THE ECOLOGY AND ANCHORAGE MECHANICS OF KELP HOLDFASTS

by

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Abstract

The intertidal zone on wave-swept shores is among the most stressful environments on earth. The ability of organisms to survive and thrive in such environments depends on their ability to withstand breakage and wave dislodgement. The research presented in this thesis investigated two aspects of the biology of kelp holdfasts. I first examined whether the recruitment of the kelp Hedophyllum sessile was facilitated by the presence of holdfasts of adult conspecifics and how canopy cover and wave-exposure mediated this interaction. Field experiments indicated that adult holdfasts and substrata of high structural complexity, such as articulated coralline algae, enhanced recruitment. However, the ability of structurally complex substrata to facilitate recruitment depends largely on the extent of canopy cover and to a lesser extent on wave-exposure. Mechanisms by which canopy cover mediates substratum-specific recruitment processes may hold significant implications for population persistence and successful recruitment, especially following periods of high disturbance. Secondly, I investigated the functional morphology of the holdfast of the kelp Laminaria setchellii in relation to its role in providing attachment to the substratum and resistance against wave dislodgment. Results of field investigations indicated that the thallus of L. setchellii responds to increased wave exposure by decreasing blade size and increasing holdfast size; a concomitant increase in holdfast attachment force was not observed. At high wave exposure sites, the integrity and attachment of L. setchellii holdfasts is jeopardized by the presence of barnacles and burrowing crabs. Field investigations further showed that L. setchellii exhibits asymmetry with respect to the prevailing wave direction. The blade and upper part of the stipe are oriented with their longer axis perpendicular to the flow so that reconfiguration and bending is facilitated. The lower part of the stipe and holdfast are oriented with their longer axis parallel to the flow, resisting bending. By exhibiting such pattern of asymmetry along it thallus, L. setchellii avoid large hydrodynamic forces while still avoiding large swaying and remaining off the substratum in water of higher light intensities and velocities.
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Figure 5.9. a) Number of tagged *Laminaria setchellii* dislodged per sampling interval; b) Daily maximum water velocity (m/s) at Prasiola Point, Barkley Sound, BC from December 2001 to January 2004. Black arrows indicate date at which hapteral removal treatments were applied. First hapteral removal was applied in January 2002 (Jan 27-30) and the second in September 2002 (Sept. 6-8). Vertical dotted line indicates the end date of survival experiment (July 11-17, 2003).

Figure 5.10. Break location occurrences for *Laminaria setchellii* pulled off the substratum. Break locations are holdfast/substratum interface (HF/Sub), holdfast (HF), stipe (St). Frequencies of stipe breaks due to the tag artefacts or of individuals that exceeded the capacity of the scale are not illustrated. Frequency differences among break locations were significant, \( \chi^2 = 76.57, N = 105, p = 0.001 \).

Figure 5.11. *Laminaria setchellii*. Mean detachment force ± 1 SE (N) of control (Con) individuals and those with their seaward (Sea, n=), shoreward (Sho) or lateral W or E (LW or LE) haptera. x
removed (see Material and Methods for details). Haptera treatment sharing a common letter are not significantly different, $p>0.05$. See Table 5.3 for sample sizes.

**Figure B.1.** Locations of the five study sites along the Southeast shores of Barkley Sound, Vancouver Island. Bordelais Is. (Bor), Seppings Is. (Sep), Prasiola Point (Pra), Eagle Bay (Eag), and Dixon Is. (Dix). Open arrow indicates the direction of prevalent winds and swells into the Sound. Star indicates the location of the Bamfield Marine Sciences Centre (BMSC).

**Figure B.2.** Maps of the five study sites showing details of intertidal and depth contour of surrounding waters. Sites are (from left to right and top to bottom) Bordelais Is., Seppings Is., Prasiola Point, Eagle Bay and Dixon Is. Star indicates the location of the Bamfield Marine Sciences Centre (BMSC). North is towards top of page.

**Figure D.1.** Beach casts. a) *Laminaria setchellii*, *Pterygophora californica* and *Lessoniopsis littoralis* clump attached to the tests of dead barnacles; b) Close-up of the inside of one of the barnacle test, showing haptera penetrating through the aperture of the test and attaching to its inside walls; c) Underside of the holdfast of *P. californica*. Note outer layer of haptera that were attached to the substratum and inner cavity; d) Underside of the holdfast of *P. californica*. Note outer ring of haptera, inner cavity and inner ring of regenerating haptera (r.h.; light brown).
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\(^1\) Sophie-ism for brainstorming
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Chapter 1 General Introduction

The benthic marine environment is to a large extent one of moving water. Benthic organisms living in the shallow subtidal zone are subjected to a back and forth motion produced by the orbital motion of waves passing overhead. Organisms living in the intertidal zone are subjected to the impact of waves breaking on the shore and the subsequent rapid surge of water up and down the shore. Wave-induced water velocities on rocky intertidal shores can attain speeds of 10-25 m·s⁻¹ (Jones and Demetropulos, 1968; Denny et al., 1985; Gaylord et al., 1994; Gaylord, 1999; Denny et al., 2003) with concomitant accelerations exceeding 400 m·s⁻² in areas exposed to large breaking waves on open coasts (Denny et al., 1985; Gaylord et al., 1994). While sessile organisms subjected to these hydrodynamic forces may suffer severe tissue damage and, ultimately, dislodgement, they can also directly benefit from the increased water turbulence. For example, as water rushes around sessile macroalgae, depleted supplies of dissolved gases and nutrients are replenished, while metabolic waste products are carried away and propagules dispersed (Hurd, 2000). The ability of sessile organisms to survive and thrive in environments such as these depends on their ability to withstand these hydrodynamic forces and to remain attached to the substratum. Thus, the structures and mechanisms by which sessile organisms anchor themselves to the substratum play a fundamental role in the survival of individuals and persistence of populations in the intertidal and shallow subtidal zones.

In this chapter I give an overview of the structures and mechanisms by which sessile organisms, specifically macroalgae and kelps, anchor themselves to the substratum and describe the fundamental role kelp holdfasts play in individual, population and community scale dynamics. I first explore the diversity of means by which macroalgae attach to the substratum. I then review the ecological and biomechanical functions on kelp holdfasts, and I identify gaps in our current knowledge to act as a framework within which this research is set.

Macroalgae are primarily sessile plants that anchor themselves to the substratum by means of a holdfast (Figure 1.1). Temperate macroalgae exhibit a wide array of attachment structures; in its simplest form, attachment to the substratum is provided by a basal cell (Figure 1.2a; Boney, 1966). More elaborate attachment devices include uni- or multicellular rhizoidal holdfasts (Figure 1.2b and c) and crustose bases (Figure
1.2d) and discoid holdfasts (Figure 1.2e; Abbott and Hollenberg, 1976). Within the large brown algae known as kelps (Heterokontophyta, Laminariales), holdfasts also exhibit a range of forms. Kelp holdfasts can consist of a simple discoid holdfast (e.g. Laminaria ephemera and Cymathere triplicata; Figure 1.2e) or of a complex prostrate, branched rhizome bearing multiple stipes (e.g. Macrocystis integrifolia or Laminaria sinclairii; Figure 1.2f). More commonly, though, a kelp holdfast is composed of a mass of intertwined, root-like haptera that, as they grow and branch towards the substratum, create crevices and hollows between the tangled strands. These haptera can grow into a highly compact mass with haptera of older plants much abraded to the point of resembling a discoid holdfast as in Egregia menziesii (Figure 1.2g), or grow in a very loose manner such as the holdfast of Macrocystis pyrifera (Figure 1.2h). Unlike their temperate counterparts, tropical macroalgae have evolved highly specialized holdfast structures that enable them to stay anchored in soft, sandy, or muddy sediment (Figure 1.2i), a habitat rarely colonized by macroalgae of colder temperate waters.

While the holdfast of macroalgae acts primarily as a means of attachment to the substratum, it has also been suggested to serve several other functions in kelps. Patterns of translocation indicate that the holdfast of large kelps such as Macrocystis integrifolia may act as a reservoir for photosynthates. Photosynthates produced by the mature blades are translocated towards the base of the plant and stored in the holdfast in the autumn (Lobban, 1978b; a). When active growth resumes in the spring, translocation is reversed and photosynthates are moved towards regions of active growth. Similarly, (Germann, 1989) observed an increase in mannitol (a photosynthate) content and in dry weight of the kelp Pleurophycus gardneri perennial structures (stipe and holdfast) prior to the occurrence of blade abscission in the autumn. Thus, holdfasts may facilitate the regeneration of blades after winter loss by providing stored photosynthates.

The holdfast of kelps also serves as habitat for a large number (10,000 organisms per m² of Laminaria ochroleuca bed; Christie et al., 2003; Arroyo et al., 2004) and a large variety of invertebrates (up to 238 species/taxa; Christie et al., 2003). Past studies have provided details on the taxonomic assemblages of invertebrates inhabiting holdfasts, on aspects of their population dynamics, faunal community organization, and of the environmental factors affecting holdfast community structure.
Figure 1.1. Typical morphology of a kelp (*Laminaria setchellii*). Rule: 10 cm. Modified from Scagel (1967).
Figure 1.2. Holdfast types. (a) basal cell of the filamentous green alga *Ulothrix* Rule: 20μm; (b) unicellular rhizoidal holdfast of *Polysiphonia rubrorhiza* Rule: 100 μm; (c) multicellular rhizoidal holdfast of *Platysiphonia decumbens* Rule: 200 μm; (d-e) crustose holdfasts: (d) *Mazzaella cornucopia* Rule: 1 cm, (e) *Corallina vancouveriensis* Rule: 1 cm; (f-g) discoid holdfasts: (f) *Laminaria ephemera* Rule: 5 cm, (g) *Cymathere triplicata* Rule: 2 cm; (h-i) Rhizomatous holdfasts: (h) *Macrocystis integrifolia* Rule: 7 cm, (i) *Laminaria sinclairii* Rule: 5 cm; (j) holdfast of *Egregia menziesii* Rule: 12 cm;
(k) holdfast of *Macrocystis pyrifera* Rule: 1 m. (l-m) rhizoidal plugs: (l) *Penicillus capitatus* Rule: 2 cm, (m) *Halimeda incrassata* Rule: 2 cm. [(a) Boney (1966); (b) Hollenberg (1968); (c) Wynne (1969); (d) Abbott (1971); (e and f) Abbott and Hollenberg (1976); (g and h) Scagel (1967); (j) modified from Carefoot (1977); (k) modified from Scagel et al. (1984); (l and m) Van Den Hoek et al. (1995); all with permission].
(Ghelardi, 1971; Edwards, 1980; Ojeda and Santelices, 1984; McLay and Hayward, 1987; Smith, 1996; Smith et al., 1996; Smith, 2000). With the exception of Cancino and Santelices (1980), Ojeda and Santelices (1984) and McLay and Hayward (1987), few studies have considered the ecological role(s) of holdfasts with respect to their invertebrate fauna. Kelp holdfasts serve to shelter fauna from wave impact and supply a refugium from predators, and nursery grounds (Ojeda and Santelices, 1984). More recent studies have investigated the use of the holdfast macrofaunal community as a tool for evaluating anthropogenic effects on hard substrata coastal environments, and as a system to test ecological theory in marine systems (e.g. founder effects, Thiel and Vasquez, 2000). However, none of these studies has considered the algal flora associated with kelp holdfasts, and only two have considered the role holdfast in kelp recruitment (Anderson et al., 1997; McConnico and Foster, 2005).

The ability of kelp holdfasts to fulfill these functions at the individual, population and community scales, presupposes that holdfasts are successful at remaining firmly attached to the substratum. Despite this, few studies have investigated the attachment mechanisms of kelps and of algal holdfasts in general. A few authors have examined the attachment mechanisms in newly settled spores (Oliveira et al., 1980) and juvenile sporophytes (Tovey and Moss, 1978). In newly settled individuals of *Laminaria saccharina* and of *Nereocystis luetkeana*, adhesive plaques secreted by the spore mediate attachment (Oliveira et al., 1980). As the spore germinates and grows into a young sporophyte, rhizoids are produced, penetrating microscopic crevices and filling available spaces in the microstructure of the substratum. There is a strong possibility that adhesive compounds are also implicated in this attachment. Tovey and Moss (1978) mention that the line of juxtaposition between the substratum and rhizoidal cells from haptera is filled by mucilage. Microscopy, tensile tests of individual hapteron of adult sporophytes and the contour-filling capacity of haptera indicate that *Laminaria digitata* adheres to the substratum mainly by mechanical means (Roscoe and Walker, 1995). Sockton et al.(1980) suggest that high levels of the polyguluronate alginate (up to ~50%) relative to mannuronate alginate levels cause a stiffening of the haptera in *L. digitata* and *Alaria esculenta* holdfasts and thus may enhance attachment through mechanical interlocking of the haptera and substratum. Separately, Kain (1971) was amongst the first to give some consideration to the holdfasts of kelps in a synopsis of *Laminaria hyperborea* populations on the coast of England. She described the annual
production of whorls of haptera that coincide with periods of rapid growth. In certain cases, the number of hapteral rings can be used in combination with stipe growth rings to estimate *L. hyperborea* age. Novaczek (1981) used the same approach to estimate the age of *Ecklonia radiata* in New Zealand. Other aspects of the biology of kelp holdfasts, such as growth with canopy reduction or with wave exposure, are mentioned briefly in a few other studies (McCleneghan and Houk, 1985; Sjotun and Fredriksen, 1995).

While the mechanisms by which kelp holdfasts adhere to the substratum are understood to a certain extent, the mechanics of holdfast anchorage, that is the functional morphology of holdfast systems in relation to their role in providing attachment and stability, are not. As waves pass by, macroalgae comply and streamline with the flow, putting their thalli and holdfasts in loading (Koehl, 1982; 1984; Koehl, 1986; Carrington, 1990; Boller and Carrington, 2006). The magnitude of the forces exerted on the holdfast depends not only on the force of the water flow, but also on the morphological characteristics and intrinsic mechanical properties of kelps (Koehl, 1982; 1984; Koehl, 1986; Carrington, 1990; Boller and Carrington, 2006). Thallus design will also influence the nature of the stresses incurred by the holdfast (Denny et al., 1998; Koehl, 1998). Ultimately, holdfast architecture will be determined by both the type and magnitude of the forces they must withstand.

As the diversity of thallus forms attests, macroalgae have evolved various strategies to cope with the hydrodynamic forces and loads to which they are subjected. Koehl (1982; 1984; 1986) and other authors (Koehl and Wainwright, 1977; Friedland and Denny, 1995; Utter and Denny, 1996; Denny et al., 1997; Gaylord and Denny, 1997) have examined in detail the mechanical design of kelp thalli in a number of species and compared their performance. However, none of these have extended their investigation to the holdfast system of kelps. A better understanding of holdfast anchorage mechanics is needed before we can adequately evaluate the functional and ecological significance behind the wide variation in holdfast forms observed in nature.

The root system of terrestrial plants, in contrast, has been the subject of much research over the past two decades. The roots of land plants differ in two major ways from the anchorage system of kelps. Roots serve two primary functions: (1) nutrient and water absorption and (2) anchorage, whereas holdfasts primarily function as anchorage structures and have no special abilities to harvest nutrients (with the
exception of certain tropical algae; Williams, 1981). Furthermore, the root system of terrestrial plants is embedded in soil. Hence the ability of a plant to resist uprooting will depend to a certain extent on the properties of the soil in which it is rooted (Coutts, 1983; Ennos, 1990; 1994). The holdfast of kelps, in contrast, meets the substratum on one interface only. In spite of these differences, certain parallels can be drawn between the anchorage systems of marine and land plants. A closer examination of the theories and models developed for terrestrial systems may give us clues as to the mechanical properties and functioning of kelp holdfasts.

Mechanical analysis of the anchorage systems of terrestrial plants stems from the engineering theory of beams. A plant may be viewed simply as a free-standing beam that is fixed at the base. When the beam (stem) is subjected to a lateral force (i.e. wind force), the windward and leeward sides of the beam behave differently. On the windward side, the tissue is loaded in tension, whereas on the leeward side, the tissue is loaded in compression. In due course, these forces will be transmitted to the anchorage system. Hence the roots on the windward side of the stem will initially bend slightly and then pull in tension, whereas the roots on the leeward side of the stem will be subjected to bending and compressive forces. Because bending stresses are proportional to the length of the beam, the stresses in the tissues near the attached end (i.e. the base of the trunk) of a plant bent in flowing water will be greater than those near its free end (Niklas, 1992). Moreover, the magnitude of the tensile and compressive stresses associated with bending is inversely proportional to the cube of the radius of the beam. Hence a small increase in radius can significantly reduce stress. In fact many organisms that stand upright in a moving fluid, whether air or water, are widest and most heavily reinforced near their base (Koehl, 1982; Niklas, 1992).

The design of anchorage systems in terrestrial plants largely depends on the types of forces they must withstand (Ennos, 1991; Ennos and Fitter, 1992). Climbing or procumbent plants that are loaded in tension (when pulled upwards by grazing animals), for example, have flexible "fibrous" roots that resist tensile stress well, like ropes (Figure 1.3a). Upright plants with a stiff stem, on the other hand, are loaded in bending and require a more rigid anchorage system to resist the rotational moments transmitted by the stiff stem (Figure 1.3b; Ennos, 1991; 1993). This rigid component can consist of a tap-root that will directly stabilize the plant, acting like the point of a stake, or a plate system, which will stabilize the plant by the resistance of the windward roots to tension

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Figure 1.3. Alternative types of anchorage systems in terrestrial plants. (a) A fibrous system with narrow, rope-like roots anchor a plant against uprooting; Plants may also develop rigid elements to transmit bending forces into the soil. In a tap-root system (b) or a plate system (c) the rigid component resists bending and rotation imposed by horizontal forces such as that of winds (modified from Ennos, 1993; 1994).
and of the leeward roots to compression (Figure 1.3c; Ennos, 1991; Ennos and Fitter, 1992; Ennos, 1993). Likewise, the design of kelp holdfasts should depend on the type of forces their thalli are subjected to.

Kelps exposed to unsteady flow, such as in the low intertidal or shallow subtidal zones, will encounter a number of different hydrodynamic forces. Drag, lift (usually considered to be negligible for flexible algae, Gaylord et al., 1994) and the acceleration reaction are the hydrodynamic forces most commonly discussed in the literature, though, certain kelps may also be subjected to buoyancy forces (Friedland and Denny, 1995) and perhaps torsional forces\(^2\). The magnitude of the flow-induced forces a kelp will have to withstand and the distribution of mechanical stresses sustained by its thallus will be affected by the shape and size of the plant (Koehl, 1982; Denny et al., 1985; Koehl, 1986; Gaylord et al., 1994). On the other hand, the type of stresses transmitted through the thallus to the holdfast will depend mainly on the design and biomechanical properties of the kelp.

The main objective of this research is to assess the role played by kelp holdfasts in structuring macroalgal populations and influencing benthic community dynamics. To attain this objective, I first determined the importance of kelp holdfasts in facilitating recruitment of juvenile kelp sporophytes. Secondly, I investigated the mechanics of holdfast anchorage systems in kelps with the goal of identifying the functional reasons behind the wide variation in holdfast form observed in nature and the factors affecting holdfast dislodgment and kelp survival.

This thesis is organized into 6 chapters, including this introductory chapter (Chapter 1), four data chapters (Chapter 2-5) and a summary chapter (Chapter 6). This general introduction to the ecology and anchorage mechanics of kelp holdfasts is intended to introduce the reader to the role of kelp holdfasts at individual, population and community scale dynamics, to expose gaps in our knowledge of this topic, and to act as a framework within which following chapters can be placed.

\(^2\) Torsional forces are most likely negligible in highly flexible kelps as they can readily reconfigure their blades in water flow. However, for species such as *E朝鲜ia arborea* and perhaps *Lessoniopsis littoralis*, which have a stiff stipe that branches laterally, protruding blades side-ways, torsional forces might be of importance. As Vogel (1995) argues with respect to trees "only a spatially uniform wind on a completely symmetrical tree would not induce torsion". The importance of torsional forces relative to other hydrodynamic forces in these species remains unclear.
In Chapter 2, I examine the role that adult kelp holdfasts play in facilitating kelp recruitment. Anecdotal observations suggested that juvenile *Hedophyllum sessile* (C. Agardh) Setchell and of other kelp species were frequently found growing on the holdfasts of *H. sessile* adults. Thus, *H. sessile* was chosen as a focus species to investigate recruitment facilitation by adult kelp holdfasts. I present the results of a field study in which I monitored the recruitment of juveniles of the low intertidal kelp, *H. sessile*, onto the holdfasts of adult *H. sessile* relative to other naturally occurring substrata. While the holdfast of kelps possess several characteristics that make them suitable as a substratum for recruitment, the presence of a dense canopy layer may mitigate their beneficial characteristics. For example, the presence of a canopy could inhibit recruitment and survival through canopy shading and/or sweeping. To understand the influence of canopy cover on juvenile recruitment, I experimentally manipulated the canopy cover of *H. sessile* and monitored juvenile recruitment onto available substrata. Canopy manipulation reflected natural seasonal fluctuations but also stochastic fluctuations (associated mainly with El Niño/Southern Oscillation events). I hypothesized that, first, the recruitment success, assessed as the percentage of recruits found on a particular substratum, would be greater on adult *H. sessile* than on other substrata. Secondly, I hypothesized, based on the literature, that the presence of a dense canopy cover would decrease recruitment success onto adult *H. sessile* due to either shading and/or sweeping. The results of this experiment show that the holdfasts of adult *H. sessile* play an important role in facilitating recruitment when the canopy layer is reduced. In contrast, turfs of articulated coralline algae facilitate the recruitment of juvenile *H. sessile* under a dense canopy cover. All other commonly occurring substrata in the intertidal inhibited recruitment. These results indicate that topographically complex substrata such as the adult holdfasts of *H. sessile* and articulated coralline turf facilitate juvenile recruitment over less complex substrata. Moreover, canopy dynamics can significantly alter facilitating interactions.

Chapter 3, 4 and 5 examine the anchorage mechanics of kelp holdfasts. This research was carried out on the low intertidal stipitate kelp, *Laminaria setchellii* P.C. Silva. *L. setchellii* was chosen as a focus species to examine the anchorage mechanics of kelp holdfasts due to its morphological features (single blade, stipe and hapteral holdfast) and its well-developed, woody stipe, which holds the blade erect in the water column. These morphological features allowed me to use theories developed for
terrestrial plants to investigate the anchorage mechanics of *L. setchellii*. More specifically, Chapter 3 investigates the morphological and biomechanical plasticity of the low intertidal stipitate kelp, *Laminaria setchellii*, along a wave exposure gradient. I hypothesized that the morphological and biomechanical attributes of *L. setchellii* vary with wave-exposure to decrease the risk of breakage and dislodgement associated with increases in hydrodynamic drag. Most specifically, I predicted that morphological and biomechanical adaptation to wave exposure would result in smaller blades, longer stipes and larger and stronger holdfasts at wave-exposed sites, effectively reducing drag forces by reducing the surface area exposed to waves and by allowing the stipe to bend with the flow (for a given diameter, a longer cylinder will bend more than a shorter one) and increasing the surface area of attachment and thus, attachment force to the substratum. The data I obtained indicate that *L. setchellii* morphology differs among sites of varying wave-exposure as predicted. However, the same is not true for *L. setchellii* biomechanical characteristics, specifically the force of attachment; this lack of concurrence is most likely due to a biological interaction with a burrowing intertidal crab.

Chapter 4 investigates the variability in morphology and shape of *L. setchellii* relative to the direction of the oncoming wave surge. Again, I hypothesized that *L. setchellii* morphology and shape vary to decrease the risk of breakage and dislodgement associated with hydrodynamic drag and bending stresses. Specifically, I predicted that the upper part of the thallus, in particular the blade, would be oriented perpendicular to the wave surge so that bending is maximized, decreasing hydrodynamic drag, whereas the lower part of the thallus would be oriented with its largest axis (diameter) parallel to the wave surge to resist the bending stresses that develop within the lower part of the stipe and holdfast. The morphological data I present in this chapter support the above hypotheses and predictions: the blade and upper part of the stipe are oriented with their largest axis (blade width or stipe diameter) oriented perpendicular to the direction of oncoming flow, while the lower part of the stipe and the holdfast (diameter for both) are oriented with the largest axis parallel to the flow. I conclude this chapter with a discussion of the implications of thallus axial asymmetry for *L. setchellii* biomechanics and survival to breakage and wave dislodgement.

Lastly, in Chapter 5, I examine the importance of thallus orientation, specifically holdfast asymmetry, for individual survivorship. I hypothesized that *L. setchellii* allocate more biomass to the holdfast in the direction parallel to the strongest flow to counteract
the bending stresses that develop in this region. Thus, I predicted that individual *L. setchellii* that have had their seaward or shoreward haptera removed are more weakly attached to the substratum and thus more susceptible to dislodgement by waves than individuals that have had their lateral haptera removed. To test this hypothesis and prediction, I set up a field experiment in which I monitored the survival of *L. setchellii* individuals that had one of their four holdfast quadrants (seaward, shoreward, lateral right or lateral left) removed or none removed (control). The results of this experiment show that the removal of a quarter of the holdfast decreases significantly individual survivorship compared to control individuals and suggests that survival is dependent on the haptera quadrant that has been removed. Data of the force required to detach *L. setchellii* from the substratum support this. Manipulated *L. setchellii* required less force to be detached from the substratum than control individuals. Furthermore, individuals lacking haptera in the direction parallel to the wave surge (seaward and shoreward) were more weakly attached to the substratum than ones lacking their haptera in the direction perpendicular to the surge (lateral right and left). These results suggest that the haptera laid down in the direction parallel to the wave surge play a greater role in the anchorage mechanics than lateral haptera.

Finally, Chapter 6 summarizes the findings presented in the previous four chapters and suggests direction for future research.

1.1. References


Tovey, D.J., Moss, B.L., 1978. Attachment of haptera of *Laminaria digitata* (Huds) Lamour. Phycologia 17, 17-22.


Chapter 2 Habitat Modification and Recruitment Facilitation by *Hedophyllum sessile* (C. Agardh) Setchell

2.1. Introduction

Ecosystem engineers are organisms whose presence or activity significantly modifies their abiotic and/or biotic environment and thereby alter the availability of resources available to other species. By doing so, ecosystem engineers directly affect the distribution and abundance of other species (Jones et al., 1994; 1997). Ecosystem engineers such as plants and algae can significantly alter environmental conditions simply through their physical presence. For example, seagrass beds or kelp forests modify the flow of water around and through them, which dampens wave impact, reduces currents and retains propagules (Eckman et al., 1989; Leonard, 1999; Johnson, 2001). Their three-dimensional structure creates living space for a variety of organisms, providing to some a refuge from predation as well as from flow, or acting for others as nursery grounds (Dommasne, 1968; 1969; Coull and Wells, 1983; Gibbons and Griffiths, 1986; Eckman, 1987; Eckman et al., 1989; Gibbons, 1991; Moreno, 1995; Connell, 2003). Kelp canopies create a microhabitat that can differ substantially from non-canopy areas. For example, the presence of a canopy attenuates light penetration, shading understory organisms from sun exposure and extremes in temperature but also reduces light available for photosynthetic organisms (Reed and Foster, 1984; Kennelly, 1989; Wing et al., 1993). The sweeping action of kelp fronds upon the substratum can also create an herbivore-free area in the immediate vicinity of the kelp holdfast, providing protection to young sporophytes (Velimirov and Griffiths, 1979; Konar, 2000; Gagnon et al., 2003).

The holdfast of kelps also acts as a habitat-modifier, providing habitat for a large number (10,000 organisms [all invertebrates] per m$^2$ of *Laminaria ochroleuca* bed; Arroyo et al., 2004) and a wide variety of invertebrate taxa (up to 156 taxa; Ghelardi, 1971). Few of these studies, however, acknowledge the habitat-modifying role of kelp holdfasts in the recruitment and demographics of understory algae. Recruitment dynamics play a critical role in determining population structure, and for ecosystem engineers such as kelps, successful recruitment can exert a strong influence on community processes. Recruits, however, are generally more vulnerable (to abiotic and biotic stresses) than older juveniles and adults (Santelices, 1990; Vadas et al., 1992).
Among the challenges recruits face are obtaining light and nutrients, tolerating fluctuations in temperature and salinity, and resisting wave action. Competitive interactions, as well as grazing, all affect the outcome of recruitment. Nevertheless, successful recruitment does occur.

Although anecdotal reports suggest that young sporophytes are found associated with, or in close proximity to, holdfasts of mature kelps, it is only recently that the potential role played by holdfasts as a refugium for recruits has been proposed. Anderson et al (1997) suggest that the holdfast of Ecklonia maxima, a South African kelp, provides refuge to young sporophytes from herbivores. These authors found that in heavily grazed areas the recruitment of young E. maxima sporophytes is strongly limited to the holdfasts of mature kelps, whereas in areas where herbivore densities are low, juveniles recruit on a variety of substrata. Although their conclusion is purely correlative, they argue that the holdfast of mature E. maxima plants provides an irregular surface from which herbivores may easily be dislodged by waves and thus provides an effective refugium for young sporophytes against grazers.

Kelp holdfasts exhibit a wide range of morphologies. Many species attach to the substratum by means of hapteral holdfasts, which consist of a mass of branched haptera that form numerous interstices and hollows as they entwine. These holdfasts possess several characteristics that make them suitable as a secondary substratum for recruitment. The interstices formed by the haptera offer a microenvironment where propagules can recruit through depositional eddies and where water velocities, and thus hydrodynamic forces, are lower. The surface of kelp holdfasts offers a very irregular surface onto which herbivores such as chitons, gastropods and sea urchins may have difficulty grazing (Anderson et al., 1997). Fine detritus and silt caught amongst the haptera and secretions from invertebrate fauna inhabiting the holdfast may constitute a source of nutrients for recruits (Kennelly, 1983). Moreover, recruits settling in the intertidal, where mortality due to thermal stress and desiccation is high, may benefit from settling amongst the holdfast haptera. Besides, the holdfasts may provide a refuge from mechanical disturbance like canopy scouring. The presence of a dense canopy may mitigate the beneficial effects of holdfasts by inhibiting recruitment and survival through canopy shading or sweeping. Successful recruitment of young kelp sporophytes on holdfasts is likely the result of a combination of interacting mechanisms.
This study investigated the ecological role played by mature kelp holdfasts of *Hedophyllum sessile*¹ (hereafter *Hedophyllum*), as physical ecosystem engineers. More specifically, I evaluated the role of adult *Hedophyllum* holdfasts in facilitating recruitment by providing a refugium for conspecific kelp recruits at both a wave-sheltered and a wave-exposed site. In addition, I evaluated the effects of canopy cover on recruitment. I posed the following questions:

1. Do the holdfasts of mature kelps, such as *Hedophyllum*, facilitate the recruitment of juvenile sporophytes?
2. What is the contribution of other substrata in facilitating *Hedophyllum* recruitment?
3. What are the effects of canopy cover and wave exposure on this facilitation process and how do they interact?

**Study site and species**

The study area stretched along both sides of a rock ridge approximately 30 m wide and 80 m long (Figure 2.1) in the rocky intertidal zone of Prasiola Point on the southeast edge of Barkley Sound, Vancouver Island, British Columbia, Canada (48°49'4" N, 125°10'4" W). The western side of this ridge was characterized as wave-exposed and the eastern side as wave-sheltered according to the prevailing direction of the oncoming waves. Biological indicators of relatively higher wave exposure, such as *Lessoniospsis littoralis* (kelp) and *Pollicipes polymerus* (gooseneck barnacle), were common on the western side of the ridge but absent on the eastern side where protected shore species, such as *Phyllospadix scouleri* (surf grass) and *Egregia menziesii* (kelp), were found. These sites differ significantly in wave-impact during the late autumn and throughout the winter (Milligan and DeWreede, 2000). The low intertidal zone of Prasiola Point, at both the wave-sheltered and wave-exposed sites, is dominated by a canopy of *Hedophyllum*. At the wave-sheltered site, this canopy can

¹ Based on a multi-gene molecular investigation, the genus *Hedophyllum* was subsumed and the genus *Saccharina* resurrected (Lane et al., 2006). For ease, I retained and use the scientific name *Hedophyllum sessile* as a synonym of *Saccharina sessile* (C. Agardh) Kuntze.
Figure 2.1. Map of study sites at Prasiola Point (48°49' 4" N, 125°10' 4" W), Barkley Sound, Vancouver Island, BC
be intermixed with patches of another canopy-forming kelp, *E. menziesii*, but this rarely occurs at the exposed site. The understory algal assemblage underneath this kelp canopy is composed of several species of crustose algae (coralline algae and fleshy red and brown crusts), articulated corallines, foliose and filamentous red algae and a few green ephemeral algae (Milligan, 1998; personal observations). The understory macrofauna commonly includes sea cucumbers, sea anemones, sea stars, sponges, colonial tunicates, and several species of herbivores (predominantly *Katharina tunicata* [chiton], *Lottia pelta* [limpet] and *Strongylocentrotus purpuratus* [purple sea urchin]). In addition of the understory community, a wide variety of other invertebrate taxa are found within *Hedophyllum* holdfasts (personal observations).

*Hedophyllum* is one of the few kelp species that can be found in the intertidal zone of semi-protected to exposed rocky shores of the northeastern Pacific. Members of the Laminariales exhibit a heteromorphic alternation of generations, in which the macroscopic sporophyte releases meiospores that settle to the bottom before germinating to produce microscopic filamentous gametophytes. Gametophytes mature to produce either female gametes (oogonia, which remain attached to the female gametophyte) or male gametes (antheridea, which are released in the water). Successful fertilization results in sporophyte development. Thus, patterns of recruitment are the product of processes acting during the dispersal, settlement and post-settlement phases of *Hedophyllum* microscopic life stages and during the early stage of sporophyte development. The juvenile sporophyte has a short, flattened stipe that rapidly disappears, leaving the blade sessile on the holdfast. Adult plants at sheltered sites are characterized by a few large blades (30-50 cm long and up to 80 cm wide), whereas at exposed site, each blade tatters into many short, strap-like blades. The blade(s) are attached directly to the substratum by numerous intertwined haptera arising from the thickened basal margins of the plant (Abbott and Hollenberg, 1976; Milligan, 1998).

Anecdotal observations suggest that mature *Hedophyllum* plants are frequently composed of several individual plants whose holdfasts have fused (Milligan K.L.D., pers. comm.; S.D. Boizard, pers. obs.), which suggests that recruits settled onto a previously existing holdfast and/or in clusters. Holdfast fusion was also observed in *E. maxima* (Anderson et al., 1997). Recruitment of new *Hedophyllum* plants occurs during spring and summer months (March-July) (Milligan, 1998). Evidence shows that
recruitment is substratum dependent, with higher recruitment on *Hedophyllum* holdfast and articulated coralline algae (Milligan, 1998). These observations indicate that mature *Hedophyllum* holdfasts may indeed provide a refugium to recruits

2.2. Material and Methods

*Experimental design and sampling*

A total of 42 experimental plots were haphazardly selected (30 at the sheltered site and 12 at the exposed site). Experimental plots were located within the *Hedophyllum* zone on moderate to gentle slopes, and ranged in vertical height from 0.86 to 1.45 m above Canadian Chart Datum at the sheltered site and from 1.37 to 1.74 m at the exposed site. In each experimental plot, a quadrat (0.25 m x 0.25 m), initially randomly placed, was permanently marked at two corners with galvanized bolts drilled into the rock surface and subsequently flagged. All quadrats contained at least two *Hedophyllum* adult holdfasts and an initial *Hedophyllum* canopy cover of at least 80%.

All 42 quadrats were initially sampled in July 1999. The percent cover of *Hedophyllum* canopy at each permanent quadrat was recorded by counting the number of squares occupied by *Hedophyllum* canopy using a sampling quadrat with a 2 cm x 2 cm grid. Substratum availability was measured using the random-point intercept method (Dethier et al., 1993). The substratum type under 30 random points (selected using a random number table, Zar, 1996) was recorded within the sampling quadrat grid. Substratum types included bare rock, crustose coralline and other fleshy red and brown crusts, articulated corallines, foliose turf algae, sponges, other invertebrates and holdfasts of *Hedophyllum* and *E. menziesii*. All macroscopic *Hedophyllum* recruits (e.g. those recognizable by the unaided-eye and having a visible stipe, Dean et al., 1989) inside the quadrat were counted and the substratum onto which they had settled recorded. Occasionally, recruits of other kelp species were seen, but these were uncommon. The density of benthic macro-herbivores, including *K. tunicata*, was also recorded for each quadrat. The data from this initial sampling were used in a cluster analysis (using Ward’s method to combine clusters and to compute similarities and dissimilarities; Kent and Coker, 1992; Norusis, 1993), and quadrats that diverged substantially from the rest of the group were dropped from the experiment. This was
done to reduce the variability at the sheltered site that resulted from the site covering a
greater area than the exposed site.

Twelve quadrats per exposure treatment were retained for the experiment. While
I realized that 'wave exposure' is not replicated in this design and may be interpreted as
a case of pseudo-replication, the proximity of the 2 sites to each other and the well-
characterized difference in wave regime (Milligan and DeWreede, 2000) suggest that
the critical difference between these two sites for Hedophyllum is wave exposure.
Consequently, the differences among sites are attributed herein to wave exposure and
will be referred to as such. Six were randomly assigned to a Hedophyllum canopy
control group and the other half to a Hedophyllum canopy removal group. The canopy
removal treatment consisted of removing the Hedophyllum canopy within an
experimental quadrat by cutting back all Hedophyllum blades within, and impinging into,
the experimental quadrat. Blades were cut one cm above the holdfast, leaving the
meristem (region of active blade growth) intact. This manipulation simulated natural
disturbance due to autumn and winter storms and stochastic disturbance (mainly El
Niño/Southern Oscillation events; Paine and Trimble, 2004). This treatment was first
applied in September 1999 just before the onset of reproduction in Hedophyllum and
was maintained thereafter. The permanent quadrats were sampled (monthly to bi-
monthly) as described above, weather permitting, for the following 18 months.

A differential recruitment index (DRI), based on Ivlev's (1861) electivity index was
used to assess if the recruitment of Hedophyllum sporophytes onto a given substratum
type occurred independently of its availability. This index relates the percentage of
recruits sampled growing on a given substratum type to the percent cover (obtained
using the random-point intercept method) of that substratum available for recruitment.

\[
\text{DRI} = \frac{(r_i - n_i)}{(r_i + n_i)}
\]

where DRI is the Ivlev's electivity measure for substratum \(i\), the measure of the
substratum \(i\) suitability for recruitment, \(r_i\) is the percentage of juvenile Hedophyllum
found onto substratum \(i\), and \(n_i\) is the percent cover of substratum \(i\) available for
recruitment. DRI ranges from -1 to 1. A DRI value equal to 0 indicated that recruitment
was totally random, whereas a DRI value > 0 showed that recruitment was enhanced
onto the given substratum (i.e. conditions were beneficial for spore settlement, gametophyte and sporophyte development). A DRI value < 0 indicated that recruitment was inhibited onto that substratum (i.e. conditions prevented spore settlement and/or gametophyte/sporophyte development).

DRI was also compared between the holdfasts of adult *Hedophyllum* and the various other substratum types enumerated to determine if recruitment was higher on the holdfasts of mature *Hedophyllum* than onto other substrata types. Thus DRI is interpreted as an index of the relative recruitment success of young sporophytes onto different substrata, recognizing that this process involves several intermediate steps.

**Data analysis**

Data were analyzed using repeated-measure ANOVA; homoscedasticity of variances was tested using Cochran's C test on the data and Levene test on the residuals (Zar, 1996; Underwood, 1997). Sphericity assumption was evaluated using Mauchly's test statistic. If the assumption of sphericity was not met, sphericity was corrected using the Greenhouse-Geisser correction (Field, 2000).

Logit log-linear analysis (Heisey, 1985; Manly et al., 1993) was used to test if substratum-specific recruitment patterns occurred and if so, if they occurred independently of canopy cover and wave exposure. I created five nested logit log-linear models for the data representing five hypotheses about recruitment patterns: H0: Juveniles recruit onto a substratum in proportion to its availability (DRI = 0); H1: Substratum-specific recruitment patterns occur and are constant across canopy cover and wave exposure (DRI ≠ 0); H2: Substratum-specific recruitment patterns occur independently of canopy cover (DRI x Canopy ≠ 0); H3: Substratum-specific recruitment patterns occur independently of wave exposure (DRI x Wave ≠ 0); H4: Substratum-specific recruitment patterns occur independently of canopy cover and wave exposure (DRI x Canopy x Wave ≠ 0). I evaluated differences among nested logit models using a likelihood-ratio test (Heisey, 1985; Manly et al., 1993).

All statistical analyses were performed using SPSS V.11 for Macintosh (SPSS Inc. Chicago, Illinois). Unless stated otherwise, the level of significance for all statistical tests was evaluated using a value of α=0.05. All error values around the mean, whether in the text or on graphs, are ± one standard error.
2.3. Results

Canopy cover manipulation

Initial sampling showed that the *Hedophyllum* canopy covered 92.65 ± 2.10% (all site pooled) of the substratum at Prasiola Point. The canopy manipulation significantly reduced the canopy cover (Figure 2.2; Table 2.1 a, canopy effect), which remained below 10% throughout the autumn and early winter of 1999. With the onset of the growing season (February-March), canopy cover increased by 10-30% of the total area within canopy removal plots between successive sampling visits (Figure 2.2). A year after the start of the canopy manipulation (October 2000), canopy cover had recovered to 60-70% of its original (July/August 1999) cover and canopy removal plots were indistinguishable from canopy control plots (Figure 2.2). This was true at both the wave-sheltered and wave-exposed site.

Effects of Canopy and Wave exposure

Substratum availability (percent cover)

Several macroalgal and invertebrate taxa were inventoried at Prasiola Point as potential substrata for *Hedophyllum* recruitment (Appendix A). Most of the available substratum consisted of adult kelp holdfasts (HF; 18%), crustose coralline algae (CC; 22%) and bare rock (BR; 17%). These were equally prevalent and jointly accounted for approximately 57% of the substratum cover in July 1999. Articulated coralline algae (AC) were the next most abundant substratum (14%), followed by fleshy crusts (FC, 8%; including "Petrocelis", which is the tetrasporic phase of *Mastocarpus papillatus, Hildenbrandia occidentalis* and *Ralfsia* sp.). The remaining rock was covered by invertebrates, including sea anemones (*Anthopleura elegantissima*), sponges (*Haliclona* sp., *Halichondria* spp.), and colonial tunicates, gastropod herbivores (e.g. *K. tunicata, Tectura scutum* and *Lottia* spp.) and other invertebrates including *Pisaster ochraceous, Cucumaria pseudocurata*; these, individually, accounted for less than 6% of the available substratum (except for sea anemones which covered, at times, as much as 12% of the available substratum). For that reason and because most of these
substrata were judged to be unsuitable for recruitment, they were grouped into an 'Others' category and omitted from further discussion.

At the start of the experiment (July 1999), the holdfasts of adult *Hedophyllum* individuals covered between 12.78 and 24.45% of the rock surface. Holdfast cover decreased steadily over the course of the winter due to dislodgement by storms, natural degeneration and possibly undercutting by *K. tunicata* (Figure 2.3; Table 2.1 b, time effects). After a year (July 2000), kelp holdfasts covered approximately half (range: 3.89 and 15.00%) of the rock surface they had covered the previous year. There were no visible effects of canopy cover nor of wave exposure (with the exception of July 1999) on holdfast cover, until the spring of 2000. Holdfast cover decreased at a slightly greater rate in canopy removal than canopy control plots (Figure 2.3; Table 2.1 b, time x canopy effect) and differences in cover were greater at the wave-exposed site than at the wave-sheltered site (Figure 2.3; Table 2.1 b, time x site (wave) effect).

In contrast to *Hedophyllum* holdfasts, the percent cover of articulated coralline algae increased over time (Figure 2.4; Table 2.1 c, time effect), and articulated coralline algae were more abundant in canopy removal plots than in canopy control plots (Figure 2.4; Table 2.1 c, canopy effect). Articulated coralline algae showed more variability in percent cover from month to month at the wave-sheltered site than at the wave-exposed site (Figure 2.4; Table 2.1 c, time x site (wave) effect), indicating that articulated turf may respond faster to environmental changes at the wave-sheltered site. Wave exposure, however, had overall no detectable effects on the availability of articulated coralline algae for recruitment (Table 2.1 c, site (wave) effect).

The availability of crustose coralline algae, fleshy crustose algae and bare rock varied little with time, canopy or wave exposure. The availability of crustose coralline algae as a substratum for recruitment varied seasonally ranging between 12-20% in the summer and 12-28% in the winter (Figure 2.5; Table 2.1 d, time effect;) but did not differ significantly with canopy cover nor wave exposure (Figure 2.5; Table 2.1 d, canopy, site (wave) effects). The availability of fleshy crustose algae remained constant with time, canopy and wave exposure, ranging between 8-22% in cover (RM ANOVA, p>0.05 for all between and within subject main effects and interactions; Figure 2.6). The availability of bare rock for recruitment varied with time of sampling (Figure 2.7; Table 2.1 e, time effect) depending on the degree of wave exposure (Table 2.1 e, time x site (wave) effect).
Figure 2.2. *Hedophyllum sessile* canopy cover (percent) at Prasiola Point, over the course of the experiment (July 1999-December 2000). a) at the wave-sheltered site; b) at the wave-exposed site. Full circles represent canopy control plots and open circles canopy removal plots. Error bars represent ± 1 SE.
Table 2.1. Statistical analysis of the effects of time of sampling, canopy removal and wave exposure on *Hedophyllum* canopy cover and substratum availability (percent cover). Data were analysed with a repeated-measures ANOVA. Effects that are significant are indicated in bold.

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<th>F</th>
<th>p</th>
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<tr>
<td>Between subjects (average over time)</td>
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<tr>
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<tr>
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<td>Error</td>
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<td><strong>b) HF %</strong></td>
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<tr>
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*Greenhouse-Geisser correction for sphericity applied.*
Figure 2.3. *Hedophyllum* holdfast percent cover in wave-sheltered (a) and wave-exposed (b) canopy control (full circle) and canopy removal (open circle) plots at Prasiola Point, over the course of the experiment. Data are means ± 1 SE.
Figure 2.4. Articulated coralline algae percent cover in wave-sheltered (a) and wave-exposed (b) canopy control (full circle) and canopy removal (open circle) plots at Prasiola Point, over the course of the experiment. Data are means ± 1 SE.
Figure 2.5. Coralline crustose algae percent cover in wave-sheltered (a) and wave-exposed (b) canopy control (full circle) and canopy removal (open circle) plots at Prasiola Point, over the course of the experiment. Data are means ± 1 SE.
Figure 2.6. Fleshy crustose algae percent cover in wave-sheltered (a) and wave-exposed (b) canopy control (full circle) and canopy removal (open circle) plots at Prasiola Point, over the course of the experiment. Data are means ± 1 SE.
Figure 2.7. Bare rock percent cover in wave-sheltered (a) and wave-exposed (b) canopy control (full circle) and canopy removal (open circle) plots at Prasiola Point, over the course of the experiment. Data are means ± 1 SE.
Recruitment densities

*Hedophyllum* recruitment occurred during spring and summer months. *Hedophyllum* recruits started to appear in late winter/early spring (February 2000), with juvenile densities peaking to 344 ± 96 juveniles per m$^2$ three months later (May 2000) at the sheltered site and to 1555 ± 402 juveniles per m$^2$ in June 2000 at the exposed site. By late summer (August 2000), most of the individuals that were left had lost their stipe, and initiation of blade splitting had started. Recruitment of juvenile *Hedophyllum* in permanent quadrats was much higher in 2000 than in 1999, making comparisons between years difficult. Juvenile densities at the sheltered site were 5-9 times greater in 2000 than the previous summer and 97-183 times greater at the exposed site (Figure 2.8). *Hedophyllum* recruitment varied spatially as well as temporally; the number of juveniles tallied in two quadrats a meter apart could differ by as much as one order of magnitude. While there were significantly more juveniles at the wave-exposed site than at the wave-sheltered site (Figure 2.8, Table 2.2, site (wave) effect), the absence of canopy cover in canopy removal plots had no effects on the overall abundance of juvenile *Hedophyllum* compared to canopy control plots (Figure 2.8, Table 2.2, canopy effect).

Recruitment patterns (proportion of juveniles)

The distribution of juveniles clearly shows differential recruitment among the various types of substratum. For example, in July 2000, juveniles recruited disproportionately onto the holdfast of adult *Hedophyllum* (1-32%) and onto articulated coralline algae (57-94%), whereas 1.5-3.5% of juveniles recruited onto crustose coralline algae, 0-2.5% onto fleshy crusts, and 0-5.5% onto bare rock. The proportion of juveniles growing onto the holdfast of *Hedophyllum* and onto articulated coralline algae changed significantly with canopy cover but not with wave exposure (Figure 2.9-2.10; Table 2.3), and time of sampling significantly influenced the proportion of juveniles growing on articulated coralline algae but not of those growing onto *Hedophyllum* holdfast (Figure 2.9-10; Table 2.3). The proportion of juveniles found growing on articulated coralline turfs increased with time, while it remained more or less constant on *Hedophyllum* holdfasts (except in sheltered, canopy removal plots were it decreased with time). Canopy cover had an opposite effect on the proportion of juveniles found growing onto the holdfasts of *Hedophyllum* than onto articulated coralline turfs. A greater proportion of juveniles were
found growing onto the holdfasts of adult *Hedophyllum* individuals when the canopy cover was reduced than when it was lush (Figure 2.9), while a lower proportion of juveniles were found growing onto articulated coralline under reduced canopy cover (Figure 2.10).

Juveniles growing onto adult *Hedophyllum* holdfasts were found in greater proportion (sheltered, 5 times; exposed, 3 times) in canopy removal plots than in canopy control plots. While wave exposure had no significant effects on juvenile distribution, juveniles growing onto holdfasts tended to be 1.75 times more abundant in canopy control plots at the wave-exposed site than at the wave-sheltered site (Figure 2.9). In contrast, juveniles growing onto articulated coralline algae were found 1.5 more often in canopy control plots than in canopy removal plots whether at the wave-sheltered or exposed site (Figure 2.10).

The proportion of juveniles found growing onto crustose coralline, fleshy crustose algae, and bare rock remained low throughout the course of the experiments (RM ANOVA, within subjects, time and all interactions $p>0.05$ for all 3 substrata; Figure 2.11) and did not differ among canopy or wave exposure treatments (RM ANOVA, between subjects, canopy, wave and interaction $p>0.05$ for all 3 substrata; Figure 2.11).

*Recruitment patterns (DRI index)*

Overall, recruitment patterns of juvenile *Hedophyllum* exhibited substratum-specific recruitment patterns (Table 2.4, $H_1$: DRI≠0). Recruitment patterns differed significantly between canopy treatment plots (Table 2.4, $H_2$: DRI x Canopy ≠0) but did not differ across wave exposure levels (Table 2.4, $H_3$: DRI x wave ≠0).

Recruitment was facilitated onto the holdfast of *Hedophyllum* (DRI>0) under a reduced canopy cover but not under a full canopy cover (DRI<0; Table 2.5). This pattern was the same whether at the wave-sheltered or exposed sites (Figure 2.12). Articulated coralline algae facilitated (DRI>0) juvenile recruitment regardless of canopy cover or wave exposure (Figure 2.13). However, recruitment on articulated coralline turfs was not as favourable under low canopy cover as it was under a thick, natural canopy cover (Figure 2.13).
Figure 2.8. *Hedophyllum sessile*. Juvenile density (#/m$^2$) within sheltered, canopy control and canopy removal plots during the course of the experiment (July 1999-December 2000): a) at the wave-sheltered site; b) at the wave-exposed site. Full circles represent canopy control plots and open circles canopy removal plots. Error bars represent ± 1 SE.
Table 2.2. Statistical analysis of the effects of time of sampling, canopy cover and wave exposure on the density of juvenile *Hedophyllum sessile* (number per 1-m²). Data were analysed with a repeated-measures ANOVA. Effects that are significant are indicated in bold.

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<th>p</th>
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<td><strong>Within subjects</strong> (change in effect over time)&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>Time x canopy x site (wave)</td>
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<sup>a</sup> Greenhouse-Geisser correction for sphericity applied.
Figure 2.9. *Hedophyllum sessile*. Proportion of juvenile (%) within a) wave-sheltered and b) wave-exposed canopy control (full circles) and canopy removal (open circles) plots found growing on the holdfast of *Hedophyllum* during the period of April to October 2000. Error bars represent ± 1 SE.
Figure 2.10. *Hedophyllum sessile*. Proportion of juvenile (%) within a) wave-sheltered and b) wave-exposed canopy control (full circles) and canopy removal (open circles) plots found growing on articulated coralline algae during the period of April to October 2000. Error bars represent ± 1 SE.
Table 2.3. Statistical analysis of the effects of time of sampling, canopy removal and wave exposure on the proportion of juvenile *Hedophyllum* found growing onto the holdfasts of adult *Hedophyllum* and onto articulated coralline algae. Data were analysed with a repeated-measures ANOVA. Effects that are significant are indicated in bold.

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<th>F</th>
<th>p</th>
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<td><strong>Between subjects</strong></td>
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<tr>
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<td>0.646</td>
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* Greenhouse-Geisser correction for sphericity applied.
Figure 2.11. *Hedophyllum sessile*. Proportion of juvenile (%) within a) wave-sheltered and b) wave-exposed canopy control (full circles) and canopy removal (open circles) plots found growing on crustose coralline (CC), fleshy crustose (FC) algae, and bare rock (BR) during the period of April to October 2000. Error bars represent ± 1 SE.
Crustose coralline, fleshy crustose algae and bare rock inhibited (DRI<1) the recruitment of juvenile *Hedophyllum* sporophytes regardless of canopy cover or wave exposure (Figure 2.14; RM ANOVA, \( p>0.05 \) for all between subjects and within subjects, main effects and interactions for 3 substrata). In the few instances when DRI differ between canopy treatments, recruitment DRI index is less negative for canopy removal plots than canopy control plots, indicating that when juveniles manage to recruit onto one of these flat substrata, they are more likely to do it if the canopy cover is low (Figure 2.14).

**Katharina tunicata and other herbivores**

*K. tunicata* density changed in space but not in time (Figure 2.15). *K. tunicata* density was significantly greater in wave-exposed plots compared to more wave-sheltered ones (Figure 2.15; Table 2.6 a, site (wave) effect). The removal of *Hedophyllum* canopy, however, had no detectable effect on the density of *K. tunicata* (Figure 2.15; Table 2.6 a, canopy effect).

Other species of herbivores (limpets, chitons and juvenile sea urchins) were censused within the experimental plots over the course of the experiment. Their numbers fluctuated slightly but remained similar among canopy treatment groups and wave exposure sites with the exception of September and October 2000 when a large pulse of limpet recruits was recorded (Figure 2.15). This recruitment pulse was observed in canopy removal, exposed plots only. This resulted in a significant canopy x wave interaction, while the canopy and wave main effects were not (Table 2.6b).

### 2.4. Discussion

**Ecosystem engineers**

The importance of ecosystem engineers in creating, maintaining and modifying habitat for other organisms is now well recognized (Jones et al., 1994; 1997; Crooks, 2002). Some authors (Bruno and Bertness, 2001; Coleman and Williams, 2002) have directly referred to kelps as ecosystem engineers, however, the discussion is usually centered around the canopy formed by kelps. Although not named as such, the holdfasts of several species of kelp have been shown to act as ecosystem engineers by providing refuge from predation (McLay and Hayward, 1987), from flow.
Table 2.4. Results of Logit log-linear likelihood ratio tests for differences in *Hedophyllum sessile* recruitment patterns (July 2000 data).

<table>
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<tr>
<th>Model</th>
<th>Hypotheses</th>
<th>Likelihood ratio</th>
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<th>( \Delta \chi^2 )</th>
<th>( \Delta df )</th>
<th>( p )</th>
</tr>
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<tr>
<td>( H_0 )</td>
<td>Juvenile recruits onto substratum in proportion to their availability (DRI = 0)</td>
<td>539.51</td>
<td></td>
<td>17</td>
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<td>( H_1 )</td>
<td>Substratum-specific recruitment patterns occur and are constant across canopy cover &amp; sites (wave exposure) (DRI ( \neq 0 ))</td>
<td>77.76</td>
<td>461.76</td>
<td>13</td>
<td>4 &lt;0.0001</td>
<td>3</td>
<td>***</td>
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<td>( H_2 )</td>
<td>Substratum-specific recruitment patterns differ across canopy cover (DRI x Canopy ( \neq 0 ))</td>
<td>17.01</td>
<td>60.75</td>
<td>10</td>
<td>3 &lt;0.0001</td>
<td>3</td>
<td>***</td>
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<td>( H_3 )</td>
<td>Substratum-specific recruitment patterns differ across sites (wave exposure levels (DRI x Wave ( \neq 0 ))</td>
<td>75.27</td>
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<td>10</td>
<td>3 0.478</td>
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<td>ns</td>
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<td>( H_4 )</td>
<td>Substratum-specific recruitment patterns differ across canopy cover depending on site (wave exposure). (DRI x Canopy x Wave ( \neq 0 ))</td>
<td>6.92</td>
<td>10.09</td>
<td>7</td>
<td>4 0.039</td>
<td>4</td>
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Table 2.5. Statistical analysis of the effects of time of sampling, canopy removal and wave exposure on substratum-specific pattern of recruitment of juvenile *Hedophyllum*, growing onto the holdfasts of adult *Hedophyllum* individuals and onto articulated coralline algae. Data were analysed with a repeated-measures ANOVA. Effects that are significant are indicated in bold.

<table>
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*Greenhouse-Geisser correction for sphericity applied.*
Figure 2.12. *Hedophyllum sessile*. Differential recruitment index (DRI) within a) wave-sheltered and b) wave-exposed canopy control (full circles) and canopy removal (open circles) plots found growing onto the holdfast of *Hedophyllum* during the period of April to October 2000. Error bars represent ± 1 SE.
Figure 2.13. *Hedophyllum sessile*. Differential recruitment index (DRI) within a) wave-sheltered and b) wave-exposed canopy control (full circles) and canopy removal (open circles) plots found growing on articulated coralline algae during the period of April to October 2000. Error bars represent ± 1 SE.
Figure 2.14. *Hedophyllum sessile*. Substratum suitability for recruitment as measured by the differential recruitment index (DRI) within a) wave-sheltered and b) wave-exposed canopy control (full circles) and canopy removal (open circles) plots found growing on crustose coralline (CC), fleshy crustose (FC) algae, and bare rock (BR) during the period of April to October 2000. Error bars represent ± 1 SE.
Figure 2.15. Changes in density (#/m²) of a) *Katharina tunicata* and b) other species of herbivores in wave-sheltered, canopy control and canopy removal and in wave-exposed, canopy control and canopy removal plots at Prasiola Point, over the course of the experiment (July 1999-December 2000). Full circles represent sheltered, canopy control plots, open circles sheltered, canopy removal plots, full squares exposed, canopy control plots and open squares exposed, canopy removal plots. Error bars represent ± 1 SE.
Table 2.6. Statistical analysis of the effects of time of sampling, canopy cover and wave exposure on the density of *Katharina tunicata* and other herbivores (number per 1-m²). Data were analysed with a repeated-measures ANOVA. Effects that are significant are indicated in bold.

<table>
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<th>Source of variation</th>
<th>df</th>
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<tr>
<td><strong>a) Katharina tunicata densities</strong></td>
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<td><strong>Between subjects</strong> (average over time)</td>
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<tr>
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<tr>
<td><strong>Within subjects</strong> (change in effect over time)⁵</td>
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<tr>
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<td><strong>b) Herbivores densities</strong></td>
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⁵Greenhouse-Geisser correction for sphericity applied.
Cancino and Santelices, 1980) and acting as a settlement substrate or nursery ground for a wide diversity of invertebrates and fish species (Andrews, 1945; Ghelardi, 1971; Christie et al., 2003). However, remarkably little work has examined directly the facilitative role of holdfasts on kelp recruitment (however see Anderson et al., 1997; McConnico and Foster, 2005) and none as a function of canopy cover and wave exposure. Using the intertidal kelp *Hedophyllum* as a model system, I examined the ability of *Hedophyllum* holdfasts to act as ecosystem engineers by facilitating the recruitment of young conspecific sporophytes under two varying levels of canopy cover and wave exposure.

My results indicate that the holdfasts of adult *Hedophyllum* individuals do facilitate the recruitment of juvenile *Hedophyllum* sporophytes, but that their suitability as a recruitment substratum is regulated by canopy cover. Turfs of articulated coralline algae also facilitated *Hedophyllum* sporophyte recruitment, and their suitability as a recruitment substratum was also affected by canopy cover, but to a smaller extent. Wave exposure exerted little influence on the pattern of recruitment of juvenile sporophytes onto adult *Hedophyllum* holdfasts (but see below) or articulated coralline turf. Other common substrata such as crustose coralline, fleshy crustose algae and bare rock consistently inhibited the recruitment of juvenile *Hedophyllum* sporophyte, independently of canopy cover or wave exposure.

These results suggest that both the holdfast of adult *Hedophyllum* individuals and turf of articulated coralline algae can positively influence *Hedophyllum* recruitment by offering more suitable microhabitat conditions.

### Similarities between *Hedophyllum* Holdfasts and Articulated Coralline Turfs as Substrata

*Hedophyllum* holdfasts and articulated coralline algal turfs impart three-dimensional structures to the mid-to-low intertidal rocky habitats. The mass of interwoven haptera of the holdfast of *Hedophyllum* and the intertwining branches of articulated coralline turfs produce semi-rigid to rigid structures that protrude above the substratum and form projections and interstices of various sizes. The three-dimensional matrix thus created hosts a diverse number of invertebrates, fish and algae. Qualitative and quantitative comparisons of faunal assemblages between the kelp holdfast and
articulated coralline mat microhabitats show considerable similarities (Dommasne, 1968; Dearn, 1987). This suggests that the mechanisms through which these two substrata alter the understory abiotic and biotic environment to create favourable microhabitat for a variety of organisms are similar.

Mechanisms by which Hedophyllum Holdfasts and Articulated Coralline Turfs Modify Resources Availability

Several mechanisms have been proposed through which increases in habitat complexity, especially due to plant biomass, can alter the abiotic and biotic environment, creating a microhabitat favourable for recruitment. Hedophyllum holdfast and articulated coralline mats may alter the flow and chemical environments, decrease desiccation stress, or decrease herbivory. Successful recruitment of young kelp sporophytes on Hedophyllum holdfasts and articulated coralline mats is most likely the result of a combination of these mechanisms.

Modification of flow environment

The three-dimensional matrix formed by holdfasts and articulated coralline mats alter flow patterns around and within the matrix. Several studies have shown that substratum morphology plays a key role in determining propagule delivery and settlement, and dislodgement of developing sporophytes (Harlin and Lindbergh, 1977; Norton, 1983; Johnson, 1994). Spore delivery and entrapment may be enhanced through direct interception by haptera or coralline fronds or indirectly through the formation of depositional eddies within depressions of the matrix (Anderson and Charters, 1982; Abelson and Denny, 1997; Harvey and Bourget, 1997). Reduced water flow through the matrix will result in longer residence time for propagules, increasing the probability that they will settle successfully.

Lower flow velocities and depositional eddies may also affect fertilization success for gametophytes that have settled within the matrix, as well as other potential factors that are density dependent (Taylor and Schiel, 2003). Low dilution rates associated with slower velocities and eddies result in higher pheromone concentrations and a greater probability of encounter between gametes (Amsler pers. comm.; Abelson and Denny, 1997).
Slower flow velocities around and within the holdfast and coralline matrices will also provide developing sporophytes with a temporary refuge from dislodgement by waves, allowing them to develop their holdfast and firmly attach themselves before they are exposed to substantial hydrodynamic forces (Norton and Fetter, 1981; Norton, 1983; Vadas et al., 1990).

**Modification of chemical environment**

*Hedophyllum* holdfasts and articulated coralline mats may favour juvenile sporophyte recruitment by altering the chemical environment within their matrix. Several authors have suggested that kelp holdfasts and articulated coralline mats provide suitable habitat for invertebrates due to their ability to capture particulate matter and other nutrient-rich detritus on which invertebrates feed (Dommasne, 1969; Moore, 1972; Hicks, 1986; Gibbons, 1988; Smith, 1996; Melville and Connell, 2001). High concentrations of nutrients in holdfasts and coralline mats due to the accumulation of particulate matter or excretory nitrogenous wastes from invertebrates living within the matrix (Taylor and Rees, 1998) may give a competitive advantage to both the gametophytes and the developing sporophytes. Moreover, Amsler and Neushul (1989) found that kelp spores responded to their chemical environment. Spores swam towards nutrients when these were present at concentrations that stimulate growth and gametogenesis. Thus, *Hedophyllum* holdfast and articulated coralline mats may attract spores and promote development through the modification of nutrient concentrations within their matrices. This could be of significant importance for organisms living in the surf zone where approximately only 0.01-0.1% of the eggs released by a single individual are fertilized (Denny and Shibata, 1989).

**Modification moisture and temperature levels**

At low tide, the intertwined haptera and intermingled coralline fronds trap moisture more effectively than flat substrata (S.D. Boizard, pers. obs.; Dromgoole, 1980; Padilla, 1984; Gibbons, 1988; 1991), buffering *Hedophyllum* recruits growing on and within these matrices from desiccation stress. Padilla (1984) showed that finely branched articulated corallines, such as *C. vancouveriensis*, could hold more water than more coarsely branched species, preventing drying during periods of emersion. Using
agarose beads, Brawley and Johnson (1993) demonstrated that articulated corallines provided protection from desiccation for zygotes of *Pelvetia fastigata*, a fucoid. Developing sporophytes may also gain protection from desiccation by growing onto holdfast and articulated coralline mats indirectly due to the common occurrence of water-saturated sponges, growing amongst the haptera and coralline frond matrices.

Desiccation is probably a more important source of mortality for developing sporophytes than for other microscopic stages (spores and gametophytes) in BC. Spore settlement, gametophyte development and fertilization take place at a time of the year when the lowest low tides occur at night and precipitations are high. Recruits, on the other hand, become visible to the naked eye in the spring when the lowest low tides occur in the day, compounding the effects of temperature, solar radiation and desiccation (Brawley and Johnson, 1991).

**Modification of grazing levels**

The holdfast of adult *Hedophyllum* individuals and mats of articulated coralline algae may also facilitate sporophyte recruitment by offering a herbivore-free space. The mass of intertwined haptera and intermingled coralline fronds provides an irregular surface from which herbivores such as chitons and limpets may be easily dislodged by waves or by predators. Steneck (1982) suggested that a close fit between *Acmea testidunalis*, a limpet, and the substratum was necessary to prevent dislodgement by waves. Anderson *et al.* (1997) found a positive correlation between density of the major herbivores (*Parechinus angulosus*, a sea urchin and *Haliotis midae*, an abalone) and the number of juveniles of *E. maxima* growing onto the holdfast of adult individuals. At sites where herbivores were rare, few juvenile sporophytes were found growing onto the holdfast of adult *E. maxima* compared to other substrata, whereas at sites where herbivores were abundant, juvenile *E. maxima* were found prevalently on the holdfast of adult *E. maxima*. *Corallina officinalis*, also an articulated coralline alga, has also been suggested to facilitate recruitment of *Lessonia nigrescens* by allowing recruits to escape herbivory by the chiton, *Enplochiton niger* (Camus, 1994). It is important to note, though, that mesograzers, such as amphipods, associated with the turfs of articulated coralline algae, were not enumerated in this study and are likely an important source of mortality for juvenile *Hedophyllum* sporophytes.
In contrast, crustose coralline algae, fleshy crustose algae, and bare rock consistently inhibited the recruitment of juvenile *Hedophyllum*. This was expected. These three substrata are more or less flat and add very little structure to the intertidal. As a result, they offer little protection from waves, dry out quickly at low tide, and offer an ideal surface for herbivore to attach to and graze on (Steneck, 1982; Day and Branch, 2002). Moreover, crustose coralline algae and some fleshy crustose algae, such as *Hildenbrandia* sp., can actively inhibit colonization by epiphytes through epithelial sloughing (Masaki et al., 1981; Masaki et al., 1984; Johnson and Mann, 1986; Camus, 1994; Keats et al., 1997 and refs therein) or through the production of a chemical deterrent (Underwood, 1980; Underwood and Kennelly, 1990).

The few juvenile *Hedophyllum* sporophytes observed growing on crustose corallines, fleshy crusts or bare rock were usually in crevices (33-69% of juveniles growing on these substrata) or other such small topographical irregularities. Irregularities such as shallow cracks in the rock or that are produced by the growth edges of crustose coralline algae may also offer some level of protection to newly settled spore and developing sporophytes from dislodgment (Harlin and Lindbergh, 1977; Norton and Fetter, 1981; Norton, 1983; Johnson, 1994), desiccation and grazing (Steneck et al., 1991; Day and Branch, 2002).

Interestingly, up to 38% of the juveniles found growing on smooth bare rock at the wave sheltered site were found emerging from aggregations of the sea cucumber *Cucumaria pseudocurata*. This sea cucumber forms dense aggregations under the canopy of *Hedophyllum* and around the turf of articulated coralline algae, retaining moisture at low tide, and effectively decreasing the negative effects of desiccation on both themselves and on the juveniles growing among them.

It is worth noting that many of the mechanisms by which the holdfasts of *Hedophyllum* and mats of articulated coralline algae facilitate the recruitment of young sporophytes are linked to their complex three-dimensional structure. *Hedophyllum* holdfasts and mats of articulated corallines add topography and structural complexity to the intertidal and by doing so create microhabitats which have abiotic and biotic characteristics that favour the recruitment of juvenile sporophytes. The holdfasts of adult *Hedophyllum* act as ecosystem engineers by facilitating recruitment through
habitat modification. The same is true for articulated coralline algae, but not for structurally simple substrata such as crustose coralline algae, fleshy crusts and bare rock. McConnico and Foster (2005) also concluded that selective recruitment of *Alaria marginata* occurred among the interstitial spaces of residual holdfasts from the same species and suggested that recruitment is enhanced, indicating that residual holdfasts offer refuge or attachment sites for juvenile *A. marginata*. Articulated coralline algae were found to facilitate the recruitment of *Hedophyllum* and have also been reported to be the primary recruitment substrate for *Alaria marginata* (McConnico and Foster, 2005). However, articulated coralline algae have also been found to inhibit recruitment in other kelp species, such as *Macrocystis pyrifera* (Wells, 1983; Reed and Foster, 1984).

*Effects of Canopy Cover*

Canopy cover had no effect on the overall density of juvenile *Hedophyllum* sporophytes that recruited at Prasiola Point. However, canopy cover had a strong influence on the recruitment pattern of *Hedophyllum*. Juvenile *Hedophyllum* recruited abundantly onto the holdfasts of adult *Hedophyllum* when canopy cover was low but rarely when the canopy cover was high. Articulated coralline mats favoured recruitment under a low canopy cover, but were not as effective under high canopy cover. Interestingly, the presence/absence of canopy did not affect the recruitment patterns of *Hedophyllum* onto smooth substrata (coralline and fleshy crusts or bare rock), nor did it affect the densities of herbivores.

These patterns suggest that the canopy has very little influence on recruitment onto topographically simple substrata, indicating that the unsuitability of a smooth substratum for recruitment is due to its physical and biological characteristics and not to interactions with the canopy. The holdfast of *Hedophyllum* and mats of articulated corallines, on the other hand, are structurally complex and their ability to provide a suitable microhabitat for the successful recruitment of *Hedophyllum* varied with canopy cover.

Several mechanisms could explain the processes by which the presence/absence of a canopy can influence microhabitat conditions within the holdfast of *Hedophyllum* and the mats of articulated coralline algae. A thick canopy cover may act as a physical barrier to spore settlement (Hruby and Norton, 1979), limit light (Reed
and Foster, 1984; Kennelly, 1989; Toohey et al., 2004), and cause damage and
dislodgement through whiplash (Kennelly, 1989; van Tamelen et al., 1997). However,
the presence of a canopy can also offer protection from thermal and desiccation
stresses (Brawley and Johnson, 1991; van Tamelen et al., 1997).

Hruby and Norton (1979) experimentally demonstrated that a thick canopy of
Enteromorpha intestinalis could significantly decrease the density of algal spores
reaching the substratum. Hedophyllum blades emerge directly from the holdfast (adults
lack a stipe). Thus, under a thick canopy, the holdfast is mostly covered by blades,
potentially shielding the holdfast from spore settlement. Furthermore, if spores do settle
onto a Hedophyllum holdfast under a thick canopy, light levels would likely be
insufficient to sustain further development. Canopy shading is a common mechanism
by which adult canopy can inhibit recruitment (Reed and Foster, 1984; Kennelly, 1989;
Toohey et al., 2004). While developing sporophytes might initially benefit from canopy
cover through protection from sun radiation and heavy desiccation, eventually they will
reach a size at which the shade created by the canopy will reduce or stop growth
(Kirkman, 1981; Brawley and Johnson, 1991). Spores settling in low canopy cover
areas would have greater access to adult holdfasts and would suffer less from shading.
It is possible that some spores reach the holdfast of the parent plant, even under a thick
canopy, by trickling down the blade to the haptera in a similar fashion as Postelsia
palmaeformis (Paine, 1979). If these spores have the ability to stay dormant, they could
form a seed bank within the holdfast. Low recruitment on holdfasts of Hedophyllum
under a thick canopy could also be the result of scouring by the Hedophyllum blades.
Thallus scouring has been shown to play a role in structuring foliose algal assemblages
directly by affecting their recruitment and survivorship, and indirectly by reducing the
presence of sessile invertebrates and mobile herbivores (Velimirov and Griffiths, 1979;
Santelices et al., 1980; Konar, 2000; Gagnon et al., 2003). Given that Hedophyllum is
stipeless, thallus scouring could have a substantial effect on recruits growing on the
holdfasts of adults. However, it is unlikely, because the blades emerge from the
holdfast in no particular pattern and they can be oriented parallel, diagonally, or
perpendicular to each other. This arrangement suggests low flexibility of the basal part
of the frond, making scouring of the substratum more important away from the holdfast
than closer to it (however, see below).
Spore preemption and light limitations are less likely to affect recruitment patterns onto articulated coralline mats under high canopy cover because these mats tend to be associated with gaps in the canopy (Melville and Connell, 2001). Recruits growing within articulated coralline mats are also less likely to come into contact with the canopy blades because the calcium carbonate matrix offers protection to recruits from canopy whiplash.

However, under low canopy cover, recruits growing onto articulated coralline mats were less favoured than ones growing under high canopy cover. While both articulated coralline mats and *Hedophyllum* holdfasts can trap water during low tides, desiccation stresses due to prolonged exposure to sun and wind in the absence of canopy will likely be more important in articulated coralline mats than holdfasts, because kelp tissue contains more water than articulated coralline fronds do. Recruits found within articulated corallines showed greater signs of desiccation stress than ones found on adult holdfasts (S.D. Boizard, pers. obs.). This suggests that articulated coralline mats are not as effective at providing suitable microhabitat conditions for recruitment when the canopy cover is low, particularly in terms of thermal and desiccation stresses.

It is interesting to note that canopy cover had no effect on the density of herbivores. This suggests that *K. tunicata*, the major herbivore in this community, is not susceptible to canopy whiplash and does not require the shade provided by the canopy to survive during period of emersion as was found for another *K. tunicata* population in the San Juan Islands, WA, south-east of Barkley Sound (Burnaford, 2004).

The recruitment pulse observed in canopy removal plots at the exposed site is worth noting, mainly because it occurred solely at the wave-exposed site.

*Effects of Wave Exposure*

Wave exposure had few effects on recruitment patterns of *Hedophyllum* at Prasiola Point. Articulated coralline mats facilitated the recruitment of *Hedophyllum* as much at the wave-exposed site as at the wave-sheltered site. The same was also generally true of *Hedophyllum* holdfasts with one nuance. The difference in both the proportion of juveniles and the electivity index between canopy control and canopy removal plots was much more pronounced at the sheltered site than at the exposed site (Figure 2.9 and 2.12). Interestingly, months with electivity index values close to zero in
canopy control, wave-exposed plots (May, June, July) are also the months of highest recruit densities. This suggests that distribution patterns during these months reflected random recruitment as opposed to inhibition. The mechanism responsible for the differences in recruitment patterns observed onto the holdfast between the sheltered and exposed sites are unknown. However, the co-occurrence of peak recruitment and random recruitment patterns suggest that the presence of a canopy at the exposed site does not influence recruitment onto the holdfast as much as it does at the wave-sheltered site. This might be due to the fact that exposed *Hedophyllum* holdfasts have generally a greater number of blades but of smaller size than sheltered individuals, and thus might not cover the holdfast as much as it is the case at the wave-sheltered site.

Nevertheless, it is interesting to note that little difference in substratum-specific recruitment patterns were observed between the two sites even though they differed in terms of wave exposure and overall recruitment. Overall juvenile densities were 9 times greater at the exposed site than at the sheltered site, yet, the same substratum-specific patterns were observed. Given that these two sites have been shown to significantly differ from each other in terms of wave exposure (Milligan and DeWreede, 2000), these results suggest that flow as it interacts with substratum microtopography may be more important than its magnitude in explaining the recruitment patterns observed in this study.

**Consequences for Population Persistence and Recovery after Disturbances**

The facilitation processes reported in this study may have important consequences for population persistence and recovery of *Hedophyllum* beds following disturbances. *Hedophyllum* populations undergo seasonal fluctuations in canopy cover and density due to late fall and winter storm disturbances (Duggins and Dethier, 1985; Milligan and DeWreede, 2000). Storm damage results in either entire individuals being dislodged or tattering of the blades (Duggins and Dethier, 1985). With the advent of spring, blades regenerate and new ones are formed, usually resulting in a quick and total recovery of the canopy. Under these conditions juvenile recruitment should occur prevalently on articulated coralline turfs. In contrast, recovery after severe stochastic disturbances such as an El Niño is likely facilitated by the presence of adult holdfasts as well as by articulated coralline algae. El Niño events are associated with severe decrease in canopy cover and slow recovery (*Lessonia nigrescens*, Camus et al., 1994)
(Hedophyllum, Milligan et al., 1999) For example, in February 1998, < 1% of the substratum at Prasiola Point was covered by a Hedophyllum canopy (Milligan et al., 1999). This was due to entire individuals being dislodged or blade tattering, leaving only perennating holdfasts with a few blades of greatly reduced length (Milligan et al., 1999). A significant decrease in articulated coralline algae was also observed at Prasiola Point (one site out of 4) following the 1997 El Niño (Milligan et al., 1999). Similar canopy losses were also observed on Tatoosh Island, WA (approx. 57 km from Barkley Sound), where Hedophyllum canopy cover following the 1997 El Niño event was the lowest observed in a 20 yr-period (Paine and Trimble, 2004). The results of my study suggest that under such conditions (low canopy cover), perennating holdfasts will play an important role in the successful recruitment of Hedophyllum. Moreover, if decreases in articulated coralline cover commonly occur following El Niño event, recruitment facilitation by adult holdfasts might represent the main mechanism by which Hedophyllum populations persist and recover after severe disturbances.

Conclusions

In conclusion, the results of this study showed that sporophyte recruitment in the intertidal kelp, Hedophyllum, is substratum-specific. Not all commonly found substrata offer suitable conditions for recruitment. Substratum suitability was dependent on the structural complexity of the substratum and how the three-dimensional structure of a substratum interacted with the environment to alter abiotic and biotic conditions. Both the holdfasts of Hedophyllum adults and turfs of articulated coralline algae facilitated the recruitment of juvenile Hedophyllum sporophytes. These substrata are both complex in structure. While this study did not aim at identifying the mechanism(s) by which these substrata modify resource availability through abiotic and biotic conditions, it is clear that the mechanism(s) responsible is/are a result(s) of increase in substratum heterogeneity.

Furthermore, the results obtained in this study indicate that the persistence of Hedophyllum populations through recruitment will largely depend on the availability of structurally complex substrata provided by ecosystem engineers and that their ability to recover after severe stochastic disturbances, such as El Niño events, is dependant upon the availability of adult holdfasts and to some extent structurally complex substratum, such as turfs of articulated corallines. Given that Hedophyllum is a
dominant member of the mid to low intertidal in the northeast Pacific, owing to both its
cover and biomass, successful, rapid recovery after severe disturbance will have major
consequences on the numerous species of invertebrates, fish and algae that inhabit
Hedophyllum beds.

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Chapter 3 Morphological and Size Variations of Kelp Thalli and Holdfasts along a Wave Exposure Gradient

3.1. Introduction

Morphological plasticity is a widespread phenomenon in nature, particularly in terrestrial plants and marine algae. The ability of macroalgae to change thallus shape in response to their physical environment is thought to enhance their survival and fitness, allowing them to expand into physically different environments (Gerard and Mann, 1979; Gerard et al., 1987; Slatkin, 1987).

Morphological differentiation in response to changes in the hydrodynamic environment has been documented in many species of brown algae, e.g. Laminariales (Svendsen and Kain, 1971; Gerard and Mann, 1979; Druehl and Green, 1982; Koehl and Alberte, 1988; Blanchette et al., 2002; Roberson and Coyer, 2004; Fowler-Walker et al., 2006; Sundene, 1964) and some species of Fucales (De Paula and De Oliveira, 1982; Back, 1993; Blanchette, 1997). Macroalgae growing at sites protected from wave exposure or strong currents have thin, wide fronds with undulated margins or bullations (bumps), while ones at exposed sites have thicker, narrower and smoother fronds (Svendsen and Kain, 1971; Gerard and Mann, 1979; Druehl and Green, 1982; Cheshire and Hallam, 1988; Koehl and Alberte, 1988; Sundene, 1964).

Variation in stipe morphology in response to wave exposure has also been documented, but the pattern is not consistent across species. Mann (1971) and Chapman (1973) described an increase in stipe length and hollowing of the stipe with decreasing wave exposure in Laminaria longicruris on the Atlantic coast of Canada, and Kain (1971) reported similar results for Laminaria saccharina in Shetland, U.K.. A similar tendency for increasing stipe length with decreasing wave exposure was also found in Durvillaea potatorum in southeastern Australia (Cheshire and Hallam, 1988). In addition, D. potatorum stipes from high-wave exposure environments were thicker than ones from low-wave exposure sites. On the west coast of British Columbia, however, Laminaria groenlandica exhibit the opposite trend: individuals growing in heavy surf have long stipes and ones in moderate surf have a short stipe (Druehl, 1967). The same is also true of Durvillaea antartica (South and Hay, 1979) and Laminaria setchellii (Klinger and DeWreede, 1988): individuals with longer and thicker stipes occur at high wave exposure sites.
Much less attention has been given to morphological and biomechanical variation of the holdfast as a function of wave exposure. In fact, when collected in the field, macroalgae, especially kelps, are commonly cut at the stipe just above the holdfast (Cheshire and Hallam, 1988; Molloy and Bolton, 1996; Fowler-Walker et al., 2006). While several authors note that sheltered individuals generally have smaller poorly developed holdfasts with few haptera (in the case of Laminariales) and a weak attachment to the substratum (Kain, 1971; De Paula and De Oliveira, 1982; Roberson and Coyer, 2004) compared to exposed individuals, few investigators have quantified this pattern.

The ability to alter blade, stipe, and holdfast morphology in response to the environment may be of functional and ecological significance for the algae. Variations in thallus morphology have been hypothesized to be an adaptation to local water flow. Sheltered fronds have a high surface area:biomass ratio, which enhances light and nutrient absorption (Gerard and Mann, 1979). Undulation of the frond’s margins and bullation on the surface creates turbulence at low water velocities, thereby reducing the boundary layer at the blade surface resulting in increase nutrient uptake (however see Hurd et al., 1996). Conversely, thick, flat, narrow fronds of wave-exposed plants are streamlined, decreasing the hydrodynamic forces, specifically drag, to which they are subjected, and reducing the breakage or dislodgement in high wave exposure areas (Koehl, 1986).

The adaptive value of having a thicker and potentially stronger stipe for individuals exposed to a high wave environment is obvious. However, from the literature, it is not clear that stipe length is as influential. While morphological differentiation of the frond may decrease drag and ultimately reduce the magnitude of the stresses transferred down the stipe to the holdfast, the holdfast still needs to be strong enough to remain attached and prevent dislodgement.

While wave dislodgment can be an important cause of mortality, dislodgment itself is often the result of the combined effects of herbivory on the stipe and holdfast (Black, 1974; Munoz and Santelices, 1989; Tegner et al., 1995; Duggins et al., 2001) and the hydrodynamic forces imposed on the thallus by water motion (Black, 1974; Munoz and Santelices, 1989; Tegner et al., 1995; Duggins et al., 2001). Grazers, such as gastropods and sea urchins, are at greater risks of wave dislodgement while foraging; thus, grazing intensity is generally thought to decrease with an increase in
wave exposure (Duggins et al., 2001). As a result, macroalgal mortality due to the interactive effects of herbivory and water motion is usually non-linear (sensu Duggins et al., 2001). Sheltered sites have a high proportion of damaged macroalgal thalli due to high herbivore activity, but because wave exposure is low, damaged individuals are rarely exposed to hydrodynamic forces large enough to cause breakage or dislodgment mortalities. At wave-exposed sites, macroalgal thalli show little sign of damage due to grazing because of reduced herbivore activity, and intact thalli are well adapted to cope with the large wave-generated forces they are subjected to. Peak mortality occurs at sites of intermediate flow exposure, where periods of low flow velocities that permit significant grazing to occur are interspersed with periods of high flow velocities, which impose large enough hydrodynamic forces on the damaged thalli to cause breaking and dislodgment. This leads to the prediction that macroalgal mortality may be maximized in regions of intermediate or variable flow energy or where macroalgal attachment is maximized when herbivores are present.

In this paper, I examine the morphological and biomechanical characteristics of the understory stipitate kelp, *Laminaria setchellii* P.C. Silva and the occurrence of herbivore damage to the holdfast along a wave exposure gradient in Barkley Sound, Vancouver Island, BC. *L. setchellii* is a perennial kelp (Laminariales, Ochrophyta) common in the low intertidal and shallow subtidal of exposed rocky shores of British Columbia. Young sporophytes have a disc-shaped primary holdfast that gives rise to a short stipe and lanceolate blade. The mature sporophyte is characterized by a well-developed woody stipe, which holds erect in the water column a single, repeatedly dissected, deciduous blade, and which is anchored to the substratum by a sturdy hapteral holdfast (Abbott and Hollenberg, 1976).

*L. setchellii* can reach an age of more than 17 yr (Klinger and DeWreede, 1988). As in other perennial kelps, *L. setchellii* growth is seasonal and strongly linked with the annual daylength cycle (Dieck, 1991). Blade initiation is triggered by the winter shift from minimum daylength to increasing daylength and is followed by an increase in stipe girth, which corresponds to the formation of a growth ring and the production of a new ring of haptera (Klinger, 1984; Dieck, 1991).

I predicted that morphological characteristics related to drag force would decrease with greater exposure to waves, while biomechanical characteristics would increase to reflect the ability of kelps to resist breakage and dislodgment as wave.
exposure increases. Further, I predicted that the occurrence of damage to the holdfast of *L. setchellii* would decrease with increases in wave exposure.

More specifically this study was designed to answer the following questions:

1) Does the morphology and size of *L. setchellii* thalli and holdfasts vary among sites of differing wave exposure?
2) Does the attachment force of *L. setchellii* holdfasts vary among sites of differing wave exposure?
3) Does the occurrence of holdfast damage vary among sites of differing wave exposure?

### 3.2. Materials and Methods

This study was carried out on the West coast of Vancouver Island, Barkley Sound, BC in the vicinity of the Bamfield Marine Sciences Centre. Prevalent winter winds come from the Southeast but the ocean swells associated with storms generally come from the southwest, creating a gradient of wave exposure from the entrance of Barkley Sound to the mouth of the Alberni Inlet. Five study sites along the southern edge of Barkley Sound were chosen to represent a range of wave exposures (Figure 3.1). Two of these sites, Bordelais (Bor) and Seppings (Sep) were located on the northwest side of the Deer Group Archipelago along Imperial Eagle channel, and the three other sites, Prasiola Point (Pra), Eagle Bay (Eag) and Dixon Island (Dix) were located on the southeast side of Trevor channel. The five sites spread over approximately 10.25 km of coastline, ranging in location from fully exposed to open ocean swell (Bor) to semi-protected sites located half way into the Sound (Dix). All five sites were chosen so that they had a similar orientation (W to NW) and exposure to sun.

Wave exposure at the five sites was assessed using two methods. The first method used meteorological data on wind speed and direction supplied by Environment Canada buoy data service (La Perouse Bank buoy 46206, 48° 50.1' N, 125° 59.9 W) to produce a Relative Exposure Index (REI, Fonseca and Bell, 1998):

\[ REI = \sum_{i=1}^{8} (V_i \times P_i \times F_i) \]

Where \( i = i \) th compass heading (1=N, 2=NE, 3=E, etc. [45° increments]), \( V = \) average
Figure 3.1. Locations of 5 study sites along the Southeast shores of Barkley Sound, Vancouver Island. Bordelais Is. (Bor), Seppings Is. (Sep), Prasiola Point (Pra), Eagle Bay (Eag), and Dixon Is. (Dix). Open arrow indicates the direction of prevalent winds and swells into the Sound. Star indicates the location of the Bamfield Marine Sciences Centre. See Appendix B for detailed descriptions and map of sites.
monthly maximum wind speed in m/s, \( P = \) percent frequency with which wind occurred from the \( i \) th direction, and \( F = \) effective fetch (m). Effective fetch (as opposed to simple fetch) allows one to account for the effects of irregularities of the shoreline on the development of wind waves at a particular site (U.S. Army Coastal Engineering Research U.S. Army Coastal Engineering Research Center, 1977). Effective fetch was computed by measuring fetch (distance from the site to the nearest shoreline along a given compass heading) along 4 radials on either side of the \( i \) th compass heading (at intervals of 11.25°), and along the \( i \) th compass heading (total of 9 radials). A maximum fetch value of 1000 km was used for unobstructed (open ocean direction) fetch radials (J.R. Harper, pers. com.). Effective fetch was then calculated by taking the average of the product of each of the 9 fetch distances (km) \( \times \) cosine of the angle of departure from the \( i \) th compass heading.

The second method used wave dynamometers (Bell and Denny, 1994) to estimate the maximum water velocity at each site. Each wave dynamometer consisted of a practice golf ball attached by a monofilament line to a spring inside a PVC housing that is attached to the rock by an anchor bolt. As a wave passed over the dynamometer, drag acting on the ball extended the spring and moved a small rubber disk located inside the housing that recorded the maximum extension of the spring. Three to four dynamometers were deployed concurrently at all sites during the first low tide of a series. Maximum spring extension was recorded during each following low tide and re-zeroed each time. Dynamometers were calibrated by hanging known masses and measuring associated spring extensions. Force measurements were converted to maximum wave velocity measurements using a published calibration curve (Bell and Denny, 1994). Wave dynamometers were deployed in May (16-18), June (14-18) and November (20-24) 2003.

Between 30 and 60 \textit{Laminaria setchellii} individuals of approximately the same size were collected at each site during the summer of 2002 and 2003. Individuals were randomly selected along a transect placed within the \textit{L. setchellii} bed (0-0.3 m above chart datum). In 2002, samples were removed from the rock with a butter knife to ensure that the holdfast remained intact. In 2003, individuals were pulled off the rock using a spring scale attached to a winch to measure the force of attachment of \textit{L. setchellii} holdfasts. Individual \textit{L. setchellii} were clamped at the base of the stipe using two pipe clamps lined with a piece of fine grain sanding cushion to prevent the clamps
from slipping along the stipe. The two clamps were linked together by a piece of small gauge stainless steel wire to which a 500-N spring scale was hooked. The use of a boat trailer winch was necessary to ensure that individuals were pulled at a constant rate and to give us the strength to dislodge *L. setchelli*. The winch was positioned so that samples were pulled shoreward and parallel to the substratum to simulate flow.

Samples were brought back to the laboratory where morphological parameters were measured. Morphological parameters were blade length, surface area (maximum projected area) and biomass (blotted weight), stipe length, basal diameter parallel and perpendicular to the direction of flow and biomass (blotted weight), holdfast surface area (maximum projected area), diameter parallel and perpendicular to the direction of flow biomass (blotted weight) (Figure 3.2). Surface area measurements were made from digital pictures using SigmaScan Pro 5.0. Holdfasts were cleaned of rocks, invertebrate shells and any other visible debris before weighing. Holdfast integrity was quantified by estimating the proportion of a holdfast that was damaged due to the burrowing activity of the crab *Oedignathus inermis* or that was found growing on the test of barnacles (*Semibalanus cariosus*). Holdfast surface area was corrected by subtracting the area of the holdfast not in contact with the substratum due to the presence of a crab cavity or the presence of barnacle tests.

Age was estimated by counting the number of growth rings in three cross-sections of the stipe, 1-2 cm above the stipe-holdfast junction (Klinger and DeWreede, 1988). Growth rings were counted independently by two observers. Kolmogorov Smirnov tests and Mann-Whitney U tests showed no significant differences (*p*>0.05) in age distribution or estimates between the two independent age assessments, indicating that age could be consistently estimated. Age estimates were used as covariates to account for morphological differences among sites due to differences in population structure.

*Data analysis*

Morphometric and biomechanical data were compared among sites using analysis of covariance (ANCOVA) to account for the effect of plant size on the various characters. Age was used as a covariate. In a few cases, morphometric characters were not significantly correlated with age, and a one-way analysis of variance (ANOVA) was used instead. *A posteriori* multiple comparison tests were carried out using the
Figure 3.2. Schematic representation of *Laminaria setchellii* showing the eleven morphological characters measured. These are blade maximum length (BL), blade surface area (BSA), blade biomass (BB), stipe length (SL), basal stipe diameter parallel (SDPA) and perpendicular (SDPE) to the flow, holdfast surface area (HSA), holdfast diameter parallel (HDPA) and perpendicular (HDPE) to the flow and holdfast biomass (HB).
Sidak method. This method is similar to the Bonferroni method, but it provides tighter bounds and was chosen to avoid the loss of power that is associated with Bonferroni corrections (Norusis, 1993; Field, 2000). Principal components analysis (PCA) was performed using the following variables: age, blade maximum length, blade surface area, blade biomass, stipe length stipe diameter parallel and perpendicular to the flow, holdfast diameter parallel and perpendicular to the flow, holdfast surface area, holdfast attachment force, holdfast attachment strength. Eleven variables were used in the analysis. PCA, followed by orthogonal rotation (VMAX), was carried out. PCA axis scores were then calculated for each plant and used in subsequent analyses. The effects of wave exposure on plant morphology and biomechanics PCA axis scores were analyzed using a one-way ANOVA procedure as described above. Gabriel's post hoc tests for unequal cell sizes were carried to identify differences among sites (Norusis, 1993; Field, 2000). All statistical analyses were performed using SPSS V.11 for Macintosh Statistical Software (SPSS Inc.).

3.3. Results

Wave exposure

Relative Exposure Index (REI)

REI ranked the sites along a wave energy gradient similar to that expected from their location within Barkley Sound (Table 3.1). Bordelais and Seppings ranked relatively higher in term of their exposure to wind-driven waves than the three other sites. Prasiola and Eagle Bay had very similar exposure indices, while Dixon ranked the lowest (Table 3.1).

Maximum water velocity

Daily maximum wave velocity measurements obtained at each of the 5 sites using the wave dynamometers varied temporally and spatially within site and among sites. Of the 5 intertidal sites, Eagle Bay and Prasiola Point had the lowest mean maximum daily water velocities (Table 3.1). Bordelais and Seppings sites had the highest maximum daily water velocities (Table 3.1). Mean maximum daily water
Table 3.1. Wave exposure ranking of study sites based on the relative index of exposure (REI) and based on dynamometers maximum water velocity measurements (see methods for details). Sites with no significant differences ($p>0.05$) share a common grouping letter.

<table>
<thead>
<tr>
<th>Site</th>
<th>REI</th>
<th>Rank$^2$</th>
<th>Max. velocity</th>
<th>Rank$^3$.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>mean</td>
<td>SE</td>
</tr>
<tr>
<td>Bordelais Is.</td>
<td>14022</td>
<td>1</td>
<td>4.27</td>
<td>0.39</td>
</tr>
<tr>
<td>Seppings Is.</td>
<td>12598</td>
<td>2</td>
<td>4.66</td>
<td>0.42</td>
</tr>
<tr>
<td>Prasiola</td>
<td>11633</td>
<td>3</td>
<td>3.49</td>
<td>0.25</td>
</tr>
<tr>
<td>Pointt</td>
<td></td>
<td></td>
<td>3.08</td>
<td>0.29</td>
</tr>
<tr>
<td>Eagle Bay</td>
<td>11108</td>
<td>4</td>
<td>4.12</td>
<td>0.31</td>
</tr>
<tr>
<td>Dixon Is.</td>
<td>10867</td>
<td>5</td>
<td>4.08</td>
<td>0.31</td>
</tr>
</tbody>
</table>

1 Sites are listed by location from the southwest (at the entrance of Barkley Sound) to the northeast (near the mouth of the Alberni Inlet).
2 Ranking based on REI.
3 Ranking based on maximum wave velocity.

Table 3.2. Correlation of offshore maximum daily significant wave height from La Perouse buoy (no. 46206, 48°50'06" N, 129°58'54" W) with maximum daily water velocities at five intertidal sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>n</th>
<th>intercept</th>
<th>slope</th>
<th>$r^2$</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bordelais Is.</td>
<td>7</td>
<td>2.33</td>
<td>1.14</td>
<td>0.91</td>
<td>0.001</td>
</tr>
<tr>
<td>Seppings Is.</td>
<td>7</td>
<td>3.77</td>
<td>0.37</td>
<td>0.23</td>
<td>0.274</td>
</tr>
<tr>
<td>Prasiola Pt</td>
<td>50</td>
<td>1.18</td>
<td>1.20</td>
<td>0.52</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Eagle Bay</td>
<td>7</td>
<td>1.86</td>
<td>0.55</td>
<td>0.76</td>
<td>0.011</td>
</tr>
<tr>
<td>Dixon Is.</td>
<td>6</td>
<td>4.70</td>
<td>-0.27</td>
<td>0.21</td>
<td>0.365</td>
</tr>
</tbody>
</table>

a Site are listed by location from the southwest (at the entrance of Barkley Sound) to the northeast (near the mouth of the Alberni Inlet).
Figure 3.3. Water velocities and wave heights in May, June and November 2003. a) Daily mean maximum water velocities (mean± 1 SE) at the five intertidal study sites; and b) maximum significant wave height at La Perouse Bank offshore Buoy (no. 46206, 48°50′06″N, 129°59′54″W).
velocities at the Dixon site varied inconsistently compared to the other four sites (Figure 3.3).

The water velocities measured in the intertidal followed a similar pattern to the maximum significant wave heights measured at the La Perouse offshore buoy (Figure 3.3). Wave height was significantly correlated with water velocity at three of the five sites, Bordelais, Eagle Bay and Prasiola (Table 3.2), accounting, at these sites, for 56 to 91% of the observed variation in daily maximum water velocities. In contrast, maximum water velocities at Seppings and Dixon were not correlated with wave height at the La Perouse buoy (Table 3.2).

Sites were ranked in terms of their relative exposure to waves using maximum water velocity measurements as opposed to REI (see discussion).

Age estimates

Sampled Laminaria setchellii ranged in age from 2 to 9 years old. Mean age differed among sites (Welch ANOVA, $F=49.170$, $Df_{1,2}=4$, 103, $p<0.001$). The youngest beds sampled were Bordelais (3.8±0.1 yrs; min.=2.5, max.=5 yrs) and Prasiola Point (4.0±0.1 yrs; min.=2, max.=7 yrs), and the oldest beds were Dixon (6.3±0.2 yrs; min.=3, max.=9 yrs) and Eagle Bay (5.9±0.2 yrs; min.=4, max.=9 yrs), while the mean age at Seppings was 5±0.3 yrs (min.=3, max.=9 yrs).

Morphological patterns

Within a site, blade size, as measured by blade maximum length or surface area, was not correlated to age. They were some exceptions to this pattern (both blade length and surface area of individuals collected at Dixon and blade surface area of individuals collected at Eagle Bay were significantly correlated with age), however, age accounted only for a small percentage ($<$18%) of the observed variation. Differences in blade morphological characters were, thus, analyzed using a one-way ANOVA. Both blade maximum length and blade surface area showed significant differences among sites (One-way ANOVAs, blade max. length: $F=34.37$, $df_{1,2}=4$, 109, $p<0.001$; blade surface area: $F=47.43$, $df_{1,2}=4$, 105, $p<0.001$; Figure 3.4). Blade morphological characteristics showed a trend towards shorter and smaller blades with increasing wave exposure at 4 out of the five sites. Individuals from the most wave-exposed sites, Bordelais and
Seppings, had the shortest and smallest blades, while individuals from one of the most wave-sheltered sites, Eagle Bay, had the longest and largest blades. Individuals collected at Dixon, the site at which wave-exposure varied inconsistently, had significantly shorter and smaller blades than individuals from Eagle Bay. Individuals from Prasiola Point, which experience low wave forces, did not fit this pattern. The blade of a large number of Laminaria setchellii individuals at this site consisted of a blade stub, characteristic of blade initiation at the beginning of the season of fast growth (later winter) or of blade regeneration following damage. A few individuals were completely lacking a blade. Incidental observations suggest that blade atrophy at Prasiola Point was likely the result of an infestation by a stipe-borer amphipod (see Discussion).

Stipe length increased linearly with age at 3 of 5 sites, namely Seppings, Prasiola and Eagle Bay (Figure 3.5; Appendix C). There was no clear relationship between stipe length and age at Bordelais because there was little variance in age, whereas at Dixon stipe length at a given age varied (Figure 3.5; Appendix C). The regression slopes for the 5 sites were homogeneous (interaction of sites and age on stipe length, p= 0.628; Figure 3.5; Table 3.3), making it possible to analyze these data by ANCOVA. Stipe length differed significantly among sites, once variation due to age was accounted for (Figure 3.6; Table 3.3). However, there was no clear relationship between stipe length and wave exposure (Figure 3.6). Individuals at the two less wave-exposed sites, Prasiola and Eagle Bay, had longer stipes than individuals at either Seppings (wave-exposed) or Dixon (intermediate wave exposure), but did not differ in stipe length from individuals at Bordelais, the second most wave-exposed site.

Holdfast size, as measured by the surface area of attachment of the holdfast to the substratum, was generally greater in older individuals than younger ones, except at Bordelais (Figure 3.7). The regression slopes for the 5 sites were homogenous (Table. 3.3), making it possible to analyze these data by ANCOVA. Holdfast surface area differed significantly among sites (Figure 3.8; Table 3.3). The two most wave-exposed sites, Seppings and Bordelais, had larger holdfast than the most wave-sheltered site, Eagle Bay (Figure 3.8). In contrast, holdfast surface area of Prasiola Point individuals was similar in size to that of the two most wave-exposed sites (Bordelais and Seppings), while holdfasts at Dixon were similar in size to those of the most wave-sheltered individuals (Eagle Bay).
Figure 3.4. *Laminaria setchellii*, blade maximum length (mean±1 SE) and blade surface area at each study site. Sites with no significant differences (Gabriel’s post hoc multiple comparisons, \( p<0.05 \)) share a common grouping letter.
Holdfast biomass increased linearly with age at all sites except Eagle Bay, and the slope of all regression lines except Eagle Bay were homogenous (Figure 3.9; Appendix C). As a result, holdfast biomass data from Eagle Bay could not be included in the ANCOVA analysis. ANCOVA results for the four remaining sites indicates a highly significant ($p<0.001$) effect of site, with holdfast biomass being greater at the two most wave-exposed sites (Seppings and Bordelais) compared to the intermediate (Dixon) or the most wave-sheltered (Prasiola) sites (Figure 3.10; Table 3.3).

**Holdfast break location and removal/break/attachment force**

Of the 102 thalli selected to measure the force required to dislodge individuals from the substratum, 41 (40%) failed at the point where the holdfast attaches to the substratum. For these individuals, dislodgement was caused by either the failure of the algal adhesive bond or of the substratum itself. The types of substrata that most often failed were rock, coralline algal crusts, and in some cases, barnacles. In 37% of cases, the holdfast failed at the haptera, leaving either a portion of the haptera attached to the substratum or at least half of the holdfast including the primary holdfast (first year or two of holdfast growth). Of the remaining thalli, 14 (14%) failed at the stipe, usually, just above the holdfast. Lastly, nine of the thalli selected were too strongly attached to the substratum to be dislodged with the available equipment, exceeding the capacity of the 500-N spring scale.

While older *L. setchellii* individuals had, in general, a larger holdfast both in terms of surface area and biomass (Figures 3.7 and 3.9), they were not more strongly attached to the substratum than younger individuals ($p>0.05$ for all sites; Figure 3.11; Appendix C). Age accounted only for a small percentage ($<13\%$) of the observed variation in the force with which holdfasts are attached to the substratum (Appendix C). Holdfast attachment force was also not correlated with holdfast size (surface area) (Figure 3.12; Appendix C). This was true for all sites except Bordelais (Bor: $r^2=0.33$, $F=8.782$, n=18, $p=0.010$). Differences in holdfast attachment force among sites of varying wave exposure were, thus, examined using a one-way ANOVA. Individuals growing at more wave-exposed sites did not require greater force to be detached from the substratum than ones growing at more wave-protected sites (One-way ANOVA, holdfast attachment force: $F=2.174$, $df_{1,2}=4$, 98, $p=0.077$; Figure 3.13).
Figure 3.5. *Laminaria setchellii*. Relationship between stipe length and age for the five study sites. Slopes of all regression lines are significant (except for Bordelais and Dixon) and homogenous. Note that the fitted lines for Prasiola and Eagle Bay overlap.
Table 3.3. *Laminaria setchellii*. Analyses of covariance testing for differences in stipe length, holdfast surface area and holdfast biomass among sites of differing wave exposure. Sites with no significant differences (p>0.05) share a common underline. Bordelais Is. (B), Seppings Is. (S), Prasiola Pt (P), Eagle Bay (E), Dixon Is. (D).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age vs stipe length</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>4</td>
<td>143.257</td>
<td>8.364</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Age</td>
<td>1</td>
<td>587.329</td>
<td>34.289</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Error</td>
<td>155</td>
<td>14.599</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Equality of slope</td>
<td>4</td>
<td>11.179</td>
<td>0.649</td>
<td>0.628</td>
</tr>
<tr>
<td>B P E S D</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age vs holdfast surface area</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Site</td>
<td>4</td>
<td>1886.216</td>
<td>17.870</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Age</td>
<td>1</td>
<td>7792.235</td>
<td>73.823</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Error</td>
<td>225</td>
<td>105.553</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Equality of slope</td>
<td>4</td>
<td>175.935</td>
<td>1.687</td>
<td>0.154</td>
</tr>
<tr>
<td>S B P E D</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age vs holdfast biomass</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>3</td>
<td>1600.537</td>
<td>17.212</td>
<td>&lt;0.001</td>
</tr>
<tr>
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85
Figure 3.6. *Laminaria setchellii*, stipe length (adjusted-means evaluated for a plant of age 4.5 yrs ± 1 SE) at each study site. Sites with no significant differences (p>0.05) share a common grouping letter.
Figure 3.7. *Laminaria setchellii*. Relationship between holdfast (HF) surface area and age for the five study sites. Slopes of all regression lines are significant (except for Bordelais) and homogenous. Data on x axis are staggered for clarity.
Figure 3.8. *Laminaria setchellii*, holdfast (HF) surface area (adjusted-means evaluated for a plant of age 4.9 yrs ± 1 SE) at each study site. Sites with no significant differences ($p>0.05$) share a common grouping letter.
Figure 3.9. *Laminaria setchellii*. Relationship between holdfast (HF) biomass and age at the five study sites. Slopes of all regression lines (except for Eagle Bay) are significant and homogenous. Data on x axis are staggered for clarity.
Figure 3.10. *Laminaria setchellii*, holdfast (HF) biomass (adjusted-means evaluated for a plant of age 4.8 yrs ± 1 SE) at each study site. Sites with no significant difference (p>0.05) share a common grouping letter. Eagle Bay was excluded from analysis due its heterogeneous slope.
Holdfast strength

Holdfast attachment strength (attachment force/surface area) was not correlated with age. This was true for all sites except Prasiola Point, where age explained 16.8% of the variance observed; Figure 3.14). It is interesting to note that while the relationship between attachment strength and age at Prasiola Point is weak, it is negative (Hf Strength=274.127 - 27.702*(Age); r²=0.17 p=0.027). For the kelps that I was able to detach, holdfast attachment strength did not differ significantly among sites of different wave exposure (One-way ANOVA, holdfast attachment strength: F=1.040, df₁,₂=4, 85, p=0.392; Figure 3.15).

Holdfast integrity

The proportion of holdfasts that had their integrity compromised either because they were found growing on barnacles or because they had been burrowed through by the crab Oedignathus inermis differed significantly among sites (KW χ²=42.972, df=4, p <0.001). Eighty-two and thirty-nine percent of the individuals found at Seppings and Bordelais, respectively, showed signs of crab burrows or were found growing on barnacle shells. Prasiola and Eagle Bay individuals showed little sign of holdfast damage, with only 6% of the holdfasts affected, while holdfasts at Dixon were never found growing on barnacles nor were damaged by burrowing crabs.

Principal Component Analysis (PCA)

The proportion of the stipe length variance (communality) accounted for by the PCA was low (0.233); thus, this variable was not included in the analysis. A PCA of the morphometric and biomechanical data revealed four PCA axes with eigenvalues greater than 1.0 that accounted for 86.0% of the variance. Orthogonal rotation resulted in the eigenvalues and PCA axes loadings shown in Table 3.4. PCA axis 1 (25.6% of the total variance) was heavily weighted by positive loadings for holdfast diameter both parallel and perpendicular to the flow and holdfast surface area and thus was labeled "Holdfast". PCA axis 2 (25.0%) was heavily weighted by positive loadings for blade maximal length, blade surface area and blade biomass and thus was labeled "Blade". PCA axis 3 (21.9%) was heavily weighted by positive loadings for age, stipe diameter at the base of
Figure 3.11. Laminaria setchellii. Relationship between force required to remove holdfast from substratum and age for the five study sites. Slopes of all regression lines are non-significant. Arrows represent lower bound estimate of removal force (>500 N). Data on x axis are staggered for clarity.
Figure 3.12. *Laminaria setchellii*. Relationship between force required to remove holdfast from substratum and holdfast surface area for the five study sites. Slopes of all regression lines (except for Bordelais) are non-significant. Arrows represent lower bound estimate of removal force (>500 N).
Figure 3.13. *Laminaria setchellii*, holdfast attachment force (mean±SE) at each study site. Sites with no significant difference ($p>0.05$) share a common grouping letter.
Figure 3.14. *Laminaria setchellii*. Relationship between holdfast (HF) strength of attachment and age for the 5 study sites. Slopes of all regression lines (except for Prasiola Point) are non-significant. Data on x axis are staggered for clarity.
Figure 3.15. *Laminaria setchellii*. Holdfast attachment strength (mean±SE) at each study site. There was no significant difference in holdfast attachment strength between sites. Sites with no significant difference ($p>0.05$) share a common grouping letter.
Table 3.4. Summary of principal components analysis (PCA) results: eigenvalues, percentage of total variance accounted for by each component and PCA loadings for each variable, after orthogonal rotation. Factor loadings <0.500 are not included.

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<td>25.0</td>
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**PCA Loadings**

Variable measured

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<tr>
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<td>Blade surface area</td>
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</tr>
<tr>
<td>Blade biomass</td>
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<td></td>
</tr>
<tr>
<td>Stipe basal diameter parallel</td>
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<tr>
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<tr>
<td>Holdfast diameter perpendicular</td>
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<tr>
<td>Holdfast surface area</td>
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<td>Holdfast attachment force</td>
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Figure 3.16. PCA analysis loadings for PCA 1, 2 and 3. The points representing the eleven variables lie in four clusters. Points representing blade surface area and blade biomass overlap.
Figure 3.17. Mean PCA scores for (a) PCA 1, ‘Holdfast’; (b) PCA 2, ‘Blade’; (c) PCA 3, ‘Age & stipe diameter’; and (d) PCA 4, ‘Holdfast attachment’ at the 5 study sites. Error bars are ± 1 SE.
the holdfast parallel to the flow and stipe diameter at the base of the holdfast perpendicular to the flow and thus was labeled “Age and Stipe diameter”. PCA axis 4 (13.6%) was heavily weighted by positive loadings for holdfast attachment force and attachment strength and thus was labeled “holdfast attachment”. These data are graphically represented in Figure 3.16. The mean PCA loading scores for each sampling site are shown in Figure 3.17. PCA 1 axis score (Holdfast), PCA 2 axis score (Blade) and PCA 3 axis score (Age & Stipe), but not PCA 4 axis score (Holdfast Attachment), varied significantly among sites of differing wave exposure (One-way ANOVA, p<0.01). Dixon and Eagle Bay individuals had negative PCA 1 axis loading scores, indicating smaller holdfasts, whereas Seppings and Prasiola individuals at positive loading scores, indicating larger holdfast. Bordelais individuals had a small negative PCA 1 axis loading, indicative of a weak influence of site on Bordelais holdfasts. Bordelais, Seppings and Eagle Bay had positive PCA 2 axis scores, indicative of larger blades, while Prasiola and Dixon had negative loading scores. PCA 3 axis had strong negative influence on Prasiola loading scores and positive influence on Eagle Bay and Dixon, indicating older and thicker stipe diameter at their base compared to Prasiola. Bordelais and Seppings had weak PCA 3 axis scores.

3.4. Discussion

Wave exposure patterns

Wave exposure has been long recognized as an important factor in determining the distribution and abundance of marine organisms (Lewis, 1968) and a common cause of morphological variation (Gerard and Mann, 1979; Cheshire and Hallam, 1988; Molloy and Bolton, 1996; Blanchette et al., 2002; Roberson and Coyer, 2004; Wernberg and Thomsen, 2005). Despite its importance, quantifying wave exposure has remained a challenge (Gaylord, 2000). I selected five study sites along the Deer Group Archipelago and the southeast shore of Barkley Sound. The five sites were selected to span across a wave exposure gradient (Figure 3.1). I expected sites located at the entrance of Barkley Sound and thus closest to the open ocean (Bordelais Is.) to be the most exposed, whereas I expected sites located halfway within the Sound (Dixon Is.) to be least exposed. During sampling, it became obvious, however, that the relative exposure of some of these sites differed from my a priori expectations. For instance,
sampling conditions at Seppings Is. were often more hazardous than at Bordelais Is. due to large intermittent waves sweeping the site.

The relative wave exposure at each site varied depending on the quantification method used. REI ranked the five sites as expected based on site location along the wave energy gradient. Bordelais Is., had the highest REI, followed by Seppings Is., then Prasiola and Eagle Bay (which had similar REI values) and Dixon Is. having the smallest REI (Table 3.1). Rankings based on daily maximum water velocities differed from those based on REI measurements. On average, Seppings experienced greater maximum water velocities than Bordelais Is. and Dixon Is., which experienced greater velocities than either Prasiola Point or Eagle Bay (Figure 3.3). Daily maximum water velocities were temporally (one day to the next) and spatially (within site, ≤ 2 m) variable, which resulted in few significant differences in maximum water velocities among sites.

While REI estimates based on fetch measurements and wind speed and frequency data are commonly used to determine wave exposure (Murphey and Fonseca, 1995; Fonseca and Bell, 1998; Ruuskanen et al., 1999; Hovel et al., 2002) or see (Baardseth, 1970; Fowler-Walker et al., 2006) for variants of this method, this type of estimate ignores bottom topography. Local site variability in slope and adjacent seafloor topography can dramatically alter wave exposure (Bell and Denny, 1994; Denny et al., 2003). Maximum water velocity measurements, on the other hand, are obtained in situ, and are the resultant of a combination of factors (wind wave, ocean swells, local shore and bottom topography). Bordelais Is. is located closest to the open ocean, yet it experienced similar wave velocities to that of Seppings Is. At Bordelais, however, ocean swells broke on two shallow reefs (within 20 m of the sampling site; Appendix B, Figure B.2), before they reached the shore, which may explain the lower than expected water velocities measured at this site. Quick shallowing at the Seppings site (Appendix B, Figure B.2) lead to an abrupt increase in wave height, resulting in greater wave velocities than expected given its location and exposure to wind and ocean swell. The presence of small-scale surge channels and a shallow, narrow rock ledge below the water line at Dixon Is. may have contributed to the inconsistency and higher than expected water velocities I recorded. Moreover, the Dixon site is oriented toward the west, perpendicular to wave trains travelling down Trevor Channel. As a result, this site may be subject to greater wave impact than a site oriented in a direction
more parallel to the wave trains (e.g. Eagle Bay). Consequently, I used maximum water velocity measurements to determine the relative wave exposure of the five sampling sites.

High spatial variability in wave velocity within a site was likely the result of topographical complexity. Topography has been shown to be responsible for high local variability in exposure to wave-driven flow on rocky intertidal shores (Shanks and Wright, 1986; Bell and Denny, 1994; Denny et al., 2003; Helmuth and Denny, 2003). Of the four dynamometers deployed at the Seppings site, one recorded velocities close to zero while the other three dynamometers, only 1 to 3 m away, consistently recorded water velocities > 4 m/s. This demonstrates the difficulty of assigning a single value and ranking of wave exposure to a sampling site, when it likely represents a mosaic of exposure microhabitats. Within-site variability in the maximum water velocities recorded is likely a reflection of this mosaic and may explain why significant differences in maximum water velocity among sites were few.

Morphology patterns

In this study, *Laminaria setchellii* thallus morphology differed among sites of high, moderate and low wave exposure. There were, however, some inconsistencies, which suggests that factors other than wave exposure may affect thallus morphology.

Blade length and surface area varied significantly with wave exposure; blades were generally shorter and smaller at exposed sites compared to more sheltered sites. These results are similar to those reported for other kelps (Gerard and Mann, 1979; Koehl and Alberte, 1988; Blanchette et al., 2002; Duggins et al., 2003), fucoids (De Paula and De Oliveira, 1982; Blanchette, 1997), and red algae (Shaughnessy et al., 1996; Shaughnessy and DeWreede, 2001) and are consistent with known physiological and mechanical responses to wave exposure (Hurd, 2000 and references therein). For example, the large blades of wave-sheltered individuals maximize surface area for nutrient exchange and light harvesting, while the small blades of wave-exposed individuals minimize drag resistance, preventing breakage and dislodgement (Koehl and Alberte, 1988).

Plants at Prasiola Point had blades that were shorter and smaller than any of the other sites. The blades of a large number of individuals at Prasiola consisted of blade stubs, which had the characteristic heart shape of newly rejuvenated blades (Druehl,
However, samples were collected in July (2003), several months after the onset of rapid growth, suggesting that *L. setchellii* blade development was delayed compared to other sites. Moreover, the blade data suggests that individuals collected in 2003 had significantly smaller blades than those collected in 2001 (unpublished data). Prasiola Point did not differ from the other sites in any way that could explain this phenomenon, except that a large number of individuals at this site also exhibited signs of stipe damage and rotting. Time series data from another experiment (Chapter 5) suggest that grazing by the snail *Lacuna vincta* at the blade stipe transition zone in the late winter and spring was associated with subsequent blade and stipe deterioration, which ultimately lead to the death of the grazed plant. The combined grazing action of gastropods (various species) and of the stipe-boring amphipod *Peramphithoe stypotrupetes* (Chess, 1993) is known to cause mortality in kelps. Gastropod damage to the blade and transition zone of *L. setchellii* impedes photosynthesis and blade regrowth, and it offers a port of entry to the amphipod. *P. stypotrupetes* that feeds on stipe tissues, forming a brooding chamber where successive broods will feed and grow, eventually causing the death of the host (Conlan and Chess, 1992). Severe infestations and subsequent destruction of a large proportion of *L. setchellii* beds appears to coincide with years of calm fall and winter months (unpublished data; Chess, 1993), which occurred during the late fall and winter of 2001-2002 (unpublished data).

The stipe length of *L. setchellii* also differed among sites but not consistently with wave exposure. Other studies have documented significant effects of wave exposure on stipe length for a number of macroalgae, including *L. setchellii* (Klinger and DeWreede, 1988 see Introduction), however, the direction of these effects is not consistent across species. Increased wave exposure has been thought to result in longer stipes (Druehl, 1967; South and Hay, 1979; Klinger and DeWreede, 1988) as well as shorter stipes (Kain, 1971; Mann, 1971; Chapman, 1973; Cheshire and Hallam, 1988).

In deeper or turbulent waters, long-stiped individuals will benefit from having their fronds closer to the light because turbulence is associated with greater surface reflection (Burrows, 1956; Cousens, 1982). Deep water individuals with long flexible stipes also benefit by ‘going with the flow’, effectively reducing water velocity relative to themselves, thereby reducing the hydrodynamic forces to which they are subjected (Koehl and Wainwright, 1977; Koehl, 1982; 1984; Koehl, 1986). This strategy is likely
not as beneficial for shallower species that are exposed to large waves (Friedland and Denny, 1995; Gaylord and Denny, 1997), because swaying would result in blade damage as the blades beat against the substratum (Gaylord and Denny, 1997). The distribution of *L. setchellii* extends into the low intertidal where it is exposed to more violent water motion and the impact of breaking waves. Excessive swaying and concomitant blade abrasion is likely of more importance for intertidal *L. setchellii* than it is for its subtidal conspecific and other stipitate kelps that are restricted to the subtidal (e.g. *Pterygophora californica* or *Eisenia arborea*). Further exploration of the consequences of variations in stipe length with wave exposure would require more detailed data of the shape and material properties of the stipe. Unfortunately, few studies have documented both morphological and material properties of algal thalli as a function of wave exposure or flow dynamics and habitat.

**Holdfast morphology and attachment**

Older *L. setchellii* generally had larger holdfasts than younger individuals, both in terms of surface area and biomass. Once variation due to age was accounted for, individuals from wave-exposed sites (Seppings and Bordelais Is.) were found to have significantly larger holdfast than those of individuals growing at the least wave-exposed site (Eagle Bay). However, individuals from Prasiola Point and Dixon Is. did not fit this pattern. At Prasiola Point plants had large holdfasts similar in size to those at Bordelais Is., one of the most wave-exposed sites. Dixon Is. plants had small holdfasts similar to those of Eagle Bay, the least wave-exposed site, suggesting that wave exposure is not be the only factor influencing holdfast size.

Holdfast size has been shown to be positively correlated to wave exposure in a few species of Laminariales (*Laminaria hyperborea*, Sjøtun and Fredriksen, 1995; *Eisenia arborea*, Roberson and Coyer, 2004) and Fucales (De Paula and De Oliveira, 1982; Norton, 1986; Malm et al., 2003). Differences in hapteral growth and branching patterns have also been recorded in some species of kelp. Holdfasts at wave-sheltered sites generally have few, long, loosely packed haptera, which may not attach to the substratum, whereas holdfasts from wave-exposed sites were composed of many small haptera that formed a compact mass securely anchored to the substratum (Kain, 1971; Duggins et al., 2003; Roberson and Coyer, 2004).
An increase in holdfast size with age and wave exposure would be of significant benefit to *L. setchellii* if it resulted in a stronger attachment, however, older *L. setchellii* were not more strongly attached to the substratum than younger ones (Figure 3.11). This result was not too surprising because older individuals did not have longer or larger blades than younger individuals, which suggests that young and old *L. setchellii* may be subjected to similar hydrodynamic forces.

Older individuals, however, did have larger holdfasts (Figure 3.7 and 3.9). The holdfast of *L. setchellii* increases in size by adding a new ring of haptera (usually annually) to the outside of the existing holdfast in a similar way to other Laminariales (Kain, 1971; Novaczek, 1981). As a result, the holdfast core of older individuals is composed of tissues that are sometimes rotting, and only the outer layer of haptera are alive (Ghelardi, 1971; Kain, 1971). Although in this study the holdfasts of older *L. setchellii* individuals did not show signs of rotting, it is possible that the bond between core haptera and the substratum decays as holdfast tissues age. Thus as the holdfast grows in size and ages, the surface area and biomass of haptera actively involved in anchorage may remain constant, which could explain why older, larger *L. setchellii* holdfasts were not more strongly attached to the substratum than younger, smaller ones (Figure 3.11).

The *L. setchellii* plants collected at the most wave-exposed sites (Seppings and Bordelais Is.) had larger holdfasts (surface area) than those collected at the most wave-sheltered site (Eagle Bay; Figure 3.8), but they were not more strongly attached to the substratum than the wave-sheltered plants (Figure 3.14). Greater attachment at exposed sites may not be necessary because individuals at Seppings and Bordelais had smaller blades, which reduced the hydrodynamic forces to which they were subjected. Furthermore, the longer blades and large surface area of the *L. setchellii* plants at Eagle Bay may have required an attachment force equal to that of more wave-exposed sites due to the greater resistance their blades offered to flow.

If, indeed, *L. setchellii* overcomes the need to attach itself more strongly to the substratum at high wave exposure sites by decreasing its thallus size, then why, for a given age, does it grow much larger holdfasts at those sites? Allocating biomass to the holdfast will come at a cost, but offers no apparent benefit.

*L. setchellii* samples at Seppings and Bordelais were easily detached from the substratum despite their large holdfasts. Eighty-two percent and thirty-nine percent of
the *L. setchellii* holdfasts collected at Seppings and Bordelais were inhabited by the crab *Oedignathus inermis* or were found growing on barnacle tests of *Semibalanus cariosus*. Kelp holdfasts can support a diverse invertebrate community, including herbivores that feed on kelp tissues and accelerate decay in the holdfast core (Ghelardi, 1971; Tegner et al., 1995). *O. inermis* likely takes advantage of the grazing activity of early colonizers to gain access to an holdfast. Little is known of the ecology of *O. inermis*; MacGinitie (1937) described it as a filter feeder, found in rock crevices, macroalgal holdfasts and in other cryptic habitats. However, *O. inermis* is also known to prey on small invertebrates and may eat algae and algal detritus (Dr. G. Jensens, pers. comm.). *O. inermis* appears to actively maintain the size of its burrows, by scraping the burrow walls to prevent the haptera from regenerating. Holdfast cavities inhabited by *O. inermis* have smooth walls, whereas empty chambers regenerated hapteral stubs (pers. obs.; Figure 3.18). Thus, the presence of *O. inermis* within a holdfast may reduce how well the holdfast is attached to the substratum (pers. obs.).

Barnacles may also affect attachment strength. At wave exposed-sites, a substantial proportion of *L. setchellii* holdfasts were attached to the tests of the barnacle *Semibalanus cariosus*, and dislodgement occurred as a result of both haptera and substratum (barnacle test) failure. Barnacle tests that *L. setchellii* were growing on were brittle compared to those that were free of *L. setchellii*. In fucoids, attachment of the holdfast is achieved by the combined action of mucilage stickiness, the penetration by rhizoids of micropores of the substratum and hapteral development (Hardy and Moss, 1979). Barnes and Topinka (1969) further suggested that *Fucus vesiculosus* exudes an acidic material that partially digests calcareous substrate. *L. setchellii* haptera may smother the barnacles, which could lead to starvation and death in the barnacle and might decrease barnacle test strength. The larger size of holdfasts found growing on barnacle tests at the more wave exposed sites and the likely weaker nature of the holdfast attachment onto this secondary substratum suggests that *L. setchellii* might grow larger holdfast to offset the likelihood of being dislodged due to substratum failure.

At the wave-exposed sites, barnacles likely suffer less predation because predators are more likely to be dislodged by waves (Menge, 1972; 1974; 1978a). Reduced predation allows barnacles to reach larger sizes and extend their distribution into the lower intertidal where *L. setchellii* occur (Connell, 1970). At wave-sheltered
Figure 3.18. a) Oedignathus inermis inside a burrow; b) and c) Underside of the holdfast of two Laminaria setchellii. Note cavity with smooth roof in Figure b); d) Underside of the holdfast of a L. setchellii that settled onto the test of the barnacle Semibalanus cariosus. Note haptera starting to grow through aperture of barnacle test. Similar cavities are found in the holdfasts of other stipitate kelps, see Appendix D for further examples.
restricted to the mid to high intertidal zone.

The presence of crabs and barnacles within the holdfast of *L. setchellii* increased with wave exposure, and the combined effect of wave impact and reduced holdfast integrity (due to crabs and barnacles) increased the chance of holdfast dislodgement. The lack of differences in attachment force among wave-exposed and wave-sheltered plants supports this conclusion. Moreover, the plants sampled at Bordelais and Seppings were on average younger than those sampled at more wave-sheltered sites, suggesting that *L. setchellii* life expectancy is lower at wave-exposed sites.

Past studies have shown that tissue damage resulting in the breakage or dislodgement of a macroalga is lower at sites with high wave exposure in part because organisms causing the damage, either through grazing or other activities, can be dislodged by wave action and reduce their level of activity when subjected to high wave exposure. The results of this study show the opposite trend. *L. setchellii* is more likely to be dislodged through the activities of invertebrates at wave-exposed sites compared to wave-sheltered sites. This is due to the increased abundance of *O. inermis* in hapteral cavities and the change in the vertical distribution, abundance and size of barnacles at more wave-exposed sites.

**Conclusion**

As in many other algal species, the patterns of morphological variations observed across sites of varying wave exposure in *L. setchellii* suggest that individuals are well adapted to the flow regime in which they occur. Plants at sheltered sites had longer blades with greater surface area and smaller holdfasts compared to plants at exposed sites. These patterns support the hypothesis that plants must balance the need to maximizing light capture and nutrient exchange and minimizing hydrodynamic forces. However, there were inconsistencies to these morphological patterns and *L. setchellii* plants at wave-exposed sites were not more strongly attached to the substratum than those at wave-sheltered sites, as I predicted. The morphological and biomechanical inconsistencies reported in this study were the result of interactions between wave exposure and biological factors, which lead to severe tissue loss (snail-amphipod infestation at Prasiola Point) and in some case mortality or to the compromise of the holdfast attachment to the substratum (crabs and barnacles). These results imply that
the effects of wave exposure on algal morphology and ultimately mortality cannot be seen entirely as separate from other local processes. The indirect effects of wave exposure on biological factors such as herbivory may override the direct effect on algal morphology and mortality. Moreover, this study shows that the indirect interaction between wave exposure and herbivory can vary spatially and temporally and do so at different scale.

3.5 References


Chapter 4 Preferred Orientation and Thallus Asymmetry of Laminaria setchellii with Respect to the Direction of Oncoming Waves.

4.1. Introduction

Marine benthic intertidal and shallow subtidal habitats of wave-swept shores host some of the most diverse and productive marine communities on earth (Connell, 1978; Leigh et al., 1987; Hurd, 2000). However, wave-swept shores are also among the most stressful flow environments (Denny, 1999; Denny et al., 2003). For example, water velocities associated with breaking waves can exceed 27 m/s, with accelerations in excess of 400 m/s² (Denny et al., 1985; Gaylord et al., 1994; Gaylord, 1999; Denny et al., 2003). Organisms living under these conditions, such as macroalgae, have to contend with large hydrodynamic forces if they are to prevent breakage and dislodgement from the substratum (Koehl, 1984; Denny et al., 1985; Koehl, 1986; Gaylord et al., 1994).

Macroalgae exposed to variable flow such as that of the low intertidal or shallow subtidal zones will encounter different hydrodynamic forces. Drag, lift (usually considered to be negligible for flexible algae, Gaylord et al., 1994) and acceleration (also considered to be negligible for intertidal organisms due to the small spatial scale [<1 cm] at which acceleration occurs; Gaylord, 2000) are the hydrodynamic forces most commonly discussed in the literature, although certain kelps may also be subjected to buoyancy forces (Friedland and Denny, 1995; Stevens et al., 2002; Stewart, 2002) and perhaps torsional forces¹. The magnitude of the flow-induced forces macroalgae will have to withstand, and the type and distribution of mechanical stresses they sustain, will be affected by the size, shape and biomaterial properties of the plant (Koehl, 1984; Denny et al., 1985; Koehl, 1986; Gaylord et al., 1994).

Macroalgae have developed a range of strategies that exploit morphological and biomechanical characteristics and thallus design features to survive the mechanical stresses imposed by hydrodynamic forces. An alga can reconfigure its blades or

¹ Torsional forces are most likely negligible in highly flexible kelps as they can readily reconfigure their blades in water flow. However, for species such as Eisenia arborea and perhaps Lessoniopsis littoralis, which have a stiff stipe that branches laterally and protrudes blades side-ways, torsional forces might be of importance. As Vogel (1995) argues with respect to trees "only a spatially uniform wind on a completely symmetrical tree would not induce torsion". The importance of torsional forces relative to other hydrodynamic forces in these species remains unclear.
branches in high water velocities to achieve a more streamlined shape, and thereby lower its drag coefficient. For instance, when *Nereocystis luetkeana* is subjected to flow, its blades form a bundle, effectively reducing the blade surface area subjected to flow (Koehl and Wainwright 1979; Koehl and Alberte 1988). Other algae that have highly flexible stipes are deflected towards the substratum in response to hydrodynamic forces, where flow velocities are slower (Koehl, 1984). Another strategy, referred to as "going with the flow", occurs in large subtidal kelps subjected to wave-induced oscillatory flow (Koehl, 1986). If an alga is long enough, it will move with the flow and stretch, but it will never reach its full extension before the water washes back. Algae with flexible and highly extensible thalli may sustain large hydrodynamic forces before they break (Koehl 1984). Others such as *Lessonia nigrescens*, have opted for strength in that the stiffness of their stipe limits bending, while still allowing them to sway with the ambient flow and resist breakage (Koehl, 1984). Thus, reconfiguration, flexibility, extensibility and strength interact to determine the extent to which hydrodynamic forces are transmitted to the holdfast and determine the nature of the stresses imposed on the holdfast system.

Stipitate kelps, such as *Laminaria setchellii*, are characterized by a well-developed woody stipe that is anchored to the substratum by a sturdy holdfast and that holds a single blade (and in some species, a number of sporophylls) erect in the water column (Fig. 4.1 a). Mechanically, a stipitate kelp can be viewed as a free-standing beam fixed at one end (Fig. 4.1 b). When the beam is subjected to a lateral force and bends, the side of the beam facing the force and the side opposite to it behave differently. The side of the beam facing the force is loaded in tension, whereas the opposite side is loaded in compression (Fig. 4.1 c). These forces will be transferred along the beam to its base. Hence, when a stipitate kelp is subjected to lateral force induced by a passing wave, the stipe tissues and the haptera on the seaward (facing the oncoming wave) side of the stipe will be loaded in tension, whereas the stipe tissues and haptera on the shoreward (opposite) side of the stipe will be subjected to compressive stress. The magnitude of the associated tensile or compressive stress is defined as

\[
\sigma_p = \frac{F \times I \times y}{I}
\]
Figure 4.1. a) a stipitate kelp (*Laminaria setchellii*); b) a free-standing beam fixed at the base; c) the same beam subjected to a lateral force and showing the pattern of tensile ($\sigma_t$) and compression ($\sigma_c$) stresses that develop along the side of the beam in response to the bending force ($F$). Bending stress ($\sigma_b$) is proportional to the force applied on the beam ($F$), the length of the beam from its free end to a point being considered along the beam ($l$; here the base of the beam) and the distance along the radius of the beam from the neutral axis of bending ($y$) and is inversely proportional to the second moment of area ($I$).
where $\sigma_b$ is the bending stress (tensile or compressive), $F$ is the lateral force being applied to the beam, $l$ is the length of the beam from its free end to the point along it being considered (where the product, $F \times l$, represent the bending moment, $M_b$), $y$ is the distance from the neutral axis of bending to the point being considered ($y$ is equal to the radius of the beam when the point being considered is located on the outer circumference of the beam) and $I$ is the second moment of area of a cross-section (a measure of the shape of the cross-section or more precisely, of the distribution of material around the neutral axis of bending). Thus, bending stress at a point $x$ along the beam will be proportional to the distance of that point from the free end of the beam and to the axis of bending and inversely proportional to the second moment area of the beam (Figure 4.1 c). Any decrease in the magnitude of the force applied to a stipitate kelp or changes in morphology that lead to a reduction in hydrodynamic forces will result in a decrease in stress.

The cross-sectional shape (described by $I$, the second moment of area) of a stipitate kelp bent by the flow can also have large effects on the bending stress. The second moment of area, $I$ is described by

$$I_c = \frac{\pi \times r^4}{4} \text{ (circular beam)},$$

where $r$ is the radius of the beam. As bending stress is inversely proportional to $I$ and thus to the radius raised to the fourth power, a small increase in radius can significantly reduce stress (Fig. 4.2 a). In fact many organisms that stand upright in a moving fluid, whether air or water, are widest and most heavily reinforced near their base and taper at their tip (Koehl, 1982; Niklas, 1992). Another cost-effective way to decrease bending stress is to allocate biomass preferentially to areas of greater stress, i.e. to tissue located along the axis of bending. This would result in an asymmetrical beam of elliptical cross-section with its major axis oriented parallel to the axis of bending (Fig. 4.2 b), with $I$ defined as

$$I_e = \frac{\pi \times a \times b^3}{4} \text{ (elliptical beam)},$$

where $a$ is the semi-axis of an ellipse perpendicular to the axis of bending and $b$ is the semi-axis of an ellipse parallel to the axis of bending. I-beams used in engineering and construction are based on the same principle. In contrast, the second moment area of a
Figure 4.2. Cross-section and second moment of inertia for a circular beam (a), and an elliptical (asymmetrical cross-section) beam with its major axis oriented parallel (b) and perpendicular (c) to the direction of the applied force; \( r \) is the beam radius, \( a \) and \( b \) are the semi-axes oriented perpendicular and parallel to the direction of the applied force. Bending stress \( (\sigma_b) \) is inversely proportional to the second moment area and thus to the radius raised to the fourth power for a beam of circular cross-section and bending stress for a beam of elliptical cross-section is inversely proportional to the product of the semi-axis oriented perpendicular to the force (a) and the cube of the semi-axis oriented parallel to the force (b). Bending stress will be lower for an elliptical beam oriented with its major axis parallel to the direction of the applied force (as in [b]) than perpendicular (c) to it.
beam with its major axis oriented perpendicular to the axis of bending will be smaller
and thus will incur greater stress when subjected to a lateral force (Fig. 4.2 c). The
degree of bending of a stipe deflected by a lateral force or flexural stiffness is defined as

\[ \text{Flexural stiffness} = EI, \]

where, \( E \) is Young’s modulus of elasticity and \( I \) is the second moment of area. A stipe
with an elliptical cross-sectional shape and with is greater axis oriented parallel to the
flow will have a greater \( EI \) value and thus be stiffer than a stipe oriented with its major
axis oriented perpendicular to the flow.

Asymmetrical thickening of the stem along the axis of prevailing wind and the
axis of bending is common in terrestrial plants (Jacobs, 1954; Telewski, 1995). Similarly,
biomass allocation among the roots of trees is asymmetric; greater biomass
is allocated to the windward and/or leeward roots of the tree, and has been shown to
have large effects on tree stability (Robertson, 1991; Nicoll et al., 1995; Stokes et al.,
1995b; Nicoll and Ray, 1996). Trees, thus, allocate assimilates to those parts of the tree
under the greatest stress, thereby optimizing the use of available resources to stabilize
the tree and modulate increases in wind movement.

Terrestrial plants contend with the forces they are exposed to largely by resisting
them. Their anchorage systems and stems show adaptive growth responses that cope
with wind forces and self-loading (gravitation) by resisting bending. Stiffness, however,
is not always the ultimate strategy. In many plant species, the petiole of the leaf exhibit
cross-sectional asymmetry that takes advantage of both stiffness and flexibility (Niklas,
1998). The petiole’s elliptical cross-section is oriented so that its major axis is
perpendicular to the ground, resisting gravity, and its minor axis is parallel to the
direction of lateral winds, reducing the bending stiffness of the petiole and allowing the
leaf to reconfigure with the wind. On the whole though, trees resist bending. Most
macroalgae, on the other hand, seem to capitalize on flexibility, bending to reconfigure
and move with the flow.

Several authors have noted that the thallus of macroalgae often exhibit signs of
asymmetry with respect to the direction of the main flow. For example, Neushul (1972)
reported that the primary dichotomy in species of the subtidal kelp *Eisenia* is oriented
perpendicular to the surge direction. The stipe of *Pterygophora californica* is asymmetrical at its apex, one side being much wider than the other, the flatter side
being oriented perpendicular to the oncoming wave direction (De Wreede et al., 1992). While Friedmann and Roth (1977) found that the stipe and capitulum of *Penicillus* spp. (Chlorophyta) growing in habitats subject to one predominant wave direction are also asymmetrical, with the flatter side oriented perpendicular to the oncoming wave direction. However, in deeper waters where wave action is insignificant or in habitat where wave direction is inconsistent, the stipe and the capitulum are symmetrical. Collado-vides et al. (1998) also noted that the thallus of *Udotea flabellum*, a green coenocytic alga of the order Bryopsidales, grows with its blade oriented perpendicular to the direction of the oncoming wave. The same phenomenon has been observed in a congener, *U. conglutinata*, and in *Avrainvillea levis* (Friedmann and Roth, 1977). Similarly the palm (flattened part of the lobbed frond) of the fucoid *Durvillaea potatorum* was found to be oriented perpendicular to the direction of prevailing waves, and this was observed for several populations both intertidal and subtidal (Cheshire and Hallam, 1988). Asymmetry and body orientation have also been noted in several species of gorgonians (Théodor and Denizot, 1965; Wainwright and Dillon, 1969; Leversee, 1976; Boller et al., 2002) and on land in several species of trees (Coutts, 1983; Vogel, 1984; Stokes and Guitard, 1997; Mickovski and Ennos, 2003). While thallus asymmetry and thallus orientation with respect to flow seem to be common phenomena in sessile organism, they have rarely been quantified, especially for macroalgae (see Friedmann and Roth, 1977 for exception to this).

In the present study, I investigate the orientation of the blade, asymmetry of the stipe and of the holdfast relative to the direction of the prevailing waves and biomass allocation among haptera around the stipe, in the stipitate kelp, *L. setchellii*. I ask the following general question: “Does the thallus of *L. setchellii* exhibit adaptive growth with respect to the direction of oncoming waves?” More specifically:

1. Does the blade of *L. setchellii* show a preferential orientation with respect to flow direction?
2. Does the stipe of *L. setchellii* show asymmetrical growth with respect to flow direction, and if so, is asymmetry localized or does it occur along the whole stipe?
3. Does the holdfast of *L. setchellii* show asymmetrical biomass allocation with respect to the flow direction?
4.2. Material and Methods

Samples of *Laminaria setchellii* were collected in the summer of 2002 and 2003 at five sites located along the southern edge of Barkley Sound, Vancouver Island, BC. These sites were chosen because they were the locations of simultaneous studies of the morphology and biomechanics of *L. setchellii* along a wave exposure gradient (Chapter 3, Figure 3.1). At all sites, between 30 and 60 samples were randomly selected along a transect placed within the *L. setchellii* bed in the low intertidal (0.1 m below to 0.3 m above Canadian chart datum). Each sample was scored at the base of the stipe on the seaward side using a butter knife to indicate the direction of the oncoming waves before being pried off the substratum, taking care not to damage the haptera. Samples were brought back to the laboratory, where morphological parameters were measured; these were blade orientation (plane of blade oriented parallel or perpendicular to the flow), stipe diameter at the transition zone, stipe diameter at the stipe base, stipe diameter half way up the stipe and holdfast diameter (Figure 4.3). Vernier calipers were used to measure stipe and holdfast measurements.

All stipe and holdfast diameter measurements were taken with respect to the direction of oncoming waves (Figure 4.3), i.e. parallel with the direction of the oncoming wave (seaward and shoreward direction) and perpendicular to it (lateral W and lateral E).

Stipe taper (*T*) was calculated as

\[ T = \frac{c_{sa_p} - c_{sa_d}}{c_{sa_p}} \]

where *c_{sa_p}* is the cross-sectional area of the stipe proximal to the holdfast, *c_{sa_d}* is the cross-sectional area of the stipe distal to the holdfast. The tapering of the stipe was measured between the stipe base and its midway point and between its midway point and the transition zone.

Once the morphological parameters were taken, the stipe of each sample was cut off at its base. The holdfasts were placed onto a wooden cutting board, divided into 4 quadrants and cut into four sections, a seaward, shoreward, lateral W and lateral E.

---

2 Quadrants located perpendicular to the flow were referred to as Lateral W(est) and E(ast) to stay consistent with a survivorship experiment set at Prasiola Point, where the shore is aligned parallel to the West-East direction (see Chapter 5).
quadrants, with a meat cleaver (Figure 4.4). The haptera within each quadrant were blotted dry and weighed to obtain biomass measurements.

Blade orientation data were coded and analyzed using a Chi-square test (Sokal & Rohlf 1997). Asymmetry in stipe and holdfast diameter was assessed by comparing the difference between the diameter parallel to the direction of the oncoming wave and that perpendicular to the direction of the oncoming wave using a paired t-test (Sokal & Rohlf 1997). Stipe diameter at the stipe/blade transition zone violated the normality assumption and could not be transformed. These data were tested using a two-related-samples Wilcoxon signed-rank test (Siegel and Castellan, 1988; Norusis, 1993). Asymmetry in haptera biomass allocation was tested by comparing the distribution of differences in biomass between hapteral quadrants parallel to the oncoming flow (seaward and shoreward) and ones perpendicular to it (lateral W and Lateral E) using a paired t-test. Stipe taper of the lower and upper thallus was tested using a one-sample t-test with mean of zero. Difference in taper between the lower and upper thallus was tested using a paired t-test. The normality assumption was checked visually by examining normal probability plots and tested by calculating the Kolmogorov-Smirnov test (Norusis, 1993; Field, 2000). Holdfast biomass data violated the assumption of normality and were ln(x+1) transformed. One-way ANOVAs were used to test if the difference in morphological characters varied among sites of differing wave exposure. The level of asymmetry (ratio of character parallel to perpendicular) did not differ among sites (see Results section), thus data were pooled to perform the analyses. However, since there were good reasons to think that L. setchellii individuals growing at the Prasiola Point site might be exposed to a more uni-directional flow than at other sites (see Chapter 5), I performed the same analyses as described above separately on the Prasiola Point data. Welch ANOVAs were used when heteroscedasticity could not be resolved by transformation (Norusis, 1993; Field, 2000). All statistical analyses were performed using SPSS V.11 Statistical Software for Macintosh (SPSS Inc.).

4.3. Results

Of the 246 Laminaria setchellii individuals collected, 36 were lacking a blade, and the tip of their stipe had rotted away, which prevented me from determining the orientation of the blade with respect to the direction of oncoming waves. For the 210 remaining individuals, 91% had the plane of their blade orientated perpendicular to the
Figure 4.3. Schematic representation of *Laminaria setchellii* showing the morphological characters measured. These are blade orientation (BO), stipe diameter at the transition zone (TZSD), half way up the stipe (HWSD) and at the base of the site (BSD), and holdfast diameter (HD). Each of these characters was measured (or coded as in the case of blade orientation) in the direction parallel (PA) and perpendicular (PE) to the direction of oncoming waves. Arrows represent direction of oncoming waves.
Figure 4.4. Schematic representation of *Laminaria setchellii* holdfast, showing the stipe/holdfast junction where the stipe was cut and the four haptera quadrants (Seaward, Shoreward, Lateral W and Lateral E) into which the holdfast was divided for biomass measurements. Red triangle represent the notch made in the field to mark seaward side of the stipe.
direction of oncoming waves. Separate analyses for each site revealed the same pattern; blades are predominantly oriented perpendicular to the oncoming waves independently of the site they were collected from. Of the five sites, Eagle Bay had the highest proportion of plants (32%) with blades oriented parallel to the oncoming wave, followed by Bordelais with 21%, while less than 7% of individuals at Seppings, Dixon and Prasiola Point were so oriented. Mean value for stipe diameter at the transition zone for both parallel and perpendicular direction to the flow are illustrated in Figure 4.5. These data could not be analyzed statistically because the few *L. setchellii* individuals that had their blade oriented parallel to the oncoming flow caused extreme skewedness in the data, which could not be resolved with transformation. In most samples (91%), the ratios ranged between 0.07-0.36 and reached values up to 3.96-10.85 in the remaining fraction (9%) of the samples.

The stipe diameter ratio midway along the stipe did not differ among sites (One way Anova F=0.563, MS=0.080, df=4, 119, p=0.690), thus, data were pooled. *L. setchellii* stipe diameter ratio halfway down the stipe was significantly lower than 1 (Table 4.1), indicating that the diameter of the stipe at that position is greater in the direction perpendicular to the flow than in the direction parallel to the flow (Figure 4.5).

While the upper part of *L. setchellii* was orientated with its larger axis in a direction perpendicular to the flow, its lower part was not. At its base, the stipe of *L. setchellii* was thicker in the direction parallel to the flow than in the direction perpendicular to the flow (Figure 4.5; Table 4.1). Note that although the basal stipe diameter ratio is statistically different from 1, the departure from 1 is small (3%, Table 4.1). The holdfast of *L. setchellii* also exhibited some asymmetry, both in diameter and in biomass. Holdfast diameter was greater in the direction parallel to the flow than in the direction perpendicular to it (Figure 4.5; Table 4.1). However, as was the case for stipe, the asymmetry is small (6%, Table 4.1). This asymmetry was also reflected by the pattern of biomass allocation. The biomass of seaward and shoreward haptera was greater than that of the lateral right and left haptera (Figure 4.5; Table 4.1). Figure 4.6 illustrates the degree (departure from 1) and direction change (parallel or perpendicular) of asymmetry along the thallus of *L. setchellii*.

Similar analyses carried out using only data from the Prasiola Point site shows the same level of asymmetry along the thallus of *L. setchellii* as for the five sites pooled. The only difference is in the allocation of biomass to holdfast quadrants. At Prasiola
Figure 4.5. *Laminaria setchellii* stipe diameter, holdfast (HF) diameter parallel and perpendicular to the direction of oncoming waves and holdfast biomass for seaward-shoreward quadrants (par.) and lateral W-E (per.) quadrants. Data are means ± 1 SE.
Table 4.1. Results of statistical analyses testing the null hypothesis that the stipe diameter ratios (transition zone, midway and base), holdfast diameter ratio and holdfast biomass ratio are equal to 1, where the ratio represents the value of the morphological character measured in the direction parallel to the oncoming flow to the value of the character measured in the direction perpendicular to the oncoming flow. Midway stipe diameter and holdfast biomass data were $\log_{10}(\log_{10}(x+0.5))$ transformed.

<table>
<thead>
<tr>
<th>Character</th>
<th>Mean ratio</th>
<th>95% CI</th>
<th>t</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stipe diameter (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Midway</td>
<td>0.92</td>
<td>(0.90, 0.93)</td>
<td>-6.725</td>
<td>123</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>base</td>
<td>1.03</td>
<td>(1.02, 1.04)</td>
<td>7.69</td>
<td>287</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Holdfast diameter (mm)</td>
<td>1.06</td>
<td>(1.03, 1.09)</td>
<td>3.48</td>
<td>175</td>
<td>0.001</td>
</tr>
<tr>
<td>Holdfast biomass (g)</td>
<td>1.10</td>
<td>(1.05, 1.14)</td>
<td>4.60</td>
<td>134</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

a Stipe diameter ratio at the transition zone is not included because data were severely skewed and could not be statistically analysed.

Table 4.2. Prasiola Point. Results of statistical analyses testing the null hypothesis that the stipe diameter ratios (transition zone, midway and base), holdfast diameter ratio and holdfast biomass ratio are equal to 1, where the ratio represent the value of the morphological character measured in the direction parallel to the oncoming flow to the value of the character measured in the direction perpendicular to the oncoming flow. Basal stipe diameter data were $\log_{10}(\log_{10}(x+0.5))$ transformed and stipe diameter at the transition zone and holdfast biomass data were $\log_{10}(x)$ transformed.

<table>
<thead>
<tr>
<th>Character</th>
<th>Mean ratio</th>
<th>95% CI</th>
<th>t</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stipe diameter (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transition zone</td>
<td>0.18</td>
<td>(0.16, 0.20)</td>
<td>-26.61</td>
<td>24</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Midway</td>
<td>0.91</td>
<td>(0.86, 0.95)</td>
<td>-4.66</td>
<td>26</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>base</td>
<td>1.03</td>
<td>(1.01, 1.04)</td>
<td>4.14</td>
<td>114</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Holdfast diameter (mm)</td>
<td>1.06</td>
<td>(0.98, 1.14)</td>
<td>1.59</td>
<td>28</td>
<td>0.124</td>
</tr>
<tr>
<td>Holdfast biomass (g)</td>
<td>1.16</td>
<td>(1.06, 1.23)</td>
<td>3.38</td>
<td>29</td>
<td>0.002</td>
</tr>
</tbody>
</table>
Table 4.3. Stipe asymmetry and orientation and stipe taper. Second moment of area (I) calculated for a stipe cross-sectional ellipse oriented in the same direction as that observed in the field (normal) and opposite to that at three positions along its length (transition zone, midway and at the base. Comparison between I, flexural stiffness (EI) and bending stress (σ) of a stipe oriented with its larger axis oriented parallel to the flow and perpendicular to the flow for three positions along the length of the stipe. Stipe taper (T) of the upper and lower portion of the stipe.

<table>
<thead>
<tr>
<th>Position</th>
<th>I (10^8 m^4)</th>
<th>I_{par}</th>
<th>E_{I_{par}}</th>
<th>σ_{par}</th>
<th>T^b</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>normal</td>
<td>opposite</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>transition zone</td>
<td>0.088</td>
<td>0.856</td>
<td>0.10</td>
<td>0.10</td>
<td>3.13</td>
</tr>
<tr>
<td>midway^a</td>
<td>0.463</td>
<td>0.533</td>
<td>0.85</td>
<td>0.85</td>
<td>1.09</td>
</tr>
<tr>
<td>base</td>
<td>2.015</td>
<td>1.899</td>
<td>1.06</td>
<td>1.06</td>
<td>0.97</td>
</tr>
</tbody>
</table>

^a Assuming that E does not vary along the length of the stipe.

^b Dimensionless.

Table 4.4. Asymmetrical vs symmetrical stipe. Second moment of area (I) calculated for an asymmetrical stipe with cross-sectional ellipse oriented in the same direction as that observed in the field (asym.) and for a symmetrical stipe (sym.) at three positions along its length (transition zone, midway and at the base. Comparison between I, flexural stiffness (EI) and bending stress (σ) of an asymmetrical and symmetrical stipe for three positions along the length of the stipe.

<table>
<thead>
<tr>
<th>Position</th>
<th>I (10^8 m^4)</th>
<th>I_{asym}</th>
<th>E_{I_{asym}}</th>
<th>σ_{asym}</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>asym.</td>
<td>sym.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transition zone</td>
<td>0.088</td>
<td>0.028</td>
<td>3.13</td>
<td>3.13</td>
</tr>
<tr>
<td>Midway</td>
<td>0.463</td>
<td>0.432</td>
<td>1.07</td>
<td>1.07</td>
</tr>
<tr>
<td>Base</td>
<td>2.015</td>
<td>1.843</td>
<td>1.09</td>
<td>1.09</td>
</tr>
</tbody>
</table>

^a Assuming that E does not vary along the length of the stipe.
Figure 4.6. Degree of asymmetry (departure from one of the ratio of character parallel to the flow to character perpendicular to the flow) and direction of asymmetry (major axis oriented parallel or perpendicular to the flow) along the stipe and holdfast of *L. setchellii*. Data at transition zone are for blade perpendicular to flow only.
Point, *L. setchellii* allocates slightly more biomass (16% as opposed to 10%, Table 4.1 and 4.2) than when all the sites are combined.

The stipe showed significant tapering along its length (lower thallus: \( t=43.62, \) \( df=122, \) \( p<0.001 \); upper thallus: \( t=37.938, \) \( df=101, \) \( p<0.001 \)). The difference in stipe taper between the upper and lower portion of the stipe was small, but significant (mean difference=0.06± 0.02, \( t=2.903, \) \( df=100, \) \( p=0.005 \)), with the greatest level of tapering being observed along the lower portion of the stipe (Table 4.3). Tapering of the lower portion of the stipe was 0.57 and corresponded to a 4 fold decrease in \( I \) and equivalent decrease in flexural stiffness (Table 4.3). Tapering of the upper portion of the stipe was 0.51, which corresponded to a 5 fold decrease in \( I \) and equivalent decrease in flexural stiffness (Table 4.3)

### 4.4. Discussion

The growth and development of sessile macroalgae are known to respond to physical stimuli by adaptively altering the size and morphology of their thallus, pattern of biomass allocation, and mechanical properties of tissues (Denny et al., 1985; Gerard, 1987; Kraemer and Chapman, 1991; Johnson and Koehl, 1994; Sjotun and Fredriksen, 1995; 1997; Kawamata, 2001; Blanchette et al., 2002). The data reported in this study suggest that the thallus of *Laminaria setchellii* exhibits asymmetrical growth with respect to the flow direction it is subjected to. Moreover, changes in the direction of asymmetry between the upper and lower thallus suggest that *L. setchellii* trade-off between an upper thallus configuration that can quickly reorient itself with the flow thereby reducing hydrodynamic drag it is subjected to, and a lower thallus configuration that increases the resistance to bending of the lower stipe, diminishing concomitant bending stress.

Previous studies have noted preferred orientation to the flow of flexible planar organisms such as macroalgae and gorgonian corals (Théodor, 1963; Théodor and Denizot, 1965; Wainwright and Dillon, 1969; Leversee, 1976; Friedmann and Roth, 1977; Cheshire and Hallam, 1988; Collado-Vides et al., 1998; Boller et al., 2002). Théodor and Denizot (1965) suggested that organisms planar in shape would achieve mechanical stability only if oriented with their plane perpendicular to the direction of flow. Wainwright and Dillon (1969) further demonstrated that sea fans of the genus *Gorgonia* oriented with their fan at angles other than 90° to the flow incurred large twisting moments and increased risks of fracture. Macroalgae such as *L. setchellii*.
Udotea spp., and Avrainvillea spp., that hold their blade erect into the water column, offer maximum surface area for drag to act upon by having their blade perpendicular to the flow. However, flexibility allows their blades to rapidly reorient themselves with the major flow force, effectively diminishing the drag force with which they have to contend. The blade of L. setchellii further streamlines by folding on itself, which genera such as Udotea and Avrainvillea cannot achieve due to the calcification of their blades (personal observations; Collado-Vides et al., 1998). Thus, the high flexibility of the blade of L. setchellii and its orientation perpendicular to the flow maximize its ability to rapidly reconfigure itself with the prevailing flow, directly reducing drag while minimizing torsional stress.

The upper part of the stipe of L. setchellii exhibited asymmetry similar to that of the blade, i.e. with its major axis perpendicular to the flow. The stipe flattens out and fans out at its tip where it gives rise to the blade. Thus, it is not surprising that the stipe cross-section at the transition zone is oriented with its larger axis perpendicular to the flow, as was the case for the blade. Flattening of the stipe tip also occurred in Pterygophora californica with its flat side also oriented perpendicular to the flow (DeWreede et al., 1992), and while the stipe of Eisenia arborea is dichotomously branched, the distal portions of its stipe are markedly flattened and oriented perpendicular to the prevailing flow (Neushul, 1972). Marked flattening of the stipe tip and orientation normal to the flow for these two species presumably hasten reconfiguration of the blade-sporophylls bundle while also limiting torsional stress. Below the transition zone, the stipe cross-sectional shape of L. setchellii becomes elliptical but remains oriented with its major axis perpendicular to the flow. Hence, both the blade and upper part of the stipe are oriented so as to facilitate bending and the reconfiguration of the drag-bearing part of the thallus.

In contrast, the lower part of the thallus exhibits asymmetry in the opposite direction to that of the upper thallus. Below the stipe midway point, the major axis of the stipe is oriented parallel to the direction of prevailing flow. The holdfast exhibits similar asymmetry. The holdfast of L. setchellii is greater in diameter in the direction parallel to the flow than perpendicular to the flow and allocates more biomass to haptera in seaward and shoreward quadrants than in lateral ones. Asymmetrical radial growth along the plane of bending has been shown to occur in the stem of a number of tree species (Jacobs, 1954; Larson, 1965; Telewski and Jaffe, 1986a; b; Telewski, 1995)
(Osler et al. 1996). A number of other studies do not measure stem asymmetry but account for it by rotating specimens over the course of the experiment so that exposure to mechanical stimuli is symmetrical (Gartner, 1994; Osler et al., 1996). Recently, studies have focused on the response of root systems to mechanical stimulation (Stokes et al., 1995a; b; Nicoll and Ray, 1996; Stokes and Guitard, 1997; Mickovski and Ennos, 2003). These studies have shown that mechanically perturbed trees adapt to greater bending stress and an increased risk of toppling by increasing biomass allocation to the root system as well as producing more and thicker roots in the direction parallel to the axis of flexing. Stokes et al. (1995a) has shown that changes in the size and architecture of the root system due to mechanical stimulation increased anchorage strength in Sitka Spruce and Larch. The asymmetry observed in holdfast diameter and biomass allocation suggests that the haptera on the seaward and shoreward side of the stipe (along the axis of bending) are subjected to greater stresses than haptera located in lateral quadrants. Allocation patterns of biomass to holdfast quadrants showed more pronounced asymmetry (10-16%) than the pattern of holdfast diameters (6%). Allometric scaling predicts, given that shape remains constant, that small changes in length will correspond to larger changes in mass/volume. However, biomass allocation patterns observed in the holdfasts of *L. setchellii* are lower than what allometric scaling would predict, suggesting that some other factors affect this relationship. These findings suggest that *L. setchellii* produce either a greater number of haptera or larger haptera on the seaward and shoreward side of the stipe in response to greater stress. Given what is known of root anchorage mechanics from the terrestrial literature and of the physical properties of materials, an increase in haptera diameter and cross-sectional areas would result in greater resistance of the haptera to bending, while an increase in haptera numbers but of smaller diameter would decrease stiffness but allow a more rapid transfer of tensile forces to the substratum (Coutts, 1983; Stokes et al., 1995b). The present study measured the gross morphology of *L. setchellii* holdfasts. A more detailed examination of the holdfasts would likely reveal more subtle functional differences among seaward, shoreward and lateral haptera.

The degree of asymmetry (departure from one) ranged from greatest at the blade to smallest at the stipe base and increased again at the holdfast but to a much smaller extent than that observed in the blade (Figure 4.6). The degree of asymmetry along the stipe below the transition zone was small (<3-6% if considering data for Prasiola Point).
but highly significant. If the second moment of area (I) is calculated at three positions along the length of the stipe using data from Figure 4.5 and is compared to the value obtained if the cross-sectional ellipse at these positions was oriented in the opposite direction, I can determine a) the change in I and b) the change in $\sigma_b$ (bending stress) as a function of orientation (Table 4.3). Moreover, if I assume that $E$, the Young's modulus of elasticity does not vary along the stipe, I can determine the effect of stipe orientation on the flexural stiffness ($EI$) of the stipe (Table 4.3). If the stipe at its midway point was oriented with its major axis parallel to the flow instead of perpendicular to it, I would increase by 15% (with a concomitant increase in stiffness) and $\sigma_b$ would decrease by 9% (Table 4.3). If the stipe at its base was oriented with its major axis perpendicular to the flow as opposed to parallel, a 6% decrease in I (with a concomitant decrease in stiffness) and a 3% increase in $\sigma_b$ would be observed (Table 4.3). This would lead to an increase in stiffness at the midway point of the stipe and a slight decrease in stiffness at the base. This suggests that the degree of asymmetry the stipe cross-sectional area exhibits at its midway point has a greater influence on the bending behaviour of the stipe than at the stipe base. Yet, due to the tapering of the stipe, the flexural stiffness of the basal portion of the stipe remains greater than that of the middle portion of the stipe, and thus, will offer more resistance to bending than the upper part of the stipe (Table 4.3).

The same exercise can be done for an asymmetrical stipe and a symmetrical stipe of same cross-sectional area. If the stipe at the transition zone had a circular cross-sectional area as opposed to an elliptical (highly flattened) one, I would increase by 68% (with concomitant increase in stiffness) and $\sigma_b$ would decrease by 77% (Table 4.4). However, since $\sigma_b$ is proportional to $I$ (length of the stipe from its tip end to the point along it being considered) and thus the magnitude of $\sigma_b$ close to the stipe tip will be small whether the stipe is asymmetrical or symmetrical. If the stipe at its midway point was circular instead of elliptical, I would increase by 7% (with a concomitant increase in stiffness) and $\sigma_b$ would decrease by 4% (Table 4.4). If the stipe at its base was circular as opposed to slightly elliptical, a 3% decrease in I (with a concomitant decrease in stiffness) and a 2% increase in $\sigma_b$ would be observed (Table 4.4). Changes in bending behaviour between an asymmetrical and symmetrical stipes are similar but less pronounced to that discussed above for asymmetrical stipes oriented in
opposite direction with regards to the flow. These comparisons indicate that asymmetry and orientation can have notable effects on the bending behaviour of *L. setchellii*, but the degree to which they will affect bending largely depends on the degree of asymmetry exhibited.

Likewise, Sitka Spruce exposed to winds have a shorter, more tapered stem toward its top and a lower $E$ than trees located within a stand where they are sheltered from winds (Bruchert and Gardiner, 2006). High taper and low stiffness of exposed spruce allow for flexural stiffness at the stem base due to the larger diameter and a higher flexibility in the crown region of the stem to prevent wind damage. Furthermore, short, tapered trees when exposed to wind sway to a smaller amplitude and frequency than trees with a long, slender stem, which is thought to help prevent weakening of the root system (Bruchert and Gardiner, 2006). Similar growth and development patterns, resulting in stem taper, have been observed in a number of angiosperm and gymnosperm species exposed to mechanical perturbations, whether wind or mechanically-induced (See for review Telewski, 1995). Tapering of the stem maintains elastic or geometric similarity between growth in stem diameter and height, ensuring a constant factor of safety against wind-induced mechanical failure (Wilson and Archer, 1979; Lawton, 1982; Telewski and Jaffe, 1986b; a; Holbrook and Putz, 1989; Telewski, 1995). An even load distribution is advantageous in that it will exempt the stem from weak (overloaded) points or waste material in underloaded areas of the stem.

In *L. setchellii*, changes in the direction of asymmetry occur concurrently to tapering of the stipe and will have direct consequences in the stress distribution along the stipe. The rapid change in cross-sectional shape (from fat ellipse at the stipe to a flattened ellipse at the blade) at the stipe transition zone is likely acting as a hinge point. The cross-sectional areas on either side of the transition zone are likely similar (personal observations), indicating that past the transition zone, the blade is subjected to tensile stress.

While a number of studies have noted preferred orientation of the blade or stipe tip of macroalgae with respect to prevailing flow, few have investigated asymmetry along the rest of the thallus and its effects on mechanical behaviour. The results of this study suggest that *L. setchellii* exhibits asymmetry in two planes, laterally (cross-sectional shape of the stipe) and longitudinally (cross-sectional size or taper). The upper thallus orientation (blade and stipe) and small diameter (stipe) facilitate bending
with the flow, avoiding large drag forces, whereas the larger diameter at the stipe base and cross-sectional shape (minimally) increase the lower stipe stiffness. These results suggest that *L. setchellii* trades-off between bending with the flow to avoid large hydrodynamic forces and limiting the development of large bending stress at the base of its stipe by resisting bending. The resistance of the lower stipe to bending may also benefit *L. setchellii* by keeping the photosynthetic blade upright in the water column, closer to light and thus shading competitors, and by elevating the reproductive tissues into a zone of higher flow velocity. The process by which bending stresses are transmitted to the holdfast haptera is not well understood, but the asymmetry (especially in biomass allocation) suggests that *L. setchellii* subjected to a prevailing flow responds by allocating more biomass to areas of the holdfast that undergo large tensile and compressive stresses. The lack of variations in asymmetry with increases in wave exposure suggests that low levels of wave exposure are enough to induce asymmetrical growth patterns. Furthermore, while it is clear that asymmetry allows *L. setchellii* to trade-off between remaining exposed to light and avoiding exposure to large waves, the small departures from symmetry observed indicate that asymmetry comes at a cost. More pronounced patterns of stipe asymmetry would put *L. setchellii* at severe risk if hit by a random wave coming from a different direction than the prevailing flow.

The role of asymmetry and tapering has been given little attention in the studies of macroalgal biomechanics. More detailed work examining the asymmetry of the stipe and holdfast of *L. setchellii* in relation to mechanical properties is needed before we can understand more clearly its dynamic response of under load.

4.5. References


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5.1 Introduction

Wave-swept shores can be physically challenging for the organisms that inhabit them. Although water action is only one of a suite of physical factors that characterize these shores, the hydrodynamic forces waves generate have been shown to play a central role in determining the size, morphology, distribution and abundance of intertidal organisms (Lewis, 1968; Seymour et al., 1989; Vadas et al., 1990; Dudgeon and Johnson, 1992; Denny, 1994; Blanchette, 1997; Gaylord, 1999). The water velocities macroalgae experience on wave-swept shores are equivalent to wind speeds in excess of 430 m/s on land (allowing for the greater density of water; Norton, 1991). Ultimately, the survival of sessile macroalgae in high-energy environments will depend on their ability to remain anchored to the substratum. Despite its fundamental importance, the holdfast of kelps (large brown algae in the order Laminariales) has been largely ignored in biomechanical studies.

While there exist fundamental differences between the anchorage system of marine algae and of terrestrial plants, certain parallels can be drawn, and a closer examination of the theories and models developed for terrestrial systems may provide information on the mechanical properties and functioning of kelp holdfasts. Mechanical analysis of the anchorage systems of terrestrial plants stems from the engineering theory of beams. A plant may be viewed simply as a free-standing beam that is fixed at the base (Figure 5.1). When the beam (stem) is subjected to a lateral force (i.e. wind force), the windward and leeward sides of the beam respond differently. On the windward side, the tissue is loaded in tension, whereas on the leeward side, the tissue is loaded in compression (Figure 5.1). In due course, these forces will be transmitted to the anchorage system. Hence, the roots on the windward side of the stem will initially bend slightly and then be pulled in tension, whereas the roots on the leeward side of the stem will be subjected to bending and compressive forces (Figure 5.1). Roots located at right angles to the direction of the wind will be subjected to twisting forces, but torsional stresses are very small and probably unimportant for small angular
Figure 5.1. a) a free-standing beam fixed at the base (i) and a stipitate kelp showing parts of the thallus (ii). b) the same beam (i) and stipitate kelp (ii) subjected to a lateral force (e.g. wave) and showing the pattern of tensile and compression stresses that develop along the side of the beam and stipe and anchorage system in response to the bending force.
displacements (Coutts, 1983). Because bending stresses are proportional to the length of the beam, the stresses in the tissues near the attached end (i.e. the base of the trunk) of a plant bent in the wind or flowing water will be greater than those near its free end (Niklas, 1992). The design of anchorage systems in terrestrial plants largely depends on the types of forces they must withstand (Ennos, 1991; Ennos and Fitter, 1992; Ennos, 1993). Likewise, the design of kelp holdfasts should depend on the type of forces to which their thalli are subjected.

Kelps exposed to variable flow, such as in the low intertidal or shallow subtidal zones, will encounter a number of different hydrodynamic forces. Drag, lift (usually considered to be negligible for flexible algae, Gaylord et al., 1994) and the acceleration reaction are the hydrodynamic forces most commonly experienced by kelps, though certain kelps may also be subjected to buoyancy forces (Friedland and Denny, 1995) and perhaps torsional forces\(^3\). The magnitude of the flow-induced forces a kelp will have to withstand and the distribution of mechanical stresses sustained by its thallus will be affected by the shape and size of the plant (Koehl, 1982; Denny et al., 1985; Koehl, 1986; Gaylord et al., 1994). On the other hand, the type of stresses transmitted through the thallus to the holdfast will depend mainly on the design and biomechanical properties of the kelp.

Kelps have developed a range of strategies that exploit morphological and biomechanical characteristics and thallus design features to survive the mechanical stresses imposed by hydrodynamic forces. An alga can reconfigure its blades or branches in high flow to achieve a more streamlined shape, and thereby lower its drag coefficient. For instance, when *Nereocystis luetkeana* is subjected to flow, its blades form a bundle, effectively reducing the blade surface area subjected to flow (Koehl and Wainwright, 1977; Koehl and Alberte, 1988). Other algae with highly flexible stipes take advantage of the slowly moving water in the boundary layer by lying near the substratum, thus reducing the amount of drag (Koehl, 1984). Another strategy, referred to as "going with the flow," occurs in large subtidal kelps subjected to wave-induced

\(^3\) Torsional forces are most likely negligible in highly flexible kelps as they can readily reconfigure their blades in water flow. However, for species such as *Eisenia arborea* and perhaps *Lessoniopsis littoralis* that have a stiff stipe that branches laterally, protruding blades side-ways, torsional forces might be of importance. As Vogel (1995) argues with respect to trees "only a spatially uniform wind on a completely symmetrical tree would not induce torsion". The importance of torsional forces relative to other hydrodynamic forces in these species remains unclear.
oscillatory flow (Koehl, 1986). If an alga is long enough, it will move with the flow and
stretch, but it will rarely reach its full extension before the water washes back. Algae
with flexible and highly extensible thalli may sustain large hydrodynamic forces before
they break (Koehl, 1984). Other kelps have opted for strength in that the stiffness of
their stipe prevents bending, and allows them to resist breakage (Koehl, 1984). Thus,
reconfiguration, flexibility, extensibility and strength interact to determine both the extent
to which hydrodynamic forces are transmitted to the holdfast and the nature of the
stresses imposed on the holdfast system.

The purpose of this study is to evaluate if holdfast attachment exhibits
asymmetry with respect to the direction of the oncoming waves and evaluate
consequences for the anchorage mechanics of kelp holdfast and, ultimately, for
individual survivorship. The anchorage mechanics of Laminaria setchellii holdfast can
be considered in terms of static or dynamic systems. Dislodgement by waves is clearly
a dynamic process. Gaylord and Denny (1997) have described the bending dynamics
of Pterygophora californica and Eisenia arborea, two other species of stipitate kelps, as
their thallus interacts with passing waves. Ideally, the components of holdfast
anchorage should be included in such dynamic models, because the holdfast's haptera
are subjected to the oscillating forces transmitted by the stipe. However, our lack of
knowledge of the mechanics of kelp holdfast anchorage and the complexity of the
system suggest that an investigation of holdfast detachment when subjected to a static
load may also provide useful information.

I used a stipitate kelp, L. setchellii, which could easily be modeled using beam
theory. L. setchellii is characterized by a well-developed, woody stipe that holds a large
repeatedly dissected blade upright in the water column and that is anchored to the
substratum by means of a hapteral holdfast. I chose to focus on the biology and
biomechanics of the holdfast, although I acknowledge that mortality likely occurs due to
stipe breakage as well as holdfast dislodgement. L. setchellii were tagged, before
removing haptera in one of four quadrants around the stipe. I monitored their survival
and haptera regeneration and the force they required to be detached from the
substratum. By monitoring differences in survival and detachment force among L.
setchellii with undamaged holdfasts and ones missing one of four haptera quadrants, I
investigated the anchorage mechanics of L. setchellii under both dynamic loading
(survival experiment) and static loading (detachment experiment).
I predicted that *L. setchellii* individuals with damaged (removed by manipulation) holdfasts would have a lower survivorship and require less force to be detached from the substratum than undamaged (control) individuals. I further predicted that *L. setchellii* individuals with damaged haptera along the axis of bending (seaward or shoreward haptera) would be more likely to be dislodged by waves and winter storms than individuals with damaged haptera perpendicular (lateral haptera) to the axis of bending. Similarly, I predicted that *L. setchellii* individuals with damaged seaward or shoreward haptera would require less force to be detached from the substratum than individuals with damaged lateral haptera. Finally, I predicted that regeneration of damaged seaward and shoreward haptera should occur faster than that of damaged lateral ones.

5.2 Materials and Methods

*Study site*

This study was conducted on a *Laminaria setchellii* population in the rocky intertidal zone of Prasiola Point, Barkley Sound, on the west coast of Vancouver Island, British Columbia (48°49' 4" N, 125°10' 4" W; Figure 5.2). The prevailing ocean swells originate from the southeast. Ocean swells entering the Sound travel down Trevor channel and curve around Prasiola Point before hitting the study site perpendicular to the shore line (Figure 5.2). The study site consists of a moderate slope that opens shoreward to a large tide pool and surge channel system (Figure 5.2). Waves reaching the top of the slope spill into a large tidepool and then out through two side channels. This tidepool-surge channel configuration results in a more or less uni-directional water movement up the slope, with most of the water evacuating through the pool-channel system, as opposed to washing back down the slope.

*Study Species*

*L. setchellii* is a perennial brown alga in the order Laminariales. It occurs vertically from the low intertidal (+0.3 m above Canadian chart datum) to the shallow subtidal (-10 m) and latitudinally from Attu Island, Alaska to Baja California (as *Laminaria dentigera*, Abbott and Hollenberg, 1976). *L. setchellii* distribution extends above any of the other stipitate kelps, such as *Pterygophora californica* and *Eisenia*
Figure 5.2. Map of study site at Prasiola Point, located on the southeast edge of Barkley Sound, on the west coast of Vancouver Island, British Columbia (48°49'4" N, 125°10'4" W). ▲’s indicate the locations of La Perouse Bank (LP) and South Brooks (SB) offshore data buoys. Middle panel indicates the direction in which swells travel into Trevor Channel, wrap around Prasiola Point and hit the study site (highlighted in red). Bottom panel is a close up of site at Prasiola Point. Thick black arrow indicates the movement of water upshore, spilling into the tidepool and exiting in large part through the side surge channels, with some backwash. Seaward (Sea), shoreward (Sho) and lateral (LW and LE) directions with respect to the direction of oncoming waves and direction of stipe flexing.
arborea, exposing it to greater wave action. The sporophyte stage is composed of a hapteral holdfast, an erect woody stipe, and a single blade repeatedly dissected (Figure 5.1a[iii]). The holdfast and stipe are perennial, while the blade is annual. The period of rapid growth coincides with the onset of longer daylight and consists of the initiation and elongation of the blade, increases in stipe girth and length, and the addition of a ring of new haptera (Klinger, 1984; Klinger and DeWreede, 1988; Dieck, 1991). L. setchellii can be aged by counting the number of concentric growth rings in cross-sections of the base of the stipe. L. setchellii as old as 17 yrs have been recorded in Barkley Sound (Klinger and DeWreede, 1988).

**Experimental design**

A hundred and thirty-four randomly chosen L. setchellii individuals were tagged and mapped in the field in the summer of 2001. Individuals with healthy blades and not growing in clumps or on a ledge were tagged with a piece of coloured flagging tape and two colour-coded nylon cable ties (coloured nylon cable ties with coloured plastic coated wire) cinched around the stipe base. The flagging tape allowed for easy relocation, while colour-coded cable ties allowed individual identification. Each individual was also mapped by recording its location (distance along and above/below) in reference to a permanent horizontal transect line placed across the middle of the bed. Morphometric data (blade length, stipe length and diameter and holdfast diameter) were collected for each individual when originally tagged. These data are discussed in Chapters 3 and 4. Individuals of similar size (stipe length) and closely located were grouped into series of four plants. The holdfast of each individual L. setchellii was divided around the central axis of the stipe into quadrants (seaward [Sea], shoreward [Sho] and two lateral quadrants [LW and LE]; Figure 5.3 a). Within each group of four, three L. setchellii were randomly assigned to one of three haptera removal treatments and the fourth to a control group. The three treatment groups consisted of the removal of all haptera in one quadrant, the seaward, the shoreward or one of the lateral quadrants (Figure 5.3 b).

The first haptera removal manipulation was applied after the onset of the storm season, in January 2002. Individual survivorship was monitored at monthly intervals for 9 months. A second haptera removal manipulation was applied in September 2002 and kelp survival monitored from Sept 2002-through July 2003 (for an additional 9 months).
Figure 5.3. *Laminaria setchellii*. a) Division of holdfast into haptera quadrants: seaward (Sea), shoreward (Sho), laterals (LW and LE); Sea and Sho quadrants are aligned with the direction of the oncoming waves and the direction of stipe flexing; LW and LE haptera quadrants are perpendicular to the direction of oncoming waves and stipe flexing; b) Side and top diagrammatic views of *L. setchellii* holdfast showing the removal of seaward quadrant haptera.
Each month, flagging tape or tag loss was recorded. These data were used to estimate the rate at which tags were lost and to correct, if necessary, the observed rate of mortality for tagged individuals. Qualitative data of damaged haptera regeneration and holdfast growth were recorded 1, 2 and 4 months after the first haptera removal and 1 and 3 months after the second manipulation. Haptera regeneration was characterized visually as the absence of haptera outgrowth along the cut edges of the removed quadrant (0), the presence of 1 to 3 haptera outgrowths, usually <1 cm long (1), the presence of 1 to 3 newly grown haptera (2), total regeneration of the holdfast quadrant where the cut quadrant is indistinguishable from the other three quadrants (3). Holdfast growth was characterized visually as the absence of a characteristic ring of haptera around the stipe (0), the presence of a new but incomplete ring of haptera (new haptera growing around part of the stipe, but not on all sides; [1]), the presence of a new ring of haptera with haptera growing on all sides (2).

Holdfast detachment force and break location

A third haptera removal manipulation (identical to the first and second manipulations; see above for details) was applied to all remaining individuals in July 2003. All plants were then pulled off the substratum to measure the force required to detach them. *L. setchellii* individuals were clamped at the base of the stipe (approx. 2-3 cm above the holdfast-stipe junction) using two small (1.5 cm) pipe clamps lined with a piece of fine grain sanding pad (1 cm thick foam pad with a non-slip surface) to prevent the clamps from slipping along the stipe. The two clamps were linked together by a piece of downrigger cable (75 Kg) to which was hooked a 500-N spring scale. A hand crank was used in line with the spring scale to pull on the samples, to ensure that all individuals were pulled at a constant rate. The hand crank was mounted on a platform that was easily moved around in the intertidal but that could be held in place by the weight of the person operating it. All samples were pulled in a direction parallel to the oncoming wave until detachment. The force required to detach each individual was recorded and whether the break occurred at the stipe, stipe/holdfast junction, holdfast or holdfast/substratum interface.

During each sampling period, three dynamometers were deployed at the site to measure maximum wave force, which was converted to maximum water velocity following Bell and Denny (1994). These data were correlated with data from the
Fisheries and Oceans Canada La Perouse Bank buoy (46206-48°50.1′N, 125°59.9′W) to obtain wave forces for the site during times when sampling did not occur. La Perouse Bank buoy was non-functional from September 2001 to the end of January 2002. I used significant wave height data from the South Brooks offshore buoy (46132-49°44.01′N, 127°55.0′W, located approx. 156 km north east of La Perouse Bank buoy), which are closely correlated to those of La Perouse Buoy \( (LP_{wh}=0.6225 \times SB_{wh}+0.5589, r=0.865, N=763, p<0.0001) \), to estimate significant wave height at La Perouse when data for this buoy were not available.

Data analysis

Survivorship of \textit{L. setchellii} was compared among haptera treatment groups in several ways. First, the proportion of tagged individuals surviving to each sampling date was calculated and plotted as a cumulative percentage to construct survival plots for each haptera treatment group. Second, a Kaplan-Meier analysis (Krebs, 1999) was used to determine the mean survival time of individuals for each haptera treatment group. Lastly, the Log Rank test (Collett, 1994) was used to compare survival times of \textit{L. setchellii} between haptera treatment groups.

The force required to detach \textit{L. setchellii} was compared among haptera treatment groups using a random block ANOVA (block: series of 4 individuals; factor: haptera treatment groups). Categorical data for haptera regeneration and holdfast growth were analyzed using Chi-square contingency table analyses. Normality and variance heterogeneity among treatments were tested using Kolmogorov-Smirnov and Cochran’s tests (Siegel and Castellan, 1988; Underwood, 1997). Data were transformed when necessary to meet these assumptions or, if this was not possible, a non-parametric statistical equivalent was used (Siegel and Castellan, 1988). All parametric and survival analyses were performed using the SPSS version 11 for Macintosh Statistical Software (SPSS Inc.), while non-parametric analyses were performed manually with the aid of a Microsoft® Excel spreadsheet.
5.3 Results

Flagging tape and tag losses

Tag and flagging tape loss was low. Two individuals out of 134 tagged ones lost both their tags and flagging tape. These individuals, however, were relocated using the reference map. Thus, overestimation of mortality due to tag loss was not a problem and correction of survival estimates not necessary.

Survival

Overall, the survivorship of *Laminaria setchellii* was high. Of the 114 individuals included in the experiment, 78 (68%) remained alive throughout the length of the experiment. Of the 36 (32%) individuals that died during the experiment, only 14 (39%) were dislodged from the substratum (these included both individuals that broke at the holdfast/substratum interface and ones that broke at the holdfast, usually leaving behind the tips of haptera). Other causes of mortality included grazing of the blade and stipe by amphipods, limpets and snails (28%), and stipe breakage (25%). Stipes that had snapped at the tag were recorded as tag mortality and accounted for 8% of mortalities. Only individuals that died due to dislodgement, i.e. detachment of the holdfast at the holdfast-substratum interface or due to holdfast/aptera breakage, were included in the survival analysis.

In the 18 months over which this experiment was conducted, there was no mortality due to dislodgement in the control group (Figure 5.4). In contrast, individuals that had damaged holdfasts (Sea, Sho, LW or LE) were more likely to be dislodged from the substratum (Log rank statistic=4.98, df=1, \( p=0.026 \)).

A detailed analysis showed that not all damaged holdfasts are as likely to be dislodged from the substratum and that damage in specific locations of the holdfast might not even jeopardize attachment (Tables 5.1 and 5.2). Individuals that were missing their LE haptera experienced no mortality, as was also the case for control individuals (Figure 5.5). LE survival (in excess of 18 months) was higher, although not significantly, than that of either seaward (16.74 ± 0.84 months) or shoreward (16.28 ± 0.74 months) hapteral treatment groups (Sea: log rank statistic=2.05, df=4, \( p=0.153 \); Sho: log rank statistic=2.81, df=4, \( p=0.094 \); Figure 5.5). The survival of seaward and
Figure 5.4. Kaplan-Meier estimates of survival functions for damaged (seaward, shoreward or lateral haptera removal treatment groups) and undamaged (control) Laminaria setchellii holdfasts.
Table 5.1. Survival comparison among control and haptera treatment groups. Log Rank statistic and (significance), df=4. Significant differences are highlighted in bold.

<table>
<thead>
<tr>
<th>Group</th>
<th>Control</th>
<th>Seaward</th>
<th>Shoreward</th>
<th>Lateral W</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seaward</td>
<td>4.25</td>
<td>(0.039)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shoreward</td>
<td>5.70</td>
<td>0.16</td>
<td>(0.691)</td>
<td>(0.991)</td>
</tr>
<tr>
<td></td>
<td>(0.017)</td>
<td></td>
<td>(0.017)</td>
<td>(0.691)</td>
</tr>
<tr>
<td>Lateral W</td>
<td>9.09</td>
<td>1.32</td>
<td>.50</td>
<td>(0.003)</td>
</tr>
<tr>
<td></td>
<td>(0.003)</td>
<td>(0.251)</td>
<td>(0.481)</td>
<td>(0.003)</td>
</tr>
<tr>
<td>Lateral E</td>
<td>0.00</td>
<td>2.05</td>
<td>2.81</td>
<td>4.57</td>
</tr>
<tr>
<td></td>
<td>(0.99)</td>
<td>(0.153)</td>
<td>(0.094)</td>
<td>(0.032)</td>
</tr>
</tbody>
</table>

Table 5.2. Mean survival times (months) and standard error (SE). Survival comparison among control and haptera treatment groups. Log Rank statistic and (significance), df=4.

<table>
<thead>
<tr>
<th>Treatment group</th>
<th>Mean survival time (months)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>18*a</td>
<td>b</td>
</tr>
<tr>
<td>Seaward</td>
<td>16.74</td>
<td>.84</td>
</tr>
<tr>
<td>Shoreward</td>
<td>16.28</td>
<td>.74</td>
</tr>
<tr>
<td>Lateral W</td>
<td>15.07</td>
<td>1.25</td>
</tr>
<tr>
<td>Lateral E</td>
<td>18*a</td>
<td>b</td>
</tr>
</tbody>
</table>

*a Survival estimate represents a lower bound of estimate.
b Standard error of survival estimate could not be computed since all observations are censored (endpoint of interest, death due to dislodgement, was not observed).
Figure 5.5. Kaplan-Meier estimate of survival functions for control (Cont) and hapteral removal treatment groups. Hapteral removal treatment groups consisted of seaward (Sea), shoreward (Sho), lateral W (LW) and lateral E (LE). LE survival function is identical to that of Cont; thus, LE survival function was staggered.
shoreward hapteral treatment groups did not differ between the two groups (log rank statistic=0.16, df=4, \( p=0.691 \)). In contrast, LW individuals tended to have the lowest survival of all groups (15.07 ± 1.25 months). Their survival, however, was not significantly different from that of seaward or shoreward hapteral treatment groups (Sea: log rank statistic=1.32, df=4, \( p=0.251 \); Sho: Log rank statistic=0.50, df=4, \( p=0.481 \); Table 5.1).

A detailed look at the dislodgment events indicated that size was likely not a factor in dislodgment. Dislodged individuals ranged in thallus size (thallus surface area) from 0.0064 to 0.0491 m\(^2\), with the majority of them (11 out of 14) having thalli smaller than 0.0276 m\(^2\) (Figure 5.6). However, mapping the location of dislodged individuals along the transect showed that a large number of dislodgement events (11 out of 14) clustered in the vicinity of topographical irregularities (tide pool, surge channel and rock wall; Figure 5.6).

**Haptera regeneration and holdfast growth**

*L. setchellii* can regenerate damaged haptera, but the rate at which they do so depends on the season. One month after the first haptera removal (February 2002), 38% of the individuals had started to regenerate the damaged haptera and 57% after two months (Figure 5.7). Three months after removal, 80% of the individuals showed signs of hapteral regeneration, ranging from the presence of haptera stubs (22%), through regeneration of a few haptera (26%) to a complete regeneration of the damaged haptera (32%). Individuals that had completely regenerated their damaged haptera were indistinguishable from control individuals. Regeneration after the second haptera removal (September 2002) was much slower (Figure 5.7). After four months, only 32% of the individuals showed signs of hapteral regeneration and only 2% had completely regenerated their haptera. Natural holdfast growth was also observed during the late winter and spring of 2002 (46% of individuals), but not during the fall of 2002. Holdfast growth consisted of the addition of a new ring of haptera at the base of the stipe, and was independent of hapteral regeneration.

Hapteral regeneration and holdfast growth occurred independently of the quadrant of haptera that was removed (k independent sample Chi-squared tests, \( p>0.05 \)).
Figure 5.6. Map of tagged *Laminaria setchellii* along the transect. Black-filled circles represent control group; wedges represent hapteral treatment groups, with wedge pointing in the same direction as the hapteral quadrant removed. Size of bubble around each data point represents individual thallus size (blade surface area m$^2$). Grey-filled bubbles represent dislodged individuals.
Figure 5.7. *Laminaria setchellii* haptera regeneration in response to seaward (Sea), shoreward (Sho), lateral 1 (L1) and 2 (L2) haptera removal; a) Spring regeneration 4 months after the first haptera removal (January 2002); b) Fall regeneration 3 months after the second haptera removal (September 2002).
**Wave Force**

Offshore significant wave height at La Perouse Bank and water velocity at Prasiola Point were closely correlated ($P_{\text{ave}}=1.197 \times \text{LP}_{\text{wht}} + 1.183$, $r=0.72$, $N=49$, $p<0.0001$; Figure 5.8), and thus was used to evaluate wave velocity patterns at Prasiola Point between sampling periods (Figure 5.9). While the total number of dislodged *L. setchellii* was low, the number of dislodged plants per sampling month was nonetheless correlated to the maximum water velocities encountered at Prasiola Point (Figure 5.9).

**Detachment force**

*L. setchellii* broke primarily at the holdfast (Chi-squared test, $\chi^2=76.57$, $N=105$, $p<0.001$; Figure 5.10). In half of the cases, small remnants of haptera or a larger part of the holdfast were left on the rock, while individuals that broke at the holdfast/substratum interface often detached with some of the underlying substratum (either rock or encrusting coralline algae). *L. setchellii*, rarely broke at the stipe, but when it did, it usually broke at the base of the stipe, close to the holdfast. Break location was independent of whether or not some of the haptera had been removed and of the quadrant of haptera that had been removed (Chi-squared test, $\chi^2=16.77$, $N=101$, $p>0.05$). The process of failure, that is, where the first sign of failure occurs in the holdfast, could not be determined even under close observation due to the rapidity at which detachment occurs.

The force required to detach *L. setchellii* from the rock ranged from 68 N to more than 500 N. In 11% of the samples, the spring scale reached its maximum extension (500 N) before the alga detached from the substratum, hence for these samples, the estimates of detachment force are conservative. Damaged holdfasts had a weaker attachment to the substratum than undamaged ones (haptera treatment groups pooled vs. control, student-\(t\) test, $t_{87}=4.183$, $p<0.0001$). A mean force of $330.7 \pm 24.3$ N was required to detach undamaged holdfasts from the substratum, while a mean force of $219.8 \pm 13.9$ N was required to detach damaged holdfasts. Detachment force also depended on the quadrant of haptera that had been removed (seaward, shoreward, lateral W or E; Table 5.3). The removal of seaward haptera significantly decreased the force required to detach an individual from the substratum compared to both control and
Figure 5.8. Relationship between offshore daily maximum significant wave height at La Perouse Bank Buoy (46°20.6'-48°50.1'N, 125°59.9'W) and daily maximum water velocity at Prasiola Point (48°49'4" N, 125°10'4" W), Barkley Sound, BC from January 2001 to November 2004 (PRAvel=1.830+1.197 x LPwht, r=0.720, N=49, p<0.0001).
Figure 5.9. a) Number of tagged *Laminaria setchellii* dislodged per sampling interval; b) Daily maximum water velocity (m/s) at Prasilo Point, Barkley Sound, BC from December 2001 to January 2004. Black arrows indicate date at which hapteral removal treatments were applied. First hapteral removal was applied in January 2002 (Jan 27-30) and the second in September 2002 (Sept. 6-8). Vertical dotted line indicates the end date of survival experiment (July 11-17, 2003).
Figure 5.10. Break location occurrences for *Laminaria setchellii* pulled off the substratum. Break locations are holdfast/substratum interface (HF/Sub), holdfast (HF), stipe (St). Frequencies of stipe breaks due to the tag artefacts or of individuals that exceeded the capacity of the scale are not illustrated. Frequency differences among break locations were significant, \( \chi^2 = 76.57, N = 105, p < 0.001 \).
Table 5.3. Results of random block ANOVA and Hochberg post hoc multiple comparisons analyses comparing the force it took to detach *Laminaria setchellii* from the substratum among control (Con, n=24), seaward (Sea, n=23), shoreward (Sho, n=19), lateral W and E (LW, n=10 and LE, n=13) haptera treatment groups. Significant differences are highlighted in bold.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type IV SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p-value</th>
</tr>
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<tbody>
<tr>
<td>Haptera removal treatment group</td>
<td>239122.03</td>
<td>4</td>
<td>59780.51</td>
<td>9.69</td>
<td>0.014</td>
</tr>
<tr>
<td>Block</td>
<td>445991.33</td>
<td>26</td>
<td>17153.51</td>
<td>2.78</td>
<td>0.129</td>
</tr>
<tr>
<td>Hapt treat x Block</td>
<td>551484.29</td>
<td>53</td>
<td>10405.36</td>
<td>1.69</td>
<td>0.295</td>
</tr>
<tr>
<td>Error</td>
<td>30859.28</td>
<td>5</td>
<td>6171.86</td>
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</table>

Hochberg post hoc test

<table>
<thead>
<tr>
<th></th>
<th>Sea</th>
<th>Sho</th>
<th>LW</th>
<th>LE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Con</td>
<td>182.46) a</td>
<td>79.23</td>
<td>40.30</td>
<td>61.68</td>
</tr>
<tr>
<td></td>
<td>(0.004)</td>
<td>(0.138)</td>
<td>(0.813)</td>
<td>(0.374)</td>
</tr>
<tr>
<td>Sea</td>
<td>-103.23</td>
<td>-142.16</td>
<td>-120.80</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.053)</td>
<td>(0.033)</td>
<td>(0.045)</td>
<td></td>
</tr>
<tr>
<td>Sho</td>
<td>-38.93</td>
<td>-17.57</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.856)</td>
<td>(0.997)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LW</td>
<td></td>
<td>21.36</td>
<td></td>
<td></td>
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<p>| | | | |</p>
<table>
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<tr>
<th></th>
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</thead>
</table>

a Mean difference [row-column] (significance)
Figure 5.11. *Laminaria setchellii*. Mean detachment force ± 1 SE (N) of control (Con) individuals and those with their seaward (Sea, n=), shoreward (Sho) or lateral W or E (LW or LE) haptera removed (see Material and Methods for details). Haptera treatment sharing a common letter are not significantly different, \( p>0.05 \). See Table 5.3 for sample sizes.
lateral treatment groups (Figure 5.11, Table 5.3). There was no significant difference between the force required to detach seaward and shoreward individuals from the substratum \((p=0.053)\); however, a larger sample size might reveal a significant difference. \(L.\ setchellii\) with holdfasts missing their shoreward haptera quadrant or one of their lateral haptera quadrants required slightly less force to be detached than control \(L.\ setchellii\), but the differences were not significant (Figure 5.11; Table 5.3).

5.4. Discussion

Previous studies have shown that, while wave-induced disturbance can have profound effects on macroalgal survivorship, macroalgae, especially kelps, have developed a number of strategies to contend with wave-generated forces. Most studies to date, however, have focused on variations in blade and stipe attributes that minimize or resist wave-induced stresses (Koehl and Wainwright, 1977; Biedka et al., 1987; Denny et al., 1989; Carrington, 1990; Shaughnessy et al., 1996; Blanchette et al., 2002). This study is unique in that it is the first attempt at investigating the mechanics of kelp holdfast anchorage and its relative importance for kelp survival.

The results of this study show that the holdfasts of the low intertidal stipitate kelp, \(Laminaria\ setchellii\) were attached very firmly to the substratum and that mortality due to wave dislodgement occurred infrequently. Dislodgment was generally associated with the occurrence of heavy storms with large waves and high water velocities. Plants with damaged holdfasts were more weakly attached to the substratum than undamaged ones, and thus were more likely to be dislodged during winter storms. Despite this, wave dislodgement remained low even for individuals with damaged holdfasts (Figure 5.4). While \(L.\ setchellii\) with damaged holdfasts are more vulnerable to wave dislodgement, their ability to quickly (during the fast growth season) and fully regenerate damaged haptera will decrease the risk of them being dislodged due to holdfast failure.

When \(L.\ setchellii\) was subjected to a natural regime of wave force (dynamic force), the seaward and shoreward hapteral removal groups both had significantly lower survival than control plants and lower, but not significantly so, survival than LE plants, which underwent no mortality. It is worth noting that the lack of significant differences between the survival of LE and seaward or LE and shoreward groups (even though LE incurred no mortality) can be explained by the difference in sample size \((n_{LE}=12, n_{sea}=28, n_{sho}=29)\). If we consider only these results, these suggest that the seaward-
shoreward hapteral quadrants, located parallel to the direction of oncoming waves, may play a more important role in the anchorage of the holdfast to the substratum than lateral quadrants, located perpendicular to the oncoming waves, supporting the hypothesis that anchorage asymmetry occurs. However, dislodgment events were few, and individual treatment sample sizes were overall small and differed among treatment groups, likely leading to non-significant differences among hapteral treatment groups. Furthermore, LW survival, which was the lowest of all, do not support this idea.

The results of the detachment experiment, in which *L. setchellii* were subjected to a static load, also seem to suggest that holdfast anchorage exhibits some asymmetry. The effects of removing a quadrant of haptera differed depending on its location around the stipe and its location with respect to the axis of bending. When *L. setchellii* was subjected to a static force, the seaward individuals required the least force to be detached from the substratum, more precisely 55% less force than to detach control plants. In contrast, the removal of lateral haptera quadrants (LW or LE) had little effect on holdfast attachment (required 12 and 19 % less force than controls), and the force to detach these did not differ from that of controls but was significantly greater than that of seaward treatment plants. The pattern is not as clear for shoreward haptera treatment plants. These required noticeably (but not significantly) more force than seaward plants before breaking off the substratum and were as strongly attached to the substratum as lateral (LW or LE) and control plants. These results suggest, in part, that haptera located perpendicularly to the axis of bending are not a major source of anchorage for *L. setchellii* when subjected to a static load. Under these loading conditions, the major source of anchorage for a *L. setchellii* holdfast is provided by the seaward haptera, which are held in tension, while the shoreward haptera subjected to compression stresses seems to be less important.

Results from both the survival experiment (dynamic loading) and the detachment experiment (static loading) suggest that anchorage asymmetry occurs in *L. setchellii* and that haptera located parallel to the axis of bending (seaward-shoreward direction in this case), particularly ones held in tension, are the major component resisting detachment from the substratum. These results, however, do not explain why LW hapteral treatment group underwent the greatest mortality when subjected to a natural hydrodynamic regime.
Several explanations could account for the unexpectedly high LW individual mortality as compared to control and other haptera treatment groups. A detailed look at the data reveals that of the six LW individuals that were dislodged, two individuals’ holdfast were burrowed through by the crab, *Oedignatus inermis*, and the other four individuals were located next to topographical features that may have altered the flow in their proximity. The presence of a crab burrow would clearly undermine the attachment of a holdfast to the substratum (See Chapter 3), resulting in quick dislodgement once the haptera removal manipulation was applied. In fact, both individuals with signs of crab damage were dislodged within a month of haptera removal. The micro-hydrodynamic patterns over the site were not studied in detail. It is clear though that the presence of a rock wall (to the east) onto which part of the surge was reflected and the presence of the two surge channels to the west of the site altered the flow. In fact, of the remaining four LW dislodgements, two of these were located close to the surge channel, the third one within half a meter of the rock wall, and the fourth one on the edge of a small depression. As a result, individuals in close proximity to these topographical irregularities were likely subjected to the eastward-westward forces as well as seaward-shoreward ones. In truth, eleven out of the fourteen dislodged individuals, irrespective of their treatment group, were located in the proximity of the tidepool/surge channels system (Figure 5.6), suggesting that flow velocities in the proximity of these topographical features might have differed in magnitude and direction than that flowing over the rest of the site.

This site was chosen because the presence of the tidepool and surge channels canalized to a certain extent the flow pattern over the site, resulting in a more or less uni-directional water movement up the slope, with most of the water exiting out through the surge channels as opposed to rushing back down the slope. However, as others (Bell and Denny, 1994; Duggins et al., 2003; Eckman et al., 2003) have observed and as I have observed in this study, the presence of topographical features such as rocky outcrops, surge channels and other small features can dramatically alter flow patterns at a site at small-scales (< 1m). Denny et al. (2003) demonstrated that water velocities experienced by organisms living in the intertidal can be greatly amplified due to the interaction of waves with the local topography. They showed that the jet generated by the collision of a wave and a rock promontory can have twice the velocity of the incident wave, and these velocities can be further enhanced (1.3 to 1.6 times) if the jet
encounters a rock wall or a surge channel. In fact, of the three dynamometers deployed at this site, one of the dynamometers (one to the east, closest to the rock wall) consistently recorded higher velocities than the other two. The intertidal likely represents more of a mosaic of microhabitats as opposed to a uniform flow environment (Bell and Denny, 1994).

While this study suggests that holdfasts exhibit anchorage asymmetry, small samples, low dislodgement events and high variability rendered few significant differences among haptera removal treatment groups. It must also be remembered that categorizing haptera as "seaward," "shoreward" or "lateral" is a generalization. While one wave direction may dominate at a site, local topographical features (see above) that alter water flow and alter the dynamic nature of wave action that subjects kelps to a backward-and-forward motion, will likely subject all haptera to both tensile and compressive forces at one point or another. Nevertheless, the use of this generalization and the study of holdfast mechanics under static and dynamic loading suggest that haptera resisting tensile stresses play an important role in securing the holdfast to the substratum. However, a more detailed investigation is needed before we understand how the need for anchorage influences the overall morphology of kelp holdfasts.

**Comparison with other algal taxa**

*L. setchellii*, in comparison to other algal taxa for which field attachment forces have been measured, is anchored exceptionally strongly to the substratum. It took, on average, 331 N (137 to upwards of 500 N) to detach the holdfast of *L. setchellii* from the substratum, whereas *Agarum fimbriatum*’s attachment force, for example, ranges between 18-36 N, *Costaria costata*’s between 20-47 N (Duggins et al., 2003), *Laminaria japonica*’s between 16-49 N (Kawamata, 2001) and *Hedophyllum sessile*’s 75-110 N (Milligan and DeWreede, 2000). These kelp species are comparable in size to *L. setchellii* (*A. fimbriatum*: thallus area 0.131 m²; *C. costata*: thallus area 0.062 m²; *L. japonica*: thallus area 0.091 m²; *H. sessile*: thallus area 0.146 m²; vs. *L. setchellii*: thallus area 0.064 m²). These kelps, with the exception of *H. sessile*, which is found in the mid to low intertidal, are found in the shallow subtidal and thus would be exposed to different flow dynamics than the population of *L. setchellii* sampled here. Up to date, only one kelp species, *Laminaria schinzii*, and one fucoid species, *Durvillaea antartica*, have been found to have a greater attachment to the substratum than that recorded in
this study for *L. setchellii*. It took on average approximately 526 N for *L. schinzii* and 1161 N for *D. antartica* to be removed from the substratum (Molloy and Bolton, 1996; Smith and Bayliss-Smith, 1998; Thomsen and Wernberg, 2005). These two species are however much larger than *L. setchellii* (*L. schinzii*: thallus area 1.7 m$^2$, up to 5 m in length; *D. antartica*: thallus area 9.7 m$^2$, up to 10 m in length) and would be subjected to much larger hydrodynamic forces than *L. setchellii* even though they are exposed to similar flow dynamics.

**Predicting dislodgement velocities and thallus size at dislodgement**

Dislodgement by waves will occur if the hydrodynamic forces imposed on the thallus of a *L. setchellii* exceed the force with which its holdfast is attached to the substratum. For a first approximation, I ignore lift and acceleration force because they are considered to be negligible for flexible intertidal organisms such as macroalgae (Gaylord et al., 1994; Gaylord, 2000) and consider solely drag force. The drag equation,

\[ F_d = \frac{1}{2} \rho A S_d U^\gamma \]

expresses drag force as a function of fluid density ($\rho$, 1025 kg m$^{-3}$ for seawater), the planform area (A) of the organisms (its maximal frontal area), the shape coefficient of drag ($S_d$), the fluid velocity relative to the organisms (U) and the velocity exponent ($\gamma$). By inserting the detachment force measured for *L. setchellii*, it is possible to calculate the theoretical water velocity that would be required to dislodge *L. setchellii* from the substratum. To estimate dislodgement velocities for *L. setchellii*, I used measurements of planform area (surface area) for both an average and a large bladed *L. setchellii* (Table 5.4). These measurements are representative of low intertidal *L. setchellii* in Barkley Sound (see Chapter 3). I used the average force required to detach *L. setchellii* with an undamaged holdfast (control: 330 N) and *L. setchellii* with a damaged holdfast (pooled hapteral removal treatment groups: 220 N). The shape coefficient of drag and the velocity exponent represent the tendency of a flexible organism to reconfigure and streamline with increases in flow (Gaylord et al., 1994; Gaylord and Denny, 1997; Gaylord, 2000). $S_d$ and $\gamma$ data were not measured for *L. setchellii*, but $S_d$ and $\gamma$ values have been published elsewhere (Gaylord and Denny, 1997). The theoretical water velocity...
required to dislodge *L. setchellii* from the substratum was estimated based on values of $S_d$ and $\gamma$ for *E. arborea*, values of $S_d$ and $\gamma$ for *P. californica* and based on their average values (Table 5.4). Given these numbers, dislodgement velocities were estimated to range between 33.6 to 114.5 m/s for an average sized and between 12.0 to 31.2 m/s for a large sized *L. setchellii* individual, depending on the values of $S_d$ and $\gamma$ used (Table 5.5). Predicted dislodgment velocities differ appreciably depending on what assumptions are made regarding *L. setchellii* reconfiguration characteristics (Table 5.5). *L. setchellii* with similar reconfiguration characteristics as *E. arborea* would require wave velocities 10 to 15 m/s slower to be dislodged from the rock than *L. setchellii* behaving more closely to *P. californica*. It is also interesting to note that damage to the holdfast has a much greater effect on dislodgement velocity for a *L. setchellii* assumed to behave closely to *P. californica* ($\Delta$Undamaged - damaged dislodgement velocity: 8.8 m/s for *P. californica*-like plants and 5.4 m/s for plants with average reconfiguration characteristics) than ones assumed to behave similarly to *E. arborea* (3.6 m/s). Water velocities of 10 to 25 m/s have been recorded in the intertidal during heavy storm on open ocean shores (Denny et al., 2003).

Until recently, water velocities greater than 25 m/s had not been recorded except as associated with rare events such as Tsunami waves (Mishra and Rajasekhar, 2005; Schiermeier, 2005). These velocities, however, remain below the velocities and accompanying forces required to explain the pattern of size distribution and mortality observed in the intertidal (Denny and Gaylord, 2002; Denny et al., 2003). As Denny et al. (2003) have shown, flow patterns in the intertidal can be chaotic, and flow amplification associated with topographical features may explain some of the discrepancies found between observed and predicted dislodgement events.

Using long-term buoy data from La Perouse Bank dating from 1989 to 2004, I estimated the average daily water velocity at Prasiola Point to be approximately 5 m/s. Dislodgement events, however, are more likely to be the result of unusual high water velocities that are associated with large winter storms (Seymour et al., 1989). The largest maximum daily water velocities experienced at Prasiola were estimated (based on La Perouse Bank Buoy data) to be as high as 19 m/s. Drag forces imposed by such waves would result in the dislodgement of the largest thalli of *L. setchellii*, especially ones with damaged holdfasts that behave similarly to *E. arborea* or that have average reconfiguration characteristics (Table 5.5). However, average sized *L. setchellii*
### Table 5.4. Morphological and drag parameters used to estimate dislodgment velocity for *Laminaria setchellii*.

<table>
<thead>
<tr>
<th>Morphological parameters</th>
<th>Thallus size (blade surface area)</th>
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<td></td>
<td>Average blade</td>
<td>0.0451 m²</td>
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<td></td>
<td>Large blade</td>
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</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Drag parameters</th>
<th><em>Eisenia arborea</em>&lt;sup&gt;a&lt;/sup&gt;</th>
<th><em>Pterygophora californica</em>&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><strong>S&lt;sub&gt;d&lt;/sub&gt;</strong></td>
<td>0.041</td>
<td>0.042</td>
</tr>
<tr>
<td></td>
<td><strong>&lt;sup&gt;Y&lt;/sup&gt;</strong></td>
<td>1.55</td>
<td>1.23</td>
</tr>
</tbody>
</table>

<sup>a</sup> Gaylord and Denny (1997)

### Table 5.5. Estimates of the velocity required to dislodge *Laminaria setchellii* with undamaged (control) and damaged (pooled hapteral removal treatment groups) holdfasts. Average force to detach *L. setchellii* with undamaged holdfasts is 330 N and with damaged holdfasts is 220 N. Calculations are based on equation 1 and Table 5.4 parameters.

<table>
<thead>
<tr>
<th></th>
<th>Velocity (m/s)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Thallus size</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>average</td>
<td>large</td>
<td></td>
</tr>
<tr>
<td>a) based on average S&lt;sub&gt;d&lt;/sub&gt; and &lt;sup&gt;Y&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Undamaged holdfast</td>
<td>66.9</td>
<td>21.2</td>
</tr>
<tr>
<td>Damaged holdfast</td>
<td>49.9</td>
<td>15.8</td>
</tr>
<tr>
<td>b) based on <em>E. arborea</em> S&lt;sub&gt;d&lt;/sub&gt; and &lt;sup&gt;Y&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Undamaged holdfast</td>
<td>43.7</td>
<td>15.6</td>
</tr>
<tr>
<td>Damaged holdfast</td>
<td>33.6</td>
<td>12.0</td>
</tr>
<tr>
<td>c) based on <em>P. californica</em> S&lt;sub&gt;d&lt;/sub&gt; and &lt;sup&gt;Y&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Undamaged holdfast</td>
<td>114.5</td>
<td>31.24</td>
</tr>
<tr>
<td>Damaged holdfast</td>
<td>82.2</td>
<td>22.4</td>
</tr>
</tbody>
</table>
(with or without damage to their holdfast) and large sized P. californica-like individuals would remain securely attached to the rock.

If we adjust this value of water velocity by a factor of 3.5 to include the potential amplification effect of small-scale topography, it would result in localized flow speeds of 66.5 m/s. Using equation 1, Table 5.4 and an average force of 330 N and of 220 N to dislodge intact and damaged holdfasts, one can predict the size of the smallest L. setchellii that would be dislodged from the substratum assuming that velocity amplification occurs. Water velocities in the range of 66.5 m/s would put at risk of dislodgement any intact L. setchellii with a thallus surface area larger than 0.023 m² (for Eisenia-like individuals), 0.088 m² (for P. californica-like individuals). L. setchellii with damaged holdfasts and thalli as small as 0.016 m² (E. arborea-like indiv.) and 0.059 m² (P. californica-like indiv.) would be at risk of being dislodged.

The same sensitivity analysis can be carried out for more commonly encountered wave velocities such as that associated with late fall and winter storms. On the West Coast of British Columbia, hurricane force storms are common in the late fall and winter and are generally associated with seas of 8 to 10 m high (West Coast Island South, Environment Canada data), which would be equivalent to wave velocities of 10.8 m/s to 13.1 m/s at Prasiola Point. Using a value of 12 m/s, I calculated the size of the smallest L. setchellii that would be dislodged during such a storm (Table 5.6). Given this, I would expect after a severe storm that the largest intact L. setchellii thalli remaining to be smaller than 0.048 m² (for E. arborea-like indiv.) and 0.115 m² (for P. californica-like indiv.).

Storm waves with velocities approaching 19 m/s do not occur frequently (once between 1989 and 2004). However, during this particular storm, which occurred in January 1997, maximum significant wave height >6 m (reaching up to 11 m high waves) were recorded for 14 consecutive hours. Wave velocities > 12 m/s were observed more often during the 15 yrs period and accounted for 24% of daily observations. Thus, while L. setchellii is firmly attached to the shore, large thallus area individuals are likely to be exposed over their lifespan (as old as 17 yrs for some populations; Klinger and DeWreede, 1988) to wave velocities high enough to cause dislodgement, especially if their holdfast integrity has been jeopardized. Moreover, if the potential for velocity amplification resulting from the interaction of flow and shore topography is considered,
L. setchellii with thallus size much smaller than the large thallus sized individuals could be at risk of dislodgement.

Mass mortality of other kelp species due to wave dislodgement has also been associated with the occurrence of unusually severe fall and winter storms and concomitant large waves (Dayton, 1975; Seymour et al., 1989). The occurrence of severe storms and concurrent high water velocities associated with weather anomalies such as ENSO events are predicted to increase in frequency and intensity with climate change (Bacon and Carter, 1991; Trenberth, 1993; Wellington and Dunbar, 1995; Mcphaden, 1999) and may become a more serious cause of severe mortality events for L. setchellii and kelps in general.

These estimates of dislodgment velocities indicate that L. setchellii is well designed to resist the hydrodynamic forces imposed even by very large waves and predict that subsequent dislodgement should be rare unless flow amplification is considered. It should be emphasized, however, that these dislodgement velocities are estimates only, based on the thallus response to flow of two subtidal kelps, P. californica and E. arborea, that are similar to L setchellii in that these three species have long, woody stipes but these likely differ in their biomechanics. Estimates of dislodgment velocities should be further refined by applying size, form and flow specific drag coefficients obtained for L. setchellii to substantiate these estimates.

Despite the strong attachment provided by the holdfast, the results of this study shows that damage to the holdfast of L. setchellii can have significant consequences for its survival. L. setchellii with damaged holdfasts were more likely to be dislodged by waves (Figure 5.3) and required, on average, 33% less force to be detached from the substratum than undamaged ones. Further, estimates of dislodgement water velocity indicate that plants with damaged holdfasts could be dislodged by measurably slower waves than intact holdfasts (see above). While it is well known that the holdfasts of kelps host a diverse invertebrate fauna (Ojeda and Santelices, 1984; McLay and Hayward, 1987; see Chapter 1), the subsequent effects on holdfast integrity, attachment forces and survival of the kelp have rarely been documented (Tegner et al., 1995).

Holdfast cavitation has been used mostly to refer to the burrowing activity of sea urchins that find refuge in the holdfast of kelp, leading eventually to its structural failure (Tegner et al., 1995; Rios et al., 2003). The holdfasts of L. setchellii and other intertidal
Table 5.6. Estimates of the smallest *Laminaria setchellii* thallus (blade surface area m²) that would be predicted to be dislodged by the maximum estimated wave velocity encountered at Prasiola Point during 1989-2004 (19 m/s) and for a water velocities commonly encountered during late fall and winter storms (12 m/s) assuming that water velocities are amplified by a factor of 3.5 by topographical features (see text for further explanations). Average force to detach *L. setchellii* with an undamaged holdfast is 330 N and with a damaged holdfast is 220 N. Calculations are based on equation 1 and Table 5.4 parameters.

<table>
<thead>
<tr>
<th>Velocity (m/s)</th>
<th>Thallus size (m²)</th>
<th>12</th>
<th>19</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>a) based on average S_d and γ</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Undamaged holdfast</td>
<td>0.086</td>
<td>0.045</td>
<td></td>
</tr>
<tr>
<td>Damaged holdfast</td>
<td>0.057</td>
<td>0.030</td>
<td></td>
</tr>
<tr>
<td><strong>b) based on <em>E. arborea</em> S_d and γ</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Undamaged holdfast</td>
<td>0.048</td>
<td>0.023</td>
<td></td>
</tr>
<tr>
<td>Damaged holdfast</td>
<td>0.032</td>
<td>0.016</td>
<td></td>
</tr>
<tr>
<td><strong>c) based on <em>P. californica</em> S_d and γ</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Undamaged holdfast</td>
<td>0.155</td>
<td>0.088</td>
<td></td>
</tr>
<tr>
<td>Damaged holdfast</td>
<td>0.103</td>
<td>0.059</td>
<td></td>
</tr>
</tbody>
</table>
kelps such as *Hedophyllum sessile* are more commonly inhabited by the soft abdomen crab, *Oedignathus inermis* (unpublished data). *O. inermis*’ burrowing activity can substantially reduce the surface of attachment to the substratum of a *L. setchellii* holdfast, effectively increasing its vulnerability to dislodgement by waves (Chapter 3). While few *L. setchellii* holdfasts showed signs of cavititation at Prasiola Point, up to 81% of the holdfasts collected at Seppings, a nearby site of greater wave exposure, were burrowed through by *O. inermis*. This suggests that holdfast damage could potentially be an important source of mortality for *L. setchellii* but that its effects will be site-specific. Dislodgement might also be increased due to substratum failure. Milligan and DeWreede (2000) suggested that coralline algae under large *H. sessile* holdfasts showed signs of bleaching and degradation, increasing the risk of dislodgement by substratum failure. *L. setchellii* at Prasiola Point were commonly found growing on crustose coralline algae and onto the test of barnacles at more wave-exposed sites in Barkley Sound (see Chapter 3). Holdfast attachment in the Fucales and some of the Laminariales is achieved by the combined action of mucilage stickiness, rhizoid penetration of micropores in the substratum and haptera interlocking with the substratum contour (Tovey and Moss, 1978; Roscoe and Walker, 1995), and it has been suggested that *Fucus vesiculosus* exude an acidic substance that partially digest calcareous material (Barnes and Topinka, 1969). This may explain, at least in part, the common occurrence (28%) of substratum failure in *L. setchellii* and other kelps and macroalgae (Barnes and Topinka, 1969; Grace, 1999; Milligan and DeWreede, 2000). This would suggest that the mechanisms by which kelps attach to the substratum may, in part, accelerate substratum degradation and substratum failure.

**Regeneration**

*L. setchellii* with damage to their holdfasts can effectively heal and regenerate damaged haptera, thereby reducing the likelihood of being dislodged. However, its ability to do so is seasonal. The process of wound-healing and regeneration has been studied in detail in several fucoid species (Moss, 1964a; b; Fagerberg and Dawes, 1976). While wound-healing and regeneration are also known to occur in several species of kelps, much less is known about the process, and studies have mostly focused on the regenerative ability of blade and stipe (Setchell, 1905; DeWreede et al., 1992), with the exception of one study (Markam, 1968) showing that portions of
Laminaria sinclairii haptera could produce outgrowths, giving rise eventually to entirely new plants.

The seasonality of wound-healing and tissue-regeneration observed in L. setchellii has also been reported in other species of brown algae (Setchell, 1905; Moss, 1964a; Fagerberg and Dawes, 1976). The decreased ability of L. setchellii to regenerate damaged haptera coincides with short daylength, decreased overall growth and the peak of the reproductive phase (Klinger, 1984; Dieck, 1991). The lack of hapteral regeneration during the autumn is likely the result of a decrease in photosynthetic activity and thus of available photosynthates for growth and increased energy allocation to reproduction. The greatest response in hapteral regeneration occurred from February through May, and coincided with the time during which L. setchellii undergoes rapid new-growth, leading to the formation of a brand new haptera ring.

Conclusions

L. setchellii is very firmly attached to the substratum. Its flexibility allows it to bend with the flow, effectively lowering the forces imposed on its thallus, and its strong holdfast allows it to remain attached to the substratum. As a result, healthy L. setchellii subjected to large hydrodynamic waves may suffer mortality more frequently as a result of stipe breakage (9 individuals out of 114 broke at the stipe) than as a result of holdfast dislodgement (none of the control holdfasts were dislodged). Nevertheless, mortality due to dislodgement does occur. L. setchellii individuals are commonly found washed up on the shore following winter storms (pers. obs.). Damage to the holdfast of L. setchellii significantly decreased survival and the force required for dislodgment. While sometimes the likely cause of dislodgement is clear (the presence of crab burrows in the holdfast or attachment to barnacles rather than to a rocky substratum), other cases are not as obviously explained. Understanding the mechanics of kelp holdfast anchorage will not only allow us to better understand how these organisms can so firmly remain anchored to the rock on wave-swept shores, but it may also shed some light on the functional reasons behind the diversity in holdfast systems observed in macroalgae.
5.5 References


Tovey, D.J., Moss, B.L., 1978. Attachment of haptera of *Laminaria digitata* (Huds) Lamour. Phycologia 17, 17-22.


Chapter 6 Conclusions

Kelp species represent the largest and structurally most complex of the brown algae, and are the most prominent constituents of the lower intertidal and subtidal zones of temperate and subpolar rocky shores (Lobban and Harrison, 1994; Mann and Chapman, 1975). As canopy and sub-canopy species, they form dense beds, or 'kelp forests', that support a rich understory flora and fauna. Worldwide, kelp forests have been described as the most ecologically dynamic and biologically diverse habitats on the planet (Birkett, et al., 1998; Dayton, 1985; Graham, et al., 2003; Mann, 1973). Kelp species have also been referred to as *Keystone* species, *Foundation* species and *Ecosystem engineers* (Dayton, 1975; Graham, 2004; Mann, 1982; Vasquez, et al., 2006). They are major contributors to coastal primary production, and the highly structured three-dimensional habitat they form provides sites for settlement, early development and refuge for a wide diversity of understory algae, invertebrates, fish, and mammals, many of which are economically important. Furthermore, a significant amount of detritus produced by kelp forests is exported to nearshore aquatic habitats and terrestrial ecosystems (Graham, et al., 2003). Kelps appear particularly well adapted to survive the harshness of wave-swept shores and, by doing so, likely contribute to sustaining the high diversity and productivity of coastal ecosystems.

The main objective of this research was to assess the role played by the holdfasts of kelps in structuring macroalgal populations and influencing the dynamics of kelp communities. In Chapter 2, I examined the role played by kelp holdfasts in facilitating the recruitment of juvenile conspecifics. The results of this chapter showed that the holdfast of *Hedophyllum sessile* (hereafter *Hedophyllum*) plays a crucial role in the recruitment dynamics of *Hedophyllum* in the intertidal zone of Barkley Sound, BC. Recruitment of this intertidal kelp is substratum-specific and occurs predominantly on topographically complex substrata such as the holdfasts of conspecific adults and the
turs of articulated coralline algae. The mechanism(s) by which recruitment is facilitated by the adult holdfasts and articulated coralline turfs is yet to be identified; however, it is clear that substratum suitability is dependent on the structural complexity of the substratum and how the three-dimensional structure of a substratum interacts with the environment to alter abiotic and biotic conditions. It is also clear that the canopy cover provided by the blades of adult *Hedophyllum* can have a positive or negative influence on juvenile recruitment, depending on the type of substrata. These results indicate that the persistence of *Hedophyllum* populations through recruitment will largely depend on the availability of topographically complex substratum. Moreover, the rate of recovery following severe stochastic disturbances, such as El Niño events, which are associated with a dramatic reduction in kelp canopy cover, is likely increased by the availability of adult *Hedophyllum* holdfasts.

The three-dimensional matrix created by the holdfast of adult *Hedophyllum* and the turfs of articulated coralline algae share similarities, and as a result, likely alter the understory abiotic and biotic conditions in similar ways to create a favourable microhabitat for juvenile kelp recruitment. However, canopy cover affects holdfast and turf microhabitats in opposite ways, suggesting that the mechanism(s) by which these substrata create favourable recruitment microhabitats differs in some ways. Future research should focus on identifying the mechanism(s) and their relative contributions to the recruitment dynamics of *Hedophyllum*.

In the second part of this thesis (Chapters 3-5), I investigated the functional morphology of the holdfast of the stipitate kelp, *Laminaria setchellii*. The impetus for this research was to understand the mechanics of kelp holdfast anchorage systems, i.e. how the hydrodynamic forces imposed on the upper thallus are transmitted to the holdfast and substratum, and to shed light on the functional reasons behind the diversity in holdfast systems observed in macroalgae. While the macrofauna of kelp holdfasts has been well studied, much less is known of the holdfast itself, how it develops and attaches to the substratum, and how it responds to exposure to increased wave action. The type and magnitude of the stresses with which a holdfast has to contend depend largely on the type and magnitude of the forces imposed on the thallus. Thus, I focused my studies to investigate how changes in hydrodynamic conditions affect the morphology and attachment mechanics of the holdfast in relation to the rest of the thallus.
In Chapter 3, I investigated the morphological and biomechanical plasticity of the low intertidal stipitate kelp, *Laminaria setchellii*, along a wave exposure gradient. As is commonly the case with macroalgae, *L. setchellii* exhibits morphological variation with varying wave exposure; this suggests that individuals are well adapted to the flow regime in which they occur. Plants at wave-sheltered sites have longer blades of greater surface area and have smaller holdfasts, while plants at wave-exposed sites have smaller blades and larger holdfasts. I found a lack of concurrency between holdfast size, attachment and wave-exposure. I also found the crab *Oedignathus inermis* and barnacle tests within *L. setchellii* holdfasts at wave-exposed sites. These observations suggest that *L. setchellii* growing at wave-exposed sites may grow a larger holdfast in response to its weakening due to both the burrowing of *O. inermis* and to the friability of the barnacle tests to which the holdfast is attached. A direct comparison between intact holdfasts and crab-damaged or barnacle-weakened holdfasts at wave-exposed sites would confirm this possibility. Unfortunately, intact holdfasts were few and prevented such comparison for this study. Pursuing this line of investigation may shed some light as to why an overwhelming number of macroalgal species, in particular kelps, seem to be over-engineered, having a holdfast that is much larger and much stronger than required given the wave regime to which they are exposed. The morphological and biomechanical inconsistencies I reported in this study, which resulted from the indirect interaction of wave exposure with herbivory, emphasize the fact that wave exposure cannot be seen as entirely separate from other processes. The indirect effects of wave exposure on biological factors such as herbivory may override its direct effect on algal morphology and mortality.

The results presented in Chapter 4 show that stipitate kelps such as *L. setchellii* exhibit asymmetry with respect to the flow to which they are exposed. Two forms of asymmetry are distinguished, lateral asymmetry (cross-sectional shape of the stipe) and longitudinal asymmetry (cross-sectional size or taper). Changes in the direction of lateral asymmetry along the length of the stipe reaffirm the trade-off macroalgae are faced with: avoiding large hydrodynamic forces while maximizing light and nutrient capture, and propagule dispersal, which in the case of stipitate kelps means staying upright. More importantly, the presence and switch of lateral asymmetry and the tapering of the stipe suggest that biomechanical models of stipitate kelps based on a cylindrical beam may not be an accurate reflection of the mechanical behaviour of these
kelps under loading. Future work should examine the asymmetry of the stipe in relation to its mechanical properties to understand more clearly the dynamic response of *L. setchellii* under load and to evaluate the magnitude of the stresses that are transferred to the holdfast and substratum.

Lastly, in Chapter 5, I evaluate the consequences of holdfast asymmetry for anchorage mechanics and individual survivorship. Over a period of a 1.5 years no mortality due to wave dislodgement was recorded for *L. setchellii* with intact holdfasts (controls), while experimental plants with a quarter of their holdfasts removed showed 20% mortality due to wave dislodgement. These results indicate that intact *L. setchellii* is anchored very firmly to the substratum. Furthermore, the holdfasts of *L. setchellii* exhibit some anchorage asymmetry and attachment is largely due to haptera resisting stress in tension. Given a more or less uni-directional orientation of high forces associated with breaking waves, seaward haptera would fulfill that role. However, topographical irregularities in the intertidal may alter flow velocity and direction, exposing individuals to waves from unpredictable directions. The results of this study suggest that only the highest winter storm waves, subjected to wave amplification due topographic irregularities, are likely to dislodge *L. setchellii* from the rock. Dislodgment does occur nonetheless and cannot always be attributed to the interaction between flow and biological factors (crabs, substratum failure). Are the holdfasts of kelps over-engineered or are our models over-simplified? The measurement of attachment forces by pulling individuals from the substratum by mean of a spring scale disregard the dynamic component of holdfast attachment. Understanding the role of repeated exposure to sub-maximal forces, tissues fatigue, and the mechanisms that regulate tissues allocation and repair will likely have important implications for kelp dislodgement.

Like most research projects, this one raises further questions, and the answers it provides open the stage for more detailed experiments examining the dynamics of kelp holdfast anchorage. It also highlights the need for a multidisciplinary approach linking what one knows of the natural history and ecology of an organism to aspects of tissue growth and remodeling, material science and hydrodynamics. It also reaffirms the need to look outside the ‘quadrat’ and the importance of interactive effects between biological and physical factors in explaining observed patterns.
6.1 References


### Table A.1. Understory algal and invertebrate organisms present as potential substratum for *Hedophyllum sessile* recruitment.

<table>
<thead>
<tr>
<th>Substratum category</th>
<th>Phylum</th>
<th>Species</th>
<th>Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bare rock (BR)</td>
<td>--</td>
<td>--</td>
<td>A</td>
</tr>
<tr>
<td>Articulated corallines (AC)</td>
<td>Rhodophyta</td>
<td></td>
<td>A&lt;sup&gt;5&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Corallina vancouveriensis</em></td>
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<td></td>
<td></td>
<td><em>Bossiella plumosa</em></td>
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<tr>
<td></td>
<td></td>
<td><em>Calliarthron tuberculosum</em></td>
<td></td>
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<tr>
<td>Coralline crusts (CC)</td>
<td>Rhodophyta</td>
<td></td>
<td>A&lt;sup&gt;5&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Lithophyllum sp.</em></td>
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<tr>
<td></td>
<td></td>
<td><em>Lithothamnion sp.</em></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td><em>Pseudolithophyllum spp.</em></td>
<td></td>
</tr>
<tr>
<td>Fleshy crusts (FC)</td>
<td>Rhodophyta</td>
<td></td>
<td>A&lt;sup&gt;5&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Hildenbrandia sp.</em></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td><em>Petrocellis</em> tetrasporophytic stage of <em>Mastocarpus papillatus</em></td>
<td></td>
</tr>
<tr>
<td>Kelp Holdfast (HF)</td>
<td>Heterokonphyta</td>
<td><em>Ralfsia</em> sp.</td>
<td>A</td>
</tr>
<tr>
<td>Others</td>
<td>Rhodophyta</td>
<td><em>Polysiphonia senticulosa</em></td>
<td>C</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Porphyra</em> spp.</td>
<td>U</td>
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<tr>
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<td></td>
<td><em>Cryptopleura</em> sp.</td>
<td>C</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Calithamnion pikeanum</em></td>
<td>U</td>
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<tr>
<td></td>
<td></td>
<td><em>Microcladia coulteri</em></td>
<td>U</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Microcladia borealis</em></td>
<td>C</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Mazzaella splendens</em></td>
<td>C</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Mastocarpus papillatus</em></td>
<td>C</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Odonthalia floccosa</em></td>
<td>C</td>
</tr>
<tr>
<td>Chlorophyta</td>
<td></td>
<td><em>Ulva</em> spp.</td>
<td>C</td>
</tr>
<tr>
<td>Magnoliophyta</td>
<td></td>
<td><em>Enteromorpha</em> spp.</td>
<td>C</td>
</tr>
<tr>
<td>Porifera</td>
<td></td>
<td><em>Codium setchellii</em></td>
<td>U</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Phyllospadix scouleri</em></td>
<td>U</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Haliclona permollis</em></td>
<td>C</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Halichondria panicea</em></td>
<td>C</td>
</tr>
<tr>
<td>Substratum category</td>
<td>Phylum</td>
<td>Species</td>
<td>Abundance</td>
</tr>
<tr>
<td>--------------------</td>
<td>-------------</td>
<td>--------------------------------</td>
<td>-----------</td>
</tr>
<tr>
<td>Cnidaria</td>
<td>Anthopleura elegantissima</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td>Annelida</td>
<td>Dodecaceria concharum</td>
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<tr>
<td>Bryozoa</td>
<td>Flustrellida corniculata</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td>Mollusca</td>
<td>Calliostoma ligatum</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Vetulina sp.</td>
<td>C</td>
<td></td>
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<tr>
<td></td>
<td>Lacuna spp.</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Katharina tunicata</td>
<td>A</td>
<td></td>
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<tr>
<td></td>
<td>Acmea mitra</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lottia pelta</td>
<td>A</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tectura scutum</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Unidentified juvenile limpets</td>
<td>A</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tonicella lineata</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mopalia lignose</td>
<td>U</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lepidochitona dentiens</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cryptochiton stelleri</td>
<td>U</td>
<td></td>
</tr>
<tr>
<td>Arthropoda</td>
<td>Pollicipes polymerus</td>
<td>U</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Chthalamus dalli</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td>Echinodermata</td>
<td>Pisaster ochraceus</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Leptasterias hexactis</td>
<td>U</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Strongylocentrotus purpuratus</td>
<td>U</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cucumaria pseudocurata</td>
<td>A</td>
<td></td>
</tr>
<tr>
<td>Urochordata</td>
<td>Unidentified species of colonial tunicates</td>
<td>C</td>
<td></td>
</tr>
</tbody>
</table>

\(a\) Herbivorous species;

\(b\) A= abundant; C= common; U= uncommon; Most uncommon species encountered in the permanent quadrats are common in other zones;

\(\$\) Relative abundances of each species in substratum categories "AC", "CC", and "FC" were not quantified in the field.
Figure B.1. Locations of the five study sites along the Southeast shores of Barkley Sound, Vancouver Island. Bordelais Is. (Bor), Seppings Is. (Sep), Prasiola Point (Pra), Eagle Bay (Eag), and Dixon Is. (Dix). Open arrow indicates the direction of prevalent winds and swells into the Sound. Star indicates the location of the Bamfield Marine Sciences Centre (BMSC).
Table B.1. Detailed description of five study sites located on the southeast edge of Barkley Sound, B.C. See Figure A.3.2

<table>
<thead>
<tr>
<th>Site name</th>
<th>Abbrev.</th>
<th>Location (Lat. Long.)</th>
<th>Descriptions and comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bordelais Is.</td>
<td>Bor</td>
<td>48° 49.108' N, 125° 13.875' W</td>
<td>Shore is steep (θ &gt; 40°), aspect WNW, continuous bedrock</td>
</tr>
<tr>
<td>Seppings Is.</td>
<td>Sep</td>
<td>48° 50.309' N, 125° 12.421 W</td>
<td>Shore is steep (θ &gt; 40°), aspect W, continuous bedrock</td>
</tr>
<tr>
<td>Prasiola Pt.</td>
<td>Pra</td>
<td>48° 49.074' N, 125° 10.007' W</td>
<td>Shore is gently sloping (θ &lt; 20°), aspect NW, continuous bedrock</td>
</tr>
<tr>
<td>Eagle Bay</td>
<td>Eag</td>
<td>48° 50.068' N, 125° 08.840' W</td>
<td>Shore is steep (θ &gt; 40°), aspect NW, continuous bedrock</td>
</tr>
<tr>
<td>Dixon Is.</td>
<td>Dix</td>
<td>48° 51.102' N, 125° 07.394' W</td>
<td>Shore is shallow to steep (20° &lt; θ &gt; 40°), aspect SW, continuous bedrock</td>
</tr>
</tbody>
</table>
Figure B.2. Maps of the five study sites showing details of intertidal and depth contour of surrounding waters. Sites are (from left to right and top to bottom) Bordelais Is., Seppings Is., Prasiola Point, Eagle Bay and Dixon Is. Star indicates the location of the Bamfield Marine Sciences Centre (BMSC). North is towards top of page.
Appendix C

Table C.1. *Laminaria setchellii*. Relationship between morphological properties (blade maximum length [cm], blade surface area [cm$^2$], stipe length [cm], holdfast surface area [cm$^2$], holdfast biomass[g]), biomechanical properties (removal force [N], removal strength [Nm$^{-2}$]) and age (number of annual growth rings). Best-fit slopes, intercepts, for each regression. Significant relationships ($p<0.05$) are highlighted in bold.

<table>
<thead>
<tr>
<th>Site</th>
<th>n</th>
<th>Slope</th>
<th>Intercept</th>
<th>$r^2$</th>
<th>$p$</th>
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<td><strong>Age vs. blade length</strong></td>
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<tr>
<td>Bordelais</td>
<td>53</td>
<td>2.38</td>
<td>39.72</td>
<td>0.03</td>
<td>0.202</td>
</tr>
<tr>
<td>Seppings</td>
<td>31</td>
<td>1.32</td>
<td>45.64</td>
<td>0.04</td>
<td>0.282</td>
</tr>
<tr>
<td>Prasiola</td>
<td>89</td>
<td>2.24</td>
<td>22.54</td>
<td>0.03</td>
<td>0.102</td>
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<tr>
<td>Eagle Bay</td>
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<td>4.48</td>
<td>40.33</td>
<td>0.08</td>
<td>0.060</td>
</tr>
<tr>
<td>Dixon</td>
<td>42</td>
<td>5.29</td>
<td>14.26</td>
<td>0.18</td>
<td>0.005</td>
</tr>
<tr>
<td><strong>Age vs. blade surface area</strong></td>
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<tr>
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<tr>
<td><strong>Age vs. stipe length</strong></td>
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<tr>
<td>Bordelais</td>
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<td>$&lt;$0.001</td>
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<tr>
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<td>18.82</td>
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<tr>
<td><strong>Age vs. holdfast surface area</strong></td>
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<tr>
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<tr>
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<td><strong>Age vs. holdfast biomass</strong></td>
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<tr>
<td>Bordelais</td>
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<td>4.05</td>
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</tbody>
</table>

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Figure D.1. Beach casts. a) *Laminaria setchelli*, *Pterygophora californica* and *Lessoniopsis littoralis* clump attached to the tests of dead barnacles; b) Close-up of the inside of one of the barnacle test, showing haptera penetrating through the aperture of the test and attaching to its inside walls; c) Underside of the holdfast of *P. californica*. Note outer layer of haptera that were attached to the substratum and inner cavity; d) Underside of the holdfast of *P. californica*. Note outer ring of haptera, inner cavity and inner ring of regenerating haptera (r.h.; light brown).