan de Fuca to the San Juan Islands in the south, and down the Queen Charlotte Strait in the north and with which the disappearance of these species appears to be correlated will be repeated in every small bay, or in every lee position in which they are regularly absent on the open coast. The physical conditions in the latter clearly need investigation, but it is most unlikely that they will differ drastically in all such areas from those of the nearby open sea, and indeed, the existence of category C species lends support to the view that conditions there are not so extreme or difficult as in the Strait of Georgia. If this assessment is correct their absence or scarcity must be ascribed to other facets of the exposure-shelter gradient such as those outlined on p. 5. In view of the diversity of the species involved (categories B1 and B2) and their very different needs and life

cycles the ultimate controlling factor(s) will probably differ markedly from one species to another (or even for the same species in slightly different situations) and can only be elucidated by experiment and long-term observations of all phases of the life cycles. The facet to which attention should be directed initially is the extent to which the reproductive stages are carried from the wave-swept sites and actually make contact with a suitable substratum in sheltered situations. Experience with this type of problem in British waters with the barnacle Chthamalus stellatus, (generally regarded as a reliable "indicator" of exposure) suggests that larvae are not carried to all parts of the shoreline as regularly as might be expected. Thus, some apparently suitable situations lack the species while some others that are sheltered do not, and the deciding factor appears to be whether or not a particular situation faces directly into the path of larvae-bearing water moving under the influence of tidal streams or winds. Although waves appear to bring about the final contact of larvae with rock, gentle lapping movement can suffice and there is no need for the violence of a typical exposed site. "Anomalous" occurrences in shelter of the open coast alga Himantalia elongata also demonstrate that the physical conditions of land-locked bays and channels are not necessarily harmful and that some species can thrive there, provided the reproductive phase reaches these sites in the first place and is not then overwhelmed by other forms. Further evidence that reproductive phases are not ubiquitous and settling everywhere comes from recolonization experiments in which the spread of Fucus has been a slow, progressive affair over several years, even in the absence of grazing molluscs (again observations in Britain).

Clearly questions of dispersal and settlement will be related not only to water movement but also to the size of the breeding population, the success of reproduction in any particular year, and the duration of the motile phase in a viable condition. There are probably open coast species of such density and fecundity that dispersal could be very widespread and this aspect ignored. Nevertheless, the suggestion that problems of transportation and settlement might apply to some species is supported by a number of observations. In a small bay near Ucluelet for example, a small promontory that faced the narrow opening but otherwise deemed "very sheltered" supported a typical semi-exposed population of Mytilus californianus, Acmaea digitalis, Pelvetiopsis and Endocladia, as well as such indicators of shelter as Tegula and Macrocystis. In several other very sheltered situations there were isolated and "anomalous" patches of M. californianus (and occasionally of Acmaea digitalis) the age of which suggested that they had settled many years previously and that there had been little or no subsequent recruitment. It would appear that these exposed shore species are capable of living under sheltered conditions but that in the normal course of events their larvae reach these sites very infrequently.

In this context the experiments and discussion of Young (1941) are relevant. Although he found that reduced salinities had an adverse effect upon the reproduction and larvae of M. californianus he was unable to relate absence to the salinity regimes of particular sites. On San Juan Island for example, he found a difference of only 0.5% between the sites with and without Mytilus and concluded, as Shelford had done earlier (1935) that turbulent water was required. However, as stated above, Mytilus can thrive in areas without turbulence and so there seems a good case for distinguishing between the physical qualities of turbulent water per se and the transportation role. Normally the two go together

on open coasts but there are clearly instances where the latter operates in non-turbulent sites.

Another example of these different facets of water movement involving other species was perhaps seen on the uniformly sloping stony beaches just west of Whiffin Spit. Species such as Collisella digitalis, Littorina sitkana, Egria and Phyllospadix were equally as abundant as Hedophyllum, Ulva, Macrocystis, and Zostera. This most unusual juxtaposition of exposed and sheltered species at all shore levels suggests that although the turbulence is lacking, the beach is sufficiently open to be bathed by water carrying the reproductive phases of exposed shore species and of suitable quality for their successful growth. Similarly a small population of Lepas anatifors, a typically open ocean species, was found to have settled on a buoy near Nanaimo in the Strait of Georgia.

Even with an ubiquitous species such as Balanus glandula the larvae of which are probably abundant in all coastal waters there were indications that settlement was greatly increased by small waves actually washing against the shore. Thus at Pipers Lagoon (near Nanaimo) the high level B. glandula belt at the entrance, facing N.E. into the Strait of Georgia comprised in August 1968, 53% animals in their first year whereas within the Lagoon itself this figure fell to only 4% at the same level and to a maximum of 17% elsewhere. The dominance of very old animals in the Lagoon population suggests that settlement was rather infrequent and depended not only on larvae entering the Lagoon, but on winds from the right direction to drive the surface waters within the Lagoon against the rocky outcrops. On a broad, geographical scale this type of event has been recorded by Barnes (1956) with Balanus balanoides, but support for the contention that very local water movement controls very local settlement densities necessitates counts of larvae adjacent to the shore under differing wind conditions. There is no indication such investigations have been made, but that such control could be possible was obtained by a casual observation on a lake suffering from a phytoplankton bloom. There was just sufficient wind to concentrate the bloom into a green scum on the down-wind shore and it was most noticeable that this scum washed against the windward side of small boulders but left a ragged "tail" of clear water on the leeward side. Although invertebrate larvae are not such passive drifters as phytoplankton this type of phenomena could well contribute to some of the observed differences between the windward and leeward sides of boulders or rocky outcrops.

Attempts to explain all the local vagaries of distribution are clearly doomed to failure. If settlement is not observed it isn't known what local mortality factors have operated, but even more fundamentally it cannot be certain that the larvae are indeed uniformly spread throughout the coastal waters. Floating debris is often distributed in long "slicks" or discrete patches as a result of convergences, and the predators of planktonic larvae may be patchy and highly mobile so that "chance" factors of this type may intervene even before the settlement phase is reached. In species with a long reproductive period and/or larval phase such aspects may even themselves out during the season, but with a short intensive reproductive period patchy settlement on the shore should perhaps be regarded as the norm rather than requiring explanation.

In drawing attention to the presumed importance of transportation of reproductive stages it is not implied that failures of this nature necessarily

account for the absence of so many Pacific coast species from the Strait of Georgia. Nevertheless, their partial or complete absence from enclosed sites elsewhere points to another major problem in their distribution, and the solution of these more local problems may well throw more light on the major one.

*Scudenberg 1968
Ecology 42, 1062*

*Menge 1972
Ecology* *Dayton 1972
Ecol. Monogr.*

THE ROLE OF PISASTER OCHRACEUS

The predatory activity of Pisaster ochraceus has been commented upon and investigated by a number of previous workers of whom the most recent are Feder (1959) and Stephenson and Stephenson (1961). The former found that 29 species were used as food but there was a marked preference for acorn barnacles and mussels when available, and the latter related the existence of a "bare zone" in the lower shore at Departure Bay to starfish activity.

As the present survey was conducted entirely at ebb tide little direct evidence of predation actually taking place was obtained, but various types of circumstantial evidence point to Pisaster playing a far more important role in determining the character of littoral populations than has previously been suggested.

In areas where Pisaster is lacking the main midshore invertebrate populations extend unbroken to low-tide levels. Two such habitats, very different physically, are the most wave-swept steep faces of Pacific coasts, (i.e., some of the "Postelsia sites"), and the landlocked Pendrell Sound that experiences very high summer temperatures and severe salinity fluctuations. Probably because of these physical conditions Pisaster is either permanently or seasonally absent and the M. californianus/Polycipes communities and Crassostrea, respectively cover the entire mid and lower shores.

Locally too, where the only concentrations of Pisaster occur in shaded clefts on otherwise smooth open slopes with a continuous cover of barnacles, mussels or oysters (an example of the latter existing in Ladysmith Harbour), a cleared area a metre or more exists on either side of the Pisaster retreat.

On open Pacific coasts, except the most exposed or those with a heavy Fucus cover, there is often an abrupt division of the shore into an upper area of barnacles and mussels, and a lower belt with various populations all of which include Pisaster. The lower margin of the upper belt often has a "raw edge" of partly broken, columnar B. cariosus or of large, occasionally gaping M. californianus and adjacent bare rock with byssal remains. Within the lower zone areas of Mytilus/Polycipes still remain, but the distinctive and relevant feature is the existence of the following populations:

(1) The dominating wealth of algae (+ Phyllospadix) that has already been described (p. 3) and which is virtually ubiquitous on the wave-swept areas.

(2) Patches of B. cariosus and Chthamalus dalli that are only one or two years old, are less crowded than the cumulative cover in the upper shore, and

are clearly newly-established populations of relatively short duration.

(3) Occasional patches of exceptionally old and large M. californianus which one presumes have escaped, or are of a size capable of resisting, predation.

(4) Sheets of the small anemone Anthopleura elegantissima several meters in extent and particularly common on verticals rising out of deep water. As this species is believed to reproduce by fission (Stephenson and Stephenson 1961) such extensive growths probably indicate a stable and long-lived population not based upon the chance settlement of motile larvae. Although Pisaster is not found on Anthopleura itself, it is usually present in the areas of bare rock, thin Balanus and small algae that intervene between the anemone sheets.

This division into upper and lower zones is less striking in the Nanaimo area, because M. californianus is absent, and the lower-shore algae are less dense and conspicuous than on Pacific coasts. Nevertheless, on Brandon Island middle and lower levels support a bewildering mosaic of patches of barnacles, oysters and mussels in varying densities and ages (sizes) and of bare rock or fine algae, throughout which individuals or aggregations of Pisaster were irregularly distributed. Such mosaics, showing no correlation with physical conditions, are only explicable in terms of patchy predation and recolonization by competing species extending over several previous years.

Accepting that the algae or the Anthopleura, once established, will do much to prevent or delay re-occupation of the rock by mussels and barnacles (or oysters where appropriate) the age, size and density that the latter can attain, leads to the belief that they would provide the dominant rock cover were they not subject to intensive predation at these levels. Whether algae alone could regularly displace them requires experimental investigation, but seems improbable in view of the large numbers of Acmaea that actually live on the surface of M. californianus, B. cariosus and Crassostrea. Equally the thesis that Pisaster is the primary agency bringing about the instability and apparently illogical mosaic distribution among these animals themselves may need experimental verification, but the field observations leave no real alternative explanation. In long-term studies on British coasts intermittent incursions of predominantly sublittoral starfish - Asterias rubens - have had a similar effect, opening up mussel-dominated areas for short-term occupation by barnacle/limpet communities or less frequently by red algae.

On the open Pacific shores the most impressive consequence of presumed Pisaster predation was not so much that space was made available for reoccupation by short-lived animal communities, but that this space was predominantly occupied by algae. Recalling that this algal belt was virtually non-existent on the most exposed sites where Pisaster was also lacking we must assume that

(a) its establishment requires the prior removal of mussels and barnacles, or

(b) these algae, like Pisaster, are absent because of the severity of wave action.

The latter is a difficult hypothesis to prove or disprove, but where M. californianus can be found occasionally at low levels in less exposed places there tends to be an accompanying dearth of algae, and accordingly one inclines to the view that the first explanation is more likely.

Accepting then that Pisaster predation opens the way for algae it must next be asked why this abundant food resource is not "exploited" and held in check, locally at least, by grazing animals as happens to some extent on British coasts with comparable algal populations. Although experimental support is needed a possible explanation is as follows. Littorinids and trochids are virtually absent and although some Acmaea mitra and Notoacmaea scutum are present at low levels the principal limpet of the open coasts is Collisella pelta of which the vast majority are very small (< 1 cm in August) and much less abundant in the algal zone than on and among Mytilus. There remain the chitons of which Katharina tunicata is large and widespread and would appear capable of taking over the principal grazing role. If Pisaster destroys the mussels and barnacles, and is unable to extend upshore beyond the "predation line" (because of excessive desiccation) it must be assumed that there is either a sufficient annual recruitment of Mytilus/Balanus/Polycipes to supply the year-round needs of Pisaster and/or that an alternative food source exists. In the experiments by Feder (1959) Acmaea sp. and Katharina were eaten, but did not rank highly, although another chiton Mopalia muscosa was taken preferentially. In this survey Mopalia was not common on Pisaster shores, but it is perhaps significant that on the few occasions when Pisaster was observed feeding, its prey was Katharina. The dearth of large C. pelta may also be due to predation and when Pisaster was pulled from the rock surface small Collisella pelta often adhered to the tube feet. Although this may not happen when the starfish walk over limpets naturally it is another possible source of limpet destruction (Margolin 1964).

Thus one may postulate that Pisaster encourages algal colonization initially by removing the attached fauna, and then retards the grazing rates by feeding on or otherwise damaging the chitons and limpets. If these hypotheses can be substantiated the most distinctive feature of the exposed Pacific shores, i.e., the division into an upper barnacle/mussel belt and a lower algal belt, will thus be more a biologically than a physically controlled phenomenon. (In this context it may be noted that the dearth of sublittoral algae on some Pacific shores is apparently attributable to the grazing of other echinoderms, the urchins Strongylocentrotus purpuratus and S. franciscanos.) Pisaster ochraceus is primarily an intertidal species and as such constitutes an "in situ" predatory agency in marked contrast with the intermittent littoral incursions of Asterias in European waters and thus it has a much greater influence upon littoral populations.³

³At the time of this survey the work of Paine (1966) was unfortunately not known. In this and later studies (1971) Paine concludes that Pisaster and other sea stars are responsible, through predation, for increasing the diversity of animal communities on rocky shores. The observations recorded here are clearly in accord with this view, but also go further in suggesting that the ultimate consequence of persistent Pisaster predation is low-level algal dominance. Decline of Pisaster because of lack of prey could restart the entire cycle but much would depend upon the efficiency of the algal turf in preventing mussel and barnacle settlement.

You also don't seem to know about J.H. Currell, and his students
Hanger, Wandenberg, Stimson, or about Paine's student Dayton Menge.
So what, jerk!

(The role of other predators, especially Thais gastropods has not been enlarged upon because although locally they cause severe damage to B. cariosus they did not seem to be sufficiently abundant over large areas to do more than marginally supplement the effects of Pisaster. This again is a point of contrast with British shores where a single species, T. lapillus, is the principal midshore predator.)

All Connell Ed. Mar. 1971
Dayton Ed. Mar. 1972.

GRAZING MOLLUSCA

The principal intertidal grazers in temperate latitudes are limpets of various types, littorinid and trochid snails, supplemented at lowest levels by a greater variety of animals including chitons and possibly echinoids in special circumstances. In British Columbia the latter are primarily subtidal or confined to pools and damp clefts, but the chitons Katharina tunicata and Mopalia muscosa are of such size and abundance that they probably play an important role in the mid/lower levels of rocky shores (see also p. 16).

Of the various trochids only Tegula funebris is abundant and even so is restricted to semi- and fully-sheltered bays on the open Pacific coast, being completely absent from the Strait of Georgia and innermost parts of Juan de Fuca Straits. When present it is primarily associated with boulder and stony beaches, backshore gullies and pools, and is especially abundant when drift weed accumulates in the higher shore. Without performing clearance experiments it is not clear what part this species plays in cropping standing algae or removing sporeling stages (Best 1964). As a detritus feeder its role parallels in part that of Littorina littorea, Gibbula umbilicalis and Monodonta lineata in Europe, but it was not found, as they may frequently be, on bare rock surfaces with microphytes as the only algal food. Although Calliostoma sp. occur in the lower levels their numbers are small so that the trochids in general are a limited component of the grazing population compared with the littorinids and limpets that are dealt with separately below. The turbinid Astraea gibberosa is probably the most important grazer on semi-protected ocean shores in certain areas.

Littorina. Littorinid-type snails not only characterize most shores of the world but because some of them are highly adapted to resisting desiccation the group is one of the major contributors to the upper levels of rocky shores in conjunction with encrusting black lichens and microphytes. In British Columbia there are two species only, Littorina scutulata and L. sitkana. The former is virtually ubiquitous and although its numbers vary greatly it lives in both exposed and sheltered situations on Pacific and Strait of Georgia coasts, and extends throughout much of the tidal area. It is found in high level pools, in spray zone clefts and cracks, among barnacles and Mytilus californianus, on stable midshore shingle and low-level gravel, and amongst high-level Fucus.

L. sitkana by contrast is much more localized, even erratic, and its distribution in relation to its mode of reproduction and dispersal would repay detailed study. Generally it is absent from wave-swept situations or confined there to protected niches, and although it can occur in very sheltered areas,

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often on mid/upper shore Fucus, it is absent from other equally sheltered sites such as the innermost parts of Sooke Harbour where L. scutulata is abundant. Greatest numbers were found on the stable boulder and shingle beaches at and westwards from Whiffin Spit and near Jordan River (on the Juan de Fuca shoreline). Here large drifts of algal debris were virtually obscured by L. sitkana, the species performing the algal scavenger role undertaken by Tegula in the Pacific coast bays.

Although one or both Littorina species can be found on all shores they play a relatively less conspicuous role than their counterparts elsewhere. To some extent this reflects the absence of a large species, a counterpart to L. littorea on N. Atlantic shores, but this apart, the classical "Littorina zone" of the upper shore was less well developed than for example in Europe (Lewis 1964) or Florida (Stephenson and Stephenson 1952). Such a zone was recorded by Stephenson and Stephenson (1961a, b) on Brandon Island and near Victoria, but the wider range of shores visited in this survey suggest that it is to be found in midsummer mainly on semi- and fully-sheltered situations that are shaded, damp or gently sloping. On dry, barnacle (or oyster) slopes and faces in full sunlight L. scutulata is concentrated among the upper barnacles and relatively few, if any, extend above Chthamalus. On Pacific coasts with severe exposure and summer mists to offset desiccation an extensive fringe zone was expected but L. scutulata was unexpectedly scarce and confined mainly to clefts. Its abundance among Chthamalus and Balanus glandula below suggest that its scarcity at the higher level may stem from a susceptibility to dislodgement, a point previously made by Boch and Johnson (1967). The latter also suggest that as L. scutulata (in California) prefers macroscopic algae for food an upper limit of distribution is set by the absence of such plants. Algae are scarce above the barnacle line of exposed sites but there is an equal scarcity in the Chthamalus/B. glandula belt where small L. scutulata can be most abundant. Microphytes presumably are the main food source here in midsummer.

Acmaea. The Acmaea populations of British Columbia comprise not only large numbers of individuals but also 11 intertidal species and thus offer a very marked contrast with the northeast coast of America where only one species occurs in the lowest intertidal area and plays little part in the biology of the shore. In N.W. Europe Acmaea is restricted to low levels and the main limpet population of the tidal area is the genus Patella with 1-4 species according to geographical locality and habitat conditions. Of these P. vulgata is virtually ubiquitous and where it occurs alone occupies a range of habitats and levels that in British Columbia is occupied by several different species of Acmaea. Ignoring those species of Acmaea with very restricted habitats (e.g., on algae or other molluscs) the main intertidal populations appeared to comprise six species: Collisella digitalis, Collisella pelta, Notoacmaea persona, Notoacmaea fenestrata and A. mitra. The latter is confined to the lowest tidal levels on the open coast and is subtidal in the Strait of Georgia, while N. fenestrata was seen only in the Jordan River area and near Tofino on stable boulders and shingle close to sand.

Although Collisella digitalis extends as far east as Saanich it is completely absent from the Strait of Georgia. Generally it behaves as a typical exposed-shore species dying out, sometimes abruptly, sometimes more gradually, at the entrance to bays and enclosed channels. Usually it is confined to

bedrock but was unexpectedly common on stable boulders and stones west of the entrance to Sooke Harbour, an area that presumably offers a rare combination of open coast hydrographic conditions that do not disturb the stability of a potentially unsuitable substratum. In full exposure it is abundant among the upper barnacles but does not penetrate far into the Mytilus californianus belt. Among and on the closely packed Balanus cariosus, C. digitalis is usually of small size (< 10-15 mm) reflecting perhaps intense competition both intra-specifically and with C. pelta with which its vertical range overlaps. Where some individuals rise above the barnacle line, especially on shaded verticals, a larger size can be attained (i.e., < 25 mm). This may, as with Patella vulgata in Britain, result from easier grazing and faster growth in the absence of barnacles, or may be due to differences in the age/structure of the population at different levels (see also Frank 1965). Restriction of the species to both the upper shore and to exposed sites raises interesting problems of dispersal and settlement of the larval stages.

N. persona has a rather restricted distribution. Test (1945) says it occupies "the inverted horizontal or semi-horizontal substrate in dim light," and if added to this is the fact that such situations are usually in high clefts and overhangs of sheltered bays or backshore regions of otherwise exposed shores, most of the population would be covered. However, its range of habitat tolerance was shown to be appreciably wider when large numbers were found in full sunlight on the stable boulders west of Sooke Harbour and at Jordan River. Only two such sites were examined, but its abundance at both and the prevalence of such shores along the shores of Juan de Fuca Strait suggest that it may be widespread in this habitat in this area. Because of proximity to shingle and sand - it shared boulders with N. fenestrata - the shells were often eroded and atypical at first sight.

N. scutum is more ubiquitous than either N. persona or C. digitalis there being few sites on which some individuals could not be found in midtidal levels. The wide range of habitats includes stable shingle in lower tide gullies and lagoons and the surface of columnar Balanus cariosus as well as the usual bedrock. Greatest abundance and maximum sized individuals occur on fairly sheltered faces or stable boulders that lack attached animals and have fine, soft growths of sporeling Ulva, Enteromorpha and small Rhodophyceae or films of Cyanophyceae. Such conditions prevailed extensively west of Whiffin Spit where N. scutum up to 5 cm in length formed a remarkably conspicuous population (with the chiton Mopalia muscosa) below the mid/upper zones of N. persona and C. digitalis to which reference has already been made. In the upper shore generally N. scutum may overlap into the shaded habitat more typical of N. persona and the two are often the only limpets present in sheltered and brackish backwaters where high-level rock gives way to muddy gravel at half-tide level.

C. pelta was classed by Test (1945) as the most eurytopic acmaeid in California, but whether this applies around Vancouver Island is a moot point. It is perhaps less common in shelter than N. scutum but on the other hand is able to live on the stipe of Postelsia as well as the more usual range of substrata. The most impressive aspect, apart from the wide range of habitats occupied, is the abundance on exposed coasts. At Amphitrite Point, for example, densities of up to 30/5x5 cm of very small animals were found in August 1968 on the rock surface between mixed M. californianus and B. cariosus. Large areas of bare rock are not

of course available on such shores, but the total surface area of mussel and barnacle shells far exceeds that of the rock space occupied by these two species. Although C. pelta was not as abundant on shells as on bare rock the total numbers of limpets could well have been within the range 5-10,000/m² of shore community. This phenomenally high density recorded in 1969 may be a regular transient feature of each post-settlement phase or the consequence of two exceptionally successful reproductive seasons. Such numbers cannot be conceived as persisting for long as size increases, and indeed a size-frequency analysis of approximately 400 individuals taken from a mixed area of mussels/barnacles/bare rock/damp cleft shows less than 10% greater than 10 mm in length. This suggests either exceptional mortality of juveniles regularly, or that the 1968 and 1969 year-classes were unusually successful, or that high density leads to very slow growth; but without long-term population studies no conclusion can be reached.

In the Strait of Georgia where C. digitalis is absent C. pelta is frequently the limpet which occurs at the highest tide level, especially on barnacle, oyster or mussel slopes facing south (e.g., Brandon Island) but its wide vertical tolerance is revealed by its presence with N. scutum on stable shingle in low-water channels in Pipers Lagoon.

By comparison with Patella in N.W. Europe a most distinctive feature of acmaeid populations on Vancouver Island is the small size of most individuals relative to the associated fauna, and the consequent lack of visual impact (irrespective of how much this is compensated for by abundance). Animals above 25-30 mm length are common only on backshore faces and overhangs (usually persona or scutum) and on stable boulders and stones (scutum, pelta and atypically persona). As these situations have algal growth of one sort or another and usually lack barnacles and mussels, the combined effects of easy movement, plentiful food and absence of other animals increase both the maximum size and conspicuousness of the limpets. Among dense barnacles, mussels or oysters the majority of limpets are small - probably because grazing is difficult and intraspecific competition is high, a situation paralleled by Patella in Britain. Because the acmaeids are small, M. californianus (large), and B. cariosus (small), the latter often supports a high proportion of the local limpet populations. By contrast Patella sp. are rarely if ever found on the much smaller barnacles and Mytilus edulis of European exposed coasts and probably for this reason the extensive beds of small M. edulis in N.W. Europe often support a blanketing layer of small red algae (Lewis 1964). The belts of M. californianus and B. cariosus, although not lacking in algae, present to European eyes a remarkably "bare" appearance.

Other situations in which algae are curiously patchy or unexpectedly scarce are the mid/upper levels of sheltered shores in the Strait of Georgia and the inner passages northwards towards Prince Rupert. To some extent this may stem from the steepness of many of these shores (as it does in N.W. Europe), but nevertheless furoid algae dominate sheltered situations in British Columbia to an extent that is much less than in Europe. Presumably there are N. Atlantic furoids adapted to sheltered conditions and with a vegetative persistence or reproductive capacity which offsets the grazing of littorinids, trochids and limpets. Greatest luxuriance in shelter (especially of Ascophyllum nodosum, an algae of large size absent from the Pacific) is associated with a scarcity of rock-living molluscs and one suspects that this scarcity may in part be a consequence of the algal luxuriance as well as its initial cause.

The situation in British Columbia where so many sheltered areas are dominated by barnacles, oysters (and mussels) is presumably related to some of the following:

(i) The smaller size of Pacific Fucaceae and absence of any other large and fully intertidal perennial genera. (This is in marked contrast with the subtidal situation where Pacific Phaeophyceae are both larger and much more diverse than those in the N. Atlantic.)

(ii) A possible low reproductive output by existing furoids, relative to the grazing rate of the littorinids and acmaeids.

(iii) A possible very short period during which the fertilized egg is viable and able to carry successfully to other shores.

(iv) A possible need for non-desiccating conditions at the early sporeling stage. Certainly the shores of the Nanaimo area were exceptionally dry in July/August, 1968 and furoids were most abundant on shaded faces, but desiccation would not seem to be a recurrent physical feature of shores to the north of Vancouver Island.

There are of course situations physically suitable for furoids in which their absence can reasonably be ascribed to the presence of many large acmaeids, L. sitkana and even chitons, but the comparative scarcity of furoids in other sheltered areas where such biological influences appear minimal is a sufficiently distinctive feature to warrant comment and speculation.

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