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An experimental study on interactions structuring the lower rocky intertidal community in eastern Canada

Diplomarbeit

vorgelegt von

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Abstract

On exposed and semi-exposed rocky shores of Nova Scotia, Canada the low intertidal zone is dominated by a short turf of the red alga *Chondrus crispus*. In contrast, the mid shore is covered by a canopy of large fucoid algae. Factors accounting for the absence of *Fucus evanescens* from the lower zone were tested experimentally for different life stages of *Fucus*.

I tested effects of *Chondrus* on recruitment of *Fucus* in the absence of grazers. *Fucus* zygotes were released on experimental plots where *Chondrus* presence was manipulated. Initial settlement density of *Fucus* was enhanced by presence of *Chondrus* crustose holdfasts and *Chondrus* canopy, and reduced on sandblasted bare rock. However, subsequent survival and growth were heavily suppressed when *Chondrus* was present. A fucoid canopy established only on bare rock.

A second experiment tested effects of (a) *Chondrus* presence and (b) grazing on two intermediate size classes of *Fucus* (2 mm and 6 cm length). Presence of *Chondrus* canopy and grazers independently depressed *Fucus* net growth rates, but only a combination of both factors resulted in significant weight loss of *Fucus*. Effects were the same for 2-mm and 6-cm plants. Presence of *Chondrus* crust alone had no effect on growth of these size classes of *Fucus*. The magnitude of effect for grazing was >twice that of competition from *Chondrus*. Moreover, procedural controls showed that this is likely a conservative estimate because cages may have mitigated grazer effects. Clearly, grazing is the main factor affecting *Fucus* in the smaller macroscopic stage.

Survival of *Fucus* (2 mm and 6 cm) in the mid-shore fucoid zone was significantly higher, suggesting an increased grazing pressure in the *Chondrus* zone. Also, a reciprocal transplant experiment of adult *Fucus* (30-40 cm length) and *Chondrus* plants showed that adult *Fucus* has the potential to grow and reproduce in the *Chondrus* zone, but suffers from intense, spatially variable grazing. *Chondrus* transplants lost weight in the *Fucus* zone, probably due to desiccation and heat stress.

To further investigate differential grazing between zones, grazer density was sampled at 6-weekly intervals from May to October. At the same time,

grazing pressure was measured directly with a grazer assay, using area losses from standardized strips of *Ulva* tissue. In the *Chondrus* zone, grazer density was 44% higher and grazing pressure was 52% higher than in the *Fucus* zone.

In this study *Chondrus* was shown to have higher resistance to grazing, higher competitive ability and reduced resistance to physical stress in comparison with *Fucus*. Also it is much slower growing than *Fucus*. This contradicts two general contentions: (a) that competitive ability relates directly to growth rates and (b) that good competitors are relatively more susceptible to grazing. Moreover a general trade-off between stress tolerance and growth rates is not verified here. However, stress tolerance is inversely correlated with competitive ability, which is in accord with a model of competitive hierarchies.

Photographs

Photo 1: Zonation pattern at the experimental site: the mid shore is covered by a dense canopy of *Fucus* spp., while the low intertidal region is dominated by *Chondrus crispus* red algal turf.

Photo 2. The lowest part of the *Fucus* belt is dominated by *Fucus evanescens*. There is a sharp boundary towards the *Chondrus* zone. A grazer-exclusion cage is shown. Cages measured 15x15 cm. They were made from an aluminum angle frame, covered with 1-mm Nylon mesh. They were fastened to the rock with four wedge anchors.

Photo 3. Recruitment of *Fucus evanescens* in the *Chondrus* zone: cages were filled with fertile *Fucus* plants for 24 hr to initiate recruitment on experimental plots ("seeding"). Here, a sandblasted control plot is shown (no *Chondrus* present).

Photo 4. Recruitment of *Fucus evanescens* on bare rock, 4 mo after "seeding". Plants were enclosed by grazer-exclusion cages. Some *Chondrus* grew back from crust remnants along the plot perimeter.

Photo 5. Effects of grazers (juvenile *Littorina littorea*) on 6-cm *Fucus* transplants in the *Chondrus* zone after 6 d.
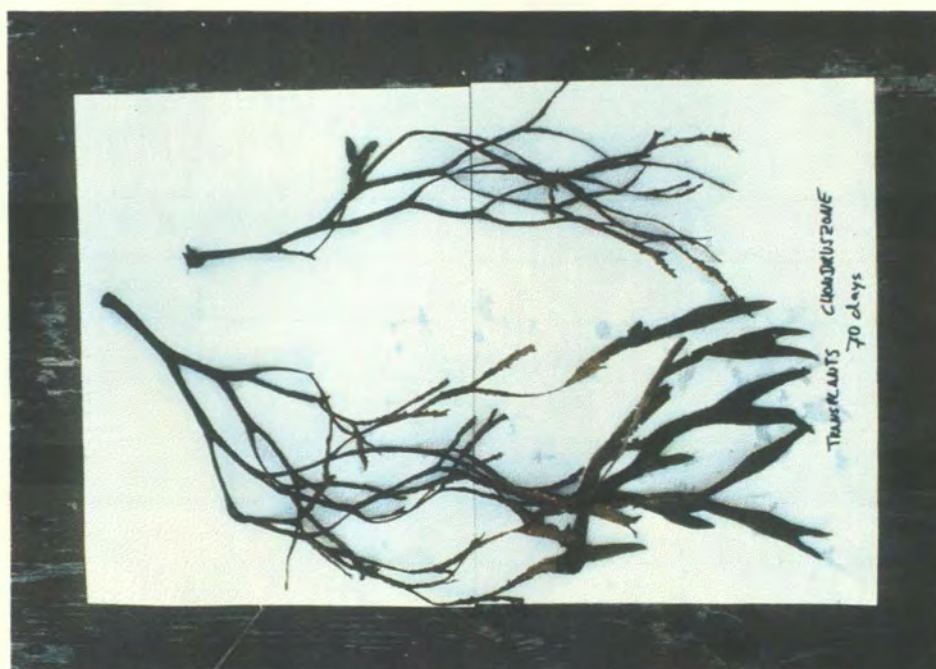

Photo 6. In a reciprocal-transplant experiment adult *Fucus* transplants (30-40 cm size class, after 70 d) were heavily grazed in the *Chondrus* zone. Controls in the *Fucus* zone (not shown) showed no grazing marks.

1. Introduction

Experimental community ecology greatly increased our understanding of how species interactions and environmental conditions locally determine the configuration of multi-species assemblages. In addition, general models of community structure and dynamics have emerged. Several authors (e.g. Menge & Farrell 1989) pointed out that rocky shores have proven to be excellently suited for the study of community structure and for testing these general models.

On exposed and semi-exposed rocky shores in Nova Scotia, Canada the upper and mid-intertidal regions of marine rocky shores are dominated by dense canopies of the three rockweeds *Fucus spiralis*, *Fucus vesiculosus* and *Fucus evanescens* at progressively lower zones. There is a sharp boundary towards the low intertidal, where *Chondrus crispus*, a red turf-forming alga dominates. The distributional boundary between the *Fucus evanescens* zone and the *Chondrus* zone is of particular interest for this study.

A similar pattern can be found in tidepools on the mid-shore. *Fucus vesiculosus* and *Fucus evanescens*, which dominate on emergent rock are found rarely within the pools, which are dominated mainly by *Chondrus crispus* , *Corallina officinalis* and green ephemeral algae (Lubchenco 1982). Possible non-exclusive explanations for these phenomena are:

(1) *Fucus* cannot exist under extended periods of submergence within the *Chondrus* zone or in tide pools (lower distributional limit of *Fucus* is set by physical factors),

(2) *Chondrus crispus* cannot withstand longer periods of emergence (upper limit set by physical factors). Where it occurs, it outcompetes *Fucus evanescens* (lower limit of *Fucus* is set by competition),

(3) *Fucus* cannot establish on the lower shore and in tide pools because of the higher abundance, activity or efficiency of grazers, against which *Chondrus* is more resistant (lower limit of *Fucus* is set by grazing).

There is no evidence that fucoids in general need emergence (Chapman 1995), with the exception of one European species, *Pelvetia canaliculata*

(Rugg & Norton 1987). In contrast, there is good experimental evidence that the upper distributional limit of *Chondrus crispus* is set by physical factors (Dudgeon *et al.* 1989, Kübler & Davison 1993). Lubchenco (1980, 1982) and Lubchenco & Menge (1978) gave experimental and observational evidence that competition and herbivory are the primary determinants of the described zonation pattern at the coast of Maine. They found that competition by *Chondrus* prevented *Fucus* generally from colonising the low zone, while grazing only affected the abundance of *Fucus*, rather than its presence or absence. *Chondrus* normally forms a dense canopy, which grows from a crustose holdfast. Natural disturbance during winter storms may remove up to 30% of the canopy (Dudgeon & Johnson 1992) leaving the persistent crust, from which a canopy can regrow. Results of Lubchenco (1980) indicate that both, *Chondrus* crust and canopy prevent *Fucus* from colonizing.

However, these studies have shortcomings. For example Lubchenco (1980) did not manipulate the presence of herbivores experimentally. Instead she chose two sites of very different geographic location and exposure to waves. *Littorina littorea* was absent at the exposed site. Other grazers, which are known to prey heavily on *Fucus* such as the snail *Lacuna* (Thomas & Page 1983) and probably gammarid amphipods (Parker *et al.* 1993) were abundant. Competition by *Chondrus* may be confounded with effects of grazers which are associated with *Chondrus* (apparent competition, Connell 1990) and effects of *Littorina* presence may be confounded with site. The experiments, in general, lacked true replication as only one large area per treatment was experimentally cleared and then sampled with several small quadrats (pseudoreplication, Hurlbert 1984).

Moreover, Lubchenco (1980) suggested further investigation on the mechanism of competitive exclusion. Other authors (Connell 1990) also emphasized the importance of revealing the underlying competitive mechanisms and controlling consumer effects, while studying competition. Connell (1990) pointed out that there is a lack of studies that follow these recommendations.

Spatial dominance is maintained by the balance of three processes: mortality, recruitment and growth (Petraitis 1995). If *Fucus* has the ability to re-

cruit and grow on the low shore, one or more of the vital parameters must be influenced by *Chondrus* presence, or by interaction with a third species to exclude *Fucus* from the low intertidal zone.

Lubchenco (1980) observed that adult *Fucus*, once established in the *Chondrus* zone, was able to grow and reproduce for several years. She suggested that *Fucus* germlings are mainly affected and that chemical interference is a mechanism of exclusion.
An alternative explanation would be that *Chondrus* simply outcompetes small *Fucus* germlings for light, which may be reduced under *Chondrus* turf. In addition, there may be effects of *Chondrus* crust on attachment and survival of *Fucus* zygotes. Thus it is necessary to determine mechanisms affecting *Fucus* at different life stages. In this study I tested experimental effects on zygotes, two different size classes of juveniles and adults of *Fucus* in separate experiments.
Fucoid zonation on the mid-shore in Nova Scotia served as a model system (Chapman 1995) to test the competitive-hierarchy concept, put forward by Keddy (1989). Results on the mid-shore are only partially concordant with the general model. This proposes that competitive ability and tolerance to environmental stress are inversely correlated among species which are zoned on an environmental gradient. At the benign (lower) end of its realized distribution, each species is restricted by competition with the species ranking next higher in competitive ability. The upper limit is set by physical factors. I evaluated some of these predictions for the lower intertidal zone: *Chondrus* was hypothesized to be competitively superior to *Fucus* on the low shore, but unable to exist on the mid-shore. *Fucus* may be able grow on the low shore, if released from competition.

2. Materials and methods

Study site and species

The experimental site was at Nowland's point, Lower Prospect, Nova Scotia (44°27'N, 63°43'W, Fig. 2.1), a semi-exposed granitic headland, which is largely undisturbed by human activity. The tidal range in this area is 2.1 m at spring tides. The maximum wave height at this site is 2-3 m during winter storms (personal observation). Surface water temperature ranges from 0°C-18°C. The rocky substratum is relatively even, allowing the tight fitting of grazer-exclusion cages.

A broad belt of *Fucus* canopy dominates the mid shore, with *Fucus evanescens* inhabiting the lower part (hereafter simply referred to as *Fucus* zone, *Fucus evanescens* referred to as *Fucus*). A strikingly sharp boundary (Photo 1, 2) exists towards the lower intertidal level, which is almost completely covered by dense *Chondrus crispus* canopy (hereafter referred to as *Chondrus* zone).
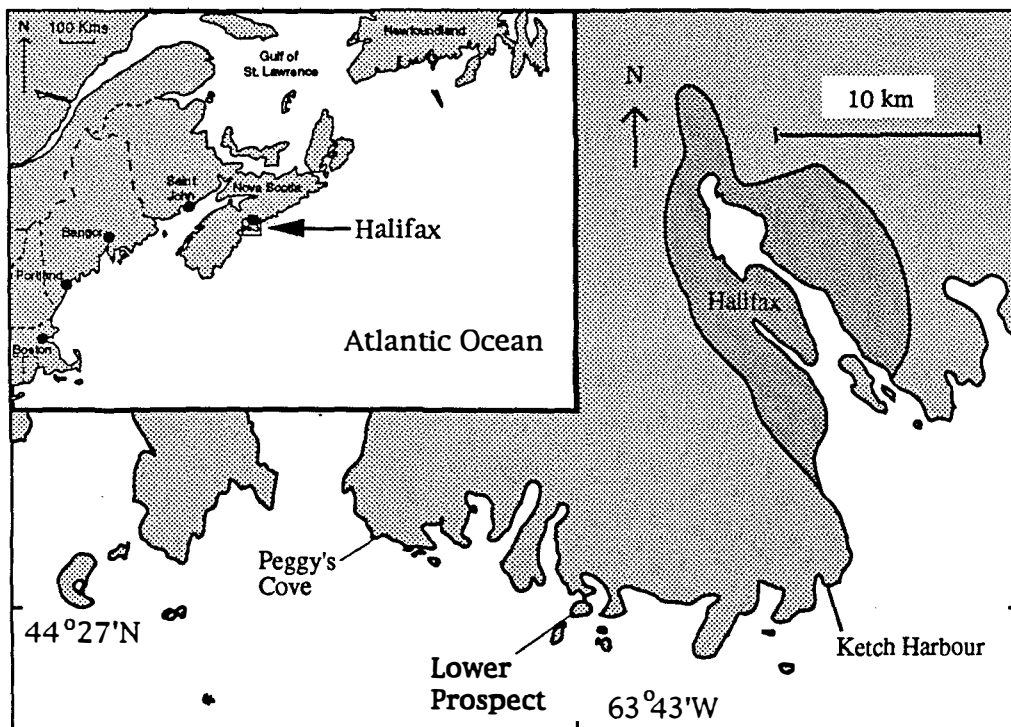

Fig. 2.1. Location, of the study site at Lr. Prospect near Halifax, Nova Scotia, Canada

Towards the subtidal *Chondrus* canopy gets increasingly interspersed with patches of *Corallina officinalis* and scattered individuals of a broad, small form of *Fucus evanescens*, until finally kelps (*Laminaria longicruris*, *Alaria esculenta*) dominate secondary space.

This general zonation pattern is consistent for most exposed and semi-exposed shores in Nova Scotia and New England (Stephenson & Stephenson 1972, Lubchenco & Menge 1978, Lüning 1990, personal observation). *Fucus evanescens* and *Chondrus crispus* may interact on the low shore. *Chondrus* is a small, sturdy, turf-forming red alga. The dense turf is 5-8 cm high and grows from extensive encrusting holdfasts. Thus *Chondrus* can occupy a large portion of primary and secondary space. Contrary, *Fucus evanescens* is a large (30-40 cm), canopy-forming alga that grows from a small (<1 cm diameter) holdfast. At low tide, the large adult plants cover the substratum in multiple layers.

This study aims to explain the absence of *Fucus evanescens* and spatial dominance of *Chondrus* in the lower intertidal zone. The working hypothesis was that *Chondrus* canopy and/or grazers prevent the growth of *Fucus* on the low shore. In a series of experiments, I tested the effects of *Chondrus* presence and grazer activity on recruitment, growth and mortality of different life stages of *Fucus evanescens*. The general experimental concept was to establish *Fucus* individuals in the *Chondrus* zone, either by transplantation or by releasing *Fucus* zygotes on experimental plots, and to measure growth and survival after several months, manipulating *Chondrus* and grazer presence.

Zonation pattern
The vertical distribution of dominant space occupants on the low shore was estimated at three replicate locations at the experimental site November 7-10, 1995. The chosen areas were characteristic for the site and physically very similar. They showed a relatively even surface and a constant slope. At each location, eleven 4.5-m transects (spaced 0.5 m apart) were run across the shore gradient from 0.0-1.1 m above LAT (lowest astronomical tide level). At 10-cm intervals, I recorded the species crossed by the tran-

sect line. Percent cover of each species at each 10-cm interval was calculated by dividing intercepts by number of transects and multiplying by 100.

Chondrus and *Fucus* percent cover and biomass were sampled on Nov 3, 1995 in random 20x20-cm plots (n=5) along a horizontal transect of 5 m length. Percent cover was estimated with a plexiglas frame with 60 random dots. Three levels on shore were sampled : *Chondrus* zone, *Fucus* zone and a transition zone, where natural recruitment of *Fucus* had occurred in the summer. Recruitment of *Fucus* in the *Chondrus* zone was only seen here, thus it is an unreplicated observation. The patch measured ca. 1.5x4 m and had probably been ice scoured previously. *Chondrus* cover was very sparse and *Fucus* recruits were first seen in August. By November secondary space was largely occupied by *Fucus*. Statistical analysis was not attempted, because results for the transition zone may be regarded pseudoreplicated (Hurlbert 1984).

Grazer density and grazing pressure
One of the central hypotheses during this study was that *Fucus* may not grow in the *Chondrus* zone due to a possibly higher density, activity or efficiency of grazers. To investigate this contention, two separate studies were undertaken: I estimated grazer density in both zones periodically along three transects. Six predominant species were sampled and weighed. But since grazer abundance may not be a direct measurement of actual grazing pressure on plants a grazer assay was developed to compare grazing pressure between zones.

Grazer abundance: Grazer density and wet weight (WW) were censused in 6-week intervals with replicate quadrats placed in the *Fucus* zone and the upper *Chondrus* zone corresponding to the level on shore used in other parts of this study. A pilot study on May 23, 1995 revealed only six mesograzers of significant numbers: Periwinkles: *Littorina littorea* and *Littorina obtusata*, gammarid amphipods: *Gammarus oceanicus* and *Hyale nilsonii*, the isopod *Idothea phosphorea* and the small limpet *Tectura testudinalis*. Sample plots for the two zones were randomly distributed along 10-m

transects at three different locations at the experimental site. Twelve replicate 15x15 cm quadrats per zone were placed along each transect line, giving 36 replicates per zone and census date. Sampling was always done on three consecutive, calm days to assure similar physical conditions for comparison of dates. Grazers collected in each plot were stored in separate seawater containers, before counting and weighing them in the laboratory. Results for total grazer density [g WW$*$m^{-2}] were analysed by three-way ANOVA with "zone" (two levels: *Chondrus* zone and *Fucus* zone) and "date" (four levels: June, July, August, October) as the main factors and "transect" (three levels) for the block effect. Data were log-transformed and homogeneity of variances was tested graphically and with Cochran's test.

Grazer assay: To measure grazing pressure a grazer assay was developed (Fig. 2.2). I used strips of a robust form of *Ulva lactuca* that were standardized to the size of a microscopic slide (2.5x7.5 cm) and fixed with Hoffman stainless steel aquarium-hose clamps. The complete array was cable-tied to wedge anchors that were placed at 3-m intervals along 10 m transects.
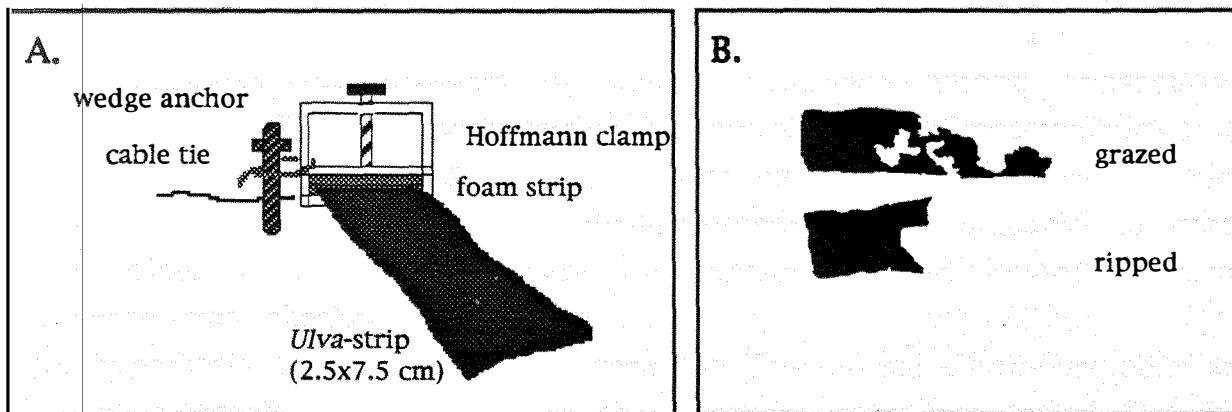
Fig. 2.2. A grazer assay to quantify grazing pressure: A. Assay arrangement in the field. A standardized strip of *Ulva lactuca* tissue is held by a Hoffmann clamp. A foam strip prevents the *Ulva* strip from slipping. B. Scanned images of two *Ulva* strips, after 24 hr in the field. Irregular grazing marks (from *Littorina* spp. and amphipods) can be clearly distinguished from strips that were ripped by severe wave action (<5% in this study). Thus, losses due to grazing are easy to identify and can be quantified as proportional area loss per time unit.

Transects and level on shore were identical with the grazer-density study. Four replicates were installed per transect and zone, giving 12 replicates per zone and date. Assay measurements were always done during the same periods as grazer-density counts, on very calm days. However in August only, a 1-m swell was present during the sampling period. Losses of *Ulva* tissue due to grazing could be distinguished very clearly from physically ripped strips, which showed smooth edges (Fig. 2.2 B). The experimental period was only 24 hr, as grazing on the assay was very intense. Measurements on ungrazed strips showed that no autogenic changes were detectable during this period.

Upon retrieval, the strips were arranged on plastic paper und dried, then photocopied and scanned. Area loss was determined using computer image analysis.

Data were analysed by two-way MANOVA, with data from each date treated as a dependent vector. This was necessary, because measurements between dates were not independent, as I chose fixed locations for the assay clamps. The multivariate analysis has a greater power of detecting a real difference than independent univariate ANOVAs for each sampling date. At the same time, it minimizes the risk of committing a type I error and eliminates the problem of non-independence among consecutive sampling dates. For hypothesis testing I chose the Pillai Trace-statistic. It is recommended by Johnson & Field (1993) as being most robust against violations of multi-normality and multi-homoscedascicity, compared to other multivariate statistics. Data were log-transformed and homogeneity of variances was checked graphically

The hypothesis that differences between the *Fucus-* and *Chondrus* zone are part of a grazing gradient across the intertidal zone was tested Oct 10, 1995. Assay measurements (n=12) were done across the intertidal gradient. The factor "zone" had four levels: the *Chondrus* zone was compared with three progressively higher levels in the fucoid belt that are dominated by *Fucus evanescens*, *F. vesiculosus* or *F. spiralis* respectively. Results were analysed by two-way ANOVA.

Effects of *Chondrus* on *Fucus* recruitment

Experimental concept: in this experiment I tested effects of *Chondrus* canopy and crust on recruitment and subsequent growth of *Fucus evanescens* in the absence of grazers. I hypothesized that attachment success of *Fucus* zygotes is reduced on *Chondrus* crustose holdfasts and growth of germlings is inhibited by shading under the turf-forming canopy. Zygotes were released from fertile *Fucus evanescens* on 15x15 cm plots, enclosed by grazer-exclusion cages. Attached zygotes were counted after 8 d and growth to visible size monitored for 4 mo.

Experimental design and sampling: Two sub-experiments were conducted. To ensure similar initial propagule densities, I seeded experimental plots with zygotes from fertile *Fucus* plants over 24 hr (Photo 3). Zygote release was induced by keeping plants dark at 10°C for 2 d, prior to seeding. Both sub-experiments were replicated in one randomized block design (n=6). All plots were enclosed by 15x15x10-cm cages (Photo 2, 3) made from an aluminum angle frame fastened to the rock with four wedge anchors (Parker *et al.* 1993). Cages were covered with 1-mm nylon mesh and sealed tightly against the rock with a foam gasket. This allowed exclusion even of smaller amphipod species (*Hyale nilsonii, Amphithoe rubricata*) and juvenile snails ≥ 1 mm size (*Littorina littorea, Littorina obtusata*). All cages were checked for grazers at least every 2 wk.

In a first sub-experiment, *Chondrus* presence had two levels: i. *Chondrus* canopy removed and crustose holdfast present, ii. *Chondrus* canopy and crust absent (sandblasted bare rock). A second sandblasted treatment was not treated with fertile *Fucus*. This served to quantify natural recruitment levels on bare rock. Plots were cleared May 10-11, 1995 using paint scrapers to remove *Chondrus* canopy and a portable sandblaster to remove the crustose holdfast. The sandblaster was connected to SCUBA dive tanks and the first stage of a diving regulator that reduced pressure to 5 bar. However, the crust was so persistent that remnants had to be removed manually with a knife. Seeding was done May 15-16, 1995. After 9 d, all plots were sampled non-destructively *in situ*, using a dissecting microscope adapted for field use. Within a 10x10-cm grid, eight 1-cm² subsam-

ples were selected randomly, and attached zygotes were counted. Two blocks were not sampled quantitatively because fouling by *Pilayella littoralis* and benthic diatoms reduced visibility of zygotes. Heavy fouling by *Chordaria flagelliformis* occurred in most cages in June. This canopy was removed with scissors, leaving the substratum undisturbed. *Fucus* juveniles grew rapidly and visible stages (>1 mm) in eight 1-cm^2 subsamples/plot were counted on August 10, 1995. Finally, all plots were sampled destructively by scraping 10x10-cm areas with razor blades on September 25-26, 1995. All *Fucus* >1mm were collected and counted.

In the second sub-experiment *Chondrus* canopy was seeded with *Fucus* zygotes May 15, 1995 and also October 13, using new plots. Because zygote density could not be examined *in situ* under *Chondrus* canopy, it was necessary to cut randomly placed rock segments (ca. 6x3 cm) from within treatment plots with a gasoline-powered diamond saw. To check for natural recruitment under *Chondrus* canopy, control rock segments were cut 1 m away from blocks, on the same level on shore. Rock segments were cemented to tiles and held for 5 d under a seawater sprinkler. Exposure to strong fluorescent light intensified zygote pigmentation and helped with identification on the very heterogeneous substratum. On each rock segment, a central 4x2-cm area was examined after cutting away the *Chondrus* canopy. Zygotes were categorized according to the substratum to which they were attached. Sampling was done 10 d after seeding, on May 26, 1995 and after 4 mo, on September 26, 1995. Plots seeded in October were sampled after 10 d on October 24.

Statistical analysis: Results for the first sub-experiment were analysed by one-way ANOVA for each sampling date separately. *Chondrus* canopy treatments were analysed by two-way ANOVA with "seeding" and "month" (experiments in May and October) as experimental factors. The dependent variable was mean number of fucoid germlings. Data were log-transformed and homogeneity of variances was tested by Cochran's procedure.

Effects of grazer presence and competition by *Chondrus* on two intermediate size classes of *Fucus evanescens*
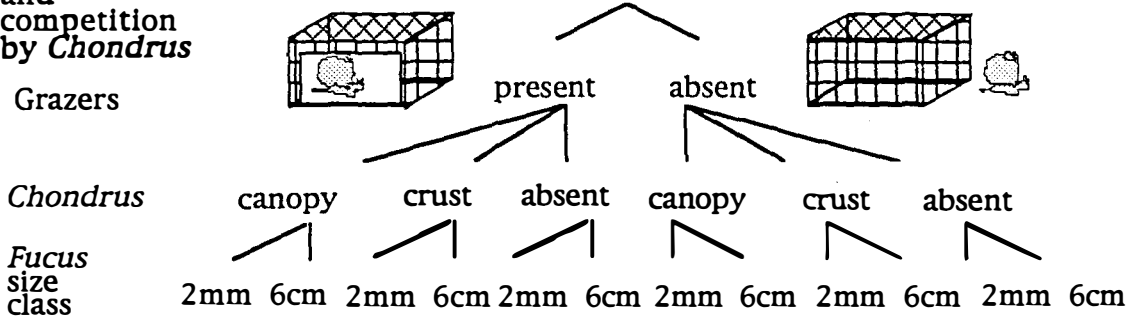
Experimental concept:. I tested for effects of presence of grazers and presence of *Chondrus* canopy and crust on net growth of transplanted juvenile *Fucus evanescens*. My hypothesis was that high grazer densities found on the low shore zone and/or shading by *Chondrus* canopy prevent *Fucus* juveniles from growing.

Lubchenco (1983) proposed an escape from grazing with plant size for *Fucus vesiculosus*. She found that *Littorina littorea* and *Littorina obtusata* affected germling (<2 cm) cover, but did not show any effect on plants >5 cm. Moreover, in the *Chondrus* zone, *Fucus* plants >5-6 cm can exceed height of the *Chondrus* canopy and may be less affected by competition for light than germlings. To test for this, juveniles of 2 mm and 6 cm length (hereafter called 2-mm *Fucus*, 6-cm *Fucus*) were used in this experiment, and orthogonally crossed with the other factors. The experimental period was 65 d, from July 3 - September 14, 1995. Transplanted *Fucus* grew on small granite rock segments, that were cemented into pre-cut grooves within 15x15 cm plots in the *Chondrus* zone.

Experimental design: in the main experiment (Fig. 2.3 A) three experimental factors were tested on replicate (n=4) transplants in a completely orthogonal design. Grazer presence was manipulated with grazer-exclusion cages (Photo 2, Fig. 2.4). In treatment combinations with grazers present, the nylon mesh was removed from the side facing the shore. Grazers readily entered these cages within days (personal observation).

There were three levels of the factor "*Chondrus*": i. canopy, ii. crust and iii. control (*Chondrus* absent). In crust treatments the canopy was removed two wk prior to transplantation with a paint scraper, leaving the crustose holdfast (65% cover ± 3% SE, n=25). In control plots the holdfasts were removed by sandblasting.

A. Effects of grazer presence and competition by *Chondrus*

Grazers

present   absent

Chondrus   canopy   crust   absent   canopy   crust   absent

Fucus size class

2mm 6cm 2mm 6cm 2mm 6cm 2mm 6cm 2mm 6cm 2mm 6cm

B. Control Experiment for cage artifacts

Cage

open   none

Chondrus   crust   canopy   crust   canopy

Fucus size class

2mm 6cm 2mm 6cm 2mm 6cm 2mm 6cm
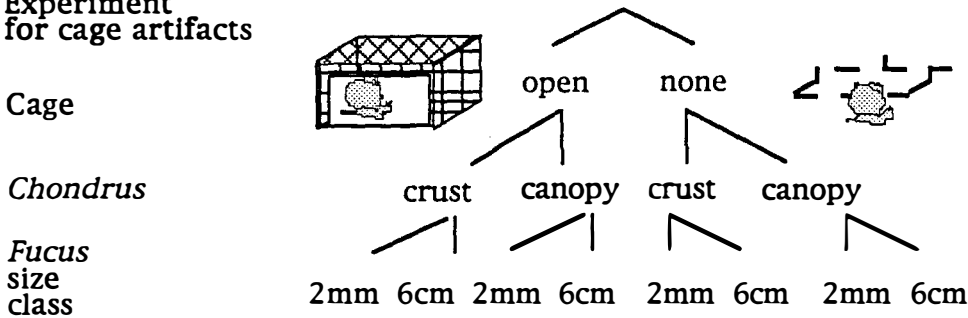
C. Effects of level on shore and *Chondrus* presence

Level on shore   *Fucus* zone   *Chondrus* zone

Chondrus   crust   canopy   crust   canopy

Fucus size class

2mm 6cm 2mm 6cm 2mm 6cm 2mm 6cm

Fig. 2.3. Experimental design of three sub-experiments testing for (A) the effects of grazer presence and competition by *Chondrus* on two size classes of *Fucus* (2-mm and 6-cm plants), (B) cage artifacts for treatment combinations with *Chondrus* crust or *Chondrus* canopy present, (C) differences in *Fucus* survival between zones (with grazers present) and *Chondrus* present as either crust or canopy. The design was completely orthogonal with 20 treatment combinations, each replicated 4 times. All treatment combinations were arranged in one completely randomized block design.

Fig. 2.4. Graphical representation of two treatment combinations (among 12 in Fig. 2.3). Grazers (mainly *Littorina littorea*) were either present or absent, *Fucus evanescens* belonged to two size classes: 6-cm plants or 2-mm germlings, growing on rock segments that were cemented into pre-cut grooves. All plots were installed in the *Chondrus* zone at the same level on shore.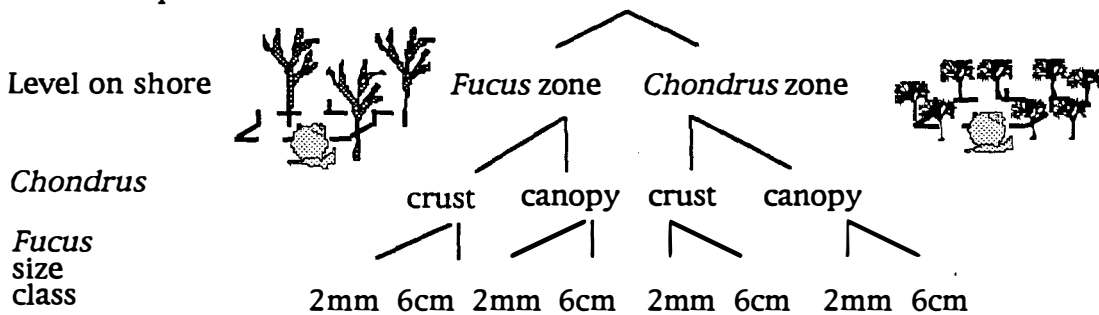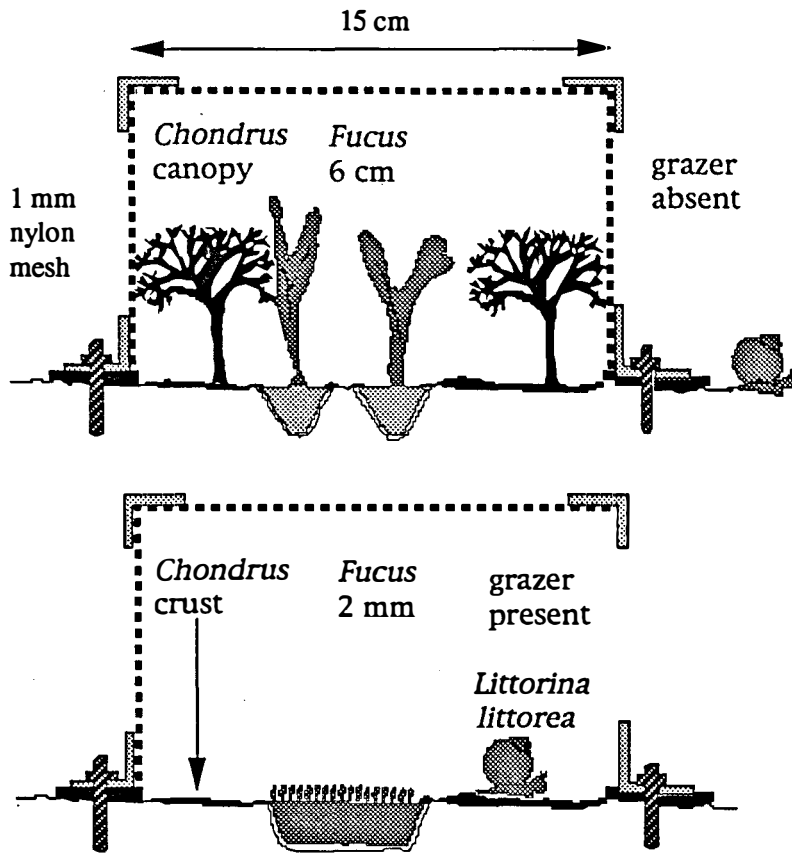 Cages were made from an aluminum angle frame, covered with 1 mm nylon mesh, fastened with four wedge anchors and tightly sealed against the rock with a foam gasket.

There were two levels of the factor "*Fucus* size class": 2-mm plants and 6-cm plants. 2-mm plants were grown in the laboratory using a modified procedure after Chapman (1973): Fertile *Fucus evanescens* plants were collected at Sandy Cove, N.S. (44°28'N, 63°33'W) on May 9, 1995 and kept in the dark for 2 d. To release gametes, plants were placed in seawater dishes and exposed to strong light. Zygotes were concentrated by siphoning off the lower portion of the water column after 3 hr, and poured over pre-cut, clean granite rock segments (6.8 ± 0.1 cm x 2.5 ± 0.04 cm, means ±1 SE, n=35). After 3 d (water was changed daily) the colonized segments were placed in a seawater sprinkler and exposed to strong light. Water pressure

was increased weekly to initiate good attachment. Zygotes grew to a size of 2 mm within 7 wk. One segment was transplanted into each plot (Fig. 2.4). 6-cm *Fucus* were collected on June 30 and July 2 from two previously ice scoured patches (6-10 m^2) within a broad bed of *Fucus evanescens* at Sandy Cove. Individuals were between 5 and 7 cm high and had an initial thallus area of 6.26 ± 0.21 cm^2 (±1SE, n=80). They were collected on small pieces of granite rock, cut with a gasoline-powered diamond saw. Only un-fouled and ungrazed individuals were chosen. Two individuals were transplanted into each plot (Fig. 2.4).

A control experiment (Fig. 2.3 B) was designed to test for potential cage artifacts. This control experiment was done for the *Chondrus* levels "crust" and "canopy" only, as these are most likely to occur naturally. Both *Fucus* size classes were included in the design. Grazers were present in all treatments. *Fucus* performance was compared among plots with and without open cages.

In a second sub-experiment (Fig. 2.3 C) I tested for differences in Fucus mortality among two tide levels on the shore. I assumed that grazing is the only cause of mortality, which was strongly supported by observations. I hypothesized that survival is higher in the *Fucus* zone than in the *Chondrus* zone because of lower grazing pressure on individual plants. Moreover, *Chondrus* presence (two levels: crust and canopy) may affect grazer behaviour. However, *Chondrus* density was reduced under the fucoid canopy. *Fucus* canopy itself was not manipulated.

Treatment combinations of all 3 sub-experiments were arranged in one completely randomized block design with 4 blocks. Treatment combinations were assigned to the pre-marked plots using random number tables.

Sampling: All *Fucus* plants were transplanted July 3-4 1995. Segments were cemented into pre-cut grooves. An acclimatization period of 8 d was allowed before initial measurements were done, to rule out random losses during the first days. All cages were closed during this period. I checked cages repeatedly for grazer intrusion. However, uncaged plots suffered a very severe grazer impact during this period. Densities of 2-mm *Fucus*

were sampled photographically after 1 d and thallus area of 6-cm *Fucus* plants was traced onto plastic paper.

In the main experiment, initial data were obtained July 11-12, 1995. I standardized density of 2-mm plants to 130 individuals on a 6 cm^2 (1.5x4 cm) area, that was permanently marked with a small diamond saw. Initial thallus area of 6-cm plants was traced. There were no significant differences in initial thallus area between treatment combinations, although there was a non-significant trend for *Chondrus* canopy treatments (2x3-ANOVA, $F_{2,15}=3.226$, $p=0.683$) that might reflect early effects of *Chondrus* canopy on growth of 6-cm *Fucus* during the acclimatization period.

To assess short-term effects, sampling was repeated July 12-13, 1995 on all uncaged plots, and July 17-18, 1995 on caged plots, counting 2-mm plants within the marked 6 cm^2-area and tracing 6-cm *Fucus* thallus area. All closed cages were controlled for absence of grazers at least every 2 wk. The experiment was terminated after 65 d, September 14, 1995. All segments were chiselled out from their grooves and analysed in the laboratory. Dry weight of *Fucus* was determined to the nearest mg, after drying plants for 48 hr at 80^0C.

To calculate initial dry weight of 2-mm *Fucus*, 50 individuals of 2 mm size were weighed. For 6-cm *Fucus* plants, initial thallus area [cm^2] was converted from field tracings into dry weight [g], by establishing a regression for *Fucus evanescens* individuals of 3-10 cm height with y=-0.016+0.015x, $r^2=0.92$, $p<0.001$***, n=40.

Statistical analysis: Analysing measured absolute or relative increase in dry weight with a linear model such as ANOVA would assume a linear relationship between final weight (hereafter W_2) and initial weight (hereafter W_1).

However for *Fucus* at the juvenile stage it is much more appropriate to suggest a logarithmic relationship between W_1 and W_2 which can be linearized by a logarithmic model such as the instantaneous growth rate.

Form. 1. $\delta W/\delta t=$ (ln W_2 - lnW_1)/t_2-t_1 dimensions=[g/g*d]

However, only plants in grazer-exclusion cages may increase weight exponentially. Plants which are exposed to grazing show a very different net growth rate, which might even be negative when losses exceed gains.

To model measured net change in dry weight according to the instantaneous growth rate (in order to analyse effects of competition and grazing simultaneously) the following **assumptions** must be met:

(1) weight gain results from exponential growth and is constant over the experimental period (constant instantaneous growth rate),

(2) the rate of tissue loss to grazing is also logarithmic and constant. Mortality of *Fucus* was not linear over time (Fig. 3.9, Results). Moreover, grazers were not observed to feed continuously on one transplant unit (linear grazing rates), but to enter and leave cages frequently. This evidence suggests a logarithmic rather than a linear model,

(3) grazing is the only significant factor, accounting for weight loss. I examined *Fucus* transplants that were protected by grazer-exclusion cages. For both size classes there was no evidence of loss of tissue or individuals independently of grazing,

(4) some plots showed zero weight after 65 d due to heavy grazing. A 2-point model (only W_1, W_2 known) has to assume that zero weight was achieved after 65 d, although actual time may have been <65 d. This may result in a more conservative estimate of the grazer effect. To include plots with zero final weight into the analysis a minimum measurable weight of 0.001 g was added to all weights so the dependent variable was chosen as:

Form. 2. $\delta W / \delta t = \ln (W_2 + 0.001) - \ln(W_1 + 0.001) / 65$ d*1000 dimensions= [mg/g*d]

Results of the main experiment (Fig. 2.3 A) were analysed by three-way (2x2x3) ANOVA. Homogeneity of variances was tested using Cochran's procedure. The magnitude of effects for the experimental factors were calculated (Howell 1992, p.407).

Form. 3. $\omega^2 = (SS_{treat} - (k-1)MS_{error})/(SS_{total} + MS_{error})$
where k=number of treatments, SS=sums of squares, MS=mean squares
and treat=treatment

The control experiment for cage artifacts (Fig. 2.3 B) could not be analysed
statistically because the two levels of the main factor "cage" were separa-
ted in time, due to a very severe grazer impact on open plots during the
acclimatization period. Hence time is a potentially confounding influence.
For the second sub-experiment (Fig. 2.3 C), no statistical analysis was at-
tempted for the final results (after 73 d), because >50% of plots showed
zero dry weight due to intense grazing. Short term effects, measured after
9 d, were analysed for each life stage separately by two-way (2x3)
ANOVA, The dependent variable was number of live plants. For 6-cm
plants, a plant was arbitrarily defined as dead when only the mid rib was
left and thallus area <1 cm^2.

Reciprocal transplants of adult *Fucus* and *Chondrus*

Experimental concept: From Keddy's (1989) theory of competitive hierar-
chies along environmental gradients it follows that the upper distributional
limit of a species along an ecological gradient is set by its fundamental ni-
che breadth, i.e. physical factors. Contrary the lower limit is set by com-
petition. Lubchenco (1980) found that *Fucus* plants can grow and repro-
duce in the *Chondrus* zone. I hypothesized that transplanted large adult
Fucus plants will not be affected by competition by *Chondrus* and may
grow better in the *Chondrus* zone than in the *Fucus* zone due to more fa-
vorable environmental conditions. Transplanted *Chondrus* may not be able
to grow in the *Fucus* zone due to its narrower fundamental niche breadth.

Experimental design: In a randomized block design, adult *Fucus* plants
were transplanted into the *Chondrus* zone and controls into the *Fucus* zone.
The same was done with rock segments bearing a full cover of *Chondrus*
canopy. To compensate for possible losses of transplants, each of 4 blocks
contained 2 replicates of each of the four treatments, (n=8).

Chondrus and *Fucus* plants were collected July 16, 1995 at the experimental site. Only unfouled individuals of healthy appearance were chosen. *Fucus* transplants were cut along a 4-m stretch of shoreline on small segments of rock measuring ca. 2.5x5 cm. The plants were ca. 30-40 cm long, wet weight was 35.10 ± 4.72 g (mean ±1SE, n=7). Rock segments with *Chondrus* canopy were all cut within a 0.5 m² area. The segments measured ca. 10x3 cm, *Chondrus* wet weight was 21.41 ± 2.17 g (n=15) and canopy height ca. 6 cm.

All transplants were weighed 3 times to the nearest 10 mg after draining them for 20 s, then marked individually and cemented into pre-cut grooves July 17, 1995. The grooves were located within the upper *Fucus evanescens-* and the upper *Chondrus* zone. Transplants were checked weekly for grazing marks and general appearance. The experimental period was July 16 - September 25, 1995. Transplants were re-weighed three times and relative growth rates (after subtracting weight of the rock segment) were calculated.

Statistical analysis: Growth rates were analysed by one-way ANOVA (factor "zone") for *Chondrus* only, because six *Fucus* transplants have been lost during a severe storm after 1 mo. Homogeneity of variances was tested by Cochran's test.

3. Results

Zonation pattern

Species distribution at the experimental site (Fig. 3.1, Photo 1) clearly follows the general zonation pattern for semi-exposed and exposed shores in Nova Scotia. In the upper part of the lower intertidal zone *Fucus vesiculosus*, *Fucus evanescens* and *Chondrus crispus* form dense canopies of ca. 100% cover at progressively lower levels on the shore gradient. Boundaries between zones are remarkably sharp. Dominance of *Chondrus* declines in the lowest part of the intertidal zone. In its place, *Corallina officinalis* becomes increasingly abundant. This pattern continues in the subtidal zone (unquantified observation).
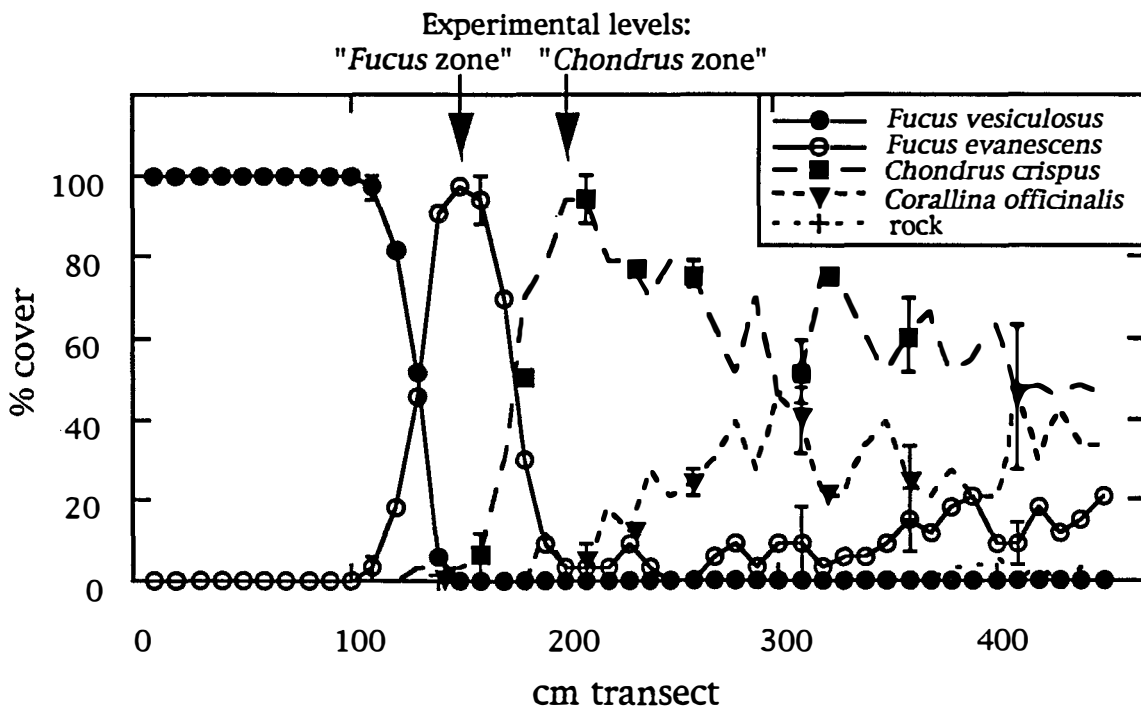

Fig. 3.1. Distribution of dominant space occupants along the lower intertidal shore gradient. Each point represents mean percent cover (±1SE, in 50 cm-intervals, n=3) at 10 cm-intervals along 4.5 m transect lines across the shore gradient. 0 cm is equivalent to 1.1 m above LAT (lowest astronomical tide level), 450 cm to 0.0 m above LAT. Of particular interest in this study was the sharp distributional boundary between *Fucus evanescens* ("*Fucus* zone") and *Chondrus crispus* ("*Chondrus* zone"). Difference in tidal height between experimental levels was only 10-15 cm.

This configuration on the low shore, however, is less rigid than the striking zonation on the upper shore. In Fig. 3.1 this is represented by fluctuating curves and high variability indicating patchy distribution of both species. A small portion of the low zone that is normally dominated by red algal turf, is occupied by scattered individuals or small clusters of *F. evanescens*, with a distributional maximum along the subtidal boundary. These individuals commonly co-occur with *Corallina* patches and only very rarely with *Chondrus* canopy. The morphology (broad, leafy, leathery thalli) is different from individuals in the *Fucus* zone. Single *Fucus* individuals were found to a depth of 6 m at the experimental site. This suggests that *Fucus evanescens* is capable of growing under constant submergence, but may be excluded from the *Chondrus* zone by other than physical factors.

Fucus and *Chondrus* biomass and percent cover are inversely correlated (Fig. 3.2). Both species showed high and similar biomass and percent cover, when the other species was absent (*Chondrus* zone: 5.53 ± 0.45 kg WW/m², 93.0 ± 1.78% cover, *Fucus* zone 4.97 ± 0.7 kg WW/m², 95.3 ± 0.97% cover, means ±1SE, n=5). *Fucus* was largely absent from the *Chondrus* zone, while a sparse *Chondrus* understorey was found under the fucoid canopy.

y=114.39 - 1.08x   r²=0.84
p<0.001

% cover *Fucus*

% cover *Chondrus*

y=1.88 - 2.38 log(x)   r²=0.72
p<0.001

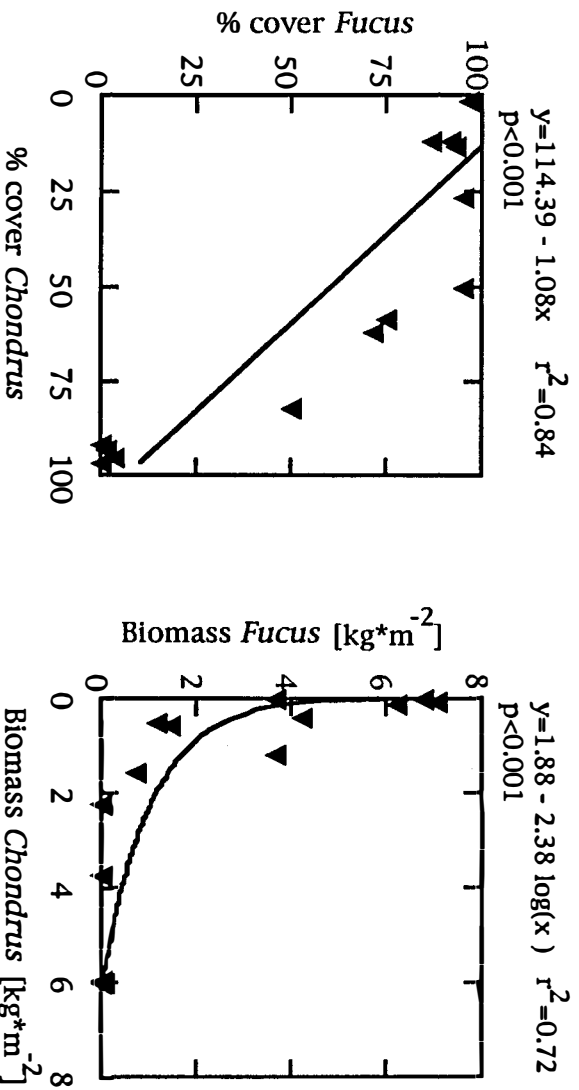Biomass *Fucus* [kg*m⁻²]

Biomass *Chondrus* [kg*m⁻²]

Fig. 3.2. Relation of percent cover and biomass (wet weight) of *Fucus* and *Chondrus* in fifteen 20x20 cm plots, sampled Nov 3, 1995. Five samples were obtained for the *Fucus* zone, the *Chondrus* zone and a transition zone that was previously ice scoured and recently recolonized by *Fucus*. Samples were placed randomly along 5 m transects.

In a recently recolonized ice scoured patch both species show high percent cover, but low biomass. Here I observed a low density *Chondrus* canopy in spring, 1995. Nevertheless *Fucus* succeeded in colonizing this patch. This was never seen in dense *Chondrus* canopy. The ability of *Fucus* to settle and grow in the presence of *Chondrus* may be related to *Chondrus* density.

Grazer density and grazing pressure between zones

I measured density of mesograzers and grazing pressure on *Ulva* tissue in the *Fucus* and *Chondrus* zone in three 10-m transects at four sampling dates June-October 1995 (Fig. 3.3). The dominant observation was very high variability in both measures between zones and dates but also between the three transects.

On average, grazer density in the *Chondrus* zone (340 $\pm$ 33 g/m^2, mean $\pm$1SE, n=144) was elevated by 44% compared with the *Fucus* zone (237 $\pm$ 32 g/m^2, n=144). This effect was highly significant in the analysis (Table 3.1). However, the factor "zone" accounted only for 5.3 % of total variance in the data. Spatial differences between transects explained 8% and the factor "date" 3.8% of the total variance. More than 80% of the variance remained unexplained. This may reflect high lateral variability in grazer abundance on a scale of meters.

Littorina littorea represented a dominant and increasing proportion of total grazer weight (52.1 $\pm$ 4.9% in June to 81.6 $\pm$ 4.2% in October, means $\pm$1SE, n=72, Fig. 5.2, appendix). *Littorina obtusata*, *Gammarus oceanicus* and *Idothea phosphorea* were only abundant in early summer and decreased in abundance constantly through October (Fig. 5.1, appendix). All species, except *Littorina obtusata,* were more abundant in the *Chondrus* zone. These results as well as direct observations on *Fucus* transplants indicate that *Littorina littorea* is the key grazer species on the low shore.

The effect of sampling date was tested for each transect separately, since there was a significant date*transect interaction. In two of three transects was no difference (p> 0.33, Table 3.2) between dates detectable.
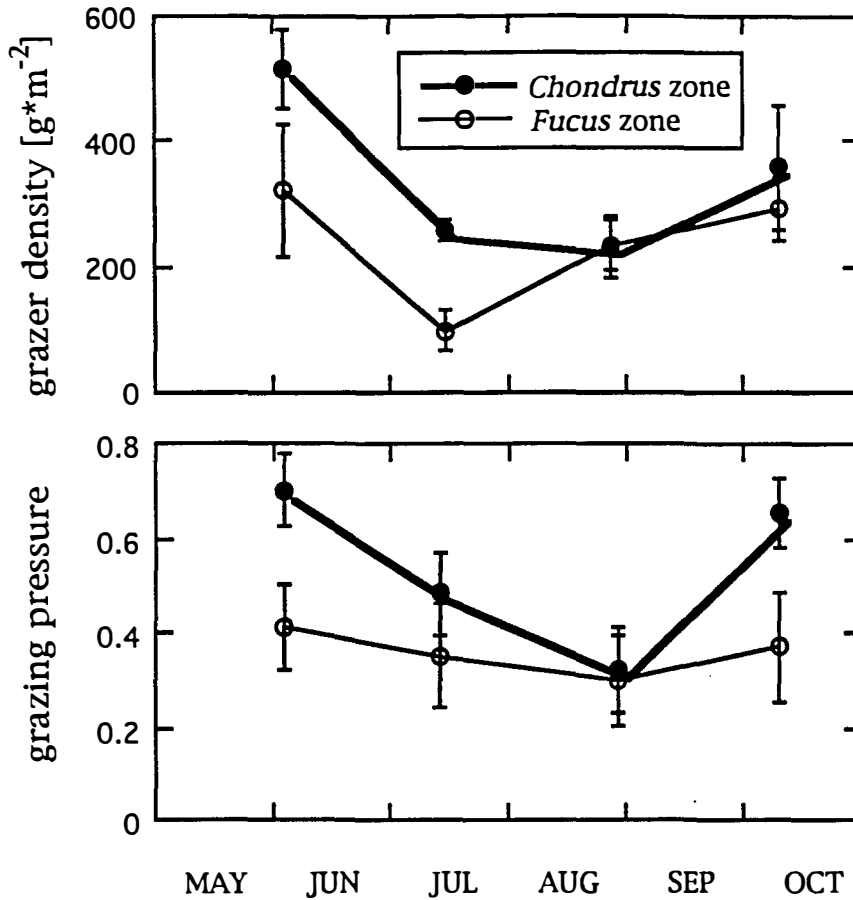
Fig. 3.3. Grazer density and grazing pressure measured at 4 dates during the growth period. Total grazer density is expressed as mean grazer wet weight per m² (±1SE, n=36), based on replicate counts within randomly placed 15x15-cm quadrats. Grazing pressure is expressed as proportional area loss of a 21-cm²strip of *Ulva lactuca*, that served as a grazer assay (n=12). For statistical analysis see Tables 3.1-3.2 and Fig. 3.4.

source of variation	df	MS	F	p	conclusion
zone	1	2.704	20.59	0.001	* * *
date	3	0.734			not tested
transect	2	2.051			not tested
transect*date	6	0.483	3.68	0.0016	* *
error	275	0.131			

Table 3.1: Three-way (2x3x4) ANOVA: effects of level on shore (*Fucus* zone, *Chondrus* zone), transect and sampling date (June-October) on total grazer density. Only the effect of zone can be tested for all replicates pooled. The effect of date was analysed for each transect separately (Tab. 3.2), since there was a significant date*transect interaction. Homoscedascicity was tested by Cochran's procedure.

source of variation	df	MS	F	p	conclusion
transect 1					
date	3	0.304	0.915	0.4370	n.s.
zone	1	2.448	22.093	0.0001	* * *
error	91	0.111			
transect 2					
date	3	0.15	1.154	0.3318	n.s.
zone	1	0.855	6.821	0.0105	*
error	91	0.13			
transect 3					
date	3	1.478	10.053	0.0001	* * *
zone	1	0.155	1.057	0.3066	n.s.
error	91	0.147			

Table 3.2. Two-way (4x2) ANOVAs: effects of sampling date and zone on grazer densities, analysed for each transect separately. In transect 3 only, grazer densities in July are significantly lower, than in June (***), August (*) and October (***). There were no significant date*zone interactions. Data were log-transformed and homoscedascicity was tested by Cochran's procedure.

In one transect grazer densities in July were significantly lower compared to all other months. This effect was very pronounced, but only present for this particular transect. Overall differences between dates seem to be neglectible with the exception of a localized decrease of grazer density in July.
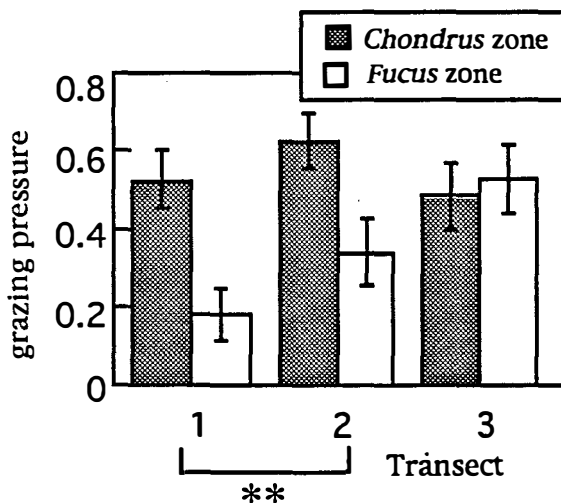

Fig. 3.4. Grazing pressure between zones is different among three sampled transects (two-way MANOVA, Pillai trace=1.027, $F_{8,26}$=3.429**). Transect 1 & 2 show elevated grazing pressure in the *Chondrus* zone (2-way MANOVA, Pillai trace=0.853, $F_{4,8}$ =11.59**), while there is no difference among zones in transect 3.

Averaging over all dates (Fig. 3.3), grazing intensity was increased by 52% in *Chondrus* zone (54.5 ± 4.4% of *Ulva* assay eaten within 24 hr, means ±1SE, n=46) compared with the *Fucus* zone (35.8 ± 5%, n=47). Results were analysed by two-way MANOVA. There was a significant zone*transect interaction (Fig. 3.4). In two transects grazing pressure was significantly higher in the *Chondrus* zone, while there was no difference between zones in a third transect.

The difference in grazing pressure between the *Chondrus* zone and the *Fucus evanescens* zone is not part of a continuous grazing gradient. in Fig.. 3.5 is shown that grazing pressure was increased by 78% in the *Chondrus* zone, compared with three progressively higher zones in the fucoid belt. There are no differences in grazing pressure within the fucoid belt.

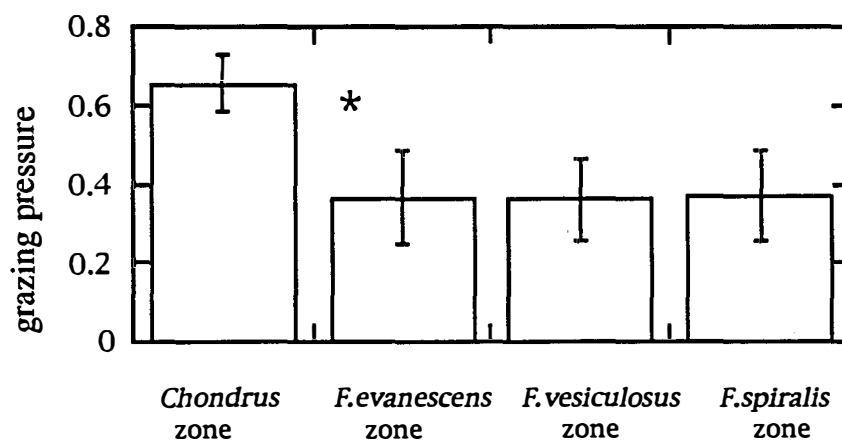

Fig. 3.5. Grazing pressure (±1SE, n=12) measured Oct 10, 1995 at four levels on shore throughout the intertidal zone. Grazing pressure was remarkably similar across the *Fucus* belt, and significantly increased (by 78%) in the *Chondrus* zone (Table 3.3 for analysis).

source of variation	df	MS	F	p	conclusion
Zone	3	0.446	4.195	0.013	*
Transect	2	0.66	6.206	0.005	* *
Zone*Transect	6	0.204	1.922	0.109	n.s.
Error	31	0.106			

Table 3.3. Two-way (4x2) ANOVA: grazing pressure at four levels across the shore gradient. Grazing pressure in the *Chondrus* zone was significantly increased relative to zones higher on shore, which were dominated by *Fucus evanescens, F. vesiculosus* and *F. spiralis*. Data were log-transformed to meet assumptions of homogeneity of variances.

Grazing pressure and grazer density were significantly correlated (Fig. 3.6), but only 45% of variance in grazing pressure was explained by grazer density.

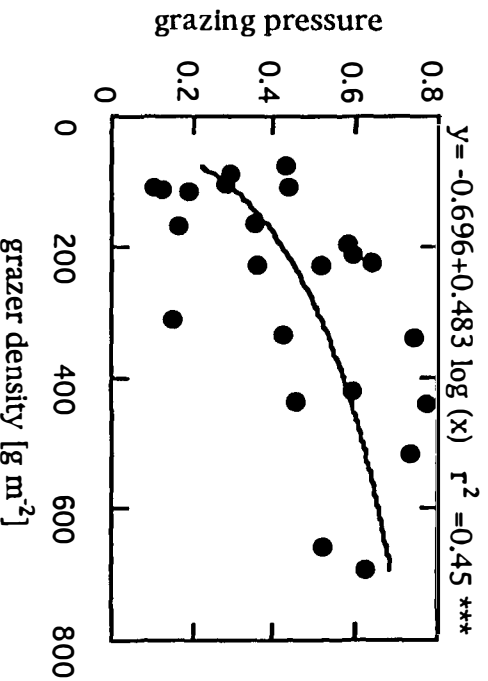$y = -0.696 + 0.483 \log (x)$ $r^2 = 0.45$ ***

Fig. 3.6. Grazing pressure is significantly correlated with log (grazer density). Points represent means of four replicate grazer assays and twelve replicate grazer density counts along 10-m transects. Three transects were sampled at four dates June-October in the Fucus zone and the Chondrus zone. Results for both zones are combined here, since regression lines were not significantly different (p>0.46).

Effects of Chondrus on Fucus recruitment

Chondrus initially facilitated Fucus zygote settlement but inhibited Fucus recruitment to visible stages (Fig. 3.7). Densities of 9-d old microrecruits were highest in the presence of Chondrus crust, relatively low on sand-blasted rock and lowest on unseeded rock (Table 3.5 for analysis). Settlement under Chondrus canopy was also high and increased by experimental seeding in May and October (Fig. 3.7 B, Table 3.4). However, subsequent growth of Fucus to visible stages >1 mm was drastically depressed in the presence of Chondrus crust and canopy. In plots with Chondrus crust present, densities decreased exponentially, and only 0.5% ± 0.4% SE, n=5) of Fucus recruits in May were present as visible stages by the end of September. In the presence of Chondrus canopy, only 0.15% ± 0.15% SE, n=5) of Fucus recruits grew to visible size. However, some zygotes may have remained under the canopy, where they were inhibited by shading. In September, Fucus zygote density in canopy treatment plots was only 3.9% ± 2.4% SE,

n=6) of the density found in May. Clearly, not only growth, but survival of *Fucus* recruits is low in the presence of *Chondrus*. On sandblasted plots recruit densities remained stable and were significantly higher than in other treatments in August and October. Only in the absence of *Chondrus* was a fucoid canopy (3-5 cm high, 4 plants cm⁻²) present after 4 mo (Photo 4).
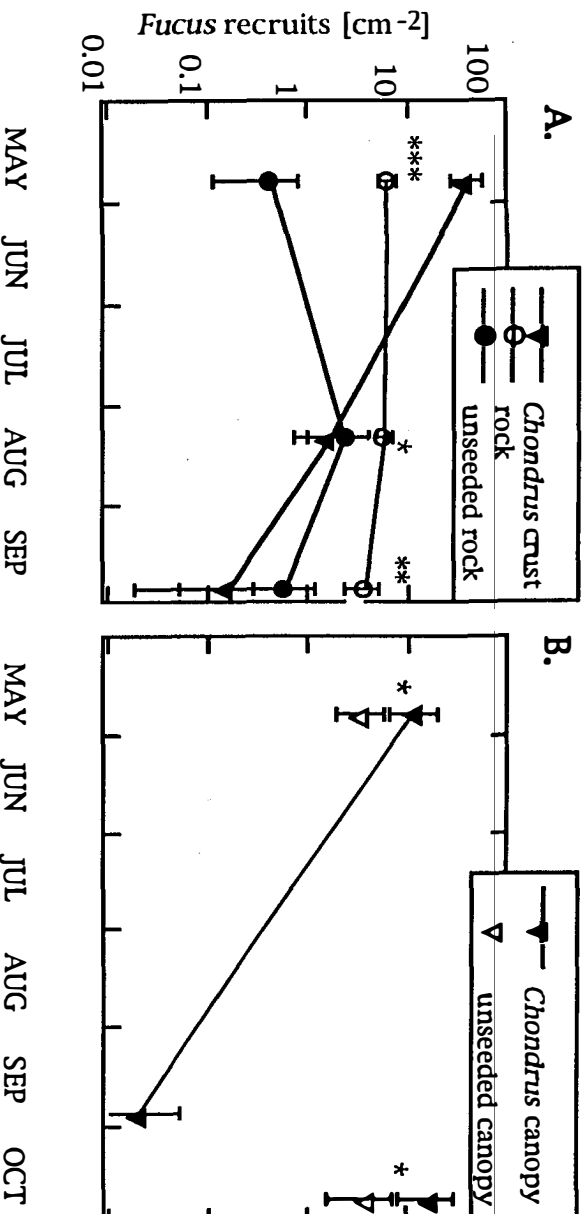

Fig. 3.7. Effects of *Chondrus* presence on recruitment of *Fucus evanescens*. *Fucus* zygotes were released from fertile plants ("seeding") on 15x15-cm plots. Two sub-experiments were conducted: A. *Chondrus* canopy was cut and the crustose holdfasts left or removed (sandblasted rock). Plots with unseeded rock controlled for natural recruitment, B. *Chondrus* canopy was left intact and seeded in May and October. Unseeded plots controlled for natural recruitment below *Chondrus* canopy. Figures for May show mean zygote densities ($\pm$1SE, n=4). In August and September only visible stages >1mm were counted (n=5). For canopy treatments, zygote densities in a second experiment in October (n=6) are included. Significance of differences (Table 3.4, 3.5 for analysis) is indicated by asterisks, with $p<0.05$=*, $p<0.01$=**, $p<0.001$=***.

source of variation	df	MS	F	p	conclusion
Seeding	1	2.458	7.016	0.0154	*
Date	1	0.008	0.022	0.8832	n.s.
Seeding*date	1	0.002	0.007	0.9347	n.s.
Error	20	0.35			

Table 3.4. Effects of seeding with *Fucus* zygotes and date on *Fucus* recruit densities in treatments with *Chondrus* canopy present. Seeding significantly enhanced recruit densities in both experiments, in May and October, but there is no difference between dates. Data were log-transformed and homogeneity of variances was tested by Cochran's procedure.

Table 3.5. One-way ANOVAs: effects of *Chondrus* presence on *Fucus* recruit densities May 25, 1995 (zygote densities, 9 d after releasing zygotes on experimental plots), August 10, 1995 (visible stages >1 mm) and September 26, 1995 (visible stages >1 mm). Means of eight 1-cm² subsamples per plot were analysed in May and August. In September all visible recruits per plot were counted. Data were (log+1)-transformed to meet assumptions of homogeneity of variances.

source of variation	df	MS	F	p	conclusion
May-25					
Chondrus	2	1.797	16.375	0.0007	***
Error	9	0.11			
Aug-10					
Chondrus	2	0.311	7.979	0.0124	*
Block	4	0.161			
Error	8	0.039			
Sep-26					
Chondrus	2	4.069	13.456	0.0028	**
Block	4	1.834			
Error	8	0.302			

Proportional recruit densities on the different substrata present under *Chondrus* canopy were measured on 24 rock segments cut from canopy treatment and control plots in May and October (Fig. 3.8).
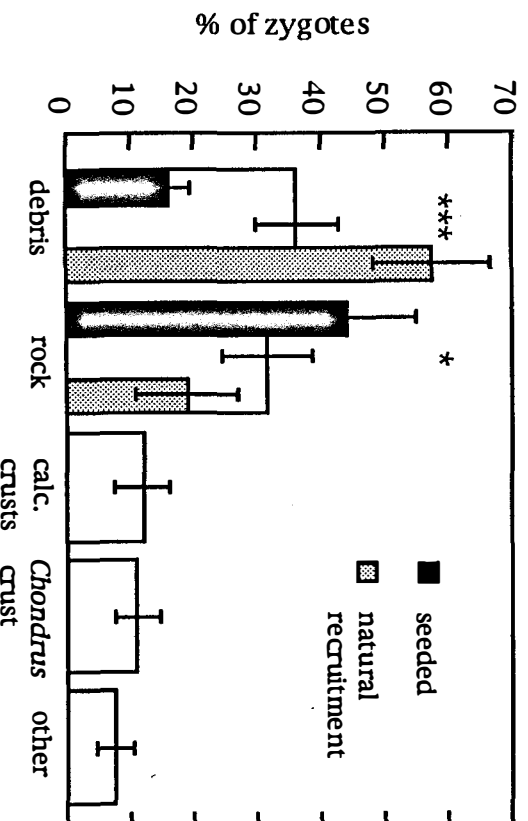

Fig. 3.8. Attachment of *Fucus* zygotes on different substrata present under *Chondrus* turf. Bars represent mean (±1SE, n=24) proportion of zygotes on a substratum relative to total number of zygotes on rock segments cut from the *Chondrus* zone. Debris refers to abundant calcareous debris, trapped under the dense *Chondrus* turf. Calc. crusts = *Phymatolithon* spp. There were significant effects of experimental seeding on relative zygote densities on debris (two-way ANOVA, angular transform. $F_{1,20} = 18.8$ p<0.001=***) and rock ($F_{1,20} = 7.2$, p<0.05=*), but not on the other substrata.

There was direct fucoid recruitment on *Chondrus* crust, but in much lower proportion (11% ± 2.4% SE, n=24) than expected by average percent cover of this substratum (65% ± 3% SE, n=25). Highest recruit densities occurred on unstable calcareous debris. Experimental procedures (cutting canopy perimeter to install cages, regular controls for grazers) may have reduced debris under the canopy: in unseeded controls >50% of zygotes were attached to debris, while in seeded plots only 16% of zygotes were found on debris.

Effects of grazer presence and competition by *Chondrus* on two intermediate size classes of *Fucus evanescens*

I measured growth of 2-mm and 6-cm *Fucus* in the presence/absence of *Chondrus* crust or canopy and in the presence/absence of grazers. Results are shown in Fig. 3.9 and Table 3.6. *Chondrus* canopy and grazer presence both significantly depressed net growth rates of *Fucus*. Generally, there was no significant difference in growth among *Fucus* size classes.

Growth rates in the absence of grazers and *Chondrus* canopy were very constant (27.8+ ± 0.3 mg/g*d, mean ±1SE, n=16). There was no effect of *Chondrus* crust on growth of either *Fucus* size class. *Chondrus* thalli regenerated only slowly from crusts and had obviously no potential to shade *Fucus* transplants.

Growth of both size classes was depressed by one order of magnitude in the presence of *Chondrus* canopy (2.6 ± 6.1 mg/g*d, n=8). Shading is the most likely cause. When grazers were present, individual growth rates were extremely variable, probably reflecting spatial variability in grazing pressure. In most plots, losses due to grazing exceeded gains due to growth. Again there was no significant difference among *Fucus* size classes and between sandblasted controls vs. crust treatments. Mean (±1SE) *Fucus* net growth rate in the presence of grazers, but absence of *Chondrus* canopy was -9.7 ± 9.7 mg/g*d, n=16). However, this is not significantly different from zero growth. Significant weight loss of *Fucus* over the experimental period occured in the combined presence of *Chondrus* canopy and grazers (-49.5 ± 0.3 mg/g d).
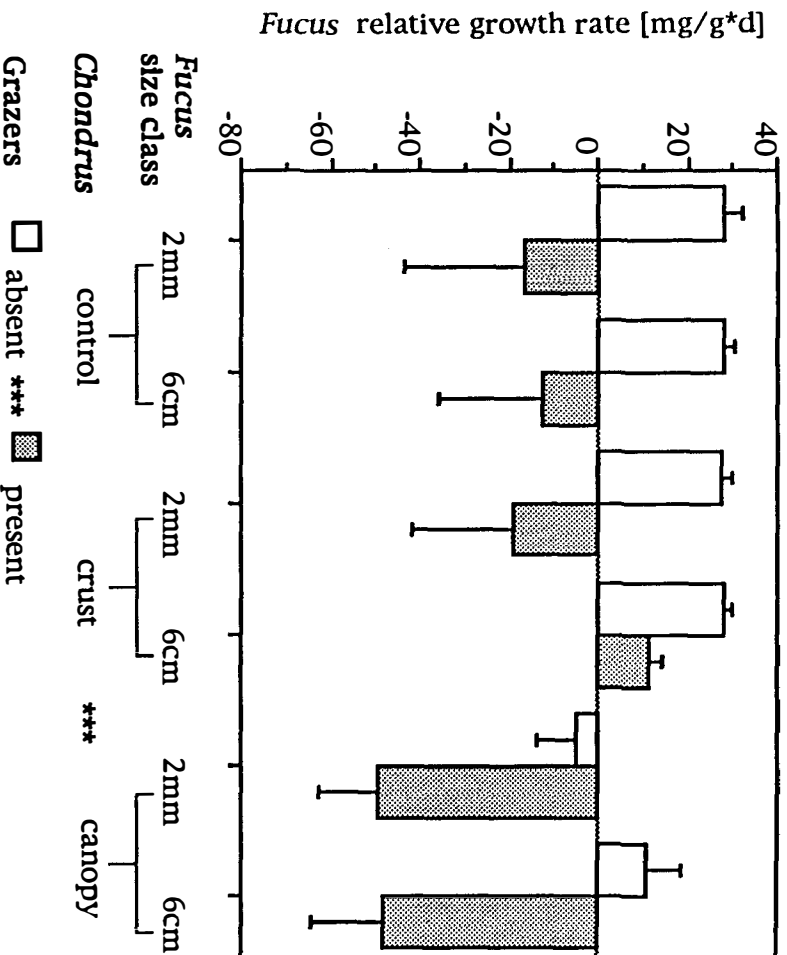
Fig. 3.9. Effects of grazer presence and competition by *Chondrus* on net growth of two intermediate size classes of *Fucus evanescens*. Mean (n=4, ±1SE) net growth rates of *Fucus* transplants are shown for all treatment combinations. Experimental period was 65 d. Significance of differences was tested by three-way ANOVA (Table 3.6). None of the differences between the two *Fucus* size classes was significant. The negative effects of *Chondrus* canopy and grazer presence were highly significant (p<0.001=***), and non-interactive.

source of variation	df	MS	F	p	conclusion
Grazer	1	212512	33.783	0.0001	***
Chondrus	2	5748.74	9.028	0.0006	***
Fucus size class	1	932.7	1.465	0.2333	n.s.
Block	3	1262.09			
Error	40	636.784			

Table. 3.6. Three-way (2x2x3) ANOVA: effects of grazers, *Chondrus* presence and *Fucus* size class on the net growth rate of *Fucus*. None of the possible 2-way or 3-way interactions were significant (p>0.49), thus they were pooled with the error term. Homoscedasticity was tested by Cochran's procedure.

Presence/absence of grazers accounted for 32.5%, presence/absence of *Chondrus* canopy for 15.8% of the total variance in growth of juvenile *Fucus evanescens* (both size classes).

There was no significant interaction between the two main factors. I conclude that they suppressed *Fucus* growth additively and independently. Instantaneous grazing- and competition rates can be calculated from measured growth rates. The specific loss rate due to grazing was 37.4 ± 9.2 mg*g/d (n=16, 16), presence of *Chondrus* canopy depressed *Fucus* growth rates by 25.1 ± 11.3 mg/g*d (n=16, 8).

A control experiment was designed to compare *Fucus* growth in plots with and without open cages to test for cage artifacts. However, these treatments were separated in time. Transplants in uncaged plots were heavily grazed during an initial 8-d acclimatization period, while all cages remained closed for this time. Initial densities of 2 mm plants were standardized to 130 individuals/6 cm^2 in open cages after 8d. This was not possible in uncaged plots, where initial density was conservatively estimated to average 250 individuals per plot, using photographs, taken after 1 d. Due to these different procedures the two treatment combinations could not be statistically compared to reveal cage artifacts. However, the differences in mortality were very clear (Fig. 3.10 A). Both *Fucus* size classes suffered a higher mortality in uncaged plots, compared to those in open cages. This was especially evident for 2-mm *Fucus* plants, with a 99% loss of individuals over the first 9 d. This could be due to grazing and physical forces. However, I directly observed intense grazer activity in uncaged plots during this period and proportional loss correlated well with grazer presence. *Littorina littorea* was most often observed feeding on *Fucus* transplants, followed by gammarid amphipods.

I conclude that cages may have mitigated grazer effects. Thus the magnitude of grazer effects in the main experiment should be seen as a rather conservative estimate, though it already accounted for most of the variance in the data. Finally, differences in mortality between 2-mm and 6-cm *Fucus* might also be influenced by diatom cover which was present on 2-mm plants only and disappeared quickly within a few days after transplantation. This film may have artificially enhanced grazing by

Littorina littorea, for which diatoms are a preferred food source (Norton *et al.* 1990).
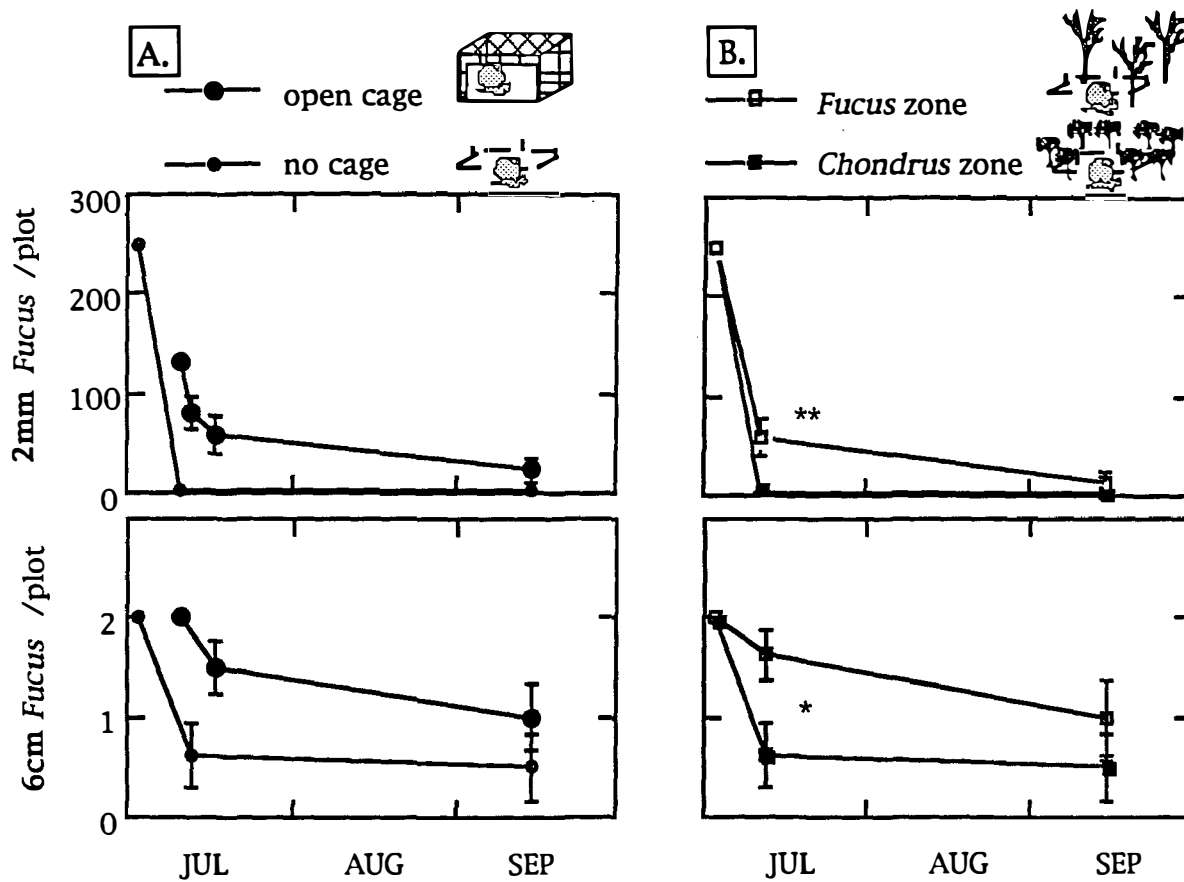

Fig. 3.10. Survival of *Fucus* (two size classes: 2 mm: above, 6 cm: below) in two sub-experiments. Points represent means of n=8 replicates (±1SE). **A.** Control experiment for cage artifacts. Effects of cages on survival of *Fucus*: Comparison of open (incomplete) cages with uncaged controls. Statistical analysis was omitted since treatments were separated in time. **B.** Survival of *Fucus* in the *Fucus*-and *Chondrus* zone. The difference after 9 d was significant (p<0.01=**) for 2-mm *Fucus* and for 6-cm *Fucus* (p,0.05=*). Mortality of 6-cm plants was increased below *Chondrus* turf compared to *Chondrus* crust. See Table 3.7 for analysis.

In a second sub-experiment, the effect of level on shore (*Fucus* zone, *Chondrus* zone) was compared among both *Fucus* size classes in uncaged plots (Fig. 3.10 B). Fucus survival was clearly elevated in the Fucus zone. Two-mm plants were nearly completely destroyed in both zones, while some 6-cm plants survived (and grew), mainly in the *Fucus* zone. Results on survival of *Fucus* after 9 d already show this trend, which is statistically

significant (Table 3.7). Grazing marks on plants and direct observations suggested that plant losses were entirely due to grazing. Thus, these results suggest that grazing pressure on *Fucus* juveniles of both size-classes is significantly lower in the *Fucus* zone, possibly due to a lower predator/prey ratio.

Due to high mortality of *Fucus* in uncaged plots growth rates could not be calculated and cage artifacts on *Fucus* growth could not be tested. Instead, I compared regrowth of *Chondrus* fronds in *Chondrus* crust treatments after 90 d. Fig. 3.11 shows that there is no difference in mean length (±1SE) of *Chondrus* fronds in open and closed cages and in uncaged plots Although this may not be true for *Fucus* plants, it gives some evidence that cage artifacts on growth, if they exist, may not be strong. In strong contrast to Fucus, *Chondrus* growth is not depressed in the presence of grazers. Also I never observed grazing or visible grazing marks on *Chondrus*.

source of variation	df	MS	F	p	conclusion
2 mm *Fucus*					
Zone	1	16.625	11.345	0.0071	* *
Chondrus	1	2.276	1.553	0.2411	n.s.
Block	3	9.116			
Error	10	1.465			
6 cm *Fucus*					
Zone	1	1.207	7.685	0.0197	*
Chondrus	1	0.803	5.111	0.0473	*
Block	3	0.189			
Error	10	0.157			

Tab. 3.7. Two-way (2x2) ANOVAs: effect of level on shore (*Chondrus* zone, *Fucus* zone) and *Chondrus* presence (*Chondrus* canopy or *Chondrus* crust present) on survival of 2 mm *Fucus* and 6 cm *Fucus* after 9 d. The Zone*Chondrus* interactions were not significant (p>0.42). The dependent variable was ln (no. *Fucus* +1). Homogeneity of variances was tested using Cochran's test.
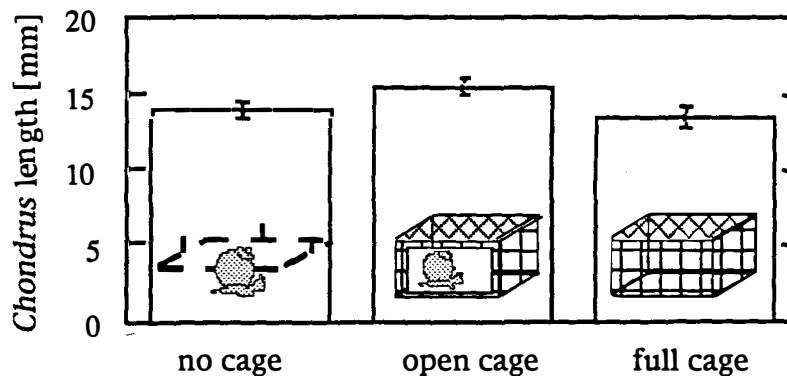
Fig. 3.11. Effect of cages and grazer presence on *Chondrus* regrowth from cru
Figures represent means (±1SE) of n=8 replicates with 4 randomly placed subsamples
per plot. *Chondrus* length was measured September 28, 1995, 90 days after instalment
of cages.

Reciprocal transplants

Fig. 3.12 shows mean net growth rates of adult *Chondrus* (6-cm canopy)
and *Fucus* (30-40-cm individuals) transplants.

All replicates of *Fucus* in the *Chondrus* zone showed severe grazing damage
after 1 wk, some were reduced to the mid rib within 2 wk (Photo 6).
Controls in the *Fucus* zone remained ungrazed. This is surprising, given the
minimal horizontal (<2m) and vertical (<20 cm tidal height) distance
between experimental levels. *Littorina littorea*, followed by gammarid
amphipods, was most often observed feeding on *Fucus*. However, despite
significant grazing damage, in two replicates *Fucus* net growth was higher
in the *Chondrus* zone (11-17 mg/g d) compared to ungrazed controls in the
Fucus zone (4-8 mg/g d). This may indicate that *Fucus* potentially grows
better in the *Chondrus* zone, possibly due to more favorable physical
conditions. All but one very heavily grazed plant grew fertile. *Chondrus*
transplants rapidly lost weight in the *Fucus* zone. Physical factors are the
most likely cause. Observations indicated that plants desiccated quickly
during submergence.

Results from this experiment suggest that *Chondrus* cannot grow in the
Fucus zone and may be limited by physical factors. *Fucus* can grow and re-
produce in the *Chondrus* zone, but suffers from increased grazing pressure.
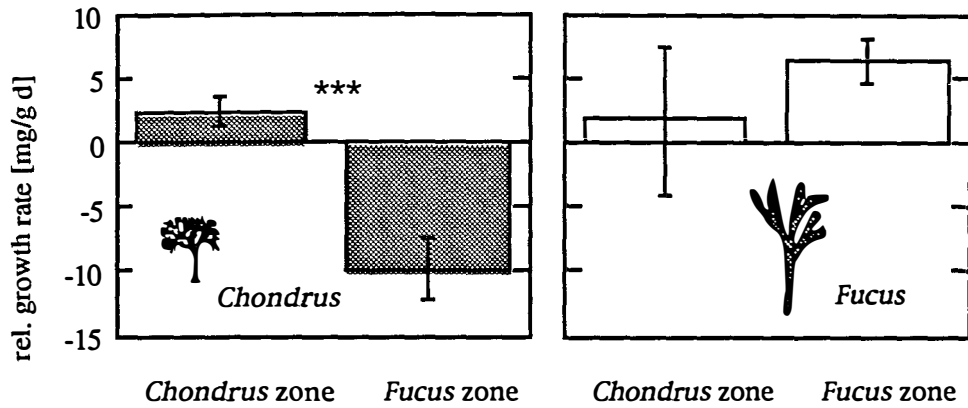
Fig. 3.12. Relative net growth rates (±1SE) of adult *Chondrus* and *Fucus* reciprocal transplants July 17 - Sep 25, 1995. Differences among zones were highly significant for *Chondrus* (n=8) transplants (Table 3.8). Results for *Fucus* were not analysed due to loss of replicates (n=2 in *Fucus* zone). High variation of *Fucus* growth rates in the *Chondrus* zone (n=5) was due to very variable loss of tissue to grazing.

source of variation	df	MS	F	p	conclusion
zone	1	554.66	19.219	0.0007	* * *
error	13	28.86			

Table 3.8. One-way ANOVA: Differences in net growth rates of *Chondrus* transplants in the *Fucus* and *Chondrus* zone Homogeneity of variances was tested using Cochran's test.

4. Discussion

In this study I attempted to answer the question: why is *Fucus evanescens* largely absent from the lower intertidal zone?
The results of my experiments indicate that both competition by *Chondrus* and an elevated grazing pressure by *Littorina littorea* and gammarid amphipods act to exclude *Fucus* from the low shore. Different mechanisms are effective for different life stages of *Fucus*.

Fucus **recruitment**: Of particular importance were competitive effects of *Chondrus* on *Fucus* recruitment. Initially, microrecruit densities were highest on plots with *Chondrus* crust (or canopy) present, probably due to favorable physical conditions, i.e. increased substrate heterogeneity and lower desiccation, compared with sandblasted plots. Brawley & Johnson (1991) showed that mortality of fucoid microrecruits (<1 wk old) is high, and short-term survival is increased under red algal turf compared to rock. Thus in my experiment, initial age-specific mortality may have been highest on exposed rock (*Chondrus* absent). At the first census date (after 9 d), germlings may have passed the most susceptible stage and densities remained stable thereafter.
Settlement of *Cystoseira* spp. under red algal turf is elevated compared to calcareous crusts (Benedetti-Cecchi & Cinelli 1992). However, post-settlement fucoid recruit mortality under the turf reversed the expected pattern of *Cystoseira* abundance. I observed the same process. Under *Chondrus* canopy >95% of zygotes were lost after 4 mo, <<1% grew to visible size. When only *Chondrus* crust was present 4% of zygotes grew to visible size after 2 mo, but only 10% of these survived 4 mo. In contrast, on bare rock with no *Chondrus* >85% of fucoid recruits grew to visible size and 65% of these survived 4 mo. Since grazers >1mm size were excluded, I conclude that *Chondrus* may have directly induced *Fucus* recruit mortality. Although allelopathic effects (Fletcher 1975) cannot be ruled out, epidermal surface "sloughing" has already been reported for many crustose algae, (Johnson & Mann 1986) and also for *Chondrus* (Sieburth & Tootle 1981). Furthermore, high (>50% in untreated controls) mortality of *Fucus* recruits may be ex-

pected due to settlement on calcareous debris that is trapped under the turf. This represents a preferred but highly unstable substratum for *Fucus* zygotes.

In subtidal habitats, algal turfs may also have strong negative effects on canopy species recruitment. Coralline and fleshy red algal turfs effectively suppressed kelp (several spp.) recruitment in southern California (Dayton *et al.* 1984). Also, after removal of abundant red algal turf (mostly *Phyllophora truncata*), a 10-fold enhancement of visible sporophyte density of *Laminaria longicruris* and *Laminaria digitata* occurred (Chapman 1984). In contrast, removal of adult *Laminaria* canopy had no significant effect. Like *Chondrus, P. truncata* is slow growing, but may outcompete very fast growing *Laminaria* plants by recruitment inhibition. This might be a general evolutionary strategy of turf-forming species, in contrast to large canopy-forming species.

Effects of grazing on *Fucus* recruits were not tested in this first experiment. Recruitment inhibition by *Chondrus* (crust or canopy) presence alone may explain why *Fucus* cannot invade the low shore. However, grazers can potentially enhance this inhibition. Parker & Chapman (1994) reported high mortality of *Fucus distichus* germlings through gammarid grazing in high shore pools. Chapman & Johnson (1990) showed that *Littorina littorea* had similar and strong effects on 14-d old recruits of *Fucus spiralis, F. vesiculosus* and *F. distichus*. However, *F. evanescens* germlings were little affected. This test was performed in the *Fucus* zone. Little can be inferred on grazer effects in the *Chondrus* zone, where grazing pressure is higher (discussed below) and substratum topography is very different.

Controls, which were not treated ("seeded") with fertile *Fucus* plants showed variable and significantly lower *Fucus* microrecruit densities than seeded plots. I conclude that I successfully manipulated recruitment with this method, achieving comparable initial conditions among treatments. After seeding, settlement densities were 5x (*Chondrus* canopy: 7*cm^{-2}) to 12x (sandblasted plots: 13*cm^{-2}) higher than in controls. This is still well within the range of natural microrecruit densities for fucoids, found by Schiel (1988; 3*cm^{-2} for *Sargassum sinclairii*), Ang (1991; 10-20*cm^{-2} for

Fucus distichus), Benedetti-Cecchi & Cinelli (1992; $0.5\text{-}2*\text{cm}^{-2}$ for *Cystoseira* spp.).

In conclusion, competitive effects on *Fucus* recruits appear to be strong.. The zonation pattern, seen for adult *Fucus* and *Chondrus*, seem to be at least in part determined by direct inhibition of *Fucus* recruitment by *Chondrus* .

Fucus juveniles and adults; competition and grazing: Despite strong negative effects of *Chondrus* on *Fucus* recruitment, there may still be successful recruitment in gaps where disturbance has created areas of completely bare rock, or where *Chondrus* crust cover is reduced. As much as 20-30% cover of *Chondrus* may be lost during winter storms on exposed sites (Dudgeon & Johnson 1992). *Chondrus* crust may be removed by sporadic ice scouring.

I transplanted *Fucus* juveniles (2 mm and 6 cm) into small scale (ca. 4x8 cm) gaps among *Chondrus* turf or *Chondrus* crust. *Chondrus* was completely absent from sandblasted controls. Presence of *Chondrus* crust had no effect on growth of 2-mm and 6-cm *Fucus* but *Chondrus* turf effectively depressed growth of both size classes. *Chondrus* seems to be competitively dominant to *Fucus* plants within the size range tested. Larger *Fucus* plants might escape competition for light by growing above the *Chondrus* canopy. However, increased grazing pressure (52% higher in the *Chondrus* zone, see below) represents a second biological force to keep *Fucus* in check. Most of the variance in *Fucus* growth (33%) was explained by grazer presence, rather than by *Chondrus* presence (16%). Moreover, procedural controls indicated that grazer effects were probably still underestimated, because they were mitigated by cages. Thus it seems that grazing is the major factor affecting *Fucus* in the smaller size classes when recruitment occurs on the low shore. However, *Fucus* growth in the presence of grazers only was not significantly different from zero growth. Only if *Chondrus* canopy and grazers were present, significant weight losses of *Fucus* occurred. If *Fucus* growth is inhibited by shading of the *Chondrus* canopy, losses due to grazing may not be compensated. A combination of both factors may explain *Fucus* absence from the low shore for this life stage.

These effects are direct and additive. No indirect (higher order) interactions, which would result in a significant *Chondrus* * grazer interaction, were detected.

Lubchenco (1983) reported differential grazing on germlings and juveniles of *Fucus vesiculosus*. She proposed size-related herbivore escapes (based on synthesis of chemical defense compounds in larger plants) as a central concept in explaining intertidal vegetation structure. Denton *et al.* (1990) approached this hypothesis by measuring phlorotannin (grazer-repellent chemicals, Hay & Fennical 1988) concentrations in three *Fucus* species. Increased (75%) concentrations with size were found only for *Fucus vesiculosus. F. evanescens* and *F. spiralis* showed no difference in phlorotannin concentrations between large and small plants. Results of my experiments also gave no evidence of size-related escapes from grazing for *F. evanescens*. Six-cm plants suffered the same losses from grazing as 2-mm plants and even 35-cm adult *Fucus* was heavily affected.

However, there may be an escape from grazing on a population basis. There is anecdotal evidence that where *Fucus* germling density is locally very high, grazers are unable to remove all individuals (Lubchenco 1983). I observed this in one patch (ca. 1.5x4 m) at my experimental site, where *Chondrus* was present but at very low density in spring. *Fucus* invaded this patch, and, although grazing pressure may have been high, a fucoid canopy (72 ± 9% cover, mean ±1SE, n=4) was present by November. I hypothesize that patch size might be an important factor affecting per capita grazer effect on *Fucus* plants. Farrell (1989) and Sousa (1984) reported higher densities of herbivorous limpets with decreasing patch size in an intertidal rocky shore community in California. Both authors suggested that this may be due to the tendency of limpets to aggregate at the patch perimeter rather than the centre for shading and shelter from waves and predatory birds. Smaller patches have a higher perimeter/centre ratio than larger patches and thus support higher total herbivore densities. Limpets were rare in the intertidal zone at my site, and patch size effects on *Littorina* and amphipod behaviour are unknown at this point.

Local predator-prey ratios are also important. Theory strongly suggests that per capita prey (*Fucus*) loss rates are dependent on predator-prey ratio

(Berryman 1992). This ratio is clearly lower in larger *Fucus* patches, assuming there is no strong aggregative behaviour of the predator (*Littorina*, amphipods). In this study I only used small (3x7 cm) patches of *Fucus* transplants. Because *Fucus* is otherwise absent from the *Chondrus* zone, local predator-prey ratios were very unfavorable. This may be an artifact of my experimental concept. Spatial scales of naturally occurring patches of primary substratum range from centimetres to meters (personal observation) to kilometres after extensive ice-scouring (McCook & Chapman 1993). I hypothesize that relative grazer effects will decrease with patch size in this system. A field test of this prediction would be highly desirable.

A potential escape for *Fucus* individuals is local variation in grazing pressure. For every size class tested (2 mm, 6 cm and 35-cm adults) I found very variable growth rates in the presence of grazers. Also, measurements of grazer density and grazer pressure on the *Ulva* assay showed very high spatial variation between and within transects. I conclude that the distribution of grazers and their effects are very patchy and single plants may escape in areas where grazing pressure is low. Similar conclusions were drawn by Lubchenco (1983) for *Fucus* and Lubchenco & Menge (1978) for *Mytilus* on the coast of Maine.

The questions remains, why is *Fucus* so abundant on the mid-shore? First, competition by *Chondrus* may be weak or absent, since *Chondrus* canopy seems to be limited by physical factors on the mid shore. Reciprocal transplants of *Chondrus* showed negative growth rates on the mid-shore, while controls in the *Chondrus* zone increased slightly in weight. From observations on *Chondrus* transplants, I conclude that desiccation and/or high temperatures may limit *Chondrus* growth on the mid-shore. Lubchenco (1980) cleared large areas of fucoid canopy and recorded nearly 100% mortality of *Chondrus* understorey. She concluded that *Fucus* canopy may protect *Chondrus* against desiccation at its upper distributional limit. There are strong negative effects of temperatures exceeding 20°C on *Chondrus* photosynthesis (Kübler & Davison 1993). Also, freezing tolerance of *Chondrus* may be correlated with its tidal distribution (Dudgeon *et al.* 1989). Thus the

upper limit of *Chondrus* may be set by low tolerance to desiccation and high temperatures and/or freezing.

Secondly, *Fucus* seems to be less affected by grazing on the mid shore than on the low shore. Especially for adult plants, the differences were striking. This is interesting, given the minimal difference (10-15 cm) in tidal height between the two zones. This may also be a function of local predator-prey ratios. *Chondrus* has been shown to be very grazer resistant (Lubchenco 1978, Cheney 1981, Parker & Chapman 1994, this study). *Fucus* is a potential food source for *Littorina* and gammarid amphipods (Chapman & Johnson 1990, Norton *et al.* 1990, Parker & Chapman 1994, this study). Food availability is much greater in the *Fucus* zone, resulting in a lower local predator-prey ratio. Thus per capita loss rates of *Fucus* transplants were lower under the fucoid canopy. This difference may have been enhanced by higher grazer densities in the *Chondrus* zone. Grazer density (measured as total grazer wet weight) was 44% higher in the *Chondrus* zone. This was mainly due to increased abundance of *Littorina littorea*, which was by far the dominant species (see also Lubchenco & Menge 1978, Lubchenco 1980). But also, densities of other mesograzers (amphipods, isopods) were higher on the low shore. Only *Littorina obtusata* was more abundant on the mid shore.

Grazing pressure was independently estimated with a grazer assay. *Littorina littorea* is the main herbivore in this system. *Ulva* is a strongly preferred food source for *Littorina littorea* (Lubchenco 1978, Norton *et al.* 1990). Thus grazing rates on *Ulva* tissue may give an estimate of grazing pressure independently of the abundance of alternative prey. Grazing pressure on average was 52% higher in the *Chondrus* zone than in the *Fucus* zone. There is limited evidence that this difference is distinct between the fucoid belt as an entity, and the *Chondrus* zone. In October, grazing pressure was identical throughout the *Fucus* belt, but significantly increased (by 78%) in the *Chondrus* zone. Grazing pressure seemed to change abruptly with habitat characteristics, rather than gradually with tidal height.

Although grazing pressure and grazer density were significantly correlated, >50% of variation in grazing pressure remained unexplained. I believe that a direct measurement of grazing pressure gives ecologically more relevant

information than grazer density counts alone. Moreover, in my experience, it is less time-consuming and may allow comparisons of actual grazing intensity and -variability among habitats with different grazer species. *Ulva* is a preferred food source for many herbivores (Littler & Littler 1980, Norton *et al.* 1990) and is common in many temperate and tropical habitats (Lüning 1990), thus readily available for comparative studies.

While the biological factors, setting the lower limit of *Fucus* may be well understood, little is known about factors explaining the very variable lower limit of *Chondrus*. Sea urchins, when abundant, may limit *Chondrus* growth in the subtidal at some sites (Lubchenco 1980). At my experimental site, *Corallina* seems to replace *Chondrus* towards the subtidal. This is interesting, because *Corallina* is very similar to *Chondrus* in morphology. It forms a dense turf, grows from an encrusting holdfast and is very persistent (Littler & Littler 1980). Competitive interactions may be strong and symmetrical. However this remains to be tested

Another open question is the striking difference in *Chondrus* distribution in the Western and Eastern Atlantic. While *Chondrus* dominance in the lower intertidal zone is a very consistent pattern along exposed and semi-exposed shores in the NW Atlantic (Lubchenco & Menge 1978, Lubchenco 1980, Lüning 1990), *Chondrus* is present, but rarely forms a belt in rocky intertidal habitats in the NE Atlantic. Here, *Fucus serratus* dominates the low shore. (Lüning 1990, personal observation). Extensive *Chondrus* beds are completely absent.

F. serratus was introduced to North America in the 19th century (Robinson 1903). Today it is abundant in northern Nova Scotia along the Gulf of St. Lawrence and Northumberland Strait. Two isolated populations exist near Yarmouth (Dale 1982) and Lunenburg (personal observation) both in southern Nova Scotia. Lubchenco (1980) hypothesized that predictable ice scouring in northern Nova Scotia and intense limpet grazing in northern Europe may remove *Chondrus* crusts, so *Fucus serratus* can colonize the low shore. However, *Fucus serratus* may be even more affected by ice-scouring and limpet grazing or "bulldozing". The isolated populations in southern Nova

Scotia are not explained by either of these hypotheses since limpets are rare and ice scour is sporadic. Clearly, this question needs further investigation.

Synthesis and relevance to ecological theory

The general results of Lubchenco (1980) were verified by this study: biotic interactions rather than physical factors structure this low shore community. Competition by *Chondrus* and grazing by *Littorina littorea* and gammarid amphipods exclude *Fucus* from the low shore. Grazing pressure was shown to be elevated in the *Chondrus* zone. If released from competition and grazing *Fucus* grows fast and reproduces normally. The mechanism of competitive exclusion was investigated. *Chondrus* may outcompete faster growing *Fucus* by recruitment inhibition and shading of smaller size classes. Given successful recruitment (most likely in gaps, created by disturbance), and growth to visible size, grazing was found to be the most important factor inhibiting *Fucus* growth. In the presence of *Chondrus* and grazers, *Fucus* juveniles are eliminated. If single *Fucus* plants pass through these two bottlenecks and grow to adult size, growth seemed to be mainly a function of local variations in grazing pressure, and, on average plants were still heavily affected.

A central paradigm in explaining patterns of species diversity is that an organism cannot be simultaneously well adapted to all environmental factors, including strong biological interactions such as competition and predation. The concept of **strategic resource allocation** is an integrative element in most current theories dealing with diversity, competition and coexistence (e.g. C-S-R theory: Grime 1974, 1979, Functional-form model: Littler & Littler 1980, Resource-ratio model: Tilman 1982, Competitive hierarchy model: Keddy 1989). It suggests that the allocation of limited resources (e.g. light, nutrients, food) to different physiological functions (e.g. growth, reproduction, dispersal, defense mechanisms) involves energetic and material costs and requires evolutionary trade-offs between these functions. Different combinations of traits result in evolutionary life-history strategies, which may be grouped into different categories (e.g. r- and

K-strategies, MacArthur & Wilson 1967, C-S-R-strategies, Grime 1974, 1979). Species abundance is thought to follow a predictable sequence both on temporal (in succession) and spatial scales (in zoned or patchy habitats). Each species dominates a part of the environmental gradient (either a spatial or temporal gradient), where it is relatively better adapted to resource levels and patterns of stress and disturbance, i.e. where it maintains a higher growth rate and/or suffers lower mortality than other species. Moreover, it might affect other species performance not only through resource monopolization (resource competition), but by direct negative interaction (interference competition).

Grace (1990) pointed out that the discrepancies between theories often lie in how they relate species traits to competitive ability. Specific "critical" trade-offs are central assumptions in many general models.

In Table 4.1 I compare the relative performance of *Fucus* and *Chondrus* for different traits. Some important characteristics (e.g. dispersal) are not considered here. Competitive ability (*sensu* Goldberg 1990) is a function of the ability to suppress neighbors either by resource depletion or interference (net competitive effect), but it is also dependent on the ability to maintain growth at low resource levels (net competitive response). Here, competitive ability is judged to be higher in *Chondrus* as it heavily suppresses *Fucus* on the low shore, i.e. the habitat, where both species can grow. However I tested only for competitive effects of *Chondrus* on *Fucus*, not vice versa. There is, nevertheless, evidence that *Chondrus* understorey is even facilitated by *Fucus evanescens* canopy on the mid shore through protection from desiccation and heat stress (Lubchenco 1980).

In the following I examine published assumptions about critical trade-offs and relationships between species traits and competitive ability, using the available information on *Fucus* and *Chondrus*. Working within the larger paradigm of strategic resource allocation, I assume that there are costs for increasing performance of each of these traits and that critical trade-offs exist. However, McCook (1994) points out that there is no test of the general paradigm, i.e. testing the null-hypothesis of no critical trade-off.

Trait	performance *Chondrus*	performance *Fucus*	Reference
max. growth rate	(-)	(+)	Strömgren (1985, 1986), Strömgren & Nielsen (1986)
canopy height	(-)	(+)	observation: Chondrus 5-7 cm, Fucus 30-40 cm
tolerance to environmental stress	(-)	(+)	Lubchenco (1980), this study, Davison *et al.*(1989), Dudgeon *et al.* (1989), Kübler & Davison (1993)
grazer defense	(+)	(-)	Lubchenco (1978), Cheney 1981, Norton *et al* (1990), this study
primary space monopolization	(+)	(-)	observation: Chondrus crust: 65% cover, Fucus holdfasts <5% cover
inhibitory mechanisms	(+)	(?)	Lubchenco (1980), this study, Sieburth & Tootle (1981)
competitive ability	(+)	(-)	Lubchenco (1980), this study

Table 4.1. Relative performance of *Fucus* and *Chondrus* in respect to some important plant life-history traits: (+) refers to higher performance regarding this trait, (-) to lower performance, (?) means that there is no information available.

There is a general contention that high growth rates may relate to competitive ability. Moreover high growth rates are thought to be involved in strong general trade-offs that include stress tolerance and predator defense. Grime (1974, 1979) proposed a general model of plant life strategies, classifying plants into three categories: competitors, stress tolerators and ruderals (C-S-R-model). Competitors monopolize space in "favorable" habitats with low disturbance and low environmental stress. Stress tolerators are restricted to extreme habitats, where the more vulnerable competitors cannot exist. Ruderals are short-lived gap colonizers with high reproductive output, adapted to high levels of disturbance but low stress. In succession they are replaced by the competitor guild. According to Grime (1979) key characteristics that are positively correlated with competitive ability are the maximum relative growth rate and canopy height. Competitive ability in Grime's (1979) sense is the ability to outgrow neighbors by maximizing resource capture. Grime does not consider the ability to grow at low resource levels, or the role of interference competition for competitive ability. In contrast, Tilman's (1982) resource-ratio model relates competitive ability

directly to minimal resource requirements. I did not measure competitive ability in Grime's sense, i.e. *Fucus* ' ability for resource capture, but rather *Fucus'* ability to withstand competition from *Chondrus*. This may explain a part of the contradiction between Grime's model and my results:

In my study the C-S-R-model may not apply: *Chondrus* can be considered a competitor, since it dominates the least stressful end of the intertidal shore gradient and it excludes the more stress-tolerant species from the mid and upper shore. However, *Chondrus* does not show the central traits of a high maximum growth rate and a high canopy: growth rates of several fucoids and *Chondrus* were compared by Strömgren (1985, 1986) and Strömgren & Nielsen (1986). Apical length growth was shown to be closely related to increase in dry weight. The maximum light saturated growth rate of *Chondrus* was 4.4 $\mu m*hr^{-1}$, while *F. evanescens* showed maximum growth rates of 12-15 $\mu m*hr^{-1}$. Accordingly, *Fucus* might be classified as both a competitor, because of high growth rates and a high canopy, or a stress tolerator, because it is less susceptible to environmental stress (desiccation and freezing) than *Chondrus* (Davison *et al.* 1989, Dudgeon et al. 1989, Kübler & Davison 1993). The critical trade-off proposed by Grime is growth rate vs. tolerance to environmental stress. This cannot be verified here as *Fucus* maximizes both traits relative to *Chondrus*. The second assumption is that fast growth and a high canopy relate to competitive ability. However, *Chondrus* is much slower growing and smaller than *Fucus*, yet it is competitively dominant. Competitive dominance in *Chondrus* may not rely on outgrowing *Fucus* but rather on suppression of early life-stages. Slow-growing turf-forming and crustose (Johnson & Mann 1986) algae may rely on competitive strategies that are not included in Grime's (1979) general model.

A strong trade-off between competitive ability and herbivore resistance has been proposed by various authors (e.g. Littler & Littler's **functional form model**, 1980, Lubchenco & Gaines 1981). It is argued that resources invested into defense structures or -chemicals cannot be invested into growth, which may be related to competitive ability. Clearly, the *Fucus/Chondrus/Littorina* assemblage is an exception. My results indicate that *Chondrus* outcompetes *Fucus evanescens*, which verifies results by Lubchenco (1980). In addition it is very effectively protected against her-

bivory (Lubchenco 1978, Cheney 1981, Norton *et al.* 1990, Parker & Chapman 1994). *Fucus* is heavily grazed at all life stages, while grazing damage was never observed in *Chondrus* and grazer exclusion had no effect on regrowth of *Chondrus* canopy from crusts. Effective herbivore defense in *Chondrus* may be compensated by low growth rates, but this does not relate to competitive ability.

The contention of competitive ability relating to growth rates and a critical trade-off: growth rate vs. predator defense is also a cornerstone of the **keystone predator concept**. Paine (1966, 1971, 1984) proposed that a top competitor grows fast and can potentially monopolize space. A keystone predator feeds preferentially on the top competitor which is poorly defended because resources are mainly allocated to growth. Diversity is increased where predators can effectively control the top competitor. In my study the reverse mechanism applies. Herbivores help to maintain a *Chondrus* "monoculture" (*sensu* Paine 1984), by differential grazing on *Fucus*. This is because *Chondrus* has both better competitive ability and herbivore defense, relative to *Fucus* (no trade-off).

However, there is evidence that mussels (*Mytilus edulis*) can potentially outcompete *Chondrus* on the low shore in Maine (Lubchenco & Menge 1978). Predatory starfish and whelks effectively controlled mussel abundance on all but very exposed sites, preventing space monopolization by mussels. This would confirm the keystone predator concept.

I did not test for interactions between mussels and *Chondrus*. Observations at my site indicated that mussels can settle densely among *Chondrus* and whelks aggregate on mussel patches. However, mussels nowhere covered >10% of primary space at my site (personal observation). Lubchenco & Menge (1978) reported 10-70% cover of mussels on two semi-exposed experimental sites in Maine and 40-100% cover at Permaquid point (very exposed). On a variety of sites (including several very exposed) in Nova Scotia, I never observed similar spatial dominance of mussels on the low shore.

A general trade-off between stress tolerance and competitive ability is part of the competitive hierarchy concept (Keddy 1989). As early as 1910 Baker argued that intertidal zonation of *Fucus* spp. in England may be caused by competition (setting the lower limit) and physical factors (setting

the upper limit). Connell (1972) demonstrated that the lower limits of rocky intertidal animals are usually set by competition or predation, rather than by physical factors, as previously assumed. This general pattern has been demonstrated experimentally for many plant and animal species in a multitude of rocky intertidal habitats (e.g. Connell 1961, Paine 1966, 1971, Underwood 1981, Lubchenco 1986, Chapman & Johnson 1990, Farrell 1991). Exceptions seem to deal with special cases. For example, Dring (1987) suggested that the lower limit of intertidal *Fucus serratus* in the Bristol Channel is due to light deficiency during immersion in the very turbid waters in this estuary. However, this was not confirmed experimentally.

Keddy (1989) proposed a general inverse relationship (trade-off) between competitive ability and adaptation to low resource levels or environmental stress, causing a competitive hierarchy along environmental gradients. Fundamental niche size is hypothesized to be greatest in the species inhabiting the harsh end of the gradient (most stress tolerant). The lower limit of the realized niche is set by competition with the species ranking next higher in competitive hierarchy. The species inhabiting the favorable end of the gradient is predicted to be most vulnerable to stress and to rank highest in the competitive hierarchy.

There is some evidence that Keddy's model of competitive hierarchies applies in this two-species assemblage: *Chondrus* inhabits the favorable end of the shore gradient. It is the competitive dominant and its upper limit seems to be set by physical factors (low stress tolerance). *Fucus* can grow and reproduce on the low shore (fundamental niche) but is excluded at least in part by asymmetric competition (realized niche). Moreover the upper limit of *Fucus evanescens* is set by physical factors, which is also in line with the general model (Chapman & Johnson 1990).
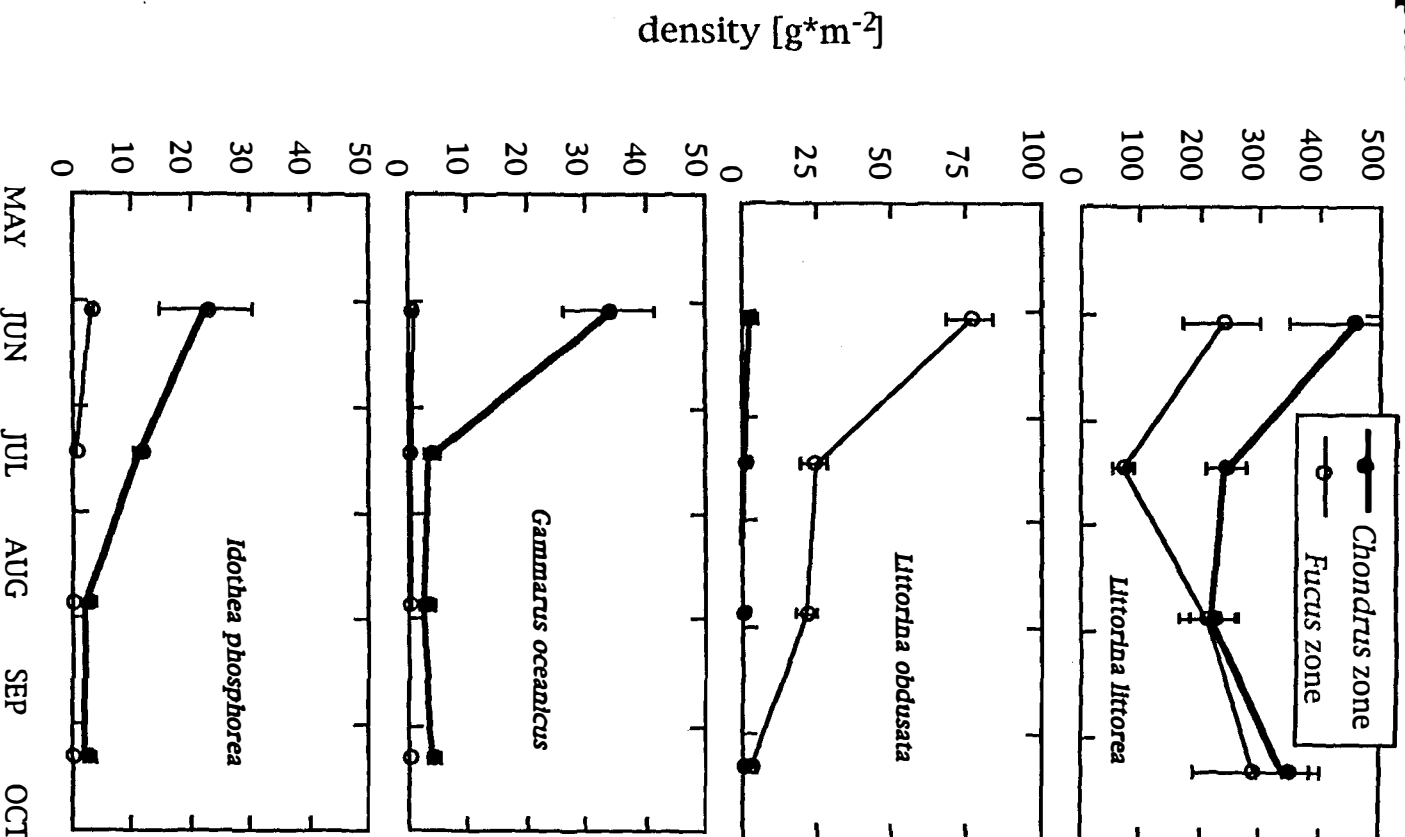
5. Appendix

Fig. 5.1. Density of the main grazer species at four sampling dates June-October. Limpets and small amphipods were sampled, but are not shown here as their densities never exceeded 5 g*m⁻². Note the different scales on the y-axis and the great dominance of *Littorina littorea* compared to other grazers. Figures represent means (±1SE), based on n=36 replicate counts.
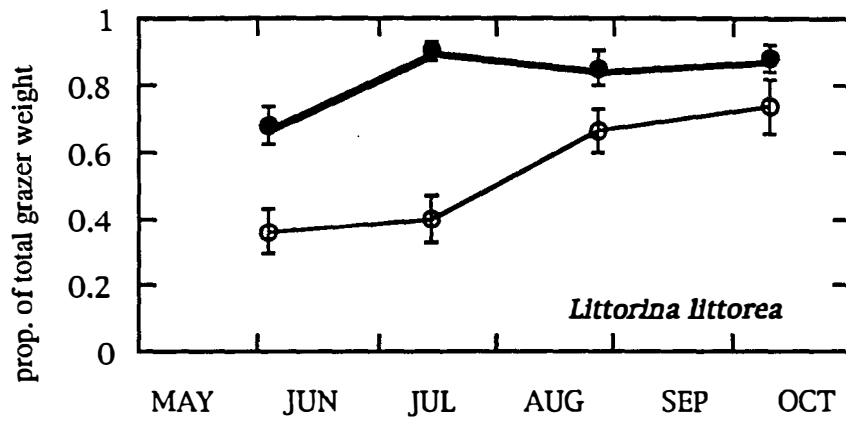
Fig. 5.2. Grazer density: *Littorina littorea* represented a dominant and increasing proportion of total grazer weight from May to October. This is more pronounced in the *Chondrus* zone. Figures represent means (±1SE), based on n=36 replicate counts.

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7.   Acknowledgements

Erklärung

Hiermit erkläre ich, daß ich die vorliegende Arbeit selbständig angefertigt und keine anderen als die angegebenen Hilfsmittel benutzt habe.

Mit der Einstellung dieser Arbeit in die Fachbibliothek Biologiezentrum, der Bibliothek des Instituts für Meereskunde sowie der Universitätsbibliothek der CAU bin ich einverstanden.

Kiel, den 16. März 1996