

THE EFFECTS OF GRAZING BY LITTORINID
GASTROPODS ON THE STRUCTURE OF ALGAL
COMMUNITIES IN NEWFOUNDLAND TIDEPOOLS

CENTRE FOR NEWFOUNDLAND STUDIES

**TOTAL OF 10 PAGES ONLY
MAY BE XEROXED**

(Without Author's Permission)

MARK D. HAWRYLUK



THE EFFECTS OF GRAZING BY LITTORINID GASTROPODS ON THE
STRUCTURE OF ALGAL COMMUNITIES IN
NEWFOUNDLAND TIDEPOOLS

BY

© MARK D. HAWRYLUK B.Sc. Hon.

A thesis submitted to the School of Graduate Studies
in partial fulfilment of the requirements
for the degree of
Master of Science

Department of Biology
Memorial University of Newfoundland
September 1992

Revised September 1995

St. John's

Newfoundland



National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

The author has granted an irrevocable non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of his/her thesis by any means and in any form or format, making this thesis available to interested persons.

L'auteur a accordé une licence irrévocable et non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de sa thèse de quelque manière et sous quelque forme que ce soit pour mettre des exemplaires de cette thèse à la disposition des personnes intéressées.

The author retains ownership of the copyright in his/her thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without his/her permission.

L'auteur conserve la propriété du droit d'auteur qui protège sa thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

ISBN 0-612-13902-6

Canada

ABSTRACT

Grazing by the littorinid gastropods, *Littorina littorea* and *L. saxatilis*, significantly affected the structure of algal communities in 10 intertidal pools on the Avalon Peninsula of insular Newfoundland. Pools were sampled approximately monthly between February and November of 1987. Diversity of the algal communities was highest at intermediate levels of grazing and lowest when a given species of algae formed a monoculture in the absence of grazing. Diversity was also low in pools with very large grazer populations which overgrazed the macrophytes. The diversity was relatively stable in moderately and heavily grazed pools but fluctuated widely in lightly grazed pools.

The greatest effect that the grazers had on the algae was to increase the amount of bare substrate and calcareous algae by removing the filamentous and blade-forming algae. *Littorina littorea* and *Littorina saxatilis* prevented blade-forming algae from establishing by grazing settling propagules but only *L. littorea* was able to significantly reduce the abundance of the adult thallus of filamentous algae which settled before the grazers became active in the spring.

The population of *L. saxatilis* increased to a peak in mid summer as individuals moved from nearby upper intertidal emergent substrata and offspring were produced in the pools. Large populations of *L. littorea* in two of the pools declined during the course of the study. The cause of this decline is not known.

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Dr. Don Steele, and my supervisory committee, Dr. A. Whittick and Mr. R. Hooper for their support and encouragement throughout this study. Assistance with the field work was generously given by Jill Bugden, Jill Hambrook, and Suzanne Nurse. The Williams family of Bay Bulls and Mr. D. LeGrow graciously provided me access to my study sites across their land. I would also like to thank Dr. P. Schwinghamer whose comments greatly improved this thesis.

Financial support for this study came from NSERC grants awarded to Dr. Don Steele and from a Memorial University Graduate Student Fellowship.

CONTENTS

ABSTRACT	ii
ACKNOWLEDGEMENTS	iii
CONTENTS	iv
LIST OF TABLES	v
LIST OF FIGURES	vi
INTRODUCTION	1
MATERIALS AND METHODS	6
Site Descriptions	6
Bauline	6
Bay Bulls	9
Portugal Cove	10
Sampling Techniques	10
Statistical Analysis	13
RESULTS	16
The Grazer Community	16
Patterns of Algal Abundance	17
Blade-forming Algae	17
Filamentous Algae	23
Encrusting Algae	26
Calcareous algae	28
Bare Rock	29
Effects of Littorinid Grazers on Species Diversity	31
Physical Characteristics of Tidepools	33
DISCUSSION	35
Summary	46
REFERENCES	48
APPENDIX A	53

LIST OF TABLES

Table 1. Physical characteristics of individual tidepools	8
Table 2. Species of macrophytic algae in each morphological group	12
Table 3. Mean grazing index and number of grazers per m ² \pm 1 sd grouped by grazing intensity	14
Table 4. Analysis of variance of % cover of morphological groups and bare rock between levels of grazing intensity	19

LIST OF FIGURES

Figure 1. Location of study sites and individual pools. All maps are oriented with true North at the top of the page.	7
Figure 2. Mean abundance of littorinids on each sampling date at Bay Bulls Pool 1 and Bauline Pool 1	18
Figure 3. Mean abundance of algae in each morphological group and bare rock at each grazing intensity level over the entire study period	20
Figure 4. Mean abundance of blade-forming algae at each grazing intensity level per month	22
Figure 5. Mean abundance of filamentous algae at each grazing intensity level per month	25
Figure 6. Mean abundance of encrusting algae at each grazing intensity level per month	27
Figure 7. Mean abundance of calcareous algae at each grazing intensity level per month	30
Figure 8. Shannon Diversity Index (H') on each sampling visit for each tidepool	32

INTRODUCTION

Although little work has been published on community structure in the Newfoundland intertidal zone (Pittman 1974, Hooper 1981, Bolton 1983, Steele 1983, Hooper and Whittick 1984), a great deal of information has been accumulated concerning factors affecting the community structure of other temperate rocky shores. Invertebrate grazers have been shown to be of primary importance in determining the structure of benthic algal communities. The most important grazers in the western North Atlantic are sea urchins in the lower intertidal and subtidal (Lubchenco and Menge 1978, Chapman 1981) and gastropods, including limpets and littorinids, in the middle and upper intertidal zone (Menge 1975, Lubchenco 1978, Branch 1981). Thorough reviews of marine plant-herbivore interactions have been done by Lubchenco and Gaines (1981) and Hawkins and Hartnoll (1983).

The focus of the present study is to determine the effects of littorinid gastropods on the algal community in tidepools on the east coast of Newfoundland. Although similar in many respects to benthic communities in New England tidepools, the tidepool communities in the present study experience lower water temperatures in higher energy environments which may cause some interesting differences. Lubchenco (1978) showed that grazing by *Littorina littorea* influenced algal diversity in New England tidepools. In the absence of grazers, a few species of fast growing ephemeral algae became very abundant at the expense of competitively inferior species, resulting

in a low diversity. On the other hand, overgrazing by large numbers of *L. littorea* removed most species and also resulted in a low diversity. In pools with intermediate numbers of grazers, competitive exclusion was prevented and diversity was high. Sze (1980) found similar results in high tidepools at the Isles of Shoals.

To a large extent, the effect that a grazer has on algal community structure is dependent on the food preferences of the herbivore. Food preference can be divided into two components: edibility and attractiveness (Watson and Norton 1985). Studies which measure feeding rates of herbivores on different species of algae examine the edibility aspect of feeding preference (for example, Barker and Chapman 1990, Inrie *et al.* 1989). Edibility is influenced by nutritional value and chemical and structural antiherbivore defenses such as polyphenols (in fucoids) and tough cell walls (in calcareous algae). Lubchenco (1978) did the classic attractiveness experiment where two algal species were added to a tank of *L. littorea* and the number of periwinkles observed on each species was counted after a given time had elapsed. This type of experiment incorporates attractiveness of a given species of algae as a habitat as well as a potential food source. Attractiveness is influenced by algal morphology as well as the factors influencing edibility. It therefore makes sense to combine algae with similar morphological characteristics into groups to investigate the effects of grazing on them.

In the present study, the macroalgae were divided into 4 morphological groups: blade-forming, filamentous, encrusting and calcareous algae based on their gross

morphology as it relates to resistance to grazing by littorinid gastropods. The blade-forming and filamentous algae were similar in that both groups were mostly comprised of short lived (ephemeral) species. The high ratio of photosynthetic tissue to structural tissue, high nutritive value and lack of chemical or structural defenses against herbivory have been shown to make these species attractive to grazers (Littler and Littler 1980, Hawkins and Hartnoll 1983) as demonstrated by Lubchenco (1978), Steneck and Watling (1982), Watson and Norton (1985), and Imrie *et al.* (1989). The filamentous algae were simply defined as those species with a non-corticated upright filamentous thallus. Steneck and Watling (1982) demonstrated that the taenioglossan radula of *Littorina* is particularly well adapted to grazing filamentous algae. Many species of algae pass through a grazer sensitive filamentous stage during early development before taking on a more grazer resistant form (Steneck and Watling 1982).

The blade-forming algae are a more heterogeneous group comprised of ephemeral thin sheetlike or tubular forms (eg *Monostroma grevillei* and *Scytosiphon lomentaria*), corticated ephemerals (eg *Chordaria flagelliformis*), and one upright perennial (*Fucus distichus distichus*). Most of the species in this group with the exception of *Fucus* are also highly or moderately preferred species of *L. littorea* (Lubchenco 1978).

In contrast, the calcareous and encrusting species have structural and/or chemical defenses which make them less susceptible to damage by grazing. In fact,

many of these grazer resistant forms have been shown to benefit directly or indirectly from grazing. *Clathromorphum circumscriptum* requires moderate levels of grazing to prevent epiphytic fouling of the thallus (Steneck 1982). Encrusting algae dominate in protected beaches in New England where grazing by *L. littorea* removes all of the upright algae (Bertness *et al.* 1983). Both species of calcareous algae in the present study (*Clathromorphum circumscriptum* and *Corallina officinalis*) are tough red algae with calcium carbonate in the cell walls. *C. circumscriptum* was considered "calcareous" rather than "encrusting" due to the increased grazer resistance provided by the calcification of its cell walls. Steneck and Watling (1982) have shown that the radula of *L. littorea* is poorly designed for excavating calcareous algae since the teeth have not been chemically hardened as have the radular teeth of *Notoacmaea testudinalis* which preferentially grazes calcareous algae.

The encrusting algae in the present study were represented mostly by *Hildenbrandia rubra* and a brown crust. Since it was difficult to determine in the field if the latter was a valid species of *Ralfsia* or an encrusting phase of *Scytosiphon lomentaria* or *Petalonia fascia*, it will hereafter be referred to as "*Ralfsia*" (*sensu* Lubchenco and Cubitt 1980). Small tightly packed cells throughout the thallus and antiherbivore chemical compounds make both encrusting species resistant to grazing (Bertness *et al.* 1983).

Scouring by pack ice in the late winter and early spring of 1987 removed almost all of the upright macrophytes from the tidepools surveyed in this study. Then,

a lens of freshwater trapped under the pack ice killed most of the invertebrates in the intertidal zone except the littorinids which survived by tightly sealing their aperture with the operculum. These events provided me with an opportunity to study the effects of grazing by *L. littorea* and *L. saxatilis* on the recolonization of tidepools by macroalgae.

Tidepools of intermediate size in the middle to upper intertidal were chosen at 3 sites, to keep the physical differences between pools as small as possible. Low intertidal pools were impossible to sample frequently due to the small tidal amplitude (0.9 m (Anonymous 1987)) and relatively exposed locations of the study sites. To avoid the theoretical and practical problems of caged manipulations (see Hawkins and Hartnoll 1983), pools were selected which varied in the numbers of *Littorina littorea*, the major grazer on rocky shores of the Northwest Atlantic (Menge 1975).

Based on the observations of grazer algal interactions in a functional form framework, the following hypotheses were tested:

1. The abundance of blade-forming and filamentous algae will be inversely related to grazing pressure.
2. The abundance of encrusting and calcareous algae will be directly related to grazing pressure.
3. Diversity will be highest in moderately grazed pools and lower in heavily and lightly grazed pools.

MATERIALS AND METHODS

Site Descriptions

The study sites are all located on the coast of the Avalon Peninsula, Newfoundland, Canada in the Western North Atlantic. They are in areas of sloping bedrock which drops off into 10 to 20 m of water just past the low water mark. This type of habitat provided a sufficient number of suitable tidepools. The three study sites were at Bauline (47° 44' N 52° 50' W) and Portugal Cove (47° 38' N 52° 52' W) in Conception Bay and Bay Bulls (47° 18' N 52° 47' W) on the east coast (Figure 1.).

Pools were selected on the basis of accessibility, relative position in the littoral zone, size, and floral and faunal community (Table 1). Accessibility was of obvious importance since the pools would be sampled monthly from spring until fall. The pools were located in the mid to upper intertidal zone; extreme upper and lower intertidal pools were not studied. Pools of intermediate size were selected since these were the most common and had the best developed algal communities. Small pools (< 0.75 m in length) were susceptible to large salinity changes due to evaporation and rainfall, and to large temperature fluctuations. Large pools (> 5 m in length) were too rare to be included. All tidepools at the three study sites within this size and littoral range were included in the study.

Bauline

Bauline is the most exposed site, with a northwest aspect. The shore is open, backed by high, steep cliffs with a more gently sloping area extending to Mean Low

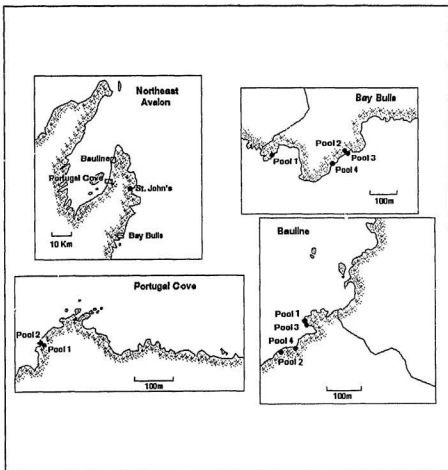


Figure 1. Location of study sites and individual pools. All maps are oriented with true North at the top of the page .

Table 1. Physical characteristics of individual tidepools.¹

	Tidepool									
	<i>Light</i>				<i>Moderate</i>				<i>Heavy</i>	
	BB3	BB4	PC1	BB2	PC2	BA2	BA4	BA3	BB1	BA1
Max. length (m)	2.0	1.5	3.1	1.4	1.3	0.8	1.2	1.1	1.7	4.9
Max. width (m)	0.7	0.9	1.6	0.8	0.7	0.5	0.8	0.6	1.2	3.3
Max. depth (cm)	18	27	20	15	17	11	36	24	23	24
Height (m) above M.L.W.	1.0	0.9	1.3	1.3	1.4	0.9	0.9	1.6	1.3	1.2
Max. temperature (°C)	15	15	20	24	25	25	22	20	19	27

¹ Pools in order of increasing grazing intensity.

Water (MLW) and then dropping rapidly to ~20 m depth. Four pools varying in exposure to wave action were sampled at this site; Pool 1 (BA1) and Pool 2 (BA2) are more exposed, Pool 3 (BA3) and Pool 4 (BA4) are less exposed.

Bauline Pool 1 is the largest pool. A 2 m high wall on its southeast side shades about half of the pool for most of the morning. Pool 3 is smaller, located in a 1 m depression in the bedrock. Its recessed position provides more protection than it would otherwise have. Pool 4 is located in a small cove in the coastline, and is protected by a few large boulders. Bauline Pool 5 is located in a very exposed position on the sloping bedrock and is exposed to insolation for most of the day. All of these pools were regularly inundated by swells during sampling at low tide.

Bay Bulls

The Bay Bulls site has more varied topography than the Bauline site. Overall, it is a slightly less exposed site, having a south aspect, but the range of exposure among the four pools is much greater than at Bauline. The least exposed pool in Bay Bulls, Pool 1 (BB1) is situated in a cove within the bay and is protected by a small spit of bedrock directly seaward of the pool. The other 3 pools are located on a more exposed shore made up of alternating surge channels and spits of bedrock outside of the cove. There are also many large boulders on this gently sloping shore. Pool 2 (BB2) is the least exposed of the outer pools being located at the head of one of the surge channels and protected by a large boulder. Pool 4 (BB4) is the next most exposed, located near the mouth of a protected surge channel. The most exposed pool,

Pool 3 (BB3), is located at the end of one of the spits between the surge channels. It was regularly inundated by swells at low tide and therefore often difficult to sample. Pools 1 and 2 were the only pools that were not often suddenly and unpredictably inundated by waves at low tide.

Portugal Cove

The west facing Portugal Cove shoreline is the least exposed of all the sites. The two pools were rarely inundated by swells during sampling visits at low tide. Steep cliffs drop down to an irregular bedrock shoreline providing variable degrees of protection to tidepools in the area. Both Pool 1 (PC1) and Pool 2 (PC2) are located in protected areas of the shoreline. The cliffs behind these pools also shade them from direct insolation for most of the morning. Pool 1 periodically experienced some terrestrial runoff resulting in a thin low salinity layer on the pool surface.

Sampling Techniques

A flexible sheet of clear plastic, 0.25 x 0.25 m, similar to the one used by Menge (1976), was used as a quadrat to sample the algal and grazer communities in the tidepools. The quadrat was weighted with lead sinkers to prevent it from floating and to minimize its movement during sampling. 100 white dots were placed on the quadrat in a stratified random manner to prevent potential excessive clumping which could occur with a completely random scheme. To determine the placement of the dots, a piece of graph paper cut to 0.25 x 0.25 m was divided into 4 even squares. 25

pairs of coordinates were selected from a table of random numbers to represent the coordinates of the dots in each of the four squares. After all 100 points were selected, the quadrat was placed over the graph paper and a white dot was marked on the quadrat at each point.

The quadrat was randomly placed in the pool and the species of algae under each dot was recorded. Identification and classification of the macrophytes follows South and Hooper (1980). Algae were then placed in one of the morphological groups: blade-forming, filamentous, calcareous, and encrusting (Table 2). Individuals of each species of mobile grazer or sessile invertebrate within the quadrat were then counted and recorded. This process was repeated for a total of 5 quadrats in each pool on each sampling date. Pools were sampled at low tide as close to monthly as possible considering time of tides and weather. A swell of 1.5 to 2.0 m in this area with a mean tidal range of 0.9 m (Anonymous, 1987) was not uncommon, and often impeded sampling. Water and air temperature were recorded using a mercury thermometer each time the pools were sampled. Salinity was measured in the field on some sample dates using a Y.S.I. salinity meter. Tidal height was measured relative to a point of known height on the shore using an inclinometer on a tripod.

The current taxonomic status of *Littorina saxatilis* is in question. On the shores of north western Europe, four species are currently recognized in the *L. saxatilis* species complex (Hill and Grahame 1990). Gilkinson and Methven (1991) have described the biology of a subtidal population of *L. saxatilis* form *saxatilis* in Trinity

Table 2. Species of macrophytic algae in each morphological group.

Blade Forming Algae	Filamentous Algae	Calcereous Algae	Encrusting Algae
<i>Alaria esculenta</i>	<i>Acrosiphonia arcta</i>	<i>Clathromorphum circumscriptum</i>	Green crust
<i>Ascophyllum nodosum</i>	<i>Ceramium rubrum</i>	<i>Corallina officinalis</i>	<i>Hildenbrandia rubra</i>
<i>Chondrus crispus</i>	<i>Chaetomorpha linum</i>		<i>Ralfsia fungiformis</i>
<i>Chordaria flagelliformis</i>	<i>Cladophora sericea</i>		" <i>Ralfsia</i> "
<i>Devalaria ramentaceum</i>	<i>Fragellaria</i>		
<i>Dictyosiphon foeniculaceus</i>	<i>Pilayella littoralis</i>		
<i>Enteromorpha intestinalis</i>	<i>Polysiphonia urceolata</i>		
<i>Fucus distichus distichus</i>	<i>Sphacelaria plumosa</i>		
<i>Fucus spiralis</i>	Tube dwelling diatom		
<i>Fucus vesiculosus</i>			
<i>Leathesia difformis</i>			
<i>Monostroma grevillei</i>			
<i>Monostroma undulatum</i>			
<i>Palmaria palmata</i>			
<i>Petalonia fascia</i>			
<i>Petalonia zosterfolia</i>			
<i>Porphyra umbilicalis</i>			
<i>Sacchoriza dermatodea</i>			
<i>Scytosiphon lomentaria</i>			

Bay, Newfoundland. Throughout the rest of this thesis, *Littorina saxatilis* will be used to describe the rough periwinkle found in the intertidal zone, with the complete understanding that the taxonomic status may be changed in the future.

Similarly, the taxonomic status of *Notoacmaea testudinalis* is also in question. This designation has been chosen for the present study to be consistent with other works from the east coast of North America (ex. Petraitis 1989).

Statistical Analysis

A grazing index was devised as a measure of grazing intensity. Yamada and Mansour (1987) have shown that *L. littorea* and *L. saxatilis* of the same size have the same ability to reduce algal standing crop. In the present study, the ratio of *L. saxatilis* wet weight to *L. littorea* wet weight was 0.083 (171 *L. littorea* and 172 *L. saxatilis* sampled at BB1 and BA1 representing the full size range for each species). Therefore, the grazing index was calculated as,

$$GI_p = n_{Ll} + (0.083 n_{Ls})$$

where GI_p is the grazing index for pool P, n_{Ll} is the mean number of *L. littorea*, and n_{Ls} is the mean number of *L. saxatilis* in pool P.

The pools were divided into three grazing intensity levels based on the mean value of the grazing index over all quadrats sampled in each pool: light, moderate, and heavy grazing. Table 3 clearly shows the differences in grazer abundance between intensity levels. In the lightly grazed pools, few if any *L. littorea* were present and numbers of *L. saxatilis* were low. In the moderately grazed pools, numbers of *L.*

Table 3. Mean grazing index and number of grazers per m² ± 1 SD grouped by grazing intensity.

Pool	Grazing Index	Number of <i>Littorina littorea</i> (per m ²)	Number of <i>Littorina saxatilis</i> (per m ²)
<u>Light</u>			
BB3	0.020	0.0 ± 0.0	3.8 ± 10.6
BB4	0.266	0.0 ± 0.0	51.2 ± 41.4
PC1	0.415	0.0 ± 0.0	80.0 ± 93.2
BB2	0.914	2.1 ± 5.5	158.9 ± 104.6
<u>Moderate</u>			
PC2	1.668	0.0 ± 0.0	321.6 ± 231.3
BA2	2.015	0.6 ± 3.2	410.2 ± 279.5
BA4	2.259	20.5 ± 25.9	190.7 ± 157.4
BA3	4.246	39.5 ± 31.7	342.9 ± 279.7
<u>Heavy</u>			
BB1	15.259	360.4 ± 466.5	159.2 ± 167.1
BA1	15.307	330.1 ± 251.8	208.0 ± 210.2

littorea were low in two of the pools but slightly higher in the other two pools. However, numbers of *L. saxatilis* were high. In the heavily grazed pools, numbers of *L. littorea* were high and number of *L. saxatilis* were moderate (i.e. lower than in the moderately grazed pools but higher than in the lightly grazed pools).

To determine the significance of differences in the abundance of algae in the 4 morphological groups and of bare rock between grazing intensity levels, one way analysis of variance was used on individual morphological groups. If a significant overall grazing effect was found at the 0.05 probability level, a Scheffé's test was used to determine which levels of grazing were significantly different from each other. Percent cover data were arcsine transformed before statistical analyses were performed (Sokal and Rohlf 1969). All figures show untransformed data.

The Shannon-Wiener index of diversity, H' , was calculated using a macro in MINITAB. The formula for the index is,

$$H' = -\sum p_i \log_2 p_i$$

where p_i is the proportion of the community belonging to the i^{th} species (Shannon and Weaver, 1949).

All statistical analyses were performed using MINITAB and SPSS* on the Digital VAX mainframe computer at Memorial University of Newfoundland.

RESULTS

The Grazer Community

The grazer communities in the tidepools were dominated by *Littorina littorea* and *Littorina saxatilis* but a number of other grazers were also present at various times during the study. Gammarid amphipods occurred in small numbers in all pools except Bay Bulls Pool 1 and Portugal Cove Pool 2. The amphipods only reached large numbers in Bay Bulls pools 3 and 4 in October among *Chordaria flagelliformis*. Early in the year, *Notoacmaea testudinalis* was present in low numbers in Bay Bulls Pools 1 and 2 and Bauline Pools 1 and 4 and *Strongylocentrotus droebachiensis* was present in low numbers in Bauline Pools 1 and 4. These species were both killed by the freshwater runoff and did not return to the pools during the course of the study.

Lacuna vincta was sporadically present in low numbers ($< 5 \text{ m}^{-2}$) throughout the study period in Bauline and Bay Bulls pools but was absent from the Portugal Cove pools. However, a fall recruitment resulted in large numbers of tiny *L. vincta* in Bauline Pool 2 (9818 m^{-2}) and Pool 3 (5453 m^{-2}). No sampling was done after the settlement of *L. vincta*, so their effects on the algal community could not be determined and they are therefore excluded from the grazer index. *Littorina obtusata* was observed on at least 1 occasion in all pools except Portugal Cove Pool 1 but was only abundant in Bay Bulls Pool 2 (49.6 m^{-2}) and Bauline Pool 4 (26.2 m^{-2}). Both of these pools had a healthy growth of furoid algae, the preferred habitat of *L. obtusata* (Steneck and Watling 1982, Hawkins and Hartnoll 1983).

Littorina littorea and *Littorina saxatilis* were the most abundant grazers with mean values over all quadrats of 97 and 193 individuals per m² respectively. *L. littorea* was only abundant in Bay Bulls Pool 1 and Bauline Pool 1 but in these two pools, it had an average abundance of 360 m⁻² and 330 m⁻² respectively. The numbers of *L. littorea* declined steadily through the study period (Fig. 2). The reason for this decline is unclear since predators of *L. littorea* were rarely seen in the tidepools. *L. littorea* did not become active until the water temperature in the pools climbed above 5°C at the end of April. Before this time, they were observed to be clumped together in cracks and crevices in an inactive state.

Littorina saxatilis was observed in all pools and was abundant (> 150 m⁻²) in all but 3 pools. It was by far the most abundant grazer in the moderately grazed pools, but was less abundant in the heavily grazed pools where *L. littorea* was abundant (Table 3). During the spring and early summer, *L. saxatilis* migrated from its overwintering cracks and crevices in the upper intertidal, to the pools. Then in the fall, the rough winkles migrated out of the pools again (Fig. 2).

Patterns of Algal Abundance

Blade-forming Algae

The mean abundance of blade-forming algae was significantly lower in the moderately and heavily grazed pools than in the lightly grazed pools (Table 4, Fig. 3). There was, however, no significant difference in abundance of blade-forming algae between moderately and heavily grazed pools ($p < 0.05$, Scheffe Test).

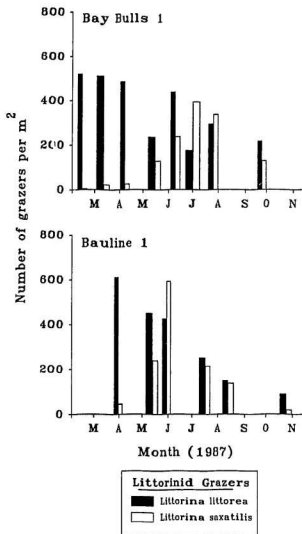


Figure 2. Mean abundance of littorinids on each sampling date at Bay Bulls Pool 1 and Bauline Pool 1.

Table 4. Analysis of variance of % cover of morphological groups and bare rock between levels of grazing intensity.¹

Blade Forming Algae						Grazing Intensity		
Source	D.F.	Sum of Squares	Mean Squares	F Ratio	Prob.	Light	Moderate	Heavy
Between Groups	2	9.2978	4.6489	47.496	<0.0001	47.57	13.42	17.75
Within Groups	264	25.8401	0.0979					
Total	266	35.1379						
Filamentous Algae						Grazing Intensity		
Source	D.F.	Sum of Squares	Mean Squares	F Ratio	Prob.	Light	Moderate	Heavy
Between Groups	2	2.7338	1.3669	18.099	<0.0001	31.58	26.115	7.736
Within Groups	264	19.9378	0.0755					
Total	266	22.6716						
Encrusting Algae						Grazing Intensity		
Source	D.F.	Sum of Squares	Mean Squares	F Ratio	Prob.	Light	Moderate	Heavy
Between Groups	2	0.4594	0.2297	15.545	<0.0001	7.195	13.73	17.03
Within Groups	267	3.9456	0.0148					
Total	269	4.4051						
Calcareous Algae						Grazing Intensity		
Source	D.F.	Sum of Squares	Mean Squares	F Ratio	Prob.	Light	Moderate	Heavy
Between Groups	2	1.5805	0.7903	33.503	<0.0001	12.55	24.765	30.2
Within Groups	267	6.2980	0.0236					
Total	269	7.8785						
Bare Rock						Grazing Intensity		
Source	D.F.	Sum of Squares	Mean Squares	F Ratio	Prob.	Light	Moderate	Heavy
Between Groups	2	2.6926	1.3463	33.628	<0.0001	10.25	27.46	31.81
Within Groups	267	10.6984	0.0400					
Total	269	13.3821						

¹ Values for morphological groups at the 3 grazing intensity levels are untransformed means. Underlined values are not significantly different at the 0.05 probability level using Scheffé's test.

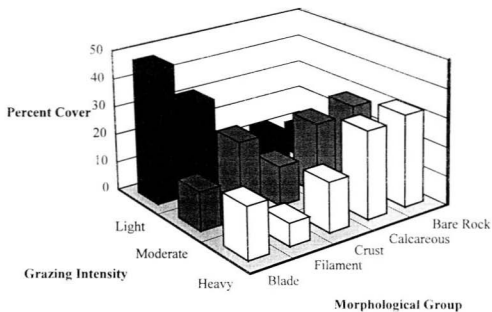


Figure 3. Mean abundance of algae in each morphological group and bare rock at each grazing intensity level over the entire study period.

In the lightly grazed pools, the abundance of blade-forming algae was high in March, then dropped precipitously to May, climbed to October and then dropped again to November (Fig. 4). The spring peak was caused by *Fucus distichus distichus* in Bay Bulls Pool 2 (the only lightly grazed pool sampled in March) where the protected, inland location of the pool prevented removal of the perennial by ice scouring up to this time. However, a few days after the pool was sampled in March, a large chunk of ice (~2 m in diameter) was observed in the pool. Movement of this ice chunk at high tide resulted in a decrease in abundance of *Fucus distichus distichus* from 84 % cover in March to 37 % cover in April. The increase in abundance of blade-forming algae to October (Fig. 4) was caused by a slight increase in *Fucus distichus distichus* in Bay Bulls Pool 2 due to growth of mature plants and regeneration from holdfasts, and a dramatic rise in *Chordaria flagelliformis* to 85 % cover in Bay Bulls Pools 3 and 4. The decrease in abundance of blade-forming algae from October to November in the lightly grazed pools was a sampling artifact. Only Portugal Cove Pool 1 and Bay Bulls Pool 2 were sampled in December. These pools both had low abundances of *Chordaria flagelliformis* throughout the study.

In the moderately grazed pools, the blade-forming algae climbed gradually to a peak in July and then declined slightly (Fig. 4). *Monostroma grevillei* declined after *L. littorea* became active and *L. saxatilis* became abundant. *F. distichus distichus* increased slightly through the study period. The peak abundance of blade-forming algae, in July, was due to *Scytosiphon lomentaria* in Bauline Pool 2 (41 % cover).

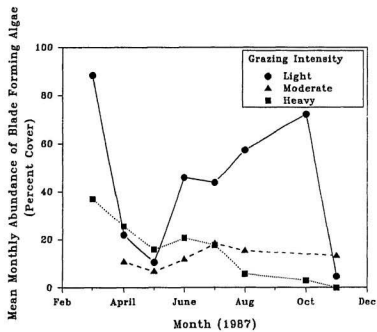


Figure 4. Mean abundance of blade forming algae at each grazing intensity level per month.

C. flagelliformis was not observed in any of the moderately grazed pools in spite of ample bare substrate on which to settle and a healthy parent population in the adjacent middle intertidal zone.

In the heavily grazed pools, blade-forming algae decreased from March to November (Fig. 4). *Monostroma grevillei* was responsible for the high abundance of blade-forming algae in the spring. The high abundance of *Monostroma grevillei* was unexpected since it is a preferred food of *L. littorea* (Lubchenco 1978). However, *M. grevillei* grew early in the year reaching peak abundance in March while *L. littorea* was still dormant and *L. saxatilis* numbers were low. *M. grevillei* declined rapidly once the littorinids began actively grazing and was not seen after May in either pool. *C. flagelliformis* did not appear in either of the heavily grazed pools despite the presence of ample bare substrate on which to settle and the abundance of parent plants in the adjacent middle intertidal zone.

Filamentous Algae

The abundance of filamentous algae was significantly lower in the heavily grazed pools than in the moderately and lightly grazed pools ($p < 0.05$, Scheffe Test). There was no significant difference between the mean abundance of filamentous algae in the lightly and moderately grazed pools (Table 4, Fig. 3).

In the lightly and moderately grazed pools, the abundance of filamentous algae increased to a peak in summer and then declined in late summer and increased again

in November (Fig. 5). The second peak was due entirely to *Cladophora serecia* in the lightly grazed Portugal Cove Pool 1 (45 % cover) and the moderately grazed Portugal Cove Pool 2 (44 % cover). The peak in May for the lightly grazed pools in Fig. 5 is due to the high abundance (68 % cover) of *Acrosiphonia arcta* in Portugal Cove Pool 1, the only lightly grazed pool sampled in May.

A. arcta was abundant during the summer (peak abundance > 30 % cover) in all of the lightly and moderately grazed pools with the exception of Bay Bulls Pool 2 (maximum 20 % cover) and Bauline Pool 2 (maximum 6 % cover). In all of these pools, it was present when the pool was first sampled in the spring and persisted at least until August (October in Bay Bulls Pool 3).

In the heavily grazed pools, the filamentous algae peaked earlier and at lower abundance than in the lightly and moderately grazed pools and then declined (Fig. 5). *A. arcta* did not become abundant during the summer. In Bay Bulls Pool 1, it increased to a peak of 26% cover in May, dropped after *L. littorea* became active and numbers of *L. saxatilis* increased but persisted in the pool until August (9% cover). In Bauline Pool 1, *A. arcta* climbed to a maximum abundance of 6% cover in June and was not found in the pool after that date.

Encrusting Algae

There was significantly less encrusting algae in the lightly grazed pools than in the moderately and heavily grazed pools ($p < 0.05$, Scheffe Test). There was no

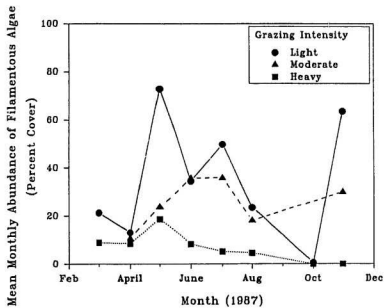


Figure 5. Mean abundance of filamentous algae at each grazing intensity level per month.

significant difference between the mean abundance of encrusting algae in the moderately and heavily grazed pools (Table 4, Fig. 3).

In the lightly grazed pools, the abundance of encrusting algae was lowest during the summer months when the ephemeral blade-forming and filamentous algae were most abundant (Fig. 6). In the moderately grazed pools, the encrusting algae, as a group, increased in abundance during the spring and then maintained a steady level throughout the study period (Fig 6). "*Ralfsia*" increased throughout the study in the moderately grazed pools. Bauline Pool 2 showed a peak in abundance of 42% cover in June, by far the highest level observed in the study. In the most heavily grazed pool, the encrusting algae decreased from March to April, increased until September and then declined to November (Fig. 6). A green crust in Bay Bulls Pool 1 was responsible for the high abundance of encrusting algae in the spring. In the most heavily grazed pool, Bauline Pool 1, *H. rubra* gradually increased in abundance from 10% cover in April to 22% cover in November demonstrating that it can survive from spring until late fall and that it is not negatively affected by intense littorinid grazing. In Bay Bulls Pool 1, *H. rubra* was absent until June. In all of the other pools where it occurred, *H. rubra* was observed on the first sampling date. This allowed vegetative spreading to increase abundance rather than new planktonic settlement as occurred in Bay Bulls Pool 1. Therefore, it is not surprising that the maximum abundance in Bay Bulls Pool 1 was only 6% cover in October.

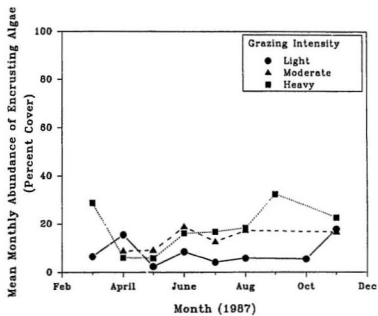


Figure 6. Mean abundance of encrusting algae at each grazing intensity level per month.

The two heavily grazed pools had different abundance patterns for "*Ralfsia*". It first occurred in Bay Bulls Pool 1 in June at 13% cover and increased to 26% cover in October. The timing of the late occurrence of "*Ralfsia*" just as *Scytosiphon lomentaria* was decreasing in abundance supports the hypothesis that these two species are alternate stages in the life cycle of the same plant (Lubchenco and Cubit 1980). "*Ralfsia*" first occurred in Bauline Pool 1 in May with 2% cover, then increased to 3% cover in June and then disappeared.

Calcareous algae

The abundance of calcareous algae was significantly different at all 3 levels of grazing and increased with increased grazing pressure ($p < 0.05$, Scheffe Test) (Table 4, Fig. 3). In Bauline Pool 1, *Corallina officinalis* increased from 2% cover in April to 14% cover in November. In contrast, *C. officinalis* went from 13% cover in April down to a low of 0.1% cover in July when the ephemeral *A. arcta* and *C. flagelliformis* were abundant in Bay Bulls Pool 3. Pools with intermediate levels of grazing showed intermediate patterns of abundance for *C. officinalis*.

Clathromorphum circumscriptum was more abundant than *C. officinalis* and had different mean abundances between the three grazing intensity levels (Table 4). In Bay Bulls Pool 3 and 4, it was abundant initially and then declined as the ephemerals became more abundant. In Portugal Cove Pool 1 and Bay Bulls Pool 2, the abundance

of *C. circumscriptum* was low throughout the study. It had a higher abundance in the moderately grazed pools and remained relatively steady throughout the study period.

C. circumscriptum was most abundant in the heavily grazed pools (Fig. 7). In Bay Bulls Pool 1, its abundance stayed relatively constant at 23% cover throughout the study. In Bauline Pool 1, its abundance increased from 12% cover in April to a maximum of 32% cover in July and then declined to 17% cover in November.

Bare Rock

In lightly grazed pools, there was significantly less bare rock than in moderately and heavily grazed pools ($p < 0.05$, Scheffe Test) (Table 4, Fig. 3).

In the absence of grazing (only 6 *L. saxatilis* and no *L. littorea* observed during the entire study period) in Bay Bulls pool 3, the large amount of bare rock observed in April (31% cover) was reduced to 0.4% cover in July once *Acrosiphonia arcta* and *Chordaria flagelliformis* settled. In the other lightly grazed pools, the amount of bare rock remained low throughout the study with the exception of Bay Bulls Pool 2 where bare rock was 20% cover throughout the study.

The moderately grazed pools had larger amounts of bare rock. These levels remained relatively constant through the study period with a dip in mid summer in all pools. This dip reflected the peaks in abundance of the ephemeral blade-forming and filamentous algae.

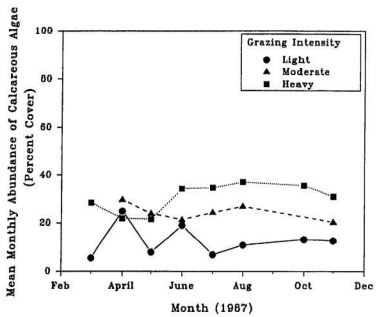


Figure 7. Mean abundance of calcareous algae at each grazing intensity level per month.

A slightly higher mean amount of bare substrate was observed in the heavily grazed pools due to the large amount of bare rock present in Bauline pool 1. The amount of bare rock ranged from 55% cover in May to 39% cover in July in this pool. In Bay Bulls Pool 1, the mean amount of bare rock was lower (21% cover) due mainly to higher levels of *A. arcta* and *Scytosiphon lomentaria*. Even so, the amount of bare rock peaked at 33% cover in July.

Effects of Littorinid Grazers on Species Diversity

The Shannon-Wiener diversity index in tidepools was greatly influenced by the grazing activity of *L. littorea* and *L. saxatilis*. In moderately and heavily grazed pools, the diversity remained fairly consistent over the entire study period (1.59 ± 0.25 sd and 1.36 ± 0.28 sd respectively). In contrast, pools with low grazer populations had a lower diversity with large seasonal fluctuations (1.22 ± 0.49 sd). The pools with the greatest fluctuations were Portugal Cove Pool 1, Bay Bulls Pool 4 and Bay Bulls Pool 3 (Figure 8.). In all of these pools, one species or assemblage obtained a maximum abundance of 85% cover or greater (*A. arcta*/*C. linum* in Portugal Cove Pool 1 and *C. flagelliformis*/*D. foeniculaceus* in Bay Bulls Pool 3 and 4). In all cases, diversity decreased until the dominant assemblage reached its maximum abundance.

In Bay Bulls Pool 2, *Fucus distichus distichus* dominated for most of the sample period. However, it only reached a peak abundance of 53% cover except for the period in March before the pool was scoured by ice. This level of dominance by

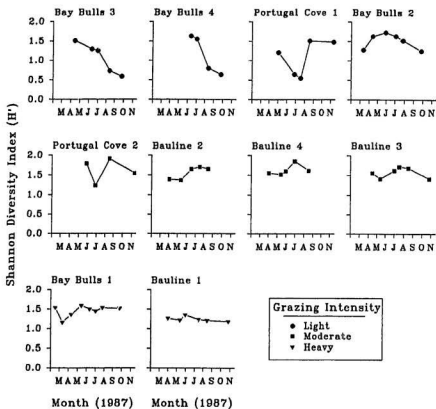


Figure 8. Shannon Diversity Index (H') on each sampling visit for each tidepool.

one species was not high enough to exclude many other species. Also, the ice scouring left patches of bare substrate which were utilized by ephemerals.

In the moderately grazed pools, no single species ever dominated, therefore diversity was higher throughout the season than in lightly grazed pools. In the most heavily grazed pools, diversity was lower than in moderately grazed pools. Species such as *Chordaria flagelliformis* were prevented from settling and other species such as *Acrosiphonia arcta* were removed earlier by the grazing littorinids.

As observed by Lubchenco (1978), the greatest diversity occurred at intermediate levels of grazing intensity. In the present study, the lowest diversity was seen in the lightly grazed pools at times when they were dominated by 2 species (Portugal Cove Pool 1, Bay Bulls Pool 3 and Bay Bulls Pool 4). Diversity was highest in pools where dominance by a single species was prevented by grazing but grazing was not so severe as to totally eliminate many species. Most of the algal species present were ephemerals which have been shown by Lubchenco (1978) to be preferred foods of *L. littorea*.

Physical Characteristics of Tidepools

One might reasonably assume that some of the biotic differences described above might be due to differences in physical characteristics of the tidepools such as distance above MLW or pool size. However, although physical characteristics varied

between individual tidepools (Table 1), there were no significant differences between levels of grazing intensity (ANOVA $p>0.05$).

DISCUSSION

In New England, grazing pressure, defined as the probability that an individual alga will be removed by herbivory during a given time period (Lubchenco and Cubitt 1980), exerted by *Littorina littorea* is maximal during the summer and minimal in the winter. The winter minimum may be caused by a decrease in numbers due to predation, cold temperature mortality or emigration (Menge 1972, Dethier 1982, Gardner and Thomas 1987), or factors decreasing foraging efficiency. In the present study, *L. littorea* became active in April when the daytime temperature in the pools reached 5°C. During the winter, the snails congregated in an inactive state in crevices and depressions in the pools. The littorinids continued to actively graze through the summer and fall until November when temperatures declined to 5°C and foraging activity ceased. Menge (1975) described a decrease in grazing activity due to storm generated wave action in the winter. Williams (1964) noted a marked reduction in the growth rate of *L. littorea* during the winter in Wales. This was due to a reduction in the number of feeding excursions caused by lethargy brought on by cold sea temperatures (~8°C). Newell (1958) described a complete cessation of activity at temperatures below 8°C.

Since the number of common periwinkles decreased throughout the year with no peak in numbers in summer and since very few small *L. littorea* were seen, a failure in recruitment from the plankton in the spring and summer seems likely (Hayes 1929). Recruitment from the plankton is patchy and irregular for many species

(Dethier 1984). Since spat settle in the subtidal or low intertidal zone, and later migrate up into the middle intertidal zone (Lambert and Farley 1968, Gardner and Thomas 1987), spring ice scouring may decrease recruitment by killing the snails directly or through starvation by removing the macrophytes. This does not however explain the gradual decrease in numbers during the study. Unexplained changes in population size and growth rate between climatically similar years have been observed by others (Williams 1964) and may be the result of normal yearly fluctuations of populations occupying the harsh and variable intertidal zone.

In the spring, *Littorina saxatilis* migrated from cracks and crevices in emergent substrata, into the pools to feed and reproduce. The maximum summer population size varied between pools and between sites depending, primarily, on the pool's proximity to a large population of *L. saxatilis* on emergent substrata in the upper intertidal zone. Recruitment of small *L. saxatilis* in early and mid summer added to the peak population size. The decline in the *L. saxatilis* population after midsummer, was likely caused by mortality and/or emigration.

Although few sea stars were observed at the study sites, other predators including sea gulls, cunners (*Tautoglabrus adspersus*), and sticklebacks (*Gasterosteus aculeatus*) were observed on occasion in some of the pools. Blue mussels, sea urchins and crabs, not gastropods, made up most of the debris found at gull anvils in the vicinity of the study sites suggesting that littorinids were not a preferred prey item. Gastropods have been found in the gut of *T. adspersus*, but they only made up a small

proportion of the total gut contents (Chao 1973, Olla *et al.* 1975). Sticklebacks may have eaten some of the smallest littorinids in the 2 pools (PC 1 and BB 1) in which they occurred but is unlikely to be a source of mortality in most pools. In the most heavily grazed pools, starvation may have resulted in the death of some rough periwinkles as described for limpets in Oregon (Cubit 1984). This, migration out of the pools into the cracks and crevices of the surrounding shore where *L. saxatilis* overwinters seems the most probable cause of its fall decline in the pools.

The differences in the distribution of the two littorinids between sites and pools (*L. saxatilis* in all pools and *L. littorea* in only two pools) is due in part to differences in larval development. Planktonic development in *L. littorea* takes about four weeks (Fretter and Graham 1980), and dispersal by currents can result in too few larvae settling in a given area to maintain a breeding population. On the other hand, the larvae of *L. saxatilis* are brooded internally and hatch as post-metamorphic juveniles (Fretter and Graham 1980). If one or more gravid *L. saxatilis* are carried to a new area via rafting on floating macroalgae, for example, the likelihood of establishing a breeding population is much greater. Johannesson (1988) showed that the presence of *L. saxatilis* and the absence of *L. littorea* in a number of isolated locations from South Africa to Greenland was due to the different modes of larval development. Similar mechanisms likely explain the ubiquitous distribution of *Littorina saxatilis* and the patchy distribution of *L. littorea* on the east coast of Newfoundland.

The population size of littorinid grazers exerts a major structuring influence on the algal communities of these tidepools. In heavily grazed pools, encrusting and calcareous species dominate. Lubchenco and Cubitt (1980) suggest that the primary adaptive value of crustose algae is their ability to persist through time while upright algae are being removed by grazers. The calcareous species, *Clathromorphum circumscriptum* and *Corallina officinalis* dominated in the heavily grazed pools in the current study. Littler and Littler (1980) have demonstrated that low calorific value and toughness due to high levels of CaCO_3 decrease the susceptibility of calcareous macrophytes to grazers. The removal of the upright algae by grazing offsets the lower growth rate of the encrusting and calcareous forms (Littler and Arnold 1982) thereby decreasing competition for primary space.

Upright ephemeral algae dominated in less intensely grazed pools. The filamentous or sheetlike thallus, lack of metabolic burden of producing chemical or structural defenses, and limited attachment points allowed a high ratio of photosynthetic area per unit biomass (Lubchenco and Cubitt 1980). Therefore, these species could grow faster and compete for space more efficiently than the encrusting and calcareous algae.

Chondaria flagelliformis is an ephemeral species which is common in environmentally harsh, physically disturbed areas. It is a major component of the successional community following ice scouring on the north western Atlantic coast (Hooper 1981, Lobban and Hanic 1984, Munda 1992). The ability of *C. flagelliformis*

to take up nitrogen when nutrient concentrations in the water are very low during the summer allows it to prosper and grow (Probyn and Chapman 1983) when the growth of many other species of macrophytes and phytoplankton is severely depressed (Platt 1971, Chapman and Craigie 1977). Despite ample lower emergent intertidal populations at all three sites, *C. flagelliformis* only became abundant in the two least intensely grazed pools. In both cases, it was first observed in June when grazing pressure in the other pools was reaching its peak. It is likely that in pools with larger grazer populations, some germlings of *C. flagelliformis* (lower in herbivore defense chemicals than adults (Geiselman 1980)) were eaten by the littorinids. Geiselman (1980), Watson and Norton (1985), and Lubchenco (1983) have shown how littorinid grazers have dislodged juvenile macrophytes while they were searching for other types of food.

With one exception (Bay Bulls Pool 2), the perennial *Fucus distichus distichus* was rare in the tidepools surveyed. Scouring by pack ice and storm generated waves removed most of the adult plants during the winter. In all cases where the abundance of *F. distichus distichus* increased during the study, young plants regrew from the remaining holdfasts which survived the winter. No newly settled juveniles were observed. This is most likely explained by the propensity of *L. littorea* to dislodge juvenile fucoids while crawling across the substratum (Geiselman 1980, Watson and Norton 1985). However, in Bay Bulls Pool 2, protected by the topography of the surrounding shore, the established canopy of *F. distichus distichus* dominated.

Although adult *F. distichus distichus* thalli did not suffer any obvious negative effects of grazing, no new sporelings settled in this pool during the study period suggesting physical disturbance by littorinids.

F. distichus distichus was completely absent from the heavily grazed pools. Although adult *Fucus* sp. have a low grazing preference rating, *L. littorea* will eat large quantities of germlings in the absence of any other macrophytes (Barker and Chapman 1990). In the most heavily grazed pool (Bauline Pool 1), while upright macrophytes were almost completely absent any germlings which settled were eaten. In Bay Bulls Pool 1, dislodgement probably played a greater role in preventing *F. distichus distichus* from attaining a foothold since during most of the study, more highly preferred algal species were present. These ephemerals provided enough high quality food that the littorinids did not have to graze the less attractive and nutritionally poorer *F. distichus distichus*.

The greater average abundance of *Monostroma grevillei* in heavily grazed pools was an artifact of the sampling not an effect of grazing. Most of the moderately and lightly grazed pools were not sampled until after *M. grevillei* had reached its peak abundance. The heavily grazed pools were sampled earlier when abundances of the blade-forming Chlorophyte were higher. *Monostroma grevillei* is similar in morphology to the highly preferred *Ulva lactuca* (Lubchenco 1978, Watson and Norton 1985) and thus should be easy to graze, providing a high return of nutrients per unit time. It occurred early in the year, persisted until mid summer in the lightly grazed

pools, but disappeared by late spring in the moderately and heavily grazed pools. The decline of *M. grevillei* was due to senescence and reproduction in the lightly grazed pools. Since the decline in the growth rate of *M. grevillei* coincided with the increase in grazing activity of *L. littorea* and the migration of *L. saxatilis* into the pools, there was a rapid decrease in *M. grevillei* in the moderately and heavily grazed pools. However, the impact of the much smaller *L. saxatilis* on the abundance of *M. grevillei* was less dramatic than that of *L. littorea*.

Scytosiphon lomentaria was most abundant during the time of peak grazing intensity in Bauline Pool 2 and Bay Bulls Pool 1. Since *S. lomentaria* is a species preferred by *L. littorea* (Lubchenco 1978), one would expect to see a low abundance of upright forms during the summer when grazers are abundant and active and a higher abundance during the winter (Lubchenco and Cubit 1980). For instance, Lobban and Hanic (1984) found that *Scytosiphon lomentaria* recolonized an ice scoured rocky shore in Prince Edward Island in the fall after a succession of mostly ephemeral species. It was not seen during the summer when grazing was most intense. However, in the present study and others (Shannon *et al.* 1988, Villard-Bohnsack and Harlin 1992, Hooper 1981, Bolton 1983) *S. lomentaria* has been observed during spring and/or summer when grazing pressure is high. Jara and Moreno (1984) observed *Scytosiphon* in herbivore addition and control plots but not in grazer exclusion plots. Thus grazing alone cannot explain the distribution of *S. lomentaria* in Newfoundland

tidepools. The role that physical factors and competitive interactions play requires further study.

Littorina littorea decreased the abundance of filamentous algae but the mechanism of algal removal was different. For most of the blade-forming species, low abundance was maintained through prevention of successful recruitment. In contrast, most of the filamentous species were present as adult plants before the grazing intensity increased and thus the littorinids had to eat the adult plants rather than juveniles. The taenioglossan radula of the littorinids is well designed for eating adult filamentous plants as well as juveniles (Steneck and Walling 1982) and many filamentous macrophytes are preferred foods of littorinids. The abundance of *Acrosiphonia arcta* was drastically reduced when *L. littorea* became active in the heavily grazed pools. No other filamentous algae became abundant once the grazers began actively feeding in the pools. In contrast, *Acrosiphonia arcta* and *Chaetomorpha linum* reached maximum abundances in mid summer in the lightly and moderately grazed pools. Although *L. saxatilis* has been reported to eat filamentous algae (Sacchi *et al.* 1981) it had a more subtle effect than did *L. littorea*. Instead of removing the filamentous algae altogether, *L. saxatilis* decreased the maximum abundance and reduced the persistence time. The inability of *L. saxatilis* to significantly decrease the abundance of adult filamentous algae combined with its negative affect on the establishment of new blade-forming algae further supports its classification by Hawkins and Hartnoll (1983), as a micrograzer.

Hildenbrandia rubra and "*Ralfsia*" were the most common and abundant encrusting algae present during the course of the study. Both species are relatively grazer resistant due to a thallus constructed of small tightly packed cells. This structure offers considerable resistance to scratching and thus causes a high degree of wear to the radular teeth of littorinids grazing on them (Bertness *et al.* 1983). The increased wear on the radular teeth makes them less effective for grazing the nutritionally richer upright ephemerals and therefore the cost of grazing the crusts is high. Bertness *et al.* (1983) found that extracts of *Hildenbrandia rubra* and *Ralfsia verrucosa* embedded in agar were eaten at lower rates than agar controls with lower nutritive value suggesting the presence of chemical defenses in the macrophytes as well as structural defenses.

The abundance of the slow growing perennial *H. rubra* was extremely low in the lightly grazed pools. Ephemerals overgrew the crust and primary space was at a premium. It was more abundant in the moderately grazed pools due to the increase in primary space caused by *L. saxatilis* removing the ephemeral algae or preventing them from settling. In the most heavily grazed pool, *H. rubra* increased in abundance by lateral spreading during the study period when all of the competing upright macrophytes were removed by grazing. In Bay Bulls Pool I, however, *H. rubra* was not present before the grazers became active and thus had to recruit from the plankton in the face of intense grazing pressure. It recruits very slowly (Bertness *et al.* 1983) and like many other macrophytes, the juveniles are probably more attractive to grazers

than the adult plants (Barker and Chapman 1990, Lubchenco 1983, Watson and Norton 1985). Once *H. rubra* appeared in this pool in mid summer, and reached a size at which it was no longer as susceptible to grazing, it gradually increased in abundance.

Although there was no significant difference between mean abundances of "*Ralfsia*" between pools, there was a consistent grazer-dependent seasonal pattern of abundance. In the lightly grazed pools, abundance was lowest during the summer when the ephemerals were present. In the moderately grazed pools and the heavily grazed Bay Bulls Pool 1, removal of the faster growing ephemerals allowed "*Ralfsia*" to increase in abundance through the study period. Only in one of the moderately grazed pools did it peak during the peak in grazing intensity as Lubchenco and Cubitt (1980) observed. In the most intensely grazed pool, however, "*Ralfsia*" was eliminated in June. Extreme levels of grazing may prevent encrusting algae from monopolizing bare rock in tidepools. Bertness *et al.* (1983) found similar densities of *L. littorea* to limit abundance of algal crusts in protected rocky beaches in southern New England.

Calcareous red algae such as *Corallina officinalis* and *Clathromorphum circumscriptum* carry structural and chemical defenses which protect them from littorinid grazers. The only weak point on *C. officinalis* is the uncalcified articulated joint but since the radula of most grazers is too wide to fit between the calcareous segments, the thallus is almost impenetrable to grazers (Watson and Norton 1985). *C. officinalis* was found to have the lowest ranking of all algae tested by Watson and Norton (1985) for both edibility and attractiveness. It was not eaten by *L. littorea*

even after 50 days of starvation (Watson and Norton 1985). *C. officinalis* grew little during the present study but removal of epiphytes such as *M. grevillei* by the littorinids may have aided the limited growth. No recruitment was observed but the structural strength of *C. officinalis* made it less susceptible to ice damage than most of the other perennial macrophytes. Tidepools on the ice scoured northwest coast of Iceland have *Corallina officinalis* as one of their chief components (Munda 1992).

Clathromorphum circumscriptum has a multilayered epithallus which protects the meristematic cells from grazing gastropods (Steneck 1982). However the thallus is prone to epiphytism in the absence of grazing by the limpet, *Notoacmaea testudinalis* (Steneck 1982). In the present study, limpets were all killed by the freshwater runoff in the spring. Most of the *C. circumscriptum* in the pools did not grow, was pale in colour and appeared heavily epiphytised. However, in the most heavily grazed pools, *C. circumscriptum* increased through the study period and eventually took on a healthy pink appearance. The high density of littorinid grazers in these pools may have mimicked the beneficial effects of grazing by *N. testudinalis* on *C. circumscriptum*.

Algal species diversity varied between pools depending on the grazing intensity. With low grazing pressure (low numbers of *Littorina saxatilis* and no *L. littorea*), diversity decreased to a minimum in mid to late summer when one of the ephemeral species became dominant. In contrast, in pools with intermediate grazing pressure (large numbers of *L. saxatilis* but low numbers of *L. littorea*), diversity remained high and constant through the year since the grazers removed enough of the dominant

ephemeral algae to decrease competition for space and reduce the frequency of competitive exclusions. Diversity was also low in pools with grazing pressures high enough to remove most of the upright algae (large numbers of *L. littorea* and moderate numbers of *L. saxatilis*). Lubchenco (1978) first described this type of relationship between grazers and diversity in New England tidepools where *L. littorea* was the only significant herbivore. In the present study, *Littorina saxatilis* was also found to play a major role in determining algal diversity.

Summary

The structure of algal communities in tidepools on Newfoundland's east coast is determined by a number of interacting biotic and abiotic factors. Frequent ice scouring prevents some perennial species from establishing by removing parent populations in localised areas. Repeated disturbance can prevent some populations from reaching maturity and reproducing. On the other hand, scouring can benefit algal populations by reducing the number of grazers as can freshwater inflows during spring.

Grazing by the herbivorous gastropods, *Littorina littorea* and *L. saxatilis* varies seasonally and spatially. The more intensely grazed pools were dominated by encrusting and calcareous species adapted to persist through time while upright algae were removed by grazers. Upright perennials are prevented from dominating by a combination of grazers removing adults and settling propagules and by physical removal through wave action and ice scouring of larger plants which have found a

temporal or spatial escape from grazing. In the less intensely grazed pools, opportunistic species with few structural or chemical defenses and high fecundity, and high growth rates outcompete the slower growing perennials for primary space.

Diversity was highest in pools with intermediate grazing pressure, and was maintained at a stable level through the year since the dominant ephemeral species are the preferred foods of the grazers. Diversity was lower in lightly grazed pools where one algal species dominated and in heavily grazed pools where all upright macrophytes were removed by grazing.

REFERENCES

- Anonymous. 1987. Canadian tide and current tables. Volume 1 Atlantic Coast and Bay of Fundy. Minister of Supply and Services Canada. Canadian Government Publishing Centre. Ottawa Canada.
- Barker, K.M. and A.R.O. Chapman. 1990. Feeding preferences of periwinkles among four species of *Fucus*. *Mar. Biol.* 106:113-118.
- Bertness, M.D., P.O. Yund, and A.F. Brown. 1983. Snail grazing and the abundance of algal crusts on a sheltered New England rocky beach. *J. Exp. Mar. Biol. Ecol.* 71:147-164.
- Bolton, J.J. 1983. Effects of short-term ice scouring on a Newfoundland rocky shore community. *Astarte* 12:39-43.
- Branch, G.M. 1981. The biology of limpets: physical factors, energy flow and ecological interactions. *Oceanogr. Mar. Biol. Annu. Rev.* 19:235-380.
- Chao, L.N. 1973. Digestive system and feeding habits of the cunner *Tautoglabrus adspersus*, a stomachless fish. *Fisheries Bull.* 71:565-586.
- Chapman, A.R.O. 1981. Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, Eastern Canada. *Mar. Biol.* 62(4):307-311.
- Chapman, A.R.O. and J.S. Craigie. 1977. Seasonal growth in *Laminaria longicervis*: relations with dissolved inorganic nutrients and internal reserves of nitrogen. *Mar. Biol.* 40:197-205.
- Cubit, J. 1984. Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. *Ecology* 65:1904-1917.
- Dethier, M.N. 1981. Heteromorphic algal life histories: the seasonal pattern and response to herbivory of the brown crust, *Ralfsia californica*. *Oecologia* 49:333-339.
- Dethier, M.N. 1982. Pattern and process in tidepool algae: factors influencing seasonality and distribution. *Bot. Mar.* 25:55-66.

- Dethier, M.N. 1984. Disturbance and recovery in intertidal pools: maintenance of mosaic patterns. *Ecol. Monogr.* 54(1):99-118.
- Fretter, V. and A. Graham. 1980. The prosobranch molluscs of Britain and Denmark. Part 5. Marine Littorinacea. *J. Mulluscan Stud.* 7:supp., 44.
- Gardner, J.P.A. and M.L.H. Thomas. 1987. Growth and production of a *Littorina littorea* (L.) population in the Bay of Fundy. *Ophelia* 27(3):181-195.
- Geiselman, J.A. 1980. Ecology of chemical defenses of algae against the herbivorous snail, *Littorina littorea*, in the New England rocky intertidal community. Doctoral Dissertation. Woods Hole Oceanographic Institute and M.I.T.
- Gilkinson, K.D. and D.A. Methven. 1991. Observations on the subtidal distributions of the intertidal rough periwinkle, *Littorina saxatilis*, and the common periwinkle, *L. littorea*, in a shallow embayment in eastern Newfoundland. *Can. Field-Nat.* 105(4):522-525.
- Hawkins, S.J. and R.G. Hartnoll. 1983. Grazing of intertidal algae by marine invertebrates. *Oceanogr. Mar. Biol. Annu. Rev.* 21:195-282.
- Hayes, F.R. 1929. Contributions to the study of marine gastropods. III. Development, growth, and behaviour of *Littorina*. *Contrib. Can. Biol. Fish. N.S.*, Vol. 4:413-430.
- Hooper, R. 1981. Recovery of Newfoundland benthic marine communities from sea ice. *Proc VIIIth Int. Seaweed Symp.*, Bangor, North Wales, pp 360-366.
- Hooper, R.G. and A. Whittick. 1984. The benthic marine algae of the Kaipokok Bay, Makkovik Bay and Big River Bay region of the central Labrador coast. *Naturaliste can.* 111:131-138.
- Imrie, D.W., S.J. Hawkins, and C.R. McCrohan. 1989. The olfactory-gustatory basis of food preference in the herbivorous prosobranch, *Littorina littorea* (Linnaeus). *J. Moll. Stud.* 55:217-225.
- Jara, H.F. and C.A. Moreno. 1984. Herbivory and structure in a midlittoral rocky community: A case in southern Chile. *Ecology.* 65:28-38.

- Johannesson, K. 1988. The paradox of Rockall: why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*)? *Mar. Biol.* 99:507-513.
- Lambert, T.C. and J. Farley. 1968. The effect of parasitism by the trematode *Cryptocotyle lingua* (Creplin) on zonation and winter migration of the common periwinkle *Littorina littorea*. *Can. J. Zool.* 46:1139-1147.
- Littler, M.M and K.E. Arnold. 1982. Primary productivity of marine macroalgal functional-form groups from southwestern North America. *J. Phycol.* 18:307-311.
- Littler, M.M. and D.S. Littler. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Am. Nat.* 116:25-44.
- Lobban, C.S. and L.A. Hanic. 1984. Rocky shore zonation at North Rustico and Prim Point, Prince Edward Island. *Proc. N.S. Inst. Sci.* 34:25-40.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive ability. *Am. Nat.* 112:23-39.
- Lubchenco, J. 1982. Effects of grazers and algal competitors on fucoid colonization in tidepools. *J. Phycol.* 18:544-550.
- Lubchenco, J. 1983. *Littorina* and *Fucus*: Effects of herbivores, substratum heterogeneity and plant escapes during succession. *Ecology* 64:1116-1123.
- Lubchenco, J. and J. Cubitt. 1980. Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. *Ecology* 61:676-687.
- Lubchenco, J. and S.D. Gaines. 1981. A unified approach to marine plant- herbivore interactions. I. Populations and communities. *Annu. Rev. Ecol. Syst.* 12:405-437.
- Lubchenco, J. and B.A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.* 48:67-94.
- Menge, B.A. 1972. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. *Ecol. Monogr.* 42:25-50.

- Menge, B.A. 1976. Organisation of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecol. Monogr.* 46:355-393.
- Menge, J.L. 1975. Effects of herbivores on community structure of the New England rocky intertidal region: distribution, abundance and diversity of algae. Ph.D. Dissertation. Harvard University, Cambridge, Massachusetts, USA.
- Mill, P.J. and J. Grahame. 1990. Distribution of the species of rough periwinkle (*Littorina*) in Great Britain. *Hydrobiol.* 193:21-27.
- Munda, I.M. 1992. Gradient in seaweed vegetation patterns along the North Icelandic coast, related to hydrographic conditions. *Hydrobiol.* 242:133-147.
- Newell, G.E. 1958. An experimental analysis of the behaviour of *Littorina littorea* under natural conditions in the laboratory. *J. Mar. Biol. Ass. U.K.* 37:241-266.
- Olla, B.L., A.J. Bejda and A.D. Martin. 1975. Activity movements and feeding behaviour of the cunner, *Tautoglabrus adspersus*, and comparisons of food habits with young tautog, *Tautoga onitis*, off Long Island, New York. *US Bureau of Fisheries Bull.* 73:895-900.
- Petratits, P.S. 1989. Effects of the periwinkle *Littorina littorea* (L.) and of intraspecific competition on growth and survivorship of the limpet *Notoacmaea testudinalis* (Müller). *J. Exp. Mar. Biol. Ecol.* 125:99-115.
- Pittman, R.C. 1974. The ecology of some tidepools of the Avalon Peninsula, Newfoundland. Thesis (M.Sc.). Memorial University of Newfoundland, St. John's, Newfoundland, Canada.
- Platt, T.A. 1971. The annual production by phytoplankton in St. Margaret's Bay, Nova Scotia. *J. Cons. int. Explor. Mer.* 33:324-334.
- Probyn, T.A. and A.R.O. Chapman. 1983. Summer growth of *Chordaria flagelliformis* (O.F. Muell.) C. Ag.: Physiological strategies in a nutrient stressed environment. *J. Exp. Mar. Biol. Ecol.* 73(3):243-271.
- Sacchi, C.F., A.O. Ambrogi and D. Voltolina. 1981. Recherches sur le spectre trophique compare de *Littorina saxatilis* (Olivi) et de *L. nigrolineata* (Gray) (gastropoda, prosobranchia) sur la greve de roscoff. II. -Cas de populations vivant au milieu d'algues macroscopiques. *Calh. Biol. Mar.* 22:83-88.

- Shannon, C.E. and W. Weaver. 1949. *The mathematical theory of communication*. University of Illinois Press, Urbana.
- Shannon, R.K., G.E. Crow, and A.C. Mathieson. 1988. Seasonal abundance and recruitment patterns of *Petalonia fascia* (O.R. Müller) Kuntze and *Scytosiphon lomentaria* (Lyngbye) Link var. *lomentaria* in New Hampshire, U.S.A. *Bot. Mar.* 33:207-214.
- Sokal, R.R. and F.J. Rohlf. 1969. *Biometry*. W.H. Freeman, San Francisco.
- South, G.R. and R.G. Hooper. 1980. A catalogue and atlas of the benthic marine algae of the island of Newfoundland. *Occasional Papers in Biology* No. 3:1-136.
- Steele, D.H. 1983. Marine ecology and zoogeography, pp 421-465. In: *Biogeography and ecology of the island of Newfoundland* (ed. G.R. South). The Hague: Dr W. Junk Publishers.
- Steneck, R.S. 1982. The limpet-coraline alga association: adaptations and defenses between a selective herbivore and its prey. *Ecology*. 63(2):507-522.
- Steneck, R.S. and L. Watling. 1982. Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Mar. Biol.* 68:299-319.
- Sze, P. 1980. Aspects of the ecology of macrophytic algae in high rockpools at the Isles of Shoals (USA). *Bot. Mar.* 23:313-318.
- Villalard-Bohnsack, M. and M.M. Harlin. 1992. Seasonal distribution and reproductive status of macroalgae in Narragansett Bay and associated waters, Rhode Island, U.S.A. *Bot. Mar.* 35:205-214.
- Watson, D.C. and T.A. Norton. 1985. Dietary preferences of the common periwinkle, *Littorina littorea* (L.). *J. Exp. Mar. Biol. Ecol.* 88:193-211.
- Yamada, S.B. and R.A. Mansour. 1987. Growth inhibition of native *Littorina saxatilis* (Oliv.) by introduced *L. littorea* (L.). *J. Exp. Mar. Biol. Ecol.* 105:187-196.

APPENDIX A

Mean % cover of algae and number per 1/16 m² of grazers on each sampling date.

Bay Bulls Pool 1

Species	Mar 1	Mar 25	Apr 23	May 27	Jun 24	Jul 14	Aug 6	Oct 5	Mean
<i>Chordaria flagelliformis</i>					0.2	1.0	2.9		0.51
<i>Monostroma grevillei</i>	15.0	57.6	33.0	18.2					15.48
<i>Scytosiphon lomentaria</i>				12.6	41.0	34.4	8.7	3.0	12.46
<i>Acrosiphonia arcta</i>		1.1	3.0	26.0	7.9	0.8	9.2		6.00
<i>Chaetomorpha linum</i>						9.7			1.21
Diatom (tube dwelling)	5.5								0.69
<i>Fragellaria</i>	5.0	5.8	10.1	8.2					3.64
<i>Clathromorphum circumscriptum</i>	23.8	17.4	24.6	13.4	26.0	22.2	28.8	27.4	22.95
<i>Corallina officinalis</i>	11.1	4.7	4.9	1.0	4.8	2.0	3.6	8.2	5.04
Green crust	36.0	20.5	2.0						7.31
<i>Hildenbrandia rubra</i>					1.3	1.8	0.9	6.0	1.25
" <i>Ralfsia</i> "					12.6	10.2	15.2	26.4	8.05
Bare rock	1.4	0.8	25.8	23.8	29.0	33.0	31.0	25.8	21.33
<i>Littorina littorea</i>	32.6	32.0	30.4	14.8	27.4	11.0	18.4	13.6	22.53
<i>Littorina saxatilis</i>	0.2	1.4	1.6	8.0	14.8	24.6	21.0	8.0	9.95
<i>Notoacmaea testudinalis</i>	0.4	1.8							0.28

Bay Bulls Pool 2

Species	Mar 26	Apr 27	Jun 11	Jul 15	Aug 7	Oct 6	Mean
<i>Dictyosiphon foeniculaceus</i>				7.3	10.1	2.90	
<i>Fucus distichus distichus</i>	82.6	37.4	30.6	53.4	41.4	46.0	48.57
<i>Monostroma grevillei</i>	5.6	4.4	1.2				1.87
<i>Scytosiphon lomentaria</i>			6.2	0.6	1.0		1.30
<i>Acrosiphonia arcta</i>	1.6	4.6	19.6	10.1	4.7	1.0	6.93
<i>Chaetomorpha linum</i>			5.4	2.2	8.3		2.65
<i>Platyella littoralis</i>	19.4	8.2	5.8	7.0	3.0		7.23
<i>Clathromorphum circumscriptum</i>	4.2	7.5	7.3	9.3	5.4	11.2	7.48
<i>Corallina officinalis</i>	1.2	2.5	2.8	4.0	0.2	2.3	2.17
Green crust	6.2	1.2					1.23
<i>Hildenbrandia rubra</i>		2.6	0.1	1.2	0.8	0.8	0.92
" <i>Ralfsia</i> "		10.0	9.9	8.8	11.8	11.1	8.60
Bare rock	22.4	21.4	15.8	14.8	20.6	26.4	20.23
<i>Lacuna vineta</i>	0.2						0.03
<i>Littorina littorea</i>			0.2	0.2	0.2	0.2	0.13
<i>Littorina obtusata</i>	2.2	0.6	3.0	3.6	5.6	3.6	3.10
<i>Littorina saxatilis</i>	3.2	13.0	20.2	7.8	7.6	7.8	9.93
<i>Notoacmaea testudinalis</i>	0.4						0.07

Bay Bulls Pool 3

Species	Apr 27	Jun 24	Jul 14	Aug 25	Oct 6	Mean
<i>Chordaria flagelliformis</i>		44.6	35.4	75.0	85.6	48.12
<i>Dictyosiphon foeniculaceus</i>				8.0		1.60
<i>Monostroma grevillei</i>	1.9	7.0	0.4			1.86
<i>Scytosiphon lomentaria</i>			39.8	2.9		8.54
<i>Acrosiphonia arcta</i>	4.7	36.6	20.4	5.3	0.7	13.54
<i>Fragellaria</i>	8.6					1.72
<i>Clathromorphum circumscriptum</i>	26.6	14.6	4.3	5.9	9.1	12.10
<i>Corallina officinalis</i>	13.2	0.2	0.1	0.4	0.8	2.94
" <i>Ralfsia</i> "	17.2	10.2	3.3	3.9	4.1	7.74
Bare rock	30.6	2.6	0.4	3.2	2.1	7.78
<i>Littorina obtusata</i>				0.2		0.04
<i>Littorina saxatilis</i>		0.2	0.4	0.6		0.24

Bay Bulls Pool 4

Species	Jun 25	Jul 15	Aug 25	Oct 6	Mean
<i>Chordaria flagelliformis</i>	20.8	48.2	69.2	84.8	55.75
<i>Dictyosiphon foeniculaceus</i>		10.0	15.0		6.25
<i>Monostroma grevillei</i>	19.2	7.9			6.78
<i>Scytosiphon lomentaria</i>	8.2	6.8	2.9		4.48
<i>Acrosiphonia arcta</i>	35.8	22.4	2.0	0.2	15.10
<i>Sphacelaria plumosa</i>		1.8			0.45
<i>Clathromorphum circumscriptum</i>	31.6	11.2	10.1	8.7	15.40
<i>Corallina officinalis</i>	0.5	0.9	7.6	7.4	4.10
" <i>Ralfsia</i> "	5.4	4.5	0.3	0.5	2.68
Bare rock	1.8	1.5	2.2	0.6	1.53
<i>Littorina obtusata</i>	0.8		0.2	0.2	0.30
<i>Littorina saxatilis</i>	3.0	5.6	2.4	1.8	3.20

Portugal Cove Pool 1

Species	May 15	Jul 10	Jul 30	Aug 28	Nov 20	Mean
<i>Chondrus crispus</i>	2.3			1.0	3.4	1.34
<i>Dictyosiphon foeniculaceus</i>	0.4	1.4	1.8			0.72
<i>Enteromorpha intestinalis</i>	4.2					0.84
<i>Fucus distichus distichus</i>	0.5	0.1	0.8	1.7	1.4	0.90
<i>Monostroma grevillei</i>	2.1					0.42
<i>Scytosiphon lomentaria</i>		2.5	2.4	1.5		1.28
<i>Acrosiphonia arcta</i>	67.8	74.6	81.0	21.3		48.94
<i>Chaetomorpha linum</i>		13.0	9.0	11.5		6.70
<i>Cladophora sericea</i>	0.1				44.6	8.94
<i>Polysiphonia urceolata</i>			0.1		2.2	0.46
<i>Sphacelaria plumosa</i>	5.0	3.3	3.1	37.2	16.8	13.08
<i>Clathromorphum circumscriptum</i>	7.8	3.5	1.3	14.2	12.6	7.88
<i>Hildenbrandia rubra</i>	2.4	2.1	0.7	4.1		1.86
" <i>Ralfsia</i> "			0.3	2.3	17.0	3.92
Bare rock	10.6	4.8	3.9	13.0	5.2	7.50
<i>Littorina saxatilis</i>	12.4	4.0	1.8	5.8	1.0	5.00

Portugal Cove Pool 2

Species	Jun 10	Jul 10	Aug 28	Nov 20	Mean
<i>Chondrus crispus</i>	5.0	1.3	4.2	6.8	4.33
<i>Chordaria flagelliformis</i>		0.7			0.18
<i>Dictyosiphon foeniculaceus</i>		2.0			0.50
<i>Fucus distichus distichus</i>	3.7	4.9	11.2	11.7	7.88
<i>Scytosiphon lomentaria</i>	3.3	6.2	0.2		2.43
<i>Acrosiphonia arcta</i>	28.0	48.6	24.4		25.25
<i>Chaetomorpha linum</i>	13.8	18.4			8.05
<i>Cladophora sericea</i>	1.0	1.8	14.4	43.6	15.20
<i>Sphacelaria plumosa</i>	6.6	3.7	7.6	10.2	7.03
<i>Clathromorphum circumscriptum</i>	11.8	5.4	12.2	13.2	10.65
<i>Corallina officinalis</i>	0.1	0.9	1.1	1.9	1.00
<i>Hildenbrandia rubra</i>	2.1	0.2	2.6		1.23
" <i>Ralfsia</i> "	1.2	1.6	8.1	7.2	4.53
Bare rock	20.0	6.0	15.0	7.6	12.15
<i>Littorina obtusata</i>		0.4	0.2		0.15
<i>Littorina saxatilis</i>	32.2	8.6	29.0	10.6	20.10

Bauline Pool 1

Species	Apr 14	May 25	Jun 12	Jul 27	Aug 26	Nov 4	Mean
<i>Monostroma grevillei</i>	17.6						2.93
<i>Scytosiphon lomentaria</i>		1.1	0.2				0.22
<i>Acrosiphonia arcta</i>		2.9	5.6				1.42
<i>Chaetomorpha linum</i>	2.2						0.37
<i>Sphacelaria plumosa</i>	1.0	0.2	3.0				0.70
<i>Clathromorphum circumscriptum</i>	12.0	21.4	26.8	32.0	28.8	17.4	23.07
<i>Corallina officinalis</i>	2.3	7.4	11.0	13.2	13.0	13.6	10.08
<i>Hildenbrandia rubra</i>	9.8	9.0	15.0	21.4	20.6	22.4	16.37
" <i>Ralfsia</i> "		2.2	3.2			0.2	0.93
Bare rock	50.6	55.4	40.6	39.0	42.4	46.8	45.80
<i>Littorina littorea</i>	38.2	28.2	26.6	15.8	9.4	5.6	20.63
<i>Littorina saxatilis</i>	2.8	15.0	37.0	13.4	8.6	1.2	13.00

Bauline Pool 2

Species	Apr 16	May 26	Jun 30	Jul 29	Aug 27	Mean
<i>Dictyosiphon foeniculaceus</i>					1.0	0.20
<i>Fucus distichus distichus</i>	0.9	0.5	1.5	1.7	2.9	1.50
<i>Monostroma grevillei</i>	11.0	5.6				3.32
<i>Scytosiphon lomentaria</i>			12.8	41.4	25.8	16.00
<i>Acrosiphonia arcta</i>	0.4	1.1	5.8	4.1		2.28
Diatom (tube dwelling)	1.8					0.36
<i>Sphacelaria plumosa</i>	0.4			0.4		0.16
<i>Clathromorphum circumscriptum</i>	13.2	16.0	16.6	12.8	12.0	14.12
<i>Corallina officinalis</i>	6.0	7.1	12.6	12.9	13.8	10.48
Green crust	0.6					0.12
<i>Hildenbrandia rubra</i>	13.8	5.9	3.2	9.0	7.6	7.90
" <i>Ralfsia</i> "		11.8	42.0	11.5	12.8	15.62
Bare rock	47.0	54.2	13.0	16.6	41.0	34.36
<i>Lacuna vineta</i>					613.6	122.72
<i>Littorina littorea</i>				0.2		0.04
<i>Littorina saxatilis</i>	9.2	37.6	43.4	27.6	10.4	25.64

Bauline Pool 3

Species	Apr 28	May 25	Jul 13	Jul 29	Aug 27	Nov 4	Mean
<i>Chondrus crispus</i>	6.8	3.4			3.0	6.6	3.30
<i>Fucus distichus distichus</i>	5.6	3.2	7.0	9.2	5.6	1.5	5.35
<i>Monostroma grevillei</i>	0.6	0.1					0.12
<i>Scytosiphon lomentaria</i>			0.6	1.6			0.37
<i>Acrosiphonia arcta</i>	10.0	22.2	31.8	21.0	8.4		15.57
<i>Sphacelaria plumosa</i>	3.8	1.9	2.1	5.0	5.6	4.9	3.88
<i>Clathromorphum circumscriptum</i>	24.6	18.0	24.0	23.4	22.6	20.6	22.20
<i>Corallina officinalis</i>	6.7	3.9	9.4	5.4	5.5	5.0	5.98
<i>Hildenbrandia rubra</i>	4.6	4.0	9.6	19.2	15.4	8.8	10.27
" <i>Ralfsia</i> "	1.0	0.6	1.4		2.6	17.0	3.77
Bare rock	40.2	39.0	26.2	21.6	35.4	37.4	33.30
<i>Lacuna vineta</i>						340.8	56.80
<i>Littorina littorea</i>	1.2	0.8	2.6	2.6	3.6	4.0	2.47
<i>Littorina obtusata</i>	0.2	0.4		0.2			0.13
<i>Littorina saxatilis</i>	6.2	42.6	35.4	27.2	12.8	4.4	21.43

Bauline Pool 4

Species	Apr 16	May 26	Jun 12	Jul 13	Aug 27	Mean
<i>Ascophyllum nodosum</i>			1.0		0.2	0.24
<i>Chordaria flagelliformis</i>				5.7		1.14
<i>Fucus distichus distichus</i>	5.4	2.6	5.6	8.2	6.7	5.70
<i>Monostroma grevillei</i>	1.9	4.9	0.8			1.52
<i>Scytosiphon lomentaria</i>		0.1	0.9	1.2		0.44
<i>Acrosiphonia arcta</i>	0.4	38.0	44.2	32.2		22.96
<i>Sphacelaria plumosa</i>	13.4	8.2	7.6	9.4	12.4	10.20
<i>Clathromorphum circumscriptum</i>	29.2	24.4	18.4	19.8	23.0	22.96
<i>Corallina officinalis</i>	9.2	2.5	4.4	7.9	17.8	8.36
<i>Hildenbrandia rubra</i>	6.4				0.8	1.44
" <i>Ralfsia</i> "		4.9	7.8	10.4	18.4	8.30
Bare rock	34.6	28.4	20.8	18.2	27.0	25.80
<i>Littorina littorea</i>		1.0	1.0	2.0	2.4	1.28
<i>Littorina obtusata</i>		3.4	3.8		1.0	1.64
<i>Littorina saxatilis</i>	0.6	19.2	16.8	18.2	4.8	11.92



