

## Benthic community modification and recovery following intensive grazing by *Strongylocentrotus droebachiensis*

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**ABSTRACT:** Intensive *Strongylocentrotus droebachiensis* grazing of a previously sampled one-hectare plot provided an opportunity for quantitatively investigating grazing impact on the benthic macrophyte community and community recovery. The changes induced by grazing are compared with changes in a similar plot located nearby which was not grazed. A total of 154 quantitative 0.25 m<sup>2</sup> quadrats were collected in mid-summer, from the two sites, over a 4-year period. The results presented indicate that *S. droebachiensis* populations in the Strait of Georgia undergo periodic, environmentally controlled, outbreaks and that these outbreaks are responsible for localized perturbation of the benthic macrophyte community. Short-term grazing, where the urchins do not remain in the area, result in a 60 percent reduction in most community parameters measured. The community requires 2 or 3 years to regain or exceed pre-grazing biomass levels while other parameters had not recovered after 3 years. An estimated 4–6 year period is required to achieve “ecological climax” (Fishelson, 1977) and “species enrichment” follows. The largest macrophyte in the Strait of Georgia, the kelp *Nereocystis luetkeana*, is a successional species whose abundance is controlled, in part, by the successional status of the community.

### INTRODUCTION

Studies of sublittoral succession and long-term variation in benthic algal communities are few in number. Recruitment and algal succession has been examined on introduced substrate (plates) by Castric-Fey (1974) and Foster (1975) while secondary succession has been studied by Jones & Kain (1967), Vadas (1968) and Paine and Vadas (1969). The latter studies were undertaken on areas grazed by sea urchins and utilized urchin removal as well as cage enclosures to obtain an urchin-free environment. The influence of the sea urchin *Strongylocentrotus droebachiensis* on algal communities has been considered by Vadas (1968) for the Pacific coast of North America and by Mann (1972), Miller & Mann (1973), Breen & Mann (1976) and Mann (1977) for the Atlantic coast of Canada. The need and justification for long-term baseline studies of littoral and sublittoral benthic communities has been stated by Price (1973), Burrows (1971) and others.

The present studies were undertaken as part of a quantitative sampling programme designed to investigate natural variations in nearshore benthic ecosystem structure and function. This investigation was initiated in 1972 using one-hectare study plots. In the early spring of 1973 one of the plots was intensively grazed by the sea urchin *S. droebachiensis* and subsequent sampling has resulted in a detailed examination of grazing impact and macrophyte recovery over a 3-year period. The results presented in this paper are an initial attempt to analyze successional events in grazed and non-grazed plots from the 4-year of data obtained to date.

### SITE DESCRIPTION

The one-hectare study plots are located within a kilometer of each other in the Flat Top Islands area ( $49^{\circ} 09' N \times 123^{\circ} 40' W$ ) of the Strait of Georgia, British Columbia, Canada. The Strait is a large, highly stratified, positive-type estuary located between the southern British Columbia mainland and Vancouver Island. The major source of freshwater in the Strait is the Fraser river and the study sites are located 30 km from, and directly opposite, the north arm of the river. The conditions at the site are typical of the central, river dominated, domain within the Strait with salinity and temperature at the site varying from 10 to 33 ‰ and 7 to 21° C, respectively.

Site B (urchin grazed) is a southeast facing area of gently sloping bedrock substrate, merging into boulders and cobbles at a depth of 7.5 m below MWL and sediment at 9 m. Site S is similar in substrate and exposure, but with a steeper slope and transition to a discontinuous boulder bottom at 8.5 m depth.

### METHODS

Figure 1 diagrammatically summarizes the sampling and processing procedures. Following an initial reconnaissance the study plots were delimited by metal markers along the beach (X) axis. Plots were selected to have a relatively homogeneous substrate along any given depth. Each plot was sampled in mid-summer, each year, by placing a 100 m marked transect line perpendicular to a randomly chosen point on the beach. Quadrats (0.25 m<sup>2</sup>) were quantitatively collected at 5 m intervals along each transect line. Prior to collection qualitative details of the physical and biotic components within the quadrat were described by a trained diver who transmitted the information to a surface operator via an underwater wireless communication system (SUBCOM, Model 130). The quadrat was then collected using a small, self-contained, airlift of the author's design with a nylon bag of 2.5 mm mesh.

The collected samples were immediately processed or preserved in 5 per cent formalin : seawater. Processing consisted of sorting all macrophytes by species and removal of all fauna. The latter were stored in neutralized formalin : seawater for later analysis. Each macrophyte species was wet weighed, sub-sampled for identification, phenology and preparation as a voucher specimen. The remaining sub-sample was reweighed, dried at 80° C for 24 hours in a forced convection oven, weighed,

ashed at 425° C for 4 hours and weighed. Wet, dry and ash-free dry weights were calculated per m<sup>2</sup>. Identification and phenology were completed at the UBC Phy-  
cological Herbarium where the voucher specimens are filed.

The data were processed and analyzed on an IBM 370 computer operated by the UBC Computing Centre.

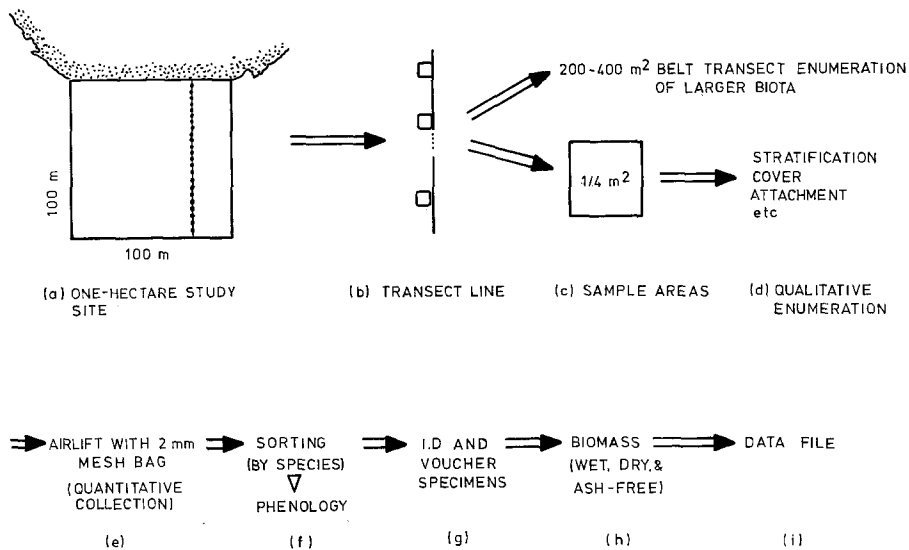


Fig. 1: Summary of collection and processing methods

Sea urchin populations were sampled during several research cruises throughout the Strait of Georgia and locally within the study area. Small quadrats ( $1/16$  to  $1/4$  m<sup>2</sup>) were collected in the denser areas of each population in order to determine maximum abundance and weight per m<sup>2</sup>. Wet and gonadal weights, and test diameter were determined for each individual.

The results which follow are based on analysis of 154 quadrats consisting of those quadrats collected at site B (urchin grazed) and site S (non-grazed) in July of 1972 through 1975. No samples were collected at site S in 1973. In this paper the site-year collections will be identified by B or S to indicate site and 72 through 75 to indicate year, i.e. B 74.

## RESULTS

### Urchin sampling

The dramatic increase in *Strongylocentrotus droebachiensis* numbers observed in the study area was an unprecedented event within the Strait of Georgia. Although

locally common in the Strait this species was generally restricted in distribution to isolated populations, in presumably favorable sites.

A survey, conducted to evaluate the extent of this phenomenon and its impact on nearshore benthic ecosystems, examined over 200 km of coastline and 130 specific sites. 21 *S. droebachiensis* populations were located and sampled. The mean number of individuals/m<sup>2</sup> was  $322 \pm 228$  (range 57 to 1072) and mean wet weight/m<sup>2</sup> was  $5,770 \pm 6065$  g (range 416 to 24,137). 15 % of the populations occupied less than 0.5 ha, 45 % 0.5 to 2 ha, and 40 % more than 2 ha of area (Foreman & Lindstrom, 1973).

Test size histograms were constructed for each population and used to estimate population age structure, based on the results of Miller & Mann (1973). 60 % of the populations were dominated by 3 to 4 cm urchins and all but 4 of the populations appeared to have juvenile recruitment in 1973. Subsequent examination of urchin populations in the vicinity of the study sites indicated no recruitment occurred in 1974 or 1975. On the basis of the histograms it was concluded (Foreman & Lindstrom, 1973), that the major recruitment occurred in 1969.

The urchins at site B appeared to have migrated through the study area from east to west along a broad front which extended from 1.5 to 8.5 m below MWL. Above 1.5 m they were exposed to emersion and gull predation and below 8.5 m the bottom became cobbly and the front interfaced with a moderate-sized population of *S. franciscanus*. The two species were not observed to mix to any great extent. By June 1973 most of site B between 1.5 and 8.5 m depth had been thoroughly grazed and some macrophyte recovery was underway in urchin-free areas. The remaining urchins within the plot were removed by divers.

### Cluster analysis

The quadrat collections were initially evaluated using cluster analysis (Clifford & Stephenson, 1975). The similarity measure used was based on ash-free dry weight. A total of 20 quadrat groups were delimited (Fig. 2). Highest similarities occurred in group 3 which consisted of 8 quadrats from B 73, the year of the urchin grazing. These quadrats were collected 5 months after grazing. The high similarities can be attributed to selective grazing by the urchins, with surviving algal species either inaccessibly located, resistant to grazing, or seasonal annuals. Similarity was also increased by the evenness of biomass distribution amongst the species present.

The upper and middle sublittoral quadrat groups from site B (groups 2, 3, 4, 5 and 6) are distinctly separated, in the dendrogram, from the non-grazed quadrats of the same depths from sites B and S (groups 7 and 8). There is also an indication that lower littoral quadrats of B 73 (group 19) were influenced by grazing. B 74 and B 75 littoral quadrats clustered with the non-grazed littoral quadrats indicating a rapid recovery of the more lightly grazed littoral region.

The trend during recovery was to decrease similarity, with most non-grazed sublittoral quadrats showing similarity values of from 0.4 to 0.55.

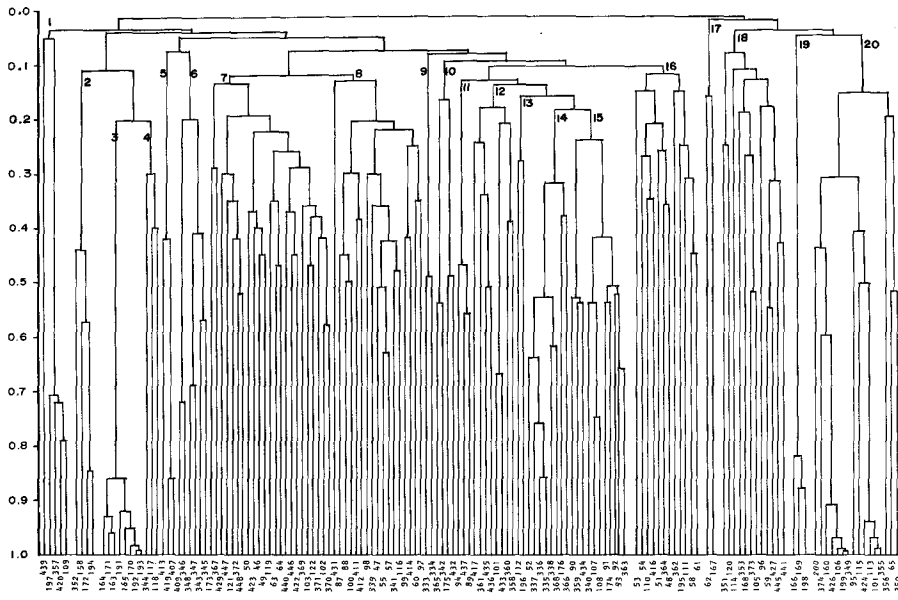


Fig. 2: Dendrogram based on cluster analysis of 154 quadrats collected from 7 site-year transects. The similarity index is plotted along the Y-axis and individual quadrats are numbered on the X-axis. Groups are delimited in bold type

$$S_{H'}$$

Quadrats from each transect were collectively analyzed using  $S_{H'}$  a similarity index based on shared species diversity (Hummon, 1974). Figure 3 is an  $S_{H'}$  similarity dendrogram of the 7 complete site-year data sets. It is evident from this figure that

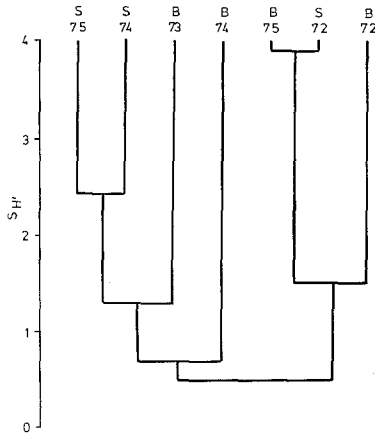


Fig. 3:  $S_{H'}$  similarity dendrogram for 7 site-year sample sets from sites B and S

B 75 was highly similar to S 72 and that the successional years of B 73 and B 74 were dissimilar from the other data sets. On the basis of these results it is hypothesized that S 72 represents a successional community with S 74 and S 75 representative of further successional development. B 72 is interpreted to be more mature than S 72 by similar reasoning.

One limitation with Figure 3 is that it includes the non-urchin grazed areas within each transect. In an attempt to improve the analyses the data sets were sub-sampled to include only samples between 1.5 and 8.5 m depth, the zone of maximum perturbation. The subsets were analyzed and the results are given in Figure 4. The unique nature of B 73 is obvious in this dendrogram as is the recovery period (B 74 and B 75). The site S collections show better affinities with each other than previously indicated and B 72 is more similar to site S than the urchin-grazed site B collections. Evident from this dendrogram is that 3 years following grazing the disturbed areas of site B are still not closely similar to the pre-disturbed condition or the non-grazed site.

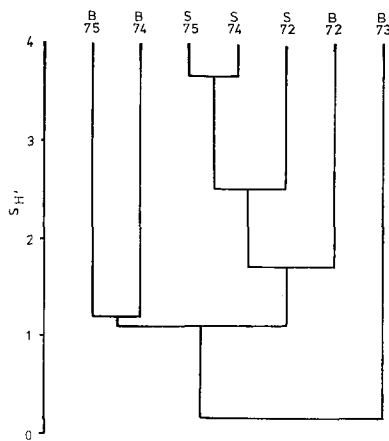


Fig. 4:  $S_H'$  similarity dendrogram for 7 site-year sample subsets from sites B and S. Each subset includes samples from 1.5 to 8.5 m depth

### Analysis of covariance

Analysis of variance was used to evaluate site and year variation for 4 dependent variables within and between sites. Quadrat variables examined were: mean number of species, mean dry weight, species diversity ( $H'$ ) and depth. In that several of these variables are known to be influenced by depth the analyses were also run using depth as a covariant. The results are given in Table 1. Duncan's Multiple Range Test ( $\alpha = 0.05$ ) was used to indicate significantly different site-year subsets.

Quadrat depths did not vary significantly within the sites due to the site selection procedures. However, the steeper slope at site S resulted in significant between-site differences in sampling depths although not supported by comparisons of individual

Table 1

Comparison of quadrat parameters for each site and year by Analysis of Variance (ANOVA), Analysis of Covariance<sup>1</sup> (COVAR) and Duncan's Multiple Range Test (alpha = 0.05)

Dependent variable	ANOVA	COVAR	Duncan subsets
BIO1 (4-years)			
1. $\bar{x}$ quadrat depth	—	n.a.	—
2. $\bar{x}$ number of species	p = 0.000001	—	(1) (2, 3, 4)*
3. $\bar{x}$ dry weight/m <sup>2</sup>	p = 0.05998	p = 0.00016	(2, 3) (3, 1, 4)
4. $\bar{x}$ species diversity (H')	p = 0.00001	p = 0.03430	(2) (4, 3, 1)
SIO2 (3-years)			
1. $\bar{x}$ quadrat depth	—	n.a.	—
2. $\bar{x}$ number of species	—	—	—
3. $\bar{x}$ dry weight/m <sup>2</sup>	p = 0.08009	p = 0.000001	(2) (3, 1)**
4. $\bar{x}$ species diversity (H')	—	—	—
Separate site-year transects			
1. $\bar{x}$ quadrat depth	—	n.a.	—
2. $\bar{x}$ number of species	p = 0.000001	—	(2, 4, 3) (3, 7, 6) (7, 6, 5, 1)***
3. $\bar{x}$ dry weight/m <sup>2</sup>	p = 0.00002	p = 0.000001	(2, 3, 6, 1, 4, 7) (6, 1, 4, 7, 5)
4. $\bar{x}$ species diversity (H')	p = 0.00011	p = 0.05219	(2) (4, 5, 3, 6, 7, 1)
<sup>1</sup> Covariant = depth			
* site-year code: 1 = B 72, 2 = B 73, 3 = B 74 and 4 = B 75			
** site-year code: 1 = S 72, 2 = S 74 and 3 = S 75			
*** site-year code: 1 = B 72, 2 = B 73, 3 = B 74, 4 = B 75, 5 = S 72, 6 = S 74 and 7 = S 75			

transects. Significant differences were obtained for the mean number of species, mean dry weight and H' at site B, but only for mean dry weight at site S.

Covariant analysis indicated a significant relationship between depth and mean quadrat dry weight, a commonly held and accepted conclusion which explains the only significant ANOVA result at site S. A similar, but not as strong, relationship was found for species diversity (H'). As expected the mean number of species per quadrat varied significantly between the grazed and non-grazed transects.

### Transect and species response to grazing

The site-year transect changes are summarized in Table 2. Although the COVAR results did not indicate significant changes at site S it is evident that all parameters, except mean number of species per quadrat, varied considerably during the sampling period with 1974 having considerably less biomass. The trends at site B, however, were more consistent. Following a pronounced decrease in all parameters in 1973 there was a general increase in all values over the next two years. Except for biomass, site B had not attained pre-grazing levels in any of the parameters by 1975.

A total of 160 taxa were identified at the two sites during the 4 year sampling period. The trends of these taxa are shown in Table 3. Following perturbation 60% of the species known to occur at site B in 1972 were eliminated as opposed to 25% elimination of site S species. Nearly half of the eliminated species at site B were recovered in 1974 and 1975 versus only 20% recovery at site S. Another 25% of the

Table 2  
Summary of site-year data

Parameters	BIO1				SIO2		
	1972	1973	1974	1975	1972	1974	1975
Total number of species	94	63	75	60	83	83	59
$\bar{x}$ Number of species/0.25 m <sup>2</sup>	21	10	14	13	27	25	27
$\bar{x}$ Dry weight (g/m <sup>2</sup> )	270	93	200	376	378	233	328
$\bar{x}$ Species diversity (H') (Shannon & Weaver, 1949)	1.90	0.77	1.66	1.60	1.63	1.80	1.76
Total dry weight (g)	9207	3449	7007	13174	13236	8182	11504

Table 3  
Summary of species representation, based on standardized number of occurrences, for BIO1 and SIO2 (1972-1975)

Trend	Site	
	BIO1	SIO2
No change	5	24
Decreased	11	20
Decreased, recovered	13	2
Eliminated	28	17
Eliminated, recovered	12	3
Eliminated, recovered, increased	12	1
Eliminated, recovered, eliminated	6	0
Increased	7	15
Variable	5	6
Transients: 1973 only	16	n.a.
1974 only	7	16
1975 only	12	15
73 + 74 only	8	n.a.
74 + 75 only	0	2
Not found at site	18	39
Total number of taxa	160	160

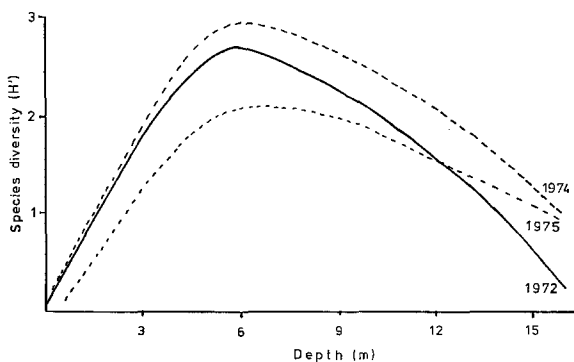


Fig. 5: Trends in the relationship between species diversity (H'), depth and year at site S (non-grazed)



B 72 species declined in occurrence while the remaining 15 % increased in number or exhibited no change. 50 % of the site S species increased in occurrence or exhibited no change while 25 % decreased. Twenty-four new taxa occupied site B in 1973, 33 % of which were also collected in 1974.

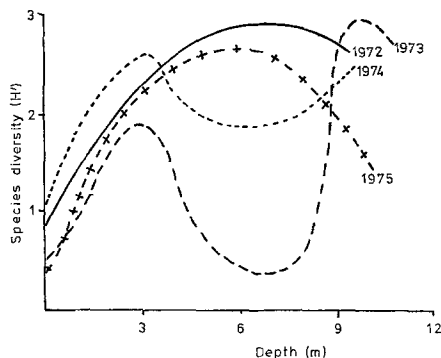


Fig. 6: Trends in the relationship between species diversity ( $H'$ ), depth and year at site B (grazed)

Generalized trends in species diversity ( $H'$ ) as related to quadrat depth are given in Figures 5 and 6. Both figures indicate a maximum  $H'$  occurs at about 6 m below MWL and  $H'$  follows a similar curve in all of the non-grazed transects. The shallower sampling depths at site B are responsible for the truncated curves in Figure 6. Following grazing the site B curve (1973) was sharply depressed in the areas of maximum impact. By 1974 recovery had occurred at shallower depths with the depressed region of the curve largely the result of *Nereocystis* development accompanied by high biomass values invested in this, a single, species.

### Community composition

The 160 macrophyte taxa collected were arbitrarily categorized into 10 groups on the basis of taxonomic class and growth form. The total number of occurrences and total dry weight per  $m^2$  were determined by group and transect and the resulting matrices standardized to eliminate differences arising from variations in quadrat number per transect. These values were summed, percent by group determined and the latter values used to prepare Figures 7 and 8. Mean dry weight per occurrence was determined by dividing total dry weight by total number of occurrences for each group and transect with the results given in Table 4.

Figure 7 indicates that the occurrence of green algae varies only slightly from year to year and site to site. The contribution to the total weight, as shown in Figure 8, is significantly greater at site B in the first and second years following perturbation. Mean dry weight per occurrence increased 15-fold from 1972 to 1973, declining to 8-fold by 1974.

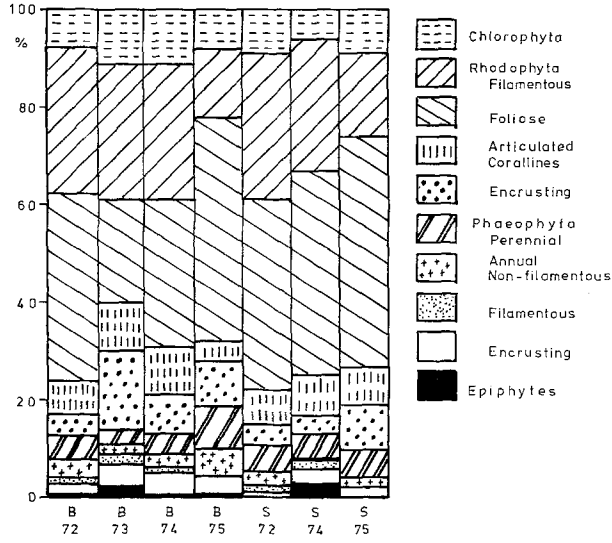


Fig. 7: Percent total number of occurrences for 10 macrophyte groups and 7 site-year sample sets

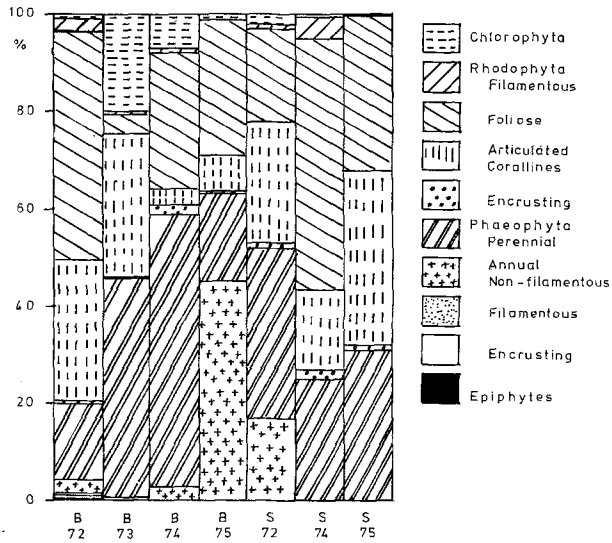


Fig. 8: Percent total dry weight for 10 macrophyte groups and 7 site-year sample sets

Filamentous red algae, although occurring frequently, contribute a maximum of 4% of the total biomass in the study areas. The fluctuations of their mean dry weight per occurrence at site B indicate that they were also influenced by the grazing and recovered gradually.

Foliose red algae dominated the upper sublittoral region prior to urchin grazing and their occurrence and contribution to the total biomass decreased dramatically in 1973. The mean dry weight per occurrence in 1973 was only 13 % of the previous year's. By 1975 biomass levels had surpassed the pre-grazing level. Observations suggest that the recovery was accompanied by a significant increase in individual performance in that the individual plants were noticeably larger in 1974 and 1975.

Table 4

Mean dry weight per occurrence, in grams, for each macrophyte group and site-year transect

Algal groups	BIO1				SIO2		
	1972	1973	1974	1975	1972	1974	1975
Chlorophyta	1.26	16.4	8.91	4.16	4.1	1.4	1.3
Rhodophyta							
Filamentous	0.8	0.1	0.4	0.5	0.7	1.9	0.2
Foliose	14.63	1.88	12.98	16.27	9.1	14.2	12.3
Articulated corallines	53.9	28.12	4.68	54.6	65.4	24.7	87.5
Encrusting	1.5	0.2	3.63	2.2	4.7	6.5	2.4
Phaeophyta							
Perennial	39.8	130.0	186.1	51.5	107.7	52.0	100.9
Annual, non-filamentous	8.8	0.01	11.6	242.9	93.6	0.6	1.2
Filamentous	0.40	0.003	1.38	—	0.2	0.3	0.4
Encrusting	0.64	0.03	0.2	1.8	5.2	1.8	0.2
Epiphytes (all classes)	0.005	0.001	0.03	0.0004	0.006	0.1	—

Articulated coralline algae exhibited a non-significant decline in 1973, although the decrease in mean weight per occurrence suggests that this group was also grazed. Himmelman & Steele (1971) noted *S. droebachiensis* grazing of coralline algae. The variations in coralline algae occurrence and biomass are probably indicative of the more patchy nature of their distribution when compared to filamentous and foliose forms. Encrusting red algae exhibit similar variations and, in addition, are poorly sampled by the techniques employed in this study.

Perennial brown algae varied non-significantly in occurrence, largely because they occurred outside the areas of major grazing impact. They were, however, increasingly important in their contribution to the total community biomass. In that the actual weights did not change significantly this increase is more a reflection of a decline in other groups than an increase in this group. At site B occurrence and total weight increased in 1974, followed by increased recruitment and a lower mean dry weight in 1975. The contribution of perennial brown algae to the total transect biomass decreased in 1975, largely as a result of an increase in annual brown algae.

Annual brown algae, notably the large kelp *Nereocystis luetkeana*, underwent the largest variations of any group following grazing. By 1975 the total weight of annual brown algae was 2000 times the B 72 level and 60,000 times the B 73 biomass. The increase in biomass was accompanied by major changes in community structural complexity caused by the development of an upper, *Nereocystis*, surface canopy between 4 and 8 m depth. Annual brown algae exhibited a steady decline at site S during the study period.

The remaining groups did not contribute significantly to the community biomass, although removal of understory species appeared to improve conditions for encrusting forms. Epiphyte data exhibit considerable variation probably as a result of difficulties in consistently sampling these small and microscopic forms.

Community recovery

The contribution of the 40 most important algal species during succession was evaluated by determining the periods of maximum species importance (frequency x

Table 5

Periods of maximum species importance values following perturbation (solid lines). Dashed lines indicate periods of increasing or decreasing values

Species	YR 1	YR 2	YR 3	YR 4	YR 5	YR 6
<i>Enteromorpha</i> sp.	—					
<i>Desmarestia ligulata</i>	—					
<i>Polysiphonia pacifica</i>	—	---				
<i>Ulvaria fusca</i>	—	---				
<i>Ulva fenestrata</i>	—	---				
<i>Odonthalia floccosum</i>	—		---			
<i>Calliarthron tuberculosum</i>	—		---			
<i>Peyssonelia pacifica</i>	—			---		
<i>Amplisiphonia pacifica</i>	---		---			
<i>Gymnogongrus leptophyllum</i>	—		---			
<i>Laminaria</i> sp.	—			---		
<i>Nereocystis luetkeana</i>	—			---		
<i>Antiithamnion defectum</i>	—				---	
<i>Sargassum muticum</i>	—			---		
<i>Microcladia borealis</i>	—			---		
<i>Botryoglossum rüprechtiana</i>	—				---	
<i>Ceramium pacificum</i>	—				---	---
<i>Iridaea cordata</i> v. <i>cordata</i>	---					
<i>Ralfsia fungiformis</i>	---				---	
<i>Rhodomenia pertusa</i>	---					
<i>Plocamium coccineum</i> v. <i>pacificum</i>	---					
<i>Rhodoglossum roseum</i>	---					
<i>Callophyllis violacea</i>	---					
<i>Pterosiphonia dendroidea</i>	---					
<i>Platythamnion villosum</i>	---					
<i>Constantinea subulifera</i>	---					
<i>Corallina officinalis</i> v. <i>chilensis</i>	---					
<i>Rhodoptilum plumosum</i>	---					
<i>Callophyllis flabellulata</i>	---					
<i>Herposiphonia plumula</i>	---					
<i>Bonnemaissonia nootkana</i>	---					
<i>Laurencia spectabilis</i>	---					
<i>Agarum fimbriatum</i>	---					
<i>Gelidium purpurascens</i>	---					
<i>Platythamnion pectinatum</i>	---					
<i>Pterosiphonia gracilis</i>	---					
<i>Corallina frondescens</i>	---					
<i>Prionitis lanceolata</i>	---					
<i>Nienburgia andersoniana</i>	---					

mean biomass) for a 6-year period (Table 5). Table 5 is predicated on the assumption that B 76 would be equal to S 72. The species are arranged on the basis of the first year of high importance value and the duration of high importance values. As a result the table divides into four groups of species corresponding to the year of initially achieving a high importance value.

The species having high importance values in year 1 were predominantly members of the class Chlorophyceae and species which possessed some grazing resistant feature such as an encrusted perennating structure or calcareous thallus. The Chlorophyceae species are mainly annuals whose occurrence was little influenced by the urchin grazing, but which benefited greatly from the removal of potential competitors.

The second year of succession is marked by the development of upperstory species, such as *Laminaria* sp. and *Nereocystis luetkeana*, in the mid-sublittoral. Several of the lower littoral – upper sublittoral species, notably *Amplisiphonia pacifica*, *Sargassum muticum* and *Botryoglossum ruprechtiana*, are the initial indicators of what will become a foliose red dominated upper-sublittoral community. The latter two species are typically found in the mature community in much smaller quantities.

Major upper-sublittoral development occurs in year 3 when the two dominants of this community, *Constantinea subulifera* and *Iridaea cordata* var. *cordata* attain their pre-impact levels. *Plocamium coccincum* v. *pacificum* attains its maximum importance value at slightly greater depths. These developments are accompanied by understory development at all depths.

Species reaching maximum importance values in year 4 are predominantly representatives of the Laminarian deep-water community and include *Agarum fimbriatum* and *Laurencia spectabilis* as well as a number of smaller and filamentous forms. Continued development of the upper sublittoral community is indicated by increased importance of *Prionitis lanceolata*, *Corallina frondescens* and *Herposiphonia plumula*.

It appears that community re-establishment preceeds from shallow to deeper depths and, hence, that recovery times vary in relation to depth. The upper sublittoral community reaches pre-urchin biomass and diversity levels within 3 years while this is not the case for deeper sublittoral communities until at least the 4th year. Further, the middle sublittoral is dominated by *Nereocystis luetkeana* which attains maximum biomass in the 3rd year and then undergoes a gradual decline until eliminated in the latter stages of development. The time required to eliminate *Nereocystis*, or decrease it to pre-urchin levels, is unknown. It would appear to dominate the middle sublittoral community for a period of 4 to 6 years.

## DISCUSSION

Previous investigations of algal succession and recovery following perturbation have indicated rapid development of macrophyte communities. Paine & Vadas (1969) observed algal succession for periods of up to 3 years using urchin removal and wire exclosures to provide urchin-free environments. They noted an immediate increase in speciation followed by the establishment of a canopy of larger algae which ultimately resulted in most of the biomass invested in a single species. The final step was the

establishment of an understory of smaller algae. The latter being more pronounced in the littoral areas. Jones & Kain (1967) also observed a rapid increase in macrophytes the first year with *Laminaria* sp. development the following year. Development on artificial substrates was examined by Foster (1975) in a *Macrocystis pyrifera* bed. He concluded that algal diversity (H), number of species, and evenness (J) all reached a peak within 100 to 200 days regardless of the time blocks were started. The diversity and number of species then fell as ephemeral species disappeared. Once gone they did not reappear, reportedly because of their inability to compete with perennial species.

In general these studies indicate a rapid recolonization of available substrate, initially by fast growing ephemerals or opportunistic species followed by perennial forms. The latter occurring in the latter part of the first year and attaining dominance in the second year. There has been little consideration of potential differences between previously colonized surfaces and new surfaces as provided in plate experiments. Historical baseline data has typically been lacking and, as a result, the conclusions are often difficult to interpret or apply outside of the specific study area.

At present our knowledge of benthic macrophyte communities and their interactions is limited and it is difficult to conceptually formulate successional events. Fishelson (1977) presents a diagrammatic "model" of community dynamics consistent with the present findings. His model consists of a period of succession terminating in an "ecological climax" and followed by an "enrichment period" during which new species are gradually added to the community. Assuming, on the basis of Figures 3 through 9, that B 76 would be comparable to S 72 it would appear that in the study area a minimum of 4–6 years is required to attain "ecological climax" in the mid-sublittoral regions dominated by *Agarum* or *Laminaria*. The shallower sublittoral communities appear to develop somewhat faster, requiring 3 to 5 years. Fishelson's term is used here to indicate the restoration of community parameters to pre-urchin levels and not, necessarily, the restoration of the exact, pre-urchin, community. The major species in the pre-urchin communities have, however, re-established their dominance by this time. A further 4 or more years appears to be required for "enrichment".

The increase in *S. droebachiensis* populations in the Strait of Georgia probably resulted from a favorable plankton bloom in the spring of 1969, following the suggestions of Himmelman (1976) as to factors initiating spawning, coupled with an unusually long period of cool water temperatures (Foreman & Lindstrom, 1973). Stephens (1972) concluded that cold winters may extend the fertility period and improve larval survival with the upper limit for larval development being about 10° C. Development time followed an inverse logarithmic relationship with temperature in the range of –1 to 9° C. The water temperatures recorded for the Strait by Hollister & Sandnes (1972) indicate that the Strait must normally be marginal for *S. droebachiensis* development and that temperature conditions in the spring of 1969 were a record 20-year low.

The marginal suitability is also reflected in the previously localized distributions of *S. droebachiensis* populations and irregular age class distributions which indicate sporadic recruitment. It is, however, important to recognize that present population levels in the Strait are considerably higher than pre-1969 and, thus, the potential for further outbreaks is enhanced.

The primary effect of urchin grazing at site B was the selective elimination of 60 percent of the macrophytes known to have occurred in the area the preceding year. Foliose macrophytes were preferentially removed, showing the greatest decline in occurrence and biomass. The next most effected group were the filamentous forms followed by articulated corallines and encrusting forms. The latter did not appear to be influenced adversely and there is some indication that they benefited from the removal of canopy species. Ephemeral species also benefited from the grazing. At site B significant declines (Tables 1 and 2) were noted for mean number of species per quadrat, down 50 %; mean dry weight per m<sup>2</sup>, down 65 %; total dry weight, down 60 %; and H', down 60 %.

During recovery the initial phases were dominated by ephemeral species (predominantly Chlorophyceae) and transient or successional species which occupied the substrate for 1 or 2 years before being eliminated by competition with other species or environmental modification (probably shading). A total of 43 transient species were noted, or about 35 % of the total number of species found at site B. This compares with 33 transient species at site S (Table 3). It would appear that many of the transients are species with sporadic reproduction or rare in occurrence, and that only a few are true successional forms. By the second year many of the original species eliminated by grazing from site B had returned and other species were increasing in abundance. This trend continued through 1975, the last year of the study. Total biomass during this period doubled each year. However, biomass was the only parameter to recover or exceed pre-urchin grazing levels by 1975. This suggests a much longer recovery time than that indicated by the previously mentioned authors. This conclusion is supported, indirectly, by the fact that 28 species known to be in the study area in 1972 have not been collected since versus 17 at site S.

The longer recovery time is also indicated by the continued presence of *Nereocystis luetkeana* which, because of its dominant role in community structure exerts a strong influence on understory development. Three years after perturbation this species is still increasing in biomass whereas Paine & Vadas (1969) noted that it dominated their sites the first year only. This difference could be a result of their method which utilized selected habitats for experimentation.

Undoubtedly several factors are influential in establishing recovery rates. Timing and quantity of spore release as well as effective dispersal distance are important considerations. Observational data indicate that reproduction in some macrophyte species may only occur in favorable years while the existence of long-lived resistant stages cannot be overlooked. The present level of knowledge is not-sufficient to permit a detailed discussion of this problem.

Perhaps the most important modification at site B is that of *Nereocystis luetkeana*. This is the only large, buoyed, kelp species in the Strait of Georgia and its role in providing upper strata to the benthic macrophyte community and importance to benthic primary production is of interest. In 1972 *Nereocystis* was present, in roughly equal quantities, at both site B and S. The successional tendency at site S was to eliminate *Nereocystis* and only a few plants were observed in the study plot in 1974, 1975, and 1976. At site B this species was eliminated by urchin grazing and very few

plants were observed in 1973. This was followed by an increase in 1974 and a dramatic increase in 1975.

The presence of this species appears to be contingent upon disturbance or perturbation of the understory environment, probably because of a high light requirement for gametophyte or juvenile sporophyte development. Understory development effectively shades out this species. It is somewhat paradoxical that the final, mature community in areas capable of supporting *Nereocystis* growth, is less stratified than the successional community. Such a reduction in stratification and biomass is not considered to be a "normal" successional trend by most authors. The *Nereocystis* community is unique in this regard because of the annual life-cycle of the dominant species and it is this feature which leads to its elimination.

If the presence of *Nereocystis* is dependent on disturbance then its continued presence in an area is indicative of a continual disturbance or perturbation of the understory community. Surveys conducted in 1946, B. C. Research Council (1948) indicated that *Nereocystis* density in the Strait of Georgia was considerably higher than present levels and, thus, that at least the last decade has been relatively disturbance free with no large scale urchin outbreaks. This interpretation is consistent with eyewitness accounts which imply that a minor urchin outbreak occurred 15 to 20 years ago. It would appear then that urchin outbreaks occur irregularly and result from combinations of favorable environmental conditions. The outbreaks are followed by a large increase in benthic primary production which peaks 3 to 6 years after the maximum urchin impact has occurred and the urchin populations have declined. This is followed by a period of biomass decline and species enrichment with about 8 to 10 years required to complete the cycle.

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#### LITERATURE CITED

- Breen, P. A. & Mann, K. H., 1976. Changing lobster abundance and the destruction of kelp beds. *Mar. Biol.* **34**, 137-142.
- British Columbia Research Council (ed.), 1948. Marine plants of economic importance in British Columbia coastal waters, Part II. *Tech. Bull. Br. Columb. Res. Coun.* **10**, 1-37.
- Burrows, E. M., 1971. Assessment of pollution effects by the use of algae. *Proc. R. Soc. Lond. (B)* **177**, 295-306.



- Castric-Fey, A., 1974. Les peuplements sessiles du benthos rocheux de L'Archipel de Glenan (Sud Bretagne) ecologie descriptive et experimentale. Thèse, Univ. Paris, 333 pp.
- Clifford, H. T. & Stephenson, W., 1975. An introduction to numerical classification. Acad. Press, New York, 229 pp.
- Fishelson, L., 1977. Stability and instability of marine ecosystems, illustrated by examples from the Red Sea. *Helgoländer wiss. Meeresunters.* **30**, 18–29.
- Foreman, R. E. & Lindstrom, S. C., 1973. Urchin survey report. Rep. Fish. Res. Bd Pacif. biol. Stn **1973**, 1–59.
- Foster, M. S., 1975. Algal succession in a *Macrocystis pyrifera* forest. *Mar. Biol.* **32**, 313–329.
- Himmelman, J. H., 1976. Factors regulating the reproductive cycles of some west coast invertebrates. Thesis, Univ. of British Columbia, Vancouver, 128 pp.
- & Steele, D. H., 1971. Foods and predators of the green sea urchin *Stronglyocentrotus droebachiensis* in Newfoundland waters. *Mar. Biol.* **9**, 315–322.
- Hollister, H. J. & Sandnes, A. M., 1972. Sea surface temperatures and salinities at shore stations on the British Columbia coast 1914–1970. *Environm. Can. pacif. mar. Sci. Rep.* **72-13**, 1–93.
- Hummon, W. D., 1974.  $S_H'$  A similarity index based on shared species diversity, used to assess temporal and spatial relations among intertidal marine gastrotricha. *Oecologia* **17**, 203–220.
- Jones, N. S. & Kain, J. M., 1967. Subtidal algal colonization following the removal of *Echinus*. *Helgoländer wiss. Meeresunters.* **15**, 460–466.
- Mann, K. H., 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic Coast of Canada. I. Zonation and biomass of seaweeds. *Mar. Biol.* **12**, 1–10.
- 1977. Destruction of kelp-beds by sea-urchins: A cyclical phenomenon or irreversible degradation? *Helgoländer wiss. Meeresunters.* **30**, 455–467.
- Miller, R. J. & Mann, K. H., 1973. Ecological energetics of the seaweed zone in a marine bay on the Atlantic Coast of Canada. III. Energy transformations by sea urchins. *Mar. Biol.* **18**, 99–114.
- Paine, R. T. & Vadas, R. L., 1969. The effects of grazing by sea urchins, *Stronglyocentrotus* spp., on benthic algal populations. *Limnol. Oceanogr.* **14**, 710–719.
- Price, J. H., 1973. Advances in the study of benthic marine algae since the time of E. M. Holmes. *Bot. J. Linn. Soc.* **67**, 47–102.
- Shannon, C. E. & Weaver, W., 1949. The mathematical theory of communication. Univ. of Illinois Press, Urbana, 117 pp.
- Stephens, R. E., 1972. Studies on the development of the sea urchin *Stronglyocentrotus droebachiensis*. I. Ecology and normal development. *Biol. Bull. mar. biol. Lab., Woods Hole* **142**, 132–144.
- Vadas, R. L., 1968. The ecology of *Agarum* and the kelp bed community. Ph. D thesis, Univ. of Washington, Seattle, 282 pp.

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