

FACTORS INFLUENCING THE DISTRIBUTION  
OF THE INTERTIDAL CHLOROPHYTE,  
*CODIUM FRAGILE* (SURINGAR) HARIOT  
IN BARKLEY SOUND, BRITISH COLUMBIA

by

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## ABSTRACT

The purpose of this research was to quantify the occurrence of the chlorophyte, *Codium fragile* (Suringar) Hariot in Barkley Sound, British Columbia habitats and explore several factors that may be correlated to its patchy distribution. *Codium fragile* is a unique species for study as it is a coenocytic seaweed found in physically-stressful habitats; specifically, rocky intertidal areas. Many previous studies have focused on the invasive nature of a closely-related subspecies (*Codium fragile* ssp. *tomentosoides*), however, few studies have examined the biology and ecology of native *C. fragile* on NE Pacific shores.

I monitored *Codium fragile* at four different field sites from 1998-2001 and found that plants were unevenly distributed over time (e.g. seasonal and annual population fluctuations) and space (e.g. differed in abundance from one location to another). I hypothesized that herbivory, sand burial, wave exposure (or a combination of these factors) could account for the patchy distribution patterns at Prasiola Point, Second Beach, Seppings Island and Scott's Bay.

I conducted feeding preference, absorption efficiency, and macroalgal diet vs. fitness experiments using generalist herbivores (e.g. purple urchins and black chitons) and three common intertidal seaweeds (e.g. *Codium fragile*, *Hedophyllum sessile*, *Mazzaella splendens*). My results show that compared to the two other seaweeds, *C. fragile* is not preferred by purple urchins or black chitons, it has the lowest (short-term) nutritional value, and did not significantly increase somatic or reproductive growth for either herbivore species.

Field observations indicated it was possible that infrequent sand burial events restricted the occurrence of *Codium fragile* at Scott's Bay. Experimental

results show that adult *C. fragile* plants buried in sand (for five weeks) grew less compared to control plants (no sand). This information provided insight to the fate of *C. fragile* adults at Scott's Bay, but did not explain the irregular distribution of plants at Prasiola Point or Second Beach (where no sand burial occurred).

This is the first study exploring biomechanical properties of a coenocytic algal species from temperate shores. I estimated maximum wave forces for each of my four study sites in order to classify them as wave-protected or wave-exposed. I measured the force to remove or break *Codium fragile* plants from their attachment on rocky substratum, comparing size classes as well as origin of representative *C. fragile* plants. These experiments showed that *C. fragile* possesses removal forces comparable to those recorded for other (multi-cellular) algal species. There were no differences in removal forces related to size; however, there were significant differences depending on where *C. fragile* plants originated. Measured drag coefficients show that *C. fragile* conforms to increased water velocities (similar to other algal species). Calculations using known data were used to project what water velocities were required to break or dislodge individuals based on size or habitat. Large *C. fragile* plants are more susceptible to increased velocities than smaller plants; plants growing at Scott's Bay are more likely to break or detach compared to plants from other locations.

My research suggests that wave forces limit both size and survival of *Codium fragile* at wave-exposed habitats (e.g. Prasiola Point), yet many individuals remain healthy and persist over time. A combination of factors (e.g.

herbivory and wave forces) might be causative for the irregular occurrence at Prasiola Point.

This thesis advances our minimal knowledge of native *Codium fragile* plants in NE Pacific habitats, compared to the wealth of information on the invasive subspecies, *C. fragile* ssp. *tomentosoides*. My research is original as it measures the effects of both biotic and abiotic factors on a coenocytic macroalgal species found in rocky, intertidal habitats. Of the three factors I chose to study, herbivory is widespread throughout published ecological literature whereas effects of sand burial are few. Furthermore, my wave action results contribute to an emerging field of study in marine science—increasing our understanding of how seaweeds persist in wave-swept environments.

## TABLE OF CONTENTS

Abstract	ii
Table of Contents	v
List of Tables	vii
List of Figures	viii
Acknowledgement	x
Chapter One - Introduction	
1.1 Introduction to the chlorophyte, <i>Codium fragile</i> .....	1
1.2 Distribution of <i>Codium fragile</i> in Barkley Sound.....	7
1.3 Justification for research questions.....	28
Chapter Two – Herbivory	
2.1 Introduction to how herbivory influences seaweeds in rocky, intertidal habitats.....	32
2.2 Comparison of “specialist” vs. “generalist” herbivores.....	37
2.3 Introduction	
2.3.1 Spatial pattern analysis of black chitons.....	40
2.3.2 Feeding preference experiment.....	41
2.3.3 Feeding absorption efficiency experiment.....	46
2.3.4 Fitness vs. macroalgal diet experiment.....	48
2.4 Materials and Methods	
2.4.1 Spatial pattern analysis of black chitons.....	50
2.4.2 Feeding preference experiment.....	51
2.4.3 Absorption efficiency experiment.....	52
2.4.4 Fitness vs. macroalgal diet experiment.....	54
2.5 Results	
2.5.1 Spatial pattern analysis of black chitons.....	58
2.5.2 Feeding preference experiment.....	59
2.5.3 Absorption efficiency experiment.....	60
2.5.4 Fitness vs. macroalgal diet experiment.....	61
2.6 Discussion	
2.6.1 Spatial pattern analysis of black chitons.....	67
2.6.2 Feeding preference experiment.....	68
2.6.3 Absorption efficiency experiment.....	72
2.6.4 Fitness vs. macroalgal diet experiment.....	76
2.7 Conclusion.....	77
Chapter Three – Sand Burial	
3.1 Sand burial as a physical disturbance.....	79

3.2 Seaweed adaptations to, and consequences of, sand burial.....	81
3.3 Other studies examining the effects of sand burial.....	82
3.4 Introduction	
3.4.1 Comparison of algal assemblages.....	84
3.4.2 Sand burial experiment.....	85
3.5 Materials and Methods	
3.5.1 Comparison of algal assemblages.....	86
3.5.2 Sand burial experiment.....	87
3.6 Results	
3.6.1 Comparison of algal assemblages.....	88
3.6.2 Sand burial experiment.....	92
3.7 Discussion	
3.7.1 Comparison of algal assemblages.....	94
3.7.2 Sand burial experiment.....	96
3.8 Conclusion.....	100
 Chapter Four - Wave Action	
4.1 Introduction to seaweed adaptations and survival in wave-swept environments.....	102
4.2 Materials and Methods	
4.2.1 Comparison of maximum wave forces.....	106
4.2.2 Biomechanic study.....	109
4.2.3 Drag coefficient study.....	112
4.2.4 Transplant experiment.....	114
4.3 Results	
4.3.1 Comparison of maximum wave forces.....	114
4.3.2 Biomechanic study.....	120
4.3.3 Drag coefficient study.....	122
4.3.4 Transplant experiment.....	126
4.4 Discussion	
4.4.1 Comparison of maximum wave forces.....	133
4.4.2 Biomechanic study.....	135
4.4.3 Drag coefficient study.....	137
4.4.4 Transplant experiment.....	139
4.5 Conclusion.....	143
 Chapter Five - Conclusion	
5.1 General conclusion.....	144
5.2 Recommendations for future research.....	148
 Bibliography.....	151

## List of Tables

Table 1.1 – Comparison of field sites on/near Vancouver Island, British Columbia.....	10
Table 2.1 – Spatial pattern analysis of the black chiton, <i>Katharina tunicata</i> , at Prasiola Point, Barkley Sound.....	58
Table 2.2 - Feeding preference results from purple urchins ( <i>Strongylocentrotus purpuratus</i> ) and black chitons ( <i>Katharina tunicata</i> ) fed two-choice macroalgal diets .....	59
Table 2.3 – Absorption efficiency values derived from purple urchins, <i>Strongylocentrotus purpuratus</i> , and black chitons, <i>Katharina tunicata</i> , offered one of three macroalgal diets.....	60
Table 3.1 – List of species present at Scott's Bay and Seppings Island, Barkley Sound, British Columbia .....	90
Table 3.2 – Algal species sampled from Scott's Bay and Seppings Island, Barkley Sound, British Columbia.....	91
Table 3.3 – Comparisons of initial measurements of <i>Codium fragile</i> plants before sand burial experiment.....	93
Table 3.4 – Sand burial experiment results.....	94
Table 4.1 - Occurrence of damaged thallus tissue (= broken branch tips), and/or loosened holdfasts from <i>Codium fragile</i> sampled in the field. ....	115
Table 4.2 – Representative plant and animal species found at field sites in Barkley Sound, British Columbia.....	117
Table 4.3 – Comparison of mean maximum wave forces between different elevation heights at Prasiola Point.....	120
Table 4.4 – Comparison of mean breaking forces of <i>Codium fragile</i> plants per size class at Seppings Island.....	121
Table 4.5 – Comparison of mean breaking forces for <i>Codium fragile</i> plants (of the small size class) at different field sites.....	122
Table 4.6 – Predicted wave velocities required to break <i>Codium fragile</i> plants of different size classes in Barkley Sound. ....	125
Table 4.7 – Predicted wave velocities required to break <i>Codium fragile</i> plants located at different field sites in Barkley Sound.....	126

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List of Figures:

Figure 1.1 – *Codium fragile* (Suringar) Hariot. ....2

Figure 1.2 – Life cycle of native *Codium fragile*.....6

Figure 1.3 – Map of study sites. ....9

Figure 1.4 – Bedrock platform study site at Prasiola Point, Vancouver Island, British Columbia. .... 11

Figure 1.5 – Mean number of *Codium fragile* plants per 1m<sup>2</sup> quadrat at Prasiola Point - High Intertidal. ....12

Figure 1.6 – Mean number of *Codium fragile* plants per 1m<sup>2</sup> quadrat at Prasiola Point - Middle Intertidal.....13

Figure 1.7 – Mean number of *Codium fragile* plants per 1m<sup>2</sup> quadrat at Prasiola Point - Low Intertidal.....14

Figure 1.8 – Distribution of *Codium fragile* size classes at Prasiola Point (High Intertidal) .....16

Figure 1.9 – Distribution of *Codium fragile* size classes at Prasiola Point (Middle Intertidal).....17

Figure 1.10 – Distribution of *Codium fragile* size classes at Prasiola Point (Low Intertidal) .....18

Figure 1.11 – Rock mound study site at Second Beach, Vancouver Island, British Columbia.....19

Figure 1.12 – Mean number of *Codium fragile* plants per quadrat at Second Beach. ....20

Figure 1.13 – Distribution of *Codium fragile* size classes at Second Beach.....21

Figure 1.14 – Rock mound study site at Scott's Bay, Vancouver Island, British Columbia.....23

Figure 1.15 – Total number of *Codium fragile* plants recorded at Scott's Bay.....24

Figure 1.16 – Distribution of *Codium fragile* size classes at Scott's Bay .....25

Figure 1.17 – Study site at Seppings Island, British Columbia.....26

Figure 1.18 - Mean number of *Codium fragile* plants per quadrat at Seppings Island. ....27

Figure 1.19 – Distribution of *Codium fragile* size classes at Seppings Island ....29

Figure 2.1 – Shallow tidepools at Prasiola Point.....	38
Figure 2.2 – Both black chitons, <i>Katharina tunicata</i> , and purple urchins, <i>Strongylocentrotus purpuratus</i> , have access to many algal species that are found at Prasiola Point.....	45
Figure 2.3 – Experimental apparatus used in macroalgal diet vs. herbivore fitness study.....	56
Figure 2.4 – Mean % change urchin test diameters for purple urchins, <i>Strongylocentrotus purpuratus</i> , offered one of four macroalgal diets.....	62
Figure 2.5 – Mean % change urchin biomass for purple urchins, <i>Strongylocentrotus purpuratus</i> , offered one of four macroalgal diets.....	63
Figure 2.6 – Mean urchin gonad mass for purple urchins, <i>Strongylocentrotus purpuratus</i> , offered one of four macroalgal diets.....	64
Figure 2.7 – Mean % change chiton biomass for black chitons, <i>Katharina tunicata</i> , offered one of four macroalgal diets.....	65
Figure 2.8 – Mean chiton gonad mass for black chitons, <i>Katharina tunicata</i> , offered one of four macroalgal diets.....	66
Figure 4.1 – Maximum wave force recorder used to measure wave forces at wave-exposed and wave-protected sites in Barkley Sound.....	110
Figure 4.2 – Comparison of mean wave forces measured at Prasiola Point, Second Beach, Scott's Bay and Seppings Island, Barkley Sound.....	119
Figure 4.3 - Drag coefficients from 0.5 to 4.0 m/s <sup>-1</sup> velocity on a representative <i>Codium fragile</i> thallus.....	123
Figure 4.4 - Results from first trial of transplant experiment where <i>Codium fragile</i> plants collected from Seppings Island were transplanted to wave-exposed Prasiola Point and wave-protected Scott's Bay .....	128
Figure 4.5 – Results from second trial of transplant experiment where <i>Codium fragile</i> plants collected from Seppings Island were transplanted to wave-exposed Prasiola Point and wave-protected Scott's Bay.....	129
Figure 4.6 – Comparison of mean thallus lengths for <i>Codium fragile</i> plants surviving at either Scott's Bay or Prasiola Point .....	130
Figure 4.7 – Condition of <i>Codium fragile</i> transplants at Scott's Bay study site..	132

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## CHAPTER 1

### Introduction to the chlorophyte, *Codium fragile*

#### 1.1 Introduction

The macroalgal genus *Codium* (Chlorophyta: Codiaceae) contains approximately 100 described species, making it one of the most diverse genera of marine algae (Silva, 1962). This genus is unique compared to many other chlorophytes, as it is comprised of large unicellular plants, often exposed to harsh extremes within intertidal environments. The most abundant and widely distributed species within this genus is *Codium fragile* (Suringar) Hariot, commonly known as "sea staghorn", "oyster thief" or "dead man's fingers".

*Codium fragile* grows erect as coenocytic filaments entwine to form axial "cables". From these cables, outward swollen and club-shaped branches (known as utricles) form a compact "cortex" or palisade. These utricles have a short, sharp, outward point which superficially resembles an old-fashioned light bulb. Within the utricles are disc-shaped chloroplasts (lacking pyrenoids) which are crowded near its apex. As a coenocytic species, there are no true cross walls, but septa (partitions) are formed in the cables. The dichotomously-branched thallus arises from a broad, spongy basal disk, producing several orders of cylindrical branches 3-10 mm in diameter (Figure 1.1a) (Scagel, 1971). *Codium fragile* is dark green in color with a velvet texture. Mature plants may grow up to 40 cm in height (Scagel, 1971).

*Codium fragile* has been used as a model seaweed for a diversity of research topics, ranging from algal physiology (Hanisak, 1979; Dromgoole, 1980; Benson et al., 1983), endo-symbiosis (Williams and Cobb, 1992; Trowbridge, 1993), and heavy metal accumulation (Burdin and Poljakova, 1984) to invasion

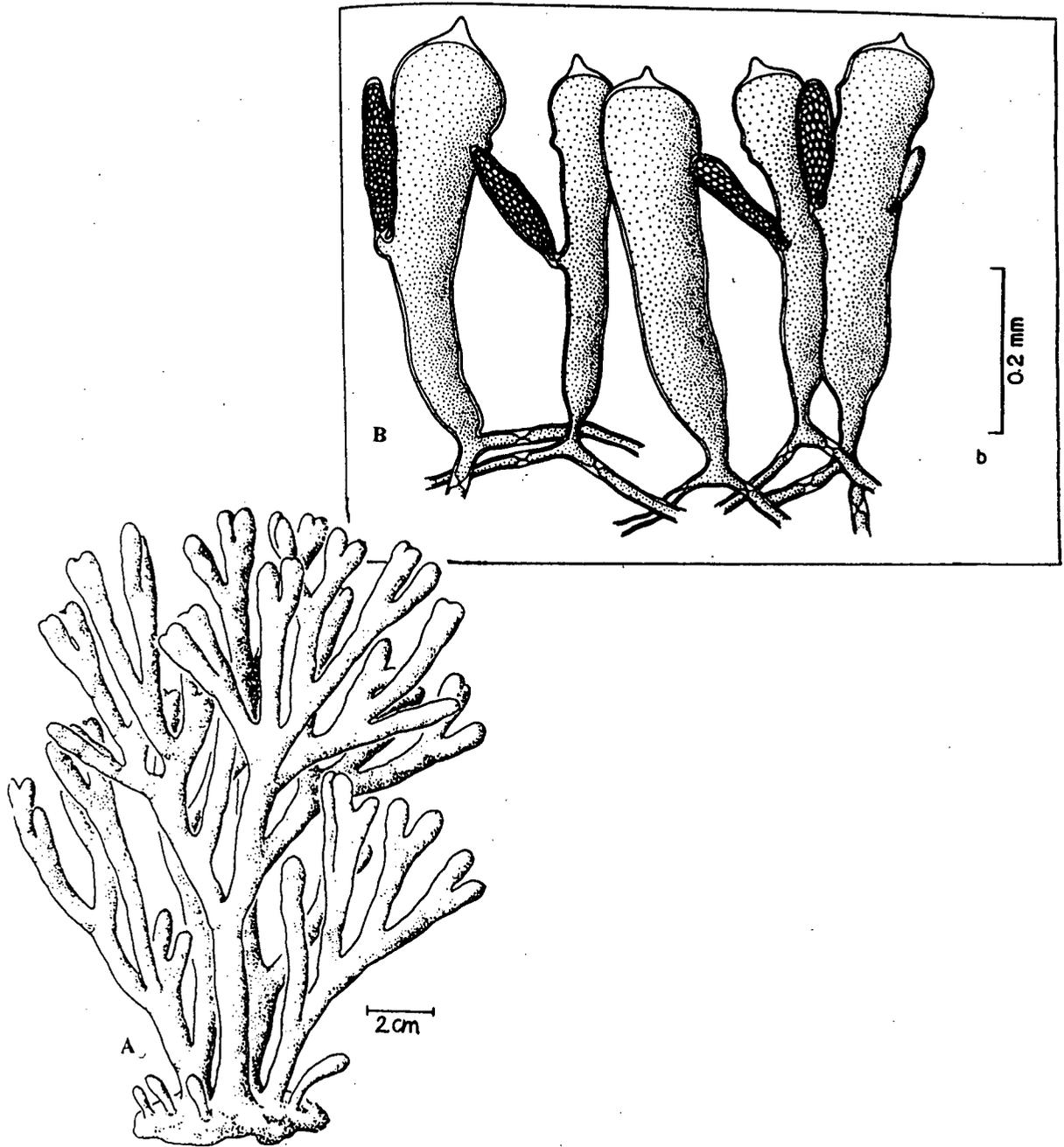


Figure 1.1 – *Codium fragile* (Suringar) Hariot. (A) Dichotomously-branched plant attached to rocky substrate (from Abbott and Hollenberg, 1976); (B) enlarged view (in transverse section) of surface region of the plant, showing filamentous structure of the plant, swollen terminal utricles, and gametangia (from Scagel, 1971).

ecology (Carlton and Scanlon, 1985; Trowbridge, 1995; Trowbridge, 1996a), algal genetics (Goff et al., 1992; Coleman, 1996), and natural products (Henrikson and Pawlik, 1995; Van Alstyne et al., 2000). It is also a seaweed species of economic value: it is cultivated as food in Asia (Arasaki and Arasaki, 1986), used as invertebrate food in mariculture projects (Pan and Yu, 1992), is a source of bioactive compounds (antibiotic, anticarcinogenic, immunosuppressive, anti-insect, and antihelminthic activity) (Amer et al., 1991; Ballesteros et al., 1992), as well as a model indicator of pollution as it accumulates heavy metals (Denton and Burdon-Jones, 1986; Costantini et al., 1991). However, *C. fragile* is also labeled as a "pest" both in natural and cultivated shellfish beds. For example, the alga smothers blue mussels and bay scallops by attaching to bivalves' shells and (by overgrowth) keeping them shut (Fralick, 1970). Also, when large thalli photosynthesize and trap gas bubbles inside their fronds, their buoyancy lifts shellfish off the beds. These thalli are transported by waves and currents away from the shellfish beds and are frequently left stranded on the shore as drift algae, resulting in the death of the shellfish (hence, the name "oyster thief") (Trowbridge, 1998).

*Codium fragile* is cosmopolitan; this species has a temperate, bipolar, and antarctic circumpolar distribution (Silva, 1962). According to Trowbridge (1998), it occurs from 29° to 54° S latitude and 33° to 70° N latitude and is a common to locally common seaweed found on many rocky shores throughout the world. *Codium fragile* often occurs on wave-exposed rocky shores. Many authors

report that N.E. Pacific *C. fragile* populations occur in the mid and low intertidal, as well as the subtidal (Scagel, 1971; Gunnill 1980 & 1985; Trowbridge, 1993).

*Codium fragile* is currently recognized as a single species with six described subspecies. Two of the six described subspecies are recognized as introduced (potentially originating from Japan) and a third subspecies may be introduced as well (Trowbridge, 1998). However, one of these subspecies, *Codium fragile* ssp. *tomentosoides*, is among the most invasive seaweeds in the world, with extensive transoceanic and interoceanic spread this past century (reviewed by Carlton and Scanlon, 1985; Trowbridge, 1995; Trowbridge, 1998). *C. fragile* ssp. *tomentosoides*, as an introduced species, has been documented to occur in the N. Atlantic, Mediterranean, New Zealand, S.E. Australia, and the N.E. Pacific (Trowbridge, 1998). However, its sole recorded occurrence in N.E. Pacific waters was in San Francisco Bay, California (Silva, 1979). It has not been found in N.E. Pacific habitats since.

Our native species, *Codium fragile* ssp. *fragile*, has a broad geographical range from Sitka, Alaska to Baja, California (Abbott and Hollenberg, 1976). It is this native species that is the focus of this study. *Codium fragile* has often been described as a perennial seaweed; meaning that mature thalli are able to persist for more than one year. Gunnill (1980, 1985) monitored *C. fragile* populations near La Jolla, CA during 1973-1977 and 1982-1983. He found that standing stocks varied from year to year; native plants had a patchy distribution both temporally and spatially. According to Gunnill (1980, 1985), *C. fragile* "recruitment" occurs from May to November for southern California populations.

However, re-establishment of a *C. fragile* population may be from settling zygotes, regrowth on perennial holdfasts, and/or growth and differentiation from filamentous mats. In severe winters (e.g. 1995-96), Trowbridge (1998) found that entire thalli (including holdfasts) are ripped from the substratum; however, during most years, thalli overwinter and there are typically a range of frond lengths on each thallus.

*Codium fragile* reproduces sexually by fusion of anisogamous gametes from separate male and female plants (Figure 1.2) (Borden and Stein, 1969). On the utricles, small club-shaped lobes develop and are walled off by a cross partition. These function as gametangia (Figure 1.1b) and produce either male or female anisogametes. The discharge of gametes has also been described for *C. fragile*; in this species, the internal layers of the gametangium wall soften and swell when wetted by a returning tide. The apical cap splits and opens as a lid through which a large mass of mucilage is extruded. Running lengthwise through the center of the mass and continuous with the cavity of the gametangium is a narrow canal. Through this canal, the gametes are released with flagella developing soon afterward. The zygote germinates to form a diploid gametophyte immediately by developing an elongated vesicle which eventually forms differentiated branches (rhizoids and vertical filaments). Clifton and Clifton (1999) report many tropical, coenocytic green algae to be "holocarpic" (e.g. algal biomass is compromised when gamete release causes the plant to fragment), which results in drastic reductions of algal density and percentage cover during periods of peak reproduction. Though *C. fragile* is coenocytic, it is not

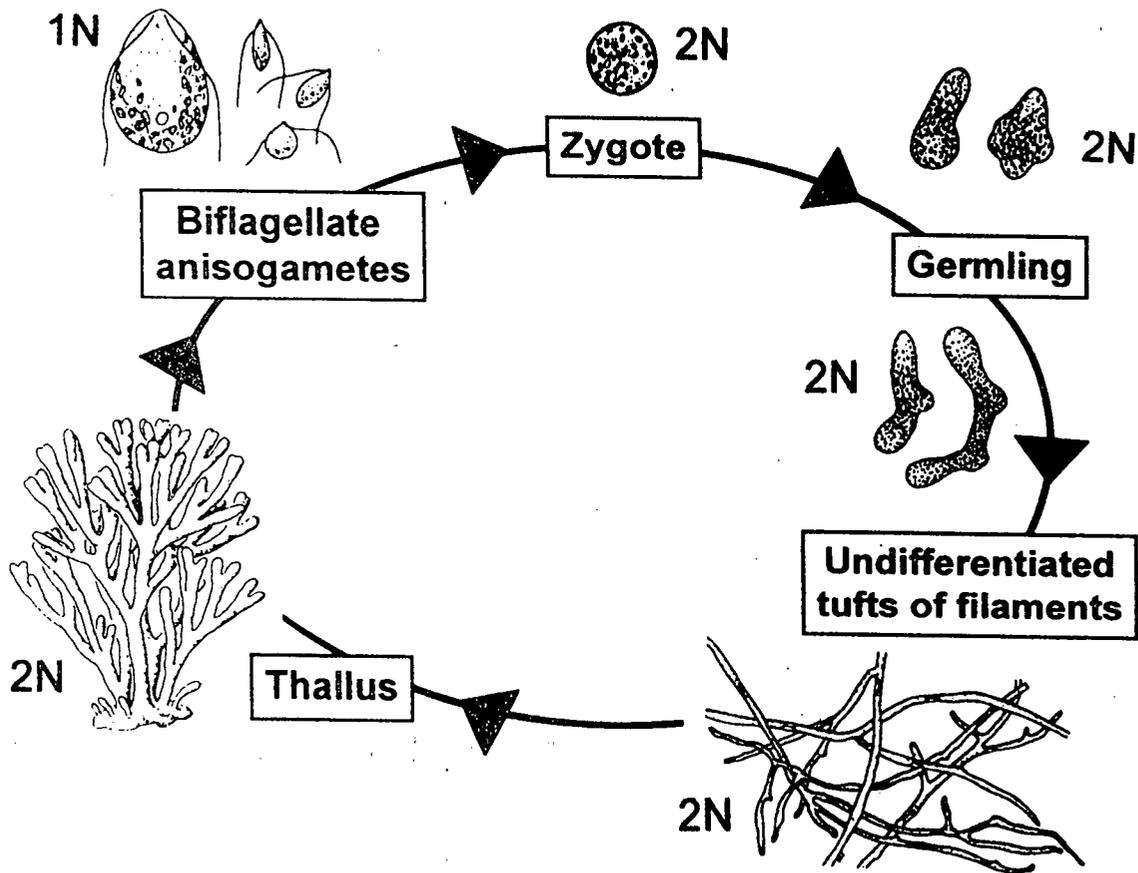


Figure 1.2 – Life cycle of native *Codium fragile*. “2N” refers to diploid life stages, whereas “1N” is haploid. (From Trowbridge, 1998)

holocarpic; this attribute may allow it to retain its space from year to year in a given habitat.

Trowbridge (1998) states, "In contrast to the wealth of taxonomic information on *Codium (fragile)*, ecological information on the alga, particularly on the native species, is meager and almost exclusively descriptive." With the exception of the reproductive studies conducted by Borden and Stein (1969), little is known of how *C. fragile* plants are distributed in the northern range of N.E. Pacific shores. Based on unpublished data (R. DeWreede, 1995) and my early field observations, the occurrence of *C. fragile* is irregular both temporally and spatially on wave-exposed, rocky shores near Prasiola Point, Vancouver Island. Transect data from July-December 1995 indicated that mature plants disappear in winter months (R. DeWreede, personal communication). This information coincides with descriptive information for both Oregon and California populations. However, what causes these irregular distribution patterns? Trowbridge (1998) states that "the study of *Codium* biology would progress much more rapidly if researchers would quantify observed patterns and test hypothesized causal processes, rather than asserting subjective opinions". Therefore, I have documented the occurrence of *C. fragile* at several field sites near Vancouver Island from June 1998 to September 2002, and tested several factors that were hypothesized to influence *C. fragile*'s abundance.

## 1.2 Distribution of *Codium fragile* in Barkley Sound

This research is part of a broader study examining factors that determine seaweed growth and abundance. Twenty years of previous studies have been

conducted at First and Second Beaches (near Prasiola Point) on Vancouver Island, with which mine will be incorporated, leading to an integrated study of seaweed dynamics. The location of these field sites is important for studying aspects of marine ecology because they are largely undisturbed by human activity, highly diverse in both seaweeds and invertebrates, and are accessible by inlet or ocean. Four field sites near Bamfield Marine Sciences Centre (Figure 1.3) were utilized within the course of this study: Prasiola Point, Second Beach, Scott's Bay, and Seppings Island. *Codium fragile* plants were located at all field sites (though variable both seasonally and spatially throughout the duration of this research). Table 1.1 summarizes similarities and differences between field sites.

#### *Prasiola Point*

Prasiola Point, a bedrock platform, was initially chosen based on the abundance of *Codium fragile* in summer 1998. Plants were distributed throughout the intertidal zone, from the higher intertidal (approximately 1.43 m above chart datum) to the edges of a subtidal urchin-filled pool (exposed only during lowest low tides) (Figure 1.4). *Codium fragile* plants were monitored at 4 month intervals within 1 x 3 m<sup>2</sup> permanent belt transects located at each intertidal elevation (i.e. High (1.43 m above chart datum), Middle (0.93 m above chart datum), Low (0.33 m above chart datum)), from June 1998 to October 2001. Mean abundances of *C. fragile* plants were highest in summer 1998 at all elevations (Figures 1.5-1.7). Mean number of plants did not fluctuate much in the higher intertidal over time while seasonal declines (October) were apparent in

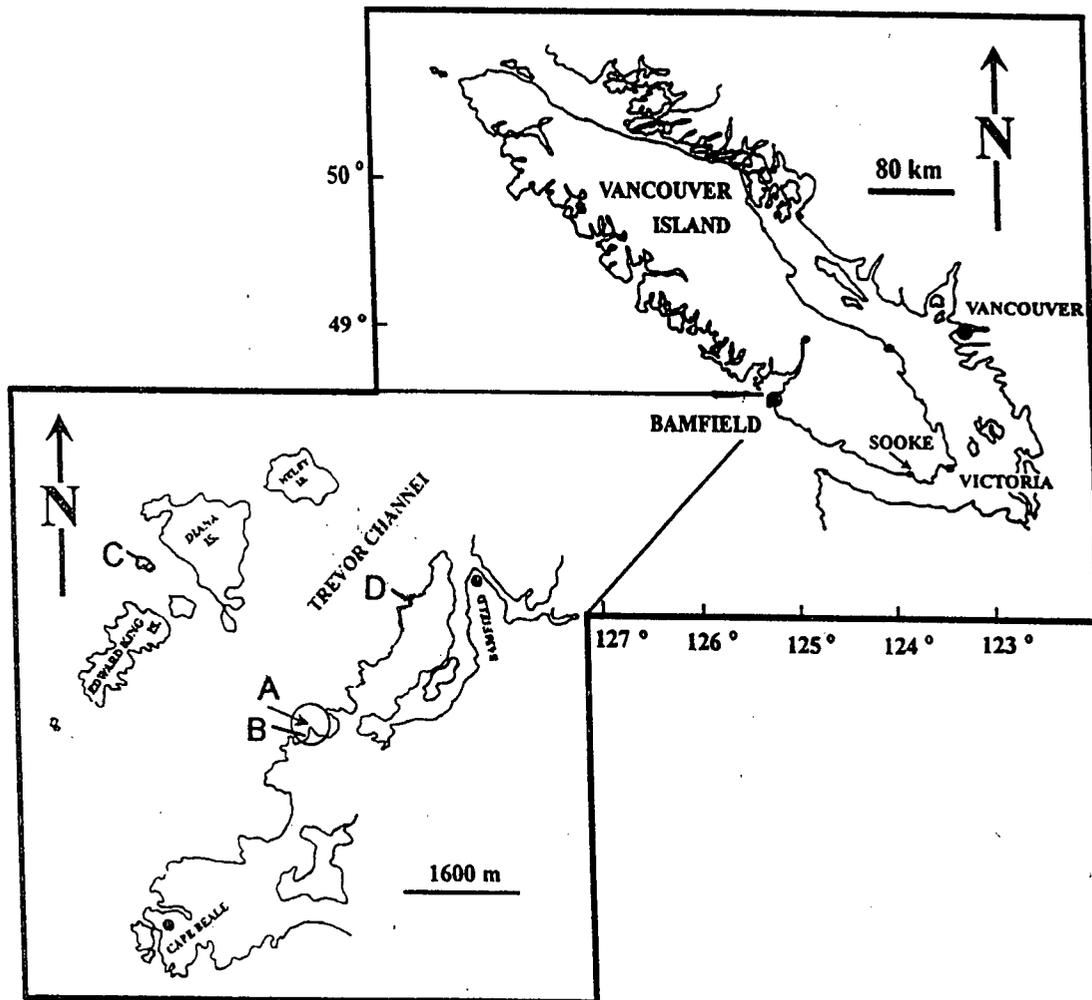


Figure 1.3 – Map of study sites. “A”= Prasiola Point, “B”= Second Beach, “C”= Seppings Island, and “D”= Scott’s Bay, Vancouver Island, British Columbia. (Modified from Milligan, 1998)

Table 1.1– Comparison of field sites on/near Vancouver Island, British Columbia. Locations were derived from GPS readings within *Codium fragile* zones. Mean elevations were derived from field surveys and published mean lowest tide predictions. Wave-action type was based on presence/absence of representative plant and animal species associated with either wave-protected or wave-exposed shores.

Site:	Location:	Mean Elevation: (m)	Substratum:	Wave Action:
Prasiola Pt.:	N 48°49.035' W125°10.135'		rocky platform	wave-exposed
		HIGH 1.43 MIDDLE 0.93 LOW 0.33		
Second Beach	N 48°48.959' W125°10.077'	1.19	rock boulders on pebble/sand beach	wave-exposed
Scott's Bay	N 48°50.033' W125°08.768'	1.03	rock mound on sandy beach	wave-protected
Seppings Isd.	N 48°50.420' W125°12.392'		boulder-strewn beach	wave-protected
		HIGH 1.25 MIDDLE 1.08 LOW 0.81		



Figure 1.4 – Bedrock platform study site at Prasiola Point, Vancouver Island, British Columbia.

13-

## Prasiola High Intertidal

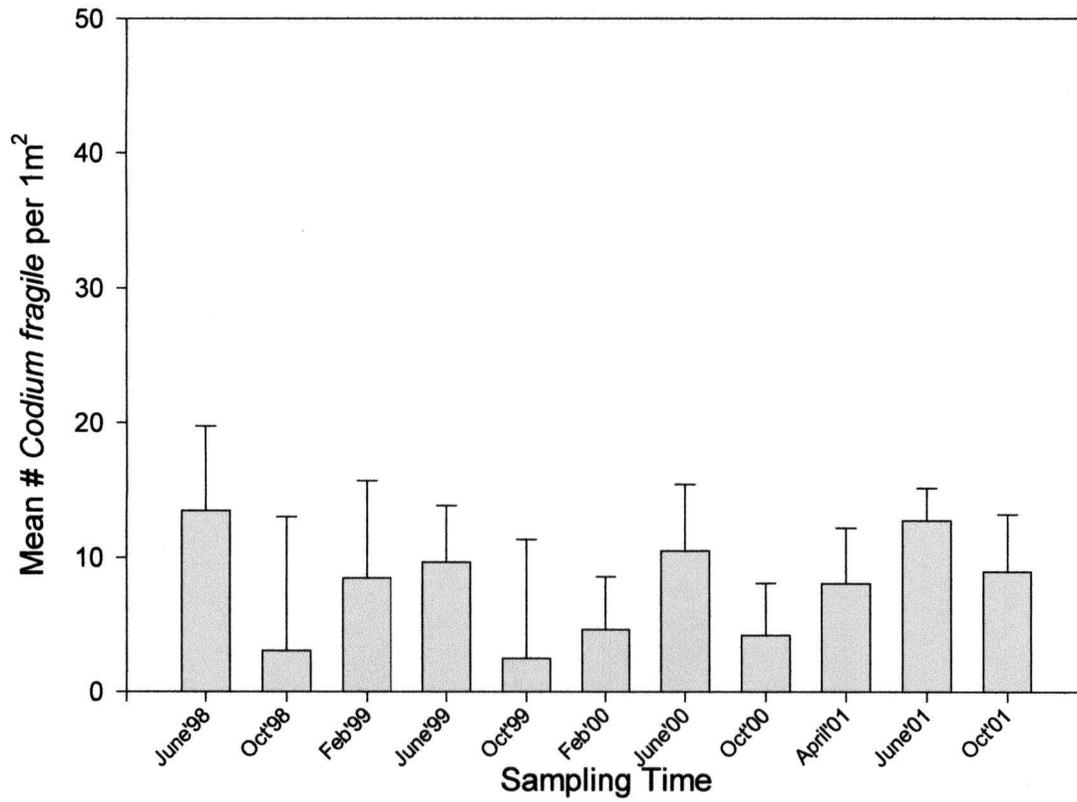


Figure 1.5 – Mean number of *Codium fragile* plants per 1m<sup>2</sup> recorded at 4-month intervals from June 1998 to October 2001 at Prasiola Point – High Intertidal. (95% confidence intervals are shown.)

## Prasiola Middle Intertidal

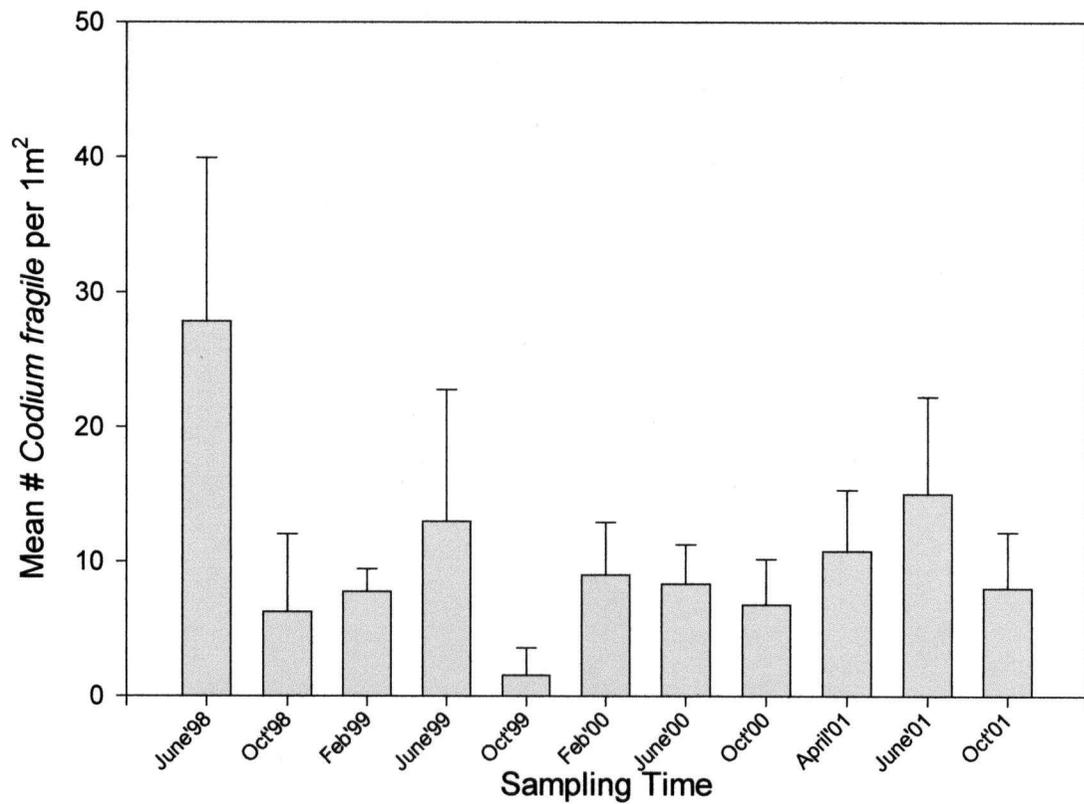


Figure 1.6 – Mean number of *Codium fragile* plants per 1m<sup>2</sup> recorded at 4-month intervals from June 1998 to October 2001 at Prasiola Point – Middle Intertidal. (95% confidence intervals are shown.)

## Prasiola Lower Intertidal

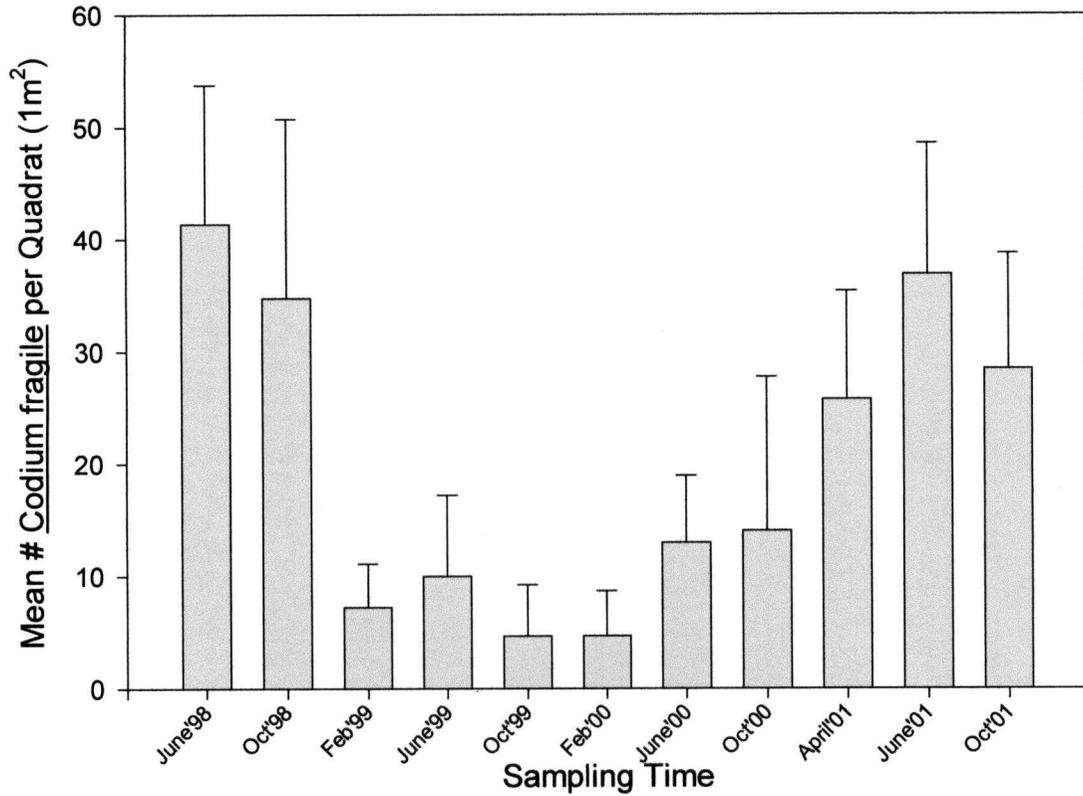


Figure 1.7 – Mean number of *Codium fragile* plants per 1m<sup>2</sup> recorded at 4-month intervals from June 1998 to October 2001 at Prasiola Point – Low Intertidal. (95% confidence intervals are shown.)

the middle intertidal zone (followed by increases each June). However, at the lowest elevation, mean number of plants showed a significant decline following winter storms of 1998-99. "Recovery" occurred over two years. Size classes were variable at all elevations (Figures 1.8-1.10). However, smaller plants (0-6 cm in length) occurred more frequently than larger plants.

#### *Second Beach*

The Second Beach site is characterized by a cluster of emergent rock mounds, surrounded by sand and beach pebbles (Figure 1.11). *Codium fragile* plants were observed at this site in February 1999 and monitored until October 2001. *Codium fragile* plants were mapped and measured at 4 month intervals within 1 x 3 m<sup>2</sup> permanent belt transects located on specific rock mounds approximately 1.19 m above chart datum. Mean number of *C. fragile* plants decreased in 2000, then increased in spring 2001 (Figure 1.12). Smaller plants (0-6 cm) were dominant during all sampling periods, followed by intermediate sizes (6-12 cm) (Figure 1.13). Large plants were present to a lesser degree, which differed from the complete absence of large plants at the same intertidal elevation at nearby Prasiola Point.

#### *Scott's Bay*

Scott's Bay is characterized by a small rock cobble field in the lower intertidal bordering both a higher rocky substratum and a sandy beach. I conducted an annual census counting all adult *Codium fragile* plants on an emergent rock mound (1.03 m above chart datum) in the middle intertidal zone

### Prasiola High Intertidal

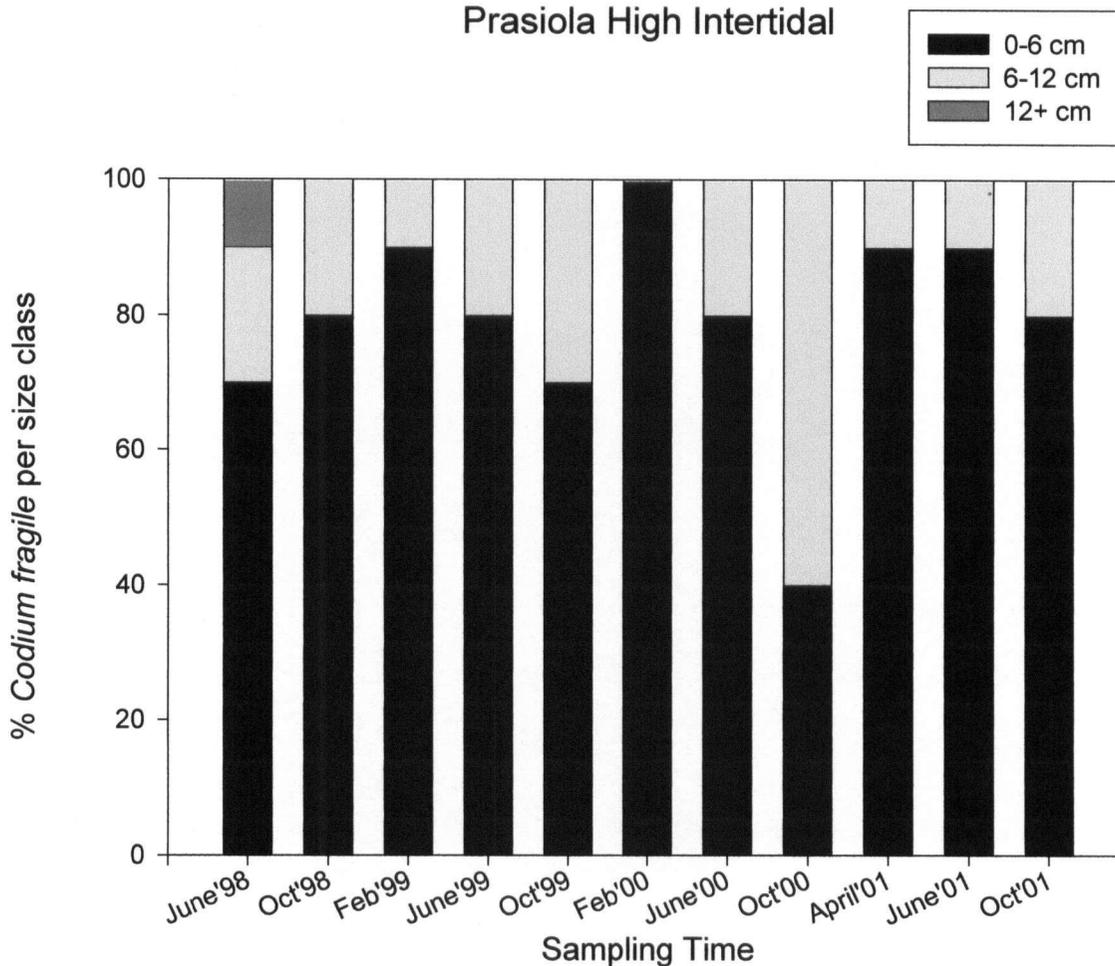


Figure 1.8 – Distribution of *Codium fragile* size classes at Prasiola Point (High Intertidal) from June 1998 to October 2001. Ten randomly selected plants were measured for total thallus length (cm).

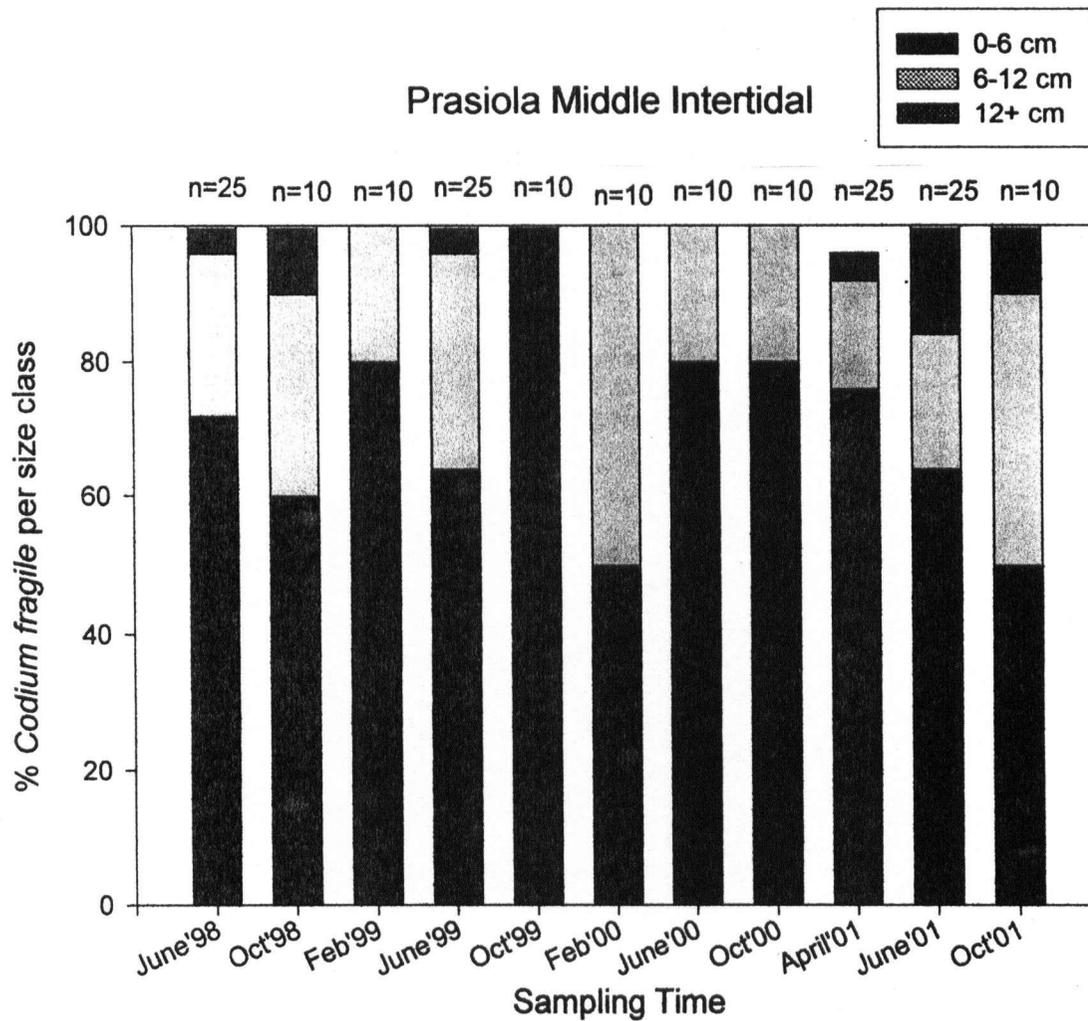


Figure 1.9 – Distribution of *Codium fragile* size classes at Prasiola Point (Middle Intertidal) from June 1998 to October 2001. “N” indicates number of randomly selected plants that were measured for total thallus length (cm).

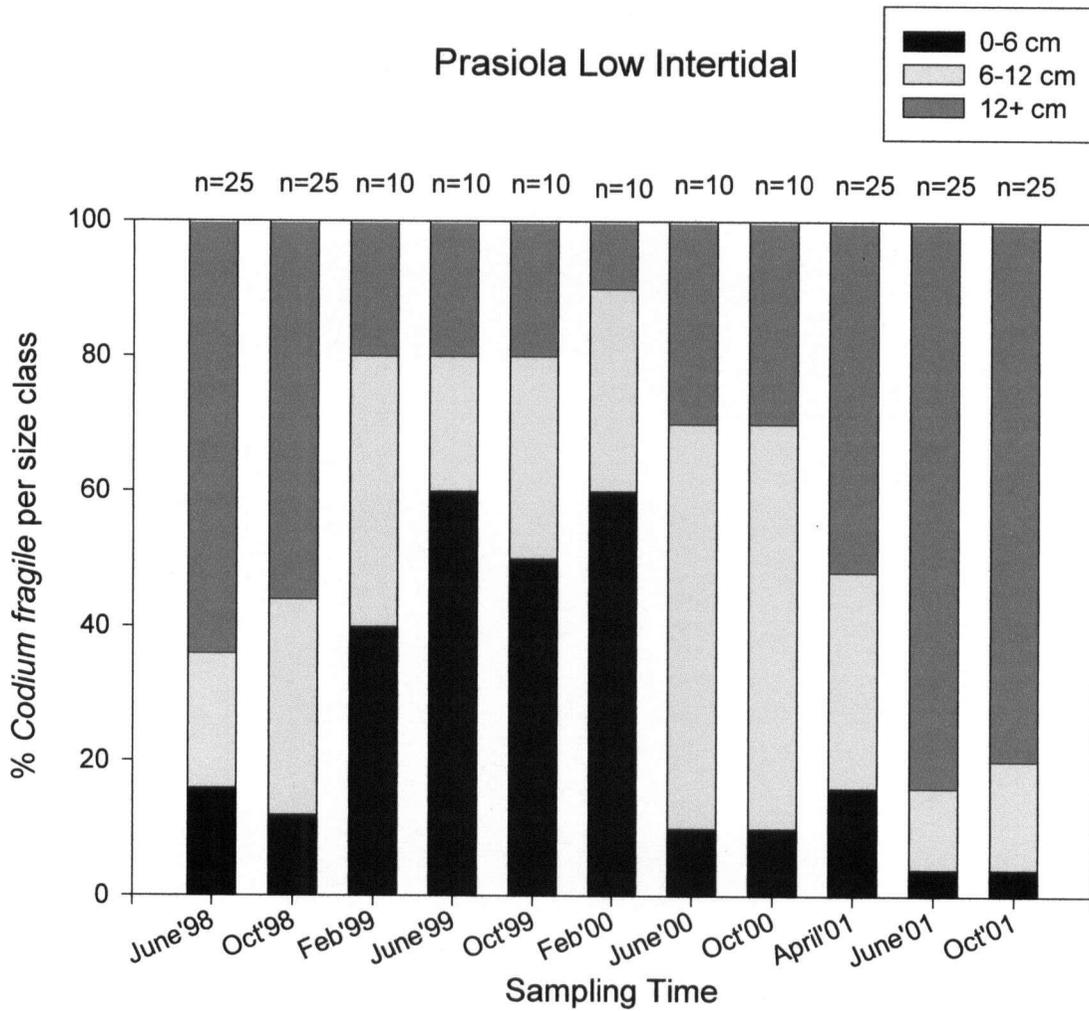


Figure 1.10 – Distribution of *Codium fragile* size classes at Prasiola Point (Low Intertidal) from June 1998 to October 2001. “N” indicates number of randomly selected plants that were measured for total thallus length (cm).



Figure 1.11 – Rock mound study site at Second Beach, Vancouver Island, British Columbia.

## Second Beach Boulders

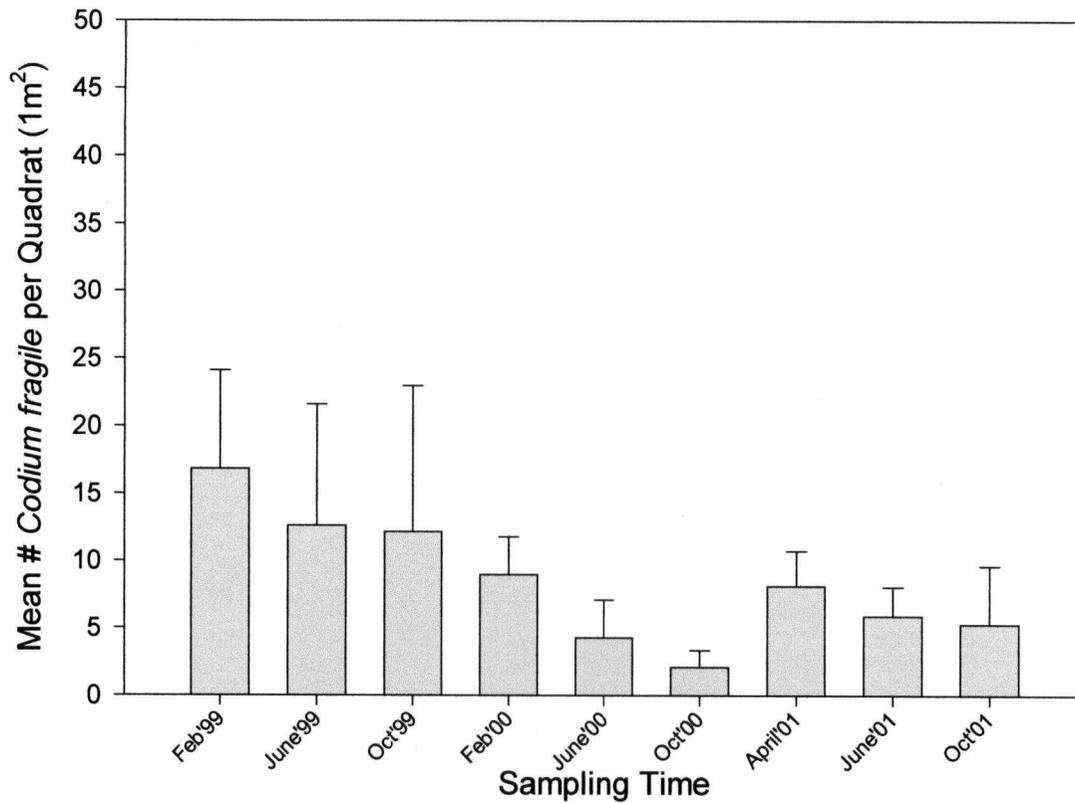


Figure 1.12 – Mean number of *Codium fragile* plants per 1m<sup>2</sup> recorded at 4-month intervals from February 1999 to October 2001 at Second Beach. (95% confidence intervals are shown.)

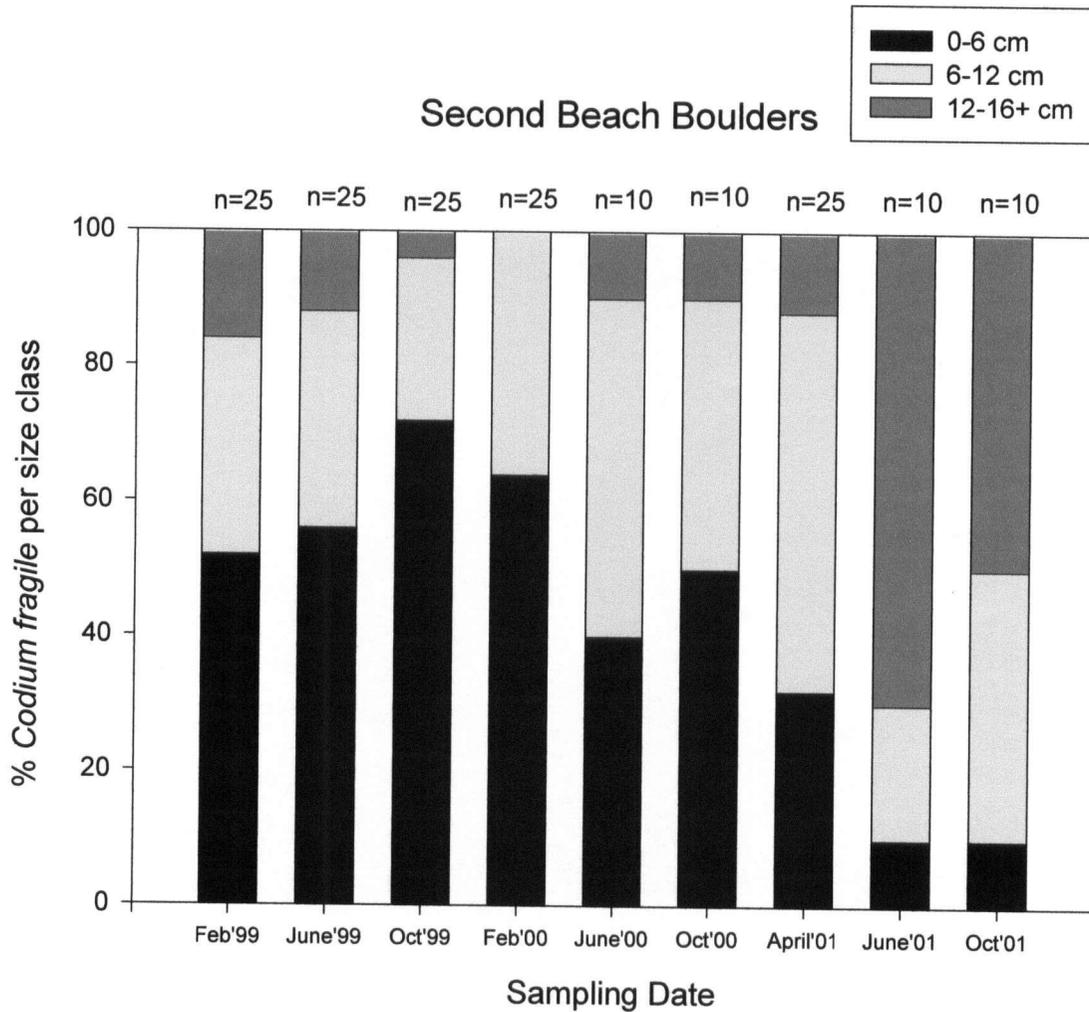


Figure 1.13 – Distribution of *Codium fragile* size classes at Second Beach from February 1999 to October 2001. “N” indicates number of randomly selected plants that were measured for total thallus length (cm).

from August 1998 to August 2001. The emergent rock mound encompassed an approximately 2.5m X 2m area (Figure 1.14). Mean number of measurable *C. fragile* plants decreased from 1998 to 2001 (Figure 1.15). "G" indicates the presence of numerous germlings in both 2000 and 2001, which covered up to 50% of the mound rock surface. However, this "carpet" of germlings did not appear to develop into small plants during my observation time. In August 2000, this study site was covered with up to 1.5 cm of sand. It is unknown whether this impacted juvenile *C. fragile* development. Large plants (12+ cm in length) were dominant in August 1998. The following year, all large plants had disappeared and were replaced by the smaller size classes. From 1999-2001, small and intermediate-sized plants showed slight increases in mean percentages with the return of a few large plants in 2001 (Figure 1.16).

#### *Seppings Island*

Seppings Island was not included until Summer 2000, when it became necessary to find another location to collect *Codium fragile* without removing monitored plants from other field sites (e.g. Prasiola Point, Second Beach, Scott's Bay). This field site is characterized by a large boulder field, with an abundance of mature *C. fragile* plants at all intertidal heights (Figure 1.17). One m<sup>2</sup> quadrats were randomly placed on permanent transect lines to measure *C. fragile* plants at each intertidal height (i.e. High (1.25 m above chart datum), Middle (1.08 m above chart datum), Low (0.81 m above chart datum)). In July of 2000 and 2001, *C. fragile* abundance was substantially greater per 1m<sup>2</sup> (Figure



Figure 1.14 – Rock mound (lower left corner outlined by white line) study site at Scott's Bay, Vancouver Island, British Columbia.

## Scott's Bay

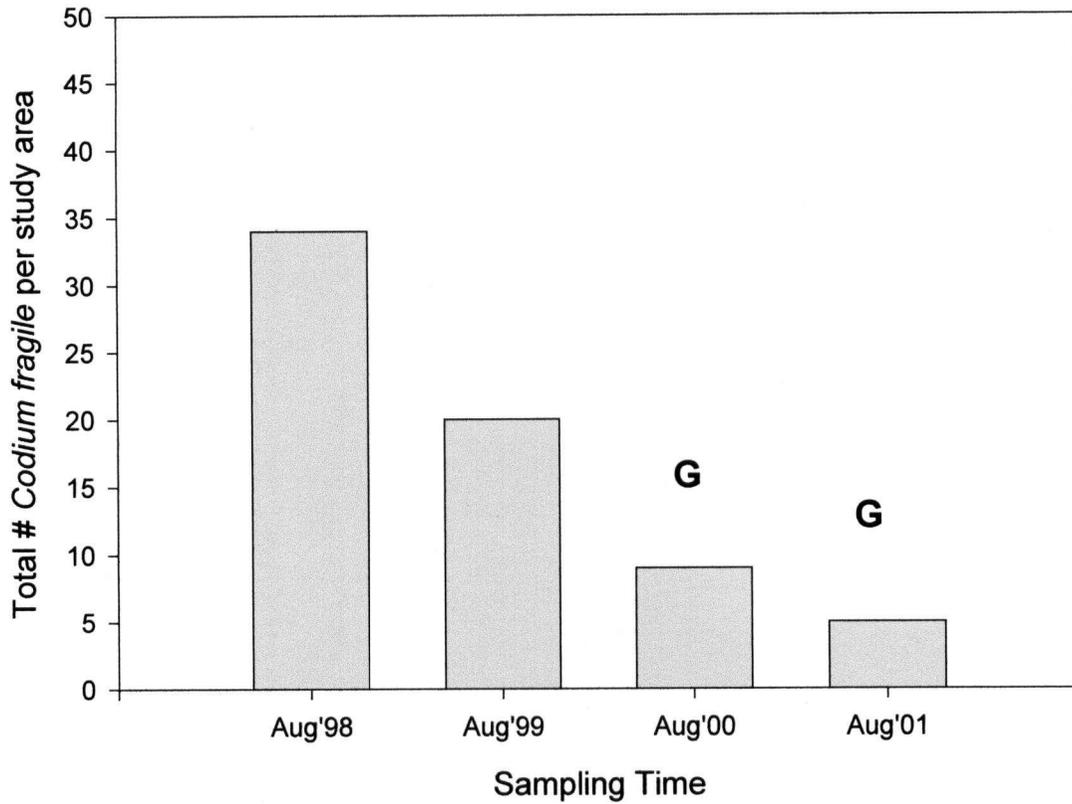


Figure 1.15 – Total number of *Codium fragile* plants *in situ* (~2.5m x 2m area) recorded annually from August 1998 to August 2001 at Scott's Bay. "G" indicates the presence of numerous germlings in both 2000 and 2001, which covered up to 50% of the mound rock surface.

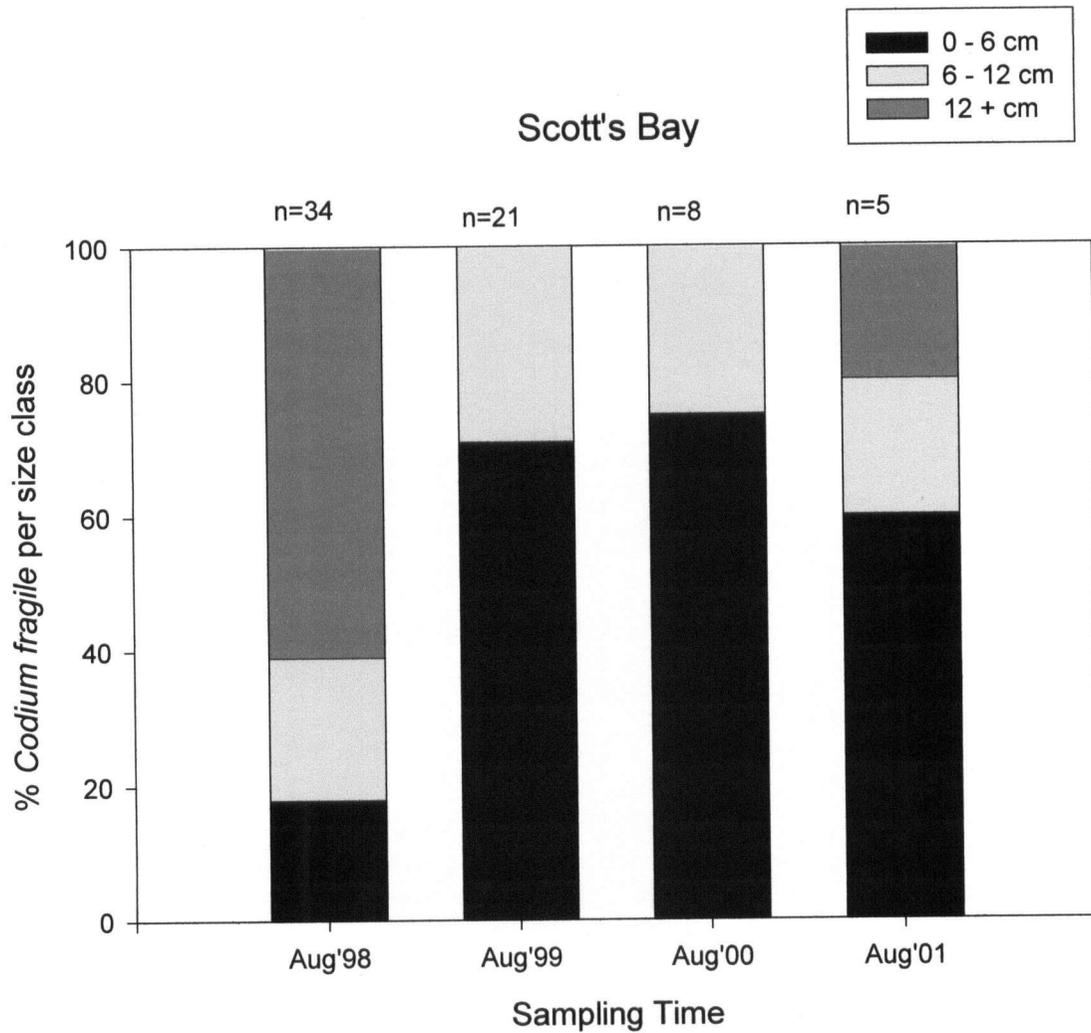


Figure 1.16 – Distribution of *Codium fragile* size classes at Scott's Bay from August 1999 to August 2001. "N" indicates number of randomly selected plants that were measured for total thallus length (cm).



Figure 1.17 – Rock boulder field study site at Seppings Island, British Columbia.

### Seppings Island

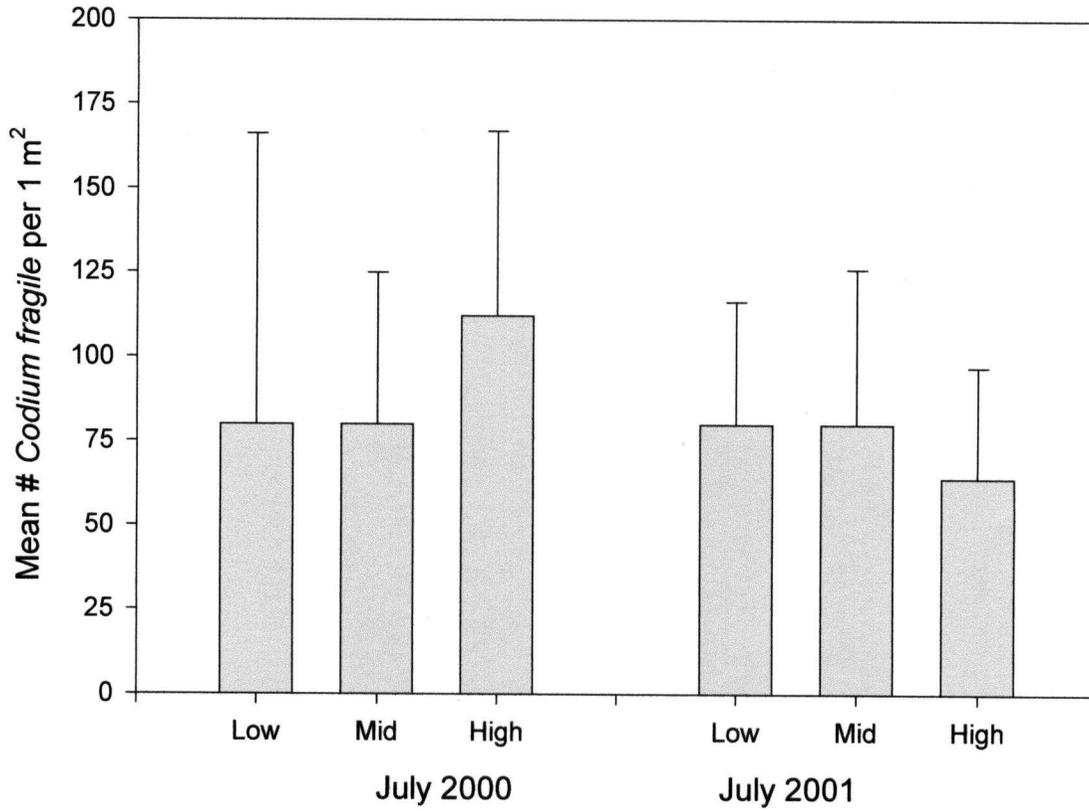


Figure 1.18 – Mean number of *Codium fragile* plants per 1m<sup>2</sup> recorded July 2000 and July 2001 at Seppings Island. (95% confidence intervals are shown.)

1.18) compared to all other field sites sampled in this study. Size-class distributions varied from July 2000 to July 2001; large plants were more abundant than the other two classes in July 2000 while small plants were more abundant in July 2001 (Figure 1.19).

### 1.3 Justification for Research Questions

My initial research questions were formulated to experimentally determine the basis of the irregular occurrence of *Codium fragile*, specifically at Prasiola Point, and more generally for the larger area of Barkley Sound. Prasiola Point supports a diversity of macroalgae and invertebrate species. *Codium fragile* and other macroalgal species fringe large tidepools containing purple urchins (*Strongylocentrotus purpuratus*) on the lower elevations of the bedrock platform. At all intertidal elevations, black chitons (*Katharina tunicata*) were present, seeking refuge beneath macroalgae at low tide. I proposed that herbivory by generalist grazers (e.g. purple urchins, black chitons) imposes size and survival limitations on *C. fragile* individuals at this location.

The herbivory hypothesis was strengthened by early field observations at Second Beach, Scott's Bay and Seppings Island. These three study sites differed from Prasiola Point topographically (bedrock platform vs. exposed rock mounds in sand/pebble beaches vs. large rock boulder field) and supported few invertebrate herbivore species. Neither purple urchins nor black chitons were found at these three study sites. Therefore, I predicted that generalist herbivores accounted for the low densities of *Codium fragile* at Prasiola Point, whereas the I tested herbivore food preference using black chitons and purple urchins. These

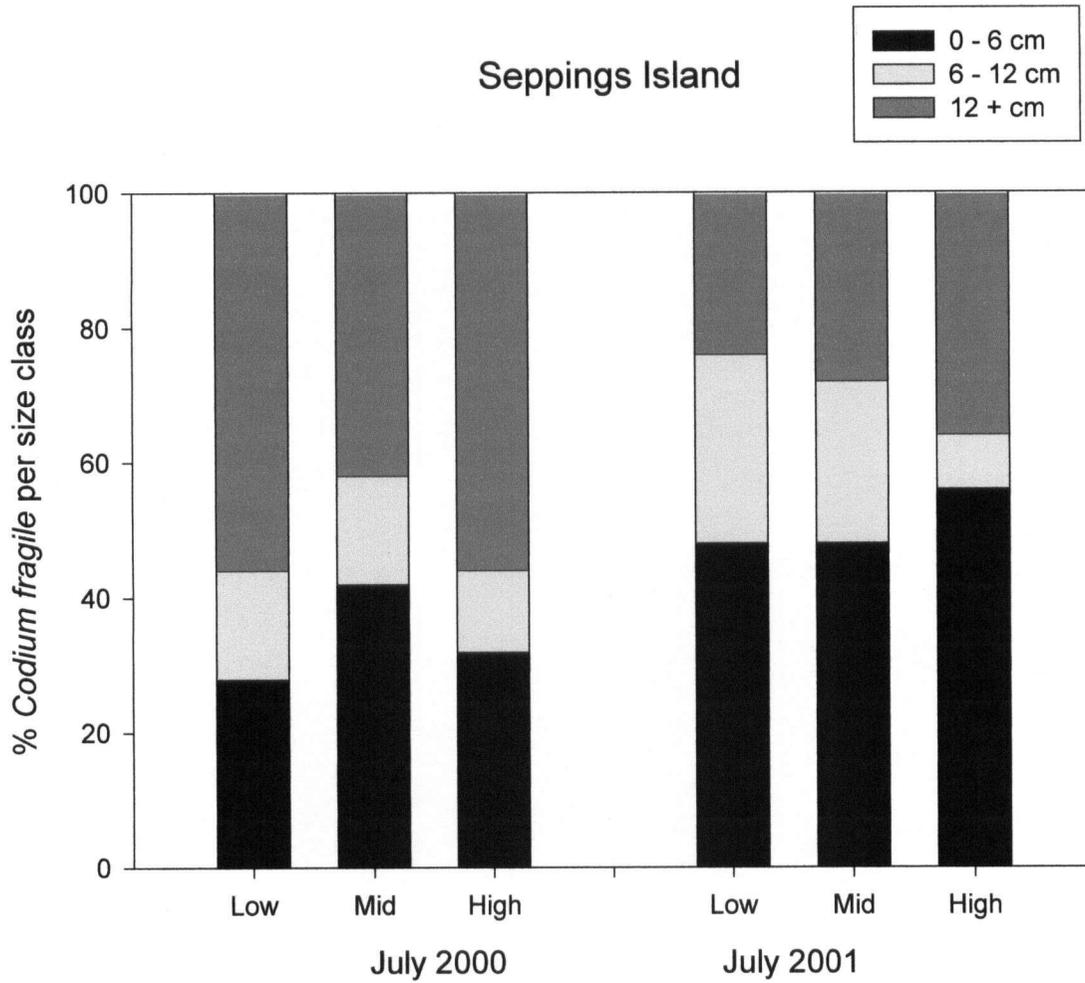


Figure 1.19 – Distribution of *Codium fragile* size classes at Seppings Island sampled July 2000 and July 2001. Twenty-five randomly selected plants within each intertidal zone were measured for total thallus length (cm).

other three sites should then support higher densities of *C. fragile*. In Chapter 2, results were used to estimate the effect that these herbivores have on *C. fragile*'s distribution at Prasiola Point.

Perhaps a physical disturbance limits *Codium fragile* survival in Barkley Sound. During Summer 1998, both *C. fragile* germlings and adult plants were observed at another Second Beach study site. Six months later, this site was covered by sand and all *C. fragile* plants were gone (as ascertained by checking under the sand). As previously mentioned, my Scott's Bay study site was covered with up to 1.5 cm of sand in August 2000. It is unknown how this natural phenomena impacted juvenile development or survival of *C. fragile* adults. I predicted that sand burial would be detrimental to *C. fragile* survival based on negative impacts reported for other macroalgal species (e.g. scouring of tissue, reduced light, reduced nutrients) (Daly and Mathieson, 1977; D'Antonio 1986; Airoidi and Cinelli, 1997). This could explain the slow recovery of *C. fragile* observed in subsequent sampling periods at Scott's Bay. Chapter 3 examines the effects of short-term sand burial on *C. fragile* plants, as has been noted to occur at these Barkley Sound beaches.

It is also possible that a different kind of physical disturbance dictates where *Codium fragile* plants occur in Barkley Sound habitats. Though a large rock wall on the southern side protects Prasiola Point from heavy wave action during spring and summer months, large waves crash over and wash around this wall during fall and winter storms. I considered Prasiola Point as a relatively wave-exposed location because there were many representative plants and

animals typical of more wave-exposed habitats, compared to my other study sites. Nearby Second Beach is also subjected to similar wave action. I proposed that wave action imposes size and survival limitations on *C. fragile* individuals at these locations as a seasonal effect. My other two field sites differed in both wave-exposure and composition of species. Scott's Bay is a wave-protected sandy/cobble beach. Furthermore, my study site on Seppings Island is protected by large rock outcroppings. When comparing early field observations, I predicted that wave action accounted for the relatively low densities of *C. fragile* at Prasiola Point and Second Beach, compared to the other mentioned sites. Finally, Chapter 4 evaluates the impact(s) of wave action on individual *C. fragile* plants by comparing breaking forces, drag coefficients and survival based on a field transplant study.

## CHAPTER 2

### Herbivory

#### 2.1 How herbivory influences seaweeds in rocky, intertidal habitats

A biotic factor that may influence population dynamics of *Codium fragile* is herbivory. Herbivory studies have shown that many invertebrate species can impact algal communities in different ways (Lubchenco and Gaines, 1981; Gaines and Lubchenco, 1982; Hawkins and Hartnoll, 1983). Herbivores sometimes play contradictory roles in community structure by grazing heavily on new seaweed recruits (a negative impact) (Trowbridge, 1992) or selectively grazing epiphytes on adult plants (a positive impact for the adult) (Trowbridge, 1993). Herbivores may even enhance a seaweed's ability to survive in a harsh physical environment. Black (1976) showed that damage by the limpet *Acmaea insessa* pruned the blades of a kelp species, *Egregia menziesii*, making it less susceptible to removal by waves via a reduction in size. However, grazing may also loosen holdfasts (Tegner et al., 1995; Milligan and DeWreede, 2000) and damage stipes (Biedka et al., 1987), causing seaweed mortality in strong wave action.

Ecologists often view herbivory as a "negative" impact on algal communities; negative due to a reduction of algal biomass or loss of reproductive potential for adult plants. Frequently, herbivore effects on plant distributions, biomass, and diversity are dramatic (Paine and Vadas, 1969; Foreman, 1977; Ayling, 1981; Harrold and Reed, 1985). It is estimated that (commonly) 10-20% of the available algal biomass passes through herbivores, whereas most goes to the detrital food web (Vadas, 1985).

Alternatively, herbivores may inadvertently "contribute positively" to algal population densities by fracturing plants and facilitating gamete dispersal or dispersal of vegetative parts. For example, the mature cystocarps of *Iridaea* sp. (now *Mazzaella*) are the preferred food of the amphipod *Hyale media*, but it eats only a fraction of the spores it breaks open. As a result, many algal spores stick to the amphipod's legs and are dispersed; some of the spores that are eaten survive and are later deposited back onto the substratum (Buschmann and Bravo, 1990). Santelices et al. (1983) reported that spores of many opportunistic algal species survive digestion by the sea urchin, *Tetrapygus niger*. Their experimental results showed that (spores of) approximately 42% of the algal species consumed by *T. niger* could survive passage through the digestive tract, producing new thalli after culturing the urchin fecal pellets.

According to Carpenter (1986), herbivores can be categorized into three groups: (1) fish (large foraging ranges, low densities), (2) urchins (intermediate ranges and densities), and (3) mesograzers (small foraging ranges and high densities). Generally, herbivorous fish occur most frequently in warmer waters (40° N - 40° S) and significantly impact tropical communities (Horn, 1989). Urchins eat mostly algae, but are considered omnivores (Lawrence, 1975; Briscoe and Sebens, 1988) and are known to utilize variable feeding strategies. Some urchins are sedentary, others are nomadic; members of a species may even behave differently depending on their density (Vadas, 1990). Furthermore, highly mobile individuals of urchin species can be selective with their food choices, whereas sedentary urchins are often generalists. Vadas (1990) found

that urchins in the tropics tend to be sedentary where grazing pressure from fish is high and search costs are also high. However, urchins in mid-latitude habitats tend to be more mobile where the algal biomass is high and herbivorous fish are few. Temperate zone urchins, such as the purple urchin, *Strongylocentrotus purpuratus*, and the large red urchin, *S. franciscanus*, are responsible for the devastation of kelp forests in southern California (as reported by Leighton et al. in 1966). Severe attacks by urchins on kelp beds (primarily in southern California and Nova Scotia) have received considerable attention in the last century due to the commercial value of kelp and invertebrates (e.g. abalone, rock lobster) associated with it (Mann, 1977; Scheibling, 1986; Harrold and Pearse, 1987; Garnick, 1989; Keats et al., 1990; Leinaas and Christie, 1996). Furthermore, mesograzers (including snails, amphipods, copepods, polychaete worms) are an important group of herbivores; but they are difficult to study because their size and activity make density manipulation challenging in the field. Small (in size) does not necessarily equate to harmless (as an herbivore); an amphipod outbreak caused a 40% reduction of kelp available for harvesting at Point Loma, California in 1986 (Merck, 1990).

Herbivory can also affect competition among seaweeds. Several studies have shown that algal species diversity is highest with intermediate grazing pressure (Paine, 1977; Lubchenco 1978). Furthermore, herbivores exhibit specific feeding preferences when food choices are diverse. Foreman (1977) found that the green urchin, *Strongylocentrotus droebachiensis*, removes foliose macrophytes first, then filamentous forms and, finally, small amounts of crustose

algae and coralline species. Brawley and Adey (1981) found that filamentous pioneer algae (e.g. *Hincksia rallsiae*, *Bryopsis hypnoides*, *Centroceras clavulatum*) were quickly grazed by gammarid amphipods, which allowed a chemically-defended alga, *Hypnea spinella*, to dominate.

Plant characteristics that may affect the probability that an herbivore will eat at least part of an encountered plant include the morphology of the plant (e.g. size, shape, toughness) (Nicotri, 1980; Cruz-Rivera and Hay, 2001), chemical composition of the plant (e.g. presence or absence of feeding stimulants/deterrents) (Van Alstyne, 1988; Paul and Van Alstyne, 1992; Hay, 1996), and factors that more directly affect the nutritional status of the plant (e.g. caloric, protein, vitamin or mineral content) (Himmelman and Carefoot, 1975; Lubchenco and Gaines, 1981). For purposes related to this study, *Codium fragile* may be a palatable food source as it is not tough or calcified, mucus production is minimal (= not a feeding deterrent), and no known chemical compounds are produced to deter herbivores at first contact. *Codium fragile's* spongy texture and unique thallus construction (e.g. coenocytic) may make this species even more vulnerable to herbivory than other multicellular algal species sharing space in the same habitats. *Codium fragile's* coenocytic thalli contain no transverse walls or septa. However, there are internal plugs or pad-shaped thickenings that hold the cell contents in place, as well as prevent the loss of an entire filament when injury occurs (Hurd, 1916; Scagel, 1966). If this "healing process" is utilized by a *C. fragile* plant following an herbivore encounter, the

tenacity of the individual plant may also be compromised in the form of reduced biomass, a damaged stipe or weakened holdfast.

In Chapter 1, I described the occurrence and abundance of *Codium fragile* at different field sites in Barkley Sound. As reviewed above, herbivory has significant effects on marine algae; thus, herbivory is a likely candidate to affect the abundance of *C. fragile*. First, I identified potential herbivores within these habitats and examined patterns of herbivore distribution in relation to *C. fragile*. Second, I compared the attractiveness of *C. fragile* to other common seaweeds (found within these habitats) by conducting 2-choice feeding experiments with generalist herbivores (e.g. purple urchins, *Strongylocentrotus purpuratus*, and black chitons, *Katharina tunicata*) found at Prasiola Point. Once it was determined that all experimental seaweeds were at least minimally consumed by these herbivores, I compared food quality of the three seaweeds to test whether feeding preferences were related to nutritive (organic) values derived from an absorption efficiency experiment. Last, I was interested in comparing effects of mono-macroalgal diets on somatic and reproductive growth of these generalist herbivores. This last experiment was necessary to determine whether short-term food preferences are correlated with long-term (four month) macroalgal diets as a means of explaining how food attractiveness is related to reproductive fitness for an herbivore. Herbivore food choices can be characterized as evolutionary adaptations within rocky, intertidal habitats used to advance a species by increasing their reproductive output. This approach (with emphasis on the herbivore) can provide insight as to the relative long-term attractiveness of *C.*

*fragile* among such generalist herbivores, which might explain lowered *C. fragile* abundance in the field over time.

## 2.2 Comparison of "specialist" vs. "generalist" herbivores

Herbivores can be divided into two categories when examining impacts on an algal population. There are "specialists", those that prey exclusively upon a select species or genus of seaweeds, and "generalists" which usually show no particular preference within an algal community as long as food is plentiful. The sacoglossan (mollusc), *Elysia hedgpethi*, is one such specialist grazer; it sucks chloroplast contents from its host, *Codium fragile*. It is small (to 25 mm), can be cryptic (same coloration as host), and has a reported range from Vancouver Island, British Columbia to Bahia Tortugas, Baja California (Behrens, 1991). Another sacoglossan, *Placida dendritica*, is common in both temperate and boreal coastal waters in the N. Pacific, N. Atlantic and Mediterranean (Trowbridge, 1992). Throughout its geographic range, it feeds on green algae of the genera *Codium* and *Bryopsis*. During the time frame of this study (Summer 1998-2001), these two species of sacoglossans were not found at any of my study sites.

However, generalist herbivores are plentiful at Prasiola Point. Shallow tidepools, containing large numbers of sea urchins (*Strongylocentrotus purpuratus* and *S. franciscanus*), are fringed with a dense stand of *Codium fragile*. (Figure 2.1) These tidepools are exposed only during low tides and also support a variety of kelp species (e.g. *Hedophyllum sessile*, *Laminaria setchellii*, *Alaria marginata*, *Desmarestia munda*), as well as some foliose reds (e.g.



Figure 2.1 - Shallow tidepools, containing large numbers of sea urchins (*Strongylocentrotus purpuratus* and *S. franciscanus*), are fringed with a dense stand of *Codium fragile* at Prasiola Point.

*Mazzaella splendens*). Therefore, food is plentiful for these species of urchins and their populations remained mostly sedentary within the lower tidepools (based on personal observations).

Laur et al. (1986) questioned whether substrate types acted as barriers to sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*), as a means of halting urchin fronts from "mowing" through an algal community. They found that soft substrates and rock walls (especially those covered with stinging anemones) impede the progress of grazing urchins, and individuals of these species move best over flat, hard surfaces. Yet, in the absence of predator control, urchins mostly surmount such barriers when water motion subsides. Though physical barriers exist at my study site (e.g. short vertical edges encompassing part of the tidepool and a ~4m high rock wall encircled part of this bedrock platform site), both species of urchins have access to all seaweeds as they are draped over the edges or growing in patches within the tidepools themselves. I investigated whether grazing by purple urchins may contribute to the irregular occurrence of *Codium fragile* at this site.

Another common invertebrate found at middle to lower intertidal heights at Prasiola Point is the black chiton, *Katharina tunicata*. *Katharina tunicata* is known to graze on many algal species that are found within the same zone as *Codium fragile* (Himmelman and Carefoot, 1975). Although exposed to air during low tide, this species is not extremely sensitive to light and is often found in the open, feeding on algae (Harbo, 1999). Duggins and Dethier (1985)

investigated the interplay between *K. tunicata* and the algal community within a low intertidal habitat in the San Juan Islands, Washington, USA. They found that over time, algal abundance and diversity increased when *K. tunicata* was removed from experimental areas. Conversely, when *K. tunicata* was added, the abundance of all plants (except crusts, diatoms, and surfgrass) decreased and overall diversity declined. I investigated whether this grazer impacts the abundance of *C. fragile* plants at Prasiola Point.

Coincidentally, both of these generalist herbivores are absent at the Seppings Island field site. Perhaps, herbivory by purple urchins and/or black chitons is the controlling factor at Prasiola Point where the occurrence of *Codium fragile* plants is irregular compared to the greater abundance of *C. fragile* plants observed at Seppings Island.

## 2.3 Introduction

### 2.3.1. Spatial pattern analysis of black chitons

Strong, interactive links between black chitons (*Katharina tunicata*), kelps, and the abundance and diversity of other algae have been demonstrated in the San Juan Islands, Washington and Oregon coastal regions (Dethier and Duggins, 1988). In Washington, the perennial brown alga *Hedophyllum sessile* increased in abundance following *K. tunicata* removal; after 2-3 years, a variety of other kelp species showed increased abundance as well. Dethier and Duggins (1988) labeled *K. tunicata* as a "strong interactor", as pronounced changes occur when it is removed from specific habitats. Piercy (1987) reported that *K. tunicata* has a wide tidal height distribution, occurs on substratum slopes

from 0-90 degrees, and has a generalist diet composed of diatoms, *Ulva* sp., filamentous algae and macrophytes. If sea urchins are associated with lower intertidal pools due to more tolerable environmental conditions (increased submersion = lower risk of desiccation) and limited (to some degree) by physical barriers, are black chitons, *K. tunicata*, positively associated with the distribution of *Codium fragile* plants? A spatial pattern analysis was conducted to address this question at Prasiola Point, Barkley Sound.

Hypotheses:

H<sub>0</sub>: Chitons, *Katharina tunicata*, are not associated with *Codium fragile* plants found at any intertidal height at Prasiola Point.

H<sub>A</sub>: Chitons, *Katharina tunicata*, are positively associated with *Codium fragile* plants found at different intertidal heights at Prasiola Point.

### 2.3.2 Feeding preference experiment

High grazing pressure can radically alter the species composition of a community. Some researchers (Paine and Vadas, 1969; Duggins and Dethier, 1985) reveal herbivore impacts by removing the dominant grazer from the community. Mooney (2001) tested the effects of sea urchin removal (*Strongylocentrotus franciscanus*) near Hot Springs Cove on northern Vancouver Island, British Columbia. Understory algal species (e.g. *Laminaria bongardiana*, *Pterygophora californica*) and canopy species (e.g. *Nereocystis luetkeana*) grew in study plots where all urchins were removed. Intermediate levels of urchin removal resulted in a patchwork of smaller urchin-dominated and kelp-dominated areas. Meanwhile, his control plots remained as urchin-dominated

barrens throughout the study period. This experimental approach (focusing on the removal of a specific herbivore) was not applicable to my study for the following reasons: (1) the topography of Prasiola Point would have posed difficulties in establishing different experimental plots, (2) wave exposure at this site made it difficult to secure any kind of semi-permanent experimental apparatus, and (3) my other intertidal field sites (e.g. Second Beach, Scott's Bay, Seppings Island) did not naturally support both *Codium fragile* and generalist herbivores (e.g. purple urchins, black chitons).

Nonetheless, herbivore food preferences are of considerable interest to ecologists, from aquatic to terrestrial habitats, and both laboratory and field-based studies have proven useful (Larson et al., 1980; Trowbridge, 1993; Scheibling and Anthony, 2001). According to Nicotri (1980), "preference" determines the quantity and quality of food ingested by a grazer; hence, affecting both the herbivores' physiological condition and overall fitness. Two components of food preference are commonly studied: (1) the selection of a potential food item (= attractiveness) and (2) the rate at which the food item is digested (= edibility). Attractiveness is usually measured by methods that allow herbivores to choose between several possible foods. Herbivores may be responding to chemoreception over some distance or to direct chemical and tactile handling of the plant (Nicotri, 1980). Conversely, methods dealing with edibility assume that herbivores consume and digest preferred foods faster. Edibility will not only reflect the speed with which the food item alleviates the physiological needs of the herbivore, but also the rate at which the item is

handled and ingested (Nicotri, 1980). It should be noted that within the scientific literature, attractiveness and edibility have sometimes been used interchangeably; however, it is clear that they are distinct and measure different aspects of feeding preference (Lawrence, 1975).

Nicotri (1980) compared the feeding preferences of two common mesograzers associated with Woods Hole, Massachusetts marine habitats. Isopods, *Idotea baltica*, and amphipods, *Ampithoe valida*, were offered different combinations of 17 macrophytes and one seagrass species, *Zostera marina*. *Codium fragile* was included in this study, as well as representative species from many common macroalgal genera (e.g. *Spongomorpha*, *Ulva*, *Ascophyllum*, *Fucus*, *Petalonia*, *Sargassum*, *Scytosiphon*, *Ceramium*, *Chondrus*, *Corallina*, *Dictyosiphon*, *Gracilaria*, *Hypnea*, *Neogardhiella*, *Porphyra*). *Codium fragile* ranked first in both attractiveness and edibility for the isopod, *I. baltica*; whereas, *C. fragile* ranked last in attractiveness for the amphipod, *A. valida* (edibility was not measured). These results indicate that there are complexities involved with herbivore feeding preferences at the mesograzer level.

Many studies have investigated feeding preferences of sea urchins in diverse macroalgal communities (Vadas, 1977; Larson et al., 1980; Scheibling and Anthony, 2001; Van Alstyne et al., 2001; Mooney, 2001). Prince and LeBlanc (1992) compared feeding preferences of the urchin *Strongylocentrotus droebachiensis* exposed to the invasive *Codium fragile* ssp. *tomentosoides* and four native macroalgae (e.g. *Agarum cribrosum*, *Ascophyllum nodosum*, *Chondrus crispus*, *Laminaria saccharina*) in Maine, USA. In multiple-diet

experiments (5 seaweed species per urchin), significantly less *C. fragile* ssp. *tomentosoides* was eaten than the rhodophyte *Chondrus crispus*, but significantly more *C. fragile* ssp. *tomentosoides* was consumed than the phaeophyte *Agarum cribrosum*. Therefore, though it is not their "favorite", sea urchins in Maine will eat *Codium* (*fragile* ssp. *tomentosoides*) when they come into contact with it. Will this hold true for native *C. fragile* in Barkley Sound? If so, this could be one explanation for the lowered occurrence of *C. fragile* plants at Prasiola Point.

During high tides at Prasiola Point, purple urchins (*Strongylocentrotus purpuratus*) (Figure 2.2a) may consume *Codium fragile* in addition to other common intertidal seaweeds. Black chitons (*Katharina tunicata*) (Figure 2.2b) were also included in this study as possible herbivores of *C. fragile* due to their abundance and proximity to *C. fragile* plants at Prasiola Point. Coincidentally, the kelp, *Hedophyllum sessile*, and the rhodophyte, *Mazzaella splendens*, also occur within the same habitats and zonation range as *C. fragile*. Both *H. sessile* and *M. splendens* are seasonally abundant and available to grazers. Since both grazers could potentially be using the same plants for food (see Figure 2.2c), it is of interest to compare the similarity of food preferences using these three algal species. Hypothetically, if these herbivores prefer the other two common and interspersed algal species over *C. fragile*, then herbivory may not be a causative factor for the observed distribution patterns of *C. fragile* at Prasiola Point.

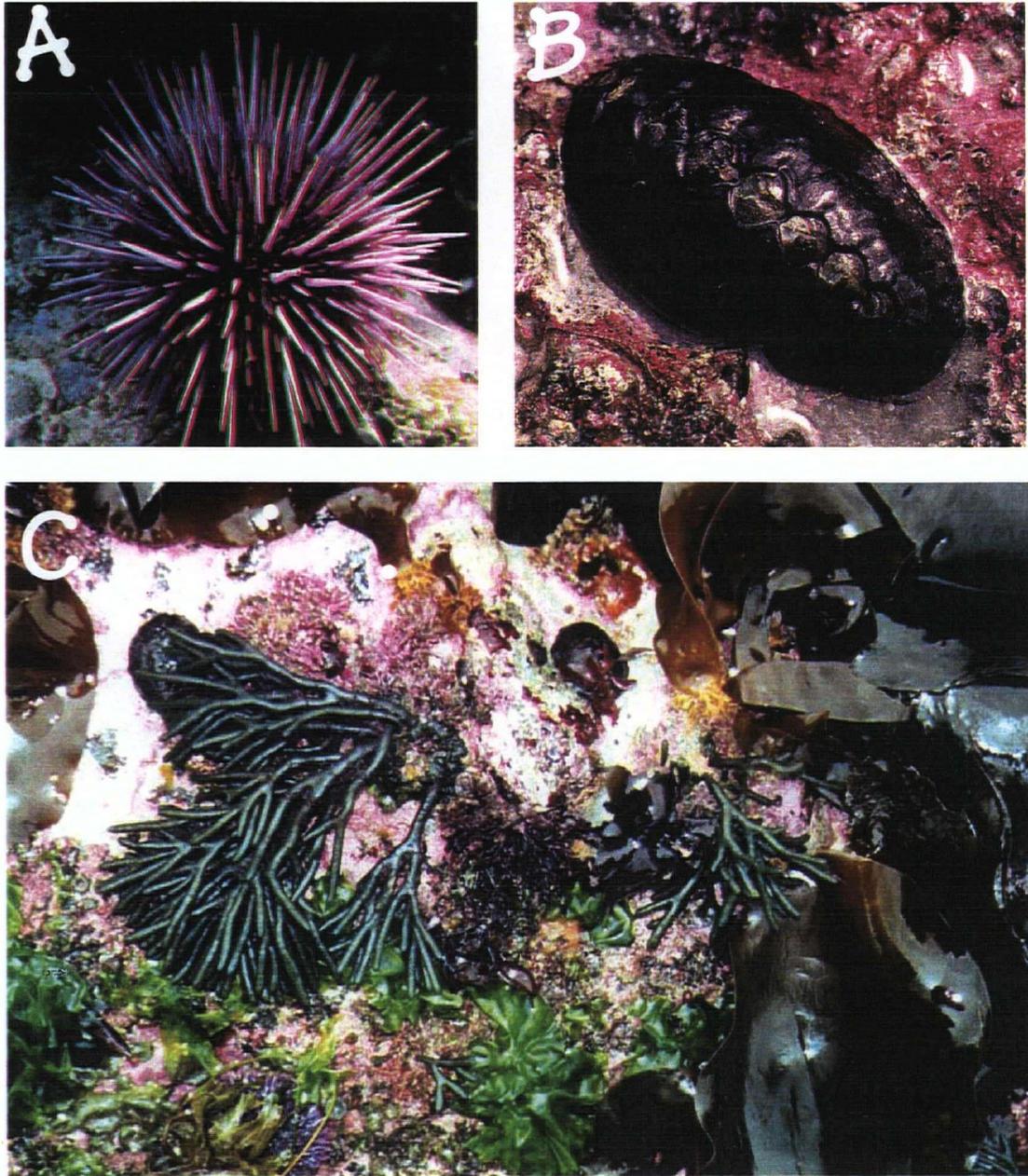


Figure 2.2 – Both (A) purple urchins, *Strongylocentrotus purpuratus*, and (B) black chitons, *Katharina tunicata*, have access to many algal species that are found at Prasiola Point (C) (e.g. *Codium fragile*, *Hedophyllum sessile*, *Mazzaella splendens*).

Hypotheses:

H<sub>0</sub>: Generalist herbivores (purple sea urchins, black chitons) show no feeding preference when offered intertidal macroalgae (*Codium fragile*, *Hedophyllum sessile*, *Mazzaella splendens*).

H<sub>A</sub>: Generalist herbivores show distinct preferences (*Hedophyllum sessile* will be consumed most often) when offered different species of intertidal macroalgae.

#### 2.4.3. Absorption efficiency experiment

Though feeding preference studies help us to define the choices herbivores make within macroalgal communities, they do not necessarily tell us what these choices are based on. For example, Nicotri (1980) examined the macroalgal preferences of the isopod, *Idotea baltica*, and the amphipod, *Ampithoe valida*. Nicotri found that *I. baltica* is attracted to large, tough, branched algae (perennials), while *A. valida* is attracted to softer, filamentous or bladed algae (annuals). Apparently, *I. baltica* responds more to algal morphology and availability, while *A. valida*'s attraction to food is related to the nutritive value of the algae. Furthermore, *I. baltica*'s mobility, possible susceptibility to fish predation and preference for moderate wave exposure may cause it to select algae as habitat, rather than as nutritious food. Perhaps, feeding preferences of purple urchins (*Strongylocentrotus purpuratus*) and black chitons (*Katharina tunicata*) are more complicated than my first assumption. As stated earlier, *Codium fragile* is morphologically different from the bladed *Hedophyllum sessile* and *Mazzaella splendens*. These herbivores may find *C.*

*fragile*'s spongy, cylindrical branches more challenging to feed on, compared to blades of different textures (soft vs. leathery). Therefore, conclusions from feeding preference studies may not give us the whole story. As scientists, we may need to explore other questions in order to make assumptions applicable to ecological interactions.

The efficiency with which ingested food is absorbed across the gut is an important parameter in studies of trophic aspects of marine ecology. In studies of animal energetics, determining the feeding or ingestion rate is not sufficient to determine the energy input for the animal. Part of this ingested food is not absorbed across the gut and, thus, passes out of the gut as feces. Farias et al. (2003) measured the physiological energetics of the green abalone, *Haliotis fulgens*, fed a balanced diet. They found that low feeding activity of abalone was compensated for by higher absorption efficiencies. As discussed earlier, feeding rates can be used as another determination of feeding preference. Therefore, less-preferred foods may not necessarily be of lesser quality to the herbivore. A knowledge of the absorption efficiency for given foods allows one to calculate the true energy input in feeding experiments where ingestion rates are known.

Previous studies by Lowe and Lawrence (1976) have used sea urchins for this type of experiment due to the fact that large quantities of feces can be easily collected over a short time period. I found that chitons also produced feces that I could collect. Since all three macroalgal species (*Codium fragile*, *Hedophyllum sessile*, *Mazzaella splendens*) are available during feeding cycles of urchins and chitons, are they of different nutritive value to these grazers? To test this

question, both purple urchins and black chitons were utilized to determine whether or not native *C. fragile* is a high quality food source for short-term use (e.g. energy), compared to the common and available *H. sessile* and *M. splendens*.

Hypotheses:

H<sub>0</sub>: Generalist herbivores (purple sea urchins, black chitons) are able to equally absorb (across the gut) all organic matter derived from mono-macroalgal diets (*Codium fragile* vs. *Hedophyllum sessile* vs. *Mazzaella splendens*).

H<sub>A</sub>: Generalist herbivores have absorption efficiencies similar to macroalgal preferences ranked by quantity consumed.

#### 2.3.4. Fitness vs. macroalgal diet experiment

Foraging models are based on the premise that strategies used in exploiting prey have evolved to maximize fitness (Pyke et al., 1977; as cited in Lemire and Himmelman, 1996). This implies that feeding behaviors represent long-term (evolutionary) adaptations to optimize growth, reproduction, and ultimately, the production of offspring. Several factors influence the fitness a predator derives from exploiting a given food source: (1) the nutritional value of the prey, (2) the time required to handle the prey, and (3) the time and energy involved with searching for the prey (Sih, 1987).

Based on field observations, the three seaweeds utilized in the previous feeding experiments are available to both purple urchins and black chitons at the same intertidal elevations and seasonally available during the feeding periods of both herbivore's reproductive cycles. Hypothetically, both types of herbivores

may spend similar amounts of time searching (if they utilize similar search strategies combined with random encounters with these three algal species). "Handling time" may be variable as these three seaweeds are different in morphology. Though *Hedophyllum sessile* and *Mazzaella splendens* (smooth blades) are morphologically different than *Codium fragile* (dichotomously branched cylinders), they are similar in size, have relatively short stipes (or none at all), and are draped on rocks when waters have receded.

Generally speaking, foods of higher nutritive value are more easily converted to energy (as they are absorbed more efficiently across the gut) by the consumer. For mobile species that are actively foraging for food over long distances, this concept is important for both short-term and long-term fitness. However, generalist herbivores (e.g. purple urchins and black chitons) at Prasiola Point are more sedentary than transient. At this field location, purple urchins remain in lower intertidal pools that are bordered by some degree of physical barrier (see discussion in 2.2). For many purple urchins in these tidepools, *Codium fragile* may be the first food they come into contact with (personal observation). Many chiton species are known to travel short distances while foraging (Focardi and Chelazzi, 1990), but have also been reported to exhibit "homing" behavior (return to a designated environmental niche after foraging for food) (Mook, 1985; Chelazzi et al., 1990). Black chitons at Prasiola Point have equal access to all three seaweeds utilized in my studies, rather than increased frequency of access to one species. For sedentary purple urchins, perhaps the conversion of high quality food to energy (used for short-term

purposes) is not as important as a steady food supply (of poor quality food) to be used for somatic and reproductive growth. I tested the long-term (= 4 months) nutritive value of these three macroalgae on purple urchins and black chitons to confirm or reject whether short-term food preferences and absorption efficiencies are correlated with long-term fitness and/or survival.

Hypotheses:

H<sub>0</sub>: Generalist herbivores (purple sea urchins, black chitons) offered one of four mono-diets (*Codium fragile*, *Hedophyllum sessile*, *Mazzaella splendens* or nothing at all) will show no differences in somatic and/or reproductive growth indices.

H<sub>A</sub>: Generalist herbivores offered one of four mono-diets will show increases in somatic and/or reproductive growth indices (*Hedophyllum sessile* > *Mazzaella splendens* > *Codium fragile*) when compared to the control.

## 2.4 Materials and Methods

### 2.4.1. Spatial pattern analysis of black chitons

Thirty-meter transect lines were laid out during low tide at Prasiola Point, Barkley Sound. Measurements were collected from three elevations (high, middle, low) in August 2001. I measured distances to the chiton from either a *Codium fragile* holdfast or a randomly chosen point on a transect line (the random points served as controls). T-tests were used for comparisons between chiton/*C. fragile* distances vs. chiton/random point distances at each intertidal height (high, middle, low). I predicted *a priori* that black chitons, *Katharina tunicata*, are not associated with *C. fragile* plants at any intertidal height at

Prasiola Point (e.g. the chitons are not closer to or associated with *C. fragile* than they are to random points).

#### 2.4.2 Feeding preference experiment

Feeding preference studies were conducted following methods outlined by Prince and LeBlanc (1992) using two species of generalist herbivores (e.g. purple sea urchins, black chitons). In October 1999, *Strongylocentrotus purpuratus* and *Katharina tunicata* were collected during low tide at Prasiola Point. All collected animals were held in outdoor sea tables at Bamfield Marine Sciences Centre, British Columbia, and starved for one week. The timing of this experiment (e.g. October) was chosen based on reported reproductive cycles for both purple urchins and black chitons on the outer coast of Vancouver Island. According to Himmelman (1976), purple urchins spawn in late spring and resume feeding shortly afterwards in order to build gonad mass for future spawning events. Black chitons, however, spawn in June and do not begin building gonad reserves until fall and winter. With this information, I chose to conduct all feeding experiments (e.g. preference, absorption efficiency, diet vs. fitness) when both species would be actively feeding in the field as part of their annual cycle. Hypothetically, this would increase the likelihood of feeding for both species when confined within the experimental cages.

This two-species-choice experimental design is described using the purple sea urchin, *Strongylocentrotus purpuratus*; the same design was used for *Katharina tunicata*. Individual sea urchins were placed in single-occupancy, flow-through containers (within a sea table) and provided with equal amounts of pre-

weighed algae (e.g. *Codium fragile* and *Hedophyllum sessile*, *C. fragile* and *Mazzaella splendens*, *H. sessile* and *M. splendens*). Identical amounts of pre-weighed algae were placed in flow-thru containers (no urchins added) within the same sea tables to serve as controls. These controls were used to record changes in algal weight (due to growth/decay). After several days of feeding, uneaten and control algae were recovered and re-weighed. Multiple replicates (n=7) were utilized for both treatments (herbivore present) and controls to increase power of analysis using before vs. final wet weights. Based on recommendations by Peterson and Renaud (1989), differences in weight loss (initial vs. final) for each pair of algal species were calculated separately for treatments and controls. Control differences were subtracted from randomly assigned treatment differences as a means of correcting treatment data. These results were then used to rank algae from most preferred to least preferred by *S. purpuratus*. Based on the findings of earlier studies (Larson et al., 1980; Prince and LeBlanc, 1992; Scheibling and Anthony, 2001), I predicted that *H. sessile* would be most preferred by purple urchins as it is a kelp species. I retained the same prediction of algal preference for black chitons (i.e. *H. sessile* would be most preferred) based on earlier findings (Himmelman & Carefoot, 1978; Markel & DeWreede, 2001).

#### 2.4.3. Absorption efficiency experiment

In October 1999, both purple urchins, *Strongylocentrotus purpuratus*, and black chitons, *Katharina tunicata*, were collected during low tide at Prasiola Point, held in outdoor sea tables at Bamfield Marine Sciences Centre, British

Columbia, and starved for one week. Experimental designs were identical for both purple urchins and black chitons; therefore, methods are described for purple sea urchins in detail. Individual sea urchins were placed in single-occupancy, flow-through containers (within sea tables) and provided with 10-20 g wet weight of either *Codium fragile*, *Hedophyllum sessile*, or *Mazzaella splendens*. A 2 g sample of each alga was collected, rinsed and dried at 90°C in a pre-weighed crucible for 48 hours. These samples were then used to determine the initial organic content of the seaweeds consumed.

Urchins were allowed to feed for two days with additional seaweed mass added as it was consumed. Feces were removed and discarded daily to avoid excretions derived from an earlier meal. On the third day, feces were removed from all compartments using a bulb pipette. Individual fecal samples were screened for debris, carefully rinsed with distilled water, transferred to a pre-weighed crucible and dried for 48 hours at 90°C. Concurrently, a small sample of each uneaten alga was collected, rinsed and dried at 90°C in a pre-weighed crucible for 48 hours. These algal samples were then used as a second estimate of organic food content, allowing for adjustments of gain (= growth) or loss (=degradation) of organic content during the feeding period. Three replicates were used in all steps of experimental design: for each alga consumed, and for initial and final organic content determinations.

All crucibles containing dried food and feces were then ashed in a muffle furnace at 500°C for 4 hours to completely oxidize any organic matter. After

cooling, each crucible was re-weighed and final values were used in the formula below:

Organic fraction for food and feces = (dry weight - ash weight)/dry weight

To determine the organic assimilation of food by urchins, Conover's (1966) equation was used:

$$U' = ((F - E)/((1 - E)F)) * 100$$

"F" and "E" are the organic fractions of food and feces respectively, and "U'" is Conover's organic absorption efficiency. Final values were then ranked accordingly; higher values are assumed to represent more "nutritious" foods as they are more readily absorbed by the gut over a specified time period.

#### 2.4.4. Fitness vs. macroalgal diet experiment

I utilized both purple urchins and black chitons for a long-term (~4 month) study to examine the effects of mono-macroalgal diets (*Codium fragile* only, *Hedophyllum sessile* only, *Mazzaella splendens* only) vs. the control (no macroalgae) on somatic and gonadal growth. These experiments were timed to coincide with the feeding behavior associated with both species' reproductive cycles in between spawning (see Himmelman, 1976). One hundred small (30 to 35 mm in diameter) sea urchins, *Strongylocentrotus purpuratus*, were collected at Prasiola Point in June 2002 and randomly divided into 5 groups of 20 individuals each. According to Lemire and Himmelman (1996), urchins of this size still have a strong potential for somatic growth yet, at the same time, are capable of producing maximum-size gonads (gonadal mass relative to total

mass). One of the five groups was sacrificed to obtain a measure of the wet mass of the gonads and test (including spines, musculature and hydrovascular system) at the beginning of the experiment. This information was used to test the assumption that collected urchins represented a homogenous population to study.

The other four groups of urchins were divided into treatment replicates. Plastic flow-through containers (19 cm x 34 cm x 11 cm) were used to house herbivores (purple urchins or black chitons) (n = 4-8 animals in each container) subjected to one of four dietary treatments: (1) *Codium fragile* only, (2) *Hedophyllum sessile* only, (3) *Mazzaella splendens* only, or (4) no macroalgae (= control). The fourth treatment served as controls for possible weight gains due to microalgal growth in the container. Individual containers (representing one of each treatment) were randomly stacked into a column and locked into a PVC tubing unit (Figure 2.3). All containers were secured within the PVC housing by cable ties to prevent the containers from sliding out due to physical movement. Each PVC unit was clipped to a nylon rope attached to a dock at Anchor Cove Marina (in Anacortes, WA); all containers were suspended at a uniform depth of 1.5 m below surface water. All containers experienced uniform environmental conditions at this location (e.g. light, low wave action, water quality parameters). Fresh seaweed (representing each macroalgal treatment) was re-supplied to the caged animals at weekly intervals to ensure uninterrupted food access and limit the effects of competition within the container. All containers were cleaned at the same time to prevent impacts from sedimentation/fouling organisms. Some



Figure 2.3 – Experimental apparatus used in macroalgal diet vs. herbivore fitness study. Plastic flow-thru containers (19 cm x 34 cm x 11 cm) were used to house herbivores (purple urchins or black chitons) ( $n = 4-8$  animals in each container) subjected to one of four dietary treatments: (1) *Codium fragile* only, (2) *Hedophyllum sessile* only, (3) *Mazzaella splendens* only, or (4) no macroalgae (control). Individual containers (representing one of each treatment) were randomly stacked into a column and locked into a PVC tubing unit. All containers were secured within the PVC housing by cable ties to prevent the containers from sliding out due to physical movement. Each PVC unit was clipped to a nylon rope attached to a dock at Anchor Cove Marina (in Anacortes, WA); suspending all containers to a uniform depth of 1.5 m below surface water.

mortalities occurred, as well as missing containers, which lowered the number of replicates for some treatments. After 115 days, all remaining urchins from all treatments were dissected at Shannon Point Marine Center, Anacortes, Washington for determination of initial vs. final growth parameters (e.g. test diameter, total biomass, gonadal mass).

The above experimental design was described using purple urchins; chitons were utilized in the same manner. One hundred chitons were collected from Prasiola Point in July 2002. Initially, twenty chitons were sacrificed to obtain a measure of the wet mass of the gonads and total mass at the beginning of the experiment. This information was used to validate the assumption that collected chitons represented a homogenous population to study. Eighty chitons were divided into the four treatments and subjected to the same experimental design described above. After 115 days, all remaining chitons were dissected at Shannon Point Marine Center for determination of initial vs. final growth parameters (e.g. total biomass, gonad mass). I predicted that results (from both herbivore species) would be similar to my results from both feeding preference and absorption efficiency studies.

## 2.5 Results

### 2.5.1. Spatial pattern analysis of black chitons

Table 2.1 shows that *Katharina tunicata* is not significantly associated with *Codium fragile* plants at middle or high intertidal heights at Prasiola Point (Middle,  $P=0.30$ ; High,  $P=0.09$ ). However, within the lower intertidal zone, *K. tunicata* is significantly associated with *C. fragile* plants ( $P=0.005$ ).

Accepted Hypothesis:

$H_A$ : Chitons, *Katharina tunicata*, are positively associated with *Codium fragile* plants only within the low intertidal zone at Prasiola Point.

Table 2.1 - Spatial pattern analysis of the black chiton, *Katharina tunicata*, at Prasiola Point, Barkley Sound. Mean distances were recorded from multiple chiton individuals and from random points to the nearest *Codium fragile* holdfast. T-tests were used for comparisons at each intertidal height (high, middle, low). N = number of chitons sampled at each height.

Location/Treatment:	N:	Mean Distance: (cm)	S.E.:	P:
<b>HIGH</b>				
<i>Katharina</i> ⇒ <i>Codium</i>	11	20.72	6.78	0.09
<i>Katharina</i> ⇒Random Pt.	11	38.36	7.23	
<b>MIDDLE</b>				
<i>Katharina</i> ⇒ <i>Codium</i>	26	16.77	2.44	0.30
<i>Katharina</i> ⇒Random Pt.	26	20.48	2.61	
<b>LOW</b>				
<i>Katharina</i> ⇒ <i>Codium</i>	26	19.27	2.20	0.005
<i>Katharina</i> ⇒Random Pt.	26	35.79	5.15	

### 2.5.2. Feeding Preference Experiment

Table 2.2 shows that both purple urchins and black chitons exhibited identical feeding preferences: *Hedophyllum sessile* > *Mazzaella splendens* > *Codium fragile*. Both purple urchins and black chitons consumed almost three times as much *H. sessile* as either *C. fragile* or *M. splendens*. Statistical analyses were not performed as my main objective was to determine preference order and that these seaweeds are consumed by urchins and chitons.

Accepted Hypothesis:

H<sub>A</sub>: Generalist herbivores show distinct preferences (*Hedophyllum sessile* will be consumed most often) when offered different species of intertidal macroalgae.

Table 2.2 – Feeding preference results from purple urchins (*Strongylocentrotus purpuratus*) and black chitons (*Katharina tunicata*) fed two-choice macroalgal diets in October 1999. Choices were: *Codium fragile* vs. *Hedophyllum sessile*, *Hedophyllum sessile* vs. *Mazzaella splendens*, *Codium fragile* vs. *Mazzaella splendens*. “N” represents number of replicates used for each treatment. Mean percent consumed values were derived from treatment values randomly corrected by control values.

Grazer/ Food Choices:	N:	Mean % Consumed:
Purple Urchins		
<i>Codium</i> / <i>Hedophyllum</i>	7	3.0 / 9.0
<i>Hedophyllum</i> / <i>Mazzaella</i>	7	16.0 / 8.0
<i>Codium</i> / <i>Mazzaella</i>	7	4.0 / 11.0
Black Chitons		
<i>Codium</i> / <i>Hedophyllum</i>	7	4.0 / 11.0
<i>Hedophyllum</i> / <i>Mazzaella</i>	7	10.0 / 7.0
<i>Codium</i> / <i>Mazzaella</i>	7	3.0 / 9.0

### 2.5.3. Absorption efficiency experiment

Table 2.3 shows that both purple urchins and black chitons can more readily absorb (across the gut) *Mazzaella splendens* > *Hedophyllum sessile* > *Codium fragile*. Using "U" values derived from Conover's equation, *C. fragile* was absorbed by purple urchins 23% and 31% less efficiently than *M. splendens* and *H. sessile* respectively. For black chitons, *C. fragile* was absorbed 17% and 33% less efficiently than *M. splendens* and *H. sessile* respectively.

Accepted Hypothesis:

H<sub>A</sub>: Generalist herbivores have absorption efficiencies similar to macroalgal preferences ranked by quantity consumed.

Table 2.3 – Absorption efficiency values derived from purple urchins, *Strongylocentrotus purpuratus*, and black chitons, *Katharina tunicata*, offered one of three macroalgal diets (*Codium fragile*, *Hedophyllum sessile*, or *Mazzaella splendens*) in October 1999. "N" represents number of replicates used for each macroalgal treatment. "U" values were calculated following Conover's equation (Conover, 1966). Final values are ranked accordingly; higher values represent foods that are more easily absorbed across the guts of herbivores.

Grazer/ Macroalgal Choices:	N:	Mean U':
<b>Purple Urchins</b>		
<i>Mazzaella splendens</i>	6	55.70
<i>Hedophyllum sessile</i>	6	42.53
<i>Codium fragile</i>	6	13.07
<b>Black Chitons</b>		
<i>Mazzaella splendens</i>	6	79.94
<i>Hedophyllum sessile</i>	6	39.90
<i>Codium fragile</i>	6	13.31

#### 2.5.4. Fitness vs. macroalgal diet experiment

Figures 2.4-2.8 show that *Hedophyllum sessile* increased urchin test size, increased both urchin and chiton biomass, and significantly increased both urchin and chiton gonadal mass (=increased reproductive potential) compared to control treatments (no macroalgae). Figures 2.4 and 2.5 show that *Mazzaella splendens* significantly increased both test size and biomass for urchins, compared to the controls. However, *M. splendens* was not significantly different than control treatments when measuring chiton biomass or both species' gonadal mass (Figures 2.6-2.8). Figures 2.4 and 2.5 show that *Codium fragile* produced the smallest increases for both urchin test size and biomass. Furthermore, *C. fragile* treatments were not significantly different from control treatments in chiton biomass and both urchin/chiton gonadal mass (Figures 2.6-2.8).

Accepted Hypothesis:

H<sub>A</sub>: Generalist herbivores offered one of four mono-diets will show increases in somatic and/or reproductive growth indices (*Hedophyllum sessile* > *Mazzaella splendens* > *Codium fragile*) when compared to the control.

## *Strongylocentrotus purpuratus*

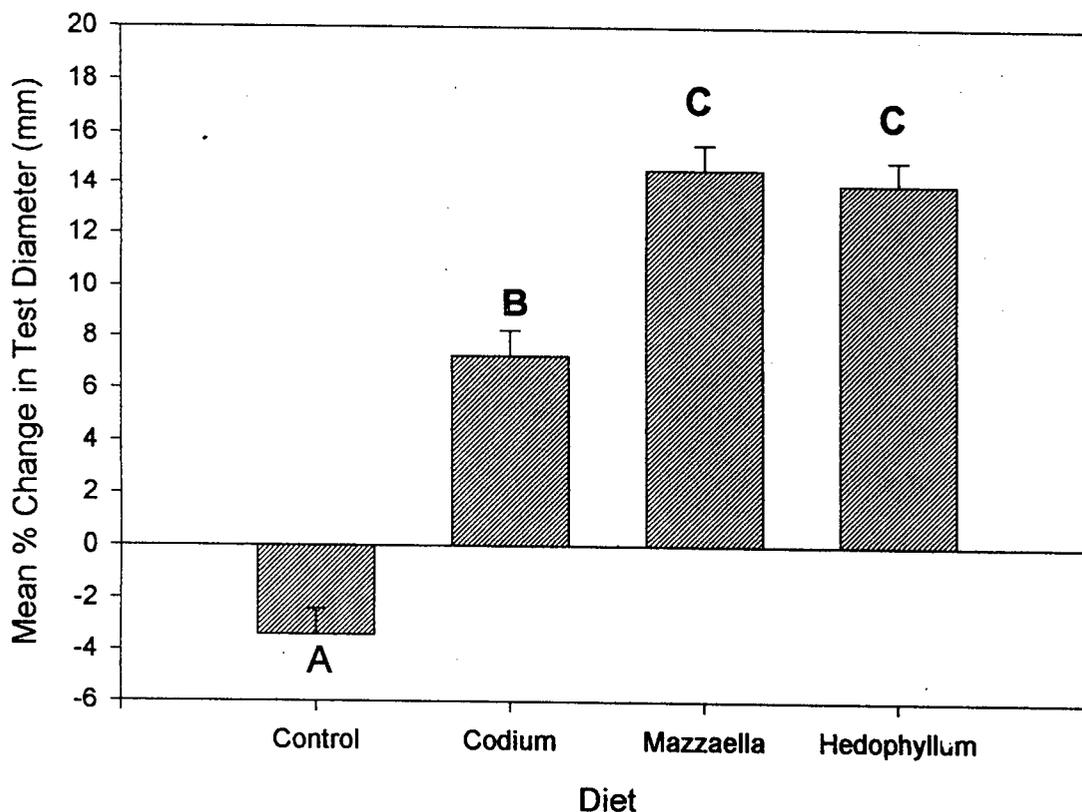


Figure 2.4 – Purple urchins, *Strongylocentrotus purpuratus*, were offered one of four macroalgal diets (*Codium fragile*, *Mazzaella splendens*, *Hedophyllum sessile*) or nothing at all (control) for ~4 months in flow-thru cages suspended from a marina dock. Initial vs. final measurements were used to calculate mean % change urchin test diameters. Standard error bars are shown. One-way ANOVA results indicate that all macroalgal diets were significantly different from the control ( $F=66.85$ ,  $P=0.01$ ). Tukey comparison of mean results indicate there were three significantly different groups (e.g. "A", "B", "C").

## *Strongylocentrotus purpuratus*

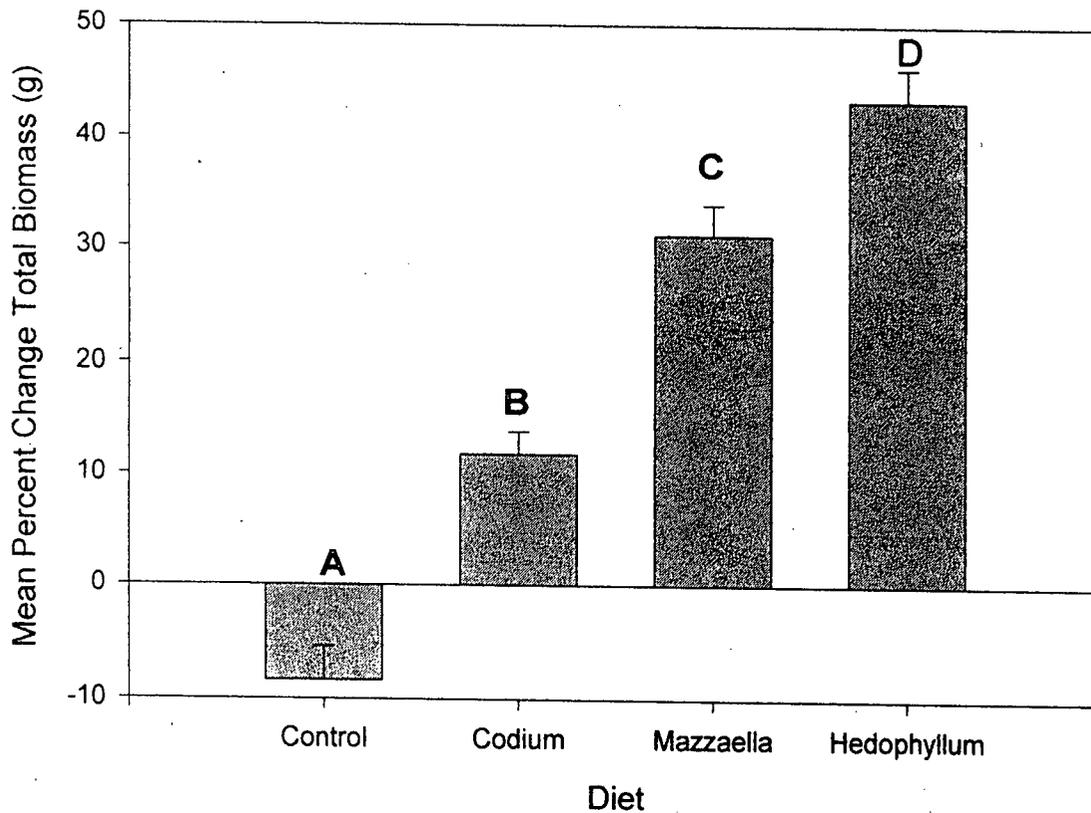


Figure 2.5 – Purple urchins, *Strongylocentrotus purpuratus*, were offered one of four macroalgal diets (*Codium fragile*, *Mazzaella splendens*, *Hedophyllum sessile*) or nothing at all (control) for ~4 months in flow-thru cages suspended from a marina dock. Initial vs. final measurements were used to calculate mean % change urchin biomass. Standard error bars are shown. One-way ANOVA results indicate that all macroalgal diets were significantly different from the control ( $F=71.1$ ,  $P=0.01$ ). Tukey comparison of mean results indicate there were four significantly different groups (e.g. "A", "B", "C", "D").

## *Strongylocentrotus purpuratus*

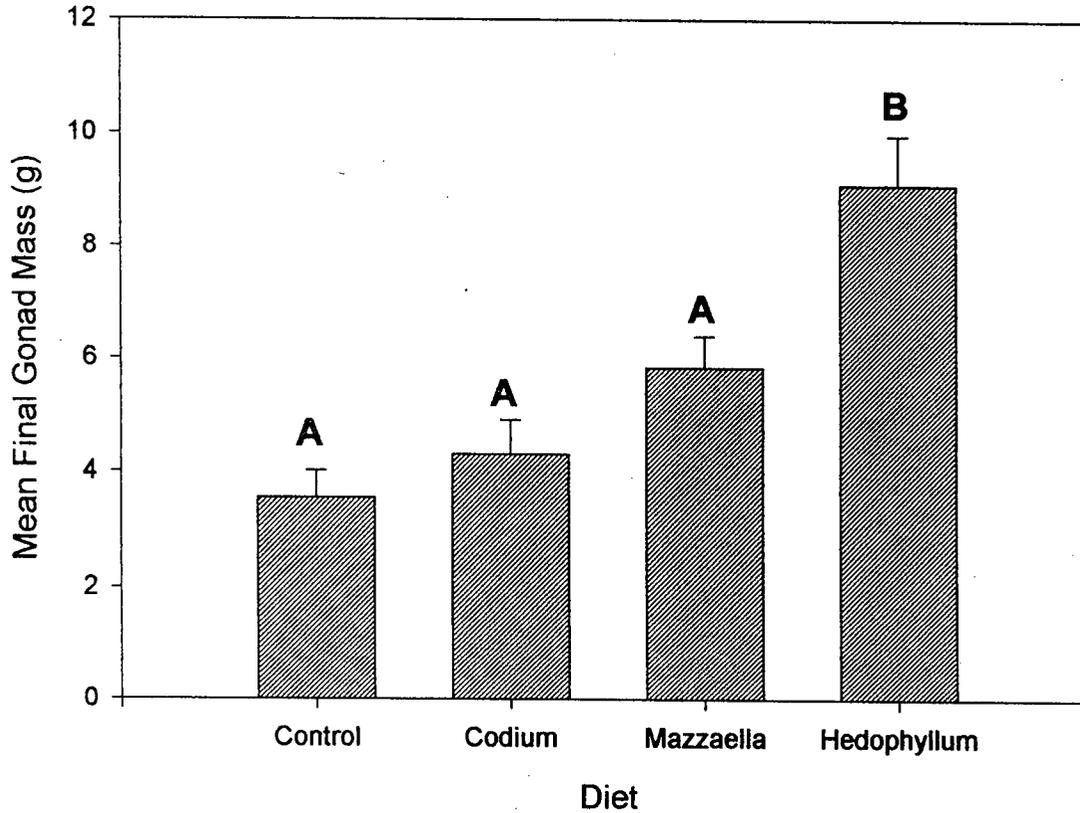


Figure 2.6 – Purple urchins, *Strongylocentrotus purpuratus*, were offered one of four macroalgal diets (*Codium fragile*, *Mazzaella splendens*, *Hedophyllum sessile*) or nothing at all (control) for ~4 months in flow-thru cages suspended from a marina dock. Final measurements were used to calculate mean urchin gonad mass. Standard error bars are shown. One-way ANOVA results indicate that neither *C. fragile* nor *M. splendens* diets were significantly different from the control ( $F=14.23$ ,  $P=0.01$ ). However, the *H. sessile* diet was significantly different from the other three treatments. Tukey comparison of mean results indicate there were two significantly different groups (e.g. "A", "B").

### *Katharina tunicata*

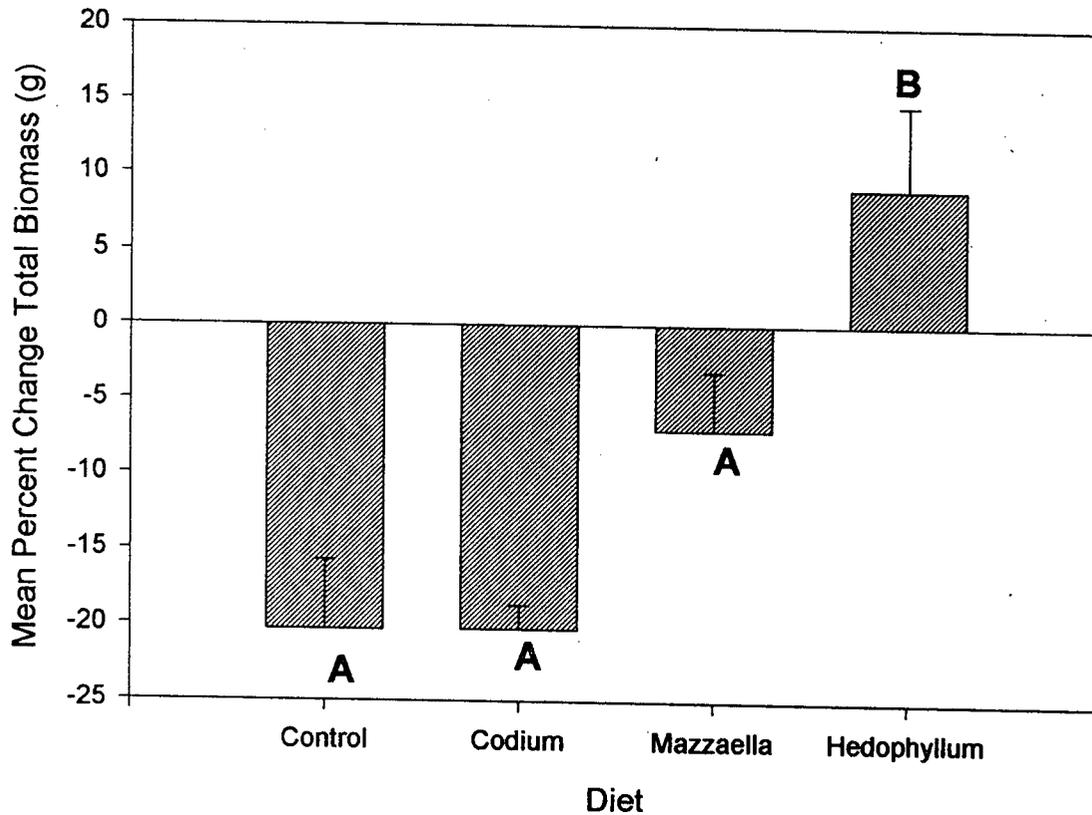


Figure 2.7 – Black chitons, *Katharina tunicata*, were offered one of four macroalgal diets (*Codium fragile*, *Mazzaella splendens*, *Hedophyllum sessile*) or nothing at all (control) for ~4 months in flow-thru cages suspended from a marina dock. Initial vs. final measurements were used to calculate mean % change chiton biomass. Standard error bars are shown. One-way ANOVA results indicate that only the *H. sessile* diet was significantly different from the control ( $F=10.3$ ,  $P=0.01$ ). Tukey comparison of mean results indicate there were two significantly different groups (e.g. "A", "B").

### *Katharina tunicata*

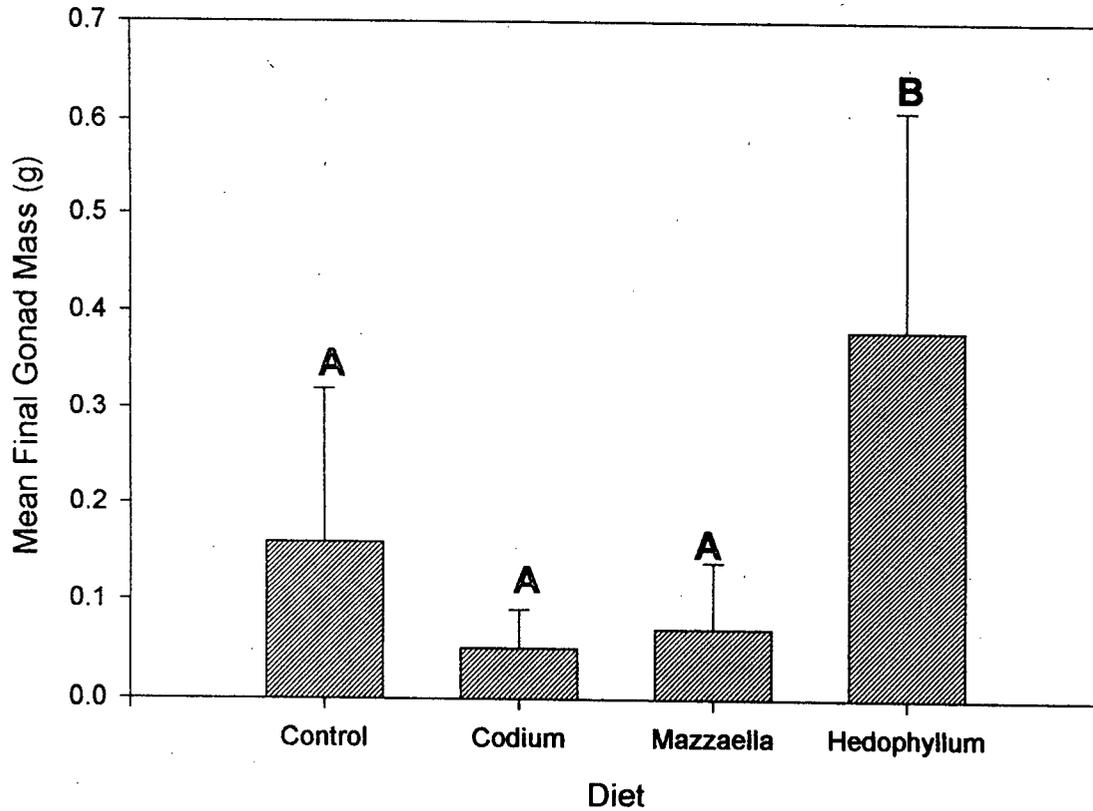


Figure 2.8 – Black chitons, *Katharina tunicata*, were offered one of four macroalgal diets (*Codium fragile*, *Mazzaella splendens*, *Hedophyllum sessile*) or nothing at all (control) for ~4 months in flow-thru cages suspended from a marina dock. Final measurements were used to calculate mean chiton gonad mass. Standard error bars are shown. One-way ANOVA results indicate that only the *H. sessile* diet was significantly different from the control ( $F=8.39$ ,  $P=0.01$ ). Tukey comparison of mean results indicate there were two significantly different groups (e.g. “A”, “B”).

## 2.6. Discussion

### 2.6.1. Spatial pattern analysis of black chitons

Results from my spatial pattern analysis experiment indicate that distances between *Codium fragile* and *Katharina tunicata* were significantly closer in the lower intertidal; whereas, distances between *C. fragile* and *K. tunicata* were nonsignificant in the high and middle intertidal zones. It is possible that there are other reasons, apart from herbivory, that may explain this close proximity. For example, both *K. tunicata* and *C. fragile* may prefer the same environmental conditions (e.g. increased submersion = reduced desiccation) within the lower limits of this habitat. Another logical explanation is that *K. tunicata* is more attracted to an algal conspecific of *C. fragile*, namely *Hedophyllum sessile*. Field observations at Prasiola Point support this idea as *H. sessile* plants are most abundant from the middle to lower intertidal heights, which overlaps with *K. tunicata*'s intertidal range. Other studies indicate *K. tunicata* has an established herbivory link with both juvenile and adult stages of *H. sessile*. For example, Dethier and Duggins (1988) examined the role of *K. tunicata* in an intertidal community and found that a persistent kelp bed developed in the absence of this herbivore. Markel and DeWreede (1998) examined herbivorous impacts of *K. tunicata* on *H. sessile* and found that grazing on juvenile plants made them susceptible to removal by hydrodynamic forces. However, Piercy (1987) found that *K. tunicata* consumes many different algal types, ranging from diatoms to macroalgae. Therefore, results from my

next three feeding studies were necessary to support or reject this spatial association between *K. tunicata* and *C. fragile* at Prasiola Point.

#### 2.6.2. Feeding Preference Experiment

Though my experimental results show that purple urchins and chitons will consume native *Codium fragile*, they consumed more of *Hedophyllum sessile* and *Mazzaella splendens*. Paine and Vadas (1969) examined the grazing effects of purple and red sea urchins on an algal community at Mukkaw Bay, Washington, USA. After removing or caging all urchins from an experimental area, they observed the rate and pattern of algal succession for a three-year period. After this time, they found that the majority of the new algal biomass was composed of a single perennial brown algal species, *H. sessile*, in the intertidal and *Laminaria* spp. subtidally. Neither of these kelp species existed in the control areas throughout their study, nor were they found initially in the experimental pools and rocks prior to urchin removal. Therefore, sea urchin grazing played a major role on the abundance of kelp species at this area, demonstrating a herbivorous relationship between purple urchins and *H. sessile* at another Pacific coast habitat.

Other studies have addressed the impacts of grazing on *Hedophyllum sessile* by black chitons (Himmelman and Carefoot, 1969; Markel and DeWreede, 2001) (see section 2.6.1). Likewise, published studies have shown herbivorous relationships between *Mazzaella splendens* and both of these generalist herbivores. Gaines (1985) reported that *M. splendens* (in either sporophyte or gametophyte reproductive phase) are readily eaten by both

*Strongylocentrotus purpuratus* and *Katharina tunicata* on Oregon shores. Furthermore, *M. splendens* persists when the herbivore *Idotea baltica* (an isopod) or *Lacuna carinata* (a snail) are present, but is rare or absent when either *K. tunicata* or *S. purpuratus* is common.

Why is *Codium fragile* such an unattractive seaweed for grazers? Van Alstyne et al. (2001) examined the role of activated defenses in marine macroalgae against generalist herbivores. Activated defenses are defenses in which a precursor compound is stored in an inactive or mildly active form. Upon damage to the prey (seaweeds), the precursor is enzymatically converted to a more potent toxin or feeding deterrent. The focus of Van Alstyne et al.'s study was the osmolyte dimethylsulfoniopropionate (DMSP) which is converted to acrylic acid or acrylate and dimethyl sulfide (DMS) following algal damage. They surveyed 39 species of red, green, and brown macroalgae from Washington and Oregon coasts and found high concentrations of DMSP in the chlorophytes *Acrosiphonia coalita*, *Codium fragile*, *Ulva intestinalis*, *U. linza*, *U. californica*, *U. fenestrata*, *U. taeniata*, and the rhodophyte, *Polysiphonia hendryi* (*Hedophyllum sessile* and *Mazzaella splendens* were not included). Concentrations of DMSP ranged from 0.04 to 1.8% of the alga's FM (fresh mass). Their results showed that *C. fragile* collected from Oregon showed mean DMSP concentrations of 0.04% FM, whereas *C. fragile* collected from Washington showed mean DMSP concentrations of 0.20% FM. In addition, feeding preference assays were conducted to test whether DMSP and/or acrylic acid served as deterrents for green urchins (*Strongylocentrotus droebachiensis*), purple urchins (*S.*

*purpuratus*) and isopods (*Idotea wosnesenskii*). They found that the precursor DMSP functioned as a feeding attractant to both urchins; acrylic acid deterred feeding by green urchins at concentrations of 0.1 –2% FM and purple urchins at 0.25 –2% FM. In contrast, isopod feeding was not deterred by acrylic acid even at concentrations as high as 8% FM.

Van Alstyne et al.'s results might explain why purple urchins in Barkley Sound are less likely to consume *Codium fragile* when *Hedophyllum sessile* and/or *Mazzaella splendens* are available. Their findings suggest that *C. fragile* has a secondary chemical defense that deters some generalist herbivores from feeding on it beyond initial contact. However, additional research must be conducted to provide sufficient evidence for this theory since neither *H. sessile* nor *M. splendens* were tested. In addition, sampling sizes were low for *C. fragile* collected from both Washington (n=2) and Oregon (n=3) sites. Furthermore, reported values for DMSP concentrations were very different for plants from the two collection sites. Is it possible that DMSP concentrations are variable based on geographical differences? *Codium fragile* plants in British Columbia have not yet been tested for presence of DMSP; it is unknown whether our native plants utilize these chemical compounds as feeding deterrents for generalist grazers. Do DMSP concentrations in *C. fragile* plants increase as they are collected from habitats at higher latitudes or at sites with increased herbivore contact? For example, Markel (1996) tested whether increased abundance of herbivores increased tannin production in *H. sessile* and found no significant association. It would also be interesting to determine if DMSP concentrations (per individual

plant) varied with age (juvenile vs. adult) and/or change seasonally. Van Alstyne et al. (2001) examined within-species food preferences of four common generalist herbivores (e.g. purple urchins, *S. purpuratus*; snails, *Lacuna porrecta* and *Tegula funebris*; isopods, *Idotea wosnesenskii*) for juvenile and adult tissues of eight common brown macroalgae (e.g. *Alaria marginata*, *Costaria costata*, *Egregia menziesii*, *H. sessile*, *Nereocystis luetkeana*, *Fucus gardneri*, *F. spiralis*, *Lessoniopsis littoralis*) from Oregon shores. Contrary to their *a priori* expectations, juvenile algal tissues were significantly preferred over adult tissues in only four of the 32 combinations of algae and herbivores tested. Van Alstyne et al. concluded that herbivores respond to a combination of morphological and chemical features of algae, rather than algal size and delicate tissues.

As mentioned earlier, the three seaweeds utilized in my feeding preference experiments were of differing morphologies; *Codium fragile* is dichotomously-branched while both *Hedophyllum sessile* and *Mazzaella splendens* are bladed. One might argue that this was an inappropriate comparison when measuring feeding attractiveness. Some researchers (Paul and Van Alstyne, 1992; Van Alstyne et al., 2001) "mask" algal morphology in feeding experiments by grinding thallus tissue and mixing it with agar/anchovy paste to create dietary compounds. Though this approach may "standardize" the food choices, other natural elements are removed from the herbivore's selection within the experimental design. For example, if natural products are present in algal tissues, these compounds may be deactivated in the "blending" process of food preparation. Therefore, herbivores might choose certain foods

willingly under laboratory conditions that they would not choose under natural conditions in the field. For this reason, I chose to test seaweeds in their natural state in order to duplicate what purple urchins and black chitons encounter at Prasiola Point.

Results from my feeding preference study indicate that purple urchins and black chitons prefer *Hedophyllum sessile* and *Mazzaella splendens* over *Codium fragile*; however, both grazers will consume the latter when hungry. As defined earlier, "preference" determines the quantity and quality of food ingested by a grazer; hence, affecting both its physiological condition and overall fitness (Nicotri, 1980). Though both purple urchins and black chitons are attracted to *H. sessile* and *M. splendens* (= short time frame), perhaps *C. fragile* is a high quality food item that affects their overall growth and reproductive fitness (= long time frame). If this were true, then these herbivores would continue to consume *C. fragile* which would account for its reduced occurrence at Prasiola Point. I conducted an absorption efficiency study to measure the food quality of these three seaweeds based on organic content and each herbivore's ability to digest these macroalgae.

### 2.6.3. Absorption efficiency experiment

How do nutritional characteristics of algae "fit" with herbivore preferences? Nicotri (1980) measured several nutritional parameters of 17 algal species (*Codium fragile* was included; see section 2.3.2 for list of species): % dry matter, % organic matter, % nitrogen, and caloric content. *Codium fragile* ranked last (= had the lowest percentages) in both dry matter (7.4%) and organic

matter (3.9%) content. *Codium fragile* was also low in nitrogen (1.38%) and caloric content (2.62 calories/mg dry weight). Nicotri then compared grazing rates of the isopod, *Idotea baltica*, fed on the same 17 macroalgal species, based on wet weight consumed, organic and caloric intake. *Codium fragile* ranked as first in wet weight consumed (mg/day per individual), ranked 7.5/17 in organic intake (mg organic matter consumed/day per individual), and ranked 5/10 in caloric intake (calories/day per individual). From these results, *C. fragile* appears to be a very poor food choice, yet is consumed more than any other species from *I. baltica*'s habitat (Woods Hole, Massachusetts).

Vadas (1977) studied feeding preferences and absorption efficiencies of three urchins (e.g. *Strongylocentrotus droebachiensis*, *S. franciscanus*, *S. purpuratus*) fed many representative macroalgal species from their San Juan Island, Washington, USA habitats (*Codium fragile* was not included). A generalized ranking of algae for green and red urchins (from most to least preferred genera) was listed as: *Nereocystis leutkeana* > *Costaria costata* > *Laminaria saccharina* > *Monostroma fuscum* > *Opuntiella californica* > *Agarum cribosum*. Vadas reported similar, but weaker, preferences for purple urchins. Coincidentally, absorption efficiencies for all three urchin species were strongly correlated with food preference rankings. Though feeding by sea urchins in nature is a compromise between food preferences and algal availability, Vadas found that urchins in his study selected algae which were ingested rapidly, absorbed efficiently, and provided the greatest nutritional value for maximizing reproductive output (measured by gonadal growth).

In my study, absorption efficiency values for *Mazzaella splendens* were higher than those reported for *Hedophyllum sessile*, which could be explained by the presence of secondary metabolites found in many phaeophyte species. The most common of the secondary metabolites are the phlorotannins, which are difficult to digest by many herbivores. Evolutionary hypotheses on plant-herbivore interactions assume that plant secondary compounds (such as the phlorotannins of brown algae) function as feeding deterrents for herbivores. However, that is not always the case. Jormalainen et al. (2001) studied the effect of seaweed quality on the feeding preferences and performance of the isopod, *Idotea baltica*. They offered *I. baltica* six species of algae, representing those most common in its intertidal habitat, in simultaneous feeding preference tests. Surprisingly, the more phlorotannin a seaweed species contained, the more it was preferred by *I. baltica*. However, isopod performance (when reared on a mono-macroalgal diet) did not match the feeding preferences determined earlier: the most preferred brown alga provided the poorest *I. baltica* growth rate. This study showed that phlorotannins in seaweeds do not function as feeding deterrents to *I. baltica*. Instead, it feeds on phenolic-rich foods that also function as a suitable habitat for this mesograzers, at the cost of decreased growth rate. If feeding preferences and habitat choice behavior evolve together, there may be other factors more important in food selection than the chemical composition of algae.

Lowe and Lawrence (1976) compared absorption efficiencies of the sea urchin, *Lytechinus variegatus*, fed six species of macroalgae which were

important components of its natural diet in the Gulf of Mexico. Their data suggest that measurements of energy and nutrient levels of food are inadequate in evaluating the "value" of different foods to an herbivore. Their ranking of foods high in total organic material (e.g. *Thalassia* > *Syringodium* > *Sargassum* > *Ulva* > *Euचेuma* > *Halimeda*) did not match the order of food absorbed most efficiently by *L. variegates* (e.g. *Thalassia* > *Halimeda* > *Ulva* > *Syringodium* > *Sargassum* > *Euचेuma*). According to Lowe and Lawrence (1976), "absorption efficiency estimates can give an inaccurate assessment of the nutritional value of foods since such determinations do not consider the levels of nutrients in the foods".

Are we interpreting absorption efficiency trends correctly? Cultured abalone in China are reported to lack high quality food sources during summer and fall. *Codium fragile* is a common intertidal seaweed during this time period in the Huanghai, Bohai, and East China seas' coastal zones. Pan and Yu (1992) conducted a growth study of the abalone, *Haliotis discus*, fed with *C. fragile*. Shell lengths increased and average monthly body weight increased by 33%. Therefore, they concluded that *C. fragile* is as suitable a food as those grown by aquacultural methods, *Laminaria religiosa* and *Undaria pinnatifida* (both phaeophytes). This information is not in agreement with reported trends from my feeding studies. Both feeding preference and absorption efficiency studies suggest that native *C. fragile* from Vancouver Island would not be as suitable a food for herbivore growth, compared to *Hedophyllum sessile* (a kelp) and

*Mazzaella splendens*. I chose to investigate this area further with a diet vs. herbivore growth study.

#### 2.6.4. Fitness vs. macroalgal diet experiment

Lemire and Himmelman (1996) measured two components of fitness, somatic and gonadal growth, for the green urchin, *Strongylocentrotus droebachiensis*, maintained on 17 different algal diets (*Codium fragile* was not included). Their field experiment, set in the northern Gulf of St. Lawrence, utilized cages containing urchins allowed to feed on a single species of seaweed for 130 days. They categorized results of earlier feeding preference experiments into three groups: preferred vs. intermediate preferred vs. non-preferred diets. They found that the relation of food preference to somatic growth was nonlinear. Test diameter, total mass, and test mass increased from non-preferred to intermediate preferred algae; however, growth rates were similar for intermediate and preferred algae. Gonadal growth increased exponentially with food preference. Lemire and Himmelman's observations suggest that urchins channel food sources toward somatic growth up to a given point, with additional reserves used for gamete production.

Scheibling and Anthony (2001) examined the potential of sea urchins (*S. droebachiensis*) to regulate the invasive *C. fragile* ssp. *tomentosoides* in Nova Scotia habitats. They used feeding experiments to compare the role of the invasive *C. fragile* species to kelp (*Laminaria* sp.) in terms of urchin somatic and reproductive growth. They found that urchins showed a strong preference for kelp (a high quality and preferred native food); they consumed more *Laminaria*

sp. than *C. fragile* ssp. *tomentosoides* in single and mixed diet treatments. Survival and somatic growth (change in test diameter) were lowest within the *C. fragile* ssp. *tomentosoides* diet. After finding that urchins on the *C. fragile* ssp. *tomentosoides* diet showed no gonadal production (compared to a marked rise on both *Laminaria* sp. and mixed diets), they concluded that *C. fragile* ssp. *tomentosoides* is an unattractive, unpalatable and poor quality food for urchins in Nova Scotia. With this information, they predicted that urchins would be more likely to graze kelp than *C. fragile* ssp. *tomentosoides* in mixed stands, thus, allowing it (*Codium*) to effectively dominate a community.

My results are in agreement with a common trend shown in earlier studies (Vadas, 1977; Larson et al., 1980; Lemire and Himmelman, 1996): despite the potential search costs associated with feeding on preferred algae, urchins must feed on intermediate to highly-preferred algae to produce gametes. Feeding on non-preferred algae (such as *Codium fragile*) permits, at most, survival through periods when preferred foods are sparse.

## 2.7 Conclusion

According to Trowbridge (1998), there is no evidence that invertebrate grazers regulate the population of *Codium fragile*, introduced or native, anywhere in the alga's geographic range. Previous studies (Malinowski and Ramus, 1973; Fralick and Mathieson, 1979; Harlin and Rines, 1993) suggesting that *C. fragile* ssp. *tomentosoides* is not extensively consumed on NW Atlantic shores is not sufficient to test the "escape from consumers" hypothesis. My laboratory studies were used to compare feeding preferences and absorption

efficiencies of generalist herbivores (purple urchins, black chitons) found within the *C. fragile* zone at Prasiola Point. These herbivores were not present at any of my other field sites in Barkley Sound (e.g. Second Beach, Scott's Bay, Seppings Island). A third experiment comparing fitness of purple urchins and black chitons offered one of four macroalgal diets was conducted within Anchor Cove Marina. This approach was necessary (for all three experiments) due to difficulties with attaching cages or experimental devices to my field site, as well as problems associated with wave exposure. Compared to common seaweeds (*Hedophyllum sessile*, *Mazzaella splendens*) at Prasiola Point, native *C. fragile* is not preferred by generalist herbivores (purple urchins, black chitons), has the lowest short-term nutritional value, and did not significantly increase somatic or reproductive growth for these herbivores. These results suggest *C. fragile* is not a good long-term food choice in this habitat. Therefore, some other mechanism must be at work that limits the distribution of *C. fragile* at Prasiola Point.

## CHAPTER 3

### Sand Burial

#### 3.1 Sand burial as a physical disturbance

An abiotic factor that may influence population dynamics of *Codium fragile* is sand burial. During the course of this study, my Scott's Bay field site was periodically covered by sand. However, the Seppings Island field site was not. As reported in Chapter 1, *C. fragile* abundances fluctuated over the sampling period at Scott's Bay (see Figure 1.15), whereas a dense stand of *C. fragile* persisted at Seppings Island (see Figure 1.18). I questioned whether this physical disturbance might account for the decreased abundance of *C. fragile* at Scott's Bay.

Sand movement on beaches is typically seasonal. On temperate zone beaches exposed to seasonal weather patterns, sand builds up in spring and is washed into the subtidal in autumn. Winter beaches may have nothing remaining but the rocky beach platform and/or cobblestones too large for winter waves to carry off. This generalization has been confirmed by many marine studies of intertidal assemblages (Seapy and Littler, 1982; Littler et al., 1983; D'Antonio, 1986; Trowbridge, 1996b). For example, D'Antonio (1986) reported that sand accumulates as wave steepness declines in the spring, with major burials occurring in the late summer along the Oregon coast. Sand is then moved seaward by wave action during fall storms.

Sedimentation can influence the distribution and diversity of seaweeds (Robles, 1982; Stewart, 1983; D'Antonio, 1986). Often isolated rocks on a sandy beach, as well as sandy areas in rocky shores, have relatively few species of

algae. At my Scott's Bay field site, *Codium fragile* plants were found attached to rock mounds surrounded by sand and/or cobble. However, *C. fragile* plants at Seppings Island were attached to rock boulders without sand in the immediate area. The prevailing theory is that high rates of sediment deposition and movement are detrimental to the overall richness and diversity of the community (Daly and Mathieson, 1977; Engledow and Bolton, 1994). It is the continuous smothering and/or scouring, as well as unpredictable nature of sedimentation that can be damaging to organisms exposed to this type of disturbance. I questioned whether algal assemblages would be different at these two sites and whether any observed differences could be correlated with sand movement.

According to Airoldi and Cinelli (1997), algal survival (following a sand burial event) is dependent on a variety of factors; for example, morphological and/or life history characteristics. *Codium fragile* is unusual in its morphology, a coenocytic species living in temperate zone habitats. *Codium fragile* is described as a perennial alga, sometimes able to persist over many seasons. Is *C. fragile* a sand-tolerant algal species? If not, does sand burial inhibit the occurrence of *C. fragile* in Barkley Sound habitats? It is important to address the role of sand burial to better understand patterns of abundance of organisms, as well as adaptations/ tolerances of seaweeds associated with near-shore habitats. After comparing species assemblages of two Barkley Sound study sites, I tested direct effects of sand burial on *C. fragile* adults to determine whether it is a sand-tolerant species.

### 3.2 Seaweed adaptations to, and consequences of, sand burial

Moving sand may scour or bury intertidal substrata. Its effects as a disturbance agent include removing plant tissue, epiphytes, or invertebrates with poor attachment to the rock surface (=effects from scouring), and decreasing light, oxygen, and substratum available to organisms (=effects from burial) (D'Antonio, 1986). Furthermore, the depth and duration of burial or even degree of water motion is important in determining the intensity of this kind of disturbance. Therefore, seaweeds must possess specialized anatomical or reproductive adaptations to persist on sand-scoured rocky shores.

Vermeij (1978) modified a three-strategy model of adaptive specialization (previously applied to terrestrial ecology) for marine organisms. According to this model, species can be categorized as (a) opportunists; which exhibit high reproductive rates, a short life span, high dispersibility, reduced long-term competitive abilities, and occupy ephemeral or disturbed habitats, (b) stress-tolerant forms; which can tolerate chronic physiological stress, exhibit low rates of recolonization, tend to be long-lived with slow growth rates and, consequently, are generally poor competitors, and (c) biotically-competent forms; which generally live in physiologically-favorable environments, have long life spans, are good competitors and have evolved mechanisms to avoid predation. In the rocky intertidal zone, Vermeij associates stress-tolerant forms with the high intertidal, while biotically-competent species are prevalent in the low intertidal. I designed

some experiments to test whether this model was applicable to *Codium fragile* in sand-inundated habitats.

According to Lobban and Harrison (1997), sand-tolerant seaweeds tend to be robust, stress-tolerant perennials (e.g. *Gymnogongrus linearis*, *Sphacelaria radicans*, *Ahnfeltia plicata*), or opportunistic ephemerals (e.g. *Chaetomorpha linum*, *Ulva* sp., *Ectocarpus* sp.). Characteristics of sand-tolerant species include the following: tough, usually cylindrical, thalli with thick cell walls; the ability to regenerate fronds quickly or by means of an asexual reproductive cycle; sexual reproduction may be timed to occur when plants are uncovered; and physiological adaptations to withstand darkness, deprivation from nutrients, and anaerobic conditions (Norton et al., 1982). By contrast, opportunistic algal species are able to settle when scouring is at a minimum and the rocks are bare; they reproduce and disappear before scouring begins again.

### 3.3 Other studies examining the effects of sand burial

The rhodophyte *Neorhodomela larix* is a good example of a sand-tolerant species in the northeastern Pacific. *Neorhodomela larix* grows well on shores unaffected by sand, but it is much more abundant where sand accumulates. D'Antonio (1986) studied the influence of sand on space occupation of *N. larix*, found along moderately exposed, sand-swept Oregon beaches. She found that most *N. larix* plants were little damaged when removed from beneath 40 cm of sand (following a 2-week major sand burial in 1981) and continued to dominate primary space along permanent transects. Coincidentally, a large percentage of these plants had mature tetrasporangia on their axes. However, effects of sand

burial on other plants (in the same habitat) were variable. Within her study site, some species remained unchanged (e.g. *Gymnogongrus linearis*, *Phyllospadix* sp.). Other species, specifically perennial red algae (e.g. *Microcladia borealis*, *Dilsea californica*, *Cryptosiphonia woodii*), disappeared. D'Antonio's results show that while *N. larix* is well-adapted for sand burial, some of its algal competitors, epiphytes, and herbivores are inhibited by the same disturbance.

D'Antonio also conducted a laboratory experiment to test sand burial tolerance by *Neorhodomela larix* and other species found in the same habitat. After 2 weeks of sand burial in sea tables, *N. larix* plants were intact but showed no increases in length. After 6 weeks, most *N. larix* plants remained intact with some tissue loss. After 14 weeks, upright portions of many *N. larix* plants were decayed but holdfasts were intact. Other macroalgal species did not fare as well. After 14 weeks, she found no trace of the rhodophytes *M. borealis*, *C. woodii* and *Gigartina papillata*; *Ulva* sp. showed a 90% tissue loss. Besides *N. larix*, only an unidentified coralline crust persisted. Many marine studies (Steneck and Watling, 1982; Dethier, 1984) have reported that crustose algal species are often more resistant (compared to erect algal species) to herbivory and scouring within intertidal environments.

*Codium fragile* may fit the description of a stress-tolerant species. In reference to Vermeij's model, *C. fragile* plants at Second Beach, Scott's Bay and Prasiola Point were slow growing, and perhaps, poor colonizers as well. However, my Scott's Bay site was disturbed by sand during Spring 1999 and Summer 2000. This site showed decreased mean abundances of *C. fragile*

plants compared to the previous sampling periods (see Chapter 1). Therefore, it seemed possible that infrequent sand burial events might be one explanation for the patchy distribution of *C. fragile* at this location. With that information, I predicted that adult *C. fragile* plants would show reduced tolerance to transitory sand burial.

### 3.4 Introduction

#### 3.4.1 Comparison of algal assemblages between study sites

Neither Second Beach, Seppings Island nor Prasiola Point sites were disturbed by sand during the course of my field studies. However, Scott's Bay was disturbed by sand during two different sampling periods. I compared algal assemblages of Scott's Bay and Seppings Island field sites, as they have similar wave-exposure (see Chapter 4). For the purposes of this study, both Scott's Bay and Seppings Island sites were described as wave-protected areas based on their location within large bays (Scott's Bay) or protection by large rock outcroppings (Seppings Island), as well as representative species (commonly associated with wave-protected habitats) present at each location (for more information, see Chapter 4). My Scott's Bay study site encompassed a single rock mound (approx. 2.5 m x 2.5 m), emergent from a sandy beach during low tides (1.03 m elevation, based on chart datum). My Seppings Island study site consisted of large (approx. 100 cm x 60 cm x 48 cm) and medium boulders (approx. 50 cm x 30 cm x 25 cm) strewn inside a wave-protected area. I used the mid-intertidal zone (mean 1.08 m elevation, based on Canadian chart datum) to standardize the comparison to Scott's Bay.

I questioned whether these two sites would be similar in species composition though they were different in sand-exposure. All sites were sampled in September 2002 to compare algal assemblages and known characteristics of seaweeds found at these habitats. I predicted that Scott's Bay would have fewer species present (compared to Seppings Island), which could be caused by occasional sand burial episodes.

#### 3.4.2 Sand burial experiment

I expected that scouring and sand burial would reduce seaweed growth. While I collected quantitative data on *Codium fragile* plants at my four field sites (see Chapter 1), I observed and recorded other trends. Monitored *C. fragile* plants showed slower growth rates at Scott's Bay compared to other field sites in this study. "Carpets" of new *C. fragile* juveniles (mapped before sand burial occurred) did not survive at another location near Second Beach. "Carpets" of new *C. fragile* juveniles at Scott's Bay were discolored and did not readily develop into mature adults after being covered with up to 3 cm of silt/sand. New *C. fragile* juveniles at Seppings Island often survived in a "sand-free" habitat, which contributed to a dense stand of plants during my field sampling period. The question remains: what happens to *C. fragile* adults when sand burial occurs? If *C. fragile* is not a sand-tolerant species, perhaps this type of physical disturbance plays a role in its irregular occurrence in Barkley Sound. Hypothetically, juvenile *C. fragile* would be most vulnerable to sand inundation as it may take only a couple of centimeters of sediment for complete burial. Light deprivation would reduce photosynthetic activity and stunt growth of new thallus

tissue. This, combined with other negative side effects of burial, would ultimately lead to juvenile mortality. Conversely, sedimentation of only a few centimeters would not completely bury *C. fragile* adults. Though they might be impacted by scouring, protruding branch tips could still be photosynthetically-active and sustain the individual for an unknown period of time. A short-term study was conducted to measure the effects of sand burial on *C. fragile* adults in a laboratory setting.

Hypotheses:

H<sub>0</sub>: *Codium fragile* individuals buried by sand for 5 weeks will show no differences in growth compared to control individuals.

H<sub>A1</sub>: After 5 weeks, *Codium fragile* individuals buried by 5-10 cm sand will show reduced growth compared to control individuals.

H<sub>A2</sub>: After 5 weeks, *Codium fragile* individuals buried by 10 cm sand will show reduced growth compared to individuals buried by 5 cm sand.

### 3.5 Materials and Methods

#### 3.5.1 Comparison of algal assemblages between study sites

In September 2002, individual 25 cm<sup>2</sup> quadrats were randomly placed at each field site. Six quadrats were sampled at Scott's Bay and Seppings Island (middle intertidal zone only). Each quadrat contained 20 random points for which plant, animal or substratum (bare rock) was recorded. Quadrat data were pooled within each study site in order to capture the occurrence of rare species. Percent occurrence of each species per total number (n=120) of sampling points was then calculated.

### 3.5.2 Sand burial experiment

To test whether adult *Codium fragile* plants are negatively impacted by sand burial, a short-term experiment was conducted at Shannon Point Marine Center in Anacortes, Washington. *Codium fragile* individuals were collected intact (with holdfasts attached to chunks of rock) from Seppings Island in November 2001 and transported to Shannon Point Marine Center. *Codium fragile* plants were placed in 1-liter plastic containers with coarse mesh sides. Each plant was subjected to one of three treatments:

Treatment 1 = control, *Codium w/o* sand (n=14)

Treatment 2 = *Codium* + ~5 cm sand (n=14)

Treatment 3 = *Codium* + ~10 cm sand (n=14)

Control plants were anchored by the chipped rocks that each holdfast was originally attached to and floated upright within their containers; Treatment #2 plants were half-buried by sand and Treatment #3 plants were buried with sand so that only branch tips were showing. Equal numbers of replicates from each treatment were placed in sea-tables with filtered, running seawater. To keep the algae aerobic, containers were elevated above the bottom of the sea-table with seawater flowing down through the sediment. All sea-tables were exposed to indirect daylight and fluorescent ceiling lamps on a 12 hr light: 12 hr dark cycle.

To test whether sand burial reduced growth or survival of *Codium fragile*, all individuals were subjected to initial vs. final measurements of total thallus length, water displacement (=volume), and wet weight (=biomass). After five weeks, percent change was calculated for changes in those parameters. Each

parameter was then statistically analyzed using a single factor ANOVA to compare all treatments. For those results showing significant differences, a Tukey comparison of means test was used for further analysis.

### 3.6 Results

#### 3.6.1 Comparison of algal assemblages between study sites

Table 3.1 shows a list of species present at both Scott's Bay and Seppings Island. Only algal species from the middle intertidal elevation at Seppings Island are shown as they were most similar to the mean intertidal elevation measured for Scott's Bay (see Chapter 1). The most abundant algal species within these habitats were the chlorophytes *Codium fragile* and *Ulva* sp., the phaeophytes *Fucus gardneri*, and *Macrocystis integrifolia*, and the rhodophytes *Halosaccion glandiforme*, *Mazzaella splendens*, *Mastocarpus papillatus*, and *Prionitus lanceolata*. Large kelp species (e.g. *M. integrifolia* and *Alaria marginata*) were present at Seppings Island, but absent at Scott's Bay. Seppings Island (middle elevation) had a large number of algal species present (n=14); in comparison, Scott's Bay possessed less than half as many algal species (n=7). Only green anemones, *Anthopleura elegantissima*, barnacles, *Balanus glandula* and sponges, *Haliclona* sp., were common to these field sites. Scott's Bay had the largest percentage of uncolonized substrate space (12.5% bare rock), whereas Seppings Island boulders were covered by both plant and animals; only 1.7% of sampled points were bare rock.

Table 3.2 compares macroalgal life histories, morphology types, and ranks the most common algal species associated with the two field sites utilized in this study. Macroalgae with annual life histories (e.g. *Ulva* sp.) were present at both field sites, though *Ulva intestinalis* was present only at the sand-exposed site (Scott's Bay). In comparison, perennial species were present at all sites, whether sand-exposed or not. Although *Codium fragile* is the only coenocytic, dichotomously-branched species present at both field sites, another multicellular, dichotomously-branched algal species was present: *Fucus gardneri*. *Codium fragile* was ranked first in abundance at the Seppings Island site and ranked second at Scott's Bay (behind *F. gardneri*).

Table 3.1- List of species present at field sites in Barkley Sound, British Columbia in September 2002. Six quadrats were randomly sampled at each field site to determine species present (n = 20 points per quadrat). Reported values = % of times species occurred in total number of measured sampling points (n=120).

Study Site:	Scott's Bay	Seppings Island
Mean Elevation Height:	1.03m	1.08m
<hr/>		
Algal Species:		
Chlorophyta		
<i>Codium fragile</i>	10.8	50.0
<i>Ulva intestinalis</i>	8.3	0
<i>Ulva</i> sp.	10.8	8.3
Phaeophyta		
<i>Alaria marginata</i>	0	0.8
<i>Fucus gardneri</i>	28.3	0.8
<i>Hedophyllum sessile</i>	0	5.0
<i>Macrocystis integrifolia</i>	0	1.7
Rhodophyta		
<i>Chondracanthus</i> sp.	0	1.7
<i>Cumagloia andersonii</i>	0	2.5
Filamentous red	5.8	0
<i>Halosaccion glandiforme</i>	0	5.0
<i>Mastocarpus papillatus</i>	0	3.3
<i>Mazzaella splendens</i>	0	5.0
<i>Neorhodomela larix</i>	15.0	0
<i>Odonthalia floccosa</i>	0	2.5
<i>Polysiphonia</i> sp.	0	0.8
<i>Prionitis lanceolata</i>	2.5	3.3
Invertebrate Species:		
<i>Anthopleura elegantissima</i>	9.2	0
<i>Balanus glandula</i>	10.0	0
<i>Haliclona</i> sp.	0	2.5
Bare Rock	12.5	1.7
<hr/>		

Table 3.2- Algal species (ranked in order of most common to least common found at field sites in Barkley Sound, British Columbia in September 2002. Life history: P = perennial, A = annual (with long season of abundance), E = ephemeral (annual with short season). Morphology type: B = bladed, BR = branched, T = tubular, S = saccate, C = encrusting, S = soft, F = firm. Field sites: ScB = Scott's Bay, SIM = Seppings Island (Middle); NS = no sand burial event, S = sand burial event.

	Life History:	Morphology Type:	Assoc. w/sand?	ScB (S)	SIM (NS)
Chlorophyta					
<i>Codium fragile</i>	P	F,Br	?	2	1
<i>Ulva intestinalis</i>	A	S,T	?	3	-
<i>Ulva</i> sp.	A	S,B	?	2	2
Phaeophyta					
<i>Alaria marginata</i>	P	F,B	N	-	7
<i>Fucus gardneri</i>	P	F,Br	N	1	7
<i>Macrocystis integrifolia</i>	P	F,B	N	-	6
Rhodophyta					
<i>Chondracanthus</i> sp.	?	F,B	N	-	6
<i>Cumagloia andersonii</i>	A	S,Br	?	-	5
Filamentous red	?	S,Br	?	4	-
<i>Halosaccion glandiforme</i>	?	F,S	?	-	3
<i>Mastocarpus papillatus</i>	?	F,B	?	-	4
<i>Mazzaella splendens</i>	A	F,B	N	-	3
<i>Odonthalia floccosa</i>	?	S,Br	N	-	5
<i>Polysiphonia</i> sp.	?	S,Br	?	-	7
<i>Prionitis lanceolata</i>	A	F,B	?	5	4

### 3.6.2 Sand burial experiment

After five weeks, there were differences between treatments. I observed that *Codium fragile* individuals in both sand treatments were less healthy than plants in the control treatment. Whether partially buried in sand or buried with only centimeters of branch tips showing, all plants were fouled with benthic diatoms and limp in texture. Some plants were easily fractured when removed from their sand treatment; sand burial caused broken branches, weakened main axes, and loosened holdfasts. Conversely, *C. fragile* that were not buried by sand (controls) were firm in texture and maintained their dichotomously-branched form when the experiment ended.

Table 3.3 shows there were no initial significant differences (e.g. mean thallus length, mean volume, mean biomass) between *Codium fragile* individuals prior to their treatment assignment. Results listed in Table 3.4 show that adult *C. fragile* buried in sand for five weeks grew less (e.g. individuals showed reductions in thallus length, volume, and biomass) than control plants (no sand). Though *C. fragile* plants in sand treatments (e.g. + sand, ++ sand) were not significantly different from control plants in % change of thallus length ( $F=1.19$ ,  $P=0.32$ ), control plants grew longer than *C. fragile* plants in the sand treatments. Control plants showed a significant increase in mean volume (8.4%), compared to -17.7% and -22.2% in the + sand and ++ sand treatments, respectively ( $F=4.01$ ,  $P=0.03$ ). When comparing mean % change in biomass (of *C. fragile* individuals), individuals in both sand treatments were significantly different from those in the control treatment ( $F=3.32$ ,  $P=0.047$ ). Plants that were partially

buried in sand showed a mean reduction of 16.5% over time, whereas the controls lost little biomass (-2%) (Tukey critical Q = 3.5, rejection level = 0.05).

Accepted Hypothesis:

H<sub>A1</sub>: After 5 weeks, *Codium fragile* individuals buried by 5-10 cm sand will show reduced growth compared to control individuals.

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Table 3.3 – Comparisons of initial measurements (e.g. mean total thallus length, mean volume, mean biomass) of *Codium fragile* plants before sand burial experiment. “N” = number of plants measured per experimental treatment. Standard error values are shown in parentheses. One-way ANOVA results show there were no significant differences between treatment groups *a priori*.

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Treatment Group:	N:	Mean Thallus Length (cm):	Mean Volume (ml):	Mean Biomass (g):
No Sand	14	13.84 (1.14)	49.29 (8.65)	58.69 (11.57)
+ Sand	13	13.16 (0.60)	44.08 (7.58)	43.34 (9.50)
++ Sand	12	13.40 (0.58)	54.50 (6.07)	51.50 (7.82)

---

(F=0.17, P=0.84)      (F=0.45, P=0.64)      (F=0.61, P=0.55)

Table 3.4 - *Codium fragile* plants subjected to one of three treatments within seatables: Treatment 1 = *Codium* w/o sand (control); Treatment 2 = *Codium* + ~5 cm sand; Treatment 3 = *Codium* + ~10 cm sand. "N" = number of plants per treatment. After five weeks, initial vs. final measurements were used to calculate mean % change in total thallus length, water displacement (=volume), and wet weight (=biomass). Standard error values are shown in parentheses. One-way ANOVA results are shown for each data set; significant results (determined by a Tukey comparison of means) are shown by "A" or "B".

Treatment:	N:	Mean %Change Thallus Length (cm):	Mean %Change Volume (ml):	Mean %Change Biomass (g):
No Sand (Control)	14	3.79 (0.02)	8.36 (0.03)A	-1.79 (0.03)A
+ Sand	13	2.0 (0.03)	-17.69 (0.10)A,B	-16.46(0.05)B
++ Sand	12	-3.83 (0.05)	-22.17 (0.08)B	-11.25(0.04)A,B

(F=1.19, P=0.32)    (F=4.01, P=0.03)    (F=3.32, P=0.047)

### 3.7 Discussion

#### 3.7.1 Comparison of algal assemblages between study sites

I measured species abundance at Scott's Bay and Seppings Island to enable a simultaneous comparison of one location infrequently buried by sand to one that is not. This comparison omits seasonal changes, but my interest was in the relative abundance of seaweeds at each location at any given time. For example, we can examine common species occurrences between these habitats, as well as identify algal species by known sensitivity/tolerance to physical disturbances.

Patches of bare rock occurred more frequently at Scott's Bay (12.5%), than at Seppings Island (1.7%). Perhaps these patches were colonized prior to

sand burial events and the former occupants did not survive. It is unknown whether this was a direct effect of sand burial and/or scouring. By contrast, rocky substratum (medium and large boulders) at Seppings Island was covered with multiple species of macroalgae. Though *Codium fragile* was the dominant algal species, many others competed for space in this habitat.

When comparing total number of algal species (for this sampling date), the sand-inundated rock mound at Scott's Bay had 7 algal species present; whereas species abundance for Seppings Island (Middle) was doubled (n=14). Results from this site comparison support the prevailing theory wherein high rates of sediment deposition and movement are correlated with reduced richness and diversity of an intertidal community (Daly and Mathieson, 1977; Engledow and Bolton, 1994). In addition to being "sand-free", the large number of algal species at Seppings Island could be attributed to their attachment to large and medium (non-moving) boulders in a wave-protected habitat. Many researchers have studied effects of physical disturbance on boulder communities (Sousa, 1979; McGuinness 1987a, 1987b). For example, McGuinness (1987a,b) sampled both tops and bottoms of boulders to determine patterns of community structure and to assess the role of disturbance. She found that small rocks were overturned more often and buried (by sand) to a greater extent than large rocks. However, sedimentation did not appear to impact algal assemblages on tops of stable boulders (regardless of size), as the tops of rocks were rarely buried in sand. Instead, the main influences on algal community structure were aerial exposure at low tide and grazing gastropods. If these attributes are applicable to other

intertidal boulder fields, Seppings Island may represent a favorable environment for seaweeds, especially *Codium fragile*. As mentioned in Chapter 2, common herbivores were absent from this habitat and wave-exposure was lessened due to large, subtidal rock outcrops that absorb the impact of breaking waves (see Chapter 4). Boulders at this site were stable during all seasons (personal observation), which allowed many perennial species to persist on the same boulder over time.

*Codium fragile* does not appear to be part of a typical sand-inundated community as it was present at both of these field locations; infrequently buried by sand or not. In fact, its greatest abundance occurred at Seppings Island (not susceptible to sand burial). According to published literature, other algal species found with *C. fragile* at Scott's Bay do not have characteristics of sandy (or highly disturbed) habitats. Unlike *Ulva* sp. (present at all sites) and *Ulva intestinalis* (found at Scott's Bay), *C. fragile* is not known to be an opportunistic species in disturbed habitats. Furthermore, it was, until my study, unknown whether *C. fragile* is sensitive or tolerant to particular physical disturbances. The experiment I conducted on sand burial answered this question.

### 3.7.2 Sand burial experiment

As stated previously, characteristics of sand-tolerant species include the following: tough, usually cylindrical, thalli with thick cell walls; the ability to regenerate fronds quickly or by means of an asexual reproductive cycle; sexual reproduction may be timed to occur when plants are uncovered; and physiological adaptations to withstand darkness, deprivation from nutrients, and

anaerobic conditions (Lobban and Harrison, 1997). Trowbridge (1996b) examined the effects of sand burial on growth of *Codium setchellii*, a crustose algal species found on sand-influenced, rocky Oregon shores. Trowbridge reports that thallus growth for *C. setchellii* was slow, and mortality rates were size dependent. For example, small thalli experienced high mortality rates in their natural environment; whereas, large thalli persisted for several years. Contrary to D'Antonio's (1986) mention of a crustose algal species' tolerance to sand burial, Trowbridge found that in laboratory experiments, *C. setchellii* lost substantial biomass during 4-5 weeks of sand burial compared to non-buried controls. *Codium setchellii* appears to lack specialized anatomical or reproductive adaptations for inhabiting sand-scoured shores, however, Trowbridge suggests that larger (*C. setchellii*) specimens may survive sand burial events (that are largely unpredictable and variable both temporally/spatially) due to their slow growth and perennial lifestyle. Based on Vermeij's model (1978), *C. setchellii* does not fit the description of a stress-tolerant species. Though it is an encrusting form, it does not regenerate thalli tissue quickly, small individuals often do not survive sand burial events and larger individuals lose biomass.

Though *Codium setchellii* possesses characteristics associated with the genus *Codium*, this species has a distinctly different morphology (=encrusting form) when compared to *Codium fragile* (=erect, dichotomously-branched form). Is *C. fragile* a sand-tolerant species? A related subspecies, *Codium fragile* ssp. *tomentosoides*, may be. In New Zealand, *C. fragile* ssp. *tomentosoides* is usually found in wave-protected habitats covered by sand (e.g. harbors,

estuaries and channel margins) (Trowbridge, 1996b). On the North American East Coast, Ramus (1971) found that dense beds of *C. fragile* ssp. *tomentosoides* cause decreased rates of water flow, resulting in increased sedimentation. This, in turn, impacts water clarity and substrate quality. It is often reported that *C. fragile* ssp. *tomentosoides* species have perennial holdfasts while thalli often die back in winter. Malinowski and Ramus (1973) found that *C. fragile* ssp. *tomentosoides* holdfasts can survive burial in silt and still produce new thalli in the spring. Furthermore, Hanisak (1979) documented that germlings of *C. fragile* ssp. *tomentosoides* have significantly reduced irradiance requirements relative to mature thalli. As settlement and germination often occur in dense beds of shading seaweeds, reduced light-saturation requirements offer a possible competitive advantage in establishment (Hanisak, 1979). Though *C. fragile* ssp. *tomentosoides* are cylindrical in form, they are not tough with thick cell walls. However, this invasive subspecies can regenerate thallus tissue quickly (up to 10 cm per month; Trowbridge, 1995), which is important to compete for light and substrate monopolization. This subspecies also utilizes an asexual, parthenogenetic reproductive cycle. According to Vermeij's model, *C. fragile* ssp. *tomentosoides* could be labeled a sand-tolerant algal species based on rapid thalli growth, an asexual reproductive cycle, and physiological adaptations to sand burial.

Is West Coast native *Codium fragile* a sand-tolerant species? By contrast, our native *C. fragile* is often associated with rocky, coastal habitats. Native *C. fragile* plants share the same cylindrical form, lacking thick cell walls. Thalli

regeneration is slower (compared to the subspecies) and reproduction is sexual, not asexual (see Chapter 1). My field observations near Second Beach suggest that *C. fragile* germlings are not able to survive burial or shading. Germlings exposed to sand at Scott's Bay were often discolored and did not develop into mature thalli over time. My laboratory experimental results showed that adult plants are also impacted by sand burial. Though the sand treatment plants were not significantly different from the controls in mean % change thallus length, a trend was apparent. *Codium fragile* plants buried in 10 cm of sand showed a reduction in plant size, which may be the result of lowered photosynthetic activity (due to burial or epiphyte shading) and/or tissue degradation. Individuals that were "sand-free" (e.g. the controls) showed twice as much growth in thalli length than their counterparts partially-buried in sand. This trend was also observed with another parameter comparing mean percent change in volume. *Codium fragile* adults without sand showed significant increases in overall size, compared to their counterparts buried with 10 cm of sand. Control plants stayed firm and healthy, while treatment plants withered and decayed due to sedimentation. Furthermore, my laboratory experiment showed that *C. fragile* adults buried with 5-10 cm of sand showed a significant reduction in biomass over a short-term burial event (= 5 weeks). Optimally, plants were "healthier" in non-sand treatments than those in either sand treatment. Field observations at Scott's Bay indicate that mature plants are stunted in growth, often discolored, and thalli tissue is weakened. These plants are further compromised when their holdfasts

are loosened due to scouring, further lessening their chances of survival in this habitat.

How does our native *Codium fragile* fit into Vermeij's model of adaptive specialization? My laboratory results show it is not "stress-tolerant"; meaning it cannot tolerate chronic physiological stress. Instead, *C. fragile* could be a "biotically-competent form"; which means it generally lives in physiologically-favorable habitats, has long life spans, is a good competitor and has evolved mechanisms to avoid predation. It is unknown whether *C. fragile* is a good competitor for space, light, and nutrients compared to other algal conspecifics in its environment. *Codium fragile* is a dominant algal species at Seppings Island and has been described to be a perennial species in published literature. Van Alstyne et al.'s (2001) results (see Chapter 2) may apply to *C. fragile* plants found in Barkley Sound habitats—*C. fragile* may utilize chemical compounds within its tissue as an activated defense against herbivores.

### 3.8 Conclusion

Sand movement, as a physical disturbance, may work on predictable timelines but does not necessarily follow regular patterns (similar to currents) of washing ashore. Though my experiments provide some insight to how *Codium fragile* plants respond to sand-burial at Scott's Bay, my results do not explain the irregular distribution patterns of *C. fragile* at Second Beach and Prasiola Point (where no sand-burial occurred). It is highly likely that other factors are linked to distribution patterns of *C. fragile* in Barkley Sound. Chapter 4 will explore wave

action as a possible physical factor that limits the abundance and/or distribution of this species.

## CHAPTER 4

### Wave Action

#### 4.1 Introduction to seaweed adaptations and survival in wave-swept environments

Waves are periodic surge events generated by wind, tides, earthquakes and landslides; small-scale surface currents are unidirectional motions that are strongly influenced by coastal topography (Graham and Wilcox, 2000). Waves and currents play an important role in structuring algal communities. For example, waves and currents provide a tremendous source of energy to near-shore environments, contributing approximately ten times more energy than solar radiation. This extraordinary energy input is related to the high productivity of coastal macroalgal communities. By constantly moving the fronds of macroalgae, waves and currents reduce shading and bring a constant resupply of inorganic nutrients to the algae (Graham and Wilcox, 2000). They also reduce nutrient depletion by decreasing the thickness of the boundary layer associated with seaweed surfaces.

Nonetheless, wave-swept shores are among the most stressful flow environments on earth. Wave-induced water velocities on rocky shores can reach 10 to 20 m/s (Denny et al., 1985; Carrington, 1990; Friedland and Denny, 1995; Denny, 1999). Furthermore, accompanying accelerations can exceed 400  $\text{m/s}^2$  (Denny et al., 1985; Gaylord et al., 1994). These extreme water motions often impose large hydrodynamic forces on exposed plants and animals. Many studies of marine habitats (Dayton, 1971; Paine and Levin, 1981; Seymour et al., 1989) show that wave-induced damage is characteristic of intertidal and shallow subtidal communities. Furthermore, water movement can remove algae from

their rocky substratum; once removed, these algae generally die. Consequently, wave-generated physical forces influence the abundance of algal populations (Bell and Denny, 1994; Shaughnessy et al., 1996; Denny, 1999).

Native *Codium fragile* plants have been reported to occur in wave-exposed habitats from California (Gunnill, 1980; Gunnill, 1985) to British Columbia (present study). Gunnill (1980; 1985) observed that in his studies, most *C. fragile* losses were individuals torn from their holdfasts. Throughout the course of my study, I observed many *C. fragile* plants with broken branches or "stumps" remaining—more so at Prasiola Point than at my other field locations. I predicted that differences in wave exposure could account for *C. fragile* losses and/or decreased abundances at Prasiola Point (see Chapter 1).

Many marine scientists have explored mechanical limits of size in wave-swept organisms (Denny et al., 1985; Koehl, 1986; Denny et al., 1989; Carrington, 1990). If we examine the gross morphology of *Codium fragile* plants, the high degree of branching might make them vulnerable to wave dislodgement (Dromgoole, 1979). It seems likely that the distribution of this seaweed, whether as individual plants or in clusters, is influenced by wave action.

Hypothetically, if wave forces are important in limiting seaweed size, waves should prune or dislodge the largest plants unless such plants increase their attachment and mechanical strength concurrently. Thallus "tattering" might also occur, in which individual branches or sections of the thallus are removed by waves, while the holdfast remains attached to the rock. For *Fucus gardneri*, thallus tattering is common and seems to be an important method of size

reduction (Blanchette, 1997). A sublethal (wave) force may break off several branches of a *F. gardneri* plant, reducing its overall area and volume. In this scenario, the plant's probability of survival is increased, since the size of the plant is reduced while its tenacity remains unchanged. Later, this individual will regrow to achieve some "optimal" size for its particular environment.

Besides increasing survivorship, thallus tattering may have other benefits. For example, fracturing may be a useful mechanism of asexual reproduction and spore dispersal for seaweeds. Broken off thallus fragments may contain spores, conceptacles, or gametes or may be able to reattach to a new substratum and grow (Norton et al., 1982). This method of dispersal could be utilized by seaweeds such as *Fucus gardneri* and *Codium fragile* that contain buoyant receptacles or branch tips; serving as a means of long-distance dispersal for their gametes.

When comparing *Fucus gardneri* to *Codium fragile*, there are similarities in both habitat and shape. Their distributions occasionally overlap within the intertidal zone; *F. gardneri* often occurs from high to middle intertidal zones while *C. fragile* is found in the middle to lower intertidal zones (Scagel, 1971). Both arise from a discoid basal holdfast and form a dichotomously-branched thallus. Mature plants of both species are often the same size class, with total lengths up to 40 cm. Both species are somewhat buoyant (Scagel, 1971; Ramus, 1978). One important characteristic they do not share (for the purposes of this study) is thallus construction. However, both *F. gardneri* (a multicellular seaweed) and *C.*

*fragile* (a unicellular, coenocytic seaweed) endure the physical forces associated with a wave-swept environment.

The coenocytic thalli of *Codium fragile* contain no transverse walls or septa. However, there are internal plugs or pad-shaped thickenings that hold the cell contents in place, as well as prevent the loss of an entire filament when injury occurs (Hurd, 1916; Scagel, 1966). When mechanical damage occurs in *C. fragile*, the partial plugs are quickly blocked and sealed by cytoplasmic organelles (which prevents extensive loss of cytoplasm) (Wassman and Ramus, 1973). Realistically, breaks could occur anywhere on a *C. fragile* thallus. Other studies using rocky intertidal (multicellular) seaweeds showed that the majority broke above the holdfast, either within the stipe/holdfast junction or at the stipe/blade junction (Carrington, 1990; Shaughnessy et al., 1996). Many of these algae can regrow from the original holdfast; thus, retaining space within the habitat. Consequently, wave action can also act as a selective force in rocky, intertidal habitats; removal of thalli from their substratum usually results in algal death (Carrington, 1990; Gaylord et al., 1994; Friedland and Denny, 1995; Shaughnessy et al., 1996; Collado-Vides et al., 1998).

Do wave forces limit native *Codium fragile* from successfully persisting in these rocky habitats? I addressed this question by comparing maximum wave forces of four study sites in Barkley Sound. I also explored biomechanical aspects of *C. fragile* by measuring drag coefficients (of individual plants exposed to flow) and breaking forces. Breaking forces were measured for *C. fragile* plants found at each location to determine what force is necessary to fracture thallus

tissue or remove them from the substratum entirely. Drag coefficients were calculated to demonstrate how individual *C. fragile* plants respond to increased (wave) velocities. I used this information to place this alga's morphological attributes into ecological context. Finally, I conducted a transplant study to determine survival of *C. fragile* plants moved to either a wave-exposed (e.g. Prasiola Point) or wave-protected (e.g. Scott's Bay) environment.

Hypotheses:

H<sub>0</sub>: *Codium fragile* individuals transplanted to either wave-exposed or wave-protected habitats will not differ in survival over time.

H<sub>A1</sub>: More *Codium fragile* individuals transplanted to a wave-exposed habitat will survive, compared to those transplanted at a wave-protected habitat.

H<sub>A2</sub>: Fewer *Codium fragile* individuals transplanted to a wave-exposed habitat will survive, compared to those transplanted to a wave-protected habitat.

## 4.2 Materials and Methods

### 4.2.1 Comparison of Maximum Wave Forces

While collecting data on *Codium fragile* abundances at four field sites in Barkley Sound, I observed that not all plants were in optimal condition. In early spring sampling periods, many were damaged with either broken branches, loosened holdfasts or had lost all their branches with only a "stump" of thallus tissue remaining. Other plants were missing from previously mapped locations within permanent quadrats at Prasiola Point. I attributed these findings to wave action; in particular, wave forces associated with winter storms. I quantified

these observations to determine whether damaged plants were site-specific or random in occurrence.

Other studies (Harper et al, 1996; Milligan and DeWreede, 2000) have utilized representative plant and animal species to characterize habitats in many ways, including wave-exposure. For example, the kelp, *Laminaria setchellii*, the surfgrass, *Phyllospadix scouleri*, and the goose-neck barnacle, *Pollicipes polymerus*, are representative species of habitats with a continuous degree of wave-exposure. During the course of my studies, I observed both *L. setchellii* and *P. scouleri* were present at Prasiola Point. Also, a substantial population of *P. polymerus* was found approximately 10 m from the bedrock platform at Prasiola Point. In September 2002, I compared species assemblages for each field site to identify the presence/absence of species that are representative of wave-exposed or wave-protected habitats. Multiple quadrats (n=6) were randomly placed at each field site to determine species present (n = 20 sampling points per quadrat).

Wave-exposure at any given tidal height will vary with topographic features which modify wave breaking patterns. For intertidal organisms, the degree of wave-exposure will be the greatest where the waves actually break. High wave action occurs at intertidal sites that are affected by ocean swells. Prasiola Point fits the definition of a wave-exposed site; whereas, Scott's Bay offers protection from strong swells and crashing waves.

The maximum force associated with maximum wave velocities and acceleration is another aspect of wave-exposure that has only recently been

measured with the purpose of site comparisons (Bell and Denny, 1994). Maximum wave force is understood to be the primary selective agent (acting on organisms in sites of high wave-exposure) since it is assumed that this force determines maximal thallus dislodgement (e.g. the force necessary to remove the organism from its attachment to the substratum) (Denny et al., 1985; Gaylord et al., 1994). The benefit derived from taking such measurements is that peak velocities can be estimated and commonly-used devices can be left in the field for any given amount of time to acquire a maximal reading.

Maximum wave force measurements were taken from both protected and exposed sites containing *Codium fragile* plants. Measurements were also recorded from three intertidal elevations (High, Middle, Low) at Prasiola Point to determine if within-site differences existed. Stainless steel eye bolts were anchored to substratum within *C. fragile* zones at each site. Overhanging algae surrounding the eye bolts were removed to prevent recorder entanglement. During the June, August, and October 2001 low tide cycles, wave force recorders (Figure 4.1; modified from Bell and Denny, 1994) were attached to these eye bolts using cable ties at each field location. Twenty-four hours later, spring extensions were measured to the nearest 0.5 mm using calipers and then reset. Spring extension data collected in the field were then converted to maximum wave force (N) using calibration data obtained in the lab.

Maximum wave force recorders were calibrated in the lab by hanging known masses from each recorder and measuring their spring extension. Forces required to extend springs within the recorders were calculated by:

$$F = Ma_g \quad (\text{Equation 1})$$

where "F" (N) is the force, "M" (kg) is the known mass, and "a<sub>g</sub>" is the gravitational acceleration (9.81 ms<sup>-2</sup>) (Bell and Denny, 1994). For each recorder, these forces were plotted against the resulting spring extensions (m). Linear regressions were calculated and plotted so that forces could be estimated in the field from the observed spring extensions. Therefore:

$$F = (kx_{\text{spring}}) + c \quad (\text{Equation 2})$$

where "k" is the spring constant which indicates the spring extension constant (Nm<sup>-1</sup>), "x<sub>spring</sub>" is the spring extension (m), and "c" is the force required to overcome the initial spring compression (Bell and Denny, 1994). After conducting initial trials, the same spring extension constant (196 N/m) was utilized for all wave force recorders.

#### 4.2.2 Biomechanic Study

What force is required to remove or break *Codium fragile* individuals from a rocky substratum? "Breaking force" can be defined as the force (N) required to break a given plant or to remove it from the substratum. Important variables that determine imposed force and may lead to breaking are: (1) surface area of the thallus and, (2) the way in which the thallus reconfigures in water flow (Carrington, 1990). The thallus surface area generates "drag forces", which can be calculated. Drag results from friction of the water as it slides over the surface of the seaweed. The volume of water trapped by the reconfigured thallus then generates "acceleration forces", which occur as a function of the rate of change

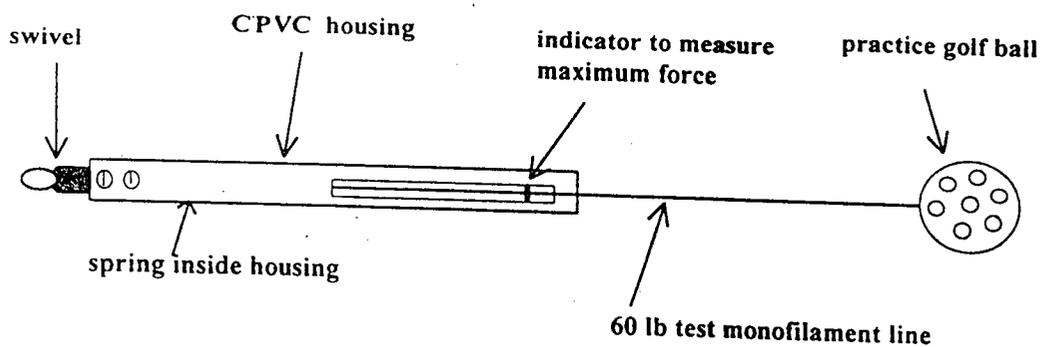


Figure 4.1 – Maximum wave force recorder used to measure wave forces at wave-exposed and wave-protected sites in Barkley Sound (modified from Bell and Denny, 1994).

of water velocity. These two forces together (frictional drag and acceleration drag) result in the "total drag", which acts on the branches, stipe and holdfast. In general, whichever of these (e.g. branch, stipe or holdfast) is the weakest will break first.

I investigated whether breaking forces for *Codium fragile* were standard for plants of different sizes or for those originating from habitats differing in wave-exposure. For the size class comparison, breaking forces of randomly selected *C. fragile* plants were measured *in situ* at Seppings Island in July 2001. To determine the force required to tear *C. fragile* from its holdfast or to detach the holdfast from the substratum, different sizes of plants were placed between clamps (padded with neoprene) attached to a tensiometer. Four to six plants were sampled per size class: "Small" = thallus lengths from 11.5-15.5 cm; "Medium" = thallus lengths from 16.0-20.5 cm; "Large" = thallus lengths from 21.0-26.0 cm. For the site comparison, several small *C. fragile* individuals were pulled from each field site with the same measuring device. In the field, individual thalli were pulled parallel to the substratum as in previous studies (Carrington, 1990; Shaughnessy et al., 1996; Milligan and DeWreede, 2000.) The place of breakage was recorded for each plant; plants were then labeled and returned to the lab for morphological measurements. Strength of the thallus break points (e.g. the stipe) was calculated by dividing the total force to break by the surface area of the break.

Field measurements of spring extensions were converted to force (N) using the calibration data. For each comparison (size vs. breaking force; site vs.

breaking force) a one-way ANOVA was used to determine if significant differences existed between treatments.

#### 4.2.3 Drag Coefficient Study

To measure whether the drag generated by seaweeds is greater or less than the breakage force (measured above), drag coefficients were calculated to determine the change in conformation of *Codium fragile* plants exposed to different water velocities. Methods for this study followed those outlined by Collado-Vides et al. (1998).

Coefficient of drag ( $C_d$ ) was measured at Bamfield Marine Sciences Centre using freshly-collected *Codium fragile*. A 1.8 m steel pole was held vertical in the water by a frame on the side of a small boat. A double beam force transducer (Showa Measuring Instruments, Type N11-MA-2-350-23) (similar in construction to that used by Denny, 1982) was attached to the pole. The transducer voltage output is directly proportional to the applied force generated by moving water on each *C. fragile* thallus. The pole and affixed transducer was positioned so that the solid beam is perpendicular to the direction of flow and submerged 1 m to avoid boat wake and surface effects. Flow velocity was measured by a pitot tube mounted 0.5 m underwater.

Individual *Codium fragile* holdfasts were fixed in a quick-set cement mold with an embedded bolt for attachment; the entire thallus was then attached to the immersed transducer with a coupler nut. This measure standardizes the orientation of *C. fragile* to flow in a fixed position, similar to that in its natural environment. The boat was driven at 0.5 m s<sup>-1</sup> intervals from 0.5 to 4.0 m s<sup>-1</sup>,

and voltage signals from the transducer were continuously recorded by a PC-interfaced multimeter (Micronta Digital Multimeter). A minimum of 30 readings were sampled at each velocity. Background drag (created by the holdfast mount) was measured by removing the *C. fragile* thallus from the mold and repeating the above method.

Drag data (corrected for background drag) for each velocity were averaged. Projected surface area (S) was estimated for each plant by measuring water displacement in a standard 500 ml graduated cylinder and using known volume to calculate the surface area of a cylinder. Drag forces were calculated using the standard drag equation (Vogel 1981):

$$D = 1/2rSU^2C_d \quad (\text{Equation 1})$$

where  $C_d$  is the coefficient of drag (dimensionless),  $D$  is drag (in Newtons, N),  $r$  is the density of seawater ( $\text{kg m}^{-3}$ ),  $S$  is the thallus projected area ( $\text{m}^2$ ), and  $U$  is flow velocity ( $\text{m s}^{-1}$ ). Equation 1 was rearranged as follows:

$$C_d = 2(D/rSU^2) \quad (\text{Equation 2})$$

in order to calculate  $C_d$  (Carrington, 1990). Sigma Plot was used to plot the relationship between  $C_d$  and  $U$  so that:

$$C_d = cU^E \quad (\text{Equation 3})$$

where  $c$  is a coefficient of fit and  $E$  is an exponent of decrease (in this case only), which illustrates the ability of plants to become more streamlined as velocity increases. This relationship was used to estimate  $C_d$  at a range of velocities for predicting drag forces.

Using the drag coefficients derived from this experiment, I also calculated what water velocity is required to generate drag forces large enough to break or to remove *Codium fragile* individuals from the rocky substratum.

#### 4.2.4 Transplant Experiment

To measure wave impact on survival and size of *Codium fragile*, mature plants from Seppings Island were collected by breaking off chunks of boulders with intact holdfasts. Healthy *C. fragile* plants were individually transplanted to either wave-exposed Prasiola Point or wave-protected Scott's Bay (within the normal intertidal range of *C. fragile*) using quick-set cement. For the first trial (Summer 2000), transplants (Prasiola Point, n=24; Scott's Bay, n=27) were monitored at monthly intervals (measuring % survival) to test the technique and determine what period of time was necessary to gain sufficient experimental results. In the second trial, transplants (Prasiola Point, n=16; Scott's Bay, n=15) were monitored monthly for survival, thallus length, and condition (e.g. presence/absence of broken branches, epiphytes) from May to September 2001. For both trials, I predicted that *C. fragile* transplants would exhibit higher survival in a wave-protected site compared to transplants in a wave-exposed site.

### 4.3 Results

#### 4.3.1 Comparison of Maximum Wave Forces

Table 4.1 illustrates the occurrence of damaged *Codium fragile* plants and/or loosened holdfasts observed at field sites in Barkley Sound. *Codium fragile* plants at Prasiola Point had the highest percentage of both broken branches (26%) and loose holdfasts (22%), compared to the three other

locations. *Codium fragile* plants at Scott's Bay ranked second in both damage categories; however, I speculate this is due to infrequent sand burial (discussed in Chapter 3) which can cause scouring, resulting in weakened tissue.

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Table 4.1- Occurrence of damaged thallus tissue (= broken branch tips), and/or loosened holdfasts from *Codium fragile* sampled in the field. N = number of plants sampled at a given location. Percentages are derived from total N per sampling.

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Location:	Sampling Period:	N:	Broken Branches:	Loose Holdfasts:
Prasiola Point	6/98-6/01	131	26%	22%
Second Beach	6/99-6/01	56	13%	8%
Seppings Island	7/00 & 7/01	87	7%	4%
Scott's Bay	8/98-8/01	42	21%	14%

---

Using species assemblage information (Table 4.2), I characterized Prasiola Point as wave-exposed as both *Laminaria setchellii* and *Phyllospadix scouleri* were present. However, I classified Second Beach, Scott's Bay and Seppings Island field sites as wave-protected due to the absence of *L. setchellii* and *P. scouleri*.

As shown in Figure 4.2, there were significant differences in maximum wave forces between sites in June 2001 ( $F=5.31$ ,  $P=0.01$ ) and October 2001 ( $F=7.31$ ,  $P=0.01$ ). [Note: October is lacking data from Seppings Island as I was unable to access it.] In June, Prasiola Point experienced significantly greater mean maximum wave forces (4.6 N) than Scott's Bay (3.1 N) and Seppings Island (3.1 N). There were no significant differences (between sites) in maximum wave forces in August 2001 ( $F=1.87$ ,  $P=0.19$ ). However, in October 2001, both Prasiola Point and Second Beach had significantly greater mean maximum wave forces (7.36 N and 6.8 N, respectively) than those measured at Scott's Bay (3.2 N).

Table 4.3 compares mean maximum wave forces between elevation heights at one location: Prasiola Point. In June, mean maximum wave forces were not significantly different at any intertidal height (one-way ANOVA;  $F=1.09$ ,  $P=0.38$ ). In August, wave forces were significantly different between higher elevations (3.9 N) and lower elevations (3.1 N) (one-way ANOVA;  $F=5.00$ ,  $P=0.03$ ). However, in October, mean maximum wave forces were again significantly different in the high intertidal zone (7.5 N) from those recorded at lower elevations (3.9 N) (one-way ANOVA;  $F=6.17$ ,  $P=0.02$ ).

Table 4.2– Representative plant and animal species found at field sites in Barkley Sound, British Columbia in September 2002. Multiple quadrats were randomly sampled at each field site to determine species present (n = 20 per quadrat). "P" = present; "A" = absent. (PPH = Prasiola Point High; PPM = Prasiola Point Middle; PPL = Prasiola Point Low; SeB = Second Beach; ScB = Scott's Bay; SIH = Seppings Island High; SIM = Seppings Island Middle; SIL = Seppings Island Low)

Species:	PPL	PPM	PPH	SeB	ScB	SIL	SIM	SIH
Algal Species:								
Chlorophyta								
<i>Cladophora columbiana</i>	A	A	P	P	A	A	A	P
<i>Codium fragile</i>	P	P	P	P	P	P	P	P
<i>Ulva intestinalis</i>	A	A	A	P	P	A	A	A
<i>Ulva</i> sp.	P	P	P	P	P	P	P	P
Phaeophyta								
<i>Alaria marginata</i>	P	A	A	A	A	A	P	A
<i>Egregia menziesii</i>	P	P	A	P	A	P	A	A
<i>Fucus gardneri</i>	P	P	P	P	P	P	P	P
<i>Hedophyllum sessile</i>	P	P	P	P	A	P	P	P
<i>Laminaria setchellii</i>	P	A	A	A	A	A	A	A
<i>Leathesia difformis</i>	A	P	A	A	A	A	A	A
<i>Macrocystis integrifolia</i>	A	A	A	A	A	A	P	A
Rhodophyta								
<i>Bossiella orbigniana</i>	P	A	A	A	A	A	A	A
<i>Callithamnion pikeanum</i>	A	A	P	A	A	A	A	A
<i>Chondracanthus</i> sp.	A	A	A	A	A	P	P	A
<i>Corallina</i> sp.	P	P	P	A	A	P	A	A
<i>Cumagloia andersonii</i>	A	A	P	A	A	P	P	P
<i>Endocladia muricata</i>	A	P	P	P	A	A	A	A
Filamentous red	A	A	A	A	P	A	A	A
<i>Halosaccion glandiforme</i>	P	P	P	P	A	P	P	P
<i>Mastocarpus papillatus</i>	P	P	P	P	A	P	P	P
<i>Mazzaella splendens</i>	P	P	A	A	A	P	P	P
<i>Membranoptera platyphylla</i>	P	A	A	A	A	A	A	A
<i>Odonthalia floccosa</i>	P	A	A	A	A	A	P	A
<i>Petrocelis</i> sp.	A	A	A	P	A	A	A	P
<i>Polysiphonia</i> sp.	A	P	P	A	A	A	P	A
<i>Porphyra</i> sp.	A	P	P	P	A	A	A	P
<i>Prionitis lanceolata</i>	P	A	A	P	P	P	P	P

Species:	PPL	PPM	PPH	SeB	ScB	SIL	SIM	SIH
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Sea Grasses:

<i>Phyllospadix scouleri</i>	P	P	P	P	A	A	A	A
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Invertebrate Species:

<i>Anthopleura elegantissima</i>	P	P	P	P	P	A	A	A
<i>Balanus glandula</i>	A	P	P	A	P	A	A	P
<i>Cucumaria</i> sp.	A	P	A	A	A	A	A	A
<i>Haliclona</i> sp.	A	A	A	P	A	A	P	P
<i>Katharina tunicata</i>	A	P	P	A	A	A	A	A
<i>Modiolus rectus</i>	A	A	A	P	A	A	A	A
<i>Pisaster ochraceus</i>	A	P	P	P	A	A	A	A
<i>S. purpuratus</i>	P	A	A	A	A	A	A	A

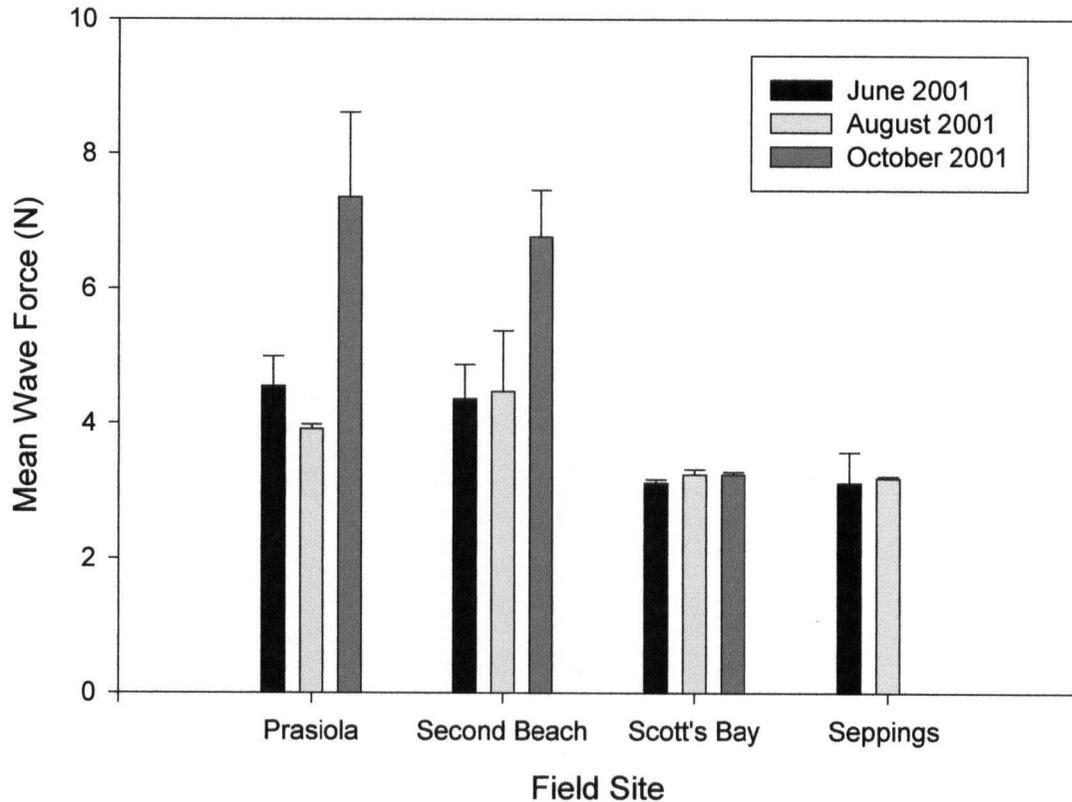


Figure 4.2 - Comparison of mean wave forces (N) measured at Prasiola Point, Second Beach, Scott's Bay and Seppings Island, Barkley Sound. Maximum wave forces were sampled in June, August, and October 2001. [Note: Data were not collected from Seppings Island in October due to high ocean swells.] (Standard error bars are shown.) There were significant differences between sites in June ( $F=5.31$ ,  $P=0.01$ ); Prasiola experienced significantly greater wave forces than both Scott's Bay and Seppings Island. There were no significant differences between sites in August ( $F=1.87$ ,  $P=0.19$ ). In October, both Prasiola Point and Second Beach wave forces were significantly different than those measured at Scott's Bay ( $F=7.31$ ,  $P=0.01$ ).

Table 4.3 – Comparison of mean maximum wave forces between different elevation heights at Prasiola Point. “High” = higher intertidal, “Middle” = middle intertidal, “Low” = lower intertidal. Mean maximum wave force (N) is shown, as well as standard error in parentheses. Multiple wave force recorders (n = 4) were deployed for 24 hours during low tide cycles of June, August and October 2001. Results were analyzed by one-way ANOVA for each month. A Tukey comparison of means test indicates which groups were significantly different from one another (e.g. “A” or “B”).

Month:	Elevation Height:	Mean Max. Wave Force (N):
June F=1.09, P=0.38	High	4.1 (1.1)
	Middle	3.9 (0.02)
	Low	3.4 (0.1)
August F=5.00, P=0.03	High	3.9 (0.4) A
	Middle	3.3 (0.1) A,B
	Low	3.1 (0.01) B
October F=6.17, P=0.02	High	7.5 (5.8) A
	Middle	4.5 (0.6) A,B
	Low	3.9 (0.7) B

#### 4.3.2 Biomechanic Study

Table 4.4 compares the mean breaking forces of different size classes of *Codium fragile* at Seppings Island. Both small and large plants were removed from the substratum (=holdfast attachment) 75% of the time. Medium-sized plants responded to exerted force by either fracturing at the holdfast-stipe region (50%) or detaching from the substratum (50%). One-way ANOVA results

indicate there were no significant differences of breaking forces between small, medium and large plants at this location ( $F=0.03$ ,  $P=0.97$ ).

However, mean breaking forces of small *Codium fragile* plants were significantly different depending on where they came from (see Table 4.5). One-way ANOVA results ( $F=9.13$ ,  $P=0.0005$ ) show that *C. fragile* plants collected at Scott's Bay had significantly lower breaking forces than plants collected at Prasiola Point, Second Beach, or Seppings Island. Furthermore, most *C. fragile* individuals at Prasiola Point, Second Beach and Seppings Island experienced holdfast failure instead of stipe or tissue failure. However, *C. fragile* plants at Scott's Bay ( $n=6$ ) broke at the stipe 50% of the time.

---

Table 4.4 – Breaking forces of randomly selected *Codium fragile* plants were measured *in situ* at Seppings Island in July 2001. "N" = number of plants sampled from different size classes: "Small" = thallus lengths from 11.5-15.5 cm; "Medium" = thallus lengths from 16.0-20.5 cm; "Large" = thallus lengths from 21.0-26.0 cm. Mean breaking forces (B.F.) and standard errors are shown. "% HD" = percent of plants within each size class that were dislodged at the holdfast. One-way ANOVA results show that there were no significant differences of breaking forces between size classes ( $F=0.03$ ,  $P=0.97$ ).

---

Size Class:	N:	Mean B.F./S.E.: (Newtons)	% HD:
Small	4	6.9 /6.7	75
Medium	6	9.4 /3.3	50
Large	4	10.3 /3.5	75

---

Table 4.5– Breaking forces were measured *in situ* for randomly selected *Codium fragile* plants (all were of the small size class) at different field sites in September 2001. “N” = number of plants sampled per field site. Mean breaking forces (B.F.) (e.g. force to remove or break *C. fragile* plants) and standard errors are shown. “% HD” = percent of plants from each location that were dislodged at the holdfast. One-way ANOVA results show that *C. fragile* plants collected from Scott’s Bay had significantly lower breaking forces than plants collected from other sites (F=9.13, P=0.0005). A Tukey comparison of means test indicates which groups were significantly different from one another (e.g. “A” or “B”).

Collection Site:	N:	Mean B.F./S.E.: (Newtons)	% HD:
Prasiola Point	7	11.10 / 0.57 <sup>A</sup>	71
Second Beach	5	11.57 / 0.10 <sup>A</sup>	100
Seppings Island	6	10.06 / 0.79 <sup>A</sup>	86
Scott’s Bay	6	5.11 / 1.65 <sup>B</sup>	50

#### 4.3.3 Drag Coefficient Study

*Codium fragile* plants exhibit differences in total thallus surface area when comparing young juveniles (<2 orders of dichotomous branching) to mature adults (3 or more orders of dichotomous branching). However, all size classes become streamlined in shape, regardless of the number of orders of branching, when subjected to water flow (personal observation). Figure 4.3 shows that this observation holds true for *C. fragile*; drag coefficients for a typical plant are highest ( $C_d = 0.7$ ) at  $1 \text{ m/s}^{-1}$  velocity and approaches a nearly horizontal asymptote ( $C_d = 0.05$ ) at  $\sim 4 \text{ m/s}^{-1}$  velocity.

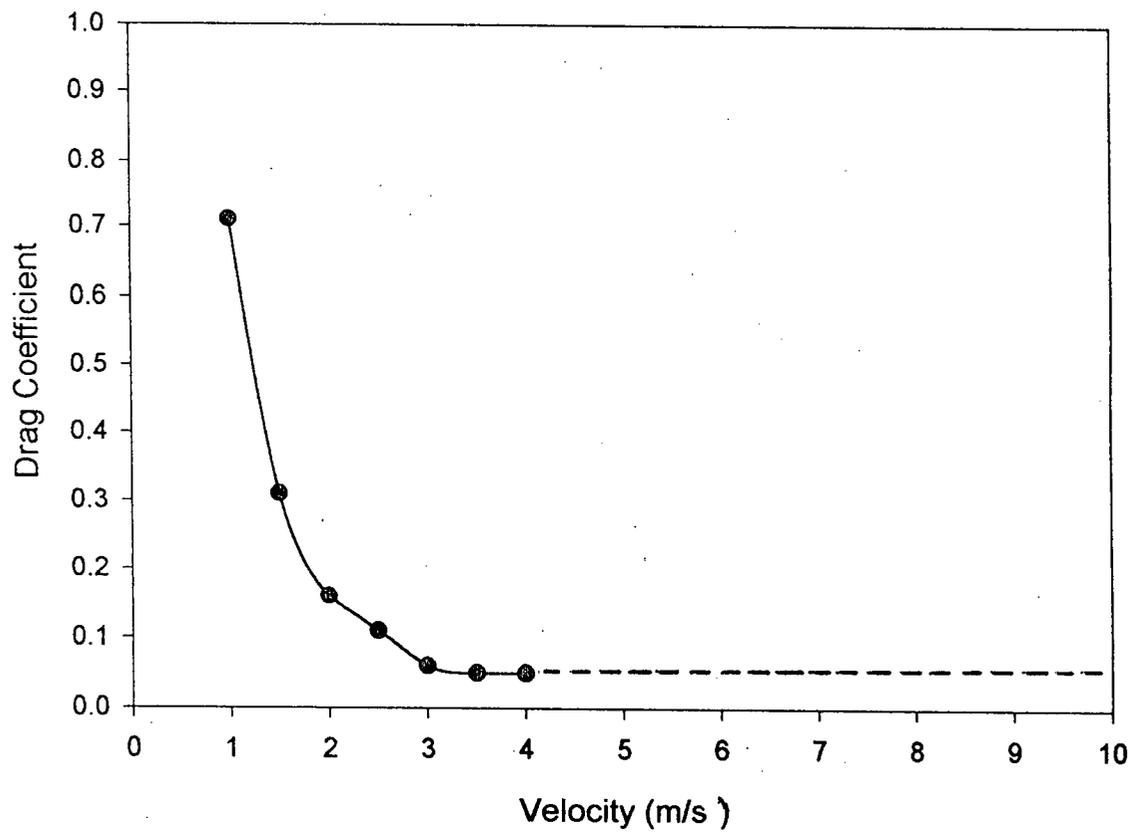


Figure 4.3 – Drag coefficients from 1.0 to 4.0 m/s velocity on a representative *Codium fragile* thallus. The dotted line represents projected velocities.

These data can also be evaluated to test whether wave forces generated during periods of high water motion (e.g. winter storms) could account for differences in *Codium fragile* abundance. Table 4.6 compares different size classes of *C. fragile* plants in relation to their range of measured breaking forces and estimations of breaking forces using known data. Results from Table 4.5 show that it would take wave velocities of 10-16 m/s<sup>-1</sup> to break or remove small and medium *C. fragile* plants from their substratum. Large *C. fragile* plants are more susceptible to waves; it is estimated that a wave velocity of 10 m/s would remove them from the substratum.

Drag coefficients from this study were also used to predict wave velocities required to break or remove *Codium fragile* plants collected from my four field sites in Barkley Sound. The range of removal forces for each size class (shown in Table 4.7) was derived from the earlier biomechanic experiment. Results from Table 4.7 show that it would take wave velocities greater than 16 m/s to remove plants from substratum at Prasiola Point, Second Beach and Seppings Island. However, waves of lessened velocity ( $\pm 10$  m/s) would break or remove *C. fragile* plants at Scott's Bay.

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Table 4.6 – Predicted wave velocities required to break or remove *Codium fragile* plants of different size classes in Barkley Sound (“Small” = thallus lengths from 11.5-15.5cm; “Medium” = thallus lengths from 16.0-20.5cm; “Large” = thallus lengths from 21.0-26.0cm). Drag coefficients (calculated from previous experiment) were used to estimate forces capable of removing plants from the substratum or breaking thallus tissue. Range of measured breaking forces (B.F.) (derived from earlier experiment) is shown in Newtons.

---

Size Class:	Range of Measured B.F.: (Newtons)	Predicted Velocity (m/s):	Realistic?
Small	5.4-9.7	10-16	Yes
Medium	6.7-12.8	10-16	Yes
Large	6.7-12.5	10	Yes

---

Table 4.7 – Predicted wave velocities required to break or remove *Codium fragile* plants located at different field sites in Barkley Sound. Drag coefficients (calculated from previous experiment) were used to estimate forces capable of removing plants from the substratum or breaking thallus tissue. Range of measured breaking forces (B.F.) (derived from earlier experiment) is shown in Newtons; “+” indicates that breaking forces exceeded the capability of the tensiometer recording range.

---

Field Site:	Range of Measured B.F.: (Newtons)	Predicted Velocity (m/s):	Realistic?
Prasiola Point	7.7-11.7+	>16	No
Second Beach	11.2-11.7+	>16	No
Seppings Island	7.0-11.7+	>16	No
Scott's Bay	1.0-9.4	+/- 10	Yes

---

#### 4.3.4 Transplant experiment

Figures 4.4 and 4.5 show that during Summer 2000 and 2001, *Codium fragile* transplants from both sites experienced decreased survival over time. After four months (Trial 1), 20% of *C. fragile* plants transplanted to Prasiola Point were still alive whereas all Scott's Bay transplants had disappeared (Figure 4.4). Furthermore, four transplants at Prasiola Point survived winter storms and persisted at Prasiola Point for 15 months (not shown in Figure). Figure 4.5 depicts similar results for the 2001 transplant trial. In September, 45% *C. fragile* transplants were present at Prasiola Point compared to 20% survival for plants at Scott's Bay. Figure 4.6 compares mean thallus lengths for *C. fragile* transplants

in Trial 2. Mean thallus lengths at Prasiola Point decreased in July, then showed successive increases in August and September. By contrast, transplants at Scott's Bay showed a mean reduction in thallus length at each monthly interval. Table 4.8 compares the condition of *C. fragile* transplants during Trial 2. At Prasiola Point, 7-8% of *C. fragile* transplants had loose holdfasts throughout the sampling period, broken branches were observed 15-67% of the time, and 40-67% of those surviving the experiment were fouled with epiphytes. By contrast, 100% of *C. fragile* transplants at Scott's Bay had loose holdfasts and broken branches after four months. It was common for them to be fouled with epiphytes (40-100%) (Figure 4.7A); however, nearly half of all surviving transplants were fouled with invertebrate larvae (e.g. mussels, fish, gastropod) (Figure 4.7B) in July and August.

Accepted Hypothesis:

H<sub>A1</sub>: More *Codium fragile* individuals transplanted to a wave-exposed habitat will survive, compared to those transplanted to a wave-protected habitat.

2000

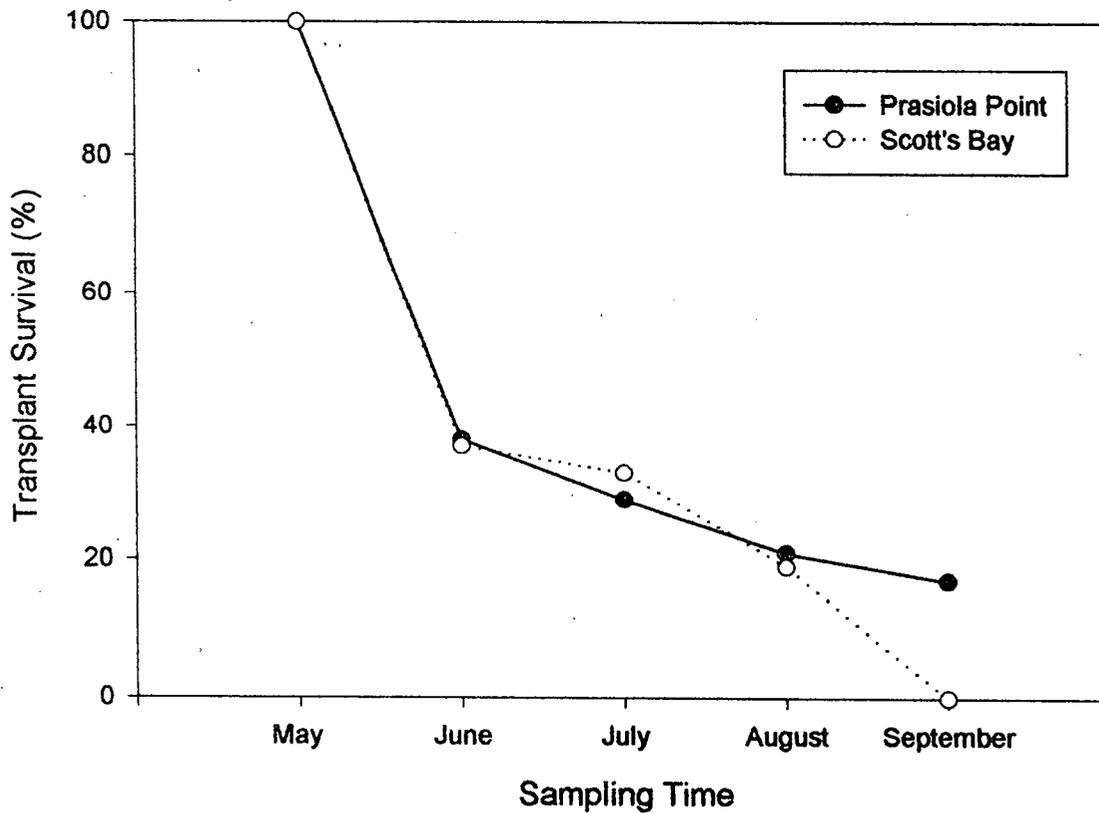


Figure 4.4 – Results from first trial of transplant experiment where *Codium fragile* plants collected from Seppings Island were transplanted to wave-exposed Prasiola Point (n=24) and wave-protected Scott's Bay (n=27). All transplants were monitored monthly from May to September 2000 for percent survival (presence/absence).

2001

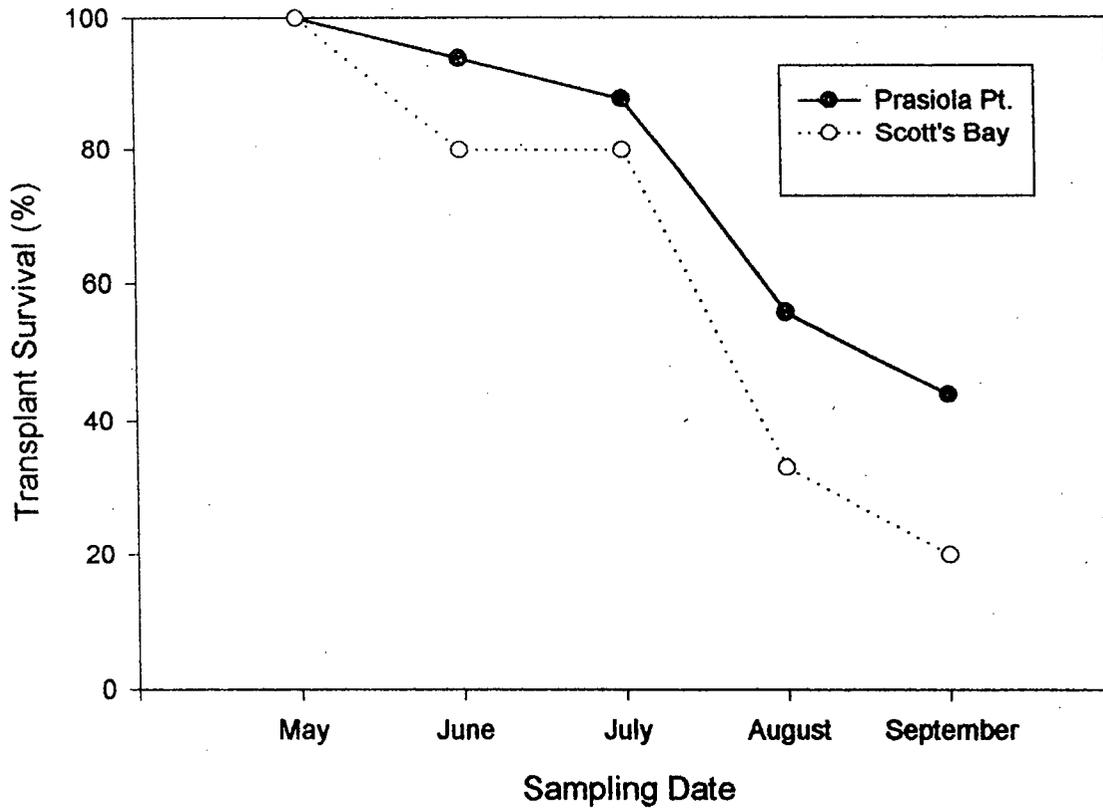


Figure 4.5 – Results from the second trial of the transplant experiment where *Codium fragile* plants collected from Seppings Island were transplanted to wave-exposed Prasiola Point (n=16) and wave-protected Scott's Bay (n=15). All transplants were monitored monthly from May to September 2001 for percent survival (presence/absence).

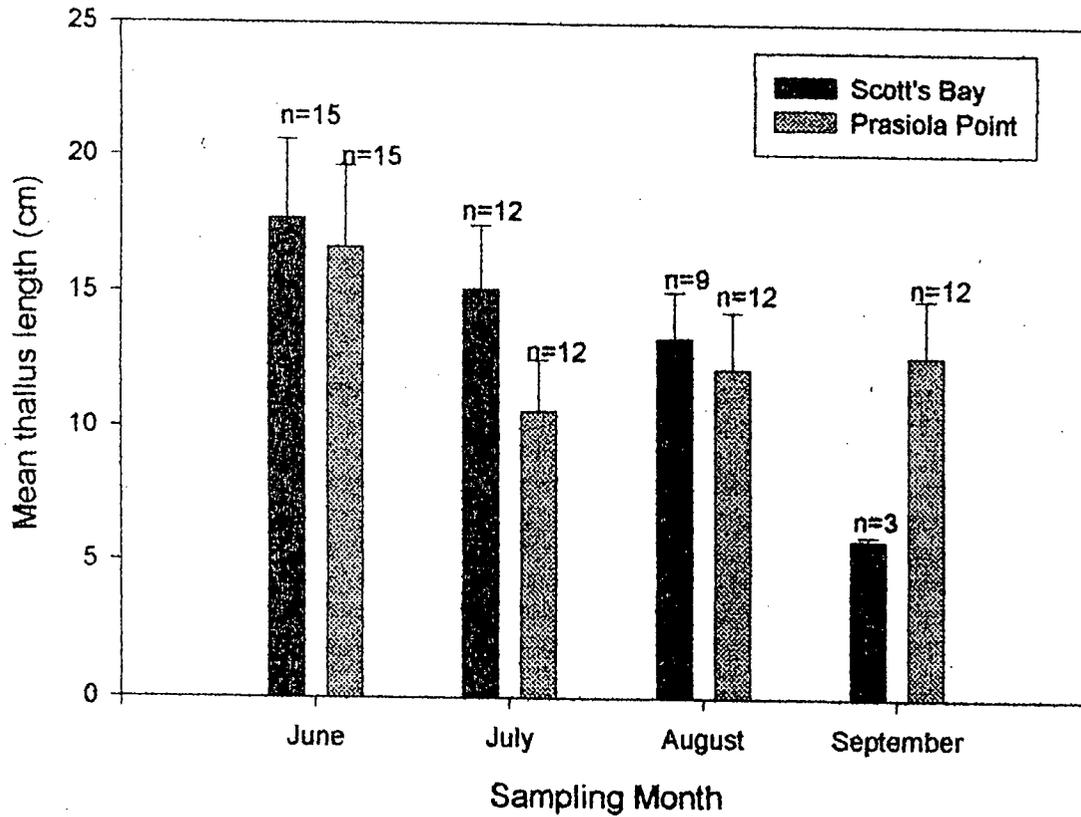


Figure 4.6 – Comparison of mean thallus lengths for *Codium fragile* plants surviving at either Scott's Bay or Prasiola Point during Summer 2001. "N" = number of plants remaining at each location. (Standard error bars are shown.)

Table 4.8 – *Codium fragile* transplants were monitored for changes in thalli condition from May to September 2001. “N” = number of transplants alive at each sampling period. Percentages are given for number of plants at each field site (Prasiola Point, Scott’s Bay) observed to have loose holdfasts, broken branches, and fouled thalli. “EF” = epiphyte fouling, “ILF” = invertebrate larval fouling.

Location:	Sampling Month:	N:	% Loose Holdfast:	% Broken Branches:	%Fouled Thalli:
Prasiola Point	May	15	0	0	40 (EF)
	June	14	7	15	40 (EF)
	July	13	8	50	58 (EF)
	August	8	8	67	67 (EF)
	September	7	8	67	67 (EF)
Scott’s Bay	May	15	0	0	40 (EF)
	June	12	7	0	40 (EF)
	July	12	8	67	25 (EF) 58 (ILF)
	August	5	67	56	44 (EF) 56 (ILF)
	September	3	100	100	100 (EF)



Figure 4.7 – *Codium fragile* transplants at Scott's Bay study site. In August 2001, (A) many plants were fouled with algal epiphytes; (B) some were fouled with invertebrate larvae. This *C. fragile* stipe was fouled with gastropod egg sacs while invertebrate larvae (juvenile mussels) were attached to upper branches.

## 4.4 Discussion

### 4.4.1 Comparison of Maximum Wave Forces

My results indicate that during the months of June and October 2001, there were significant differences in maximum wave force between the four field sites in my study. Mean wave forces at Prasiola Point were significantly higher (in June) compared to those recorded from Scott's Bay and Seppings Island. In October, mean wave forces were significantly higher at both Prasiola Point and Second Beach, compared to measurements from Scott's Bay. (Seppings Island was not included in that sampling due to precarious waves en route) This trend supports my earlier classification wherein I labeled Prasiola Point as a wave-exposed site and Scott's Bay as a wave-protected location. Data from my experiment indicate that the rock mounds at Second Beach are more wave-exposed than wave-protected, as swells of waves hit the large bedrock mass of Prasiola Point and crash on either side of it (eventually hitting the mounds at Second Beach). Data collected in the month of June suggest Seppings Island is a wave-protected location. However, a larger data set is required to further substantiate this observation.

Are these trends accurate? According to other studies monitoring wave forces in Barkley Sound (Milligan and DeWreede, 2000; Salomon, 2000), wave forces can be used to differentiate wave-exposure patterns between sites though seasonal fluctuations exist. Salomon (2000) compared maximum wave forces between nine study sites (August – October 1999) and found significant differences (between sites) in the month of September. Milligan and DeWreede

(2000) found that maximum wave forces were significantly higher from October to February in sites they judged subjectively to be wave-exposed sites, when compared to data derived from wave-protected sites.

As stated earlier, the degree of wave-exposure will be the greatest (for intertidal organisms) where the waves actually break. Though waves are breaking at all intertidal heights while the tide recedes, perhaps, wave forces are stronger (at higher elevations) during high tide. My results show that in both August and October 2001, mean maximum wave forces were ~30-50% greater in the higher intertidal zone than those measured in the lower intertidal. High maximum wave forces may severely limit both number and size of *Codium fragile* plants occurring at that elevation. If we review distribution data (from Chapter 1): 10+ *C. fragile* plants per m<sup>2</sup> were recorded 64% of all sampling periods in the lower intertidal zone, compared to 27% of the time in the high intertidal region. From June 1998 to October 2001, large (e.g. 12+ cm in length) *C. fragile* plants were found in the lower intertidal region during every sampling period. Alternately, small (e.g. 0-6 cm in length) *C. fragile* plants were the predominant size in the higher intertidal; large plants were present only in one sampling period (June 1998). This pattern may be caused by other physical stresses; specifically, desiccation of plants during daytime low tides in spring and summer months.

A common prevailing theory is that plants inhabiting intertidal areas are generally small relative to subtidal and terrestrial plants; within a species, plants on wave-exposed shores are usually smaller than those at wave-protected sites (Lewis, 1964; Menge, 1976). This generalization is true for *Codium fragile* if *C.*

*fragile* size classes are compared using Prasiola Point and Seppings Island data. For example, large (12+ cm in length) *C. fragile* plants were found ~47% of all sampling periods at wave-protected Seppings Island. However, large *C. fragile* plants were found <5% of all sampling periods at high and middle intertidal elevations at wave-exposed Prasiola Point. Large plants occurred more frequently in the lower intertidal at Prasiola Point, this may be due to lessened wave forces (as described above). When comparing (wave-exposed) Prasiola Point to (wave-protected) Scott's Bay, large *C. fragile* plants occurred <17% of all sampling periods. Though the smaller number of large plants (at Scott's Bay) is most likely caused by sedimentation (as described in Chapter 3), large plants occurred more often at this wave-protected site than at Prasiola Point.

#### 4.4.2 Biomechanic Study

My study results show that it takes a mean breaking force of ~6 N to dislodge *Codium fragile* plants from the substratum at Seppings Island (July 2001). There were no significant differences when comparing breaking forces of different size classes (e.g. small, medium, large) found at Seppings Island. The majority of the time (50-75%), most *C. fragile* plants exhibited holdfast failure, rather than stipe/tissue failure. This fact offers one explanation for the disappearance of *C. fragile* plants from Prasiola Point as holdfast failure leads to mortality. Gunnill (1985) monitored *C. fragile* populations in southern California from 1973-77. He noted that most losses (from known quadrat locations) were *C. fragile* individuals torn from their holdfasts. Other studies (Carrington, 1990; Shaughnessy et al., 1996) show that most seaweeds attached to rocky

substratum (e.g. *Mastocarpus papillatus*, *Mazzaella splendens*) break at the junction of the stipe and the holdfast. This is advantageous for these algal species as individuals may be able to maintain space and regrow thallus tissue following a break at the holdfast region. Though I documented the occurrence of *C. fragile* "stumps" at Prasiola Point, I did not observe a regrowth of thallus tissue. Gunnill (1985) observed that recruitment of new *C. fragile* individuals (and regeneration of known *C. fragile* individuals) occurred simultaneously within locations at his study site. Some kelp species are dislodged completely (at the holdfast region) which leaves new space available for recolonization (Koehl and Wainwright, 1977; Milligan and DeWreede, 2000).

Mean breaking forces were within the range of 5-12 N when *Codium fragile* plants were sampled from all four study sites (September 2001). Though sample sizes were small, these results may not be unusual. Milligan and DeWreede (2000) found that for the intertidal kelp, *Hedophyllum sessile*, holdfast weakening occurs during summer months which results in a larger proportion of loose holdfasts before early winter storm events. Other studies have reported a similar range of breaking forces for the tropical chlorophyte, *Udotea flabellum* (Collado-Vides et al., 1998) and the temperate rhodophyte, *Mazzaella splendens* (Shaughnessy et al., 1996). Consequently, I found significant differences in mean breaking forces based on where *C. fragile* plants originated. Mean breaking forces were significantly higher at Prasiola Point, Second Beach, and Seppings Island than those measured at Scott's Bay. In other words, *C. fragile* are adapted to withstand higher wave forces at these locations compared to the

wave-protected Scott's Bay habitat. Of the randomly chosen plants sampled, most *C. fragile* plants experienced holdfast failure at the holdfast (71-100%). Coincidentally, 50% of sampled plants at Scott's Bay broke at the stipe region. Perhaps *C. fragile* tissue is weaker more so at Scott's Bay than the other study sites due to the infrequent sand burial events (discussed in Chapter 3). Sedimentation may cause scouring of algal tissue, which reduces its tensile tissue strength (particularly at the stipe junction). Another explanation could be that loose holdfasts and/or weakened *C. fragile* tissue are the results from suboptimal environmental factors (other than wave action) associated with this habitat.

#### 4.4.3 Drag Coefficient Study

According to Friedland and Denny (1995), there are four forces that wave action imposes on algae: 1) drag, 2) lift, 3) buoyancy, and 4) accelerational force; it is crucial that intertidal species develop a range of strategies to survive them. One such adaptation is an alga's shape. For example, the bull kelp *Nereocystis leutkeana* forms a bundle of its blades when subjected to flow. Drag is reduced because of the bundle's streamlined shape and because the blades on the inside of the bundle are shielded from the largest water velocities.

Most uncalcified algae (which includes most temperate and noncoralline seaweeds) reconform when subjected to water flow (Collado-Vides et al., 1998). For example, the rhodophyte, *Mazzaella splendens*, "bunches" its blades in strong currents (Shaughnessy et al., 1996). Field observations suggest that *Codium fragile* utilizes this same morphological adaptation; when exposed to

incoming tides and water flow patterns, the dichotomous branches clump together and become streamlined in order to conform to the flow. Measured drag coefficients support these qualitative observations; drag coefficients for a typical *C. fragile* plant were highest ( $C_d = 0.7$ ) at  $1 \text{ m/s}^{-1}$  velocity and showed no change at ( $C_d = 0.05$ ) at  $\sim 4 \text{ m/s}^{-1}$  velocity.

When using drag coefficients and breaking forces to project what water velocities are required to dislodge *Codium fragile* individuals, I found that it would take wave velocities of  $10\text{-}16 \text{ m/s}^{-1}$  to break or remove small and medium *C. fragile* plants from their substratum. Large *C. fragile* plants are more susceptible to waves; it is estimated that a wave velocity of  $10 \text{ m/s}$  would remove them from the substratum. These data support my distribution trends at Prasiola Point (see Chapter 1)—small and medium *C. fragile* plants occurred most often in the high and middle intertidal elevations, whereas large *C. fragile* were predominantly located in the lower intertidal. These predictions are feasible for a typical rocky shore habitat; according to Friedland and Denny (1995), wave-induced velocities on rocky shores can reach  $10\text{-}20 \text{ m/s}$  during winter storms. Thus, *C. fragile* plants are susceptible to removal by higher wave forces that occur at this site from time to time.

Drag coefficients from this study were also used to predict wave velocities required to break or dislodge *Codium fragile* plants collected from my four field sites in Barkley Sound. My findings suggest that it would take wave velocities greater than  $16 \text{ m/s}$  to remove plants from substratum at Prasiola Point, Second Beach and Seppings Island. However, waves of lessened velocity ( $\sim 10 \text{ m/s}$ )

would break or remove *C. fragile* plants at Scott's Bay. This information implies that *C. fragile* individuals have adapted to specific habitats (e.g. Prasiola Point, Second Beach, Seppings Island) by developing stronger holdfasts and/or tensile tissue strength in order to withstand a range of wave velocities associated with those habitats.

#### 4.4.4 Transplant Experiment

The invasive brown seaweed, *Sargassum muticum*, is patchily distributed in localities that differ in wave-exposure and is most abundant in wave-protected habitats. Viejo et al. (1995) conducted a transplant study to test the ability of *S. muticum* to persist and grow on wave-exposed shores. After one month, they found that >80% of their transplants suffered from breakage. The remaining (undamaged) plants showed a mean reduction in size compared to control plants at the wave-protected site. Their findings suggest that the distribution of this species is limited by physical conditions associated with wave-exposed environments.

Other studies have examined relationships between size and survival of intertidal seaweeds influenced by wave action (Carrington, 1990; Gaylord et al., 1994; Shaughnessy et al., 1996). One study focused on the common intertidal seaweed, *Fucus gardneri*. Blanchette (1997) reciprocally transplanted *F. gardneri* individuals between wave-exposed and wave-protected sites at Fogarty Creek Point, Oregon. She found that mean sizes of wave-exposed plants transplanted to wave-protected sites increased significantly relative to exposed control transplants. Furthermore, mean sizes of wave-protected plants

transplanted to exposed sites decreased significantly relative to protected control transplants. Blanchette's findings suggest that wave-protected habitats are better suited for optimal growth (of *F. gardneri*), compared to wave-exposed habitats. This pattern was not repeated in my study using *C. fragile* plants.

At wave-protected Scott's Bay, *Codium fragile* transplants showed decreased survival compared to *C. fragile* transplants at (wave-exposed) Prasiola Point. Furthermore, transplants at Scott's Bay showed a mean reduction in thallus length at each monthly interval. This data suggests that physical conditions at Scott's Bay were not conducive to *C. fragile* growth. Meanwhile, *C. fragile* thallus lengths at Prasiola Point decreased in July, then showed successive increases in August and September. This implies, that past an initial acclimation period, *C. fragile* plants were growing at Prasiola Point.

*Codium fragile* individuals transplanted to Scott's Bay experienced a large degree of broken branches. At this wave-protected site, poorer water circulation may have resulted in weakened tissue strength for *C. fragile*. Furthermore, all Scott's Bay transplants became heavily fouled with algal epiphytes, invertebrate larvae, or a combination of both. Whether plant or animal, the effects of epiphytes generally are to shade the anchor species, impede gas and nutrient exchange and thereby, decrease its growth rate (Sand-Jensen, 1977; Harlin et al., 1985). These negative effects can deteriorate plant "health" and lead to increased mortality over time.

Transplant results from Prasiola Point also included a large number of *Codium fragile* plants with broken branches. This may be the effect of wave

"pruning", instead of poor water circulation patterns. Broken branches were often associated with larger *C. fragile* plants (>21 cm in length) transplanted at middle or high intertidal heights, compared to small or medium size *C. fragile*. As stated earlier, if wave forces are important in limiting seaweed size, waves should prune or dislodge the largest plants. Thallus "tattering" might also occur, in which individual branches or sections of the thallus are removed by waves, while the holdfast remains attached to the rock. For *Fucus gardneri*, thallus tattering is common and seems to be an important method of size reduction (Blanchette, 1997). A sublethal (wave) force may break off several branches of a *F. gardneri* plant, reducing its overall area and volume. In this scenario, the plant's probability of survival is increased, since the size of the plant is reduced while its tenacity remains unchanged. Later, this individual will grow to achieve some "optimal" size for its particular environment. This strategy may be utilized by *C. fragile* plants at Prasiola Point as 20-45% of the transplants survived at this wave-swept location for the 5-month experiment duration or longer.

*Codium fragile* transplants at Prasiola Point were also frequently fouled by algal epiphytes. According to Lewis (1982), native *C. fragile* plants on British Columbia shores have a diverse assemblage of 30 epiphytic species, thirteen of which are common. Throughout the course of my study, the filamentous rhodophytes, *Ceramium* sp. and *Polysiphonia* sp., were most commonly associated with *C. fragile* in the field. Though epiphyte fouling of *C. fragile* plants at Scott's Bay negatively impacts their overall condition; a high load of epiphytes may provide beneficial effects for *C. fragile* plants at Prasiola Point. For

example, dense epiphytes on *Corallina* sp. turf may alleviate desiccation stress (Stewart, 1982) at any intertidal elevation. Furthermore, epiphytism may allow shade-loving species to be exposed to well-lit conditions, by creating shade for the algal host (Weincke and Davenport, 1987). According to Norton et al. (1982), *C. fragile* ssp. *tomentosoides* is better suited to low light environments. If this is true for all subspecies (based on similar algal physiology), then the benefit of attached epiphytes (for shading purposes) may outweigh the potential increase in drag at a wave-swept environment.

Results from my transplant experiment seem counterintuitive. One might have expected *Codium fragile* transplants to fare better due to a lesser degree of physical stress (e.g. wave forces). However, poor water circulation patterns (associated with a wave-protected habitat) caused increased epiphyte-loads, weakening of thallus tissue, and eventually, mortality of many *C. fragile* plants transplanted to Scott's Bay. Conversely, *C. fragile* transplanted to wave-exposed Prasiola Point remained healthy, with minimal epiphyte coverage, for longer time periods than their counterparts at Scott's Bay. Though this habitat is more stressful for *C. fragile* plants (due to increased wave exposure), the physiological benefits of increased water circulation patterns contribute to their limited persistence. Therefore, wave action does influence the distribution of *C. fragile* plants at Prasiola Point and Second Beach; maximum wave forces (associated with winter storms) will most likely dislodge large plants (more so, than small ones) and prune others (e.g. cause broken branches).

## 4.5 Conclusion

Of the three experimental factors (e.g. herbivory, sand burial, wave action) thought to cause irregular distribution of *Codium fragile* at Prasiola Point, wave action has been shown to impact both size and survival of individual *C. fragile* plants. Experimental results from this chapter indicate that wave action plays a significant role in *C. fragile* survival at several Barkley Sound locations. By measuring maximum wave forces associated with each site, I was able to classify Prasiola Point as wave-exposed and Scott's Bay as wave-protected.

This is the first study exploring biomechanical properties of a coenocytic species from temperate shores. Biomechanical experiments show that *Codium fragile* possesses breaking forces comparable to those recorded for other algal species. There were no differences in breaking force related to size; however, there were significant differences in breaking forces depending on where *C. fragile* plants originated. Drag coefficient results show that *C. fragile* conforms to increased water velocities. Calculations using known data (e.g. breaking forces and drag coefficients) were used to project what water velocities were required to break or dislodge individuals based on size or habitat. Large plants are more susceptible to increased velocities than smaller plants; plants growing at Scott's Bay are more likely to break or detach compared to other habitats. According to results from my transplant experiment, Scott's Bay is not a suitable habitat for *C. fragile*. However, Prasiola Point is; in both transplant trials, ~20-45% *C. fragile* transplants survived at Prasiola Point, compared to 0-20% of the original transplants at Scott's Bay.

## CHAPTER 5

### Conclusion

#### 5.1 General conclusion

The green, dichotomously-branched macroalga *Codium fragile* (Suringar) Hariot 1889 (Chlorophyta: Codiaceae) is unique, as a coenocytic plant existing in temperate-zone habitats. Little is known of how native *Codium fragile* plants are distributed in the northern range of N.E. Pacific shores. I monitored *C. fragile* plants found at four different field sites in Barkley Sound, British Columbia from 1998-2001 and found a pattern of patchy distribution; *C. fragile* plants were unevenly distributed over time (e.g. seasonal and yearly population fluctuations) and space (e.g. differed in abundance from one location to another).

Of my four designated study sites, a stable population of *Codium fragile* plants was noted at Seppings Island in 1999 and documented from 2000-01. Quadrat sampling (at Seppings Island) revealed a lack of herbivores (within the *C. fragile* zone) and unique topography prevented sand burial events from occurring, as well as protecting the intertidal zone from increased wave exposure. In comparison, generalist herbivores (e.g. purple urchins and black chitons) were present at Prasiola Point and attached organisms were subjected to increased wave forces. *Codium fragile* plants were found attached to rock mounds at nearby Second Beach with no herbivores present and a lesser degree of wave exposure. Finally, a small population of *C. fragile* plants existed at Scott's Bay. Though this site supported a diversity of macroalgae on rock walls encompassing the small bay, *C. fragile* plants were found isolated on a rock mound infrequently buried by sand, considered to be a wave-protected

environment. I hypothesized that impacts caused by herbivory (at Prasiola Point), sand burial (at Scott's Bay), and wave exposure (increased wave forces at Prasiola Point and Second Beach vs. lesser wave forces at Seppings Island and Scott's Bay) were causative for the erratic occurrence of *C. fragile* in Barkley Sound.

Many studies have tested feeding choices of common herbivores as a means of measuring the impacts of grazing on macroalgal communities. None have addressed this topic using our native *Codium fragile* in British Columbia habitats. I conducted several feeding experiments to test whether generalist herbivores (e.g. purple urchins and black chitons) impact the occurrence of *C. fragile* plants at Prasiola Point. My results show that compared to two common seaweeds (e.g. *Hedophyllum sessile* and *Mazzaella splendens*), *C. fragile* is not preferred by purple urchins or black chitons, it has the lowest short-term nutritional value, and did not significantly increase somatic or reproductive growth for either herbivore species. Though *H. sessile* and *M. splendens* are better food choices for these herbivores, they are still locally abundant while *C. fragile* is patchy at Prasiola Point.

My Scott's Bay field site had fewer *Codium fragile* plants (following sand burial events), compared to previous sampling periods. Field observations showed that *C. fragile* plants at Scott's Bay were stunted in growth, often discolored, and had weakened thalli tissue. Therefore, it seemed possible that infrequent sand burial events might be one explanation for *C. fragile's* patchy distribution at this location. Experimental results show that adult *C. fragile* plants

buried in sand for five weeks grew less (e.g. individuals showed reductions in thallus length, volume and biomass) compared to control plants (no sand). Though my experiments provide some insight to how adult *C. fragile* plants respond to sand-burial at Scott's Bay, they do not explain the irregular distribution of *C. fragile* at Prasiola Point and Second Beach (where no sand burial occurred).

This is the first study exploring biomechanical properties of a coenocytic algal species inhabiting temperate shores. Other studies (Carrington, 1990; Gaylord et al., 1994; Shaughnessy et al., 1996; Blanchette, 1997; Milligan and DeWreede, 2000) have explored the role of wave action on (multi-cellular) macroalgae from temperate habitats or coenocytic species from tropical habitats (Collado-Vides et al., 1999). My experimental results indicate that wave action plays a significant role in *Codium fragile* survival at several Barkley Sound locations. By measuring maximum wave forces associated with each site, I was able to classify Prasiola Point as wave-exposed and Scott's Bay as wave-protected. Biomechanical experiments show that *C. fragile* possesses removal forces comparable to those recorded for other algal species. There were no differences in removal force related to size; however, there were significant differences depending on where *C. fragile* plants originated. Drag coefficient results show that like many other macroalgal species, *C. fragile* conforms to increased water velocities. Large *C. fragile* plants are more susceptible (to removal from substratum) when exposed to increased velocities than smaller plants; plants growing at Scott's Bay are more likely to break or detach compared

to plants at other habitats. According to my transplant experiment results, Scott's Bay is not a suitable habitat for *C. fragile*. However, Prasiola Point is; in both transplant trials, ~20-45% *C. fragile* transplants survived at Prasiola Point, compared to 0-20% of the original transplants at Scott's Bay.

Poor water circulation patterns (associated with a wave-protected habitat) caused increased epiphyte-loads, weakening of thallus tissue, and eventually, mortality of many *Codium fragile* plants transplanted to Scott's Bay. Conversely, *C. fragile* transplanted to wave-exposed Prasiola Point remained healthy, with minimal epiphyte coverage, for longer time periods than their counterparts at Scott's Bay. Though this habitat is more stressful for *C. fragile* plants (due to increased wave exposure), the physiological benefits of increased water circulation patterns contribute to their limited persistence.

In most ecological studies, it is challenging to define causative factors of observed patterns without interaction effects. Of the three factors I tested for influencing the distribution of *Codium fragile* in Barkley Sound habitats, it may be a combination of herbivory and wave forces for plants located at Prasiola Point. It has been proposed that wave exposure affects all components of a population's demography, especially mortality rates (Milligan and DeWreede, 2000). High wave forces (at wave-exposed sites) may cause mortality by dislodging organisms at a relatively higher rate than wave forces from wave-protected areas (Friedland and Denny, 1995). This is a likely explanation for the reduced abundance of *C. fragile* at Prasiola Point, compared to increased abundance of *C. fragile* plants at Seppings Island. When wave-induced damage

is combined with herbivory wounds, mortality rates are higher in wave-exposed habitats than wave-protected sites (DeWreede et al., 1992; Padilla, 1993). Results from my herbivory studies prove that *C. fragile* plants can be impacted by herbivore grazing (e.g. purple urchins and black chitons); which were present only at Prasiola Point (and absent at Seppings Island). Though these herbivores may not consume a large quantity of *C. fragile* (it is not their preferred food), plants can be wounded from herbivore feeding.

This thesis advances our minimal knowledge of native *Codium fragile* plants in NE Pacific habitats, compared to the wealth of information on the invasive subspecies, *C. fragile* ssp. *tomentosoides*. My research is original as it measures the effects of both biotic and abiotic factors on a coenocytic macroalgal species found in rocky, intertidal habitats. Of the three factors I chose to study, herbivory is widespread throughout published ecological literature whereas effects of sand burial are few. Furthermore, my wave action results contribute to an emerging field of study in marine science—increasing our understanding of how seaweeds persist in wave-swept environments.

## 5.2 Recommendations for future research

This study examined the effects of herbivory, sand burial and wave forces on adult *Codium fragile* plants. It is unknown whether these results would apply to juvenile *C. fragile* plants in field or laboratory experiments. My herbivory experiments measured feeding preferences, absorption efficiencies and fitness of purple urchins and black chitons. It would be interesting to investigate the role of mesograzers (e.g. isopods, polychaete worms) in Barkley Sound habitats and

identify whether their grazing impacts *C. fragile* populations. I also conducted a sand burial experiment to monitor changes in specific growth parameters (e.g. thallus length, volume and biomass) while *C. fragile* adults were exposed to three different treatments. Future experiments could explore physiological changes of *C. fragile* plants exposed to sand burial; for example, measure respiration and/or photosynthetic rates over time.

An algal population with high (wave-induced) dislodgement rates is often dependent on successful recruitment to maintain its population size at a particular habitat (Reed et al., 1988; Ang, 1991). For example, a large number of *C. fragile* juveniles were observed at Prasiola Point during both Summer 1998 and Summer 2001. Coincidentally, many juveniles were mapped at various intertidal locations where adults had occurred the previous year. Though most juveniles did not survive the following season, it appeared that the Prasiola Point *C. fragile* population was more successful with recruitment some years compared to others. Future studies on *C. fragile* recruitment could tell us whether this patchy distribution pattern in Barkley Sound habitats is a function of germling settlement and/or juvenile survivorship versus adult survivorship.

Gunnill (1980) postulates that fluctuations in California standing stocks of *Codium fragile* are due to environmental variations (e.g. cloud cover, aerial exposure during low tide, warmer seawater temperatures associated with El Nino years) during reproduction and recruitment. Seapy and Littler (1982) reported that organisms of upper and middle intertidal zones (in Santa Cruz, California) subjected to prolonged aerial exposure did not survive (including *C. fragile*).

Furthermore, the combination of desiccation and water motion can influence the abundance and performance of intertidal seaweeds. Haring et al. (2002) hypothesized that the intertidal seaweed, *Fucus gardneri*, can be dislodged or damaged by small waves if already weakened by the effects of desiccation. In the San Juan Islands of Washington, waves are generally small in spring and summer months, while low tides create desiccating conditions during midday. Their field experiments showed that mortality of *F. gardneri* field populations is high during these seasons; thalli that were experimentally protected from desiccation suffered fewer losses. Milligan and DeWreede (2000) tested holdfast attachment mechanics for the intertidal kelp, *Hedophyllum sessile*, and found seasonal differences in holdfast strength. Their results indicate that for *H. sessile*, holdfast weakening occurs during summer months which results in a larger proportion of holdfast failure before early winter storm events, compared to after storm events. It is possible that these physical stresses may also impact *C. fragile* populations found in wave-exposed habitats. Future experiments measuring the effects of desiccation and/or holdfast attachment strength (with a seasonal approach) may increase our understanding of *C. fragile* distribution patterns in Barkley Sound.

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