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ECOLOGY OF THE KELP LAMINARIA LONGICRURIS AND ITS PRINCIPAL GRAZERS IN THE ROCKY SUBTIDAL OF NOVA SCOTIA

by

. 'Craig Richard' Johnson

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A thesis submitted in partial fulfillment of the requirements for the Degree of Doctor of Philosophy at Dalhousie University,

November 1984

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	CONTENTS	
		,
۵	HISI OF FIGURED ,	ж ,
Ŷ		
	ТОТ О́́́ ТИПГО́́ •••••••••••••••••••••••••••••••••••	20112
		0
చి		xv
`•		
4		XAT
Þ	SVILOT S AND AREDEVIATIONS	
1 <del>-</del>		** V .≛. ≛.
•	CHAPTER 1. GENERAL INTRODUCTION	1.
		·
	CHAPTER 2. GENERAL METHODS	5
( 156		
6	2.1 Study sites and undertrater trork	5
* •	2.2 Identification of algae	8
· *	2.3 Statistical analysis	9
N	CHAPTER 3. RELATIONSHIP BETWEEN RELEASE FROM SEA URCHIN	
`-¶.	(STRONGVLOCENTROTUS DROEBACHIENSIS) GRAZING AND BECOVERY	
	(PERINTERCONTROLOGY DECONTROLOGY OF THE RECORDER OF THE RECORD	
	OF SEANEEDS	14 .
۰.	OF SEAMEEDS	14 14
۱ <b>۰</b>	OF SEAWEEDS	14 14 16
, <b>,</b>	OF SEAMEEDS	14 14 16
<b>۱</b>	OF SEAMEEDS	14 14 16 20
, • • •	OF SEAWEEDS 3.1 Introduction 3.2 Methods 3.3 Results 4 3.4 Discussion	14 14 16 20 29
۱. ۳	OF SEAWEEDS 3.1 Introduction 3.2 Methods 3.3 Results 3.4 Discussion	14 14 16 20 29
	OF SEAMEEDS 3.1 Introduction 3.2 Methods 3.3 Results 4 3.4 Discussion CHAPTER 4. INFLUENCE OF ENCRUSTING CORALLINE ALGAE ON	14 14 16 20 29
	OF SEAWEEDS 3.1 Introduction 3.2 Methods 3.3 Results 4 3.4 Discussion CHAPTER 4. INFLUENCE OF ENCRUSTING CORALLINE ALGAE ON SETTLEMENT OF NON-CALCAREOUS SEAWEEDS	14 14 16 20 29 ~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
	OF SEAVEEDS 3.1 Introduction 3.2 Methods 3.3 Results 3.4 Discussion CHAPTER 4. INFLUENCE OF ENCRUSTING CORALLINE ALGAE ON SETTLEMENT OF NON-CALCAREOUS SEAWEEDS 4.1 Introduction	14 14 16 20 29 31 31
· · · · · · · · · · · · · · · · · · ·	OF SEAWEEDS 3.1 Introduction 3.2 Methods 3.3 Results 3.4 Discussion CHAPTER 4. INFLUENCE OF ENCRUSTING CORALLINE ALGAE ON SETTLEMENT OF NON-CALCAREOUS SEAWEEDS 4.1 Introduction	14 14 16 20 29 31 31
· · · · · · · · · · · · · · · · · · ·	OF SEAWEEDS 3.1 Introduction 3.2 Methods 3.3 Results 3.4 Discussion CHAPTER 4. INFLUENCE OF ENCRUSTING CORALLINE ALGAE ON SETTLEMENT OF NON-CALCAREOUS SEAWEEDS 4.1 Introduction	14 14 20 29 31 31 37

4.3 Results ..... 40 4.3.1 Incidence and distribution of coralline genera ..... 40 4.3.2 Preliminary analysis; diversity and total blomass ... 41. 4.3.3 Multivarjate analysis; responses of individual species 4.3.4 Assessment of blas in settlement and growth of seaweeds on overturned rocks ...... ... 55 4.4 Discussion ..... ······················ 4.4.1º Mechanism of inhibition of recrultment of fleshy seaveeds on <u>Phymatolithon</u> crusts ..... 62 4.4.2 Ecological consequences of antifouling "by Phymatolithon 4.4.2.1 Effects of corallines in the absence of a kelp 4.4.2.2 Effects of corallines in the presence of a canopy .. 66 4.4.2.3 Influence of Phymatolithon on Laminaria versus 4.4.3 Grazers, sloughing of epithallfal cells and \*\*\*\*\*\*\*\*\*\* survival of crustose coralline algae . . . . . . . . 67 4.4.4 Summary and comment on implications for hard-bottom ÷ ، ب , benthos CHAPTER 5. RE-ESTABLISHMENT AND MAINTENANCE OF LAMINARIA LONGICRURIS BEDS 71 5.1 Introduction 5.2 Methods , ..... 76 ليحج C 7

iii. 5.2.1 'Index of lamina area 5.2.2. Pårtitioning of changes in canopy area into , components due to fecrultment and nortality of plants, and net growth and net loss of individual laminae 5.2.3 Recruitment of Laminaria; comparison between sites 5.3 Results 5.3.2 Partitioning of seasonal variation in the Laminaria canopy into components due to recruitment, mortality, 5.3.3 Influence of canopy removal on <u>Laminaria</u> • recruïtment 5.4 Discussion 5.4.1 Rate of recovery of Laminaria canopy and 5.4.2 · Seasonal variation in extent of Laminaria canopy ..... 102 5.4.3 Intraspecific competition density `dependent, regulation of recruitment ..... 5.4.3.1 Shading by adult conspectfice. . 104 5.4.3.2° Crowding by juvenile conspecifics ..... 105 5.4.4 Maintenance of dominance .5.4.5 The 'Grime' model of plant strategies and ъ categorization of L. longicruris **.** 109 CHAPTER 6. IMPACT OF GRAZERS ON LAMINARIA LONGICRURIS IN THE ABSENCE OF HIGH DENSITIES OF SEA URCHINS ..... 112<sup>-</sup> 5

ø	· ···································
a	
	6.2.1 Impact of limpet ( <u>Notoacnaea testudinalis</u> ) and
	chiton (Tonicella rubra) grazing on recruitment of L.
	<u>longicruris</u>
•	- 6.2.2 Impact of L. vincta on the canopy of L.
٢	longicruris •
	6.2.2.1; Description of the Lacuna population 115
ų	6.2.2.2 Dispersal ability of post-metamorphic snails
u.	6.2.2.3 Distribution of <u>L</u> . <u>vincta</u> grazing on <u>L</u> .
	Longicruris
	6.2.2.4 Intraplant distribution of polyphenolic
	compounds in L. longicruris
-	6.2.2.5 Size-specific grazing rates of L. vincta124
3.	6.2.2.6 Impact of grazing by L. vincta on the L.
•	<u>longicruris</u> canopy 125
	6.2.2.6.1 Direct consumption of laminae 125
<i>c</i> •	6.2.2.6.2 Overall impact on canopy
	$6_{p}2_{q}2_{q}$ .7 Impact of predation by <u>T</u> . <u>adspersus</u> on <u>L</u> .
	· <u>vincta</u>
	6.3 Results
	6.3.1 Influence of grazing by. N. testudinalis and T.
~3	rubra 'on recruitment of L. longicruris 132
	6.3.2 Impact of L. vincta on canopy of L. longicruris 132
	6.3.2.1 Description of the L. vincta population at
	Paul Pt. in 1983

6.3.2.2 Dispersal ability of post-metanorphic L. 6.3.2.3 Distribution of grazing by L. vinzta on L. bigicruris "..... .... 151 ° 6.3.2.4 Concentration of polyphen is within  $\underline{L}$ . longicruris plants 6.3.2.5 Size-specific grazing rates of L. vincta on L. ۰ ، مومومومومومو longicruris .... 154 6.3.2.6 Impact of grazing by L. vincta on the canopy of L. longicruris ...... ° 6.3.2.6.1 Direct consumption of laminae ...... 160 6.3.2.6.2 Overall impact on canopy ...... 160 6.3.2.7° Impact of predation by T. adsperses on L. v. vincta ..... . 🗝 169 6.3.2.7.1 Evidence from field populations of differential size-selective predation by different size classes of T. adspersus on L. vincta ..... 174 6.3.2.7.2 Evidence from a laboratory experiment of differential size selective predation on L. vincta by different sizes of T. adspersus ..... 185 6.4.1 Characteristics of L. vincta considered in · relation to its grazing pressure 6.4.2 Influence of predation by <u>T</u>. <u>adspersus</u> on the 6.4.3 Effect of grazing by L. wincta on the canopy of L.

vi. vi. longicruris 6.4.4 Ecological Implications of meduction of the L. longicruris canopy from grazing by L. vincta ..... 193 . 6.4.5 Relationship between distribution of polyphenols. and variation in toughness and nutritional quality in. L. longicruris, and Subtidal community structure in the absence of high densities of sea urchins ..... 194 . 6.4.6 Evolution of antiherbivore defenses in L. . 6.4.7 Comparison of the impact of S. droebachiensis and L. vincta on populations of L. longicruris ..... 205 APPENDIX A.1 Population censuses of sea durchins in "urchin `.' p enclosure ..... APPENDIX A.2 Evaluation of the point technique for estimating percentage cover of seaweeds ...... 218 APPENDIX A.3 Evaluation of sampling scheme for estimating percentage cover of seaweeds ..... 221 APPENDIX A:4 List of seaweed species in enclosures and a J non-merimental area at Mill Cove, ..... 222 APPENDIX A.5 Total cover of seaweeds in enclosures and 📜 🎽 8. APPENDIX A.6 Diversity of seaweeds in enclosures and non-experimental area at Mill Cove ...... 225 APPENDIX A.7 Variance absorbed by principal vectors in PCA of ې د

cover of seaweeds in enclosures and non-experimental area at Mill Cove ...... APPENDIX A.8 'Element coefficients for first 3 PC's in a ECA of cover of seaweeds a 'enclosures and' non-experimental." area at Mill Cove APPENDIX B. 1 Biomass of, seaweeds recruited on granite and 228 • Phymatolithon substrata APPENDIX B.2 Diversity and evenness of seaweed species · recruited on granite and Phymatolithon substrata ....444 234 APPENDIX B.3 Total biomass of seaweeds recruited on granite and Phymatolithon substrata · • • 235 · <sup>\*</sup> • APPENDIX B.4 Variance absorbed by PC's in a PCA of seaweeds , <sup>2</sup>..., 236 <sup>2</sup> \* recruited on granite and Phymatolithon substrata APPENDIX B.5 Element coefficients for the first.4 PC's in a. PCÅ of seaweed species, recruited on granite and " Phymatolithon substrata 237 -\* • • • • • • • • • • • • • • • • APPENDIX B.6 Variance absorbed by PC's in a PCA of seaweeds recruited on intertidal and subtidal granite substrata APPENDIX B.7 Element coefficients for the first 3 PC's in a PCA of seaweeds recruited on intertidal and subtidal granite substrata APPENDIX C.l Summary of manipulations of seaweeds in experimental plots at Paul Pt. . 240 APPENDIX C.2 Estimates of lamina area index of Laminaria longicruris, in the non-experimental areas at Mill Cove and - Paul Pt. 🚙 ..... .. 241 a0 •

viii.  $\{ \}$ APPENDIX C.3 Lamina- area index of Laminaria longicruris in experimental plots at Paul Pt. APPENDIX C.4 Partitioning of changes in the lamina area index ' of Laminaria longicruris into components due to mortality, recruitment, and net loss and net growth of laminae ..... 243 APPENDIX D.1 Use of non-repeated measures ~ ANOVA when the . `subject' term of a repeated measures.model is positive ... 244 APPENDIX D.2 Densities of Lacuna vincta on all substrata per unit area of bottom at Paul Pt. ..... 245° APPENDIX D.3 Densities of <u>Lacuna</u> vincía on <u>Laminaria</u> longicruris laminae at Paul Pt. APPENDIX D.4 Distribution of shell, lengths of Lacuna vincta on Laminaria longicruris at Paul. Pt. ł APPENDIX D.5 'Mean size of cohorts of Lacuna vincta on APPENDIX D.6 Sex ratio of Lacuna vincta on Laminaria . .. 249 longicruris at Paul Pt. APPENDIX D.7 Recolonization rates of Lacuna vincta' on Laminaria longicruris at Paul Pt. APPENDIX D.8 Distribution of damage from grazing by Lacuna vincta on laminae of Laminaria longicruris APPENDIX D.9 Variation in concentrations of polyphenols ' ... within Laminaria longicruris plants ...... 252 , APPENDIX D.10 Size-specific grazing rates of Lacuna vincta on APPENDIX D.11 Effect of removal of Lacuna vingta from

° s	
	`
Laminaria longicruris on the rate of increase in width of	
	254
APPENDIX D.12 Effect of removal of Lacuna vincta from	
Laminaria longicruris on the rate of increase in length of	
laminag	255
APPENDIX D.13 Predicted values of the lamina area index of	
Laminaria longicruris in the non-experimental area at Paul.	,
Pt. assuming damage to Laminaria by Lacuna vincta had not	
occurred	256
APPENDIX D.14 Incidence of Lacuna vincta in guts of	
Tautogolabrus adspersus	257
APPENDIX D.15 Relationship between size of largest Lacuna	, .
vincta in guts of . <u>Tautogolabrus</u> adspersus, and size of <u>T</u> .	
adspersus	258
APPENDIX D.16 Size selective predation by Tautogolabrus	o
adspersus on Lacuna vincta	259
REFERENCES	260
.)	X.

LIST OF FIGURES Fig. 2.1 Map showing location of study sites Sr. Margarets Bay ..... و Fig. 3.1 Proportion of hard substrate (a) bare and unshaded, (b) bare but shaded, and (c) overgrown by non-crustose seaweeds in the urchin and control enclosures, and in the non-experimental area at Mill Cove; and densities of sea . urchins (Strongylocentrotus droebachiensis) in the urchin 22 enclosure Fig. 3.2 Shannon diversity index (H) for seaweed community in 4 urchin and control enclosures, and in thed P 0 P Fig. 3.3 Separation of treatment/date groups on the first, three axes generated by R-type principal components analysis of the percentage cover of seaweed species ...... Fig. 4.1 Diagram of cross-section of generalized \$ 0 Fig. 4.2 Diversity and evenness of seaweed species recruited 🔬 on bare granite substratum and on an equivalent area of Fig. 4.3 Total biomass of all non-crustose seaweed species recruited on bare granite substratum and on an equivalent area of Phymatolithon crust in the absence of grazers ..... 47 ۵ } . . . . Fig. 4.4 Mean biomass of seaweed species recruited on bare granite and Phymatolithon substrata in the absence of grazers Fig. 4.5 Relationship between difference in biomass of seaweed species on granite and Phymatolithon ` substrata, and blomass on granite, ..... 57 Fig. 5.1 Summary of the Grime (1977, 1979) model, showing the location of plant strategies within a ternary framework Ŷ of different levels of competition, disturbance, and stress 73 Fig. 5.2 Diagram of treatments in experimental plots at both Paul Pt. - and Mill Cove ..... 80 Fig. 5.3 Estimate's of the lamina area index of Laminaria longicruris in the non-experimental areas at Paul Pt, Fig. 5.4 Lamina area index of Laminaria longicruris in Į.

xi. -1 experimental plots 1,2,5 and 6, and mean values for the non-experimental area, at Paul Pt. 88 . . . . . . . . . . . . . . . . . . . ° 0 Fig. 5.5 Partitioning of rate of change of lamina area index of Laminaria longicruris into components due to mortality . and recruitment of plants, and net loss and net growth of 18t Fig. 6.1 Delineation of regions of Laminaria longicruris (1) 0 assessed for grazing damage by Lacuna vincta, (ii) from which 'samples were taken for determination of polyphenol levels, and (iii) for which Chapman and Craigie (1977,1978) and A.R.O. Chapman (unpubl. data) determined levels of organic nitrogen, laminaran, Fig. 6.2 Densities of Lacuna vincta on all substrata (including Laminaria longicruris) per unit area of bottom at shallow, medium depth, and deep stations at Paul Pt.  $\dots$  136  $^\circ$ Fig. 6.3 Densities of Lacuna vincta on Laminaria longicruris laminae at shallow, medium depth and deep stations at Paul Pt. Fig. 6.4 Distribution of shell lengths of Lacuna vincta on Laminaria longicruris laminae at Paul Pt Fig. 6.5 Growth (mean shell length) of cohorts of Lacuna vincta on Laminaria longicruris laminae at Paul Pt. ..... 143 Fig. 6.6 Sex ratio of <u>Lacuna vincta</u> on <u>Laminaria</u> <u>longicruris</u> laminae at Paul Pt. ..... 146 Fig. 6.7 Rates of recolonization of Lacuna vincta on laminag of Laminaria longicruris in three groups of 4m<sup>2</sup> and 16m<sup>4</sup> plots initially cleared of snails at Paul Pt. ...... 148 Fig. 6.8 Sinking rates of Lacuna vincta with foot and antennae withdrawn and with foot and antennae extended .... 150 Fig. 6.9 Distribution of damage from grazing by Laguna vincta Fig. 6.10 Variation in concentrations of polyphenols within Laminaria longicruris plants ..... 157 Fig. 6.11 Size specific grazing rates of Lacuna vincta on tissue from the marginal frill of Laminaria longicruris (in the laboratory) 159 Fig. 6.12 Effect of removal of Lacuna vincta from Laminaria longicruris on the rate of increase in width of Laminaria

CF.

; o

	laminae 164	
Fig.	6.13 Effect of removal of <u>Lacuna vincta</u> from <u>Laminaria</u> <u>longicruris</u> ) on the rate of increase in length of Laminaria lamiñae	•
Fig.	6.14 Predicted canopy area (lamina area index) in non-experimental area at Paul Pt. assuming damage to Laminaria longicruris by Lacuna vincta had not occurred 171	
Fig.	6.15 Incidence of <u>Lacune vincta</u> in guts of <u>Tautogolabrus</u> adspersus collected from above the thermocline at Paul Pt. 173	
Fig.	6.16 Relationship between size (shell length) of largest Lacuna vincta in guts of <u>Tautogolabrus</u> adspērsus and size (total length) of <u>T. adspersus</u> 178	
Fig.	6.17 Proportion of Lacuna vincta in specific size classes consumed per fish (Tautogolabrus adspersus) of given size in 5 days in a controlled laboratory experiment	0
Fig.	6.18 Size preference index describing the preference of different sizes of <u>Tautogolabrus adspersus</u> for specific size classes of <u>Lacuna vincta</u> in a controlled laboratory experiment	
Fig.	6.19 Intraplant variation in levels of alginic acid and cellulose in <u>Laminaria longicruris</u> (A.R.O. Chapman unpubl. data)	
Fig.	7.1 Diagram summarizing the dynamics and principal interactions influencing community structure in the rocky subtidal in Nova Scotia	

1

 $P \in I$ 

1

٥

xii.

## LIST OF. TABLES

1

C.

o \*

	Table 4.1 Occurrence of species of fleshy algae onPhymatolithon,Lithothamhium, and bare granite substratain the absence of grazers	42 `
P	Table 4.2 Influence of the crustose coralline <u>Phymatolithon</u> on the recruitment of seaweeds. Results of 3-way (substratum x date x species) ANOVA of biomass	50
L	<ul> <li>granite substrata. Results of 2-way (date x substratum)</li> <li>MANOVA of principal components</li> </ul>	52
¢	Table 4.4 Biomass of seaweed species recruited on intertidal and overfurned subtidal granite rocks	58
	Table 4,5 Settlement of seaweeds on bare surfaces of overturned. subtidal. rocks, and rocks from the high intertidal. Results of 1-way ANOVA of principal components	സ
•	Table 5.1 <sup>III</sup> Recruitment of Láminaria longicruris in kelp         removal plots at Mill Cove and Paul Pt.	85
د	Table 5.2 Comparison of lamina area index of <u>Laminaria</u> longicruris in four experimental plots with estimates of the index in the non-experimental area at Paul Pt	89
	Table 5.3 Comparison of contribution of components of recruitment, mortality, net blade loss and net growth of laminae, to rates of change in the lamina area index of Laminaria longicruris. Results of 3-way (component x	, ,
	Table 5.4 Recruitment of <u>Laminaria longicruris</u> in kelp	92
	removal plots, non-removal plots, and in the non-experimental area at Paul Pt.	96
	Table 5.5 Mean size (estimated shade area of laminae) of <u>Laminaria longicruris</u> recruits in kelp removal plots, non-removal plots and in the non-experimental area at Paul Pt.	97
<b>5</b> ,	Table 5.6 Results of t-tests comparing mean size of Laminaria <u>Iongicruris</u> recruits in kelp removal plots, non-removal plots, and in the non-experimental area at Paul Pt	98`')
Ŧ	Table 6.1 Comparison of recruitment of Laminaria longicruris in two plots from which chitons and limpets were removed, with recruitment in the adjacent non-experimental area, Paul Pt.	133
		•

Ŀ

xiii.

ß

Ş

~

ę.

ł

ĉ

Table 6.2 In situ qualitative assessment of damage from grazing by Lacuna vincta on the stipes and holdfasts, and the meristem of Laminaria longicrurią 155 . . . . . . . . . . . . . . . Table 6.3 Mean change in biomass over 21 days of undamaged Laminaria 'longicruris and of plants damaged from grazing by Lacuna vincta Table 6.4 Comparison of increments in width of laminae of Laminaria longicruris in a population maintained clear of Lacuna vincta with an unmanipulated control population .... 165 Table 6.5 Comparison of increments in length of laminae of Laminaria longicruris in a population maintained clear of Lacuna vincta with an unmanipulated control population .... 168 Table 6.6 Comparison of mean size (total length) of Tautogolabrus adspersus with and without Lacuna vincta in .. 175 their guts Table 6.7 Size-preference indices of specific size classes of Tautogolabrus adspersus for Lacuna vincta in the field .... 176 Table 6.8 Size-selective predation by <u>Tautogolabrus</u> adspersus on <u>Lacuna vincta</u> in a controlled laboratory experiment. Results of 2-way (fish size x sndil size) ANOVA of proportion of snails consumed .... 181 Table 6.9 Size-preference indices of specific size classes of Tautogolabrus adspersus for Lacuna vincta in a controlled Table 6.10 Intraplant variation in organic nitrogen content in Laminaria longicruris (A.R.O., Chapman, unpubl. data) .. 197 Table 6.11 Qualitative ranking of intraplant differences in Laminaria longicruris of damage by Lacuna vincta, levels of organic nitrogen, laminaran, mannitol, alginic acid ۹. Table 6.12 Relationship between phenolic content of vegetative tissue and specific growth rate in brown algae .. 204

#### ABSTRACT

Until recently, the rocky subtidal of the. Atlantic coast of by sea úrchin/coralline Noya Scotia characterized was alga - dominated 'barren grounds', and virtual' absence of 'fleshy However, in the autumn months of 1980-1983, epizootics. macroalgae. decimated the urchin <u>(Strongylocentrotus</u> droebac populations, and seaweeds began to reappear in the subtidal. droebachiensis)

In this study, manipulative experiments indicated that recovery of the seaweeds occurred as a direct result of release from urchin grazing. In the absence of grazers, recruitment of seaweeds is inhibited by the coralline alga <u>Phymatolithon</u>. The mechanism of antifouling by the coralline is <u>likely</u> sloughing of epithallial cells from the surface of the crust, Extensive die-back of coralline crusts beneath seaweed cover did not occur.

Despite the antifouling action of Phymatolithon, the kelp Laminaria longicruris demonstrated impressive ability to recolonize and rapidly develop a closed stratum. Although the kelp canopy erodes for most of the year, rapid growth early in spring restores a closed stratum before most other seaweeds realize accelerated growth . rates. In manifesting characteristics of opportunistic, competitive and stress-tolerant strategies, L. longicruris is well adapted to maintain its dominant status in a variety of habitats of varying levels of disturbance, competition, and nutrient stress.

The gastropod Lacuna vincta was the principal grazer of L. Tongicruris following mass mortality of the urchins. Although direct consumption of plant tissue by the snails was relatively small, grazing damage promoted the tearing off of large portions of the lateral frill of the kelp laminae. The snails exhibited strong preference for the frill region, but avoided the meristem and stipe. This pattern of grazing resulted in significant reductions in canopyarea, but did not increase mortality of the kelp. Avoidance of the meristem by the snails is likely due to the high concentrations of polyphenols in this region. The tough stipe is of relatively poor nutritional value. The labrid fish Tautogolabrus adspersus is the most important predator of Lacuna vincta, but its predatory impact is limited since snails gapidly attain a size refuge safe from most ° sizes of the fish.

In overview, following mass mortality of sea urchins, L. longicruris replaced the urchins as the single most important sprong interacting species influencing community structure. However, in contrast to the side tion on barren grounds in which the urchins are the principal biological determinants of community composition and organization, the thelp influences community structure in concert with a suite of weakly interacting species.

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A large field-oriented project is never a solo effort. My supervisor, Ken Mann, was a continual source of logistic and moral My support, and along with committee members Tony Chapman, Eric Mill's and Ian McLaren, provided valuable guidance and criticism of the research and writing of the thesis throughout. Brock Bernstein, Jack McLachkan hid Robert Scheibling also gave useful discussion. Identification of seaweed species might, have been a nightmare without the frequent' and enthusiastic help of Carolyn Bird. Mark Ragan did not hesitate to interrupt a hectic schedule to perform the -polyphenol assays. Similarly, Chris Field gave many hours of advice on statistical procedures. Charlie Thompson was a great help in the building of several pieces of apparatus, and John Coates and Doug Wiseman made my life easier by clearing roads through "bureaucratic jungles of red tape. Freddy (Stan) Watts provided valuable advice and training in diving procedures. John Farley kindly allocated me most of his office space for the writing of this thesis, and provided timely opportunities for work-avoidance behaviour in his expositions on the United Frait Company, why we eat so many bananas, British Imperialism, and how schistosomiasis has changed the history of the world. I greatly appreciate the efforts of, and extend sincere thanks to, all of these persons.

Finally, because they deserve special mention, are the divers. I shall be ever grateful to Pat Young, James Smith, Blair Gill, John Houston, and others too numerous to name, for their untiring and uncomplaining efforts beyond any reasonable call of duty. They worked long hours from open boats, and in abominable conditions in winter, in helping to tally 1400 man-hours underwater on this project.

xvii. Ŵ SYMBOLS AND ABBREVIATIONS 🔍 = probability of type I error ANOVA = analysis of variance (univariate) B(t) = standing blomass of Laminaria longicruris laminae substratum at time t 1 df = degrees of freedom d(i) = value proportional to area of region i of Laminaria longicruris lamina damaged by snails D(i) = index of distribution of damage by Lacuna vincta on Laminaria <u>longicruris</u> laminae D(t) = density of snails on Laminaria longicruris lamine at time t F = F statistic <u>G</u> = column vector of the size specific grazing rates of Lacuna vincta on Laminaria longicruris laminae H = Shannon diversity index  $I_{1}$  = preference index of <u>Tautogolabrus</u> adspersus in size class i for <u>Lacuna vincta</u> in size class j J = index of evenness L = length of Laminaria longicruris lamina . 8 ~ MANOVA = multivariate analysis of variance n, = total number of Lacuna vincta consumed by Tautogolabrus adopersus of size class i Ð o = number of Lacuna vincta in size class j eaten by Tautogolabrus adspersus in size class i PCA = principal components analysis PCn =- n<sup>th</sup> principal component  $p_i = proportion cover of i<sup>th</sup> species$  $p_i = proportion$  of <u>Lacuna</u> vincta in size class j in population at large' P(i) = proportion of region i exhibiting snail damage

P(i) = average proportion of snail damage per region i, averaged over all regions

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<u>P(t) = row vector giving the proportion c</u> the <u>Lacuna vincta</u> population in each size class at time t

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r = Pearson product moment correlation coefficient

 $S_{\circ}E_{\circ} = standard error$ 

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SNK = Student-Newman-Keulg multiple range) test.

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- S(t) = total surface area of <u>Laminaria</u> <u>longicruris</u> laminae  $m^{-2}$ . substratum at time t
  - T(i) = value proportional to total area of region i of <u>Laminaria</u> longicruris lamina

W = maximum width of Laminaria longicruris lamina, \*

Y = untransformed variable

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#### CHAPTER 1

1.

#### GENERAL INTRODUCTION

Biological interactions play an important part in determining the structure of many natural communities. The recent history of the nearshore rocky subtidal of the Atlantic coast of Nova Scotia provides a particularly colourful and dynamic example of how interactions among species can radically affect community structure. In 1968, Mann (1972a) first noticed the occurrence of high densities of sea urchins (Strongylocentrotus droebachiensis) on bare rock substratum as holes in extensive beds of seaweeds in St. Margaret's Bay (see fig. 2.1). These patches expanded, and rapid destruction of the kelp beds and their replacement by what was termed `urchin-dominated barren grounds' (sensu Lawrence 1975) soon followed (Mann and Breen 1972; Breen and Mann 1976a, b; Lang and Mann 1976). Subsequently, a large scale investigation revealed that the entire Atlantic coast of the province was characterized by high densities of sea urchins but virtually no macrophytes (Wharton and Mann 1981). Moreover, unlike most herbivores that overgraze their food supply, the urchins were able to persist in 'the absence of macroalgae, and thus maintained the 'barren' condition (see reviews by Mann 1977; Johnson and Mann 1982).

It seemed then, that the 'barren grounds' represented a new, long-term configuration of the community that had far-reaching implications for 'the overall structure of the nearshore subtidal system (Mann 1977; Wharton and Mann 1981). The urchins had mediated a transition from a highly productive system dominated by the kelp Laminaria longicruris (Mann 1972a,b), to one of a low productivity.
 devoid of seaweed. With a decrease in primary production of nearly two orders, of magnitude (Chapman 1981), a collapse in secondary production could be expected, and there was evidence from lobster
 catches that this had already occurred (Wharton and Mann 1981).

However, first occurring in the autumn months of 1980, and repeated during this season in the subsequent three years, were mass mortalities of the sea urchins (see Miller and Colodey 1983; Scheibling and Stephenson 1984). Within two years, urchins were almost eliminated from shallow water (<25m) by an epizootic, the disease organism believed to be a <u>Paramoeba</u>-like amoeba (G. Jones, pers. comm.). Following removal of the urchins, seaweeds began to reappear in the subtidal (Moore and Miller 1983; C.R. Johnson personal observation).

These events prompted the raising of a number of queries concerning community structure that set the foundation for the present study. First, was it release from urchin grazing that enabled widespread recovery of seaweeds in the subtidal for the first time in over a decade? Second, the most abundant organisms following urchin mortality were crustose coralline algae. Coralline crusts are known to greatly influence the settlement and recruitment of many invertebrate species. What is their effect on the settlement and recruitment of seaweeds, and in particular of kelps? If recruitment of seaweeds is influenced by coralline algae, is this interaction likely to continue if seaweeds recover, or do corallines die and recede if dense macrophyte beds re-establish? Third, L. longicruris was the dominant seaweed in shallow water prior to the urchin outbreak, and ostensibly accounted for the single greatest portion of the net production of the seaweed zone (Edelstein et al. 1969; Mann 1972a,b). Can this kelp recover and also sustain its dominant status in the post-urchin outbreak period? Finally, what are the predominant grazers of L. longicruris in the absence of high densities of S. droebachiensis, how does their impact on this kelp compare with that of the urchins, and is the impact of non-echinoid grazers on kelp predator-limited?

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Answers to these questions should indicate the resilience of L. small-scale disturbances, longicruris to large- and aid the identification of those biological interactions that are important in structuring this community when sea urchin numbers are low, and thus considerably augment current concepts of the dynamics of this system and engender implications for others. Controlled manipulative, field experiments have emerged as perhaps, the single most powerful tool enabling ecologists to identify and quantify intra- and interspecific interactions (see Connell 1974, 1983a; Palme 1977; Quinn and Dunham 1983; Schoener 1983, but see also the cautionary comments of Dayton and Oliver 1980; Bradley 1983; Connell 1983b; Hurlbert 1984; Underwood and Denley 1984). Fn this study I employed a largely experimental approach to test several hypotheces in attempting to answer the foregoing questions. Details of the hypotheses and background to their formulation are presented later in the introductory sections of the relevant chapters. A discussion of the results of the experiments

is also given in each of the principal chapters. Thus, the final chapter is an overview attempting to integrate the general conclusions already discussed in detail earlier.

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#### CHAPTER 2 ·

#### GENERAL METHODS

Only introductory information on field work, identification of algae, the study sites and general comments on the statistical analysis are given here. Details of specific methods appear in the relevant chapters.

Study sites and underwater work

Field investigations were conducted at Mill Cove and Paul Pt. in St. Margaret's Bay on the Atlantic coast of Nova Scotia (fig. 2.1) from April 1982 through November 1983. Both sites are moderately exposed and are characterized by boulder substratum to <u>c</u>. 15-17m depth. Virtually all of the work was conducted at <u>c</u>. 9-10m depth. This is approximately the middle of the bathymetric range of <u>Laminaria</u> <u>longicruris</u> recorded by Mann (1972a) prior to decimation of kelp beds by Strongylocentrotus droebachiensis.

A major factor considered in choosing study sites was that urchin mortality occurred on the eastern side of St. Margaret's Bay one year before significant mortality was observed on the western side. At Paul Pt. sea urchins were exterminated by disease in the autumn months of 1980. In contrast, a healthy population of urchins persisted along the Mill Cove shore until September 1981. Thus, simultaneous investigation of both sites permitted comparison of two. different stages in development of the post-urchin community. It should be noted that it is not known definitely that the Paul Pt.

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site was barren of non-calcareous macroalgae prior to urchin mortality. However, the substratum and exposure characteristics of this site, and the presence of numerous empty urchin tests and a litter of spines in the sediment between boulders when the site was first visited in May 1982, suggest that the area was indeed a barren ground (sensu Lawrence 1975) prior to urchin die-off.

All underwater work was conducted using SCUBA from open boats. In the experiments that required identifying, individual kelps, the plants were tagged with numbered polyethylene strips tied loosely around their stipes. When sampling the non-experimental areas, quadrats were positioned randomly by swimming predetermined random distances along predetermined randomly generated compass headings from an initial haphazardly selected point.

2.2 Identification of algae

Two experiments (chapters 3 and 4) were conducted in which the composition of the entire seaweed community was assessed. Fleshy algae were identified according to the taxonomy given in South and Hooper (1980). Crustose coralline species were identified from information outlined in Adey (1964, 1965), South and Hooper (1980), and from an unpublished key compiled by R.S. Steneck.

Since the focus of this study was primarily ecological and not taxonomic, not all taxa were identified to species. Also, the taxonomic status of some of the algal species is currently in review (C. Bird, personal communication). Species of Cladophora,

Chaetomorpha, Spongomorpha, Ectocarpus, Stictyosiphon, Callithamnion and Fucus vere not determined. Species of Antithamnion and Antichamnionella were pooled under the generic assemblage Antithamnion 📽 spp. When identification was determined in situ underwater, taxa in the species pairs Ectocarpus spp. and Pilayella littoralis, Chorda filum and C. tomentosa, and Sphacelaria furcigera and S. cirrosa, see appendix A.4). This practice is' were not separated (e.g. unlikely to be of any consequence insofar as ecological interpretation σŕ the data is concerned. Species differences within any of these genera are established at the microscopic level, and there are no differences in macroscopic form or habit. Moreover, altogether these genera represent only a minor portion of the flora.

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2.3 Statistical analysis

The analysis largely comprised parametric techniques using the MINITAB (Ryan et al. 1976, 1980), SPSS (Nie et al. 1975; Hull and Nie 1981), and BMDP (Dixon et al. 1983) software packages MINITAB package was also used in performing analyses longhand when specific software was not available (e.g. principal components analysis @of 'variance-covariance matrices (chapter 4); testing significance of differences in slopes and intercepts in regression analysis (chapter 6); distribution-free tests of differences between frequency distributions (chapter 6)). Most commonly, procedures of analysis of variance (ANOVA) were employed. For designs with repeated measures and for the 3-way model with large numbers of within-factor categories discussed in Chapter 4, the BMDP package was used.

Otherwise, all ANOVAs, including multivariate ANOVA (MANOVA), were carried out using SPSS.

Careful attention was given to the underlying assumptions of the parametric zests. Regarding ANOVA in particular (see Scheffe 1959; Winer 1971; Sokal and Rohlf 1981; Underwood 1981), testing for non-additivity of main effects was not a problem, as in all cases replicate observations were made of all cells. There were only two occasions when independence of error terms could not be assumed, For one of these cases a repeated measures model ANOVA was followed. In the other, the repeated measures approach was not used. However it is argued (section 6.2.2.1) that for this particular case a conventional analysis without consideration of repeated measures was more conservative in testing the null hypothesis than strict adherence to a repeated measures model.

Two other properties of data assumed in ANOVA are a normal distribution of error terms and homoscedasticity, or homogeneity of sample variances. For data sets small enough to be handled by MINITAB, normality of residuals was tested by examining the correlation of the raw residuals with their normal score. The correlation coefficient can be used in a powerful test for normality  $\circ$  essentially equivalent to the Shapiro and Wilk (1965) test (Ryan et al. 1980). For data sets which could not be handled by MINITAB, normality vas assessed by visual inspection of a normal probability plot.

For MANOVA, strict testing of multinormality of error terms was

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not attempted. Instead, normality of the unidimensional marginal distributions were checked, again by visual examination of normal probability plots. While not absolutely, rigorous (Legendre and Legendre 1983), this procedure is commonly followed, and certainly provides an adequate indication of multinormality (C. Field, pers. . comm.).

Homogeneity of sample variances in univariate ANOVA was tested using the Bartlett-Box F statistic (Dixon, and Massey 1969). With multivariate data, the F statistic approximation of Box's M statistic (Morrison 1967; Cooley and Lohnes 1971) was used as the criterion for testing homogeneity in group dispersion matrices.

Frequently, rav data did not conform to the assumptions of the homoscedasticity and normality of error terms, necessitating transformation to different scales that better met these requirements. In most cases, transformations successful in stabilizing the variances normality of residuals. .also achieved Because commonly used transformations (see Sokal and Rohlf 1981; Legendre and Legendre 1983) vere rarely applicable, the objective method for finding a suitable variance stabilizing scale given by Draper and Smith (1981) was This method was successfully applied to univariate data, followed. however determining transformations for the multivariate data sets proved difficult. For the multivariate case, a unique transformation can be applied to each of the variates independently only if the variates ware uncorrelated (Press 1972). While the use of specific separate transformations may be attractive in terms of statistical

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tidiness, for the present study this practice would imply unrealistic biological assumptions; namely that there are no interactions or associations among seaweed species. The only remaining option was to treat the replicate measurements of each variate of each combination of factors as a separate group, and apply the Draper and Smith method to these groups to obtain a single best overall transformation for the entire multivariate set. This practice met with only limited success (thapter 4).

Tests for homoscedasticity and normality of error terms were conducted in conjunction with every ANOVA performed in the analysis. When necessary, scale transformations were made. In the text, transformations are described in terms of the untransformed variate, Of course, the structure of some data sets is such that no Y. monotonic transformation exists to achieve homoscedasticity or Fortunately, the robustness of ANOVA to normality of error terms. departures from its underlying assumptions is well understood; the F-statistic and level of significance are little affected by mild heteroscedasticity or non-normality, particularly in balanced designs and with relatively high degrees of freedom (Scheffe 1959; Winer 1971; Underwood 1981). In subsequent chapters when ANOVA statistics are . presented, unless explicitly stated otherwise, At can be assumed that both assumptions (homoscedasticity and normality of error terms) have been met, or at least that any departures from these conditions are · likely to be of little consequence to interpretation.

When a postcriori multiple comparisons were desirable (e.g. with

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a significant interaction of factors indicated by ANOVA), Tukey's honestly significant difference procedure was followed. This test was preferred over the more commonly used Student-Newman-Keuls (SNK) procedure as it is considerably more conservative in terms of keeping the type 1 error small (Winer 1971). However, given that the Tukey method tends to yield too few significant results, in some cases where inclusion of particular groups within a homogeneous subset appeared dubious with the Tukey method, the SNK procedure was also run for comparison.

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#### CHAPTER 3

# RELATIONSHIP BETWEEN RELEASE FROM SEA URCHIN (STRONGYLOCENTROTUS DROEBACHIENSIS) GRAZING AND RECOVERY OF SEAWEEDS

3.1 Introduction

On a global scale, sea urchins constitute the single most important assemblage of grazers influencing the structure of subtidal algal communities. The ability of urchins to overgraze extensive areas of seaweed cover is well documented and reported from tropical through high latitudes (North 1974; Lawrence 1975; Foreman 1977; Paine 1977; Estes et al. 1978; Simenstad et al. 1978; Vance 1979; Duggins 1980,1981b; Sammarco and Lawrence 1982; Dean et al. In 1984)。 tropical regions the impact of sea urchin grazing on algal community composition is important, but is second to that of fishes (Randall 196b,1965; Earle 1972; Vine 1974; Wanders 1977; Hay 1981a,b, 1984; Hay et al. 1983; Hixon and Brostoff 1983; Sammarco 1983). In contrast, urchins are far and away the most important grazers influencing subtidal community structure in temperate waters. Where areas have initially been overgrazed and urchins then removed from the system, either on a large scale or as patches in time and space (Paine and Vadas 1969; Lawrence 1975; Péarse and Hines 1979; Duggins 1980,1983; Sousa et al. 1981; Coven et al. 1982; Jangoux and Lawrence 1982; 1983; Himmelman et al 1983), or when urchins have Breen et al. switched to non-algal food sources (Duggins 1981a), the extent and rate of recovery of seaweed cover is usually dramatic.

In Nova Scotia, there has been an impressive recovery of seaweeds

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in the nearshore subtidal (Moore and Miller 1983; C.R. Johnson personal observation) following recent widespread mass mortality of sea urchins along the entire east coast (Miller and Colodey 1983; Scheibling and Stephenson 1984). An obvious and fundamental starting point to an ecological investigation of this newly instigated successional community, is to objectively determine the relationship between urchin mortality and recovery of seaweeds. This chapter outlines an experiment designed to test the premise that the recappearance of seaweeds in the subtidal was a direct result of the release from grazing by sea urchins.

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## 3.2 Methods

The experiment was conducted at Mill Cove commencing 8 June 1982, approximately eight months after mass urchin mortality at this site. Seaweed community composition in an enclosure containing sea urchins (hereinafter referred to as the urchin enclosure) was followed over a 16 month period and compared with algal community composition in the surrounding non-experimental area and in a second identifical enclosure void of urchins. The enclosure without sea urchins (hereinafter referred to as the control enclosure) acted as a control for enclosure effect.

The enclosures were square pens constructed of 25mm mesh netting, were  $16m^2$  in area, <u>ca</u>. 1.1m high, open at the top and with an inward-folding skirt at the bottom <u>ca</u>. 0.5m wide. The inner and outer edges of the skirt were weighted with chain, the top of the net buoyed with floats, and each corner of the net was supported with a large float and a guy-line leading to an anchor. This design was effective in containing urchins. Both enclosures were erected in <u>ca</u>.

The urchin enclosure was stocked with animals collected from several localities on the eastern and south shores and Bay of Fundy (appendix A.1). Continual restocking was required to overcome high mortality in the summer and autumn months in attempting to maintain densities similar to those of 8-11 year old barren grounds (see Wharton and Mann 1981).

Complete censuses of the density and size (length and width of lamina) of Laminaria longicruris were made within the enclosures, but in the non-experimental area this species was sampled with ten randomly-positioned 2m<sup>2</sup> quadrats on each sampling occasion. An in situ point estimation method was developed to assess the abundances of all other non-crustose species in terms of percentage cover. The technique consisted of dropping 3mm diameter brass rods through 30 randomly chosen holes of a possible 100 drilled in a thick plexiglass The 100 holes were equidistant within a  $0.125m^2$  area and the tablet. plexiglass platform was elevated off the substratum by three adjustable lead-filled legs of 300mm maximum extension. Species that each rod touched or through whose canopy the rods penetrated ware In this manner estimates of the percentage cover of each recorded. · species, and of the proportion of hard substratum bare and not shaded by algae, bare but shaded, and overgrown by seaweed were determined. Ten quadrats to estimate percentage cover were taken for each of the three treatments per sampling occasion. I am not aware of any other subtidal study that has used a point method of cover estimation similar to the one described here. An evaluation of the point technique and discussion of the applicability of this method and sampling scheme in próviding'quantitative data on seaweeds suitable for testing by parametric methods is given in appendix A.2.

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To avoid damaging plants within the enclosures, divers lay on and worked through a moveable aluminium frame (2.5m x 2.5m) with 0.4 w legs, and thus were always elevated off the substratum. Within the enclosures, quadrat positions were randomly determined on a 5 x 5 grid

system.

Percentage cover data for the three treatments were collected on 7 and 8 June 1982 immediately prior to addition of sea urchins to the enclosure, and subsequently in September 1982, and in January, April, August, and October 1983. Corresponding assessments of <u>L</u>. <u>longicruris</u> were undertaken in August and December 1982, and in April, August and October 1983.

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In analyzing these data, diversity was described by the Shannon

 $H = -p_i \log p_i$  (sée Pielou 1978)

where  $p_i$  was the proportion cover of the i<sup>th</sup> species.

While use of the Shannon estimate of diversity may not be theoretically strictly valid (Pielou 1966), Peet (1974) and Legendre and Legendre (1983) have pointed out that use of the alternative Brillouin index is rarely necessary or even desirable. Moreover, the Brillouin index is not applicable to measurements of percentage cover. It should also be noted that by calculating the mean and standard (error of diversity of each date/treatment <combination from the separate measures of diversity obtained from each quadrat, the overall mean is likely to be too small. However, since this practice was consistent for all date/treatment groups, comparison of diversity among groups is valid.

An R-type (Legendre and Legendre 1983) principal components

analysis (PCA) was performed on the 10 x 10 variance-covariance matrix of species abundances in the 18 date/treatment combinations in an attempt to compare community structure in a more easily perceived space of lower dimensionality. The covariance matrix was based on the mean percentage cover of all species whose mean cover in the control enclosure and non-experimental area, for all sampling dates combined; exceeded 2%. Species included in the PCA are given in appendix A.4.

3.3 Results

The experiment was plagued in it's early stages by high mortality of sea urchins in the urchin enclosure due to disease (fig. 3.1, summary data in appendix A.1). Until January 1983 most of the live animals in the pen were diseased, not feeding, and hidden in the crevices between boulders. It was not until the fourth stocking attempt in mid January 1983 that sea urchins remained healthy for any length of time. Even so, by mid July 1983 many animals were beginning to show disease symptoms, and the entire population had died by early October. Predation by crabs (<u>Cancer borealis</u>) and lobster (<u>Homarus</u> <u>americanus</u>) also, appeared to contribute significantly to sea urchin mortality in the enclosure, especially during the warmer months.

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Once the problem of high urchin mortality was overcome and a population consistent of healthy animals maintained, non-calcareous macroalgae within the urchin enclosure were rapidly eliminated between January and April 1983 (fig. 3.1, summary data in appendix A.5; the 28 species recorded over the course of the experiment are given in appendix A.3). In contrast, at least 55% of the hard substratum in the control enclosure and non-experimental area remained overgrown or shaded by algae during the same period. This marked differencé in seaweed cover was maintained at least until August, but by late October algae were again growing in the urchin enclosure. On any given sampling date, the amount of seaweed cover in the control enclosure and non-experimental area was similar.

Not suprisingly, the pattern of seaweed species diversity closely

Fig. 3.1 Proportion of hard substratum (a) bare and unshaded, (b) bare but shaded, and (c) overgrown by non-crustose seaweeds in the enclosure containing urchins (U), the control enclosure without urchins (C), and in the non-experimental area (N) at Mill
Cove; and (d), densities of sea urchins (Strongylocentrotus droebachiensis) in the urchin enclosure. Bars are S.E.

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paralleled that of amount of cover (fig. 3.2, summary data in appendix A.6). There was a dramatic decline in diversity in the urchin enclosure relative to the urchin-void treatments by April 1983, and diversity remained low in the urchin enclosure until, termination of the experiment. Throughout the experiment, algal diversity in the non-experimental area and control enclosure treatments was similar.

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In the principal components analysis, separation of, treatment/date groups on the first three principal vectors (which accounted for 85.5% of the total raw dispersion, summary data in appendix A.7) demonstrated clearly the close similarity in community structure of the three treatments at the beginning of the experiment, and later divergence in seaweed composition in the urchin enclosure (fig., 3.3, summary data in appendix A.8). This style of data presentation also emphasized the marked temporal variability in seaweed community structure in the urchin-void treatments, reflecting seasonal and/or successional effects.

The percent cover and diversity measurements do not include  $\underline{L}_{\circ}$ <u>longicruris</u>. In view of the very low recruitment and paucity of plants of this species at Mill Cove (see chapter 5), formal treatment of the data on this species would be pointless. Suffice to say that the single recruit of <u>L</u>. <u>longicruris</u> present in the urchin enclosure on 13 January 1983 had been destroyed 14 days later, whereas the two plants in the control enclosure remained for the duration of the experiment.

In summary, there was no detectable effect of sea urchins on .

Fig. 3.2 Shannon diversity index (H) for 'sealled' community in enclosure containing urchins (<u>Strongylocentrotus droebachiensis</u>), enclosure void of urchins, and in the non-experimental area at Mill Cove. Bars are S.E.

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Fig. 3.3 Separation of treatment/date groups on the first three axes generated by an R-type principal components analysis of the percentage cover of seaweed species. U = enclosure containing sea urchins (<u>Strongylocentrotus droebachiensis</u>), C = control enclosure (without urchins), N = non-experimental area (Mill Cove). 1-6 = sampling dates in June and September 1982, and January, April, August and October 1983, respectively.



seaweeds in the urchin enclosure from June through December 1982. This is attributed to high urchin mortality and cessation of feeding by the remaining, mostly diseased, animals. In less than three months after establishment of a healthy population of urchins in January 1983, seaweeds in the urchin enclosure were decimated whereas algae continued to flourish in the control enclosure and non-experimental  $\mathcal{V}$ area. No enclosure effect was evident.

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## 3.4 Discussion

The results of the experiment, are clearly consistent with the hypothesis that the re-establishment of seaweeds in the focky subtidal is due to release from grazing by sea urchins. When urchins were reintroduced into the system, the community resumed its previous configuration, namely, absence of any fleshy macrophytes. While the outcome of the experiment may not be startling, this is the first time that sea urchins have been introduced into a seaweed community in a controlled experiment.

Reappearance of seaweeds in the urchin enclosure after April 1983 was probably the result of declining urchin numbers, high grouth rates algae, and changes in the behaviour pattern of the urchins. From of January until at least the end of April 1983, urchins formed exposed and dense 'aggregations on 'the sides and tops of boulders. Over the period mid June through mid July urchins were only occasionally exposed and aggregated, and from the end of July all remaining animals were hidden. This behaviour may be temperature related. When the thermocline was above the urchin enclosure (bottom temperature 4-6 C), exposed aggregations were found. However, most urchins moved to the crevices between boulders during periods when the thermocline moved below the enclosure (bottom temperature in enclosure 10-12 °C). Movement of urchins in and out of hiding occurred over periods of only ' a few days in response to changes in the position of the thermocline. This behavioural pattern was similar to that observed by Bernstein et al. (1981) in a barren region at nearby Boutilier Pt. They found the

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proportion of urchins exposed during the day to be higher in winter than in summer, jand there was always a period in summer when virtually all urchins were hidden.

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In view of the extensive and annually repeated kills of sea urchins over the past four summers along most of the Atlantic coast of <sup>)</sup> Nova Scotia, the implications for change in the structure and dynamics Seaweeds are a major source of of the rocky subtidal are vast. production in coastal communities (Clendenning 1971; North 1971; Mann " 1973,1982; Kain 1982; Littler and Arnold 1982; Littler et al. 1983a), and provide substrata (Andrews 1925; Dommasnes 1969; Mukai 1971; Norton 1971; Sieburth et al. 1974; Cundell et al. 1977; Roland 1978; Gunnil 1982a, b, 1983; Lewis and Hollingworth 1982; Norton and Benson 1983; Kitting et al. 1984), and spatial heterogeneity and shelter (Hagermann 1966; Mitchell and Hunter 1970; Bray and Ebeling 1975; Hobson and Chess 1976; Ebeling et al. 1980a,b; Russ 1980; Sheppard et al. 1980; Anders and Moller 1983; Coull and Wells 1983; Bell and Galzin 1984; Moreno and Jara 1984; Ojeda and Santelices 1984) for a diverse array of organisms in shallow water communities. The virtual elimination of urchins and recovery of seaweed beds in Nova Scotia 1s. likely to be manifest in (1) an increase in primary production in the nearshore subtidal of about two orders of magnitude (see Mann 1972b; Chapman 1981) with concomitant increases in secondary production, (2) greater diversity, and (3) the realization of a host of interactions within and among species which may have great influence in shaping overall community structure.

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INFLUENCE OF ENCRUSTING CORALLINE ALGAE ON SETTLEMENT

OF NON-CALCAREOUS SEAWEEDS

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CHAPTER 4

4.1 Introduction

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The term 'urchin dominated barren ground' is a misnomer. Areas where grazing by sea urchins has reduced or memoved cover of fleshy. seaweeds on hard substrata are also characterized by extensive cover of crustose coralling algae (Paine and Vadas 1969; Adey and Macintyre 1973; Vadas 1977; Wanders 1977; Vance 1979; Ayling 1981; Sousa et al. 1981; Himmelman et al. 1983; Logan et al. 1984 ; Hagen 1983). A predominance of encrusting red algae has also been recorded where grazing by fish has been effective in preventing the establishment of fleshy seaweeds (Vine 1974; Wanders 1977; Hay 1981b; Hay et al. 1983). Indeed crustose corallines dominate much of the hard substrata of the photic zone from propical through arctic and antarctic latitudes (Adey 1964,1965,1966, 1970,1973; Adey and Macintyre 1973; Steneck and Adey 1976; Wanders 1977; Vance 1979; Ayling 1981; Masaki 1981; Steneck 1982; 'Hagen 1983; Masaki 1984; Littler and et al. Littler 1984).

Notwithstanding their cosmopolitan distribution and high abundance, relatively scant aftention has been paid to the ecology of corallines. Most ecologists seem to have viewed these plants as inert primary substrata. This probably stems from their very slow growth and low productivity (Goreau 1963; Adey 1970; Adey and Vassar 1975; Steneck and Adey 1976; Littler and Littler 1980, 1984; Littler and

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Arnold 1982; Littler <u>et al.</u>° 1983a). However, productivity is not the only criterion for assessing ecological importance. The magnitude and outcome of interactions among species can be of fundamental importance to the structure of communities.

consideration of interactions of coralline crusts with date other taxa has largely focused on their influence on the settlement and metamorphosis of invertebrates. The planktonic larvae of several species of invertebrates including limpets (Steneck 1982), chitons (Barnes and Gonor 1973; Morse et al. 1979; Rumill and Cameron 1983), abalone (Morse et al. 1979; Morse and Morse 1984), asteroids (Lucas 1975, cited in Morse and Morse 1984; Barker 1977, polychaetes (Gee 1965), and corals (Sebens 1983a,b) have been found to preferentially settle on crustose corallines. Moreover, for many of these species contact of the larvae with the surface of a coralline is obligatory for settlement and metamorphosis, and therefore ·succèssful recruitment, to occur. Recruitment of other invertebrate groups is inhibited on coralline crusts (Breitburg 1984).

° Other than the studies cited above suggesting that coralline cover increases when grazers limit epiphytes on their surface, the number of investigations of the interactions of crustose red algae with their non-calcareous counterparts are relatively few. Little is known of the influence of, corallines on the settlement of fleshy seaweeds in the absence of grazers, though apparently not for lack of speculation. Most crustose corallines consist of three principal anatomical layers, <u>viz</u>. a basal hypothallium, a perithallium of which

the top layer of cells is meristematic, and an epithallium derived from and overlying the meristem (fig. 4.1). Many corallines continually slough their epithallial cells, and a number of workers have suggested that this may act as an antifouling mechanism retarding overgrowth by fleshy species (Adey 1964, 1973; Johnson and Adey 1965; Giraud and, Caboch 1976; Steneck and Adey 1976; Masaki 1984). Experiments have been conducted with only one species (Lithophyllum yessoense), in which it was shown that sloughing of epithallial cells was effective in preventing fouling by Laminaria japonica (Masaki et 1981,1983). al.

In Nova Scotia, "rocky areas denuded of fleshy seaweeds by sea urchins (Strongylocentrotus droebachiensis) were also characterized by extensíve cover of crustose red algae (C.R. Johnson personal observation). Following die-off of the urchins, encrusting corallines were conspicuously the dominant species in the rocky subtidal. Crustose corallines in St. Margaret's Bay are primarily represented by the genera Clathromorphum, Lithothamnium and Phymatolithon, the dominant species being C. circumscriptum, glaciale, Ρ. L. laevigatum and P. rugulosum. In view of the recent study by Steneck (1982) on the relationship of the limpet Notoacmaea (=Acmaea) testudinalis (this grazer is also common in St. Margaret's Bay) with these genera, it seemed that an examination of the interaction of encrusting red algae with fleshy seaweeds in the absence of grazers might provide new insight into the role of corallines in structuring the newly developing seaweed community. 'This chapter outlines an experiment designed to test the null hypothesic that the coralline

Fig. 4.1 Diagram of cross-section of generalized <u>Phymatolithon-like</u> crust. ep = epithallium, hy =hypothallium, mr =meristem, pr = perithallium. (Compiled from drawings and diagrams in Adey and Macintyre (1973) and Johansen (1981)).



genera Phymatolithon, Lithothamnium and Clathromorphum have no effect on the recruitment of macroscopic fleshy algae relative to bare rock substrata in the absence of grazers.

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4.2 Methods

The cover of living coralline species on hard substrate in the non-experimental areas at the Paul Pt. and Mill Cove sites was estimated using 0.25 m<sup>2</sup> quadrats divided into 100 5x5 cm squares. Squares with estimated proportions of 1/8,2/8,3/8,...,8/8 bare of live corallines were recorded and summed, and cover of coralline algae was calculated as a percentage of the quadrat area. All non-crustose macroalgae were removed from the substratum prior to estimating coralline cover. Thirty and 25 quadrats were assessed at Paul Pt. and Mill Cove respectively in October 1983.

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To test the null hypothesis that in the absence of grazers crustose corallines neither inhibit nor promote colonization by non-calcareous macrophytes relative to bare rock substrata, settlement of fleshy species on granite rock and on the coralline genera <u>Clathromorphum, Lithothamnion</u>, and <u>Phymatolithon</u> was followed from June 1983 through October 1983. Eighteen groups of ten experimental boulders were positioned at <u>ca</u>. 9m depth at Mill Cove on 10-15 June 1982. Each group of ten consisted of five rocks with extensive cover of corallines, and five which had been overturned to expose their bare underside surface. The rocks were not shaded by seaweeds or other boulders. All.rocks were collected at <u>ca</u>. 10m depth, and all manipulations outlined following were performed at this depth."

Initially the experimental rocks were scrubbed thoroughly over their entire surface with wire brushes to remove all foliose algae and sediment. From the colour of the crusts, there was no evidence that the scrubbing treatment had an ill effect on any of the coralline species (the pink colour of corallines rapidly changes to white after death).

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Initially and on each visit, limpet (Notoacmaea testudinalis), chiton (Tonicella rubra), Mand sea urchin (Strongylocentrotus droebachiensis) grazers were removed from the experimental rocks and from.an area ca. 0.6m around each group. In 1983 the growth of algae concealed small numbers of newly recruited grazers which reached a maximum density of ca. 10 per experimental rock in August. Also, moderate densities of the gastropod grazer Lacuna vincta infested the Mill Cove site in March and April 1983, but this species was found exclusively on foliose seaweed and never on hard substrata. Lacuna appeared uniformly distributed on algae growing on all experimental substrata. It assumed that the low numbers of very small was herbivores on the experimental surfaces had a negligible effect on seaweed recruitment.

On each of six occasions (see figs. 4.1-4.3), one group of rocks was selected haphazardly, the individual rocks scaled in separate containers underwater, and taken to the laboratory and stored at <u>ca</u>. 2.0°C. Portions of rocks to be excluded from analysis (<u>e.g.</u> undersides and regions overlaid by other rocks) were delineated underwater with oil pastel crayon.

All non-crustose macroalgae on the experimental surfaces were removed, identified, dried at <u>ca</u>.  $80^{\circ}$ C, and weighed. Substratum areas were determined by dividing each surface into flat sections or sections with curvature in only one plane, tracing these sections onto transparent acetate sheets, and converting the weight, of the tracings to an area from a predetermined regression equation. Final results were calculated as dry weights of species per  $0.1m^2$  of substratum on each of the four substrata (granite + three coralline genera). Thus, on any one sampling date, five replicate observations of each seaweed species on each of the four substrata were obtained.

In analyzing these data, the Shannon index of diversity (H) (see chapter 3) and a measure of evenness (J) were used, where J is defined as  $\Rightarrow$ 

 $J = H/\log s$ 

and s is the total number of species (see Pielou 1978).

A supplementary experiment was conducted to control for the possibility that the bare undersides of overturned rocks might possess chemical characteristics to promote or inhibit seaweed settlement and growth, and thus bias the primary experiment. Twenty bare rocks were brought from the high intertidal adjacent the Mill Cove site on 21 September 1982, and placed with a second group of 20. rocks collected at <u>ca</u>. 10m depth which had been overturned. For consistency, all rocks were scrubbed with vire brushes in the manner described previously. These rocks were also maintained clear of grazers. Ten rocks of each treatment were selected haphazardly on 31 October 1983 and the biomass of seaweed species on each rock determined as described above.

## 4.3 Results

Qualitative and quantitative analyses indicated that although there were no differences in the number and composition of seaweed species that recruited on the granite, <u>Phymatolithon</u> and <u>Lithothamnium</u> substrata, the biomass of seaweeds that recruited on <u>Phymatolithon</u> was significantly less than that on an equivalent area of bare granite. The inhibitory effect of <u>Phymatolithon</u> was not species specific, and on average the biomass of a seaweed on the coralline was only 46% of its biomass on the same area of granite. Moreover, this estimate may be conservative, since significantly greater quantities of seaweeds grew on rocks brought from the intertidal than on the scrubbed surfaces of overturned subtidal rocks.

4.3.1 Incidence and distribution of coralline genera

Encrusting corallines covered 98.0% (S.E. = 0.3) of the Focky substrata at <u>ca</u>. 10m depth at Paul Pt., and 91.3% (S.E. = 0.8) at Mill Cove. At Paul Pt. where a dense seaweed canopy had prevailed for at least 18 months (chapter 5), the patches devoid of live crustose corallines were primarily those areas beneath <u>Laminaria</u> longicruris holdfasts.

The relative abundance of coralline genera on the experimental rocks was 72.3% <u>Phymatolithon</u>, 26.7% <u>Lithothamnium</u>, and only 1.0% <u>Clathromorphum</u>. The latter genus occurred in small patches usually not larger than 10-30mm diameter. The distribution of <u>Phymatolithon</u> and Lithothamnium on rocks at both sites followed a characterisitc

pattern. The top surface and the uppermost regions of the sides of rocks was covered mostly by <u>Phymatolithon</u>. Lithothamnium was largely restricted to a relatively narrow band around the base of rocks immediately above the rock/sediment interface. On larger boulders occasional small patches of <u>Lithothamnium</u> occurred higher on the side and top surfaces.

## 4.3.2 Preliminary analysis; diversity and total biomass

In view of the sparse cover of Clathromorphum and the relatively low abundance and unique spatial distribution of Lithothamnium, these genera were excluded from the quantitative analysis to avoid potential . bias stemming from differences in orientation to light and area Phymatolithon was the only genus colonization. available for comparable with the bare rock surfaces in terms of area and aspect. However, qualitative comparison of the species of fleshy seaweeds encountered on bare rock, Phymatolithon, and Lithothamnium substrata is both valid and useful. The qualitative differences among substrata in the number of species found on the experimental surfaces (table 4.1), can be attributed to effects of chance in settlement. With the possible exception of D. viridis, the species that \were not ubiquitous on all substratum types were relatively rate on the experimental surfaces (fig. 4.4, appendix B.1). Furthermore, the species absent from coralline substrata on the experimental rocks were all found growing on both Phymatolithon and Lithothamnium mearby.

There was little difference in the diversity and evenness of abundance of species in the seaweed communities that developed on the

Table 4.1. Occurrence of species of fleshy algae on <u>Phymatolithon</u>, <u>Lithothamnium</u> and bare granite substrata in experiment examining influence of crustose corallines on settlement of fleshy algae.

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(+) indicates those species recorded, (-) indicates species not encountered.

SPECIES · ·				
······	Bare	Phymatolithon	Lithothamnium	· · ·
Hlorophyta '		,	<del>⊚™©™™™©∞™∞™©™©™©™©™©™©™©™©™©™©™©™©™</del>	~~
Cladophora spp.	÷	<del>4</del> -	<b>+</b>	
HAEOPHYTA	•		,	•
Ectocarpus spp.	+	+	*	
Acrothrix novae-angliae	+	· +	÷	
Stictvosiphon spp.	÷	+-	/ +	· ·
Desmarestia viridis	+	-	/ +	
Tilopteris mertensii	`-+-	- <b>{</b> ~	/ * +	,
Sphacelaria cirrosa	· +	+	÷	-
Sphacelaria furcigera	- +	÷ ()	′ <del>_}</del>	
Sphacelaria plumosa	-+-	· • • • /	*	
Halopteris scoparia	+	· + · /	• +	
Petalonia fascla	+	· + /		
HODOPHYTA	•			
Bonnemaisonia hàmifera	.+-	- <b>-</b> -	*	
Cystoclonium purpureum	+	V 🚥	4533	
Chondrus crispus	÷	-\$-	÷	
Anithamnion spp.	-{-	÷.	-+-	
Callithannion spp:	, +	· +	+	-
Ceramium rubrum	÷	~ <del> </del> -	+	-
Polysiphofia flexicaulis	÷	· +	*	Ş
Polysiphonia harveyi	<b>6</b> 2	+ ~	, «can	°,
Polysiphonia nigrescens	÷	+	<del>,</del> *-	• '4
Polysiphonia urceolata	-{-	-+-	÷ 、	,
Rhodomela confervoides	+ `	+	+, /	

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bare and Phymatolithon surfaces (fig. 4.2, summary data in appendix B.2). However, conspicous differences were evident in the total biomass of seaweeds that recruited to the two substrata (fig. 4.3, summary data in appendix B.3). ANOVA (all samples included) indicated highly significant date interaction (ANOVA; <sub>δ</sub> a substratum x transformation =  $Y^{0.235}$ ; interaction 'effect F=6.83, df=(5,48), p<.001). Tukey's multiple range test ( $\propto =.05$ , transformation = 1n(Y)) indicated that by 9 August 1983 a significantly greater biomass of fleshy algae had recruited to the bare rock surfaces than to an equivalent area of Phymatolithon (fig. 4.3). The decline in standing biomass after 9 August 1983 reflects deterioration of the summer annuals.

4.3.3 Multivariate analysis; responses of individual species

Three-way (substratum x date x species) univariate ANOVA indicated highly significant date x species, substratum x species, and date x substratum x species interactions (table 4.2), suggesting real differences among species in their abundances on the different substrata. This test provided objective confirmation of the patterns indicated from graphical depiction of species abundances on the two substrata (fig. 4.4, appendix B.1), and suggested that it would be informative to proceed to a 2-way MANOVA treating `species' as a multivariate response vector.

For the MANOVA, several changes to the raw data were made in an attempt to circumvent problems of heteroscedasticity in group dispersion matrices and non-normality of residuals. Data from the

Fig. 4.2 Diversity (H) and evenness (J) of non-crustose seaweed / species recruited on bare granite substratum and on an equivalent area of <u>Phymatolithon</u> crust in the absence of grazers.

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Fig. 4.3 Total biomass of all non-crustose seaweed species recruited on bare granite substratum and on an equivalent area of <u>Phymatolithon</u> crust in the absence of grazers. Bars are S.E. Homogeneous subsets of substratum/date groups according to Tukey's classification are given ( $\propto = .05$ , transformation = ln(Y)).

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	Fig.	4.4	Mean	biomass of seaweed species recru:	ited o	on bare	grani e
		and	Phyma	tolithon substrata in the absence	of gra	zers.	۹
۰. ۱.			-	SPECIES	KEY	-	
1.1			•	energy and a second	anan <mark>ayan kanan kanan d</mark> ara ta		
				Chlorophyta			*
_				Cladophora spp.	1		
-				рнаеорнута			
		0		Ectocarpus spp. (a	2		
	•			Acrothrix novae-angliae	3	• •	
				Stictyosiphon spp.	4		
				Desmarestia viridis	5		
,				Tilopteris mertensii	. 6		
•				Sphacelaria cirrosa	7		
				Sphacelaria furcigera	8		
				Sphacelaria plumosa	9		
				Halopteris scoparia	10		
		1		Petalonia fascia	11		
			`	RHODOPHYTA			
		•	. '	Bonnemaisonia hamifera	12		٥
				Cystoclonium purpureum	13		
				Chondrus crispus	14		
				Anithamnion spp.	15		
				Callithamnion spp.	16		
				Ceramium rubrum	1/		
				Polysiphonia riexicaulis	10		
		•	•	Polysiphonia narveyi	17		
				rorysipnonia nigrescens	20		
			<b>`</b>	rorysiphonia urceolata	21		•
				KHODOMETS CONTELAOTOES	66		
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Table 4.2. Influence of the crustose coralline alga Phymatolithon spp. on the recruitment of seaweeds. 3-way ANOVA of substrate (2) x date (6) x species (22) model. Transformation =  $y^{0.295}$ .

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SOURCE	df	F	, b	-
Date	5	66.23	0.0000	
Substrate	1	15.25	0.0001	
Species	· 21	97.51	0.0000	
Daté x Substrate	5	11.72	0.0000	
, Date x Species	105	- 24.21	0.0000	
Substrate x Species	21	3.95	0.0000	
Date x Substrate x Species	105	2.86	0.0000	
, Error	1056	•	,	

first two sampling dates in the incipient stages of the experiment, and ten species rarely encountered, were excluded from the analysis (see fig. 4.4, summary data in appendix B.1). Also, dimension reduction of the remaining 12 species was attempted by performing an R-type (Legendre and Legendre 1983) principal components analysis (PCA) on a mean variance-covariance matrix obtained by averaging the eight group dispersion matrices (4 dates x 2 substrata = 8 groups).

The first four principal components accounted for 97.1% of the. total dispersion (appendix B.4). Therefore, restricting the analysis to these variates provided a parsimonious but quite satisfactory description of the data complex. A high degree of structure in the data was indicated further by each vector having only one species different species for each vector) with a high loading (appendix B.5). Thus, in decreasing order of importance, the species Ceramium rubrum, Bonnémaisonia hamifera, Polysiphonia nigrescens and Desmarestia viridis were responsible of 'the variance for most vithin. These were also the most abundant species date/substratum groups. recorded at any time during the experiment (fig. 4.4).

To test for significance of date and substratum effects, a MANOVA was performed on the first four principal components (table 4.3). However, interpretation of the results was not straightforward since heteroscedasticity in group dispersion matrices was still evident after transformation. Unlike the case for univariate ANOVA where the implications of heteroscedasticity on the size of the type I error are well understood (see chapter 2), the robustness of the equivalent
52. Table 4.3. Recruitment of fleshy seawaeds onto bare granite and Phymatolithon substrata. "Two-way MANOVA of principal components (PC1 - PC4) date (4) x substrate (2) model in Transformation  $\Rightarrow Y^{0^{/}_{\circ}128}$ . EFFECT - DATE (adjusted for substrate) Test Hypothesis df F Error df р Hotelling's trace 20.3. 83 0 12 77 Wilk's lambda 16.9 Univariate F-tests with (3,32) dr Våriable F, ` р ° 45.0. • PC1 n PC2 \ \ 22.2 04000 PC3 0.000 20.0 0.000 PC4 1) 22.3 / 1 EFFECT - SUBSTRATE (adjusted for date) : Hypothesis df ' Error df Test F P Hotelling's trace 5.4 : 1. 29 0.002 . Wilk's lambdà 5.4 29 0.002 Univariate F-tests with (1,32) df Variable F, · P PCl 17.9 0.000 PC2 0.007 8.3 PC3 11.3 <sup>\</sup>0.002 PC4 10.1 0.003 (Table continued overleaf)

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multivariate tests under departures from homoscedasticity is not known (see Cooley and Lohnes 1971; Press 1972).

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In any case, accepting from the preliminary analysis (section 4.3.2) that a real and significant substratum effect exists, it is not necessary to attach much importance to estimating the likelihood of a substratum effect from the multivariate treatment. The real usefulness of the SPSS MANOVA output for this analysis is in the univariate ANOVAS of each of the principal components within each. of the main and interaction effects (table 4.3). Some confidence can be placed in the univariate results as the model design was balanced, the distribution of error terms for each variate was normal, and only mild, if any, heteroscedasticity was likely. These tests indicate that all four principal components were significant components of variance within the main effects. Because each principal component had only a single species with a high loading, it may be concluded that the four species C. rubrum, B. hamifera, P. nigrescens and D. viridis (in decreasing order of importance) were largely responsible for the observed differences in the two substrata.

The rank order of these four species was in direct accord with their overall abundance on the experimental surfaces (see fig. 4.4). This indicated that for a given species, the difference in biomass on the <u>Phymatolithon</u> and granite substrata was approximately porportional to its abundance. At least among the more common species (biomass  $\geq$ 0.1g. dry weight per 0.1m<sup>2</sup> substratum) the relationship between the difference in abundance on the two substrata and the biomass on granite substratum was approximately linear  $(r^2=0.81;$  fig. 4.5). This suggests that the inhibitory effect of antifouling was similar for all algae encountered.

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In overview, it is clear that the coralline genus <u>Phymatolithon</u> supported less seaweed growth than an equivalent area of pare rock during the same period. Several observations indicated that the inhibitory effect of <u>Phymatolithon</u> was not species specific; (1) there were no real qualitative differences in the species occuring on the two substrata, (2) patterns of diversity and evenness were virtually identical on the two substrata, and (3), all species were diluted by about the same proportion, the biomass of a given species on <u>Phymatolithon</u> being, on average, 46% of its biomass on an equivalent area of granite (fig. 4.5).

4.3.4 Assessment of bias in settlement and growth of seaweeds on overturned rocks

Twenty three species were recorded in the control experiment comparing the recruitment of seaweed species on the bare surfaces of granite rocks obtained from the high intertidal and on overturned subtidal rocks (table 4.4). Of these, 22 were encountered on the intertidal rocks but only 15 were recorded from the overturned rocks. However, most of the species limited to a single substratum were relatively rare (table 4.4), indicating that the differences may be accountable by chance in settlement rather than a real substratum effect. Fig. 4.5 Relationship between difference in biomass of seaweed species on granite and <u>Phymatolithon</u> substrata, and biomass on granite (for species  $\geq 0.1$ g dry weight 0.1m<sup>-2</sup> substratum).

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Table 4.4. Biomass of seaweed species recruited on intertidal and overturned subtidal granite rocks. (\*) indicates species included in quantitative analysis.

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, ,	DRY	WEIGHT	(g 0.1	m <sup>-2</sup> )	
	<sup>¢</sup> INTERTID	DAL ROCKS	SUBTIDA	L ROCKS	
SPECIES	Mean	S.D.	Mean	S.D.	and over the second second
u b	دىنى	an a sharay manaka sha Alamahaa ahaa ahaa			
Chlorophyta			v	۰. ۲	* *
<sup>2</sup> Cladophora spp.	0.211	0.163	- 0.020	0.041	
Chaetomorpha spp.	0.001	0.002	0	0	
Rhizoclonium spp.	800.0	0.026	0	0	
* Spongomorpha spp.	0.039	0.061	0 *	0	
PHAEOPHYTA					
Ectocarpus spp.	0.002	0.006	0	0	•
Stictyosiphon tortilis	0.102	0.158	0.013	0.032	-
· Desmarestia aculeata	0.210	0.438	0	0	
· Desmarestia viridis	0.493	0.697	0.022	0,068	,
* Chorda filum	6.443 .	9.018	0.026	0.078	
<sup>*</sup> Laminaría longicruris .	0.120	0.183	0	· 0	
Saccorhiza dermatodea	0	0	0.454	1.435	
* Sphacelaría cirrosa	0.053	0.168	0.002	0.005	
* Sphacelaria furcigera	0.004	0.011	0.017	0.040	-
* Sphacelaria plumosa	0.002	0.006	0.134	0.327	
Halopteris scoparia	0.005	0.012	0.000	0.001	
RHODOPHYTA	¥				
Bonnemaisonia hamifera	0.013	0.029	0	0	
* Cystoclonium purpureum	0.489	1.263	0.235	0.366	
Chondrus crispus	0.001	0.005	0	0	
Callithamnium spp.	0.268	0.313	0.107	0.203	<b>`</b> 0
* Ceramium rubrum	0.095	0.120	.036	0.036	
* Polysiphonia nigrescens	8.205	3.039	5.543	3.068	* A(*.*)
* Polysiphonia urceolata	0.051	0.093	0.034	0.030	
* Rhodomela confervoides	0.246	0.290	0.051	0.076	
1	•				
₩₽₩₽₩₽₩₽₽₩₽₽₩₽₽₩₽₽₩₽₽₩₽₩₽₩₽₩₽₩₽₩₽₩₽₩₽₩			aliyan na ana ana ana ana ana ana ana ana a	0	

Seven rare species unlikely to contribute to real structure in the data, and the brown alga <u>Chorda filum</u>, were excluded from the quantitative analysis. Being a gregarious and fast growing plant and by far the largest of all species encountered when sampling the experimental rocks, the chance settlement of a few <u>C. filum</u> plants on . either substratum could introduce sufficient bias to suggest a real substratum effect in a MANOVA when no real effect exists. In the manner outlined in the foregoing section, an R-type FCA was performed on the mean variance-covariance matrix obtained by averaging the two group dispersion matrices of the remaining 15 species, and a MANOVA

The first three vectors cumulatively accounted for 87.7% of the raw variation (appendix B.6). Element loadings associated with these vectors indicated that <u>P. nigrescens, C. purpureum</u>, and <u>Desmarestia</u> <u>viridis</u> were the primary contributors to this variance (appendix B.7).

In the MANOVA, after attempting several transformations, it was evident that transformations resulting in least heteroscedasticity were associated with the highest values of the F-statistic calculated from MANOVA. Given this trend, and that a MANOVA using the transformation giving least heteroscedasticity indicated a significant F-statistic (table 4.5), it was concluded that a significantly greater biomass of algae recruited to rocks brought from the high intertidal than to an equivalent area on the scrubbed undersides of overturned subtidal rocks. Of the 23 species encountered, 20 were more abundant on the rocks collected from the intertidal (table 4.4).

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Table 4.5. Settlement of seaweed on bare surfaces of overturned subtidal rocks, and rocks from the high intertidal. One-way ANOVA of principal components. Transformation =  $\dot{Y}_{0.156}^{0.156}$ . (Note: residuals of marginal distributions not normally distributed, and heteroscedastic dispersion matrices Box's M = 38.96,  $= 2^{1} \times 10^{-5}$ ).

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SUBSTRATE EFFECT

p

Test name Hypothesis df Error df

Hotelling's trace. 4.25 0.022 16 0.022 Wilk's lambda 16 25

This result is somewhat enigmatic. All of the boulders were granite and the only difference was in their collection sites. Although the surfaces of the newly overturned rocks were no doubt anoxic, after the scrubbing treatment all sulphides <u>etc</u>. should have oxidized in much less than 24 hours. However, while the result may be difficult to explain, prudence demands that the difference be accepted as real. This being so, then clearly this result implies a conservative bias in the primary emperiment. To reaffirm, the differences in abundance of seaweed species recruiting to equivalent areas of <u>Phymatolithon</u> and bare granite surfaces can be expected to be at least as great as that observed between <u>Phymatolithon</u> and the bare surfaces of overturned rocks.

## 4.4 Discussion

4.4.1 Mechanism of inhibition of recruitment of fleshy seaweeds on Phymatolithon crusts

Before expanding on the ecological significance of the inhibitory effect of <u>Phymatolithon</u> on seaweed settlement, it is worthwhile speculating on the underlying mechanism. Three possible mechanisms come to mind, <u>viz</u>. (1) sloughing of surface epithallial cells, (2) chemical inhibition of settlement and/or growth of flebby seaweeds, and (3) rugosity properties of the crust surface adverse to settlement of propagules (spores, gametes or zygotes) of flesby species.

The most reasonable explanation to account for reduced macroscopic phases of fleshy seaweeds to recruitment of the Phymatolithon surfaces is 'sloughing-off of epithallial cells. Shedding of these surficial cells by Phymatolithon can occur at such a rate that frequently there is no epithallium left over relatively large areas (Adey 1964, 1973). This hypothesis is consistent with the findings of Masaki et al. (1981, 1983) who demonstrated that shedding of epithallial cells by Lithophyllum yessoense was effective in preventing overgrowth by Laminaria japonica.

Differences in the rugosity of the granite and <u>Phymatolithon</u> surfaces are unlikely to account for the differential recruitment of seaweeds on these substrata. Although rough and irregular surfaces are more favourable to seftlement and attachment of seaweeds than smooth ones (Feldman 1937; deno Hartog 1972; Harlin and Lindbergh

1977), the surface particle size range where this difference is most noticeable is in the order of 0-0.5 Em (Foster 1975b; Harlin and Lindbergh 1977 and references). Thus, while the surface texture of the bare rock was rougher than that of <u>Phymatolithon</u>, the surface of this coralline is certainly not smooth (see Adey 1964; Steneck 1982), but exhibits roughness at a grain size unlikely to retard settlement and attachment of fleshy macrophytes. Incidentally, the coralline <u>Clathromorphum circumscriptum</u> which is considerably smoother than <u>Phymatolithon</u> and does not shed its epithallium, is rapidly overgrown with fleshy algae in the absence of grazers to keep it clean (Steneck 1982).

The possibility that <u>Phymatolithon</u> chemically inhibits settlement of seaweeds also seems doubtful but is not so easily dismissed. There is much evidence indicating that surface chemistry of crustose corallines promotes the settlement and metamorphosis of many invertebrates (Gee 1965; Barnes and Gonor 1973; Morse <u>et al.</u> 1779; Rumrill and Cameron 1983; Sebens 1900a; Morse and Morse 1964) but inhibits recruitment of others (Breitburg 1984). Might there be a similar effect on the settlement of seaweeds?

Unfortunately nothing is known of the influence of chemicals' released from or available at the surface of coralline crusts on seaweed settlement and growth. Also, unlike the case for invertebrates where there is some understanding of the influence of surface chemistry on settlement of marine invertebrate larvae"(see above references plus Griop 1965, 1974; Cameron and Elinegarcher 1978;

Burke 1980), little is known of the effect of surface chemistry on the settlement of deaveeds & Den Hartog (1972) contends that with the exception of sea grasses, boring algae and parasitic algae, marine plants are indiscriminate regarding the chemical composition of their Diatons may be another group to add to den Hartog's list substratum. of exceptions, as Scheer (1945) found that diatom colonization of fouling plates was much higher when a bacterial film was present inftially. In any case, current information suggests that the surface chemistry, of crustose corallines is not likely to affect the settlement of fleshy macroalgae.

4.4.2, Ecological consequences of antifouling, by Phymatolithon

that cloughing of epithallial cells provides an Accepting effective means of reducing overgrowth of Phynatolithon by fleshy seaweeds, what is the likely ecological impact of this effect, not only on Laminaria longicruric but on the subtidal seaweed community in largaret's Bay as a whole?

4.4.2.1 Effects of corallines in the absence of a kelp canop First consider the situation at the Mill Cove site In which a kelp canopy was lacking and the seaweed community comprised mostly, filamentoys opecies. In addition 'to' merely reducing the standing crop, it is benefing to speculate that in retarding overgrowth by aweeds, shedding of epithallial cells represents a mild and predictable disturbance acting to , reduce the intensity

interspecific competition among spaweeds for substratum and canopy

64

space. In doing so, monopolization of these recources by competitively superior species is presumably reduced, resulting in the coexistence of a greater number of species than otherwise would be permitted. The role of various kinds of disturbances, both biological (<u>e.g.</u> Paine 1966,1969,1974; Connell 1970; Dayton 1971; Dayton <u>et al</u>. 1974; Menge 1976; Menge and Sutherland 1976; Sousa 1980; Ayling 1981; Dethier 1984) and physical (Dayton 1971; Lubchenco and Menge 1978; Paine 1979; Sousa 1979,1980; Paine and Levin 1981; Dayton and Tegner 1984; Dethier 1984), in preventing competitive exclusion is well entrenched in ecological thinking.

the broad spectrum from negligible through entreme anounts. of disturbance, incofar as filamentous "seaweeds are concerned, wshedding of surficial cells by Phynatolithon represents at most a moderate level of disturbance. | Several vorkers have suggested that intermediate levels of disturbance are most effective in promoting species coexistence (Paine and Vada's 1969; • Levin and Paine 1974; Connell '1978; Lubchenco 1978; Samparco 1980,1982,1983; Ayling 1981; Carpenter 1981; Paine and Levin 1981; Hixon and Brostoff 1983). there, is an important difference in the way that However. Phynatolithon affects other seaweeds and the manner of species interactions proposed and observed, in most models and examples concerning disturbance and diversity. Whe dilution effect in terms of reduced biomass on the corpliane crust is not species specific, at east anong filbnentous species. The majority of existing' models, oth enpirical and theoretical, focus on enhancing diversity through loturbance specifically limiting the abundance o£ competitively,

dominant species only. However, limitation of competitively superior species is not a mandatory prerequisite for coexistence (Menge 1976; Caswell 1978; Massel 1979; Manski 1981).

4.4.2.2 Effect of corallines in the presence of a kelp canopy

When a dense canopy covers the understorey. filamentous species, although shedding of epithallial cells from the cruct would continue, the influence of coralline antifouling on the structure of the filamentous community could be expected to be of secondary importance to the shading effect of the upper strate (supported by observations at Paul Pt.; see also chapter 5).

4.4.2.3 Influence of Phymatolithon on Laninaria versus filamentous

• species

Regarding Laminaria longicruris in particular, this species was not recorded on the 'experimental substrata; thereby preventing assessment of the effect of Phymatolithon on its quantitative recruitment. 'However, in view of the findings of Masaki and ` co-workers (1981,1983) mentioned earlier, there is no reason to suppose that Phynatolithon does not have some influence on Laninaria , Nevertheless from the community recruitment. źt clear ាំព configuration at Paul Pt. that a virtual 100% cover of coralline crusts on hard substrata tannot prevent the establishment of a closed canopy of this precies. In addition, in cloced Stands of Laminaria, any effect of Phynatolithon in limiting recruitment of this kelp would be of minor importance relative . to intracpecific competition (see

chapter 5).

A fundamental dichotomy separating large seaweeds like Laminaria from their small filamentous counterparts, is that once kelps begin to grow and their holdfast expand, sloughing of the epithallium would not increase their spaceptibility to detachment from the substratum. Regarding filementous species, it is not necessary to suppose that . shedding of surface cells primarily affects microscopic phases. Groups of cells ready to be shed were found to frequently attain sizes Inm diameter (cleaved cells are non-pignented and groups of of , ca. these cells show up as chalky white scales on the surface of the Macroscopic juvenile and adult plants of many filamentous plant). scauceds anchored wholly or partially to such scales would be suscéptible to being dislodged even in moderate surge conditions." It is possible that during seasons when virtually no recruitment occurs, sloughing of the epithallium could thin-out existing stands of filamentous algae. Thus, while release of epithallial cells by Phymatolithon likely inhibits recruitment-of all seaweed species in, St. Margaret's Bay to some extent, the impact can be expected to differ among morphological groups, culminating among the filamentous assemblage.

4.4.3 Grazers, sloughing of epithallial cells and survival, of crustose coralline algae

Some authors have suggested a co-evolved mutualistic association of coralline crusts and grazers (Steneck 1962, 1983; Morse and Morse 1984). Their thesis steps from several observations, mamely, (1) the preferential association of many grazers with crustose red algae (see introduction), (2) the extreme grazer resistant morphology exhibited by these plants (Adey 1973; Adey and Macintyre 1973; Steneck 1932,1983; Littler <u>et al</u>.. 1933a,b; Littler and Littler 1984; Morse and Morse 1984), and (3) in a few cases the apparent dependence of growth or recruitment of some corallines on grazing to prevent their overgrowth by fleshy epiphytes (Paine and Vadas 1969; Adey 1973; Vine 1974; Wanders 1977; Ayling 1981; Hay 1981b; Steneck 1982,1983).

Although - the - argument for mutualism is sound to a point, in the light of the present results the general assertation that survival of coralline crusts is dependent on grazing seems an overstatement of the case. For crusts that do not shed epithallial cells, such as spécies of Clathromorphum (Adey 1965; Steneck 1982), and for several tropical species (e.g.' see Vine 1974; Wanders 1977), grazing probably is mandatory for . survival, but for other species sloughing of the epithallium is sufficient to kimit fouling to non-lethal levels (Masaki et al.. 1981,1983). In the present study, both Phymatolithom and Lithothampion remained healthy in the absence of grazers throughout the 16 months of the experiment. Similarly, Padilla (1984)' found no change in the distribution and abundance of coralling algae within herbivore exclusion cages over a nine month period, and within urchin removal areas over two years, relative to controls. 'I contend that a general case suggesting that coralline crusts require grazing For survival. is without justification, particularly because species that do . not slough sufficial cells but retain a cohesive chithailium constitute a minority among crustose red algae (Adey /1964,

Johnson and Adey 1965; Giraud and Cabioch 1976; Steneck and Adey 1976; Masaki et al.. 1981,1983).

Certainly coralline crusts .do not require absolute protection from colonization by macroalgal epiphytes to remain viable. At Paul where a dense kelp canopy had been present for at least 18 Pτ. months, the only areas of dead crust were directly beneath Laninaria Similarly, in southern Nova Scotia (A.R.O. Chapman pers. holdfasts, comma), Norway (Hagen 1983) and Japan (No Hagen perso comma), crustose corallines thrive beneath dense turfs, and closed canopies of Laminaria hyperborea and L. japonica respectively, Extensive cover of coralline cructs under dense canopies of Macrocystis pyrifera have also been reported (Noreno and Sutherland 1982; Reed and Foster 1984). The 'ability of some corallines to grow in relatively low light levels , is also evident from physiological studies (Adey 1970). It is tempting, to suggest that in growing baneath closed canopies where low light levels restrict the development of the understorey (see chapter. 5), and thereby overgrowth by epiphytes, coralline survivorship is enhanced. Apparently, there is a marked difference in the intensity of grazing necessary to create coralline-dominated areas and that required to maintain coralline bottoms.

4.4.4 Summary and comment on implications for hard-bottom benthos

In the absence of grazers and an overstorey canopy, the crustose cotalline <u>Phymatolithon</u> spp. bignificantly inhibited recruitment of fleshy. (mostly filamentous), seaweeds on its surface. Sloughing of epithallial cells by the coralline is probably the machanism

responsible for this effect. Among smaller, mostly filamentous, species, the inhibitory effect is not species specific, but all species are diluted by approximately the same proportion (=0.45 on average). For these plants, in the absence of an overstorey canopy, it is suggested that the antifouling effect serves as a mild form of disturbance. Disturbance at this level may enhance diversity of the seaveed community in the long term by reducing resource monopolization and allowing coexistence of species.

that crustose corallines constitute a dominant Considering assemblage in subtidal hard-bottom communities worldwide and that most species do slough their epithallium, the implications of the results of the present study are more far-reaching than just for the subtidal Margaret's Bay or Nova Scotia. Although grazing might be of St. necessary to create coralline-dominated bottoms, once established, " many corallines may reduce overgrowth by epiphytes and persist in the absence of grazers by sloughing their epithallial cells. Add to this innate antifouling ability the association with coralline crusts of a diverse assemblage of invertebrate grazers, and corallines amount to a guild of prominent ecological significance in shaping the structure of subtilial hard-bottom communities. To date it seems that fet ecologists have fully appreciated the eminent ecological role of encrusting red algae, probably because more attention has been given their low productivity than their interactions with other species. Crustose corallines cannot be viewed as passive primary substrata as earller workers have done (e.g. Paine 1974; Payton 1975a; Menge <

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1976)。

## CHAPTER 5 ·

RE-ESTABLISHMENT AND MAINTENANCE OF LAMINARIA LONGICRURIS BEDS

5.1 Introduction<sup>® "</sup>

Grime (1977,1979) proposed the evolution of three primary strategies in plants which he related to different levels of disturbance and stress in the environment. He designated these principal strategies as the competitive, stress tolerant, and ruderal referred to disturbance as physically, or strategies. Grine biologically induced loss of plant biomass, and defined stress as the physiological constraints on production imposed by resource limitation. C-plants are adapted to environments of low stress and disturbance, S-plants to conditions of high stress but low disturbance, and R-plants to environments of low stress but high disturbance. Grime suggested that all plants could be categorized within a ternary framework relating competition, disturbance, and stress (fig: 5.1).

In this chapter, the response of Laminaria longicruris to disturbance on a large and small scale is examined, and then considered along with several of its life history characteristics in assessing its competitive ability. Clearly, widespread destructive grazing of macrophytes by sea urching represents a major disturbance on a large scale. Although species of Laminaria are particularly susceptible to grazing by urching because they are a preferred food (Vadao 1977; Largon et al. 1980; Dugging 1983), several species of this genus have been quick to recover following release from sea R

Fig. 5.1 Surmary of the Grime (1977, 1979) model showing the location of plant strategies within a ternary framework of different levels of competition, disturbance and stress (redrawn after . Grime 1977).

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urchin grazing (Paine and Vadas 1969; Dayton 1975b; Estes <u>et</u> <u>al</u>. 1978; Duggins 1980, 1983) ... It has been shown that in Nova Scotia release from grazing by Strongylocentrotus droebachiensis facilitates seaweed recovery (Breen and Mann 1976b; Chapter 3), but that crustose coralline algae can, inhibit recruitment of macrophytes (Chapter 4). Can Laminaria regain its status as a dominant species on a large scale, as was characteristic of the pre-destructive grazing period (see Edelstein et al. 1969; Mann 1972a,b; Wharton and Mann 1981)? Also,' if L. longicrufis does re-establish on a large, scale, is there a consistent relationship between the extent of its recovery and time . since urchin die-off? The latter question was addressed by comparing the rates of Laminaria recovery at Paul Pt. and Mill Cove. Both' of ' these sites are similar in terms of exposure, substratum and depth, they are both potential kelp habitats, and most likely supported extensive kelp cover prior to the urchin outbreak (see Mann 1972a).

74.

If subtidal community structure after mass urchin mortality were to return to a configuration similar to that in the pre-outbreak period, then not only should extensive <u>Laminaria</u> beds be restored, but cover must also be maintained. Continued dominance of <u>L</u>. <u>longicruris</u> in the absence of high densities of sea urchins would necessitate both competitive ability and the ability to recover from small scale disturbances. Thus, maintenance of the newly established <u>Laminaria</u> bed at Paul Pt. was examined both in terms of the 'seasonal variability in components acting to reduce and increase canopy area, and the response in recruitment to small scale removals of the canopy. Finally, in light of the adaptations of L. <u>longicruris</u> to smalland large-scale dicturbances, its competitive ability, life history characteristics, and response to nutrient stress (studied by Chapman and Craigie 1977; Gagne <u>et al.</u>, 1982; Espinoza and Chapman 1983), it is attempted to place this species within Grime's (1977, 1979) ternary framework.of plant strategies.

75

5.2 Methods

5.2.1 Index of lamina area

The canopy area of Laminaria longicruris laminae in the non-experimental ureas at the Mill Cove and Paul Pt. sites and in four experimental plots at Paul Pt. (see next section) was followed from October 1982 until October 1983. 'Lamina area was expressed as an index of total shade area of Laminaria blades per unit area of substratum. Estimates of the shade area of individual laminae were obtained by measuring the total length and maximum width of blades in situ and converting to shade area with one of two regression functions.

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The regression functions were obtained from measurements of 184 plants collected at Paul Pt. The plants were brought to the laboratory, laid flat on plastic sheets and their outlines traced. The tracings were weighed and converted to an area by a known function relating weight and area of the plastic. The areas were then regressed against corresponding products of blade length x maximum width. Two separate functions were obtained, <u>viz</u>. -(1) for plants  $\leq 0.5m$  famina length,

Estimated shade area = ((0.672 x length x width) -1.38) cm<sup>2</sup> (N = 124 plants; r<sup>2</sup> = 0.98 adjusted for d.f.)

(2) for plants > 0.5m lamina length,

Estimated shade area = ((0.602 x length x width)+110.38)  $\operatorname{cm}^2$ (N = 460 plants; r<sup>2</sup> = 0.98 adjusted for d.f.)

"The estimates were of shade area and not surface area of the kelp

blades. The margins of L. <u>longicruris</u> blades are highly convoluted, and therefore the surface area of one side of the lamina is considerably greater than the shade area of the same blade (see chapter 6). Also, because blades overlap and, of course, never flig exactly horizontal in the field, the index represents an overestimate of the actual shade area cast by the L. <u>longicruris</u> canopy.

On each sampling occasion, the lamina area index in the non-experimental areas was estimated by measuring all plants within 10 randomly positioned quadrats of  $2m^2$ .

5.2.2 Partitioning of changes in canopy area into components due to recruitment and mortality of plants, and net growth and net loss of individual laminae

The lamina area index, as defined in the foregoing section, was also determined in four experimental plots at Paul Pt. Within each plot, Laminaria plants of lamina length >0.2m were tagged and numbered; plants with blades less than 0.2m long were too small and delicate to tag. Excluding small plants would not significantly influence the estimates of canopy area as their contribution to the canopy was minimal.

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On each sampling occasion the dimensions of all tagged plants were measured, notes made of plants lost since the previous sampling date, and any new plants attaining a blade length of 0.2m were recorded as recruits and tagged and measured. This procedure enabled partitioning of the change in the lamina area index from one sampling period to the next into components acting to increase canopy area (net growth of existing prints and recruitment) and those serving to reduce canopy area (mortality of plants and net loss of lamina tissué). Each component was expressed as a rate of change of the canopy area index per 30 day period. Data from the four plots were averaged to obtain mean values of these rates for each component for each time period.

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The four plots were part of a large experiment involving manipulations of both innual and perennial seaweed species in a total of eight plots (fig. 5.2), but details of the complete experiment need not be given here. All plots were 2m x 2m in area and delineated by rope borders. To minimize edge effects, manipulations were performed to at least 1m outside the rope borders, giving a total manipulation area of 16m<sup>2</sup> per plot. Given the possibility that grazing by limpets (Notoacmaea testudinalie) and chitons (Tonicella rubra) might affect recruitment of Laminaria, these molluscs were removed from all plots (see chapter 6)., The seaweed species removed and dates of all manipulations are given in appendix C.1.

5.2.3 Recruitment of Laminaria; comparison between sites and influence of intraspecific competition

At both Paul Pt., and Mill Cove, the number of <u>L. 'longicruris</u> recruits in four 2m x 2m experimental plots from which <u>Laminaria</u> had initially been removed, were recorded and compared (fig. 5.2, plot no's. 3,4,7 and 8). Recruits of lamina length >0.1m and >0.2m, were censused in these plots in May 1983. These eight plots were also maintained clear of limpet (<u>Notoacmaea</u> <u>testudinalis</u>) and chitom



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(Tonicella rubra) grazera To test the null hypothesis that the L. longicruris canopy at Paul Pt. has no effect on its oun recruitment, in May 1983 recruitment of Laminaria, in plots where the canopy had best removed (plot numbers 3,4,7 and 8, fig. 5.2) was compared with recruitment in nearby plots where Laminaria had not been manipulated (plot numbers 1,2,5 and 6, fig. 5.2) and in the non-experimental area. In the non-removar ploto, only recruits of lamina length >0.2m were cencused, while in the femoval plots and non-experimental area two size classes (blade length >0.1m and >0.2m were examined. Complete censuses were taken within the experimental plots. In the non-experimental area, · recruits were counted within ten randomly positioned 2m2 quadrats.

5.3 Results

5.3.1 Rate of recovery of Laninaria canopy

The extent of the Laminaria canopy was markedly different at the two sites. At Mill Cove <u>L</u>. <u>longicruris</u> plants were sparse and scattered whereas Paul Pt. was characterized by a dense and closed cover of <u>Laminaria</u> (fig. 5.3, summary data in appendix C.2). Clearly, comparing the two sites, there was no consistent relationship between the extent of <u>Laminaria</u>; cover and time since urchin hortality. The <u>Laminaria</u> lamina area index at Paul Pt. <u>ca</u>.18-20 months after urchin mortality was about an order of magnitude greater than that at Mill Cove after an equivalent urchin-free period, Similarly, <u>Laminaria</u> recruitment, in the kelp removed plots at Eaul Pt. was about two orders of magnitude greater than in similar plots at Mill Cove (table 5.1). This difference is clearly significant (1-tailed t-tests not assuming homoscedasticity, for recruits >0.2m blade length p=0.012, for recruits >0.1m blade length p=0.005).

5.3.2 Partitioning of seasonal variation in the Laminaria canopy into components due to recruitment; mortality, loss of lamina, tissue and growth of plants

The fully developed <u>Laminaria</u> canopy at Paul Pt., exhibited significant seasonal variation in cover (fig. 5.3; ANOVA, transformation  $= Y^{0.4}$ , df=(6,63), p<0.000). The canopy steadily deteriorated from <u>ca</u>. July until early spring at which time recovery was dramatic over a 6-8 week period. In the decline phase, the lamina





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area index fell to less than half of its peak springtime value, In the four experimental plots in which Laminaria was no manipulated, plots 1, and; 2 differed from 5 and 6 in the manipulation, of annual species. However Rregarding L. longicruris, I believe that consideration of the four plots as equivalent replicates is justified. First, there was no evidence to suggest that the annual species exerted a detectable influence on the Laminaria canopy or its recruitment. It was observed that by the time annuals first appeared in the spring, the new Laminaria recruits had grown considerably and had already formed an upper stratum over the developing annuals. The differences in the number of recruits 30.2m lamina length among plots 1 and 2, plots 5 and 6, and in the Onon-experimental area, / was not significant (ANOVA, F=0.17, d.f.=2, p=0.85). Second, the pattern of temporal variation in the kelp canopy in the four experimental plots containing Laminaria was not significantly different from that of the non-experimental area (fig. 5.4, summary data in appendix c.4; table 5.2). 'Thus, it seemed valid to examine the seasonal contribution of the different components of variation in canopy area within the experimental plots and accept this pattern as being the general case for Laminaria beds in the area.

There were significant differences (table 5.3) in the contribution of each component to the net change in canopy area, depending on time of the year (fig. 5.5, summary data in appendix C.4). For most of the year mortality of larger plants and erosion and tearing-away of portions of the lamina exceeded the combined effects




TABLE 5.2. Comparison of lamina area index of Laminaria longicruris in experimental plots 1,2,5 and 6 (see fig. 5.1) with estimates of the index in the non-experimental area at Paul Pt. Results of 2-tailed t-tests; None of the comparisons, show significant differences.

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Fig. 5.5 Partitioning of rate of change of lamina area index of , Laminaria longicruris into components due to mortality and recruitment of plants, and net loss and net growth of individual laminae. Bars are S.E.

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Component (C)	<sub>0</sub> 17.67 <sup>-</sup>	(3,9)	0.000
Date (D)	2.78	(7,21)	0。033
C x D	5.76	(21,63)	0.000

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of blade growth and recruitment, of new individuals to the population, and the Laminaria canopy declined. Mortality and loss of lamina tissue was particularly high through the stormy months of October through February. Restoration of the canopy during March through mid-May was due largely to increased growth rates of already established plants. Few plants were lost or exhibited a decrease in blade size during this period. Recruitment of plants of 0.2m minimum lamina length was also greatest during the period mid-March through mid-May. However, because of the small size of individuals recruited over any 2-3 month period, their contribution in increasing net canopy area was minimal.

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5.3.3 Influence, of canopy removal on Laminaria recruitment

A theoretical complication in interpreting data from this experiment is that in the four sites where perennial dominants were removed, <u>Desmarestia aculeata</u>, as well as <u>L</u>. <u>longicruria</u>, was cleared initially. Thus, at least in theory, the influence of intraspecific competition of <u>Laminaria</u> and the interspecific interaction of <u>D</u>. <u>aculeata</u> on <u>Laminaria</u> recruitment are confounded. At the beginning of the experiment (July 1982), both perennials were classified as 'dominants' because <u>Laminaria</u> formed a closed upper strata and <u>Desmarestia</u>, although an understorey species, covered an estimated 52.7% of the hard substratum in the non-experimental area. However, subsequent behaviour of the <u>Desmarestia</u> population at Paul Pt. indicated that if <u>Laminaria</u> recruitment was influenced by removing both species, the effect could be attributed largely to the influence of the Laminaria canopy alone and not to the combined effects of <u>Desmarestia</u> and <u>Laminaria</u>. First, after starting the experiment, <u>Desmarestia</u> cover began to rapidly decline. By December 1982 the cover of this species in the non-experimental area had dropped to 16.3%, by March 1983 to 11.6%, to 5.0% in May and 3.6% in July 1983. Thus, during the period of maximum growth of newly recruited <u>Laminaria</u> sporophytes (March through mid-June, see section 5.4), <u>Desmarestia</u> cover was already much reduced. Also, the initial cover of <u>D</u>. <u>aculeata</u> in the <u>Desmarestia/Laminaria</u>, removal plots was much less (only 31.1%) than the average for the non-experimental area (52.7%).

Recruitment of longicruris beneath a canopy of adult L. conspecifics was much lower than in plots where the canopy had been removed. The number of Laminaria recruits attaining a blade length of 0.1m or greater was significantly greater in the kelp removal plots than in the non-experimental area (table 5.4). Similarly, the number of recruits of minimum lamina length 0.2m was significantly greater in the kelp removal plots than in the non-removal plots and in the unmanipulated area (table 5.4). Laminaria recruitment in the non-removal experimental plots was not significantly different from that in the non-experimental area.

Although a greater number of <u>L. longicruris</u> recruits occurred in the kelp removal plots, these plants were significantly smaller than . recruits in the non-removal plots and in the non-experimental area (tables 5.5 and 5. The difference, in the size of <u>Laminaria</u> recruits in the non-experimental area and non-removal experimental

94



TABL	5.4. Recruitment of Lami	naria longicruri	<u>s</u> in kelp remova	1
, <b></b>	plots, non-removal plots, an Paul Pt. Standard errors in	nd in the non-ex	perimental area a	12
				•
•••••	TREATMENT	"NUMBER of RE Lamina L	CRUITS m <sup>2</sup>	
`.	• • • • •	· · ≥0.1m	, ≥0°2m	,
(72	Removal plots	45.00 (7.55)	23.38 (5.50) 2.94 (1.07)	
	Non-experimental area	6.25 (1.60)	4.10 (2.23)	
		v		`` 

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- plants jo. im lamina length in significantly greater than in the non-experimental area (l-tailed t-test not assuming homoscedasticity; p=0.008) ... ۰° ک
- \*\*\*\* Recruitment of plants 30.2m lamina length was significantly greater in the removal plots than in the non-removal plots (p=0.018) and non-experimental area (p=0.022); (results of 1-tailed totests not assuming/homoscedasticity). The difference in recruitment of plants  $\geq 0.2n$  lamina length in the non-removal and non-experimental areas was not significant (2-tailed t-test not assuming homoscedasticity, p=0.524). ٥

TABLE 5.5. Mean size (estimated shade area of laminae) of <u>Laminaria</u> <u>longicruris</u> recruits in kelp removal plots, non-removal plots and in the non-experimental area at Paul Pt.

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· TREATMENT	MEAN SHADE	STANDARD	N	95% CONFIDEN
•	· AREA (cm <sup>2</sup> )	ERROR	• عو	INTERVAL FOR M
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Removal plots	218.3	9。8	374	<sup>°</sup> 198.9 - 237.0
Non-removal plots	· 503。5	48.0	47	406.8 - 600.
Mon-ovportimental area	375.7	41.1	82	294.0 - 457.
			02	
B. Recruits of lamina TREATMENT	length ≥0.lm MEAN SHADE	STANDARD	. N	95% CONFIDEN
B. Recruits of lamina TREATMENT	length ≥0.1m MEAN SHADE AREA (cm <sup>2</sup> )	STANDARD ERROR	N .	95% CONFIDEN INTERVAL FOR M
B. Recruits of lamina TREATMENT	length ≥0.1m MEAN SHADE AREA (cm <sup>2</sup> )	STANDARD ERROR	, N	95% CONFIDEN INTERVAL FOR M
B. Recruits of lamina TREATMENT	length ≥0.1m MEAN SHADE AREA (cm <sup>2</sup> ) `122.9	STANDARD ERROR ° 5.9	。N 766	95% CONFIDEN INTERVAL FOR M 111.3 - 134.

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TABLE 5.6. Results of tests (hom	oscedas	tiçity	not · assum ·
.comparing' mean size (estimate	ed · shade	e area	a) of Lamina
. <u>longicruris</u> recruits in kelp remove	l plota	s, nor	n-removal plo
and in the non-experimental area at	: Paul P	٤.	
-			۵ 
A Boomston of Longing Tomoth NO 2m			Ð
A. RECENTLY OF THEMAN TENELI 20.2m			- ``
COMPARISON	° t	df	, р
	مار میں اور اور میں میں اور می		
Removal vs non-removal plots	8.767	419	p << 0.001
Removal <u>ve</u> non-experimental area	5,535	454	p << 0.001
Non-removal vs non-experimental area	1.957	127	.05 <p< .10<="" td=""></p<>
· · · ·	، <sub>د</sub>		,
and and the second s	u	······································	an a
B. Recruits of lamina length ≥0.1m		,	,
COMPARISON	έ.	df	. D
$\sim$ )	- ·		
Removal <u>vs</u> non-experimental area	7,209	889	p <<0.001 🔅
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(\*\*) indicates 2-tailed test

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5.4 Discussion

5,4.1 Rate of recovery of <u>Laminaria</u> canopy and relationship to

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The presence of a dense stand of <u>L</u>. <u>longicruvis</u> at Baul Pt. when the sife was first visited <u>ca</u>. 18 months after urchin mortality indicates the kelp's impressive potential to recolonize and rapidly develop a closed canopy. This rapid recovery and domination of the seaweed community on a large scale is consistent with the outcome of an earlier small scale clearing of sea urchins. When Breen and Mann (1976b) removed urchins from a 7m x 8m patch in St. Margaret's Bay, <u>L</u>. <u>longicruris</u> dominated the ensuing community after only 4-5 months. Clearly, <u>L</u>. <u>longicruris</u> resembles several of its congeners in its ability to recover and rapidly dominate seaweed communities following release from grazing (Paine and Vadas 1969; Dayton 1975b; Estes <u>et al</u>. 1978; Duggins 1980,1983).

This capacity to rapidly re-establish and attain dominance is indicative of two important life history traits. L. longicruris has an enormous reproductive potential, and exhibits high growth rates during late winter and early spring. Chapman (1984) estimated this species to produce an average of <u>ca</u>. 1.5 x 10<sup>7</sup> spores  $\overline{\text{cm}}^2$  of soruc in a population at Pubnico in the south of Nova Scotia. In the Pubnico population, which is <u>ca</u>. 8-10 times less dense than that at Paul Pt., this amounted to a peak spore production of <u>ca</u>. 5.25 x 10<sup>9</sup> spores m<sup>-2</sup> substratum. The growth rate of <u>L</u>. <u>longicruris</u> in St. Margaret's Bay is also impressive. From mid-March until mid-June, blade elongation may reach <u>ca</u>. 10mm per day (Chapman and Craigie 1977; Gerard and Mann 1979; Gagne <u>et al</u>. 1982). Mann (1972b) estimated that in one year of growth, individual plants in St. Margaret's Bay would grow 1-5 times their initial length, assuming no erosion at the blade tip.<sup>1</sup> These growth rates are not abnormal. Gagne <u>et al</u>. (1982)<sup>6</sup> measured increments of blade length in other populations of this species in Nova Scotia of <u>ca</u>. 18mm per, day, and Anderson <u>et al</u>. (1981) reported rates up to 35mm per day.

The occurrence of mass urchin mortality during the autumn probably confers an advantage to <u>Laminaria</u> over other species for recolonizing. Spore production in <u>L. longifruris</u> also occurs at this time, and macroscopic sporophytes first appear in the winter. Observations in the kelp-removal plots at Paul Pt. indicated that rapid growth of these recruits beginning in late winter enabled. <u>Laminaria</u> to dominate light resources before other species attained their peak spring growth.

If <u>L. longicruris</u> is able to recolonize readily extensive areas after release from grazing, as was evident at Paul Pt., why did a dense canopy of this species not develop at Mill Cove, even after more than two years following urchin mortality at this site? The difference in the rate of recovery of the <u>Laminaria</u> populations at the two sites correlates with the distance to the nearest spore source.

had persisted throughout the urchin-coralline dominated period at Boutilier Pt., which is only ca. 0.4 nautical miles upstream on an outgoing tide. At the height of the ebb, currents in the area can be -1-1.5 knots since the main channel funneling water from Mosher cå. Boutilier Coves is between Paul Pt: and nearby Luke Is. Along and the shore from Boutilier Pt. to Paul Pt., this tidal current is evident both at the surface and at depths of at least 18m. In contrast, the closest refugial Laminaria population to the Mill Cove site grew on the Mill Cove breakwater ca. 0.6 nautical miles to the south. Moreover, this population exhibits meager, if any, sorus No other intertidal or shallow infralittoral population production. was found from south of this breakwater to north of the Fox Pt. breakwater; which lies ca. 1.5 nautical miles to the north of the Mill Cove site. Currents in the area are considerably less than at Paul It is likely then, that an effective spore source for the Mill Pt. Cove site was considerably further afield than 0.6 nautical miles.

As a general case, the absence of a nearby kelp refugium at Mill Cove was anomalous. Along most of the Atlantic coast, refuge populations persisted as a narrow band in the low intertidal and very shallow subtidal throughout the urchin-coralline period. These plants were protected from urchin grazing by wave action. Following mass urchin mortality, rates of recovery of kelp along much of the east coast indicate that this infralittoral refugium provided sufficient spores to heavily seed the contiguous subtidal area (R.E. Scheibling pers. comm.; C.R. Johnson personal observation).

These comments raise a further query, namely, by what means is dispersal achieved over distances of the order of hundreds of metres? It is known that in other laminarian genera, spores are dispersed at most 3-5m from the parent plant (Anderson and North 1966; Dayton 1973). In the case of <u>L. longicruris</u>, the distance that a spore might travel from a given parent sorus is not a critical factor in dispersal. In this species sorus production occurs in October through January (Chapman'1984), coinciding with the onset of rough weather. During this period the distal ends of blades, often supporting extensive cover of sorus tissue, are continually being eroded. Thus, portions of spore bearing drift material may travel relatively long distances releasing spores en route.

102.

other investigations of recruitment of organisms in aquatic In communifies, relatively few authors have commented on the importance the source of recruits. Among these, Himmelmann et al. (1983) of observed poor colonization of Laminaria species in a subtidal area in maintained clear Strongylocentrotus Quebec which was of droebachiensis. They attributed this to the rarity of Laminaria in the infralittoral algal fringe. Ambrose and Nelson (1982) suggested the importance of both distance to nearest spore source and current in recruitment of Macrocystis pyrifera. Gore (1982) and Ebert (1983), studying the recruitment of aquatic invertebrates, have likewise emphasized the effect of distance to sources of recruits.

5.4.2 Seasonal variation in extent of Laminaria canopy

Temporal variation in the canopy area index at Paul Pt. ' was

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consistent with patterns of growth and blade erosion previously reported for L. <u>longicruris</u> in St. Margaret's Bay. Re-development of a closed canopy by rapid growth during March through May parallels observations by Mann (1972b), Chapman and Craigie (1977), Hatcher <u>et</u> <u>al</u>. (1977), Gerard and Mann (1979), and Gagne <u>et al</u>. (1982). Elevated rates of blade erosion during stormy winter months have also previously been noted (Mann 1972b; Chapman and Craigie 1978).

103.

Rates of loss of canopy area due to mortality of plants also correlates positively with the incidence of bad weather. In storms, individual plants were torn completely from the substratum, and frequently, blades were torn from the stipes (which remain attached) below the meristematic region.

The contribution of recruits of blade length >0.2m to canopy area peaked from mid-March .through May. This peak represented the new sporophytes recruited during winter reaching this size class during the rapid growth phase in the spring. Perhaps more interesting was the consistent appearance of plants attaining this size from September through February. This is probably the result of suppression of growth of macroscopic juveniles by the canopy rather than an · indication of virtually year-round low level recruitment. Reduced growth of juvenile conspecifics under canopy plants of Ecklonia radiata has been demonstrated by Kirkman (1981). However, it should be noted that Chapman (1984) found a low level of recruitment of microscopic stages of L. longicruris during periods when sori were absent in the vicinity.

The failure of the canopy in the spring of 1983 to attain a similar density to that during the same period in 1982 is attributed largely to grazing by the gastropod Lacuna vincta (see chapter 6).

<sup>,</sup> 104.

5.4.3 Intraspecific competition; density dependent regulation of recruitment

5.4.3.1 Shading by adult conspecifics

The marked reduction in numbers of recruits of L. longicruris in the presence of an overstorey of conspecifics is probably a shading effect. In St. Margaret's Bay substratum space, is not limiting, and the substratum under the kelp canopy at Paul Pt. was particularly open.' Unlike that for several other kelp species (Black 1974; Dayton 1975a; Velimirov and Griffiths 1979; Duggins 1980; Kirkman 1981) there . was no evidence of L. longicruris locally limiting recruitment of conspecifics (or other species) by physical abrasion of kelp fronds sweeping the substratum. Whereas the distal one-third of the lamina L. longicruris may rest on the substratum, this usually occurred. of only in calm conditions. Also, the laming of L. longicruris is considerably more delicate than those of the laminarian species studied in the foregoing examples. The difference in the density of recruits in the unmanipulated area compared to the kelp removal plots, where chitons and limpets were also removed, cannot be attributed .to grazing by these herbivores. Limpet and chiton grazing had no detectable impact on kelp recruitment (see chapter 6). It seems that recruitment was limited by low light levels beneath the canopy.

Impeded recrulitment by an overstratum of adult conspecifics has also been noted in other kelps (Black 1974; Santelices <u>et al.</u> 1980; Reed and Foster 1984; Santelices and Ojeda 1984b), including <u>Laminaria</u> <u>groenlandica</u> (Duggins 1980). Indeed, the literature abounds with examples of canopy effects in which the distribution and abundance of understorey species is inhibited by upper strata (Dayton 1975a,b; Foster 1975b; Pearse and Hines 1979; Harkin 1981; Ambrose and Nelson 1982; Cowen <u>et al.</u> 1982; Moreno and Sutherland 1982; Dayton <u>et al.</u> '1984; Reed and Foster 1984; Santelices and Ojeda 1984a).

It is interesting that when Chapman (1984) removed the canopy of a mixed stand of <u>L. longicruris</u> and <u>L. digitata</u> at Pubnico in the south of Nova Scotia, recruitment of visible plants was not affected. Divergence of his results from those in St. Margaret's Bay probably stems from two major differences in these populations. First, at Pubnico the kelp canopy is considerably more sparse than at Paul Pt. Perhaps a more important distinction is that the hard substratum at Pubnico is virtually entirely covered by a turf of red algae (Chapman 1984). Removal of this turf resulted in a ten-fold increase in recruitment of <u>Laminaria</u> spp.

5.4.3.2 Crowding by juvenile conspecifics

A further density dependent effect on recruitment of  $\underline{\mathbf{L}}_{\circ}$ <u>longicruris</u> was evident in areas from which adult plants had been removed. The inverse relationship between the size and density of recruits suggests that crowding limits growth in juvenile plants. In the kelp removal plots, <u>Laminaria</u> recruits settled in dense patches.

Within these patches substratum space was locally limiting and many plants grew over or were entirely epiphytic on the holdfasts of conspecifics.

<u>،</u> 106.

The shading effects of the canopy and of crowding in the absence of a canopy thus act in opposing directions, tending to minimize variance in the biomass of juveniles per unit area within a broad range of canopy development. This tendency to maintain constant biomass in a yirtually monospecific stand regardless of plant density is in line with the behaviour of many seaweed and terrestial plant species (Cousens and Hutchings 1983). A similar crowding effect in the intertidal kelp Egregia laevigata has been noted by Black (1974). Santelices and Ojeda (1984a) also found that plant size increased with interplant distance in Macrocystis pyrifera.

5.4.4 Maintenance of dominance

Prodigious spore production, dispersion of sorus-bearing drift material, and rapid growth early in the spring before other species realize peak growth rates, facilitate recolonization and establishment of a closed canopy. Once a dense cover has re-established, these same traits enable <u>L. longicruris</u> to maintain this stranglehold on resources. Annual rejuvenation of the canopy in spring has already been emphasized. In the absence of destructive grazing, openings in the canopy are most likely to be caused by winter storms. At Paul Pt. <u>L. longicruris</u> was quick to respond to release from canopy shading. Accelerated growth early in the spring and the marked numerical response in recruitment following canopy removal resulted in <u>Laminaria</u>

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dominating the removal areas before the arrival of summer annuals (which also increased following canopy removal). The perennial nature of this species also aids its competitive ability.

This pattern is unlike those in most marine communities that are  $_{\infty}$ , subject to disturbance that is patchy in time and space. Temporal and spatial patchiness in disturbance frequently promotes community species diversity by releasing resources otherwise monopolized by competitive dominants, thus allowing the proliferation of the ruderal but poorly competitive species (<u>e.g.</u> Dayton 1971; Levin and Paine 1974; Ayling 1981; Paine and Levin 1981; Dethier 1984). At Paul Pt., <u>L. longicruris</u> is both the competitive dominant and the opportunistic species that responds most quickly to patchy disturbance.

While Laminaria may have a clear advantage over other species in recolonizing openings in the canopy formed during winter, the same eventual outcome of dominance by Laminaria could be expected whenever the canopy was removed. No other seaweeds in this community approach the potential of Laminaria to form a closed perennial canopy. In the absence of Laminaria a closed cover develops only in the summer-with the proliferation of a guild of annual species (C.R.' Johnson, unpubl. Even if summer annuals were permitted to form a closed upper data). strata, this 'canopy' disappears in the autumn. Thus, Laminaria could be expected to gain dominance by the following spring. This contrasts with the situation in many intertidal (Hay and South 1979; Sousa et 1981) and subtidal communities (Sutherland 1974; Foster 1975a; al. Sutherland and Karlson 1977; Peckol and Searles 1983), where the

season that a limiting resource becomes available may have profound impact on the composition and structure of the ensuing community.

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A fundamental characteristic of a dominant species is that it limits the distribution and abundance of others. Comparison of community structure at Paul Pt, and Mill Cove, and comparing the composition of the kelp removal versus the non-removal plots at Paul Pt., showed that the Laminaria canopy inhibited development of understorey species (C.R. Johnson, unpubl. data). In particular, the otherwise impressive proliferation of summer annuals was severely curtailed beneath kelp cover.

species are ostensibly the principal competitors Three of L. longicruris on the Atlantic coast of Nova Scotia. In general, with increasing exposure from moderate to high levels, L. longicruris is found in mixed stands with L. digitata. Except at extremely exposed sites, usually in shallow water (<5m), L. longicruris appears readily L. digitata (C.R. Johnson, personal to coexist with able observation). Desmarestia aculeata is a relatively large understorey perennial also frequently found in association with L. longicruris (Edelstein et al. 1969; C.R. Johnson, personal observation). However, qualitative observation indicates that Laminaria eventually association (A.R.O. dominates this Chapman, pers; comm.; C.R. Johnson, personal observation). With increasing depth, L. longicruris and L. digitata are normally replaced on · hard substratum by the kelp Agarum cribrosum (Edelstein et al.. 1969; Mann 1972a). The wepth of 'this changeover zone may vary from ca.10m to

greater than 20m. Indeed, within its depth and exposure, range, the only situation in which <u>L. longicruris</u> might be severely limited by other species in the long term is when dense turfs are present "(Chapman, 1984). In Nova Scotia these turfs are rare on the Atlantic coast.

5.4.5 The Grime model of plant strategies, and categorization of  $\underline{L}_{\circ}$  longicruris

L. longicrufis does not dovetail neatly with any one of Grime's (1977,1979) primary groupings, but occupies several positions within his ternary framework. Certainly, this species exhibits features characteristic of all three primary strategies. Grime argues that rapid growth and high reproductive output, are two properties of ruderal species. L. longicruris exhibits both of these features. The perennial nature and high growth rates of this kelp are traits of competitive species.

L. longicraris also displays ability as a stress-tolerant During eight months of the year, excepting December through species. March, nitrogen levels in St. Margaret's Bay are extremely low (Chapman and Craigie 1977; Gagne et al. 1982). Chapman and Craigie (1977) showed that nitrogen was the main factor limiting growth of Nonetheless, this species is well adapted to deal L. longicruris. with extended periods of nutrient stress. In St. Margaret's Bay, Laminaria accumulates nitrogen from the water when levels are high during winter, and this internal nitrogen reserve, is utilized ĉΟ

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achieve high growth rates early in the spring when light conditions. are favourable but nitrogen virtually obsent in the water (Chapman and Craigie 1977; Gagne et al. 1982; see also Espinoza and Chapman 1983).

It should be noted that in Grime's scheme, a plant must manifest competitive ability in an unstressed environment to be classified as demonstrating a competitive strategy. If St. Margaret's Bay is a nutrient-stressed environment, how does <u>L. longicruris</u> behave under conditions in which nitrogen is not limiting? At Centreville in the Bay of Fundy (fig. 2.1) where upwelling provides excess nitrogen year around (see Gagne <u>et al. 1982), L. longicruris</u> dominated the community in the absence of destructive grazing (J. Gagne, pers. comm.).

Clearly, <u>L. longicruris</u> is an opportunistic colonist, demonstrates impressive competitive ability, and is tolerant of nutrient stress. This kelp dominates subtidal communities in a range of environments in Nova Scotia, and therefore 'fits' several of Grime's primary and secondary strategies. To, emphasize this point, consider some of the environmental characteristics of several of the localities in which Laminaria flourishes. In the absence of sea wrchins, Paul Pt. is an environment of moderate levels of stress and More sheltered sites on the Atlantic disturbance. coast are characterized by nutrient stress but low disturbance, whereas on the Bay of Fundy coast, Laminaria populations thrive in environments of low stress and low or moderate levels of disturbance. In these four environments, L. longicruris adopts the C-S-R, S-type, C-type, and C-R strategies (sensu Grime) respectively. In this sense it is a non-conformist. The success of <u>L</u>. <u>longicruris</u> in a wide range of exposure and nutrient environments is undoubtedly attributable to the adaptations afforded it in adopting this flexible `non-conformist' strategy.

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How do the life history and ecological features of L. longicruris compare with other species in the genus? Collectively, species of . Laminaria constitute a dominant group on rocky substrata in most shallow temperate waters in the Northern Hemisphere (e.g. see review by Kain 1979). Parallelling the case of L. longicruris in Nova Scotia, in experimental studies in the northeastern Pacific several workers have identified Laminaria species as competitive dominants in the absence of sea urchin grazing (Paine and Vadas 1969; Dayton 1975b; . 1978; Duggins 1980,1983). Foreman 1977; Estes et al. 'As with L. longicluris, recovery and realization of dominance following urchin removal in these communities was rapid. Closed Canopies developed in less than two years, indicating impressive reproductive and growth potential. Evidently L. longicruris is not unique within the genus in exhibiting traits of both competitive and ruderal plants.

## $_{\odot}$ CHAPTER 6

## IMPACT OF GRAZERS ON LAMINARIA LONGICRURIS

## IN THE ABSENCE OF HIGH DENSITIES OF SEA URCHINS

∕6.1 Introduction

• In this chapter I examine the impact on <u>L</u>. <u>longicruris</u> of the principal grazers in kelp beds in the absence of high densities of sea urchins (<u>Strongylocentrotus droebachiensis</u>), and compare their effect on <u>Laminaria</u> with that of the urchins. The predominant grazers are the limpet <u>Notoacmaea testudinalis</u>, the chiton <u>Tonicella</u>, <u>rubra</u>, and the prosobranch mesogastropod, <u>Lacuna vincta</u>.

vincta is an annual species and occurs only where there is a L. lush cover of macrophytes (e.g. Smith 1973; Fralick et al. 1974; Thomas and Page 1983), whereas the chitons and limpets were common on the urchin/coralline barrens and are present throughout the year. 0f the three, only Lacuna grazes the macroscopic sporophyte (see Fretter and Graham 1962; Kain 1971; Fralick et al. 1974; Brady-Campbell et 1984). However, chitons and limpets might potentially limit al. macroscopic 'stages, by grazing the microscopic recruitment of gametophytes and sporophytes. The null hypotheses that chitons and limpets do not influence Laminaria recruitment, and that grazing by L. vincta has no significant effect on the sporophytes, were tested by manipulation experiments in the field.

The region of a plant on which a herbivore grazes can substantially influence the outcome of the plant/herbivore

interaction. Depending on whether a grazer consumes the entire plant or just a part of it, and whether peripheral vegetative tissue, or reproductive structures, or primary structural regions are attacked, directly affects the impact of the grazer on the reproductive output and likelihood of mortality of the plant. Thus, the distribution of grazing by <u>Lacuna</u> on sporophytes was quantified, and in light of the results of the manipulation experiments, the implications of the grazing pattern for the structure of <u>Laminaria</u> populations and subtidal seaveed community structure in general was examined. The pattern of snail grazing was related to variation in the nutritional quality and toughness of different parts of the sporophyte, and to the distribution of polyphenols within plants.

113.

Polyphenols are a class of secondary metabolites which have recently been demonstrated or strongly implicated as effective antiherbivore compounds inhibiting the grazing activities of gastropods on brown algae (Geiselman and McConnel 1981; Steinberg 1984, in press). Polyphenols are polymers of phloroglucinol that are probably ubiquitous in all orders of brown algae (Ragan 1976; Ragan and Jensen 1977; Ragan and Craigie 1976, 1978; Steinberg in press), and ostensibly constitute the principal chemical defenses of the Phaeophyta against grazers (see Steinberg 1984). The levels of polyphenols in Laminaria, and the impact of grazing by <u>L</u>. vincta and <u>S</u>. droebachiensis on Laminaria are considered in discussing the evolution of a defense strategy in this kelp.

The few studies of L. vincta in the subtidal (Fralick et al.

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1974; Brady-Campbell et al. 1984) have not been Uquantitative, and have provided only limited information on the behaviour of populations of this snail. In view of the apparent importance of Lacuna as a grazer of Laminaria (Fralick et al. 1974; Brady-Campbell et al. Johnson personal observation), and the lack of knowledge 1984; C.R. of the basic natural history of this species in the subtidal, quantitative descriptions of densities, cohort patterns, and dispersal ability of post metamorphic snails were attempted. Also, the impact of cunner (Tautogolabrus adspersus) predation on Lacuna populations was assessed. This omnivorous labrid fish appeared to be the principal (predator of Lacuna on Laminaria plants at Paul Pt., and therefore might significantly influence the impact of Lacuna on Laminaria. In western North Atlantic temperate waters, cunner occur in high densities in nearshore habitats in which cover is available (Johansen 1925; 011a et al. 1975, 1978; Pottle and Green 1979; Pottle et al. . 1981).

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6.2 Methods

6.2.1 Impact of limpet (<u>Notoacmaea testudinalis</u>) and chiton (<u>Tonicella rubra</u>) grazing on recruitment of <u>L. longicruris</u>

Recruitment of <u>L</u>. <u>longicruffis</u> ( $\geq 0.2m$  blade length) in two experimental plots (plots 1 and 2, fig. 5.1) maintained clear of limpets and chitons, was compared with recruitment in the adjacent non-experimental area at Paul Pt. in May 1983. Complete censuses of recruits were made within the plots. In the non-experimental area, recruitment was assessed within ten randomly positioned  $2m^2$  quadrats. To minimize migration, into the  $2m \times 2m$  plots, grazers were removed to a distance of <u>ca</u>. In outside the plots, giving a total manipulation area of  $16m^2$  per plot. Some animals close to the rock/sediment interface, and all those below it, could not be removed.

6.2.2. Impact of L. vincta on the canopy of L. longicruris

Densities of snails on Laminaria blades and per unit area of bottom substratum were followed at shallow (3-5m), medium depth (9-11m) and deep (15-17m) sites in the Kelp bed at Paul Pt. from February until October 1983. On each sampling occasion, densities per unat area of substratum were estimated using 15 randomly positioned  $0.25m^2$  (medium depth and deep stations) or  $0.125m^2$  (shallow station) quadrate at each depth. Estimates of densities on Laminaria blades were obtained by counting snails on 25 tagged plants in each of the shallow and deep stations, and on 50 tagged plants in' the medium depth

site. The total surface area of the lamina of each tagged plant was estimated from measurements of the length and maximum width of blades made on each sampling date. Blade surface area (including both sides of the lamina) was calculated from these dimensions using the relationship -

total surface area of lamina =  $2 \times (1.037 \text{LW} - 11.376) \text{ cm}^2$ 

where L=lamina length (cm), and W=maximum lamina width (cm).

This function  $(r^2=0.96 \text{ adjusted for d.f.})$  was obtained from measurements on 20 plants collected at Paul Pt., which represented a size range from 0.28 - 3.30m blade length. The laminae were cut, into small pieces such that each piece would lie flat. These pieces were traced onto plastic, the tracings weighed, and then converted to an area with a predetermined function relating weight and area of the plastic.

The densities of snails on Laminaria blades were compared among depths and sampling dates by ANOVA. Strictly speaking, a repéated . measures model ANOVA should have been used since the same populations of plants were measured on each sampling occasion. However, because plants with the most (or least) snails at one time tended to have most (or least) snails on the next sampling date, the `subject' term of a mode1 repeated measures would be positive. Thus, use non-repeated measures design provided a more conservative test than strict adherence to a repeated measures approach (see appendix D.1 for further explanation).

The size frequency distribution of the <u>Lacuna</u> population on <u>Laminaria</u> blades in the non-experimental area at <u>ca</u>. 10m depth was followed from January through October 1983. Samples were collected by removing all snails from haphazardly selected kelp blades with suction lifts. Cohorts vere identified from these data using graphical methods (Harding 1949; Cassie 1954).

Lacuna sex ratios were estimated from the samples collected for size frequency analysis. However, snails collected on 23 January and 29 July 1983 were not sexed. In the samples for which sex ratios were estimated, a stratified random subsample of 50 snails of identical size frequency structure to the total sample was saked.

6.2.2.2 Dispersal ability of post-metamorphic snalls

The dispersal ability of snails was assessed in terms of the rate of recolonization of Laminaria blades in  $s_{\rm L}^2/4m^2$  and two groups of  $\pm w_0$ 16m<sup>2</sup> experimental plots following the removal of snails from these plots in January 1983 using suction lifts. Recolonization was followed for 41 days after the initial clearing. Prior to 'vacuuming, all plants within the experimental plots were tagged, and the number of snails on their blades counted. After Macuuming, snails were counted on subsamples of 10-54 haphazardly selected plants. The average number of snails per plant before and after snail 'removal was and recolonization was expressed as a percentage of the compared, initial number of snalls per plant prior to vacuuming.

Snails were frequently observed to be floating in the water

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column with their foot and antennae extended fully. то test the hypothesis that protrusion of the foot and antennae by detached snails facilitates dispersion by allowing snails to spend longer in the water column, the sinking rates of Lacuna with their foot and antennae withdrawn versus extended were compared. Two groups of 35 snails, representing as large a size range as was available, were selected and 4% formalin in seawater to one group washed with ca. induce withdrawal into the shell. The sinking rates of snails vere determined in the bottom 1.00m of a resting column of seawater 1.32m high and 0.10m diameter. For both groups, sinking rate was regressed against shell length and the significance of the difference in the slope (Sokal and Rohlf 1981, p. 505) and intercepts (Kleinbaum and Kupper 1978, p.103) determined.

14

6.2.2.3 Distribution of L. vincta grazing on L. longicruris

It was observed that <u>Lacuna</u> were not evenly distributed on <u>Laminaria</u> blades, but seemed to prefer the convoluted marginal frills of the laminae. To quantify the distribution of snail grazing on blades, the laminae of 14 plants collected at Paul Pt., representative of the size range of <u>Laminaria</u> at that site, were first divided into 10 regions (fig. 6.1). The proportion of each region exhibiting <u>Lacuna</u> damage was determined by overlaying flat sections of blade with transparent acetate sheets marked with dots spaced at 6.3mm intervals, and counting the number of dots over the damaged region and over the entire flat section. The distribution of damage aeross the 10 regions was analyzed by comparing an index of damage calculated for each

Fig. 6.1 Delineation of regions of <u>Laminaria longicruris</u> (i) assessed for grazing damage by <u>Lacuna vincta</u>; (ii) from which samples were taken for determination of polyphenol levels; and (iii) for which Chapman and Craigie (1977, 1978) and A.R.O. •Chapman (unpubl. data) determined levels of organic nitrogen, laminaran, mannitol, cellulose and alginic acid.

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region. The index was independent of the total amount of damage, <u>ie</u>. was sensitive to the distribution but not the extent of damage, independent of the number of regions, and weighted for the relative size of each region. The index was defined as -

damage index for region  $i = D(1) = (P(1) / \overline{P}(1))^{n}$  (1)  $/ \sum_{n=1}^{\infty} T(1)$ where P(1) = d(1)/T(1) = proportion of region i exhibiting

and d(1) = number of dots over damaged area of region 1 . sarea of snail damage of region i T(1) = number of dots over entire region i

snail damage

 $\approx$  total area of region /1.  $\overline{P}(1)$  = average proportion of snail damage per region for

all 10 regions

 $= (\sum_{i=1}^{10} d(i)/T(i))/10$ Also, the extent of <u>Lacuna</u> damage on the stipes, holdfasts and meristems of 97 haphazardly selected plants at Paul Pt. from <u>ca</u>. 5-16m depth was qualitatively assessed <u>in citu</u> on 17 March 1983. The extent of damage was assessed on a scale of 0-4 (nil through extreme), and the severity of grazing was recorded as either surface grazing or penetrating.

6.2.2.4 Intraplant distribution of polyphenolic compounds in L.

To test the hypothesis that the observed differential distribution of grazing by Lacuna on Laminaria correlates with levels of polyphenolic compounds within plants, polyphenol levels in six regions of <u>Laminaria</u> (fig. 6.1) were determined in each of five. plants Plants were obtained from <u>ca</u>. 10m depth at Paul Pt., transported in sealed dark plastic bags on ice, and analyzed immediately,

The concentration of polyphenols in samples (ca. 1-3 g blotted fresh weight) was determined by a variation of the colorimetric method given in Ragan and Jensen (1977) using Brentamine Fast Red 2G Salt. ". After weighing, samples were ground with pestle and mortar in ca. 2-3 ml redistilled anhydrous acetone, and the supernatant collected. The sample was ground a second time in a mixture of distilled water (ca. l=2 ml) and redistilled acetone (ca. l=2 ml), and this supernatant added to the first. The aqueous acetone extract was then dried, first by rotary evaporation and then in a high vacuum evaporator. Polyphenols were dissolved from the dried extract with distilled water 5, ml), particles, removed from the resuspended extract by (ca。 centrifuging, and the supernatant decanted and diluted to 50.0 ml with distilled water. Brentamine (2.0 ml of 1 mg ml<sup>-1</sup> solution) was added 500  $\mu$ l subsamples of the 50 ml extracts, these subsamples diluted ΈO to 6.0 ml with distilled water, and incubated at room temperature for 20 minutes before reading Absorbance 445nm against blanks of the Brentamine solution (2.0 ml) with distilled water (4.0 ml) In the calculations, background readings of the subsamples diluted to b.0 ml without Brentamine were subtracted from values obtained with the salt present.

Dry weights of the tissue samples used in preparing the extracts were estimated using regression functions relating blotted fresh weight and dry weight. One of two functions were used, depending on the region of the plant from which the sample was taken. These relationships were determined from tissue samples taken contiguous to those used in preparing the extracts. Dry weights of these secondary samples were determined after 24 hours drying at ca. 105°C.

for regions S,M,A and B (see fig. 6.1),

dry weight (g) =  $(0.0679 \times \text{blotted fresh weight}) \div 0.0222$ 

(r<sup>2</sup>=0.98 adjusted for d.f.; N=32)

for regions C and D (see fig. 6.1),

, dry weight (g) = (0.1403 x blotted fresh weight)  $\div$  0.0039

 $(r^2=0.97$  adjusted for d.f.; N=17).

Polyphenol concentration was expressed as mg polyphenols g<sup>-1</sup> dry weight of plant, relative to the high molecular weight (`type' 2') non-diffusable phloroglucinol polymers in <u>Fucus vesiculosus</u> (see Ragan and Craigie 1976; Ragan and Jensen 1977).

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6.2.255 Size specific grazing rates of L. vincta

Two methods were used to estimate the size specific grazing rates of <u>L</u>. <u>vincta</u> on the frill tissue of <u>L</u>. <u>longicruris</u> laminae. Size classes of snails were in 2.0 mm increments of shell length.

<u>Method 1</u>. Depending on their size, 10-25 snails of each size class were placed in cages (76mm diameter x 127mm high) with large meshed windows allowing flow-through of water in running seawater tanks at ambient seawater temperature. Pieces of fresh kelp blade were weighed (five replicate blotted wet weights), added to the cages, reweighed after <u>ca</u>. 2 days, and the differences in the mean weights before and after the experiment calculated. Three cages containing kelp but not .snails acted as controls.

<u>Method 2.</u> Depending on their size, 4-10 snails of each size class yere placed on a piece of fresh <u>Laminaria</u> blade 82mm in diameter in a petri dish ( $c_{ij}$ ) with a mesh top. The cages were placed in running seawater tanks at ambient seawater temperature. There were three replicate cages for each size class, and four control cages containing <u>Laminaria</u> but not snails. Five replicate blotted fresh weights were made of each piece of kelp before the experiment and again after <u>ca</u>. 4 days, and the difference in the mean weight of each kelp disc calculated.

Grazing rates estimated by both methods were expressed as g wet weight snail<sup>-1</sup> day<sup>-1</sup>. Since the results from the two methods were similar, they were pooled in the analysis (giving four replicate

estimates for each size class). .

6.2.2.6 Impact of grazing by L. vincta on the L. longicruris canopy 6.2.2.6.1 Direct consumption of laminae

The total biomass of <u>L</u>. <u>longicruris</u> blade consumed by <u>L</u>. <u>vincta</u> relative to the blade biomass available for consumption in any period of T days, is given by  $\rightarrow$ 

 $\int_{0}^{T} \underline{P}(s) \times \underline{G} \times D(t) \times S(t)$ 

percent lamina consumed =  $\int_{a}^{T} B(t)$ Where =  $\int_{a}^{T} B(t)$  $V(t) = row vector giving the proportion of the snail population in <math>\int_{a}^{T} B(t)$ 

 $\underline{P}(t) = row$  vector giving the proportion of the shall population in the each size class at time t

<u>G</u> = column vector giving the grazing rates of each size class of <u>L</u>. <u>vincta on L. longicruris</u>

D(t) = density of snalls on lamina at time t

S(t) = total surface area of L. <u>longicruris</u> laminae m<sup>-2</sup> substratum at time t

 $B(\xi)$  = standing blomass of <u>L</u>. <u>longicruric</u> laminae m<sup>-2</sup> substratum at time t<sup>2</sup>.

Using estimates of these variables obtained at <u>ca</u>. 10m depth at Paul Pt., this value was evaluated over the 254 day period 23 January

1983 to 4 October 1983, which represents almost the entire season that L. vincta was present at Paul Pt. during 1983. Thus, integrating over this period provided an estimate of the direct consumption of <u>L</u>. <u>longicruris</u> by Lacuna on a seasonal basis.

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Variables were measured using methods described earlier, and it was assumed that changes in variables between sampling dates were linear. Values of S(t) and B(t) were calculated from <u>in situ</u> measurements of kelp laminae in the non-experimental area. Blade biomass was estimated from the frond dimensions with the function -

blade biomass (g wet weight) = 0.063LW - 27.501

where L=blade length (cm), and W=maximum blade width (cm).

This equation  $(r^2 \approx 0.93)$  adjusted for d.f.) was obtained from measurements on 29 plants collected at Paul Pt. representative of the size range of Laminaria at this site.

6.2.2.6.2 Overall impact on canopy

Grazing by L. <u>vincta</u> appeared to promote the loss of large portions of the frilled margins of the laminae of <u>Laminaria</u>. 'Two experiments were conducted to test the hypothesis that <u>Lacuna</u> grazing significantly reduces the size of the canopy by increasing the rate of lamina erosion.

<u>Experiment 1</u>. On 25 Februrary 1983, 20 medium-sized <u>L</u>. <u>longicruris</u> exhibiting moderate damage from <u>Lacuna</u> grazing were collected at Paul Pt., and 20 undamaged plants of similar size were selected from Cranberry Cove which lies a short distance to the south of St. Margaret's Bay. Plants were brought ashore in dark plastic bags, weighed (five replicate weights per plant), and then resubmerged and attached to a taut line about 40m long, 0.5m off the bottom, in 7m of water at Paul Pt. After 21 days the plants were brought to the surface for final weighing (five replicates per plant), the percentage difference between the initial and final mean weights of each plant calculated, and the mean change in weight of the damaged and undamaged plants compared.

Experiment 2. Length and width increments of two groups of plants, one maintained free of snails and the other unmanipulated, were compared on five occasions from 14 February through 29 July 1983 in <u>ca</u>. 10m water at Paul Pt. Over this period, the blade dimensions of sixty-one plants within a  $2m_{\rm e}x$  2m experimental plot and 50 plants in the adjacent non-experimental area (unmanipulated controls) were followed. The experimental plot was maintained clear of snails using suction lifts. Initially (February-March), vacuuming was performed <u>ca</u>. weekly, and thereafter bimonthly (April-July).

6.2.2.7 Impact of predation by T. adspersus on L. vincta

When cunner first appeared in the kelp bed at Paul Pt. early in May 1983, they were observed to be voracious predators of <u>Lacuna</u>. Predation intensity was assessed from field samples, in terms of both the proportion of fish containing snails in their, guts, and the proportion of fish in which <u>Lacuna</u> constituted the greatest portion of the gut contents by volume. Cunner were sampled above the thermocline

at Paul Pt. on three occasions (13 June, 8 and 31 August 1983), and one sample was obtained from below the thermocline on 20° July 1983. Slurp guns, spears and baited crab traps facilitated collecting samples representative of the size range of <u>Tautogolabrus</u> at this site.

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Three approaches to the analysis of the gut contents of the fish in these samples were used to determine whether cunner exhibited size. selective predation on snails. First, for each sample, the mean size (total length) of fish containing Lacuna in their guts was compared with the sizes of fish without snails. Second, the preferences of different size classes of fish (60mm size class intervals of total length) for specific size classes of snails (2mm intervals of shell length) were determined using the following index -

- $I_{ij} = o_{ij} / p_j \pi n_i$
- · where -
- I = preference index of fish in size class i for snails in size class j
- o j = observed number of snails in size class j in guts of fish in ~.
  - p = proportion of snails in the field population in size class j
    n = total number of snails of all size classes consumed by fish of
    size class i
    '''
    - and where -I<sub>1</sub> = 1 indicates no preference

 $I_{ij} > 1$  indicates preference  $0 \leq I_{ij} \leq 1$  indicates avoidance

The quantity p<sub>j</sub> was estimated from size frequency distributions of snail populations on kelp blades at <u>ca</u>. 10m depth (see section 6.2.2.1). Because the sampling times when snails were collected for size frequency analysis did not coincide with the dates when fish were sampled, the size frequency distributions of snails on the fish sampling dates were estimated assuming linear changes in the size distributions between consecutive samplings.

129

Third, three samples of fish (13 June, 20 July, and 8 August) were pooled, and the relationship between size class of. fish (30mm size class intervals of total length) and the largest size class of snail (2mm intervals of shell length) in the fish guts was determined. To validate pooling of the three fish samples, it was first necessary to demonstrate independence of the size frequency patterns of snails and fish on these dates. Independence was suggested in that all size classes of fish containing intact snails in their guts were present on all sampling occasions. Moreover, there was no significant difference among sampling dates in the distribution of the size of fishes containing intact snails (Kolmogorov-Smfrnov distribution free test, p>>0.05 for all comparisons; see Hollander and Wolfe 1973, p.219).

Because these three analyses were based on the gut contents of samples of field populations, they provided only indirect indications of the size preferences of cunner. Corroborative data were sought by conducting a controlled laboratory experiment. Cunner in three size

classes («90mm total length, 110-160mm, >180mm) were placed in six 220 l aquaria (two replicates per size'class) of running sea water maintained at ambient seawater temperature under conditions of natural Each aquarium contained a . single photoperiod. plant \ of `L. longicruris. In the two tanks containing the large fish, there were five fish per tank, but all other aquaria contained 10 fish. After 12 hours acclimation, the kelps were removed and each replaced with another plant on which 150 Lacuna were feeding. Snails on these three size classes (2.01-4.00mm, 4.01-6.00mm, plants were in 6.01-8.00mm), in the proportion 14:111:25 respectively. After 120 hours the fish were demoved and all remaining snails in each size class counted. The proportion of snails in each size class consumed per fish was calculated for each tank, averaged for each size class' of fish, and compared among fish/snail combinations. Also, the size preference index I,, defined earlier in this section, was calculated for each size class of fish. In this case -

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 $o_{ij}$  number of snails in size class j consumed by fish in size class i  $p_j$  = initial proportion of snails in size class j and  $n_i$  = total number of snails consumed by fish in size class i.

The significance of the deviation of this index from unity was tested for each fish/snail size class combination using a t-test, where the test statistic  $(t_s)$  was defined as -

$$x_{s} = \bar{x} - 1 \, \bar{7} \, (s^{*} / \sqrt{N}) \quad \text{with 9 d.f.}$$

and where -



6.3 Results

6.3.1 Influence of grazing by <u>N.</u> <u>testudinalis</u> and <u>T.</u> <u>rubra</u> on recruitment of <u>L. longicruris</u>

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The number of <u>Laminaria</u> recruits  $\geq 0.2m$  blade length in experimental plots where limpets and chitons had been removed did not differ significantly from the density of recruits of this size in the adjacent non-experimental area (table 6.1). Thus, at least on the scale of this manipulation, chitons and limpets had no detectable effect on <u>Laminaria</u> recruitment.

6.3.2 Impact of L. vincta on the canopy of L. longicruris
6.3.2.1 Description of the L. vincta population at Paul Pt. in 1983

The mean abundances of <u>Lacuna</u> on all substrata (including <u>Laminaria</u>) per unit area of bottom, and on <u>Laminaria</u> blades only, from February until October 1983 are given in figs. 6.2 (summary data in appendix D.2) and 6.3 (summary data in appendix D.3) respectively. First, consider total densities per unit area of bottom. For most of the season, total abundances declined markedly with depth, but by late July densities were low at all depths, and the snails had virtually disappeared by early October (fig. 6.2). In shallow water, snails occurred on all seaweed species only when densities were >400m<sup>2</sup>, and at the medium and deep stations <u>Lacuna</u> was found virtually exclusively on <u>L</u>. <u>longicruris</u>. This distribution suggests that snails exhibit preference for <u>Laminaria</u>, but when densities exceed a threshold level (between  $400m^{-2}$  and  $1000m^{-2}$  at Paul Pt.), they will densely colonize

TABLE 6.1 Comparison of recruitment of <u>Laminaria longicruris</u> of minimum lamina length 0.2m in two plots from which chitons (<u>Tonicella rubra</u>) and limpets (<u>Notoacmaea testudinalis</u>) were removed, yith recruitment in the adjacent non-experimental area (Paul Pt., May 1983).

TREATMENT	NUMBER of RECRUITS m <sup>2</sup>	COMPARISO	on VITH N <b>QN</b> E AREA	: XPERIMENTAL
· · · · · · · · · · · · · · · · · · ·	, , ,	î S	۲ ۳۶۰ ۲	p (d.f.=9)
Plot no.1	1 <sub>°</sub> 25 <sup>°</sup> .	۰609 م <del>ر</del>	)	>>0 <sub>e</sub> 10 ,
Plot no.2		。406	• 6,	>>0.10
Non-experimental area,	4.10 (S.E.=1.41)	,	2	·
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Fig. 6.2 Densities of <u>Lácuna vincta</u> on all substrata (Ancluding <u>Laminaria longicruris</u>) per unit area of bottom at shallow (3-5m), medium depth (9-11m) and deep (15-17m) stations at Paul Pt. Bars are S.E. Homogeneous subsets of depth/date groups according to Tukey's classification are given (o(=.05, transformation= (Y+1)<sup>0.159</sup>). 2-way ANOVA indicated significant depth/date interaction (transformation = (Y+1)<sup>0.159</sup>, F=25.1, df=8, p<0.001).



Fig. 6.3 Densities of <u>Lacuna vincta</u> on <u>Laminaria longicruris</u> laminae at shallow (3-5m), medium depth (9-11m) and deep (15-17m) stations at Paul Pt. during 1983. Bars are S.E. Homogeneous subsets of depth/date groups according to Tukey's classification are given ( $C_{4}$ =.05, transformation =  $log_{10}$  Y). 2-way ANOVA indicated significant depth/date interaction (transformation =  $log_{10}$  Y, F=26.2, df=10, p<0.001).

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other species.

Analysis of the distribution of snail sizes (fig. 6.4, summary data in appendix D.4) indicated the occurrence of three cohorts during the season, with new cohorts arriving in January (cohort #2) and May (cohort #3) (fig. 6.5, summary data in appendix D.5). Because the growth rates of both sexes are similar (Smith 1973); identification of three distinct groups from the size distribution data may be interpreted as cohorts of different ages rather than groups of similar aged animals of different sex. The increase in snail densities in shallow water between the April and June samplings is attributed to the advent of cohort #3 in May. The presence of large snails in the January sample (cohort #1) implies that a small portion of the pòpulation overwinters. Presumably ft is these overwintering snails, which are mostly females, that spawn the new cohort early in the year.

When <u>Lacuna</u> abundances were examined in terms of density per unit area of <u>L</u>. <u>longicruris</u> blade, only the very broad population trends were similar to those of the total densities. In February, the densities of snails on kelp in shallow and medium depths were not significantly different, and in March and April snails occurred on kelp in uniform densities at all depths (fig. 6.3). Thus, the magnitude of the spatial and temporal variations in densities on <u>Laminaria</u> blades was much less than the fluctuations in, total densities. These differences in /density patterns are largely explicable by, the tendency of snails to colonize algae other than <u>L</u>. <u>longicruris</u> when overall snail abundances are high.

Fig. 6.4 Distribution of shell lengths of Lacuna vincta on Laminaria



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Fig. 6.5 Growth (mean shell length) of cohorts of <u>Lacuna vincta</u> on <u>Laminaria longicruris</u> laminae at <u>ca</u>. 10m depth at Paul Pt.

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The sex ratio changed considerably from approximately equal numbers of males and females from January until the end of April, to 70% females by early October (fig. 6.6, summary data in appendix D.6). Most of the large (>8.00mm shell length) individuals constituting cohort #1 were females (78.3%, N=60), and all snails >10.00mm total length in cohort #1 were females.

6.3.2.2 Dispersal ability of post-metamorphic L. vincta

Lacuna demonstrated an impressive ability to recolonize <u>L</u>. <u>longicruris</u> blades within the  $4m^2$  and  $16m^2$  experimental plots following initial clearing of snails (fig. 6.7, summary data in appendix D.7). Recolonization rates after clearing were as high as 44.0% and 69.1% of initial densities after only three and 17 days respectively. Moreover, these estimates are conservative in that they do not take into account the decline in snail densities throughout the area during the period of the experiment.

Dispersal was achieved by spails floating in the water column and being moved by currents. On several occasions, water to <u>ca</u>. 3-5m off the bottom teemed with floating snails. In addition, <u>Lacuna</u> was extremely adept at adhering to the surface of plants with which they) made contact while floating. Floating snails extended fully their foot and antennae, and comparison of sinking rates of snalls with their foot extended versus withdrawn showed that this behaviour significantly reduces sinking rate (fig. 6.8), and therefore enhances dispersal. The sinking rate of snails withdrawn into their shell followed the relationship -



at <u>ca</u>. 10m depth at Paul Pt.



Fig. 6.7 Rates of recolónization of <u>Lacuna vincta</u> on laminae of <u>Laminaria longicruris</u> in three groups of  $4m^2$  and  $16m^2$  plots initially cleared of snails at <u>ca</u>. 10m depth at Paul Pt. Recolonization is expressed as a percentage of the initial average number of snails per plant prior to clearing. Number of plants sampled given in parentheses ( ).

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151. sinking rate (mm sec<sup>-1</sup>) = 26.1 + (16.2 x shell length) (r<sup>2</sup>=0.87 adjusted for d.f.; N=35; ANOVA determining significance of slope, p<<0.001), and with the foot and antennae extended sinking rate  $(mm \sqrt{sec^{-1}}) = -12.2 + (12.5 \times shell length)$  $(r^2=0.89 \text{ adjusted} \ for$ N=35; ANÓVA d.f.; determining significance of slope, p<<0.001), where shell lengths are in mm. The slopes and intercepts of ( the ' two regressions were significantly different (p<0.001 for both). 6.3.2.3 Distribution of grazing by L. vincta on L. longicruris Lacuna grazing on Laminaria blades was highly and significantly clumped, (fig. 6.9, summary data in appendix D.8; ANOVA, transformation =  $\arcsin^{((Y^{0.5})+.001)}, F=32.8, d.f,=9, p<<0.001).$ Snails clearly avoided the meristem and mid-portion of the blade contiguous to the meristen, but exhibited marked preference for the medium-aged regions of the frilled margins. It should be noted that the estimates of relative grazing damage to the frill are conservative in that all plants used in the analysis had lost tissue from their margins (as a result of snail grazing), which could not be included in the assessment of damage. " . The in situ qualitative assessments of damage from grazing by

Fig. 6.9 Distribution of damage from grazing by <u>Lacuna vincta</u> on laminae of <u>Laminaria longicruris</u>; damage index  $(D_i)$  for 10 regions of lamina. Bars are S.E. Homogeneous subsets according to Tukey's classification are given ( $\ll =.05$ , transformation =  $\arcsin((Y_i^{0.5}) \div .001))$ .

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snails also indicated that the meristem is not damaged by snails (table 6.2). Only 10.3% of the plants showed any sign of grazing of the meristem, and in all cases this damage was light and barely detectable. Grazing of stipes was more common, but in no case were stipes damaged to the point that they appeared significantly weakened. It is interesting however, that <u>Lacuna</u> attacked heavily the relic stipes of damaged plants which had been broken off at a point along the stipe.

6.3.2.4 Concentration of polyphenols within L. longicruris plants

The concentration of polyphenolic compounds in <u>L</u>. <u>longicruris</u> was considerably and significantly higher in the meristem than elsewhere in the plant (fig. 6.10, summary data in appendix D.9; ANOVA, transformation = ln(Y), F=11.9, d.f.=5, p<<0.001). Excluding the meristem, there were no significant intraplant differences in levels of polyphenols, which were particularly uniform throughout the rest of the lamina.

6.3.2.5 Size specific grazing rates of L. vincta on L. longicruris

The grazing rates in the laboratory of specific size classes of L. vincta on frill tissue of L. longicruris are depicted in fig. 6.11 (summary data in appendix D.10). Grazing rate was dependent on snail size according to the function -

grazing rate oc (shell length)<sup>1.57</sup>

 $(r^2=0.95 \text{ adjusted for d.f.}).$ 

TABLE 6.2 <u>In situ</u> qualitative assessment of damage from grazing by <u>Lacuna vincta</u> to the stipes and holdfasts, and the meristem of 97 <u>Laminaria longicruris</u> plants at Paul Pt., March 1983. The severity of grazing is given as either surface grazing or penetrating, and the extent of damage ranked from 0-4, where 0=none, 1=barely detectable, 2=moderate, 3=heavy, 4=extreme.

REGION	SEVERITY OF DAMAGE	EXTENT OF DAMAGE	PERCENTAGE OF PLAN EXHIBITING SPECIFI
	n	ōn	DATAGE SCORE
Meristem	· _=	0	89.7
	surface grazing	1	10.3
Stipe and	en ,	0	77.4
holdfast	surface grazing	. 1	19.6
	surface grazing	2	· 1.0
4	penetrating	1	1.0 '
	penetrating	L	1.0
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Fig. 6.10 Intraplant variation in concentrations of polyphenols in Laminaria longicruris (expressed relative to the high molecular weight 'type 2' non-diffusable phloroglucinol polymers in Fucus vesiculosus). Bars are S.E. Homogeneous subsets according to Tukey's classification are given ( $\ll =.05$ , transformation = ln(Y)).

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This relationship indicates that grazing rate, and presumably metabolic activity, is proportionally much less in larger snails than in small ones, since biomass increases proportionally to length cubed.

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Over the course of the experiment, the change in weight of the pieces of <u>L. longicruris</u> blade in the seven control cages without onails was not significant ( $t_c=0.691$ , d.f.=5, 0.7>p>0.5).

6.3.2.6 Impact of grazing by L. vincta on the canopy of L.

6.3.2.6.1 Direct concumption of leminae

The biomass of L. <u>longicruris</u> blade consumed by L. <u>vincta</u> during the period 23 January - 4 October 1983, given by  $0\int^{254} \underline{P}_t \times \underline{G} \times \underline{D}_t \times S_t$ , was estimated to be 121.05 g Freehrweight m<sup>-2</sup> substratum. This represents only 0.05% of the biomass of <u>Laminaria</u> laminae that was available for consumption over this period.

Experiment 1. When Laminaria plants damaged by Lacuna grazing were held in the sea alongside undamaged plants of similar size for 21 days, the mean increase in biomass of the damaged plants was significantly less than the weight increase of the undamaged plants (table 6.3). Several of the damaged plants had lost considerable portions of the lateral frill of the laminae. Furthermore, since the 'damaged' plants were only moderately damaged (badly damaged plants that were intact could not be found), the difference in weight change
TADLI	E 6.3	Mean	<b>c</b> hange	la, i	fresh	weight	0È	undana	aged	Lanino	<u>ria</u> `
•	longic	ruris	plant	e, and	d pla	nts dar	aged	fron gi	razing	g by <u>Lac</u>	una.
	vincia	Le Rec	sults o	f expe	rinent	run oya	er 21	days;	Febr	uary-Ila	rch
	1983,	In	<u>C2</u> .	7a wat	ter a	t Paul	Pt.	Stand	lard	errors	in •
	parent	heses:	().	The dea	n inc	reasc iņ	ı wêig	ht of	the	undana	iged
	planto	, was	cignif:	icantly	y grea	ter thân	that	of the	e plan	its dans	iged
	by one	il gra	nzing (	l-țailo	ed i-t	est not	asour	iing ho	DEOSCO	das <b>tici</b>	ty,
	€_=2.J	A, df=	-11, p=	0.028)	**			5 J			

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	LAMINARIA	R.	MAN WEIGHT CHANGE
f	POPULATION	,	(as % of initial weight)
		* * *	1
•	Damaged	1 I	+3.86 (6.36)
	Undanaged	16 .	° +17.90 (1.60) 👾 📉

Of the 40 plants initially measured, 13 were lost during the experiment. 0

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\*\* The difference in the length of laminae of the damaged and undamaged plants at the beginning of the experiment was not significant (2-tailed t-test not assuming, homoscedasticity, t =0.968, df=38, p=0.34). .

162. between the damaged and control plants is not likely to represent the maximum effect of grazing on loss of blade tissue. Experiment 2: Although the control plants adjacent to the plot where plants were maintained clear of snails were chosen at random, there was a significant difference in the blade lengths of plants in the two treatments. Decause plants of different sizes grow at different rates (Mann 1972b), the analysis was restricted to kelps whose lamina ledgths fell within the size range 0.40-1.00m. Within this range, the difference in . mean laming length abong the two treatments at the beginning of the experiment was not sighificant (2-tailed t-test not assuming homoscedasticity,  $t_{a}=1.90$ ,  $d_{b}f_{a}=59$ , 0.10>p>0.05). Plants from which shalls were removed at regular intervals grew-". much wider between February and August than plants on which "onails were grazing (fig. 6.12, cutmary data in appendix D.11; wable 6.4). However, the differences in the relative increase in . Length of the grazed and ungrazed plants were not significant (fig. 6.13, cummary data la appendix D.12; table 6.5). . From the differences in "the width increments of the control versus the snall removal plants, it was possible to predict what the canopy biomass and lamina area index might have attained had smalls not, been present in; the kelp bed bed that the blade blomass of ... h. "Jongicruris Is proportional to the product of its length and maximum; width (see section 6.2.1.6), it could be expected that by "June 1983, Laminaria would have produced 28.3% greater standing biomass if the onallo had not been present. Similarly, it was calculated that if the





. 165. TABLE 6.4 Compartson of increments in width of laminae of Laminaria longicruris in a population maintained clear of Lacuna vincta trith an unmanipulated control population at ca. 10m depth at Recults Paul Pt., February-July. 1983. o£ 2-way ANOVA (treatment x date) showing a highly significant difference in the relative change in width of Laminae of the two populations. SOURCE  $\mathbf{F}$ df <0.001 Treatment (T 10.38 1 Date (D) 12.60 3 <u><0</u>,001 0.68 T x D: 0.568

Fig. 6.13 Effect of removal of <u>Lacuna vincta</u> from <u>Laminaria</u> <u>longicruris</u> on the rate of increase. In length of <u>Laminaria</u> laminae at <u>ca</u>. 10m depth at Paul Pt. Bars are S.E. Number of plants measured given in parentheses ().





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	,	Treatment (1	')	2.30	•	1	0.131	
·	•	Date (D)	•••	59.36		3	. <0.001	
•	, <sup>k</sup> t , '	ΤxD	به ۲ بر ۴ ۳ ع	<b>1.4</b> 5	,	3	0.229	
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canopy had not been subject to grazing by snails, given all else equal, by mid July 1983 the lamina area index would have increased to 27.3% greater than that observed (fig. 6.14, summary data in appendix D.13). Furthermore, these estimates are probably conservative in that this experiment did not commence until after the peak in <u>Lacuna</u> densities had passed.

6.3.2.7 Impact of predation by T. adspersus on L. vincta

Field obsérvations. indicating that cunner were important predators on Lacuna, at least early in the summer, were supported by data from analysis of the gut contents of fish. Until early August, the guts of most fish above the thermocline contained snails, and in June Lacuna comprised the greatest proportion of the gut contents of approximately-half of the fish examined (fig. 6.15, summary data in appendix D.14). However, as the summer progressed, the proportion of fish in which snails were the most important component of the gut contents declined dramatically. By the end of August, very few fish guts contained snails. Indeed, it was first noticed early in August that snails offered to T. adspersus by divers were usually sucked Ejected snails into the fish's mouth and then expulsed. were not harmed.

It is also noteworthy that fish above and below the thermocline exhibited markedly different behaviour patterns. Above the thermocline cunner were aggressive, exposed in the water column and actively feeding, whereas in the deeper colder water they were sluggish, timid, and for the most part cought the shelter of crevices



Fig. 6.14 Predicted canopy area (lamina area index) in non-experimental region at Paul Pt. assuming damage to Laminaria Longicruris by Lacuna vincta had not occurred.



Fig. 6.15 Incidence of Lacuna vincta in guts of Tautogolabrus

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. <u>adoperous</u> collected from above the thermocline at Paul Pt.

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174. in the boulder substratum. <sup>6</sup>6.3.2.7.1 Evidence field populations of differential from by different size classes of size-selective predation adspersus on L. vincta Analysis of the gut contents of cunner indicated that all sizes adspersus preferentially fed on small Lacuna, and that this preference was most pronounced in small fish. In all samples of cunner, the mean total length of Fish containing Lacuna in their guts was greater than the; length of fish "vithout' snails, and in two cases this difference was significant (table 6.6). This trend suggested that large fish were more likely to  $^{\prime\prime}$ feed on snails than smaller ones. Values of the size preference index clearly indicated that all fish exhibited strong preference for small snails, but that the bias towards small snails was most pronounced in the smallest fish (table 6.7). Moreover, the magnitude of preference for small snails estimated using this index is conservative. Many fish contained fragments of Lacuna shells which could not be included in the size frequency analysis. Examination of the size and chickness of the . fragments' suggested that most shell pieces were of small snails, but that relatively few of the larger snails in the guts were crushed. In addition, there was a clear relationship between the size of "

the largest snails in fish guts and size of the fish. Small fish consumed only small Lacuna, but larger fish ate a larger size range of

TABLE 6.6 Comparison of mean size (total length) of <u>Tautogolabrus</u> <u>adspersus</u> with and without <u>Lacuna vincta</u> in their guts. Samples collected at Paul Pt., June-August 1983., Included are results of l-tailed t-tests, not assuming homoscedcoticity, testing H<sub>1</sub>= mean size of fish containg <u>Lacuna</u> > mean size of fish without snails. Standard errors in parentheses.().

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,	8 Aug 1	55 ,	178 (5.8)	167 (10.6)	.0° 30,	°188 '
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of the proportion of snalls in specific size classes consumed per fish of given size in 5 days. Results of 2-way ANOVA (proportion of snalls consumed by fish size and snall size).

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TABLE 6.9, Size-selective *predation by Tautogo	). olabrus adspersus on ·
Lacuna vincta ine a Controlled laborator	ry experiment. Size
, preference index (I, ) describing, the pref	Eczence of different
sizes, of fish for specific size classe	es of snalls, and the
significance of the deviation of this index	from unity.
SIZE CLASS MIDPOINT of SIZE CLASS I( (total length) of SHELL LENGTH of	) t <sub>s</sub> p <sup>r</sup> ('df='9)°
of, <u>LACUNA</u> <u>TAUTOGOLABRUS</u> (mm)	
<90 3 4.83 5	11.67 <.001
7 0.67	-1.01
	ໍ3.49 ໍີ.01>p>.001 ໌ ≏0.27 , >.100໌
· · · · · · · · · · · · · · · · · · ·	-0.72 >.100
>180 3 1.80 5 0.96	2.44 .05>p>.02 -0.14 >.100 .
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snails (fig. 6.16, summary data in appendix D.15). These data indicated that L. vincta >8.00mm shell length attain a total size refuge from T. adspersus <150-240mm total length.

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6.3.2.7.2 Evidence from a laboratory experiment of differential size-selective predation on <u>L. vincta</u> by different sizes of <u>T.</u>

The behaviour of cunner of specific size classes in consuming different sizes of snails in the laboratory closely parallelled the patterns obtained by analysis of the gut contents of animals from Consideration of the proportions of the different field samples. sizes of snails consumed by fish in each size class (fig. 6.17, summary data in appendix D.16; table 6.8), and values of the size-preference index of specific sizes of cunner, unequivocally illustrated universal preference by all fish for small snalls, but that large fish ate proportionally more large snails than their smaller conspecifics (fig. 6.18, table 6.9). Only the preference indices of fich for small snails "differed, significantly from unity " (table 6.9). However, it should be noted that since the range that I may take when an item is preferred is infinitely larger than when an item. is avoided (see section 6.2.2.7), testing the deviation of this index from unity may not be sensitive in detecting avoidance.

4 Discussion

Of the three species of grazers which might potentially affect populations of <u>L</u>. <u>longicruris</u> in the absence of high densities of sea urchins, the impact of limpets (<u>Notoacmaea testudinalis</u>) and chitons (<u>Tonicella rubra</u>) appears negligible, but the prosobrach gastropod <u>Lacuna vincta</u> can have considerable impact on the canopy structure of this kelp.

6.4.1. Characterisites of <u>L. vincta</u> considered in relation to its grazing pressure

Lacuna exhibits several features that collectively signify this species as a potentially important grazer of L. longicruris. vincta is a generalist herbivore able to utilize a Although L. variety of seaweed species, in the subtidal it demonstrates preference longicruris. At >ca.9m depth where densities never exceeded for L.  $300m^{-2}$ , snails were found virtually exclusively on ca. L longicruris and rarely occurred on other species. Only at shallow depths when densities exceeded 1000m<sup>2</sup> did snails commonly utilize Preference for Laminaria may be of other species as substrata. adaptive significance since the growth rates of cohorts feeding on Laminaria at Paul Pt. (1.46mm month  $\begin{bmatrix} 1 \\ 2 \end{bmatrix}$ ; estimate for cohort #2 prior to cunner becoming active) suggest that Laminaria might be of superior nutritional quality to other food plants. Documented growth rates of cohorts feeding on species of Fucus are much lower, ranging from 0.08-0.64mm month. (Thomas and Page 1983), and 0.11-0.83mm month. (Smith 1973). Also, at Paul Pt. snails grew substantially larger

than the largest snails found by Smith (1973), Fralick <u>et al.</u> (1974), Eretter and Manly (1977), Grahame (1977), and Thomas and Page (1983). In addition, egg masses were largely restricted to <u>L</u>. <u>longicruris</u> irrespective of depth and density. <u>Laminaria</u> blades provide relatively tough, dependable, flat surfaces suitable for the adherence of egg masses away from benthic predators. These observations are in accord with reports from both sides of the north Atlantic which indicate that although <u>L</u>. <u>vincta</u> may feed and spawn on several<sup>4</sup> 'seaweed species, with few exceptions, in the subtidal <u>Laminaria</u> species are commonly used for these activities, whereas <u>Lacuna</u> is of ten found on <u>Fucus</u> intertidally (Fretter and Graham 1962; Kaih 1971; Smith 1973; Fralick <u>et al</u>. 1974; Fretter, and Manly 1977; Grahame 1977; Thomas and Page 1983).

Snails can appear in extremely high densities within a short period of time, suggesting mass simultaneous settlement from the plankton. Early in January 1983, numbers of <u>Lacuna</u> at the Paul Pt. site were very low, but by 22 January maximum densities exceeded >300 snails plant<sup>-1</sup> at <u>ca</u>. 10m, and by mid February maximum densities of >4500 m<sup>-2</sup> were encountered in shallow (3-4m) depths. Other's have similarly reported the sudden appearance of high densities of small <u>L</u>. <u>vincta</u> on subtidal populations of <u>Laminaria</u> (Fralick <u>et al</u>. 1974) and intertidally on Fucus (Smith 1973; Thomas and Page 1983).

In addition, several cohorts, may settle in a single season. Spawning occurs for at least six months of the year, and although early mortality is high (Smith 1973; Fretter and Manly 1977), reproductive output is large (Grahame 1977, 1982). In intertidal populations of <u>L</u>. <u>vincta</u> in Britain, 'spawning occurs from <u>ca</u>. January until June, and first settlement usually takes place not 'before May-June (Fretter and Graham 1962; Smith 1973; Fretter' and Manly 1977; Grahame 1977; Fretter 1984). At Paul.Pt., spawning was observed similarly from January until mid June. However, given an egg 'life of <u>ca</u>. 2-3 weeks and a planktonic larval phase of <u>ca</u>. 6-8 weeks, settlement of <u>L</u>. <u>vincta</u> at Paul Pt. in January indicates that spawning commences earlier and lasts longer in Nova Scotia chan in intertidal populations in Britain.

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Finally, unlike snails in intertidal populations (Smith 1973; Fretter and Manly 1977), L. vincta has considerable capacity for dispersal in the subtidal. By extending fully their foot and antennae, larger snails can considerably reduce their sinking rates, and small snails can slow their sinking rates to the point where they are nearly neutrally buoyant. Also, L. vincta can produce copious amounts of mucus, and frequently snails were observed to float with neutral buoyancy suspended from mucus threads. The limpet Helcion pellucidus which feeds and lives on L. hyperborea, also produces mucus when dislodged, allowing it to float and drift to other plants (Vahl 1983). Thus, if settlement of L. vincta were patchy along a shoreline, given sufficient water movement, it is likely that areas of low settlement density would soon be invaded by dispersing snails. I have observed the water column teeming with snails several metres from the bottom, and others have collected L. vincta in large numbers in surface plankton tows (R.S. Schiebling, pers. comm.). 'It seems that

the high densities of snails recorded in shallow water were the result of floating animals being washed inshore.

6.4.2 Influence of predation by <u>T</u>. <u>adspersus</u> on the population

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Cunner were clearly the principal predators of L. <u>vincta</u>, on L. <u>longicruris</u> plants. Field observations and analysis of gut contents indicated that this fish is a voracious predator of <u>Lacuna</u> from when they first become active in late April until mid-summer. Johansen (1925) also reported <u>Lacuna</u> to be common in cunner guts. However, the dramatic decline in the density of <u>Lacuna</u> before <u>T</u>. <u>adspersus</u> became active suggests that there are other major sources of mortality. Both Smith (1973) and Fretter and Manly (1972), reported extremely high juvenile mortality in intertidal populations of L. <u>vincta</u>.

Predation on Lacuna is intense only early in the summer, since as cohorts grow, a large proportion of snails attain a size refuge from cunner, predation. Snalls >8.00mm shell length did not appear to be eaten by the largest fish (150-240mm total length) encountered. The marked preference of all sizes of fish for small Lacuna is probably indicative of the difficulty of crushing the larger shells. Food adspersus, such as pieces of sea items found in the guts of  $\cdot$  T. urchins and crustacean appendages, were frequently much larger than, the sizes of ingested snails, suggesting that large snails were not avoided because they were too large for fish to swallow. Johansen (1925) also noted that cunner were unable to crush the shells of molluscs other than small species and individuals.

Overall then, since intense predation is limited in time and space, predation on <u>Lacuna</u> by cunner, probably only slightly moderates any impact the snails have on <u>Laminaria</u>. High densities of snails can be present for some time prior to cunner becoming active, many snails quickly attain a size refuge protected from most sizes of fish, and predation does not appear to be intense below the thermocline.

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The preference of cunner for small snails likely influences two primary characteristics of the Lacuna population. First and most obviously, cunner predation would cause a shift in the size structure Af Lacuna towards a larger mean cohort size. The pronounced increase in the estimated mean size of cohort #2 between the April and June sampling dates is likely to be partially attributable to predation by <u>'</u>. adspersus. A more subtle and ecologically important consequence of cunner predation is likely to be a  $\circ$  change in the sex ratio of Lacuna, favouring "females. Both male and female Lacuna growsat the same rates, but females usually grow larger (Smith 1973). Whereas this mortality pattern in itself would lead to an increase in the proportion of females, differential predation on smaller snails would the sex ratio changed from. accelerate this trend. At Paul Pt. approximately equal numbers of both sexes early in the season to 70% females by October. Differential predation in this manner is adaptive in that enhanced survival of females would augment spawning in the next season.

This pattern of mortality is diametrically opposite that reported . by Russell-Hunter and McMahon (1975) for an intertidel population of

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<u>L. vincta</u> in Massachusetts, U.S.A. They also observed a <u>ca</u>. 1:1 sex ratio in late winter, but by June 70% of the population were males, and by the end of the summer all of the large snails were male. Different again, Grahame (1977) found approximately equal numbers of both sexes at the beginning of the spawning season in an intertidal population in Britain. Seasonal patterns of sex ratios among disjunct populations are clearly inconsistent, and there has been little work to elucidate the factors which might influence sex ratios in <u>L</u>.

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6.4.3 Effect of grazing by L. vincta on the canopy of L. longicruris

Despite their high numbers, the biomass of Laminaria blades consumed by snails was small, attaining an estimated maximum of 1.32g fresh weight day  $m^{-2}$ , and amounting to only 0.05% of the blade consumption biomass available for for 'the season period Although these estimates were based on grazing February-September. rates measured in the laboratory, there was no reason to-suppose that the laboratory rates grossly underestimated grazing in the field. During the experiment snails were actively grazing at all times when they were checked, and their grazing left the characteristic holes and scars in the blade portions similar to those observed in the field.

These estimates are much lower than the value of 48.9g dry weight  $day^{-1} m^{-2}$  given by Thomas and Page (1983) for Lacuna grazing on Fucus edentatus, even when allowing for the higher snail densities in their sites. However, they derived this value from the difference in

production  $m^{-2}$  of <u>Fucus</u> at two different positions on the shore, one which was lightly grazed and the other heavily grazed by <u>Lacuna</u>. Their value includes plant material eroded and lost as a result of grazing but which was not directly consumed. Moreover, they did not control for differences in <u>Fucus</u> production at the two positions independent of grazing.

Whereas the biomass of <u>Laminaria</u> consumed by <u>Lacuna</u> was negligible, the net effect of snail grazing on the canopy was significant. Grazing was concentrated on the frilled margins of the plant, and snails typically ate right through the blade, at first forming small holes which later coalesced. Concentrated damage in this pattern promoted tearing away large sections of the lamina margins during storms, resulting in significant reductions in the width but not the length of plants. Therefore, by the indirect effect of weakening the delicate frill of laminae, but not other portions of the plant, grazing significantly reduced the canopy area but showed no evidence of promoting <u>Laminaria</u> mortality.

Some of these observations differ from those of Fralick <u>et al</u>. (4974) who examined grazing by a dense 'population of <u>Lacuna</u> on <u>L</u>. <u>saccharina</u> and <u>L</u>. <u>digitata</u> in New Hampshire, U.S.A. In contrast to the pattern at Paul Pt. in which damage to the stipes of intact plants was not severe, even when mean snail densities exceeded  $2200m^{-2}$ , Fralick and colleages reported that stipes were, 'grazed heavily and that the contributed to extensive destruction of the kelps. No evidence of this was found after viciting several sites in Nova Scotia, although Làcuna colonized and grazed heavily the residual stipes remaining after the upper portions of Sporophytes had been torn avay by storms or divers.

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6.4.4 Ecological implications of reduction of "the L. <u>longicruris</u> canopy from grazing by L. <u>vincta</u>

The impact of <u>Lacuna</u> in effecting a significant reduction in the cover of the dominant overstorey species is unlikely to have much influence on overall community structure. The high growth rates of <u>Laminaria</u> during April and May far exceeded the effect of the loss of blade tissue as a result of snail grazing. Thus, it seems likely that the understorey species would benefit little from the reduction in canopy area since by the time most species commenced accelerated spring growth, the canopy had recovered sufficiently to form a closed stand (Lamina area index >1.5m<sup>2</sup> m<sup>-2</sup> substratum, fig. 5.2).

One effect of <u>Lacuna</u> grazing may be in fostering the continued dominance of <u>Laminaria</u> by reducing its mortality and increasing its productivity. It has already been emphasized that because snails avoided the meristem, and did little damage to the stipes of intact plants, grazing did not appear to increase <u>Laminaria</u> mortality. Indeed, by promoting the loss of lamina margins, kelp mortality may be reduced since drag on the blade in heavy surge would be reduced, which would elessen the likelihood of plants being torn from the substratum during storms. In addition, by reducing canopy cover, <u>Lacuna</u> grazing may promote the productivity of <u>Laminaria</u>. Reducing canopy area by cutting off the distal one-third of laminae is used to increase the productivity of commercial kelp beds (Tseng 1980), although severe pruning of Laminaria decreases growth rates (Luning <u>et al</u>. 1973; Chapman and Craigie 1978).

6.4.5 Relationship between distribution of polyphenols and variation in toughness and nutritional quality in L. <u>longicruris</u>, and subtidal community structure in the absence of high densities of sea urchins

It seems likely then that the interaction between L. vincta and Le plongicruris is mutually beneficial to both snail and, kelp. The nature of this interaction depends to a large degree on the distribution of grazing damage on the plant. If the distribution of grazing 'vere more uniform, the outcome of the interaction might be altogether different. Certainly, if the stipe and meristem were attacked by snails in densities similar to those encountered at Paul Pt., there seems little doubt that extensive mortality of macroscopic sporophytes would occur. With a drastic reduction in the Laminaria canopy, which would be unable to recover fully in the spring, understorey plants would flourish (C.R. Johnson unpublished data). Thus, at least temporarily, the composition of the seaweed community would undergo a major shift

Avoidance of the meristem of <u>L. longicruris</u> by <u>Lacuna</u> correlates with high concentrations of polyphenolic substances in this portion of the blade. Elsewhere in the plant levels of polyphenols are uniformly low. The role of polyphenols as antiherbivore agents in terrestial plants is widely accepted (see Feeny 1976; Rhoades and Cates 1976;

McKey 1979; Rhoades 1979; Swain 1979), and there is a small but convincing body of evidence indicating their effectiveness as defense compounds in many marine brown algae (Geiselman and McConnell 1981; Steinberg 1984, in press). Levels of polyphenols in the meristem of longicruris are slightly lower than in Fucus vesiculosus (Ragan Ľ. and Jensen 1978). Collectively, species in the order Fucales are characterized by high concentrations of polyphenolics and are, ingeneral, avoided or least preferred by a taxonomically diverse array of grazers (Steinberg in press). Thus it seems highly probable that avoidance of the meristem of Laminaria by Lacuna is a direct result of the elevated levels of phenols in this region. If this is the case, then in the absence of large numbers of sea urchins, the structure of the seaweed community in much of the rocky subtidal of the Atlantic coast of Nova'Scotia hinges to a large degree on the distribution of polyphenols in the dominant canopy species.

Intrablade variation in phenolic levels cannot account for the differential grazing of <u>L</u>. <u>vincta</u> on the stipe, and central and frill portions of the lamina. The ranking of grazing damage to these areas was lamina frill > central portion of lamina > stipe and holdfast. Two factors that might account for the differences in feeding among these regions are toughness and nutritional quality of the tissue. The stipe and holdfast of <u>L</u>. <u>longicruris</u> are considerably tougher, than the meristem and mid-region of the blade, which are tougher again than the blade frill. Most mesogastropods, including <u>Lacuna</u>, possess taenioglossan radulae (Fretter and Graham 1962; Steneck and Watling 1982). Steneck and Watling (1982) stressed that taenioglossan radulae

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are much less effective in excavating leathery macrophytes than other (docoglossan) types, and suggested, that the grazing ability of molluscs possessing taenioglossan radulae is significantly limited by the toughness of their food. Among several species of kelps all characterized by low levels of polyphenols, Steinberg (in press), found a significant negative correlation between frond toughness and the grazing rate of the gastropod <u>Tegula funebralis</u>. There is also an abundance of examples from non-kelp species showing, that increasing toughness, both within and among algal species, reduces susceptibility to grazing (Littler and Littler, 1980, 1984; Lubchenco and Cubit 1980; Slocum 1980; Hay 1981a,b; Hay <u>et al.</u> 1983; Littler <u>et al.</u> 1983a, b).

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. Differences in the distribution of damage from Lacuna grazing also correlate with variation in the nutritional quality of different' regions of L. longicruris. Intraplant variation in levels of organic " nitrogen (Chapman and Craigie 1977; A.R.O. Chapman unpublished data in table 6.10), laminaran and mannitol (Chapman and Craigie 4978), and callulose and alginic acid (A.R.O. Chapman unpublished data in fig. 6.19) in L. longicruis is summarized in table 6.11. The vast majority of the large number of marine gastropods investigated to date posséss laminarinases, alginases and cellulases (Yokoe and Yasumasu 1964; 1970; 1971: Sova al. Favorov and Vaskovsky et Hylleberg-Kristensen 1972; Gianfreda et al: 1979a,b; Elyakova <u>et</u> <u>al</u>. 1981)。 However, whereas laminarinases exhibit very high activities, cellulase and alginase activities are typically low. Thus, the structural polysaccharides are hydrolyked less well than the reserve carbohydrates in brown algae (see Livingstone and de Zwann 1983).
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` ≠ TAB	LE 6.10 Intra	lant variation i	n oreanic nitrogen	content (*) in
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, (\*\*\*) See fig. 6.1.





TABLE 6.11 Qualitative ranking of intraplant differences in Laminaria longicruris of damage by Lacuna vincta, levels of organic · nitrogén, laminaran, mannitol, alginic acid and cellulose, and overall hutritional quality. 1-5 =.least to greatest. ۰, ۲ STIPE a MERISTEMO MID-REGION NEW FRILL OLD FRILL a q of LAMINA - 9 PD. ) '2 Crazing Damage 1 3 4 5 Organic N <sup>b,d</sup> 1 4 4 \* 53 Laminaran <sup>C</sup> 3 1.5 1.5 4 5^ Mannitol <sup>C</sup> 2 1 3 4~.5 4.5 Alginate 5 3 3 1 3 2.5 5 2.5 Cellulose 2.5 2.5 2 3 **Overall** 4 5 1 Nutritional Quality See fig. 6.1. b Chapman and Craigie (1977). С Chapman and Craigie (1978). đ A.R.O. Chapman, unpublished data (see table 6.10). . . e Chapman, unpublished data (see fig. 7,19). A.R.O. . 2 £ determined assuming nitrogen, Overall nutritional quality laminaran, and mannitol enhance nutritional value, and alginate and cellulose detract from nutritional quality.

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Studies of the utilization of mannitol 'by marine invertebrates are wanting, but it is likely that this simple sugar alcohol is 'absorbed directly # and metabolized readily intracellularly (R. Brown personal communication), Therefore, assuming ` that the structural cellulose and alginate detract from nutritional polysaccharides quality, but that mannitol, laminaran and organic nitrogen enhance nutritional value, the overall nutritional quality of different regions of the plant were ranked (table 6.11).' The rank of the nutritional value of the stipe, new and old frill, and central region of the blade, matched exactly the rank of the extent of grazing by Lacuna on these regions.

Clearly, because the pattern of grazing on the stipe and frill and central portions of the blade correlated with both the targuness and nutritional quality of these portions, either or both factors may be implicated in influencing feeding of <u>Lacuna</u>. In any case, positive covariance of toughness and nutritional quality may be a consistent pattern among most macro-algae. Littler and Littler (1980, 1984) and Littler <u>et al</u>. (1983a) found caloric content to decline with increasing toughness (grazer resistance) among a diverse spectrum of algal taxa.

6.4.6 Evolution of antiherbivore defenses in L. longicruris

In this section, discussion pertains only to the development of defenses against generalist macroherbivores. Both <u>S</u>. <u>droebachiensis</u> and <u>L</u>. <u>vincta</u>, the prinipal grazers of <u>Laminaria</u> in the north west Atlantic Ocean, are generalist macroherbivores (Vadas 1977; Larson <u>et</u>

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al. 1980; section 6.4.1). By `macroherbivore', I refer not to the size of the grazer but to the size of the food particle that it can rasp or bite from the plant.

A central theme of ecological evolutionary theory maintains that allocation of the resources aquired by an organism among growth, storage, repair and defense, should optimize the organism's fitness (McKey 1979; Rhoades 1979; Calow and Townsend 1981; Janzen 1981). Also, a fundamental contention of the theory of the evolution of defense against herbivores, is that there is a cost in developing defenses. Divercing resources into defenses is done so at the expense of other resource-requiring functions such as growth, storage and repair, all of which influence firness (Feeny 1976; Rhoades and Coates 1976; Rhoades 1979). Although the costs of different defense strategies have not been evaluated in energetic terms (see Fox 1981), the cost argument is intuitively attractive and there is some indirect evidence to support the theory (Cates 1975; Rhoades 1979). Certainly, among a taxonomically diverse array of marine algae, Littler and Littler (1980, 1984) and Littler et al. . (1983a) found that species with the highest productivity were also most susceptible to herbivory.

Thus, a corollary of the defense theory outlined by Rhoades (1979), is that in highly productive species in which a considerable portion of the net photosynthate is allocated to growth and related functions such as storage, levels of chemicals for defense in vegetative tissue should be relatively low; there should be a trade-off between defense and competitive ability. Given constant q

grazing pressure, and assuming that polyphenols are the primary defense metabolites (see Steinberg 1984) and are ubiquitous in brown algae (see Ragan 1976; Ragan and Jensen 1977; Ragan and Craigie 1976, 1978; Steinberg in press), then it would be expected that phenolic levels in the vegetative tissue of highly productive brown algae would be lower than in slower growing species. The results for <u>L</u>. <u>longicruris</u> from the present study, and data available for other species support this premise. Among 26 species representing five orders of brown algae for which Steinberg (in press) determined polyphenol levels, only two did not match the predicted pattern (table 6.12).

In high productivity kelps like Alaria in which the reproductive bodies occur on relatively small sporophylls differentiated from the principal vegetative lamina, the production of high levels of unpalatable secondary metabolites in the sporophylls (see Steinberg 1984) is probably cost-effective. In contrast, in fast growing kelps like L. longicruris in which sori are borne on the single vegetative lamina, defense of the reproductive units by loading the entire lamina with high levels of toxins is not likely to be cost effective. If, given the high productivity of Laminaria, the plant is unable to produce high levels of chemical defenses in all regions, what other strategies might this plant have evolved? Since the sori are produced on the distal one-third of the central portion of the lamina, reproduction by the sporophyte is contingent upon production of a robust vegetative lamina, and therefore ultimately dependent upon the proper functioning of the intercalary maristem.. It seems reasonable

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13 SPECIES TOTAL SPECIFIC PHENOLICS a GROWTH (% dry ught) RATE 61 CI: LOW PHENOL LEVELS 용 LAMINARIALES Laminaria dentigera 0.49 high L. farlowii 0.84 high sinclairii Lo 0.30 high Costaria costata 0.31 hígh Alaria marginața 0.43 high " Pterygophora californica 1.11 high Nereocyatis leutkeana 0.44 % high Postelsia palmaeformis · 1.65 , high Egregia menziesii 0.96 high Macrocystis pyrifera high 1.07 DICTYOSIPHONALES Coilodesme californica 0.43 high HIGH PHENOL LEVELS B. LAMINARIALES Dictyoneurum californicum 5.41 10w Agarum cribosum (\*) 4.05 & 5.53 1**o**w Agarum fimbriatum (\*) 4.08 & 1.33 1010 Eisenia arborea high 3.11 FUCALES Halidrys dioica 12.54 100 3.82 Hesperophycus harveyanus ' 100 Sargassum muticum 3.77 10w Pelvetia fastigiata 4.33 100 Pelvetiopois limitata 4.93 10w 4.42 high Cystoseira osmundacea Fucus distichus 10w 4<sub>6</sub>,35 DICTYOTALES Dictyota flabellata 4.04 10w 2.99 D. binghamiae 100 Dictyopteris undulata **4**∕₀55 1077 CHORDARIALES Analipus japonicus ; 4.24 1017

T/BLE 6.12 Relationship between phenolic content of vegetative tissue and growth rate in brown algae.

<sup>a</sup> Steinberg (in press).
 <sup>b</sup> A.R.O., Chapman, J., McLachlan, R.
 Smith, personal communication. (\*) two populations.

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that in view of the small size of the meristem and the importance of meristematic activity to the integrity of the whole plant and therefore to reproductive output, that selection would favour production of chemical defenses in this region.

Once the well protected meristem has produced new tissue, how might the rest of the plant be protected against grazers? Toughness as a defense mechanism is likely to be cost-effective with respect to fitness, because it affords multiple benefits to the plant. Not only . may toughness inhibit grazers, but it provides protection from abrasion and shear and drag forces in the harsh physical environment in which kelps grow. Considering that survival and spore production in L. longicruris depends in the first instance on maintaining intact the holdfast, stipe, meristem and central region of the lamina, it seems reasonable to predict that selection should favour developing toughness of these portions over toughness of the marginal frill. Thus, given commitment of much of the resource aquisition of  $\underline{L}_{\circ}$ longicruris to production, its antiherbivore defense strategy of producing high levels of phenols in the meristem only, and of promoting toughness of the stipe, meristem and central lamina region over the lamina frill, is consistent with cost-effective arguments relating resource allocation and fitness. In addition, a strategy of high growth  $\overset{\triangleright}{}$  and reproductive rates (see chapter 5), bestows an sindirect benefit in increasing the likelihood of a given portion of the Laminaria population escaping serious grazing by swamping and satiating their herbivores,

6.4.7 Comparison of the impact of <u>S</u>. <u>droebachiensis</u> and <u>L</u>. <u>vincta</u> on populations of <u>L</u>. <u>longicruris</u>

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The effect of high densities of urchins and high densities of shails on <u>L</u>. <u>longicruris</u> differ in magnitude and possibly direction. Whereas high densities of urchins decimate <u>Laminaria</u> beds (Mann 1977; Wharton and Mann 1981), high densities of <u>Lacuna</u> do not appear to increase destruction of kelps and may even reduce <u>Laminaria</u> mortality.

CP Y Although 'both the urchins (Vadas 1977; Larson et al. 1980) and the snails are generalist herbivores that exhibit preference for L. longicruris, their modes of grazing and response to the antiherbivore defenses of Laminaria are markedly different. The urchins are well adapted to feed on Laminaria. They are a relatively large grazer and their large and powerful feeding apparatus (see De Ridder and Laurence 1982) facilitates much higher grazing rates on kelp (Vadas 1977) than Lacuna is capable of. Not suprisingly, their feeding rates are ostensibly much less influenced by the toughness of their food than are those of the snails; urchins readily feed on the holdfast and stipe of Laminaria. In common with most marine gastropods (see section 6.4.4), the urchins are able to digest the major storage (laminaran) and structural (cellulose and alginic acid) carbohydrates of kelps (Fong and Mann 1980; see also Lawrence 1982). However, unlikė Lacuna, S. droebachiensis feeds on the meristem of L. longicruris, although it is probable that the urchins prefer other regions of the plant since kelp species with elevated polyphenol levels are ther least preferred food (see Vadas 1977; Larson et al.

1980; Steinberg'in press).

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There are also considerable differences in the spatial and temporal patterns of grazing impact by these herbivores, which stem largely from dissimilarities in their life histories. As might be expected of an annual species with a lengthy planktonic life and which produces several cohorts annually, the occurrence of high densities of Lacuna is unpredictable in time and space. In 1982 and 1983; peak densities of Lacuna in St. Margaret's Bay occurred in January and February, but in 1984, qualitative observations indicated that high densities did not occur until July and August. Field · observations also shown that considerable spatial variation in Lacuna have densities can occur on a scale of kilometres. Thus, pulses of Extensive grazing of Laminaria by Lacuna potentially occur annually, but are spatially and temporally unpredictable. See .

In contrast, the time scale of the formation of high densities of  $\cdot$ urchins, either over localized or extensive areas, is in the order of several years (Wharton and Mann 1981). Also, aside from the catastophic effects of epizootics (Schiebling and Stephenson 1984; Schiebling in press), urchin populations are maintaided in the absence of macrophytes (Mann 1977; Wharton and Mann 1981; Johnson and Mann 1982), preventing the re-establishment of seaweeds. By comparison, Lacuna populations do not occur on coralline/urchin barrens, but are found only in macrophyte beds. Periods between outbreaks of sea urchins, and the length of time that high densities of urchins persist, appear to be long and may be of the order of decades.

GENERAL CONCLUSIONS

CHARTER 7

The two principal configurations of the rocky subtidal of the Atlantic coast of Nova Scotia are unproductive sea urchin/crustose coralline `barren \ grounds', and highly productive communities characterized by dense beds of seaweeds and extensive coralline crusts, but few sea urchins. We now know several details of the dynamics of both of these community states, their dominant organisms, and the relationships between them (summarized in fig. 7.1). Here, Iv attempt to integrate the results of the present study with those of other investigations in outlining (i) the adaptations of Laminaria longicruris to stress and disturbance in the subtidal, (ii) the blological interactions important in influencing the establishment and maintenance of dense stands of L. longicruris in the absence of sea urchins, and (iii) the differences between these interactions and those most important in structuring the barren form of the community.

The principal interactions that influence the structure of the two states of the community differ in humber and strength. On urchin/coralline barren grounds, community structure is largely determined by a single strongly-interacting (sensu Paine 1980) species; the sea urchin <u>Strongylocentrotus</u> <u>droebachiensis</u>. In contrast, in the seaweed-dominated configuration of the community, <u>Laminaria bongicruris</u> replaces <u>S</u>. <u>droebachiensis</u> as the single most important strongly-interacting species; but it influences community structure in concert with a suite of weakly-interacting species.

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Fig. 7.1 Diagram summarizing the dynamics and principal interactions influencing community structure in the rocky subtidal in Nova Scotia.. Notice that the major void in understanding of this system concerns the factors that lead to high densities of sea urchins in kelp beds.

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Laminaria is a strongly-interacting species in that it limits markedly the abundance of several understorey species (C.R. Johnson, unpubl. data).

The transition from urchin/coralline barrens back to lush beds of seaweeds appears to be mediated by epizodtics (Schiebling and Stephenson 1984, Schiebling in press). Recovery of seaveeds occurs as a direct result of the release from urchin grazing, and it is at this point that geveral weak interactions come into play in influencing the developing community. Immediately following mass urchin mortality, by far the most abundant and conspicuous organisms are the encrusting coralline algae; they cover virtually all rock substrata in the genus, - Phymatolithon, inhibits subtidal. The most abundant recruitment of fleshy seaweeds, probably by sloughing its epithallial. cells. It seems likely that this innate antifouling action affects both the microscopic and macroscopic stages of filamentous species, but only the microscopic forms of kelps.

The effect of coralline antifouling on the community composition of fleshy seaweed species is probably two-fold. Among filamentous plants, the antifouling effect is not species specific, but all species are limited by approximately the same proportion? Thus, not only is the standing crop reduced, but it is probable that antifouling acts as a mild disturbance preventing monopolization of resources by a few strongly competitive species, and thus promotes seaweed diversity, at least among the smaller species. Also, by retarding overgrowth by epiphytes, corallines likely augment their own survival. Extensive

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die-back of coralline crusts beneath seaweed cover, even in plots maintained clear of grazers, did not occur. Thus, antifouling by corallines is likely an enduring feature of seaweed beds in Nova Scotia. Evidently, the intensity of grazing necessary to maintain coralline crusts is much less than might be required to initially establish them. In summary, coralline algae are abundant at all times, regardless of the extent of seaweed cover or intensity of urchin grazing, but their interactions with other species are considerably more subtle than those of the urchins and kelp.

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Despite their antifouling action and omnipresence on hard substrata, coralline algae cannot prevent the recovery of lush seaweed beds. Indeed, in areas contiguous to refugial populations, extensive stands of <u>L</u>. <u>longicruris</u> forming a closed canopy can develop in less than 18 months. Recovery of <u>Laminaria</u> in areas where adjacent refugia are lacking is considerably slower, and is likely dependent upon seeding of spores by sorus-bearing drift material. The rapidity of the establishment of <u>Laminaria</u> beds reflects both the kelp's enormous reproductive capacity (Chapman 1984) and its high growth rates in spring (see also Mann 1972b; Chapmah and Craigie 1977; Gerard and Mann 1979; Gagne <u>et al</u>. 1982).

Once a closed canopy is formed, <u>L</u>. <u>longicruris</u> demonstrates considerable tenacity in maintaining its dominance in the face of nutrient stress (Chapman and Craigle "1977; Gagne et al. 1982; Espinoza and Chapman 1983), "erosion of laminae, and disturbance by storms and non-echinoid grazers. Although the canopy "of <u>L</u>.

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longicruris is eroded steadily from summer through mid-vinter, accelerated growth in the spring results in the rapid re-establishment of a closed stratum before most other species attain their peak growth rates. Similarly, the formation of holes in the canopy results in a marked numerical response in recruitment of this perennial kelp, and rapid growth in the spring soon reinstates its dominance over other species.

The primary grazer of L. longicruris following the demise of the urchins is the gastropod Lacuna vincta. Although this snail manifests preference for L. longicruris and can occur in extremely high densities, Laminaria is apparently effectively defended against attack by Lacuna, unlike the case when sea urchins occur in large numbers. This snail primarily attacks the lateral frill of the laminae, exhibits reduced grazing of the mid-region of the blade, but largely avoids the meristem and stipe. It seems likely that snails do not eat the meristem primarily because of high levels of polyphenols in this region, but toughness is also likely a deterrent, and they probably avoid the stipe and holdfast primarily because of the toughness of the toughness of the stipe.

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The consequence of <u>Lacuna</u> attack on <u>L. longicruris</u> is that concentrated damage on the frill promotes the tearing away of large portions of this region, which leads to a significant reduction in the canopy area but does not increase mortality of <u>Laminaria</u>. Loss 'of frill ticcue in this manner may even enhance continued dominance of the kelp by reducing the drag on plants in storms, and hence lessen

their susceptibility to being torn from the substratum, and by stimulating growth in response to decreased canopy area in winter and early springs

A weak interaction that probably tempers the impact of <u>louna</u> on kelp, is predation on the snails by cunner (<u>Tautogolabrus adspersus</u>). This interaction is 'weak' because intense predation by cunner on the snails occurs only in early summer, commencing after snails have been present'in high densities for some time. Furthermore, as the snails grow, a large proportion of their population quickly attains a size refuge safe from most of these predatory fish.

Clearly, the impacts on L. longicruris of high densities of Lacuna and high densities of sea urchins are vastly different. The kelp's anti-grazer defenses are effective against the snails, but not against the urchins. In view of the low preference of S. droebachiensis for algae, with low levels of polyphenolics in their vegetative lamina (see Vadas 1977; Larson et al. 1980; Steinberg in press), it is likely that if L. longicruris produced high concentrations of `phenols throughout the sporophyte, it too yould be much less susceptible to grazing by sea urchins. However, this would incur a cost in terms of the resources available for other metabolic functions, including growth. Thus, it appears that L. longicruris has evolved `a competitive, stress tolerant strategy, allowing rapid  $^{
ho}$ growth during periods when nutrients are law, at the expense of developing chemical defences against large herbivores.

In short, L. longicruris possesses a remarkable suite of

adaptations that enable it to recover quickly from decimation by sea urchins, forming and maintaining dense beds in the long term as long as urchin numbers remain low. This plant exhibits opportunistic, stress-tolerant and competitive traits that, enable it to assert dominance in subtidal habitats of a variety of levels of stress and disturbance. Moreover, when sea urchin numbers are: low, <u>L</u>. <u>longicruris</u> exerts considerable influence on seaweed community structure in severely curtailing the abundance of several understorey species (C.R. Johnson, unpubl. data).

In which direction should future research proceed? What approach might be most profitable in ameliorating our inderstanding of the mechanisms that give structure to this subtidal system? At present, we have some insight into how kelp beds and destroyed, why sea urchin populations are able to persist on 'barren grounds', how. the urchins are obliterated, and the interactions with and adaptations of L. longicruris that enable it to recover and maintain dense stands (see 7.1). However, fundamental descriptive data on many aspects of fig. the subtidal are lacking, and there are several ideas proposed in the Further details are present study that need critical testing. required of (1) the population biology of Notoacmaea testudinalis (limpet), Tonicella rubra (chiton), L. vincta and T. adspersus, and (ii) the small-scale effect of limp and chiton grazing on seaweed recruitment. In addition, experiments need to be conducted to test the hypotheses (1) that the mechanism of antifouling by Phymatolithon is sloughing of 'epithallial cells, (ii) that coralline antifouling reduces resource monopolization by competitively superior seaweeds,

(iii) that polyphenols are effective in reducing grazing by  $\underline{L}_{\circ}$ . <u>vincta</u>, (iv) that the production of high concentrations of defensive secondary metabolites in brown algae is done so at the expense of productivity, (v) that sloughing of large portions of the frill of  $\underline{L}_{\circ}$ . <u>longicruris</u>, promoted by snail grazing, reduces mortality of the kelp, and (vi) that the impact of cunner predation on  $\underline{L}_{\circ}$ . <u>vincta</u> has little influence on the snails' impact on the Lo <u>longicruris</u> canopy.

Beyond these queries, however, looms one overriding question that stands apart from all others as the major deficiency in our knowledge of the dynamics of community structure in this system: what are the factors that act to bring about the expansion of the normally sparse populations of sea urchins in kelp beds to the point that destructive grazing of seaweeds occurs? In 1984, the answer still eludes us.

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APPENDIX A.1 (	Chapter 3)。 Po	pulation censu	ses of sea	urchins
(Strongy1	ocentrotus 'dro	bebachiensis) in	urchin enclosure	at Mill
Cove. Co	llection sites	of urchins are g	iven in brackets	( )。
Date	Initial Copulation	Number of Urchins Added	Population <sup>°</sup> Afte Restocking	r

08	June	1982	0	,	600	(1)	600	4
15	July	1982	275		0		275	e.
12	Aug	1982	150		120	(1,2)	270	
05	0ct	1982	20		200	(3)	220	
07	0ct	1982	220		300	(3)	. <b>₅520</b>	
13	Jan	1983	30		600	(4)	630	
07	Mar	1983	<sup>*</sup> 550		. 0	1	່ 550	
28	Apr	1983	540		0		~ 540	
22	June	1983	' 360	3	0		- 360	
11	July	1983	360		0		360	•
15	Aug	1983	180		0		180	¢
04	Oct	1983	0		0		0	

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(1) Rood Head, Lockeport

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; (2) Halifax Harbour

- (3) Eagle Head, Liverpool
- . (4) Sandy Cove, Digby Neck

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APPENDIX A.2 (Chapter 3). Evaluation of the point technique) for seaweeds.

quantities in terms of cover has ' many species Measuring advantages over other measures such as biomass, or density or frequency of, individuals. Cover estimates permit comparisons of species of widely divergent growth forms, reveal ecological information on utilization of light and space resources not obtainable from other measures, and can be performed in situ without destroying individual plants. The latter attribute is of paramount importance in experimental studies which require following community responses ĉο specific treatments through time.

The point. technique used in the present study is particularly useful in that data may be collected on all species in a multilayered 3-dimensional community, and the method is highly objective; guesses of proportion cover are not required. The two major disadvantages are first, that the method can only be applied to relatively small species and is inappropriate for large kelps, and second, that in strong surge conditions subjective judgement is often necessary in deciding whether or not a rod passes through the canopy of a given individual.

The question should now be addressed, how accurate is a sample of ten quadrats using 30 random points of a possible 100 per quadrat in quantitativley estimating community structure at the St. Margaret's Bay sites? Consider first the consequences of using 30 points instead of 100. If it is assumed that all 100 points (N) represent the actual proportion (p) of cover in the complete population of the quadrat, then the variance of the estimate (p) of p from a sample size of n points is given by -

 $V(\hat{p}) = \frac{p(1-p)}{n} x \frac{(N-n)}{(N-1)}$  (Cochran 1977) where (N-n)/(N-1) is a correction term for finite populations. It follows that standard deviation  $(\hat{p}) = \text{standard error } (\hat{p}) = S.E.(\hat{p})$ .  $= V(\hat{p})$ , where  $S_b E_b(\hat{p})$  is a measure of the deviation of the estimate  $(\hat{p})$  from the actual value  $(p)_b$ . Following the suggestion of Elliot (1971) that it is desirable to keep  $S_b E_b(\hat{p})$  within 20% of p, it follows that for n=30 points the actual proportion cover of a species needs to be at least 0.3%. Only about nine of the 28 species encountered in the study consistently satisfied this requirement, even during months of peak abundances. It seems then, that 30 out of 100 points represents a minimum sampling intensity. However, it should be emphasized that this analysis does not consider the improvement in information quality gained in taking less than 100 points and allowing more quadrats to be sampled per unit underwater time.

Now consider the efficiency of a sample of ten quadrats (of 30 points per quadrat) in estimating community composition. Over the period 27 May to 8 June 1982, a sample of 35 percentage cover quadrats was taken in the non-experimental area at Mill Cove and the mean percent cover of all species encountered was calculated. Following Southwood's (1980) method, it was determined from these mean values that if ten quadrats were taken, only three of the five most common species had a standard error less than 20% of the mean (appendix A.3). However, it could be assumed that further species would be added to this list later in the summer when the annual species became abundant.

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Overall, it was concluded that for the Mill Cove site the sampling scheme adopted represented the minimum sampling effort necessary to obtain data on the more common species suitable for analysis by parametric statistical tests. In 'retrospect, this judgement proved sound and parametric procedures were readily performed on these data. The method and sampling scheme devised represented both a suitable approach to accurately quantifying 1. [7] 6, community structure and 🖓 satisfactory compromise of minimum underwater time versus data quality.

APPENDIX A.3 (Chapter 3). Evaluation of sampling scheme for estimating percentage cover of non-crustose seaweeds. Standard error of the estimates of percentage cover when n = 10 quadrats are expressed as a percentage of the mean. Species are the five most abundant species, in a sample of 35 quadrats taken at Mill Cove from 27 May to 8 June 1982.

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Species onnemaisonia hamifera olysiphonia urceolata hodomela confervoides ntithamnion spp. esmarestia viridis	Řean Percentage Cover (n=35)	S.E. as % of Mean when n=10		
onnemaisonia hamifera	37 . 4	√ 15		
olysiphonia urceolata	27 ° 2	` 12		
hodomela confervoides	22.9	19		
ntithamnion spp.	14,9	30		
comproped a wiredia	10 1	35		



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APPENDIX A.4 (Chapter 3). Species encountered in assessing composition of non-crustose seaweed community in urchin enclosure, control enclosure and non-experimental area in experiment at Mill Cove to determine the influence of release from sea urchin (<u>Strongylocentrotus</u> <u>droebachiensis</u>) grazing on seaweed community structure. (\*) indicates species used in principal components analysis.

#### CHLOROPHYTA

Spongomorpha spp.
 Chaetomorpha spp.
 Cladophora spp.
 Rhizoclonium spp.

#### рнаеорнута

- Ectocarpus spp./Pilayella littoralis Giffordia granulosa Chordaria flagelliformis
- \*. Acrothrix novae-angliae
- \* Desmarestia aculeata
- Desmarestia viridis
   Chorda filum/C.'tomentosa
   Laminaria longicruris
   Saccorhiza dermatodea
   Tilopteris mertensii
  - Sphacelaria furcigera/S. cirrosa
- Sphacelaria plumosa Halopteris scoparia
- , Fucus spp.
- RHODOPHYTA
  - ☆ Bonnemaisonia hamifera Cystoclonium purpureum Chondrus crispus Corallina officinalis
  - \* Antithamnion spp.
  - 🌣 Callithamnion spp.
  - \* Ceramium rubrum
  - ° Polysiphonia nigrescens
  - \* Polysiphonia urceolata
  - \* Rhodomela confervoides

222.

APPENDIX A.5 (Chapter 3). Proportion of hard substrate (1) bare and unshaded, (2) bare but shaded, and (3) overgrown by non-crustose seaweeds in the 3 treatments (urchin enclosure, control enclosure and non-experimental area) in the experiment at Mill Cove to (influence determine the of release from sea-urchin (Strongylocentrotus droebachiensis) grazing on seaweed community structure. Standard errors in brackets ( ). Laminaria longicruris not included.

PROPORTION of HARD NON-CRUSTOSE SUBSTRATE BARE and UNSHADED by MACROPHYTES D Urchin Enclosure Control Enclosure Non-experimental Date Area 01 Sept 1982 0.20 (.05) 0.16 (.03) 0.13 (.02) 0.39 (.05) 06 Jan 1983 0.47 (.05) 0.44 (.05) 18 Apr 1983 1.00 (.00) 0.35 (.05) 0.45 (.05) 05 Aug 1983 0.62 (.06) 0.20 (.05) 😳 0.18 (.04) 27 Oct 1983 0.50 (.06) 0.33 (.04) 0.36 (.05) PROPORTION of HARD SUBSTRATE BARE BUT SHADED NON-CRUSTOSE by MACROPHYTES Urchin Enclosure Control Enclosure Non-experimental Date Area

01 8	Sept	1982	0.38	(。05) 🤇	0.40	(.05)	0.48	(.03)
06.	Jan	1983	0.27	(.04)	, 0°27	(04)	0.31	(.04).
18 /	Apr	1983	0	(0)	0.36	(。02)	0.26	(.03)
05 <i>i</i>	Aug	1983	0.16	(.04)	0.30	(.02)	0.42	(₀05) ·
27 (	Oct	1983	0°23	(.03)	0.35	(.03)	0.29	(.04)
						•		

(Appendix continued overleaf) -



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PROPORTION	of	HARD	SUBSTRATE	overgrown	by	NON-CRUSTOS	E MACROPHYTES
							,
				۵			
Date		Urch	ln Enclosu	re Control	E	nclosure No	n-experimental

01	Sept	1982	0.42	(。05)	0.44 (.05)	0.39 (.03)
06	Jan	1983	0.26	(。04)	0.34 (.04)	0.26 (.04)
18	Apr	1983	0.00	(.00)	0.29 (.02)	0.29 (.03)
05	Aug	1983	0.22	(.04)	0.50 (.05)	0.39 (.06)
27	Oct	1983	່ 0₀27	(。04)	0.31 (.06)	0.35 (.03)
		•			a	

APPENDIX A.6 (Chapter 3). Diversity (Shannon index) of non-cructose seaweed community in treatments (urchin enclosure, control enclosure and non-experimental area) in the experiment at Mill Cove to determine the influence of release from sea urchin (Strongylocentrotus droebachiensis) grazing on seaweed community structures Standard errors in brackets (). Laminaria longicruria not included.

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Date	Urchin Enclosure	Control Enclosure	Non-experimental Area	
08 June 1982	2.10 (.07)	1.86 (.12)	1.71 (.08)	
01 Sept 1982	1.54 (.13)	1.81 (.08)	1.79 (.08)	
06 Jan 1983	1.38 (.15)	1.47 (.12)	1.22 (.08)	
18 Apr. 1983	0.01 (.01)"	1.68 (.07)	1.52 (.15)	
05 Aug 1983	0.66 (.08)	1.61 (.09)	1.51 (.12)	
27 Oct 1983	0.97 (.09)	1.46 (.05)	1.31 (.09)	

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APPENDIX A.7 (Chapter 3). Variance absorbed by principal vectors in an R-type principal components analysis of species abundances in the 18 date/treatment groups in the experiment at Mill Cove to determine the influence of release from sea urchin (Strongylocentrotus droebachiensis) grazing on seaweed community composition.

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*		°0	•	e (\$) - (\$)
<u></u>	Principal Component	% Variance Absorbed	Cumulative % Variance Abéorbed	4 ) 4 ) 4
		· ·		- 0
	0	· · · · · · ·		° 3
•	PC1	47.41	47.41	
	PC2	28 <b>.</b> 95 °	76.36	•
	PC3	9.14	لاي 85₀50	p
	PC4	6.16	91.66	n' (
	PC5	3.11	94.770	
	· PC6	2.67	97.44	6
	PC7	1.17	98.61	• «
1.	PC8	0.73	99,34	
	PC9	0,38	99.72	
	PC10	0,28	* 100.00	
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APPENDIX A.8 (Chapter 3). Values of the first three principal components (PC's) from a principal components analysis of species abundances in the 18 date/treatment groups in the experiment at Mill Cove to determine the influence of release from sea urchin (<u>Strongylocentrotus</u> droebachiensis) grazing on seaweed community ° composition.

		\$	URCHIN	ENCLOSI	JRE	•	,	-	J	
<i>.</i> ,		-	. Date	2	Q	PC1	1	PC2	PC3	-
, « —		, est		82			•			*
			08 June	1982		-8,48		-0.74	1.24	
			01 Sept	1982		-4.13		-2.61	2.15	0
	02	£	06 Jan	1983		-3.17		1.98·	2.18	
		-	18 Apr	1983		0.00	0	0.00	0.00	
	٠.	٩	05 Aug	1983		-0.63	•	0.31	-1.03	
» ۽			27 Oct	1983	• •	-1.36		1.75	2.11	¢
•					, <sup>D</sup>					

CONTROL ENCLOSURE

۰ 	•	N Date	2	PCL	•	PC2	PC3	ox
· .	`` ```````````````````````````````	08 June 01 Sept 06 Jan 18 Apr 05 Aug 27 Oct	1982 1982 1983 1983 1983 1983	7.14 5.23 3.90 5.35 7.21 3.19	,œ	0.69 3.21 2.52 0.72 3.89 3.56	1.23 1.03 1.98 0.67 0.14 0.98	
	î ,	1	۵.	۰.				

	,	,	,		*
7 12	· Date	PC1.	PC2	· PC3	
<u>, 19 - 19 - 19 - 19 - 19 - 19 - 19 - 19 </u>				Ċ,	-24
` 2	08 June 1982	-5.67	-0.68	0.84	
	01 Sept 1982	-4.99	3.89	-0.65	
	06 Jan 1983	-3.11	3.20	1.05	
	18 Apr 1983	· -4.29	0.67	0.44	
	05 Aug 1983	-6.44	4.29	-0.30	`
	07 0 4 1000	2 01	0 00	1 00	

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APPENDIX B.1 (Chapter 4). Biomass of seaweed species recruited on bare granite surfaces and on <u>Phymatolithon</u> crusts in the absence of grazers. Values are means of 10 rocks. Standard errors are given in parentheses ( ). (\*) indicates species included in multivariate analysis.

Sampling Date: 15 July 1982

SPECIES

DRY WEIGHT (g 0.1 m<sup>-2</sup>)

i.	, ** •	Grai	lite	Phymat	olithon
CHL(	DROPHYTA		,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,		*************************
	Cladophora spp.	, 0		0	
PHAI	сорнита				
	Ectocarpus spp.	. 0		0	
*	Acrothrix novae-angliae	0		- 0	
\$ <u></u>	Stictyosiphon spp.	, 0		0	
ş.:	Desmarestia viridis .	0		0	
\$	Tilopteris mertepsii	0		0	
	Sphacelaría cirrosa	0		0	•
•	Sphacelaria furcigéra	0		0	•
	Sphacelaria plumosa	0.01	(.01)	0	
× '	Halopteris scoparia	0	•	0	
	Petalonia fascia	0	¢.	' O	
ישני		•		*	
KnOi S		0.00	( 02)	0 20	( 15)
, "		0.02	(.02)	0.20	(01)
	Chardrug exignue	0,		0	
		0		0.	
<u>.</u>	Collithaniton Spp.	0		0	
4	Comparing subsum	0		0	
	Delgaisharia florianlia	0,		0	
	Polysiphonia Liexicaulis	0		0	,
<b>.</b> %	Polysiphonia marveyi Delectric ricescore	0	(	0	1
۰۰ رو	rorystphomia argrescens	0		. 0	
ev 23,	Polysiphonia urceolala	0			
•*	KNOUDMELA CONTETVOIDES	, 0		U	
	- 	· 、			

(Appendix continued overleaf).

## Sampling Date: 13 August 1982

SPECIES	DRY WEIGHT (g $0.1 \text{ m}^{-2}$ )		
• •	Granite	Phymatolithon	
Chlorophyta		• • •	
Cladophora spp。	0'	• •	
рнаеорнута		•	
Ectocarpus spp. "	0	0	
* Acrothrix novae-angliae	0.01 (.01)	· 0.01 (.00)	
* Stictyosiphon spp.	0.02 (.01)	0.00 (.00)	
🌣 Desmarestia viridis 🌔	0 *	× 0	
* Tilopteris mertensii 🔪	0.00 (.00)	' 0。00 <b>(。00</b> 》	
Sphacelaria cirrosa 🔪	0	0	
Sphacelaria furcigera	0	0	
Sphacelaria plumosa	0	0 、	
Halopteris scoparia 🔪	_0	° 0	
Petalonia fascia 🛛 🔪 .	` <b>0</b>	0 "	
RHODOPHYTA			
* Bonnemaisonia hamifera	0.00 (.00)	0.02 (.01)	
Cystoclonium purpureum	0	0	
🕆 Chondrus crispus .	0	· · • 0	
🌣 Antithamnion spp.	0	0	
🌣 Callithamnion spp.	0.00 (.00)	0.01 (.01)	
. 🔅 Ceramium rubrum	0.00 (.00)	0.01 (.01)	
Polysiphonia flexicaulis	0	0.00 (.00)	
Polysiphonia harveyi	0.*•*	0 -	
* Polysiphonia nigrescens ·	0	0 _	
🌣 Polysiphonia urceolata	0	0 .	
* Rhodomela confervoides	0	` 0 ·	
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(Appendix continued overleaf)

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## Sampling Date: 21 September 1982

SPECIES		DRY WEIGHT (g 0.1 m <sup>-2</sup> )						
		Grar	nite		Phymai	olitho	n	
CHLOROPI	HYTA	٥					*****	
010	adophora spp.	0			U	•		
PHAEOPH	та							
Eci	tocarpus app.	0			0			
🔅 Aci	rothrix novae-angliae	0.14	(.08)		0.14	(.12)		
° St	ictyosiphon spp.	0°02	(.01).		0			
* Der	smarestia viridis	0			0			٥
a Til	lopteris mertensii	<sub>ര</sub> 0ം02	(.01)		0.01	(.00)		•
Spl	hacelaria cirrosa	°О			0			
Spl	hacelaria furcigera	0			<u>`0</u>		7	-
Spl	hacelaria plumosa	0	(		0	(		
Ha.	lopteris scoparia	0.00	(.00)		0.13	(。05)		
Pe	talonia fascia	0			0			
RHODOPHY	YTA .							
* Boi	nnemaisonia hamifera	0.17	(.16)		<b>0</b> °08	(.04)	•	
Суа	stoclýnium purpureum	0			0	•		
s Che	ondrus crispus	0		U	0			
An An	tithamnion spp.	0			0			
Ca:	llithamnion spp.	0.83	·(°13)		1.21	(°08)		
/ ° Cei	ramium rubrum ·	0°33	(.06)		, 0 <u>,</u> 39	(:05)		
- Po:	lysiphonia flexicaulis .	0		4	0	•		
Pol	lysiphonia harveyi	0		۰	0		•	•
Pol	lysiphonia nigrescens ,	ò			0			
Po.	lysiphonia urceolata	0			0,			
) a Rhe	odomela confervoides '	· 0		0	0			
						,		-0

(Appendix continued overleaf)

Dempring Duces , increm r	,	,
SPECIES .	DRY WEIGHT	(g 0.1 m <sup>-2</sup> )
° ,	Granite	Phymatolithon
CHLOROPHYTA	0	· 0 -
PHAEOPHYTA Ectocarpus spö Acrothrix novae-angliae Stictyosiphon spp. Desmarestia viridis Tilopteris mertensii Sphacelaria cirrosa Sphacelaria furcigera Sphacelaria plumosa	$\begin{array}{c} 0.01 (.01) \\ 0 \\ 0 \\ 0.02 (.01) \\ 0.02 (.01) \\ 0.00 (.00) \\ 0 \\ 0.00 (.00) \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 $	0.01 (°.01) 0 0 0 0.19 (°.16) 0.01 (°01) 0 0
RHODOPHYTA Bonnemaisonia hamifera Cystoclonium purpureum Chondrus crišpus Antithamnion spp. Callithamnion spp. Ceramium rubrum Polysiphonia flexicaulis Polysiphonia harveyi Polysiphonia nigrescens Polysiphonia urceolata Rhodomela confervoides	0.03 (.02) 0.15 (.07) 0.35 (.35) 6.27 (1.04) 0 0.01 (.00) 0 0	0, 04 (.03) 0, 04 (.03) 0, 04 (.03) 0, 21 (.12) 0, 21 (.12) 0, 35 (1.58) 0.02 (.01) 0, 05 (.05) 0.05 (.03) 0.01 (.01)

Sampling Date: 7 March 1983

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pembring pares a wuguer's	202	<b>`</b> "-			
SPECIES	DRY WEIGHT	$(g \ 0.1 \ m^2)^{\frac{1}{2}}$			
Ū	• Granite	Phymatolithon			
	· · · ·	4			
		, L I			
CHLOROPHYTA		•			
Cladophora spp.	<sup>م</sup> ٥٥٥٥٬ (٥٥٥) <sup>°</sup>	0.00 (.00)			
	ىڭ سە	3 - 10 <sup>-</sup>			
PHAEOPHYTA, v.	ť				
' Ectocarpud spp. 🐁 🗍	0 .	0			
* Acrothrix novae-angliae	0.01 (.01)	0			
* Stictyosiphon spp	· 0 ` `	0			
. 🎂 Desmarestia viridis	1.43 (.66)	· 0			
🔅 Tilopteris mertensii	0 a	<b>0</b>			
Sphacelaria cirrosa	0 '	O			
Sphacelaria furcigera	0	0.01 (.01)			
🚬 Šphacelaria plumosa 🏻 🎽	0	0			
Halopteris scoparia	Ū .	0			
Petalonia fascia	°,0	·0			
<i>b</i> ,		• 、			
RHODOPHYTA	• •				
" Bonnemaisonia hamifera	5.50 (.83)	. 2.29 (.72)			
Cystoclonium purpureum	0.09 (.06)	~ 0			
A Chondrus crispus	· 0	- 0			
Antithamion spp.,	0.07 (.07)	0			
* Callithamnion spp.	0	"``O			
* Ceramium rubrum	5°25 (1°18)	1.32 (.34)			
Polysiphonia flexicaulis	0	0			
Polysiphonia harveyi	0	0.01 (.01)			
Polysiphonia nigrescens	0.35 (.16)	0.10 (.06)			
🔆 🔅 Polysiphonia urceolata	0.01 (.00) "	0.02 (.01)			
🤆 🌣 Rhodomela confervoides ุ	0.01 (.01)	0.04 (.02)			
× ,	•				

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(Appendix continued overleaf)

L
st.	SPECIES	dry weight			(g°0.1 m <sup>-2</sup> ) '			
,		Ç Gran	Granite			Phymatolithon		
CUIO	ν	مي <sub>ليس</sub> معالياتين مناتيا ويون مانيا من	,	*		4	8	
CRLO.	Cladophora spps°	. 0.03	(.02)		0			
, PHAE	орнута	,	,		• 5	-	•	
have a	Estocarpus spp.'	0		٩	0			
\$ <del>2</del>	Acrothrix novae-angliae	0	•		ΰ	<b>.</b> •		
슱	Stictyosiphon spp.	۰ 0°06	(.03)	•	0°08	(.04)		
\$	Desmarestia viridis (	0	•		0		•	
\$2	Tilopteris mertensii	0			0	×		
,	Sphacelaria cirrosá	0.01	(01)		0			
	Sphacelaria furcigera	0.02	(.02)	•••	0.00	(°°00)		
•	Sphacelaria plumosa	0.04	(。04)	•	<u></u> 0			
	Halopteris scoparia	` <b>0</b>			0			
	Petalonia fascia	0			0	0		
RHOD	орнута	•.	•		· ,			
23	Bonnemaisonia hamifera	1.07	(53)		0.45	(.17)		
-	Cystoclonium purpureum	0			0			
\$	Chondrus crispus	0.12	(.12)		0.01	(.01)		
, \$	Antithamnion spp.	0	• •	•	0	•	0	
, ŵ	Callithamnion spp.	.0.13	(.04)	,	0.04	(.03)		
Ċ	Ceramium rubrum	0.47	(.16)		0.02	(.01)		
,	Polysiphonia flexicaulis	0.00	(.00)	٢	۰ 0	0		
	Polysiphonia harveyi	۴ 0			0°00	(.00)		
\$	Polysiphonia nigrescens	2.94	(.68)		.0061	(.33)		
-	Polysiphonia urceolata	0.07	(007)	0	0.01	(.00)		
2	Rhodomela confervoides ,	· 0.18	(008)		0.01	(.00)		
	۰ .	/		đ	r.		٥	

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## APPENDIX B.1 (Continued)

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Sampling Date: 20 October 1983

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APPENDIX B.2 (Chapter 4). Diversity (Shannon index) and evenness of seaweed species recruited on bare granite surfaces and on an equivalent area of Phymatolithon crust in the absence of grazers.

(.4 \*2

,	DATE	GRAN	ITE	, PHYMATOLITHON		
0	,	Diversity	Evenness	Diversity	Everness	
	15 July 1982	0.288	<sup>′</sup> 0。958	` 0.000	0.000	
	13 Aug 1982	0.613	0。787	0.647	0.926	
	21 Sept 1982	. 0.540	0.639	0.491	0.631	
	07 Mar 1983.	0.171	0.171	0.265	° 0₀255	
	09 Áug 1983	0° <b>50</b> 1	0.501	0°385	0.423	
	20 Oct 1983	0。593 。	0。550	0。524	0.524	
-				·	مەسىلەر مەسىرىمە ئەر مەسىرىمە ئەسىرىمە يىر مەسىر	

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DATE	TOTAL BIOMASS - DRY V	JEIGHT (g 0.1 m <sup>-2</sup>
1°	Granite	Phymatolith
15 July 1982 13 Aug 1982 21 Sept 1982 7 Mar 1983 9 Aug 1983 20 Oct 1983	0.03 (0.03) 0.03 (0.02) 1.51 (0.34) 6.86 (1.07) 12.69 (2.32) 5.12 (0.93)	0.28 (0.15) 0.05 (0.02) 1.95 (0.17) 4.99 (1.74) 3.80 (0.99) 1.23 (0.36)
· · · · · · · · · · · · · · · · · · ·	- t	· · · · · · · · · · · · · · · · · · ·
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APPENDIX B.3 (Chapter 4). Total biomass of all non-crustose seaweeds recruited on bare granite surfaces and <u>Phymatol</u>ithon crusts in

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APPENDIX B.4 (Chapter 4).	Variance absorbed	l by principal	components
recruited on hare grat	ite surfaces and	Phymatolithon	erusts in
the absence of grazers	o barradab ana		va 60 60 - All
· · ·		v	)
a an			

Principal Component	% Variance Absorbed	Cumulative % Variance Absorbed	
PC1 o PC2 PC3 PC4 PC5 PC6 · PC7 PC8 PC9 PC10 PC11	68.42 16.25 7.58 4.85 1.86 0.33 0.27 0.18 0.05 0.02	68.42 84.67 92.25 97.10 98.96 99.29 99.56 99.75 99.93 99.98 100.00	
PC12 .	0.00	100.00	2
	,	<u></u>	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,

APPENDIX B.5 (Chapter 4). Element coefficients for the 'first four ' principal components (PC's) from a principal components analysis of the 12 most common species recruited on granite rocks and -<u>Phymatolithon</u> crusts in the absence of grazers.

. SPECIES	PC1	PC2	PC3	PC4
***************************************				میں بر ان میں
Acrothrix novae-angliae	<b>-0</b> °000	0.003	0.001	0°003
Stictyosiphon spp.	-0°000	-0 <b>.001</b>	0。004	-0.001
Desmarestia viridis	-0.095	0.064	0.101	0。983
Tilopteris mertensii	0.015	0°016	-0.005	0.020
Bonnemaisonia hamifera	` <b>−0</b> ₀251	0.959	0.083	-0°080°
Chondrus crispus	-0.002	0.047	0.023	-0.018
Antithamnion spp.	-0.018	0°034	0.003	-0.094
Callithamnion spp.	-0.010	-0.013	020 ە-0	0.011
Ceramium rubrum	-0.963	-0°522	0.015/	-0₀075
Polysiphonia nigrescens	0.003	0.075	- 0。989	-0.104
Polysiphonia urceolata	-0.002	0.021	0°012	-0.016
Rhodomela confervoides	-0.003	-0.024	-0.056	0.010
•. •			/	

APPENDIX B.6 (Chapter 4). Variance absorbed by principal components in a principal components analysis of the 15 most common species '(<u>Chorda filum excluded</u>) recruited on bare granite rocks collected from the high intertidal and on the bare surfaces of overturned 'subtidal rocks in the absence of grazers.

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	Principal	· % Variance,	Cumulative %	
	Component	Absorbed	Variance Absorbed	
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	PCL	88.53	88.53	
	PC2	_ ~ 6 <u>.</u> 87	95.40	
	PC3	2.32	97°75	,
	PC4	0.66	98°38	
	PC5	0.52	98.90	
	PC6	0.50	99。40	~
	PC7	0°32	99 <i>°</i> 22	
	PC8	0.12	99。87	
	PC9	80°0	<sup>ດ</sup> 99。95	
	PC10	0.03	99 <u>。</u> 98^	
	PC11	0.02	100.00	
	<b>FC12</b>	0.00	100.`00	
	<b>B</b> 1213	`    0°00	·100.00	
	Ϋ́ PC1	. 0.00	<b>100</b> °00	
	PC15	0.00	. 100.00	

APPENDIX B.7 (Chapter 4). Element coefficients for the first three principal components (PC's) from a principal components analysis of the 15 most common species (<u>Chorda filum</u> excluded) recruited on bare granite rocks collected from the high intertidal and on the bare surfaces of overturned subtidal rocks in the absence of grazers.

			•	
SPECIES	PC1	PC2	° PG3	
Cladophora spp.	-0.010	-0.001	-0.093	
Spongomorpha spp.	0.002	0.013	0.023	
Stictyosiphon tortilis	0.012	0.017	-0.037	
Desmarestia aculeata	0.028	-0.114	。 0。440	
Desmarestia viridis	0.047	-0.224	- 0.839	
Laminaria longicruris	-0.002-	-0.087	0.069	
Sphacelaria cirrosa	-0.009	0.041	-0.013	٠
Sphacelaria furcigera	0.001	-0.010	0.007	,
Sphacelaria plumosa	0.008	-0.024	0.012	
Cystoclonium purpureum	-0.139	-0.946	0°22	•
Callithamnion spp.	· 0°018	0.070	-0.107	
Ceramium rubrum	-0°003	0.027	-0.017	
Polysiphonia nigrescens	-0.988	0.120	0.086	
Polysiphonia urceolata	· -0.014	-0.043	-0.032	
Rhodomela confervoides	-0.013	0.097	0.047	
	i		۰ ۴	

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APPENDIX C.1. (Chapter 5). Details of manipulations of seaweeds in the eight experimental plots at Paul Pt. Limpets (<u>Notoacmaea</u> <u>testudinalis</u>) and chitons (<u>Tonicella</u> rubra) were also removed from these plots. Seaweed species removed were <u>Laminaria</u> <u>longicruris</u>, <u>Desmarestia</u> <u>aculeata</u>, <u>Polysiphonia</u> <u>urceolata</u>, <u>Antithamnion</u> <u>spp</u>., and <u>Ceramium</u> rubrum.

	PLOT NUMBER			4		REMOVALS	
	AND TREATMENT	Plot		Dàte	2	Species,	g dry wght
٩	BLOTS 1 and 2			ے۔ دی	<del></del>	<b>دهه در م</b> رود می مرد م مرد می مرد می	ca)
	PLOTS 3 and 4 Dominant perennials	3	01 05	July July	1982 1982	L. longicruris D. aculeata	911.0 326.4
·	removed	Ľ,	25 01	Máy July	1983 1982	L. longicruris L. longicruris	68.0 1824.7
		n	05 25	July May	1982 1983	D. aculeata L. longicruris	275.5 85.8
	PLOTS 5 and 6 Dominant annuals	5	06	Aug	1982	P. urceolata Antithamnion spp.	<sup>4</sup> 19.1 6.0
	removed		04	June	1983 ·	C. rubrum P. urceolata Antithemnion spn.	9°5 80°4 12°3
	۰.	б	05 •	Aug	1982	P. urceolata Antithamnion spp.	8.3 ' 13`8
	, •		04	June	1983	C. rubrum P. urceolata Antithannion spp.	*5.0 46.3 19.7
	PLOTS 7 and 8	7	08	July	1982	L. longicruris	1174.0
	and annuals removed		12 06	July, aug	1982 1982	D. aculeata P. urceolata Antithamnion spp.	92.7 10.9
	٥		24 27	May May	1983 1983	C. rubrum · L. longicruris P. urceolata	3.8 59.4 192.0
	~	8	13	July	1982	Antithaunion spp. L. longicruris	16.6 3020.3
	$\sim$		30 05	Jul) Aug	1982 1982	D. aculeata P. urceolata Antithamnion ann.	57.6 17.1 8.1
		Ś	25	May	1983	C. rubrum L. longicruris	4.3 157.0
-		•	01	June	1983	P. urceolata Antithamnion spp.	69.0 13.6
					u	(***	tin and the second s

	APPENDIX C.2. (Cha	apter 5). Estin	ates of lamina area index	of
	Laminaria lor	ngicrúris in the	non-experimental areas at Mill Co	)ve
1	and Paul Pt.	Standard error -	's in parentheses ().	
ø	, by	,		-
	` SITE	DATE	. LAMINA AREA INDEX	•
•	· · · · · ·	•	$(m^2 \text{ shade area } m^2 \text{ substratum})$	
5	Paul Pt.	19 Oct 1982	1.91 (0.30)	10000000000000000000000000000000000000
·	a	05 Jan 1983 06 Apr 1983	1.00 (0.21) 0.83 (0.16)	
	· · · · ·	24 May 1983	1.86 (0.21)	•
		19 July 1983	1.59 (0.29)	*
•	· ";	23 Oct 1983	0.73 (0.09)	
	Mill Cove	21 Dec 1982	0.01 (0.01)	•
	<b>ч</b> т	28 Apr 1983	0.13 (0.05) (0.13 (0.07)	
P	¢ ~	02 Aug 1983	0.19 (0.10)	
	• ,	18 Oct 1983	0.23 (0.09)	°
X	~ · ·	· ·		``
•••	°€ 53	Ø	ι.	•
	• `` 1.**		۰ <sup>۵</sup>	
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	a	1	L L 7	
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	Date '		P	lot		
		1	°2	3	Zş.	6
0	5 <sub>July</sub> 1982	1.65	0			
0 0	6 July 1982 2 Aug 1982	à	1.44	2.05	2.01	
1 1	4 Sept 1982 5 Sept 1982	1.63	1.67	2.26	2.04	
1	8 Oct 1982	1.57	1.76	1,78	2.01	
0 0	2 Der 1982 5 Jan 1983	1.44	`` 1•37	1.43	1.68	
1	4 Mar 1983	0.58	0.57	0,52	0.68	,
• <u>1</u>	6 May 1983	1.52	1,.23	1.20	1.38	
1 • <u>1</u>	5 Jul 1983 8 Jul 1983	1.47	0.90	0.89	ì.28	я •
0 0	l Sept 1983 3 Sept 1983	1.19	'0₀72	0.71	1.02	•
2	4 Oct 1983	0.91	0.42	0.41	0.75	•

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DAPPENDIX C.3. (Chapter 5). Lamina area index of <u>Laminaria longicruris</u> in experimental plots no's. 1,2,5 and 6 (see fig. 5.1) at Paul Pt.

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APPENDIX C.4. (Chapter 5). Partitioning of changes in the lamina area index of Laminaria longicruris in experimental plots 1,2,5 and 6 (see fig. 5.1). at Paul Pt. into components due to mortality, recruitment, and net loss and net growth of laminae. Standard errors in parentheses ().

RATE	of	CHANCE	of	LAMINA	AREA	INDEX	

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(m<sup>2</sup> lamina area m<sup>2</sup> substratum 30 days<sup>1</sup>)

TIME	
DEDIOD	

PERIOD	Recruitment	Mortality	Blade Growth	Blade Loss
$ \begin{array}{rcrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	.0026 (.0026) .0172 (.0118) .0033 (.0019) .0112 (.0099) .0638 (.0346) .0008 (.0008) .0000 (.0000) .0092 (.0039)	.0340 (.0134) .1107 (.0786) .1203 (.0597) .2141 (.0197) .0114 (.0080) .1159 (.0283) .0604 (.0188) .0915 (.0418)	.1607 (.0397) .1616 (.0463) .1013 (.0139) .0318 (.0101) .2811 (.0315) .0691 (.0192) .0154 (.0046) .0167 (.0092)	.0687 (.0257) .1742 (.0493) .1584 (.0384) .1049 (.0357) .0071 (.0022) .0467 (.0150) .0973 (.0109) .0958 (.0271)
			· · · ·	

Time	Periods:	1	•	18	July	1982	
	٦,	2	=	14	Sept	1982	
	_	3	=	18	0ct	1982	
		4	1	02	Dec	,1982	
		5		14	Mar	1983	
		6	=	16	May	1983	
	-	7	=	16	July	1983	
		8	=	01	Sept	1983	
	• • •	9	=	24	0ct	1983	

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APPENDIX D.1. (Chapter 6). Justification of use of non-repeated measures ANOVA design when the 'subject' term of a repeated measures model is positive

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Assume that several populations of plants are subject to different treatments, and that parameters of these same populations are measured on several sampling dates. In strict terms, analysis of these data should follow a repeated measures design in which any single observation Y is given by -

Y = treatment effect + date effect + date/treatment interaction + subject effect + error term

The model incorporates a subject effect because the same subjects are sampled on each date, <u>ie</u>. samples are not independent. The subject effect incorporates a measure of the covariance of the observed measure (Y) with the repeated measure (date). If the covariance is positive, then the subject effect will be positive. If the subject effect is positive, then by using a non-repeated measures. model in which the error term is in fact the sum of the error term and subject effect of the repeated measures model, the error mean square is larger than in the repeated measures case. Clearly, when the subject effect is positive, the F-otatictic is smaller and the significance level more conservative in the non-repeated measures approach than in the appropriate repeated measures model. APPENDIX D.2. (Chapter 6). Densities of <u>Lacuna vincta</u> on all substrata per unit area of bottom at shallow (3-5m), medium depth (9-11m) and deep (15-17m) stations<sup>6</sup> at Paul Pt. during 1983. Standard errors in parentheses ().

	<sup>6</sup> DATE (1983)	. <u>LA</u>	CUNA DENSITY m <sup>2</sup>	
3		3-5m	9-11m	` 15-17m
		7	N	
	) James and the second			ang panala makasanakanan genye na danam
	15 Feb	2352.0 (253.5)	303.5 (65.6)	82.7 (27.9)
	21 Apr	1209.3 (196.4)	180.0 (49.4)	65.9 (14.2)
	10 June	2161.1 (298.9)	225.1 (29.3)	17.9 (4.4)
	28 July	382.0 (104.0)	5.9 (2.5)	3.2 (1.2)
		• •		_

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	(15-17m) stat	ions at Paul Pt.	'during 1983.	Standard errors
• •	parentheses (	)。	• *	
	`. DATE (1982)	· <u>LACUNA</u> DENSIT	y 0.4m <sup>-2</sup> LAMINA	RIA LAMÎNA
`	(1963)	3⊷5 <u>m</u>	9 <b>–11́m</b>	15−17m <sup>-</sup>
,,	2 Feb 6 Mar 22 Apr 10 June 29 July	$19.6 (4.8) \\ 6.4 (1.0) \\ 2.9 (0.5) \\ 6.2 (1.1) \\ 6.3 (0.9) \\ 2.1 \\ 0.1$	26.8 (3.3) 6.5 (1.1) 3.4 (0.6) 0.7 (0.1) 0.6 (0.1)	$\begin{array}{c} 2.9 & (0.6) \\ 7.1 & (0.9) \\ 4.6 & (0.8) \\ 0.0 & (0.0) \\ 0.1 & (0.0) \\ 0.2 & (0.0) \end{array}$
	3 OCT	000 (0.0)	0.1 (0.0)	,
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	APPENDIX	D.4. (	Chapter	6). Di	sčribuj	tion of	shel	l ler	eths d	of Lacuna	L	
•			onepeer	0 ·		, 10 II	<u>One</u>					
a.	vin	cta on [	Laminari	a longi	cruris	laminae	at <u>ca</u>	. lÓn	a° dep tl	n at Paul		
,°	- 	7					$\mathcal{S}$			1		
	PCb	, Janua	ry=uctob	er 1965	0	-						
	р Фалерали			,		مىرىمى بىر بىر بىرى <u>مەر</u> كەر يېرى مىرى مىرى مىرى مىرى مىرى مىرى مىرى م	**************************************			4 	-	
~ * .	1 20.00	,		, <b>v</b> t	•						•	
ਵਾ	DATE	ч •	PERCENT	AGE OF	POPULA	cion in	SIZE C	LASS		N		
	(1983)	`	ľ.	d doo d med	~~ Å1		(	۲	<b>^</b>	٥		ъ.
		÷	â.!	παροτιιξ	OL SL	76 CT022				° D		÷
	, , ,	1 1.	3	5 <sup>`</sup>	7	9	11	`13 <sup>*</sup>	15	<u>۱</u> ۱		, 1
	4	1× 2	ta.		• • •	ş		a '	· .	s ()-		'n
	, , ,		<u>متعقب والمحمور محمور ،</u>	and the little property of the little propert	<u> </u>		on major out the Ob		<u>ь</u>		-	x
• '	23 <sup>°</sup> ໄລກ		12.2	3°2	141	0.6	0.3	0.2	-0.1	• 3465	i .	
	'5 Mar	35.5	50.8 .	10.3 .	2.2	i.0	0.1	0.1	0	1121	, . , .	-
	22 Apr	12.8	33.3	38/1	11.9	2.8	ໍ່0 <sub>°</sub> 7່	0.5	0	` 430	)	v
• •	6 June	7.9	54.1	31 4)6	5.7	`0 <sub>°</sub> 1	0.4	Q	0.1	917	7	۱
•	29 July	0.4	7°2	67.3	24.4	0.5,	- °0`,	0	0	) 816		a
	4 Oct	U ;	,U	1.1.0 1	60.1	31.01.	1.4	U	0	280	)	
				-	x		3	· ·	u a	,	٩	•
			<u>نو به مرد این اور اور اور اور اور اور اور اور اور اور</u>	***			i an		۹ ۴		- 0	i e
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• .	APPENDIX D.5. (Chap	ter 6). Mean size (shelk lengt	h) of cohorts of
•	<u>Lacuna</u> <u>vincta</u>	or Laminaria longicruris lamina	le at <u>ca</u> ., 10m depth
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APPENDIX D.6. (Chapter 6). Sex ratio of <u>Lacuna vincta</u> on <u>Laminaria</u> <u>longicruris</u> laminae at <u>ca</u>. 10m depth at Paul Pt., March-October 1983. N=50 for all dates.

<i>ħ</i>	* 7. *		· · · · · · · · · · · · · · · · · · ·	,	DATE (1983)		SEK	RATIO	(%	FEMALES)		
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APPENDIX D.7. (Chapter 6). Recolonization of <u>Lacuna vincta</u> on laminae of <u>Laminaria longicruris</u> in three groups of  $4m^2$  and  $16m^2$  plots initially cleared of snails at <u>ca</u>. 10m depth at Paul Pt., January-March 1983. Recolonization is expressed as a percentage of the initial average number of snails plant<sup>-1</sup> prior to clearing. Number of plants censused given in parentheses ( $\frac{1}{2}$ ).

17

23

32

4

16

24

35

10

23

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GROUP NUMBER, DAYS SIZE OF PLOTS, SINCE (NUMBER OF PLOTS) CLEARING Group 1 3 14

4m<sup>2</sup> (6 plots) Group 2 16m<sup>2</sup> (2 plots) Group 3 16m<sup>2</sup> (2 plots)

250.

% RECOLONIZATION

21.7 (32)

32.7 (30)

69.1 (25)

53.3 (54) 39.4 (54)

44.0 (11) 47.2 (16)

31.8 (16)

28°6 (16)

57.0 (10)

60.9 (15) 72.8 (12)

51.1 (14)

APPENDIX D.8. (Chapter-6). Distribution of damage from grazing by <u>Lacuna vincta on laminae of Laminaria longicruris</u>. Damage index  $(D_i)$  for 10 regions of lamina (see fig. 6.1, section 6.2.2.3). Standard errors in parentheses ().

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APPENDIX D.9. (Chapter 6). Variation in concentrations of polyphenols within <u>Lauinaria longicruris</u> plants. Expressed as mg polyphenols  $g^{-1}$  dry weight relative to the high molecular weight (`type 2') non-diffusable phloroglucinol polymers in <u>Fucus vesiculosus</u>. Standard errors in parentheses ( ).

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APPENDIX D.11. (Chapter 6). Effect of removal of <u>Lacuna vincta</u> from <u>Laminaria longicruris</u> on the rate of increase in width of laminae at <u>ca</u>. 10m depth at Paul Pt., February-July 1983. Standard errors in parentheses ().

DATE (1983)	of INITIAL WIDTH or 7	PROPORTION FEBRUARY 1983
σ. 9.	Control Plants (no 'removals)	Plants with Lacuna removed
- 6 Mar	0.23 (.09) n=31	0.37 (.18) n=31
. 22 Apr	. 0.59 (.11) n=30	0.87 (.17) n=30
10 June 29 July	ر 0.81 <sup>°</sup> (.11) n=27 ′ میر 0.86 <sup>°</sup> (.11) n=26	1.33 (.20) n=28 1.33 (.20) n=25
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	Laminaria	longicru	ris °on	the r	ate of	increa	se in .	length	of
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APPENDIX D.13. (Chapter 6). Predicted values of the lamina area index for <u>Laminaria longicruris</u> (see section 5.2.1) in the non-experimental area at Paul Pt. in 1983, accuming damage to <u>Laminaria</u> by <u>Lacuna vincta</u> had not occurred.

	lanina	AREA	I	NDEX	(n <sup>2</sup>	shade	area	
•	of	lanir	ıa	<sub>m</sub> 2	suboi	ratun	)	

Observed	Predicted
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24 May		1:86	2.31
' 19 July		1.59 · .	2.02
•		• • •	

DATE (1983)

APPENDIX D.14. (Chapter 6). Incidence of <u>Lacuna</u> <u>vincta</u> in guts of . .<u>Tautogolabrus</u> <u>adopersus</u> collected from above the thermocline at Paul Pt., June-August 1983.

.

•	DATE (1963) :	, N -	PROPORTION with Locuna present , in guts	PROPORTION in which <u>Locuna</u> greatest component of stomach contents by.volume	
47.0004.700	13 June 8 Aug 31 Aug	, 41 . 55, ≈ 100	0.61 0.69 0.09	0.46 0.24 0.03	, - 1
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APPENDIX D.15. (Chapter 6). Relationship between size (shell length) of largest <u>Lacuna vincta</u> in guts of <u>Tautogolabrus</u> adopersus and size (total length) of <u>T.</u> <u>adopersus</u>. Samples collected from Paul Pt., June-August 1983.

 $\bigcirc$ 

h	) MIDPOINT of size class of total length of <u>Tautogolabrus</u> (m)	MIDPOINT of size. class N of shell length of largest <u>Lacuna</u> found in fich guts (nm)	•
1	75 105 135 165 195 225	1 3 3 7 5 18 7 13 7 13 7 6	, c

APPENDIX Dùló. (Chapter 6). Size selective predation by <u>Tautogolabrus</u> <u>adopersus</u> on <u>Lacuna vincta</u> in a controlled laboratory experiment. Responsion of snalls in specific size classes consumed per fish of given size in 5 days. Standard errors in parentheses ().

Midpoint of pise class PROPORTION snable consumed fich<sup>-1</sup> 5 days<sup>-1</sup> of shell length of <u>Lacuná</u> (na)

۰ <sup>۱</sup> -	, Size	` • Class of Fish (n	ED) · · · !
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77	.008,(.008)	,₀032 (₀02́0);	°∞076 (₀012)

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