EFFECTS OF WAVE-EXPOSURE ON AN INTERTIDAL KELP SPECIES

HEDOPHYLLUM SESSILE (C. AGARDH) SETCHELL:

DEMOGRAPHICS AND BIOMECHANICS

by

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ABSTRACT

Our understanding of how wave-exposure affects a macroalgal species’ ecology is not predictive since it is unknown how the species interacts with its physical environment and the ultimate effects on recruitment or mortality rates. This thesis investigates wave-exposure effects on the population ecology of the intertidal kelp species *Hedophyllum sessile* by a series of demographic and biomechanical field experiments and physical modeling of survivorship.

Sporophyte recruitment, survivorship, and reproductive output were measured at sites of different exposure in Barkley Sound, British Columbia. Site exposures were different when offshore daily significant wave heights exceeded 2.1 m, usually during fall and winter months. Important conclusions are: (1) Recruitment is not dependent on exposure, but is different between years and substratum types, with more recruitment on articulated coralline algae; (2) The theoretical trade-off between thallus size-minimization to reduce wave-induced force and maximization to increase reproductive output was not supported; despite lower thallus surface area in the exposed site, these individuals had larger soral surface area, and; (3) Adult mortality is wave-induced; survivorship and life expectancy were lower in the exposed site.

Holdfast attachment mechanics were measured. Juveniles have differential attachment properties on different substrata types and exposures; adult attachment is firm (∼100 N), but relatively weak (∼0.07 MN·m⁻²). Site exposure did not affect adult attachment but there was a shift within each site to more resistant holdfasts after a series of early winter storms. Drag experiments and model approaches demonstrated that thallus size, not shape, effectively minimizes drag force and survival. *H. sessile’s* size is reduced by tattering. Model simulations predicted adult survival for exposed and protected sites for 3-month intervals.
during peak wave seasons. Results using only drag forces were not predictive whereas
accelerational plus drag forces approximated real survivorship.

This thesis has shown that populations in more exposed sites will be more reliant on
successful recruitment to persist because of higher adult mortality. Individuals will be at
highest dislodgment risk during storms in summer and early fall months when thalli have not
tattered sufficiently to reduce hydrodynamically-induced forces and holdfasts are weak.
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CHAPTER 1

Introduction to the intertidal kelp species *Hedophyllum sessile*
and its surf-swept environment

“All the life of the shore- the past and the present - by the very fact of its existence there, gives evidence that it has dealt successfully with the realities of its world - the towering physical realities of the sea itself, and the subtle life relationship that bind each living thing to its own community.”

*Rachael Carson 1955*

The correlation between specific biological communities and their relative exposure to waves has been well documented (e.g. Ballantine, 1961; Lewis, 1964; Dayton, 1971). Likewise, patterns of macroalgal morphological shapes, sizes and biomechanical characteristics which correlate with wave-exposure have been recorded (e.g. Koehl, 1986; Armstrong, 1987; Gerard, 1987; Armstrong, 1989; Carrington, 1990; Friedland and Denny, 1995). In contrast, the underlying mechanisms which produce the correlations between community assemblage and wave exposure, and the ecological consequences of biomechanical performance have not been well documented. The primary goal of this thesis is to document the physical and biological interactions which occur on wave-exposed shores. Specifically, questions regarding the nature of physical forces in the environment, how these parameters affect a macroalgal species’ ecology through changes in demographic parameters, and the mechanisms by which the species functions in its fluid environment will be explored.

1.1 Wave-exposure

In its simplest form, the definition of wave-exposure is the degree to which a site is exposed to the force of wave-impact. Wave-exposure at any given tidal height will vary with topographic features which modify wave breaking patterns, and with a site’s tidal height in
the intertidal and depth in the subtidal. In this case, the degree of wave-exposure will be greatest where the waves break on the intertidal. Exposure will be less in subtidal regions which may experience oscillatory flow from passing waves but not from breaking ones.

High wave-exposure occurs at intertidal sites that are in close proximity to open ocean wave swells. The impact of waves on the shore creates a compression force which is capable of damaging organisms like macroalgae since it will compress the blades against the substratum and create punctures in the tissue. However, these impact-induced forces are understood to be of low importance in terms of organism dislodgment and mortality since they assert less force on an organism's attachment than that generated by subsequent flow from wave surges (Vogel, 1981; Denny, 1988). Denny (1988) describes three different flow regimes to which intertidal organisms may be exposed: (1) flow under shallow waves, (2) jets of water onto the rock faces upon which the organisms live, and (3) onrush of turbulent flow moving parallel to the substratum surface. The latter is the most important to intertidal organisms since it typically creates the greatest hydrodynamic force.

1.2 Biological and physical interactions

Numerous aspects of a species' ecology are affected by the physical forces of their flow environment. For example, many invertebrates, such as benthic macrofauna in sandy environments, will change from deposit to suspension feeding in response to variation in moderate oscillatory flow regimes and will cease feeding entirely at high flow (Miller et al., 1992). Likewise, various flow regimes, especially those created during storms, will dislodge organisms at faster rates than in calmer regimes, such as during non-storm periods (Ebeling et al., 1985; Reed et al., 1988; Seymour et al., 1989).
Furthermore, organisms modify flow around them with consequences on nutrient or food availability and minimization of flow forces. For example, specific algal shapes can modify flow patterns in sheltered environments and in unidirectional flow and thereby increase nutrient diffusion rates to the surface of the lamina (Hurd et al., 1997; Stevens and Hurd, 1997). Highly wave-exposed sites with strong wave-driven, oscillatory flow regimes are turbulent enough that low nutrient diffusion rates are not likely limiting factors to growth and survival; instead, the primary physical limitation is from high flow-induced forces which limit algal biomass by dislodging all or some portions of the thallus. Streamlined thallus shapes and small sizes may sufficiently reduce flow-induced forces and effectively increase survival (Dudgeon and Johnson, 1992; Gaylord et al., 1994).

Changes in species assemblages along wave-exposure gradients suggest that there is a limited range of wave-exposure in which a species can successfully persist. Furthermore, demographic rates (such as recruitment and mortality) may correlate to a wave-exposure gradient within which a species is found. In contrast to the number of experimental studies on the effects of biotic interactions on macroalgal population ecology (e.g., Dayton, 1975; Dayton et al., 1984; Paine, 1984; Dean et al., 1989; Chapman, 1990; Menge, 1991), there are few studies documenting specific effects of wave-exposure on macroalgal demographic parameters within the range of wave-exposures that a species inhabits.

1.3 Use of *Hedophyllum sessile* to investigate biological and physical interactions

This thesis uses the intertidal kelp species *Hedophyllum sessile* (Laminariales, Phaeophyceae) to examine the effects of wave-exposure on macroalgal populations. It is found in the mid-intertidal zones on shores in the northeast Pacific Ocean, ranging from Attu Island, Alaska to northern California (Widdowson, 1965). The juvenile plant has a short
flattened stipe (up to 5 cm) which rapidly disappears as the blade becomes sessile on the holdfast. Adult plants are characterized by a large blade (up to 0.6 m² total surface area) and no stipe, attached by numerous haptera arising from the thickened basal margins of the plant. *Hedophyllum sessile* lives in a wide range of wave-exposures, and the primary documented mechanism of its adult mortality is wave-induced dislodgment (Duggins and Dethier, 1985; Markel and DeWreede, 1998). For these reasons, *H. sessile* provides an excellent organism for the study of the effects of wave-exposure on population parameters.

*Hedophyllum sessile* demonstrates morphological variation associated with wave-exposure (e.g., in more protected sites, the mature thallus is primarily one blade with many undulations while in exposed sites, it is tattered into many strap-like, leathery blades). In addition, there are multiple forms between these extremes. It has also been hypothesized that these morphological variations are responses to micro-habitat exposure (for example, on top of a rock vs. under a rock) to waves and air (Widdowson, 1965). Nevertheless, it has been postulated that the form with strap-like blades functions more effectively in wave-exposed sites (Armstrong, 1989).

### 1.4 Experimental research

The aim of this thesis research is to investigate interactions between *Hedophyllum sessile* and the wave-exposed environment and how changes in wave-exposure affect demographic parameters. Experiments were designed to establish site wave-exposure and test predictions that (1) demographic parameters and physical attachment properties vary with exposure; (2) thallus shape and size affect wave-induced drag forces; and (3) a physical model based solely on drag forces and holdfast attachment forces does not explain dislodgment rates in highly wave-exposed sites. To these aims, studies were initiated to
determine the biological and physical differences between sites along a wave-exposure gradient (Chapter 2), demographic responses in *H. sessile* to these differences (Chapter 3); and the physical mechanisms by which wave-exposure affects *H. sessile*'s demographic parameters (Chapter 4-6).
CHAPTER 2

Determination of site wave-exposure:
Use of physical and biological indicators to define site exposure

2.1 Introduction

Despite observations that rocky-shore intertidal populations and community structures are highly variable in time and space, species assemblages are predictable along wave-exposure gradients from extremely wave-sheltered to extremely wave-exposed sites (e.g. Ballantine, 1961; Lewis, 1964; Jones and Demetropoulos, 1968; Ricketts et al., 1968; Dayton, 1971; Paine, 1979; Menge and Farrell, 1989; Harper et al., 1996). These different assemblages can be viewed as reflections of different selective forces acting on populations at each level of wave-exposure. For example, in sites of high wave-exposure, wave-impact and resultant surges of velocities up to 14 m\(\cdot\)s\(^{-1}\) and accelerations exceeding 300 m\(\cdot\)s\(^{-2}\) may dislodge organisms (Denny et al., 1985; Gaines and Denny, 1993; Bell and Denny, 1994), and species more resistant to high flow-induced forces will be selected for in these sites. In contrast, at lower wave-exposures, where active grazing by some gastropod species may happen for longer time periods and when physical mixing of nutrients is low, biological interactions and physiological limitations become more important selective factors (Menge, 1972; Miller, 1974; Wright, 1978; Wheeler, 1980; Denny, 1988; Hurd et al., 1996). Additionally, within the wave-exposure gradient where each species can successfully exist, morphological variations related to wave-exposure are common (e.g. variations in surface area and streamlining within a species; Norton, 1969; Druehl and Kemp, 1982; Norton et
In spite of the well documented biological and ecological patterns that are correlated to wave-exposure, wave-exposure itself has never been precisely defined (Denny & Gaines, 1990; Denny, 1995). It is usually defined by the composition of the biological community, and by relative, observer-based judgments. Definition of wave-exposure based on the site’s biological community is often sufficient within a given geographic area (Ballantine, 1961) but does not allow comparisons between geographic areas. Observer-based judgments of wave-exposure are also geographic and observer specific. For example, a “highly wave-exposed” site directly exposed to oceanic swells averaging 2 m is less exposed than a “highly wave-exposed” site in a geographic area where swell size averages 4 m.

2.1.1 A review of the physical components of wave-exposure

While the above methods for determining wave-exposure are sufficient for determining relative degrees of wave-exposure, none is consistent or quantitative enough to be used in the study of mechanisms by which wave-exposure affects organisms and their ecology since they do not define the physical components of “wave-exposure”. Components of “wave-exposure” are turbulence, maximum wave forces, and wave magnitudes and frequencies. These components will vary to different degrees at any given site and are dependent on factors such as the site’s tidal height, proximity to the open ocean, and local topographies which may magnify or dampen wave forces.

Turbulence is generated wherever fluid forms eddies during and after a breaking wave and also during flow over rough substrata (Denny and Shibata, 1989). Water motion is directly related to turbulence so that low turbulence is associated with low water motion.
Both are important to diffusion-related processes such as nutrient uptake concentrations (Wheeler, 1988; Koch, 1994; Hurd et al., 1996). In sites of low water motion and turbulence, velocity and nutrient boundary layers around macrophyte blades are larger than those in high water motion conditions. Depending on the degree of nutrient limitation to a thallus, algal productivity and survival may be limited, e.g. in extremely wave sheltered sites where free-stream velocities are \(< 4 - 6 \text{ cm} \cdot \text{s}^{-1}\) (Wheeler, 1980; Hurd et al., 1996). In addition, turbulence may affect algal recruitment rates. High turbulence may dilute gamete concentrations and thus limit external fertilization rates; yet, this same turbulence will enhance propagule return to the substratum from the water column (Denny and Shibata, 1989).

Relative degrees of turbulence can be measured \textit{in situ} by integrating the total water motion over a measured time period. The most common methods use calcium sulphate blocks (Muus, 1968; Doty, 1971) or dissolving sucrose, such as candy. These measurements are sufficient for comparing sites (Gerard and Mann, 1979; Shaughnessy, 1994; Shashar et al., 1996) and provide an index of cumulative water motion.

The maximum force associated with maximum wave velocities and accelerations is another aspect of wave-exposure that has only recently been measured with the purpose of site comparisons. Maximum wave force is understood to be the primary selective agent acting on organisms in sites of high wave-exposure since it is assumed that this is the force determining maximal thallus dislodgment (Denny, 1985; Gaylord et al., 1994). Maximum wave force has been measured with numerous methods such as spring scales (Bell and Denny, 1994), drogue disks (Jones and Demetropoulos, 1968), and directional and maximum force recorders (Denny, 1982; Denny, 1988). The benefit of these measurements is that they
measure maximum force from which peak velocities can be estimated, and the devices can be successfully deployed in wave impact zones for long time periods.

The extreme oscillatory nature of flow in wave-impacted zones produces forces in the seaward and shoreward directions (Koehl, 1977; Koehl, 1984; Denny et al., 1985) and the magnitudes and frequencies of these forces may be extremely important to algal success. High accelerations (≥300 m·s⁻²) in the surf zone are common in highly exposed sites and there is evidence that forces imposed by acceleration are predominant components of the total hydrodynamic force on flexible organisms such as algae (Koehl, 1984; Gaylord et al., 1994, Blanchette, 1997). Therefore, maximum forces on algae may be dictated by the maximum rate of change in velocities as much as, if not more than, the peak velocity.

The frequency of oscillations can also affect forces to which algae are susceptible. Depending on the length of an algal thallus, a high wave frequency may not allow the thallus to become fully extended in flow, and thus the full hydrodynamic force will not be transferred to the holdfast. Lower wave frequencies cause an alga to become fully extended and thus experience the accelerational and peak velocity forces on the holdfast, potentially resulting in dislodgment (Koehl, 1984; Denny, 1988; Gaylord et al., 1994). Forces below the maximum may be important to fatigue failure (e.g. by creating minor stress fractures that weaken the attachment, thus making dislodgment risk a function of the rate of fracturing), however, this has not been studied in field populations.

To fully identify wave magnitudes and frequencies, and how they differ between sites, instantaneous velocities must be measured. In comparison to the methods used to measure maximum wave force, the techniques (e.g., propeller devices, drag sphere devices, flow meters, and laser-Doppler techniques) to measure instantaneous velocities are more
labor-intensive, usually more expensive, and less durable for extended time in the field (Denny, 1988).

2.1.2 Research objectives

In this chapter, I define the wave-exposure at two sites which were used to study the effects of wave-exposure on demographics of *Hedophyllum sessile*. Maximum wave forces and biological indicators at the sites are documented with the purpose of comparing wave forces between sites and evaluating how biological measures reflect these wave force differences.

2.2 Methods

2.2.1 Site descriptions

Two study sites were established on Prasiola Point in Barkley Sound, B.C. (Figure 2.1). The sites were characterized as wave-exposed or wave-protected depending on the primary wave direction in relation to these sites. A recent local classification guide by Harper *et al.* (1996) which is based on the presence or absence of indicator species classifies the protected site as “semi-exposed”, and the exposed site as “semi-exposed” or “exposed”. In lower tidal zones, the indicator species *Lessoniopsis littoralis* (Tilden) Reinke was common in the exposed site but absent from the sheltered site, whereas *Laminaria setchelli* Silva, *Egregia menziesii* (Turner) Areschoug, and *Phyllospadix scouleri* Hooker were present in the protected site but absent from the exposed site. For simplicity, sites will be referred to as wave-exposed and protected throughout the thesis.
2.2.2 **Physical parameter: maximum wave forces**

Daily maximum wave heights were predicted for exposed and protected sites using maximum wave force recorders and Environment Canada buoy data (La Perouse Bank buoy 46206, 48° 50.1' N, 125° 59.9' W; Figure 2.1), with the permission of the Government of Canada, © 1997 Her Majesty in Right of Canada, Department of Fisheries and Oceans. Site maximum wave forces were measured during field monitoring dates during low tide series in May, July, September, October, and December 1995, February, April, June, August, and October 1996 and February 1997. Correlations between these data and buoy data were used to calculate site forces during times when sampling did not occur.

Wave force recorders (Figure 2.2, Bell and Denny, 1994) were constructed and calibrated by hanging known masses from each recorder. Forces required to extend springs within the recorders were calculated by:

\[ F = M \cdot a_g \]  

**eq. 2.1**

where \( F \) (N) is the force, \( M \) (kg) is the known mass, and \( a_g \) is the gravitational acceleration (9.81 m \( \cdot \) s\(^{-2}\)). For each recorder, these forces were plotted against resulting spring extensions (m) and linear regressions (in SYSTAT 5.03 for Windows) were calculated and plotted so that field forces could be estimated from the observed spring extensions. Thus:

\[ F = (k \cdot x_{spring}) + c \]  

**eq. 2.2**

where \( k \) is the spring constant which indicates the spring extension constant (N \( \cdot \) m\(^{-1}\)), \( x_{spring} \) is the spring extension (m), and \( c \) is the force required to overcome the initial spring compression (Serway, 1982). Calibrations were recalculated after each field use.
During each field sampling period at low tide, three recorders were placed at each field site, attached to permanent, 0.635-cm diameter stainless steel eye bolts anchored into the rock just above the *Hedophyllum sessile* zone. Overhanging algae surrounding the bolts were clipped so that they would not entangle the recorders. Two different spring tensions were used in the recorder and are referred to as “heavy” (spring extension constant $\equiv 1.99 \text{ N} \cdot \text{mm}^{-1}$) and “light” (spring extension constant $\equiv 0.192 \text{ N} \cdot \text{mm}^{-1}$). Light springs were used when there were no visible differences between waves at the sites, typically when the swell size was small (less than 1 m). Heavy spring recorders were used at all other times.

Recorders were deployed for an entire tidal cycle and visited at each low tide (deployed for either 12 hr or 24 hr). At each visit, spring extensions were measured (to nearest 0.5 mm) and recorders reset. Spring extensions were converted to force (N) by the calibration curves.

Daily significant wave height data obtained from the La Perouse Bank buoy 46206 were extracted for time periods matching recorder deployments. Maximum wave heights were not used because these are less reliable than significant wave height data (AXYS Environmental Consulting Ltd., 1996). For each deployment period, the mean significant wave height was calculated and plotted against recorder maximum forces at each site. These were tested for significant relationships by Pearson product-moment correlation analysis in SYSTAT version 5.03 for Windows. If the relationship was significant, then the regression and its 95% confidence intervals were calculated and plotted by SigmaPlot version 2.0. Site differences were analyzed using these plots. These regressions were also used to estimate site forces during times when direct measurements were not available.
2.2.3 Top tidal heights of *Hedophyllum sessile* zone

The top elevation of the *Hedophyllum sessile* zone was measured at each site as height (m) above Mean Lower Low Water (MLLW) on January 29, 1995. It was predicted that, if the sites are different in terms of wave-exposure, the *H. sessile* zone in the exposed site would extend higher than that in the more protected site. Elevations were measured from a fixed point on shore, above the intertidal zone, using a surveyor’s scope and ranging pole. The vertical distance below the survey site to three points at water level (V<sub>water</sub>) and at the top of the *H. sessile* zone were measured at each site. The tidal height (H<sub>water</sub>) at the surveying time was calculated by Tides & Currents for Windows, version 2.0a. (Nautical Software, Inc.) which uses National Oceanic and Atmospheric Administration (NOAA) standards and reference stations.

The survey site’s elevation above MLLW was estimated by:

\[ H_{\text{survey}} = V_{\text{water}} + H_{\text{water}} \]  

where H<sub>water</sub> is tidal height (m) above MLLW and V is the vertical distance (m) below the site’s elevation. To calculate the height above MLLW of the upper edge of the *H. sessile* zone, the vertical distance below the survey site to these points was subtracted from H<sub>survey</sub>.

2.2.4 Biological community

To evaluate how the biological communities differ between the two sites and over seasons within the sites a permanent transect was established at each site in March 1995 and sampled at approximately bi-monthly intervals until February 1997. Transect ends were marked by permanent bolts, and a nylon rope was tightly extended between these bolts.
during each sampling date. Ten 0.25 m x 0.25 m quadrats were located at random along each transect line, and sampled repeatedly throughout the monitoring period.

Within each plot, percent canopy cover was visually estimated. The percent cover of understory species was estimated by a point-intersect method (Dethier et al., 1993). A monofilament grid with 1 cm² divisions was constructed within a 0.25 x 0.25 m quadrat. Thirty random points (out of a possible 676 points) were chosen and the species below each point recorded. Species were grouped by type: articulated coralline algae (AC), crustose coralline algae (CC), non-calcareous encrusting red algae (RC), other species (Tables 2.1, 2.2), and bare rock. Densities (# individuals m⁻²) of the dominant grazer (Duggins and Dethier, 1984; Paine, 1984) Katharina tunicata were estimated by counts in each quadrat.

2.2.5 Hedophyllum sessile morphological variations

Even though Hedophyllum sessile displays the strap-like, more wave-exposed morphology (such as that described by Widdowson, 1965 and Armstrong, 1989) at both sites, it is predicted that there will be morphological differences for this species between the two sites as a result of site and seasonal wave-exposure differences. Morphological parameters of each H. sessile adult were measured within the permanent plots described above throughout the sampling period. Data from each holdfast consisted of total number of blades, blade lengths, and holdfast dimensions. Holdfast area was assumed to be represented by the area of an ellipse and thus estimated by the measured dimensions using equation:

\[ A_{\text{holdfast}} = \pi \cdot a \cdot b \quad \text{eq. 2.4} \]

\( A \) is the estimated holdfast area (cm²), \( a \) is the maximum radius (cm) and \( b \) is the radius (cm) perpendicular to \( a \).
Average blade lengths and normalized blade number (# blades • holdfast area\(^{-1}\)) were compared between sites and throughout the sampling dates. It is predicted that higher wave action will be reflected in increased thallus-tattering, which results in shorter blades and more blades per holdfast area.

2.2.6 Statistical analyses

SYSTAT version 5.03 was used for statistical analyses. All data sets passed tests for homogeneity of variances (by \(F_{\text{max}}\)) and normal distributions. Only *Katharina tunicata* density data required square root transformed to achieve normal distribution. Student's grouped t-test was used to detect differences between top tidal heights. For each site and sampling date, 95% confidence intervals were calculated for biological community and morphological data. Confidence intervals for normalized blade number were calculated as in Krebs (1989) using the following equation (Cochran, 1977):

\[
95\% \text{CI} = t_{0.05} \left\{ \left( \frac{1}{\sqrt{n}} \right) \left( \frac{\bar{y}^2 - 2\hat{R} \sum xy + \hat{R}^2 \sum y^2}{n-1} \right) \right\}^{1/2}
\]

where
- \(t_{0.05}\) = Student's t value for n-1 degrees of freedom for \(\alpha = 0.05\)
- \(x\) = numerator parameter (blade number)
- \(y\) = denominator parameter (estimated holdfast area, cm\(^2\))
- \(\bar{y}\) = mean holdfast area (cm\(^2\))
- \(f\) = sampling fraction, assumed to be less than 0.05 and therefore 0 in these calculations (Krebs, 1989)
- \(n\) = sample size
- \(\hat{R}\) = mean ratio of \(x\) to \(y\)
2.3 Results

2.3.1 Maximum wave forces

Calibrations (e.g., Figures 2.3, 2.4) did not change during field use and there was a linear correlation between applied force and spring extension for all recorders (Table 2.3).

Recorder data (nearshore wave forces) were significantly correlated to offshore mean significant wave heights at both sites (exposed: $r = 0.824$, $p<0.001$, $n=57$; sheltered: $r = 0.704$, $p<0.001$, $n=57$). Regression analysis of these correlations (Figure 2.5) show that the exposed site is significantly more exposed to wave forces only when the offshore mean significant wave height is above 2.1 m. An offshore mean significant wave height of 2.1 m produces forces on the recorders of 15.6 N in the exposed site and 12.8 N in the protected site. Thus, when recorder forces exceed these site values, the sites are significantly different, $p \leq 0.05$, with the exposed site experiencing more force than the protected site.

Offshore daily significant wave heights (Figure 2.6) were used to calculate the site maximum wave forces (Figures 2.7, 2.8) for the entire sampling period. Significant site differences ($p \leq 0.05$) in site maximum wave forces occur throughout the year (Figures 2.7, 2.8) but are more frequent from February - May 1995, September 1995 - May 1996, and September 1996 - February 1997. Sites are rarely different at the 95% confidence level during the months of June, July and August.

2.3.2 Top tidal heights of Hedophyllum sessile zone

The top tidal height of the Hedophyllum sessile zone in the site predicted to be more exposed was significantly higher ($p=0.007$) than that of the site predicted to be less wave-
exposed. *Hedophyllum sessile* extended to \(+0.66\) m (± 0.073 SE) in the exposed site and to \(+0.32\) m (± 0.044 SE) in the protected site.

### 2.3.3 Biological community

Of the biological community data gathered (Figures 2.9-2.16), only percent canopy cover (Figure 2.9) shows seasonal variation, with decreased canopy cover in winter months (especially from December - April 1996 in both sites). There were no significant (p ≥ 0.05) site differences for canopy cover, holdfast cover, crustose and articulated coralline algae, and other species (Figures 2.9-2.16). The only consistent site differences were for bare rock (protected > exposed, p ≤ 0.05; Figure 2.14) and non-calcareous encrusting red algae (exposed > protected, p ≤ 0.05; Figure 2.13).

On average, *K. tunicata* was more dense in the exposed site for all sampling dates (Figure 2.16). However, densities were not statistically different (p > 0.05) except in September and October 1995.

#### 2.3.4 *Hedophyllum sessile* morphological variations

There were no significant site differences in average blade length (Figure 2.17). Blade lengths were lower in both sites during the winter months than in summer months. Overall, there were more blades per holdfast area (p ≤ 0.05) in the exposed site (Figure 2.18) except for April and June 1996 when the trend was reversed.

### 2.4 Discussion

The mechanisms of wave-exposure effects on macroalgae are not clearly understood, primarily because field studies rarely define the components of wave-exposure. For the
purposes of demographic studies (Chapter 3), I define exposure in terms of maximum wave force since this component is the one most important to macroalgal dislodgment rates (Gaines and Denny, 1993). I also investigated how different biological and physical measurements affect conclusions about wave-exposure differences between sites. The primary conclusions from this study on wave-exposure are that the two sites experience significantly different wave forces only when the offshore significant wave height is above 2.1 m and that most biological indices represent site differences but do not reveal seasonal wave-exposure patterns.

The difference between site wave-exposures was dependent on offshore daily average significant wave heights exceeding 2.1 m; such heights (exceeding 2.1 m) mostly occur in fall, winter, and early spring months. Gaines and Denny (1993) hypothesized that the measurement of mean maximum force at a site is sufficient to describe flow induced forces important to dislodgment since variations around the means are similar. However, results from the time series in this study demonstrate that the magnitude of mean measurements within a site and the extent to which sites differ in maximum forces are season-specific. The seasonal range of mean forces should therefore be measured to accurately assess site wave-exposure.

Differences in wave forces at different sites which are relevant to organisms are most likely not expressed by statistical differences. A more relevant way to evaluate site differences is to calculate a species or group of species' risk of dislodgment (Denny, 1995). Consider the following: within the range of predicted forces (Figures 2.7, 2.8) considered statistically significantly different (>2.1 m), the minimum estimated force difference between my study sites is 2.8 N (exposed = 15.7 N; protected = 12.9 N) and the maximum difference
is 18.9 N (exposed = 54.7 N; protected = 35.8 N). In order to make these measurements more general to other organisms (which, for any given wave, will generate different forces than the recorder) and less specific to the recorder, this maximum force difference can be converted to a difference in velocity using the equation:

\[ \nu = \left( \frac{F_d}{0.575} \right)^{1.93} \quad \text{eq. 2.6} \]

Where \( \nu \) is the peak velocity required to produce the drag force, \( F_d \), on the recorder and the constants are those calculated specifically for the recorders (Bell and Denny, 1994). The velocities required to achieve minimum and maximum forces (within the range of average significant wave heights when sites are statistically different) are 5.5 m \( \cdot \) s\(^{-1} \) (exposed) and 5.0 m \( \cdot \) s\(^{-1} \) (protected) and 10.6 m \( \cdot \) s\(^{-1} \) (exposed) and 8.5 m \( \cdot \) s\(^{-1} \) (protected). Thus, at force magnitudes which were statistically different, velocity differences necessary to produce these forces range from 0.5 - 2.1 m \( \cdot \) s\(^{-1} \). These velocity differences will have variable effects on different organisms, depending on the organism’s surface area, shape (which dictate the forces generated), and attachment forces (which determine the risk of dislodgment) (Denny 1988).

For example, Shaughnessy et al. (1996) predicted that, at velocities above approximately 3 m \( \cdot \) s\(^{-1} \), velocity changes of 0.5 - 2.1 m \( \cdot \) s\(^{-1} \) would produce differential survival rates in Mazzaella linearis and M. splendens based on thallus surface areas and holdfast attachment forces. But for other species at lower risk, which have lower surface areas and are more firmly attached, these velocity differences between sites may not result in differential survivorship (Gaylord et al., 1994).
In 1995, Denny proposed a system for predicting hydrodynamic forces and consequences for dislodgment risk on organisms in intertidal sites as a way to define a biologically relevant scale of site exposure. Steps towards establishing this exposure index require determination of offshore maximal wave heights, wave shoaling and refraction, patterns of breaking and consequent velocities, hydrodynamic forces and dislodgment risks. Despite the utility of this approach, he emphasized that the quantification of wave shoaling, refraction, and breaking events is extremely time-consuming and potentially inexact due to small-scale local topographic effects which can not be easily taken into account. Thus, the link between offshore wave data and local wave forces using these steps may not be efficient for ecological intertidal studies.

In this study, methods for determining site wave forces circumvented the difficulties outlined above and directly correlated offshore wave heights to onshore forces. There was substantial variation in wave forces at each site, yet correlations were significant. This is a promising result for other studies since it demonstrates that at least one component of wave-exposure can be defined in intertidal ecological studies. The force recorders are inexpensive (about 10$US per recorder) and easy to deploy (Bell and Denny, 1994). If this system is regularly used to define wave-exposure, then results from studies at different geographic sites can be more easily compared.

The biological surveys in this study reflect that there are biologically relevant site differences which were predicted by analysis of maximum wave forces. However, most of the biological parameters do not distinguish seasonal patterns in wave-exposure. The parameters which reflected overall site differences but not seasonal variation were: tidal height, non-calcareous encrusting red algae and bare rock cover. The use of indicator species
also represents site differences but overall, classification based solely on presence/absence of indicators can be misleading since it does not represent seasonal variations in wave-exposure.

Canopy cover varied seasonally but not between sites. The only biological parameter which could represent site differences throughout different seasons was normalized blade number. Unlike other biological indicators in this study such as Lessoniopsis littoralis, Laminaria setchellii, red crusts, and tidal heights, tattering reacts to seasonal changes in wave force at each site, especially in the wave-exposed site.

2.4.1 Conclusion

Seasonal variation in wave activity produces differences in the mean maximum wave forces that intertidal sites experience which biological indicators, overall, do not reflect. Variations in turbulence and wave magnitudes and frequencies were not measured in this study and require further investigation.

Wave-induced disturbance events are important to the ecology and species diversity of rocky shores (Sousa, 1979; Paine and Levin, 1981; Sousa, 1984; Sousa, 1985; Menge and Farrell, 1989). Effects of wave disturbance on the biology of intertidal sites can only be fully studied when the relative importances of wave-exposure components, individually or in combination, are quantified. The following chapters investigate how maximum wave force differences within and between the sites affect Hedophyllum sessile’s demographic features, especially that of survival, by the use of field documentation and biomechanical model approaches.
Table 2.1 Macroalgal species in exposed and protected sites. Abbreviations in site column represent the site in which the species is found, E= exposed and P= protected, and if that species contributes to the percent cover measurements (%) in each site at any sampling date. If % is not indicated for a species, then that species was observed only as a trace species in all sampling dates.

<table>
<thead>
<tr>
<th>PHYLUM</th>
<th>SPECIES</th>
<th>COMMON NAME</th>
<th>SITE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorophyta</td>
<td><em>Codium fragile</em></td>
<td>dead-man's fingers</td>
<td>P</td>
</tr>
<tr>
<td></td>
<td><em>Ulva lactuca</em></td>
<td>sea lettuce</td>
<td>P</td>
</tr>
<tr>
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<td><em>Analipus japonicus</em></td>
<td>feather boa</td>
<td>E</td>
</tr>
<tr>
<td></td>
<td><em>Egregia menziesii</em></td>
<td>sea cabbage</td>
<td>P</td>
</tr>
<tr>
<td></td>
<td><em>Hedophyllum sessile</em></td>
<td>non-calcareous, encrusting red (RC)</td>
<td>P% E%</td>
</tr>
<tr>
<td></td>
<td><em>Ralfsia sp.</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhodophyta</td>
<td><em>Bossiella plumosa</em></td>
<td>articulated coralline (AC)</td>
<td>P E%</td>
</tr>
<tr>
<td></td>
<td><em>Corallina officinalis</em></td>
<td>articulated coralline (AC)</td>
<td>P E%</td>
</tr>
<tr>
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<td><em>C. vancouveriensis</em></td>
<td>articulated coralline (AC)</td>
<td>P E%</td>
</tr>
<tr>
<td></td>
<td><em>Cryptopleura lobulifera</em></td>
<td></td>
<td>P</td>
</tr>
<tr>
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<td><em>Halosaccion glandiforme</em></td>
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</tr>
<tr>
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<td><em>Hildenbrandia occidentalis</em></td>
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<td>P</td>
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<td></td>
<td><em>Nemalion helminthoides</em></td>
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<tr>
<td></td>
<td><em>Neorhodomela larix</em></td>
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<tr>
<td></td>
<td><em>Odonthalia floccosa</em></td>
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<td>P</td>
</tr>
<tr>
<td></td>
<td>&quot;Petrocelis&quot;, (tetrasporophytic phase of <em>Mastocarpus papillatus</em>)</td>
<td>non-calcareous, encrusting red (RC)</td>
<td>P E%</td>
</tr>
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<tr>
<td></td>
<td><em>Rhodoglossum roseum</em></td>
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</tbody>
</table>

† Relative abundances of the species in groups “AC”, “CC”, and “RC” were not quantified in the field.
‡ percent cover symbol (%) refers to the whole group, not individual species.
Table 2.2 Animal species in exposed and protected sites. Abbreviations in site column represent the site in which the species is found, E= exposed and P= protected, and if that species contributes to the percent cover measurements (%) in each site at any sampling date. If % is not indicated for a species, then that species was observed only as a trace species in all sampling dates.

<table>
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<th>PHYLUM</th>
<th>SPECIES</th>
<th>COMMON NAME</th>
<th>SITE</th>
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<td>ochre star</td>
<td>P % E %</td>
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<td>Porifera</td>
<td>Halicrona sp</td>
<td></td>
<td>E</td>
</tr>
<tr>
<td></td>
<td>Halichondria bowerbanki</td>
<td></td>
<td>E</td>
</tr>
<tr>
<td></td>
<td>H. panicea</td>
<td></td>
<td>E</td>
</tr>
<tr>
<td>Urochordata</td>
<td>Synoicium parfustis</td>
<td>colonial tunicate</td>
<td>P</td>
</tr>
</tbody>
</table>
Table 2.3 Regression parameters and multiple R-square values for recorder calibrations. Each maximum wave force recorder was individually calibrated by linear regression between spring extension, $x_{\text{spring}}$ (m) and force, $F$ (N) to fit equation (2.2), $F = (k \cdot x) + c$; $k$ is the spring constant and $c$ is initial spring compression. Spring type indicates the spring tension; light springs measure lower wave forces than heavy springs. Calibration regressions were used to calculate field wave forces on recorders.

<table>
<thead>
<tr>
<th>recorder</th>
<th>spring type</th>
<th>$k$</th>
<th>$c$</th>
<th>$R^2$</th>
</tr>
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<td>184.973</td>
<td>2.884</td>
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</tr>
<tr>
<td>2</td>
<td>light</td>
<td>200.021</td>
<td>1.316</td>
<td>0.989</td>
</tr>
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<td>3</td>
<td>light</td>
<td>185.173</td>
<td>3.200</td>
<td>0.999</td>
</tr>
<tr>
<td>4</td>
<td>light</td>
<td>190.964</td>
<td>3.333</td>
<td>0.997</td>
</tr>
<tr>
<td>5</td>
<td>light</td>
<td>190.382</td>
<td>2.905</td>
<td>0.996</td>
</tr>
<tr>
<td>22</td>
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<td>200.752</td>
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</tr>
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<td>7</td>
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</tr>
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<td>9</td>
<td>heavy</td>
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<tr>
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<td>10.150</td>
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</tr>
<tr>
<td>14</td>
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<td>2014.962</td>
<td>8.068</td>
<td>0.994</td>
</tr>
</tbody>
</table>
Table 2.4 Number of individuals sampled, n, in each site for blade length (Figure 2.17) and normalized blade number data (Figure 2.18).

<table>
<thead>
<tr>
<th>sampling date</th>
<th>exposed site n</th>
<th>protected site n</th>
</tr>
</thead>
<tbody>
<tr>
<td>September 1995</td>
<td>36</td>
<td>36</td>
</tr>
<tr>
<td>October 1995</td>
<td>39</td>
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<tr>
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<td>July 1996</td>
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<tr>
<td>August 1996</td>
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<td>16</td>
</tr>
<tr>
<td>October 1996</td>
<td>13</td>
<td>9</td>
</tr>
<tr>
<td>February 1997</td>
<td>13</td>
<td>11</td>
</tr>
</tbody>
</table>
Figure 2.1 Map of study sites. All experiments were performed on Vancouver Island, British Columbia, Canada. Bamfield Marine Station is located on Trevor Channel, which opens to Barkley Sound and the Pacific Ocean. The approximate position of the LaPerouse Bank Buoy is represented by (B). Study sites were on either side of Prasiola Point (48° 49' 4" N, 125° 10' 4" W), which is marked by an arrow on the Trevor Channel/ Bamfield map.
Figure 2.2 Maximum wave force recorder used to measure wave forces at exposed and protected sites (modified from Bell & Denny, 1994). The recorders were attached by the stainless steel swivel to eye bolts embedded in the sites.
Figure 2.3 Representative calibration for heavy wave force recorder, #14. Regression parameters are listed in Table 2.3.
Figure 2.4 Representative calibration for light wave force recorder, #1. Regression parameters are listed in Table 2.3.
Figure 2.5 Comparison of wave forces at exposed and protected sites to offshore mean significant wave height, $H_{avg,m}$, n=57. $H_{avg,m}$ is the average hourly significant wave height during recorder deployments. Solid lines and symbols represent exposed site and dotted lines and symbols represent protected site. For each site, heavy lines are the regression and light lines are upper and lower 95% confidence intervals. Exposed site: $F_{max} = (6.562 \times H_{avg,m}) + 1.816$, $r=0.824$, $p<0.001$; Protected site: $F_{max} = (3.850 \times H_{avg,m}) + 4.760$, $r=0.704$, $p<0.001$. 
Figure 2.6 Daily offshore mean significant wave heights ($H_{\text{avg},m}$) from January 1995 to February 1997 at La Perouse Bank, 48° 50.1' N, 125° 59.9' W. The horizontal reference line at 2.1 m represents the $H_{\text{avg},m}$ above which sites are different, $p \leq 0.05$. (Wave height data are used by permission from the Government of Canada, © 1997 Her Majesty in Right of Canada, Department of Fisheries and Oceans).
Figure 2.7  Estimated wave forces on drogues in the exposed site, predicted by the regression between wave recorder and offshore wave height data. Forces above the horizontal reference line at 15 N are significantly greater, $p \leq 0.05$, than those in the protected site.
Figure 2.8 Estimated wave forces on drogues in the protected site, predicted by the regression between wave recorder and offshore wave height data. Forces above the horizontal reference line at 13 N are significantly less, $p \leq 0.05$, than those in the exposed site.
Figure 2.9 *Hedophyllum sessile* percent canopy cover in exposed (shaded bars) and protected (open bars) sites. Data are the mean ± 95%CI of 10 replicate 0.25 x 0.25 m plots along permanent transects in each site throughout the sampling period of March 1995 to February 1997.
Figure 2.10 *Hedophyllum sessile* holdfast percent cover in exposed (shaded bars) and protected (open bars) sites. Data are the mean ± 95%CI of 10 replicate 0.25 x 0.25 m plots along permanent transects in each site throughout the sampling period of March 1995 to February 1997 (with the exception of October 1997 due to poor weather conditions).
Figure 2.11 Articulated coralline algae percent cover in exposed (shaded bars) and protected (open bars) sites. Data are the mean ± 95%CI of 10 replicate 0.25 x 0.25 plots along permanent transects in each site throughout the sampling period of March 1995 to February 1997 (with the exception of October 1997 due to poor weather conditions).
Figure 2.12 Crustose coralline algae percent cover in exposed (shaded bars) and protected (open bars) sites. Data are the mean ± 95%CI of 10 replicate 0.25 x 0.25 m plots along permanent transects in each site throughout the sampling period of March 1995 to February 1997 (with the exception of October 1997 due to poor weather conditions).
Figure 2.13 Non-calcareous encrusting red algae percent cover in exposed (shaded bars) and protected (open bars) sites. Data are the mean ± 95%CI of 10 replicate 0.25 x 0.25 m plots along permanent transects in each site throughout the sampling period of March 1995 to February 1997 (with the exception of October 1997 due to poor weather conditions).
Figure 2.14 Bare rock percent cover in exposed (shaded bars) and protected (open bars) sites. Data are the mean ± 95%CI of 10 replicate 0.25 x 0.25 m plots along permanent transects in each site throughout the sampling period of March 1995 to February 1997 (with the exception of October 1997 due to poor weather conditions).
Figure 2.15 Percent cover of other species in exposed (shaded bars) and protected (open bars) sites. Data are the mean ± 95%CI of 10 replicate 0.25 x 0.25 m plots along permanent transects in each site throughout the sampling period of March 1995 to February 1997 (with the exception of October 1997 due to poor weather conditions). See Tables 2.1 and 2.2 for species included in these data.
Figure 2.16 *Katharina tunicata* density (# · m$^{-2}$) in exposed (shaded bars) and protected (open bars) sites. Data are the mean ± 95% CI of 10 replicate 0.25 x 0.25 m plots along permanent transects in each site throughout the sampling period of March 1995 to February 1997 (with the exception of the exposed site in October 1997 due to poor weather conditions). Confidence intervals were calculated on square root transformed data and converted back to the original scale.
Figure 2.17 *Hedophyllum sessile* average blade length per individual in exposed (shaded bars) and protected (open bars) sites. Data are the mean ± 95%CI of individuals within 10 0.25 x 0.25 m plots along permanent transects in each site throughout the sampling period of March 1995 to February 1997. See Table 2.4 for replicate numbers in each site and sampling date.
Figure 2.18 *Hedophyllum sessile* normalized blade number ( #. cm$^{-2}$ ) in exposed (shaded bars) and protected (open bars) sites. Data are the mean ± 95%CI of # blades/holdfast area for individuals within 10, 0.25 x 0.25 m plots along permanent transects in each site throughout the sampling period of March 1995 to February 1997. See Table 2.4 for replicate numbers in each site and sampling date.
CHAPTER 3

Wave-exposure effects on *Hedophyllum sessile* demographic parameters

3.1 Introduction

Variations in recruitment, mortality, and fecundity rates may reduce or increase population growth, or act together to maintain constant population size (Harper, 1977). A macroalgal population from a common gene pool may inhabit a wide range of environmental types. Dispersal distances of at least 100 m have been reported for *Laminaria* sp. and *Pterygophora* sp. (Pearse and Hines, 1979), and 10 - 50 km for *Enteromorpha* sp. (but see Kendrick and Walker, 1991 and Paine, 1979 for reports of dispersal less than 1 m). A sub-population can be defined as a subset of the entire population at a specific site; its demographic parameters will be affected by site-specific events, especially variations in frequencies and magnitudes of disturbance events, such as predation or wave forces (Dayton *et al.*, 1984; Ebeling, 1985; Deysher and Dean, 1986; Dean *et al.*, 1989).

Recruitment is the addition of new individuals to a population (Doherty and Williams, 1988). Here, macroalgal recruitment will be defined as the appearance of macroscopic sized individuals, i.e. those recognizable by the unaided eye (Dean *et al.*, 1989). Recruitment in all algal species is dependent on processes occurring during dispersal, settlement, and microscopic post-settlement phases (Figure 3.1). As is common for other macroalgal species, a substantial portion of the kelp life cycle is spent in the microscopic phase. And, for a kelp species, successful sporophyte recruitment is dependent on successful zoospore dispersal, gametophyte fertilization, and pre-recruitment sporophyte growth (Figure 3.1). In other words, a
population’s reproductive output is not necessarily an indicator of sporophyte recruitment potential, since processes occurring during the microscopic phases may uncouple reproductive output from eventual recruitment densities. For example, Ang (1991) reported that reproductive output in *Fucus distichus* L. emend. Powell was correlated to microscopic settled stages but not to macroscopic recruit stages.

Experimental evidence from macroalgal studies suggests that on the substratum there are germling banks (Santelices, 1990; Vadas *et al.*, 1992) which are composed of microscopic life phases, such as gametophytes. When larger, canopy forming mature plants are removed, the germling bank will grow quickly thus allowing faster population recovery after adult dislodgment and lower dependency on successful dispersal. Despite the potential for germling banks, the early microscopic stages are considered bottleneck periods for a population (Vadas *et al.*, 1992) during which time there is increased mortality. This high pre-recruitment mortality may eventually result in limited recruitment (Roughgarden *et al.*, 1988).

Wave-exposure has been hypothesized to affect all components of a population’s demography, especially mortality. For example, high wave force may increase mortality rates by dislodging individuals at a relatively higher rate than in more wave-protected sites (Dudgeon and Johnson, 1992; Friedland and Denny, 1995). Wave-induced damage can also combine with grazer-induced wounds to increase mortality rates; tissue loss after partial herbivore damage in wave-sheltered habitats is much lower than post-herbivore damage sustained in more exposed habitats (DeWreede *et al.*, 1992; Padilla, 1993). A population with relatively high dislodgment rates may then be dependent on successful recruitment to maintain its population size (Hoffman and Ugarte, 1985; Reed *et al.*, 1988; Roughgarden *et al.*, 1988; Ang, 1991).
Biomass loss, especially in sites of higher wave-exposure, from partial physical damage may result in lower reproductive output. Furthermore, because thallus size is restricted in high wave-exposure sites (e.g., Carrington, 1990) and thallus size and reproductive output may be positively correlated (e.g., Chapman, 1986), reproductive output may be limited in wave-exposed sites. For example, Gaylord et al. (1994) predicted that there is an optimal size for a species to maximize reproductive output but minimize dislodgment.

Effects of wave-exposure on recruitment, mortality, and reproduction are not well documented. Indirect measures of recruitment and mortality are typically accomplished by quantifying changes in plant percent covers or densities. Specific rates of recruitment and mortality are directly quantified by following the appearance of new individuals (e.g., a cohort) and fates of these individuals. Published cohort recruitment and mortality data in wave-exposed sites are limited; this is especially the case for perennial algal species, primarily due to the time and effort required to collect such demographic data. In this thesis, I use two definitions for a cohort: (1) plants initially tagged during a given survey and (2) a group of newly recruited individuals at a given survey. This study tests hypotheses that Hedophyllum sessile in a site of higher wave-exposure will have lower juvenile and adult survivorship, less blade area dedicated to reproductive tissue, and consequently lower reproductive output than H. sessile in the wave-protected site.

3.2 Methods

3.2.1 Experimental sites

Sites were established as described in Chapter 2. All survival and recruitment data were generated from natural trajectory experiments in permanent transects which were
established in March 1995 and sampled until February 1997. Transect ends were marked by permanent bolts and a nylon rope was tightly extended between these bolts during each sampling date. Ten random 0.25 m x 0.25 m quadrats were established along each transect line, resulting in ten permanent plots in each site that were sampled throughout the monitoring period.

Reproductive data were collected in both the permanent plots and random or haphazard samples from areas outside the permanent transects. Random sampling was accomplished by choosing individuals closest to random distances along a leaded line. Haphazard sampling was typically accomplished when the conditions did not allow the line to be laid in the intertidal without being washed away by waves; in this case, plants were sampled without the use of the leaded line, and randomly selected distances were instead chosen by walking through the middle of the *Hedophyllum sessile* zone and then sampling a plant after every three or four strides. In this haphazard sampling, an effort was made to not take time to choose a plant but instead to select quickly so as to simulate random sampling.

### 3.2.2 Recruitment and survivorship

All individuals within the permanent quadrats were mapped in May 1995 by an x, y coordinate system. Quadrats were strung with monofilament lines in a grid system with 1 cm² divisions. This allowed for each x and y coordinate to range from 0 - 25, and individual holdfasts were mapped to the closest grid intersection coordinate. For holdfasts larger than 1 cm², the point in the middle of the holdfast was recorded. Census dates were May, July, September, October, and December 1995, February, April, June, August, and October 1996, and February 1997. Data on all *Hedophyllum sessile* individuals were recorded at each census date. Holdfast size (maximum diameter and diameter perpendicular to maximum), number of
blades, length of blades, and reproductive status of each blade were recorded. Holdfast size was assumed to be the surface area (A) of an ellipse (equation 2.4). New individuals were always mapped and the substratum type (articulated coralline algae, crustose coralline algae, pre-existing H. sessile holdfast, non-calcareous encrusting red algae, or bare rock) on which they appeared was noted.

Recruitment rates were compared between sites at each sampling period by calculating the number of new individuals recruiting into each site. To assess if juvenile recruitment is substratum-dependent, differential recruitment was quantified by dividing the percent of individuals sampled on each substratum type (\( \frac{\# \text{ on substratum type}}{\text{total juveniles sampled}} \times 100 \)) by the available percent cover of each substratum type. This was done for the May 1995 cohort, and percent covers of substrata were extracted from the data sets (Figures 2.10 - 2.14). To evaluate the time necessary for recruits to grow into adults (designated by the disappearance of the stipe), holdfast size classes were assigned to estimated holdfast areas as size class (SC) 1 = < 0.5 cm\(^2\), SC2 = 0.5 - 4 cm\(^2\), SC3 = 4 - 7 cm\(^2\), SC4 = 7 - 12 cm\(^2\) and SC5 = > 12 cm\(^2\). Size structures for each sampling date of the May 1995 recruit cohort were then constructed.

To compare survival between sites, data from permanent plots in each site were compiled for a life table from the original cohort of juveniles mapped in May 1995 and for the adult cohort mapped in July 1995. Life tables, with age intervals in days, were constructed from cohort data which were extrapolated to a population of 1000 starting individuals. Standard life table parameters (from Chapman, 1979, except for probability of being reproductive) were calculated, where \( l_x \) is the standardized number of individuals at the start of each age interval, \( d_x \) is the number of individuals dying during the age interval (\( d_x = l_x - \))
\( l_{x+1} \), \( p_x \) is probability of surviving to next age interval \( (p_x = l_{x+1} / l_x) \), \( L_x \) is number of individuals living during the interval \( (L_x = l_x + l_{x+1} / 2) \), and \( e_x \text{ days} \) is expected longevity in days \( (e_x \text{ days} = \{(55)(T_x / l_x)\}) \) where \( T_x = \sum L_x \) from oldest age interval to and including interval \( x \); 55 is the average age interval length in days). Probability of being reproductive, \( P_R \), was calculated as the proportion of total individuals alive at the beginning of the time interval which were reproductive.

Kaplan-Meier survival proportions \( (p_k) \) and 95% confidence intervals were calculated using the July 1995 adult cohort at both sites and \( p_k \) values at each sampling date were compared. Survival proportions represent the cumulative proportion of individuals surviving to each census date and is estimated by the equation (from Machin and Gardner, 1989):

\[
p_k = \prod r_i - d_i \over r_i \tag{eq. 3.1}
\]

where \( r_i \) is the number of individuals alive before each census date, \( d_i \) is the number dead at each census date, and \( \Pi \) indicates multiplication over each time a death occurs up to and including the census date. The standard error of \( p_k \) is calculated as:

\[
SE_p = \sqrt{\frac{p_k(1-p_k)}{n'}} \tag{eq. 3.2}
\]

where \( n' \) is the effective sample size calculated as the number of individuals lost by the census date subtracted from the total number in the original cohort. The 95% confidence interval for \( p_k \) was then calculated as:
95% CI = \( p_k \pm N_{1-\alpha/2} \cdot SE \)  

where \( N \) is the appropriate value from the standard normal distribution for the 95\(^{th} \) percentile.

Active recruitment periods are considered to be times during which individuals recruit into the population. It is predicted that recruits at both sites will have differential growth rates, resulting in differential transitions into holdfast size classes. I also hypothesize that the site of higher wave-exposure has lower survivorship; if this hypothesis is to be supported, sites will have different life table values, where the exposed site has lower \( e_x \) and \( p_x \) values.

Additionally, it is expected that during times of high seasonal wave-exposure when sites consistently experience significantly different forces (October - March; refer to Figures 2.6 - 2.8), the exposed site will have a significantly lower Kaplan - Meier survivorship proportion, \( p_k \).

3.2.3 Reproductive effort and output

*Hedophyllum sessile* tatters during periods of wave stress, losing blade surface area distally and increasing the number of blades (Figures 2.17, 2.18). To test if increased thallus tattering, which results from increased wave-exposure, reduces reproduction, reproductive status in *H. sessile* was examined during the monitoring period.

Reproductive effort was estimated. Reproductive effort is the amount of resources allocated to reproduction over a defined period of time (Begon *et al.*, 1990). Instantaneous samples to represent relative reproductive efforts were collected and analyzed for soral area produced per total blade area. This method was assumed to yield analogous data to reproductive efforts as defined by Begon *et al.* (1990) since blade and soral production are continuous events (Klinger, 1984; Ang, 1991).
At each sampling date between May 1995 and May 1996, the number of reproductive blades per holdfast along the permanent transects was noted. Data on the total number of sterile and fertile blades in December 1995 was supplemented by a haphazard sampling of 30 holdfasts per site. In October 1995 and December 1995, random samples of reproductive blades were collected by cutting two blades per randomly selected holdfast. For each holdfast, the longest and shortest reproductive blades were collected by cutting them off at their bases. In October 1995, 6 holdfasts were sampled in the exposed site and 30 sampled in the protected site. In December 1995, 33 holdfasts were sampled at each site. Blade surface area was quantified by tracing each blade and its soral areas on an acetate sheet. Outlines were scanned using a flatbed scanner; Image 1.57 (National Institute of Health) was used to calculate total blade and soral surface areas (cm$^2$) for blades from both sites (Figure 3.2).

To test if tattering is correlated to the number of blades which are reproductive, Pearson product-moment correlation coefficients (R) were calculated for a regression between the total number of blades and number of reproductive blades at each site. It is expected that the increase in blade number will not reduce the number of reproductive blades, since lengthwise tears will split reproductive blades and hence create more reproductive blades. Thus the number of reproductive blades should be directly correlated to total number of blades.

For each blade sampling date (October 1995, December 1995), regressions between total blade area and reproductive area were constructed; R was calculated to test for a correlation between those parameters. To test if the exposed site has a lower reproductive area per blade than the protected site, grouped t-tests (in SYSTAT version 5.03) were performed for each sample date to compare soral areas. It is predicted that reproductive area per blade
will be correlated with total blade surface area and that the exposed site will have significantly less reproductive area per blade than the protected site in each date.

Since the exposed site may have smaller but more numerous blades than in the protected site, due to tattering effects, reproductive output per individual was evaluated in two ways. First, reproductive effort was represented by the normalized reproductive area per blade. This was calculated by dividing the reproductive area per blade by the total surface area of the blade. Confidence intervals (95%) were then constructed (equation 2.5) to compare these ratios. Since the primary location of blade loss is from their tips and sori are produced on the basal parts of the blade, it is predicted that total reproductive effort (as measured by normalized reproductive area) will be greater in the exposed site because exposed thalli tatter more.

Secondly, total reproductive area was estimated for each individual by multiplying the number of reproductive blades by the average soral area per blade; in each date, these data were compared using a grouped t-test. For all parametric statistical analyses, data were tested for normal distribution and equal variance and transformed if necessary. It is expected that differences in blade area and reproductive area per blade between sites will be reflected as lower reproductive output per individual. Thus, if blade area and reproductive area are lower in the exposed site, then the exposed site will have a lower total reproductive output per individual.

3.2.4 Implications of mortality rates for population maintenance

In highly wave-exposed sites the rate of elimination of Hedophyllum sessile may exceed that of recovery, especially if the population is isolated from dispersal from surrounding areas. In order to illustrate potential ramifications of differential mortality rates on population size, simple matrix models were constructed.
The model is a simple Leslie matrix (Leslie, 1945 and in DeWreede, 1986; Ang and DeWreede, 1990; Ang and DeWreede, 1993). The transition matrix was derived directly from May 1995 life table $p_x$ values. Transition matrix ($M$) is constructed of submatrices, each of the form (Ang and DeWreede, 1993):

$$M = \begin{bmatrix} A & C \\ B & D \end{bmatrix}$$

Where $A$ and $D$ describes the probability of staying within an age class. Since these data are age intervals, these values are 0. $B$ describes the proportion of individuals moving from age class 1 to 2 ($p_x$), and so on. $C$ is the fecundity per capita within an age class.

The transition matrices were multiplied by column vectors. Each row of the column vector represents the number of individuals within an age class. Age classes were designated as 0 - 9, where 0 represents the microscopic stage and is used to represent the time delay (here estimated to be approximately 60 days, based on study site observations) involved between reproductive output and juvenile sporophyte appearance. Each age class thereafter (1 - 9) is a class equivalent to a life table interval. Thus the column vectors were:

$$N = \begin{bmatrix} 0 (-60 \text{ to } 0 \text{ days, d.}) \\ 1 (0 - 57 \text{ d.}) \\ 2 (57 - 104 \text{ d.}) \\ 3 (104 - 154 \text{ d.}) \\ 4 (154 - 209 \text{ d.}) \\ 5 (209 - 266 \text{ d.}) \\ 6 (266 - 307 \text{ d.}) \\ 7 (307 - 370 \text{ d.}) \\ 8 (370 - 442 \text{ d.}) \\ 9 (442 - 503 \text{ d.}) \\ 10 (> 503 \text{ d.}) \end{bmatrix}$$
Population growth was then defined as:

\[ N_{t+1} = M \cdot N_t \]  \hspace{1cm} \text{eq. 3.4}

Where \( t \) is time and each time step is a time interval equivalent to sampling dates (~ every 2 months).

Population sizes for any model projection were sums of individuals alive in age classes 1 - 9. A newly recruited April cohort was simulated by starting projections from April with 1000 individuals in age class 1, and 0 individuals in all other ages. Population sizes were projected for 4 recruitment periods. Sample calculations of the model projections are in Appendix 1.

Two types of matrices per site were constructed; one assumed no recruitment and was used to depict the cohort life table data, and the other assumed 10 individuals successfully recruited by each surviving reproductive adult. The estimation that 10 individuals will successfully recruit per reproductive sporophyte is used to demonstrate how the populations rely on recruitment, since measurements of successful recruitment from a single, reproductive kelp sporophyte varies from 1 - 2 (for \textit{Laminaria longicruris} and \textit{L. digitata}, respectively, Chapman, 1984) to approximately 265 (for \textit{Macrocystis pyrifera}; Anderson and North, 1965). Also, as previously discussed, reproductive output is not necessarily correlated to eventual recruitment thus differences between proportions of reproductive individuals were not taken into account.
3.3 Results

3.3.1 Recruitment and survivorship

*Hedophyllum sessile* recruitment occurs during spring and summer months (Table 3.1). However, these recruits do not mature at similar rates (Figure 3.3). Recruitment is substratum-dependent with higher recruitment on articulated coralline algae and *H. sessile* holdfasts (Table 3.2).

Life tables of the May 1995 cohort suggest that these two sub-populations have different population parameters (Tables 3.3, 3.4). The probability of surviving ($p_x$) to the next age interval is similar from May through September. From September through December, the individuals in the exposed site have a lower probability ($p_x = 0.44$ and $p_x = 0.25$) of surviving compared to those in the protected site ($p_x = 0.81$ and $p_x = 0.77$). Life expectancy ($e_x$, days) in the exposed site declines at each age interval whereas it remains relatively constant until February in the protected site. Mean life expectancy values also reflect differences in survival by which the longevity of individuals in the exposed site is lower than the lifetime in the protected site after July 1995.

These observations are supported by Kapan-Meier survivorship analysis of the July 1995 adult cohort (Figure 3.4). During the times when wave-exposure is consistently different between sites (fall and winter months, Figure 2.6 - 2.8), adults in the exposed site have a more rapid decline in survival than those in the protected site. The cumulative probabilities as measured by the Kaplan-Meier $p_k$ of surviving to December and February are significantly less in the exposed site than in the protected site. At these census dates, 95% confidence intervals only slightly overlap. The difference in survivorship proportions (in December and
February) is primarily due to extremely low survivorship of adults in the exposed site relative to that in the protected site during the September - October time interval (Tables 3.5, 3.6). In these tables, sample sizes were extrapolated to population size of 1000 individuals and all size classes were pooled. By February, there are 333.3 individuals in the exposed site and 518.5 individuals in the protected site from the original cohort size of 1000. Additionally, the expected longevity for *H. sessile* (*ex, days*) is lower in the exposed site than in the protected site in both cohort life tables. Size structures are not shown for this cohort; in both sites in July 1995, approximately 30% of the adults are in size classes (SC) 3 - 5 and approximately 70% were in SC 1 - 2.

### 3.3.2 Reproductive effort and output

During the May 1995 - May 1996 period, soral production occurred in October and December 1995 as shown by *P*<sub>R</sub> values (Tables 3.3 - 3.6). This reproduction is plant size-dependent. One hundred percent of the juveniles in exposed site and up to 67% in the protected site were reproductive in the first year (Tables 3.3, 3.4); this correlates to plant sizes (Figure 3.3) where 100% of individuals in the exposed site were in or larger than size class (SC) 2 whereas only about 40% were larger than SC 1 in the protected site. The total number of reproductive blades per holdfast is significantly positively correlated to the total number of blades on the holdfast (Table 3.7), and the number of reproductive blades per holdfast can be predicted using a linear regression from the total number of blades (Figures 3.5, 3.6). In October, the measured number of reproductive blades per holdfast in the exposed site range from 1 to 20 whereas the number in the protected site ranges from 0 to 12. A similar pattern is repeated in December except that the number of reproductive blades per holdfast in the exposed site is 10 to 37 and the number in the protected site is 1 to 18.
Soral area is directly related to total blade surface area (Figures 3.7, 3.8). In October, the average soral area per blade in the exposed site was 61.03 (± 8.83 SE, n=12) cm², whereas that in the protected site was 93.31 (± 8.71 SE, n=60) cm². Average reproductive area per blade in December 1995 in the exposed and protected sites was 26.24 (± 1.97 SE, n=66) and 46.04 (± 3.99 SE, n=66), respectively. Within each date, data were square-root transformed to achieve normal distribution of data, and t-test results showed that the exposed site has significantly less reproductive surface area per blade (in October, p = 0.064; in December, p< 0.001). Data suggest that soral area and hence reproductive output is limited by blade surface area; total surface area and reproductive area are directly correlated, and there is significantly less soral area per blade in the exposed site.

However, when the tissue surface area dedicated to reproduction was analyzed for differences in reproductive effort per blade and reproductive output per individual, it was found that even though the exposed site blades produce less reproductive tissue, overall, this was not reflected in lower reproductive effort. In October, the reproductive effort of *Hedophyllum sessile* at both sites have similar amounts of reproductive tissue per total tissue area (Figure 3.9). However, in December, *H. sessile* has a slightly higher reproductive effort than in the protected site (Figure 3.9).

In the exposed site, the relatively low soral area per blade is not reflected in total reproductive area per individual (Figure 3.10). Within each site, the estimated mean soral area per holdfast between sampling dates was relatively constant. Contrary to original predictions, grouped t-tests within each sampling date showed that *H. sessile* in the exposed site had a
greater total thallus surface area dedicated to soral area than those in the protected site (October, \( p = 0.03 \); December, \( p = 0.002 \)).

### 3.3.3 Matrix model projections

As expected, without recruitment both populations will go locally extinct, and the exposed site population would disappear 5 months before that in the protected site (Tables 3.8, 3.9; Figure 3.11). This would only realistically occur if there was reproductive failure by adults, complete failure of dispersal (from surrounding areas), and/or no post-settlement stage survival. Predictions for populations in these sites, with successful recruitment (Tables 3.10, 3.11; Figure 3.12), demonstrate that populations are maintained but that over time, the annual population in the protected site grows more rapidly since individuals survive into the second reproductive season. Recruitment is important to both sites for maintenance; however, the exposed population is primarily dependent on annual recruitment to supply individuals.

Based on survivorship data and matrix projections, the population in the exposed site acts as an annual population, dependent on annual reproduction and recruitment. If local adult reproductive output or recruitment fails, the population in the more exposed site may be at risk of becoming locally extinct. Yet, the exposed site individuals may have a lower risk of reproductive or recruitment failure since these plants have higher reproductive effort and output which could potentially correlate to a higher probability of recruitment success.
3.4 Discussion

3.4.1 Recruitment, survival, and mortality

_Hedophyllum sessile_ populations at these study sites show different demographic patterns. The most prominent site effect is on survival rates, especially during periods when sites consistently experienced higher wave forces. Adult survivorship is higher in the protected site after October when the site has comparatively lower wave-exposures. The juvenile cohort has a longevity of 264 days in the exposed site (0.73 years) and 497 days (1.37 years) in the protected site.

The age of the adults in the July 1995 cohort is not known. In both sites, a small percentage (~30%) of these adults were in size classes (SC) 3-5 and ~70% were in SC 1-2, suggesting that the larger holdfasts survived from the previous recruitment period (February - April 1994). However it is also possible that these individuals originated from the February - April 1995 spring recruitment period since a similar proportion of individuals from the May 1995 exposed site cohort grew from size class 1 to classes 3-4 within 4 months. Longevity of these adults from July 1995 in the exposed site was 442 days (1.21 years) and in the protected site was more than 503 days (>1.37 years). These results suggest that survival time is variable, ranging from 264 days to more than 442 days in the exposed site and from 497 days to more than 503 days in the protected site.

The influence of the chiton _Katharina tunicata_ on these results can not be deduced from the data collected. Markel and DeWreede (1998) demonstrated that high _K. tunicata_ densities decrease adult _H. sessile_ survival, presumably due to their increased burrowing activity in holdfasts and consequent holdfast susceptibility to dislodgment. During fall and winter 1995, _K. tunicata_ was more abundant in the exposed site than in the protected site. This
suggests an alternate mechanism for these mortality patterns in that it is the combined influence of variable chiton densities and physical forces that determine the different longevities of *H. sessile* adults. This conclusion is valid if *K. tunicata* has a similar effect in both the exposed and the protected site; the latter is the site where Markel and DeWreede (1998) conducted their study. In this case, *H. sessile* holdfasts should be more weakly attached in the more exposed site (prior to storm events) due to the increased burrowing activity. This hypothesis is tested in Chapter 4. In any event, despite the different *K. tunicata* densities between sites, these data represent demographic patterns found at two sites of different wave-exposures. Each site is characterized by different physical and biotic factors; these data should only be interpreted within the context of effects of wave-exposure on demographic patterns. Specific mechanisms producing these demographic patterns can not be isolated by the methods here.

An increased mortality rate in the exposed site opens space, and this may be the mechanism by which there is, on average, a lower *H. sessile* canopy cover in December 1995. This increased open space may also increase recolonization rates. Peak recruitment periods occur in the spring, and differential recruitment occurs on various substrata types. There is more recruitment on articulated coralline algae and in *H. sessile* holdfasts in both sites, but juveniles also use crustose coralline algae and bare rock. These observed recruitment patterns may result from the initially different attachment forces that can be attained by holdfasts on each substratum type, various levels of protection from grazers, and/or differing degrees of protection from scouring in the different substrata.

The May 1995 cohort's size structure shifts throughout the sampling period. All recruits in the exposed site grew into larger individuals by October 1995, whereas protected
site recruits remained in the juvenile size class until April 1996. These larger individuals in both sites were reproductive by October 1995. One possible mechanism for these differential growth rates is the enhancement of the growth of recruits by more open space. When recruitment occurred in May 1995, there was a lower (but p > 0.05) average canopy cover in the exposed site than in the protected site. Other studies have concluded that an adult canopy can limit juvenile recruitment by lowering irradiance levels (Hsiao and Druehl, 1973; Deysher and Dean, 1986; Dean et al, 1989) and by increasing scouring of the understory (Santelices and Ojeda, 1984). These interactions between adults and juveniles would result in high adult mortality followed by juvenile recruitment. For example, the adult density of *Macrocystis pyrifera* (L.) C. Ag in California kelp forests fluctuates, primarily due to storm dislodgment and subsequent pulses of sporophyte recruitment which often follow these thinning events (Pearse and Hines, 1979; Kimura and Foster, 1984; Reed and Foster, 1984).

### 3.4.2 Reproduction

There is not a clear difference between *Hedophyllum sessile* reproductive output in the two sites. In the wave-exposed site, the life of the juvenile cohort consists of recruitment in spring, growth to adult sizes by early autumn, reproductive maturity by winter, and dislodgment by February. In the wave-protected site, this life-time is extended through the first February until the following fall, at which time the individuals become reproductive again. The adult survival table data modify this pattern by indicating that individuals in the exposed site may live through a second summer. However, even the adult July 1995 cohort died before the second reproductive season, suggesting that individuals in the exposed site are likely to have only one reproductive season, whereas they will have two in the protected site. It is expected that this pattern would be exaggerated in sites more sheltered than this study’s protected site.
with an increase in the number of reproductive seasons would be increased, since longevity values as high as 730 days have been reported (Steneck and Dethier, 1994). Thus, if based solely on mortality rates, it would be concluded that over their entire lifetime, exposed site individuals have lower reproductive output than individuals at the protected site.

However this pattern of seemingly lower adult reproduction in the exposed site, based on mortality rates, is counteracted by differential reproductive output between sites. Initial predictions were that *H. sessile* in the more exposed site would have a lower reproductive potential since exposed site individuals tatter more and have a lower thallus area than protected site individuals. The probability of becoming reproductive in the first year is greater in the exposed site ($P_R = 1$ in the exposed site; $P_R = 0.67$ & 0.3 in the protected site), which most likely correlates with the increased growth of juveniles in this site. For sporophyte reproduction in *H. sessile*, therefore, thallus size is a better descriptor of this demographic parameter than age, which agrees with demographic analyses for other species of algae (e.g., Chapman, 1986; Lazo and McLachlan, 1990; Ang, 1991).

Furthermore, *H. sessile* in the more exposed site had a greater reproductive effort and larger total soral area per holdfast. The increased reproductive effort is most likely an artifact of the process by which *H. sessile* tatters (soral area is produced on basal parts of the blade while tattering primarily occurs distally). Loss of total surface area from the vegetative distal ends yields a higher reproductive effort since this parameter is measured as the ratio between tissue dedicated to reproduction to the total tissue area.

This process of tattering does not explain why the more wave-exposed site had more soral area per holdfast. Here a similar process, as was described by DeWreede and Klinger (1988), could be occurring whereby increased length and reproduction occurs by rapid thallus
elongation concurrent with or followed by the onset of reproduction. In *H. sessile*, more rapid juvenile growth into mature size classes occurs but since blades are tattered distally, rapid elongation in plant length is not obvious. However, this rapid growth may still be reflected in increased reproductive tissue.

### 3.4.3 Implications of differential mortality rates to population maintenance

The contribution of zoospore output to population maintenance is probably of minimal importance since events occurring during microscopic stages would probably decouple zoospore output from juvenile sporophyte recruitment. However, site-specific survival rates found in these sub-populations may have more substantial consequences on the sizes of isolated populations. In highly wave-exposed areas (such as this exposed site and exposures greater than this site) with similar biological communities, the rate of elimination of *Hedophyllum sessile* may exceed that of recovery. The population would then become extinct in these areas, or be in a state of decline that periodically is reversed, e.g. when a recruitment "window" occurs. This could occur in spring and summer months when the exposed site does not experience high wave-exposure.

Another possible mechanism by which these populations can avoid risk of an episodic, annual recruitment failure is by maintaining a germling bank (Santelices, 1990; Vadas *et al.*, 1992). The matrix projections assumed an approximately 60-day interval between adult reproductive output and recruitment, to account for time of gametophyte development. This assumption, however, is questionable. Similar to the delayed growth seen in size class 1 juveniles in the protected site, microscopic stages (germlings) may experience delayed growth and remain at a small size and young developmental stage for a prolonged period. An indefinite germling stage may place individuals at greater risk, since predation or physical
stresses may be extremely high for this stage. On the other hand, this germling bank may increase the probability for the population's persistence by balancing fluctuations in successful dispersal (Ang, 1991) and may even uncouple recruitment from dispersal (Kendrick, 1994). Thus, despite potential limitation of recruitment by dispersal variability, a germling bank may compensate by supplying recruits.

3.4.4 Conclusion

Results from this study demonstrate that wave-exposure affects these populations' demographic parameters. The population at the exposed site is at risk of local extinction if successful annual recruitment fails. The protected population may be at risk if two successive annual recruitment periods fail. These results agree with those of numerous others which conclude that recruitment processes are important to the population structure of dominant species in intertidal and subtidal systems (e.g., Connell, 1985; Gaines and Roughgarden, 1985; Roughgarden et al., 1985). Specifically these conclusions agree with those of Duggins and Dethier (1985) who concluded that for *Hedophyllum sessile*, loss during winter storms coupled with intensive grazing on juvenile sporophytes will produce local extinction. These effects most certainly will be more pronounced and occur at a greater rate in more exposed sites.

Recruitment could occur from existing germling banks or successful dispersal from surrounding areas. Thus for the populations surveyed, population parameter differences most likely do not affect population maintenance. However, these conclusions also imply that populations in sites that are highly wave-exposed and isolated from large source populations would be more at risk to local extinction from episodic events causing recruitment failure than isolated populations in moderately wave-exposed to wave-sheltered sites.
Table 3.1 Number of new *Hedophyllum sessile* recruits throughout sampling periods in exposed and protected sites. Mean number of new recruits ± 95% confidence intervals (n=10) are shown for 0.25 x 0.25 m quadrats (0.0625 m²).

<table>
<thead>
<tr>
<th>DATE</th>
<th>EXPOSED</th>
<th>PROTECTED</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAY 1995</td>
<td>2.6 ± 1.78</td>
<td>2.6 ± 2.14</td>
</tr>
<tr>
<td>JULY 1995</td>
<td>2.2 ± 1.34</td>
<td>4.1 ± 4.6</td>
</tr>
<tr>
<td>SEPTEMBER 1995</td>
<td>0.7 ± 1.35</td>
<td>1.2 ± 1.84</td>
</tr>
<tr>
<td>OCTOBER 1995</td>
<td>0 ± 0</td>
<td>0 ± 0</td>
</tr>
<tr>
<td>DECEMBER 1995</td>
<td>0 ± 0</td>
<td>0 ± 0</td>
</tr>
<tr>
<td>FEBRUARY 1996</td>
<td>0.5 ± 0.61</td>
<td>0.2 ± 0.30</td>
</tr>
<tr>
<td>APRIL 1996</td>
<td>21.4 ± 12.59</td>
<td>46.5 ± 36.33</td>
</tr>
<tr>
<td>JUNE 1996</td>
<td>9.2 ± 8.35</td>
<td>14.4 ± 12.26</td>
</tr>
<tr>
<td>AUGUST 1996</td>
<td>1.0 ± 1.66</td>
<td>0.8 ± 0.66</td>
</tr>
<tr>
<td>OCTOBER 1996</td>
<td>0 ± 0</td>
<td>0 ± 0</td>
</tr>
<tr>
<td>FEBRUARY 1997</td>
<td>1.7 ± 1.01</td>
<td>3.4 ± 3.41</td>
</tr>
</tbody>
</table>
Table 3.2 *Hedophyllum sessile* juvenile recruitment on different substrata types in May 1995. Measured by % juvenile occurrence / % substratum cover. Total number of juveniles sampled in exposed site is 37, and total number in the protected site is 81.

<table>
<thead>
<tr>
<th>substratum type</th>
<th>exposed site</th>
<th>protected site</th>
</tr>
</thead>
<tbody>
<tr>
<td>articulated coralline algae</td>
<td>2.00</td>
<td>1.23</td>
</tr>
<tr>
<td>crustose coralline algae</td>
<td>0.24</td>
<td>0.11</td>
</tr>
<tr>
<td>non-calcareous encrusting red algae</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>bare rock</td>
<td>0</td>
<td>0.76</td>
</tr>
<tr>
<td><em>Hedophyllum sessile</em> holdfasts</td>
<td>3.59</td>
<td>0.82</td>
</tr>
</tbody>
</table>
Table 3.3 Life table of *Hedophyllum sessile* at the exposed site. See footnote 3.1 for explanation of life table abbreviations.

<table>
<thead>
<tr>
<th>interval, $x$ (days)</th>
<th>month</th>
<th>$l_x$</th>
<th>$l_{x\ 1000}$</th>
<th>$d_{x\ 1000}$</th>
<th>$p_x$</th>
<th>$L_{x\ 1000}$</th>
<th>$e_{x,\ days}$</th>
<th>$P_R$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-55</td>
<td>May - Jul</td>
<td>37</td>
<td>1000</td>
<td>421.1</td>
<td>0.58</td>
<td>789.5</td>
<td>79.6</td>
<td>0</td>
</tr>
<tr>
<td>55-112</td>
<td>Jul - Sep</td>
<td>21</td>
<td>578.9</td>
<td>342.1</td>
<td>0.41</td>
<td>407.9</td>
<td>62.5</td>
<td>0</td>
</tr>
<tr>
<td>112-155</td>
<td>Sep - Oct</td>
<td>9</td>
<td>236.8</td>
<td>131.6</td>
<td>0.44</td>
<td>171.1</td>
<td>58.1</td>
<td>0</td>
</tr>
<tr>
<td>155-209</td>
<td>Oct - Dec</td>
<td>4</td>
<td>105.3</td>
<td>78.9</td>
<td>0.25</td>
<td>65.8</td>
<td>41.3</td>
<td>1</td>
</tr>
<tr>
<td>209-264</td>
<td>Dec - Feb</td>
<td>1</td>
<td>26.3</td>
<td>26.3</td>
<td>0</td>
<td>13.2</td>
<td>27.5</td>
<td>1</td>
</tr>
<tr>
<td>264-321</td>
<td>Feb - Apr</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

3.1 Life table abbreviations are: $x$, age interval in days; month, sample months; $l_x$, actual number living at start of interval; $l_{x\ 1000}$, standardized number to 1000 individuals; $d_{x\ 1000}$, standardized number dying during interval; $p_x$, probability of surviving to the next time interval; $L_{x\ 1000}$, standardized number of plants alive between intervals; $e_{x,\ days}$, mean life expectancy in days; $P_R$, probability of being reproductive at the beginning of the interval.
Table 3.4 Life table of *Hedophyllum sessile* at protected site. See footnote 3.2 for explanation of life table abbreviations.

<table>
<thead>
<tr>
<th>interval, ( x ) (days)</th>
<th>month</th>
<th>( l_x )</th>
<th>( l_x 1000 )</th>
<th>( d_x 1000 )</th>
<th>( p_x )</th>
<th>( L_x 1000 )</th>
<th>( e_{x, \text{days}} )</th>
<th>( P_R )</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-55</td>
<td>May - Jul</td>
<td>81</td>
<td>1000</td>
<td>518.5</td>
<td>0.48</td>
<td>740.7</td>
<td>95.4</td>
<td>0</td>
</tr>
<tr>
<td>55-112</td>
<td>Jul - Sep</td>
<td>39</td>
<td>481.5</td>
<td>284.0</td>
<td>0.41</td>
<td>339.5</td>
<td>113.5</td>
<td>0</td>
</tr>
<tr>
<td>112-155</td>
<td>Sep - Oct</td>
<td>16</td>
<td>197.5</td>
<td>37.0</td>
<td>0.81</td>
<td>179.0</td>
<td>182.2</td>
<td>0</td>
</tr>
<tr>
<td>155-209</td>
<td>Oct - Dec</td>
<td>13</td>
<td>160.5</td>
<td>37.0</td>
<td>0.77</td>
<td>142.0</td>
<td>162.9</td>
<td>0.67</td>
</tr>
<tr>
<td>209-264</td>
<td>Dec - Feb</td>
<td>10</td>
<td>123.5</td>
<td>24.7</td>
<td>0.8</td>
<td>111.1</td>
<td>148.5</td>
<td>0.3</td>
</tr>
<tr>
<td>264-321</td>
<td>Feb - Apr</td>
<td>8</td>
<td>98.8</td>
<td>24.7</td>
<td>0.75</td>
<td>86.4</td>
<td>123.8</td>
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<tr>
<td>321-362</td>
<td>Apr - Jul</td>
<td>6</td>
<td>74.1</td>
<td>0</td>
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<td>74.1</td>
<td>100.8</td>
<td>0</td>
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<tr>
<td>362-425</td>
<td>Jul - Aug</td>
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<td>74.1</td>
<td>61.7</td>
<td>0.17</td>
<td>43.2</td>
<td>45.8</td>
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<tr>
<td>425-497</td>
<td>Aug - Oct</td>
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<td>12.3</td>
<td>0</td>
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<td>12.3</td>
<td>82.5</td>
<td>0</td>
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<tr>
<td>497- 569</td>
<td>Oct - Dec</td>
<td>1</td>
<td>12.3</td>
<td>12.3</td>
<td>0</td>
<td>6.15</td>
<td>27.5</td>
<td>1</td>
</tr>
</tbody>
</table>

3.2 Life table abbreviations are: \( x \), age interval in days; month, sample months; \( l_x \), actual number living at start of interval; \( l_x 1000 \), standardized number to 1000 individuals; \( d_x 1000 \), standardized number dying during interval; \( p_x \), probability of surviving to the next time interval; \( L_x 1000 \), standardized number of plants alive between intervals; \( e_{x, \text{days}} \), mean life expectancy in days; \( P_R \), probability of being reproductive at the beginning of the interval.
Table 3.5 Survival table of adult *Hedophyllum sessile* at the exposed site. See footnote 3.3 for explanation of survival table abbreviations.

<table>
<thead>
<tr>
<th>Interval, x (days)</th>
<th>Month</th>
<th>$l_x$</th>
<th>$l_x_{1000}$</th>
<th>$d_x_{1000}$</th>
<th>$p_x$</th>
<th>$L_x_{1000}$</th>
<th>$e_{x, \text{days}}$</th>
<th>$P_R$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-57</td>
<td>Jul - Sep</td>
<td>48</td>
<td>1000</td>
<td>250</td>
<td>0.75</td>
<td>875</td>
<td>154.7</td>
<td>0</td>
</tr>
<tr>
<td>57-104</td>
<td>Sep - Oct</td>
<td>36</td>
<td>750</td>
<td>270.8</td>
<td>0.64</td>
<td>614.6</td>
<td>142.1</td>
<td>0</td>
</tr>
<tr>
<td>104-154</td>
<td>Oct - Dec</td>
<td>23</td>
<td>479.2</td>
<td>145.8</td>
<td>0.70</td>
<td>406.3</td>
<td>151.85</td>
<td>1</td>
</tr>
<tr>
<td>154-209</td>
<td>Dec - Feb</td>
<td>16</td>
<td>333.3</td>
<td>0</td>
<td>1</td>
<td>333.3</td>
<td>151.3</td>
<td>1</td>
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<tr>
<td>209-266</td>
<td>Feb - Apr</td>
<td>16</td>
<td>333.3</td>
<td>125</td>
<td>0.63</td>
<td>270.8</td>
<td>96.3</td>
<td>0</td>
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<tr>
<td>266-307</td>
<td>Apr - Jul</td>
<td>10</td>
<td>208.3</td>
<td>62.5</td>
<td>0.70</td>
<td>177.1</td>
<td>82.5</td>
<td>0</td>
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<td>7</td>
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<td>0.43</td>
<td>104.2</td>
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<td>370-442</td>
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<td>3</td>
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<td>31.3</td>
<td>27.5</td>
<td>0</td>
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<tr>
<td>442-503</td>
<td>Oct - Dec</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Survival table abbreviations are: $x$, age interval in days; month, sample months; $l_x$, actual number living at start of interval; $l_x_{1000}$, standardized number to 1000 individuals; $d_x_{1000}$, standardized number dying during interval; $p_x$, probability of surviving to the next time interval; $L_x_{1000}$, standardized number of plants alive between intervals; $e_{x, \text{days}}$, mean life expectancy in days; $P_R$, probability of being reproductive at the beginning of the interval.
Table 3.6 Survival table of adult *Hedophyllum sessile* at the protected site. See footnote 3.4 for explanation of survival table abbreviations.

<table>
<thead>
<tr>
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3.4 Survival table abbreviations are: \( x \), age interval in days; month, sample months; \( l_x \), actual number living at start of interval; \( l_{x\,1000} \), standardized number to 1000 individuals; \( d_{x\,1000} \), standardized number dying during interval; \( p_x \), probability of surviving to the next time interval; \( L_{x\,1000} \), standardized number of plants alive between intervals; \( e_{x\,days} \), mean life expectancy in days; \( P_R \), probability of being reproductive at the beginning of the interval. Data not available (NA) designates that individuals were not monitored in a follow-up census date, thus values could not be calculated.
Table 3.7 Pearson correlation coefficients (R), sample sizes (n), and p-values for the correlation between total number of blades per adult holdfast and the total number of reproductive blades.

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Table 3.8 Transition matrix for *Hedophyllum sessile* in the exposed site with no adult fecundity or recruitment. Life stages 0 - 5 represent age intervals where 0 is a gametophyte, microscopic stage age interval (55 days) and 1 -5 represent macroscopic stages’ age intervals shown in Table 3.3. **1** = 0-55 days, **2** = 55 - 112 days, **3** = 112 - 155, **4** = 155- 209 days, and **5** = 209 - 264 days. Life stages on top row are those from which individuals move into life stages in the first column. Transition values are $p_x$ values from Table 3.3.

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Table 3.9 Transition matrix for *Hedophyllum sessile* in protected site with no adult fecundity or recruitment. Life stages 0 - 10 represent age intervals where 0 is a gametophyte, microscopic stage age interval (~ 60 days) and 1 - 10 represent macroscopic age intervals shown in Table 3.4. 1 = 0-55 days (d), 2 = 55 - 112 d., 3 = 112 - 155 d., 4 = 155- 209 d., 5 = 209 - 264 d., 6 = 264 -321 d., 7 = 321 - 362 d., 8 = 362 - 425 d., 9 = 425 - 497 d., and 10 = 497 - 503 d. Life stages on top row are those from which individuals move into life stages in the first column. Transition values are $p_x$ values from Table 3.4.

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Table 3.10 Transition matrix for *Hedophyllum sessile* in exposed site with adult sporophyte fecundity represented as 10 new sporophyte individuals successfully recruiting into age interval 1 per reproductive adult during that interval. Life stages 0 to 5 represent age intervals where 0 is a gametophyte, microscopic stage age interval (~ 60 days) and 1 -5 represent macroscopic age intervals shown in Table 3.3. 1 = 0-55 days, 2 = 55 - 112 days, 3 = 112 - 155, 4 = 155- 209 days, and 5 = 209 - 264 days. Life stages on top row are those from which individuals move into life stages in the first column. Transition values are $p_x$ values from Table 3.3.

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Table 3.11 Transition matrix for *Hedophyllum sessile* in protected site with adult sporophyte fecundity represented as 10 new sporophyte individuals successfully recruiting into age interval 1 per reproductive adult during that interval. Life stages 0 - 10 represent age intervals where 0 is a gametophyte, microscopic stage age interval (~60 days) and 1 - 10 represent macroscopic age intervals shown in Tables 3.4. 1 = 0-55 days (d), 2 = 55 - 112 d., 3 = 112 - 155 d., 4 = 155-209 d., 5 = 209-264 d., 6 = 264-321 d., 7 = 321-362 d., 8 = 362-425 d., 9 = 425-497 d., and 10 = 497-503 d. Life stages on top row are those from which individuals move into life stages in the first column. Transition values are \( px \) values from Table 3.4

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Figure 3.1 *Hedophyllum sessile* life cycle. A generalized kelp life cycle (modified from Cheng, 1969 in Lee, 1980 for *Laminaria japonica*). Adult reproductive sporophytes produce soral patches (A) in which unilocular sporangia (B) produce zoospores. Male and female zoospores (C, D) settle onto substratum (E,F) and form male and female gametophytes (G,H, I, J). The mature male gametophyte (J) produces sperm, which are released. The zygote (L) is formed when the egg is fertilized by sperm. This then grows into a juvenile sporophyte (M). Microscopic phases of this life cycle are from the zoospore to the microscopic juvenile sporophyte stages (B - L) and dispersal in the water column occurs by zoospores and by sperm (C, D, K). In this research, recruitment is defined as the appearance of a macroscopic juvenile sporophyte (M).
Figure 3.2 Representative outlines of *Hedophyllum sessile* reproductive blades used for quantifying reproductive effort and output. Shaded areas are vegetative tissue and open areas are sori. Blades from exposed and protected sites shown here were collected in October 1995.
Figure 3.3 Size structure over time in May 1995 *Hedophyllum sessile* cohort. Shaded bars represent exposed site and open bars are protected site. Holdfast size class (SC) 1 = < 0.5 cm$^2$, SC 2 = 0.5 - 4 cm$^2$, SC 3 = 4 - 7 cm$^2$, SC 4 = 7 - 12 cm$^2$, SC 5 = > 12 cm$^2$. 
Figure 3.4 Comparison of adult *Hedophyllum sessile* cohort survivorship at exposed and protected sites. Kaplan-Meier survival proportion ($p_k$) was calculated for each census date and represents the cumulative proportion of surviving individuals to that census date. Shaded bars are exposed site and open bars are protected site.
Figure 3.5 Number of reproductive blades as a function of total blades per holdfast in October 1995. Data points represent individual measurements for exposed site (●) and protected site (○) individuals. Solid linear regression line is for the exposed site (y = 0.7456 X - 3.686, r=0.879, p<0.001) and dotted linear regression represents protected site data (y = 0.4987 X - 0.8898, r=0.875, p<0.001).
Figure 3.6 Number of reproductive blades as a function of total blades per holdfast in December 1995. Data points represent individual measurements for exposed site (●) and protected site (○) individuals. Solid linear regression line is for the exposed site (y = 0.98213 X - 0.6501, r=0.984, p<0.001) and dotted linear regression represents protected site data (y = 0.9408 X - 0.4567, r=0.971, p<0.001).
Figure 3.7 Soral area per blade (cm²) as a function of total blade surface area (cm²) in October 1995. Data points represent individual measurements for exposed site (●) and protected site (○) individuals. Solid linear regression line is for the exposed site (y = 0.395X + 14.307, r=0.775, p=0.005) and dotted linear regression represents protected site data (y = 0.429X + 3.971, r=0.772, p<0.001).
Figure 3.8 Soral area per blade (cm$^2$) as a function of total blade surface area (cm$^2$) in December 1995. Data points represent individual measurements for exposed site (●) and protected site (○) individuals. Solid linear regression line is for the exposed site (y = 0.216X + 4.983, r=0.313, p<0.001) and dotted linear regression represents protected site data (y = 0.0648X + 30.459, r=0.661, p=0.011).
Figure 3.9 *Hedophyllum sessile* reproductive effort as measured by normalized reproductive area per blade in October (OCT) and December (DEC) 1995. Shaded bars are exposed site (EXP) and open bars are protected site (PRO). Error bars represent 95% confidence intervals as estimated by equation (2.5).
Figure 3.10 Estimated total reproductive area of mature and reproductive *Hedophyllum sessile* in October (OCT) and December (DEC) 1995. Shaded bars are exposed site (EXP) and open bars are the protected site (PRO). Error bars are standard error of the mean.
Figure 3.11 Simulation of *Hedophyllum sessile* population sizes in exposed and protected sites without successful recruitment from the initial population. Shaded bars represent the exposed site and open bars represent the protected site. Both initial populations start at 1000, newly recruited juveniles and population sizes thereafter were projected using a simple Leslie matrix model (see text for description). See Tables 3.8 and 3.9 for transition matrices.
Figure 3.12 Simulation of Hedophyllum sessile population sizes in exposed and protected sites with subsequent annual recruitment. Shaded bars represent exposed site and the open bars represent the protected site. Both initial populations start at 1000, newly recruited juveniles and population sizes thereafter were projected using a simple Leslie matrix model (see text for description). Horizontal line is at 1000 individuals; any bars above this line represent population growth from the initial population size. See Tables 3.10 and 3.11 for transition matrices.
CHAPTER 4

Holdfast attachment mechanics and their ecological implications

4.1 Introduction

Recent studies on mechanisms of wave-induced mortality in macroalgae have demonstrated that biomechanical approaches can explain species distributions and morphological patterns (Gaylord et al., 1994). For example, Shaughnessy et al. (1996) demonstrated that differences in distribution of two closely related species (Mazzaella linearis and M. splendens, Rhodophyta) in relation to wave-exposure could be predicted by a biomechanical survivorship model. Many of the studies to date focus on variations in thallus attributes, such as tissue mechanics (Koehl and Wainwright, 1977; Biedka et al., 1987; Denny et al., 1989) and thallus shape (Koehl, 1984; Carrington, 1990; Dudgeon and Johnson, 1992), which may resist and minimize wave stresses, and attachment forces that resist wave stress (Carrington, 1990; Friedland and Denny, 1995).

In general, survival in wave-exposed sites is dependent on the total forces transferred from the wave to the thallus attachment and the resistance force of the attachment. If the total hydrodynamically-induced force exceeds the attachment force, then the alga or part of the alga will be dislodged (Carrington, 1990). The majority of field measurements of attachment forces resulted in thallus breaks above the holdfast at either the stipe or the stipe/blade junction (Carrington, 1990; Dudgeon and Johnson, 1992; Shaughnessy et al., 1996). This results in partial thallus loss, with the holdfast or holdfast and stipe remaining for potential regrowth. In this case, biomass loss before reproduction reduces the number of propagules available for dispersal and recruitment. In cases of holdfast failure, the whole thallus is dislodged, and space is opened for recolonization.
Despite increased attention towards understanding effects of wave force on intertidal organisms, there is a lack of empirical studies documenting the variation in attachment properties between and within species, and across gradients such as wave-exposures, seasons, and substratum types. Biomechanical attributes, such as locations most prone to breakage, forces to break, and tissue strengths, that are observed in the field reflect the complex interactions between intrinsic (such as evolved tissue traits) and extrinsic (for example, herbivore and wave damage) factors which directly affect individual survival in wave-exposed sites.

A species' evolved tissue mechanics contribute to ways in which it resists physical damage. For example, in order to increase attachment force, either stronger (strength is measured as force/unit area) tissue or increased cross sectional area of break junction is needed. *Mazzaella splendens*, *M. linearis*, (Shaughnessy et al., 1996) and *Mastocarpus papillatus* (Carrington, 1990) increase resistance to breakage by increasing stipe cross sectional area while maintaining a constant tissue strength.

Combinations of herbivore- and wave-induced damage to a thallus, such as flaws and cracks in stipes, blades, or holdfasts, are common (Koehl and Wainwright, 1977; DeWreede et al., 1992). In stipes and blades, flaws and cracks propagate fracture lines when stressed, producing failure-prone locations (Denny et al., 1989). Damage to the holdfast base from invertebrate burrowing activity results in less holdfast area attached to the substratum (Tegner et al., 1995) and thus provides less resistance to stress. Depending on the severity of wounding from extrinsic factors, the thallus will ultimately break at locations different from those that occur in non-damaged thalli (Biedka et al., 1987).

Our knowledge of macroalgal attachment properties and factors affecting them is based primarily on species which regularly fail at the stipe or stipe/blade junction. Holdfast failure has not been studied in detail even though it is a commonly observed occurrence, especially in some kelp species (Koehl and Wainwright, 1977; Tegner et al., 1995). Holdfast loosening is a natural progression in kelp maturity, resulting from individual haptera being
detached from the substratum, usually by invertebrate burrows (McLay and Hayward, 1987), age (specifically, by increased sedimentation and shading; Ghelardi, 1971), and wave forces (Dayton et al., 1984). This loosening may influence individual biomechanical success.

The objectives of this study are to quantify the variation in holdfast attachment properties of *Hedophyllum sessile* and interpret the results in the context of *H. sessile*’s survival. *Hedophyllum sessile* is a dominant kelp species found in moderately to highly wave-exposed sites in the lower intertidal zone in the North-eastern Pacific Ocean (Abbott and Hollenberg, 1976).

In *H. sessile*, sporophyte recruitment occurs in late winter through spring and successful recruitment differs on different substrata types (Chapter 3, Table 3.2). Juveniles are characterized by a holdfast, stipe, and blade (Widdowson, 1965). Juvenile mortality has been primarily attributed to herbivore damage by the dominant grazing chiton, *Katharina tunicata* (Duggins and Dethier, 1985). The stipe is lost as *H. sessile* juveniles develop, and the adults consist of blades growing directly from the holdfast. Therefore, adult biomass loss can happen on the blades or at the holdfast. Adult mortality by holdfast dislodgment is primarily from winter storm damage (Dayton, 1975; Paine, 1980; Duggins and Dethier, 1985), and there is some evidence that *K. tunicata* will loosen adult holdfasts, making dislodgment more likely during winter storm swells (Markel and DeWreede, 1998). If thalli are cropped and tattered as a result of winter storms, the basal meristem and holdfast survive and new blade material will regenerate (Armstrong, 1987).

This chapter investigates how attachment forces vary within *H. sessile* at different developmental stages (juveniles vs. adults), wave-exposures, substratum types, and season. Since hydrodynamic force is bi-directional (shoreward and seaward) in the intertidal (Koehl, 1984), the holdfast mechanics in each of these directions are compared for adults. In addition, *H. sessile*’s holdfast removal force and strength are contrasted to those of other species found in similar environments to establish if *H. sessile* displays either a strategy of strength or increased attached holdfast surface area to resist wave forces.
4.2 Methods

4.2.1 Site description

*Hedophyllum sessile* was examined in moderately and extremely wave-exposed sites on Prasiola Point (Figure 2.1) in Barkley Sound, B.C. Sites were characterized as wave-exposed or wave-protected depending on the primary wave direction; a wave-exposed site was directly exposed to ocean swell, and a protected site was sheltered from these waves. Based on the classification by Harper et al. (1996), the exposed site is categorized as exposed/semi-exposed and the protected site is semi-exposed, based on the presence of specific indicator species. In lower tidal zones, *Lessoniopsis littoralis* was common in the exposed site, whereas *Laminaria setchelli* and *Egregia menziesii* were present in the protected site. Results from direct measurements of wave force at both sites (Figures 2.7, 2.8) illustrate that the difference in wave-exposure is seasonal, with significantly higher wave forces occurring more frequently during fall, winter, and early spring months (September/October through March).

4.2.2 Biomechanical measurements: force to remove, strength, and thallus surface area

Forces to remove *Hedophyllum sessile* were measured using a clamp and spring scale system. Juveniles were clamped just above the blade/stipe junction. Adults were clamped above the base of the blades. Two sizes of clamps (9 x 5 cm and 15 x 8 cm) were constructed from flat plates of 0.63 cm thick exterior plywood lined with rubber to distribute force evenly and reduce slippage on the thallus. Each clamp thus consisted of two flat plates, each with drilled holes at either end to fit a 0.63 cm diameter nylon screw. Threaded knobs (Small Parts, Inc., Miami Lakes, FL; KK series phenolic knobs with brass inserts) on each screw tightened the plates around the thallus. Additional holes (2 per plate) were drilled into the top of each plate, through which lines were threaded and used to attach the spring scales. Individual thalli were pulled parallel to the substratum as in previous studies (Carrington, 1990; Shaughnessy et al., 1996). The place of breakage was noted for each sample, and then thalli were returned to the lab for morphological analyses.
Spring scales were modified from Bell and Denny (1994) by attaching a monofilament line to the clamp and using 2 different spring tensions: “heavy” for adults (spring extension constant = 1.99 N • mm⁻¹) and “light” for juveniles (spring extension constant = 0.198 N • mm⁻¹). Two scales were used in progression for the adults when the removal force exceeded the first scale. If removal caused both scales to reach maximum extensions, then the total force to remove was calculated to be the sum of both maxima, thus producing a conservative estimate of removal force (this occurred in 20% of the samples). Scales were individually calibrated by hanging known masses (kg) and multiplying by the gravitational acceleration, 9.81 m • s⁻², for a relationship between spring extension (mm) and force (N). Field data were spring extension (mm), which were converted to force (N) by these calibration curves. The calibration curves were fit by linear regression analysis in SYSTAT 5.03.

Strength (N • m⁻²) is defined as the force (N) required to break the attachment divided by the cross-sectional area (m²) over which the failure occurs (Denny, 1988). Once the total force to remove was measured, each thallus was returned to the laboratory, blades were cut off at their bases, and all holdfast breaks directly scanned by placing the base of the holdfast on a flatbed scanner. These images were then used to measure the holdfast break area to nearest mm² (Image 1.57, National Institute of Health). Juvenile holdfasts consist of only a few haptera and could be freshly scanned. Adult holdfasts were made of more tightly compacted haptera and could not be scanned directly due to shadow effects. Thus, bases of break areas were photocopied and an outline drawn around the image on an acetate sheet, and these outlines were then scanned. In these cases, holdfast break area may have been slightly overestimated as individual haptera were not measured. Areas were converted to m² and strength calculated as MN • m⁻².

The blade surface area supported by each holdfast was measured in the laboratory by tracing the blade outlines on acetate sheets and area was then calculated in the same manner.
as for the holdfasts. Total wetted area, m², was estimated by doubling the calculated blade area.

4.2.3 Substratum and exposure effects on juveniles

Experiments on the effects of substratum type and wave-exposure on juvenile attachment force were performed in June 1996.

To assess the percent substratum available in each site, substratum types were grouped within sites as articulated coralline algae (AC), crustose coralline algae (CC), non-calcareous red encrusting algae (RC), and bare rock (BR). Ten 0.25 x 0.25 m plots were randomly placed in the Hedophyllum sessile zone at each site and percent cover of the substratum types was measured by point-intersect method (Dethier et al., 1993).

Juveniles were randomly sampled by clamping and pulling shoreward along horizontal transects in each site, and substratum type, force to remove, and break location were noted. Force data for holdfast breaks were grouped into treatments of substratum type and exposure. Differential recruitment was quantified by comparing the percent individuals sampled on each substratum (\( \frac{\# \text{ on substratum type}}{\text{total sampled}} \times 100 \)) to the percent cover of that substratum.

For removal force and holdfast area data, one-way ANOVA (in SYSTAT version 5.03) was used to test for group differences, and a Tukey Multiple Comparisons test was used to detect which groups were significantly different. Data were log-transformed to attain normal distribution and homogeneity of variances. Mean holdfast strength was calculated for each treatment.

4.2.4 Site and seasonal wave-exposure effects on adults

To assess if wave-exposure acts to loosen holdfasts, thus reducing the total force to remove, effects of site and seasonal wave-exposure were measured on adult holdfast attachment. Adults were measured in wave-exposed and protected sites on Prasiola Point in July (pre-storm) and October (post-storm) 1996 (Figure 4.1). At each site, horizontal transect lines were placed in the middle of the Hedophyllum sessile zone and random points chosen
along the lines. Adults closest to each point were chosen, and thalli were clamped and pulled. Pre-storm adults were pulled shoreward. In post-storm sampling, adults were pulled both shoreward and seaward at both wave-sheltered and wave-exposed sites to test if pull direction affects attachment.

Force to dislodge was measured and break location noted. Thalli were returned to the laboratory for thallus surface area and holdfast break area determination. If the entire thallus was not dislodged (holdfast and blade material were left on the substratum), the remaining thallus was subsequently pulled to test if partial holdfast loss would loosen the surviving portion.

Pull direction data from the post-storm survey were log transformed to achieve normal distribution. All data were tested for homogeneity of variances and transformed if necessary. Data were analyzed by one-way ANOVA. Treatment groups were site exposures and pull directions. If no differences were detected in pull directions in each site, then all pull direction data within each site were pooled for further comparisons to pre-storm data.

To compare site and seasonal effects on holdfast attachment, force data from complete holdfast dislodgment were grouped into sites and seasons, log transformed to achieve normal distribution and homogeneity of variances, and tested for differences by a one-way ANOVA. The same procedure was used to test effects on holdfast break area.

To further test how increased exposure affects variation of holdfast forces, cumulative probability distributions of normalized removal forces were constructed using methods of Gaylord et al. (1994), Denny (1995), and Friedland and Denny (1995). Each set of force data from exposed and sheltered sites in pre- and post-storm months was normalized by dividing the actual force to dislodge *H. sessile* by the mean removal force for that set, yielding values for normalized breaking forces ($f_n$). $f_n$ values were ranked in ascending order; ties were assigned the same rank. The equation:
was used to plot the cumulative probability \( p \) of a holdfast having less than a given \( f_h \). The rank of the sample is represented by \( i \), and \( n \) is the total number of samples. A generalized cumulative probability function,

\[
p = \exp \left[ -\left( \frac{a - bf_n}{a - bc} \right)^{\frac{1}{b}} \right]
\]

was fit to the observed probabilities from equation (4.1) using a nonlinear curve fitting routine in SigmaPlot version 2.0a. Confidence intervals (95%) were calculated for the cumulative distribution coefficients, \( a \), \( b \), and \( c \) in this curve-fitting routine. These intervals were used to determine if the estimated probability distributions for each site and season were different.

It is predicted that larger holdfasts are more firmly attached. Pearson product-moment correlation analysis was used to test if there is a relationship between holdfast area and the force required to remove thalli. To test if larger holdfasts support more blade area, data from each sampling group were analyzed for a correlative relationship between holdfast area and blade area using Pearson product-moment correlation and regression analyses. Blade areas were then compared between groups by calculating the wetted area per holdfast area; averages and 95% confidence intervals for these ratios were calculated (Cochran, 1977).
4.3 Results

4.3.1 Substratum and exposure effects on juveniles

Relative to the percent cover of substrata types open for recruitment (Figure 4.2), the number of juveniles found on each type were different (Table 4.1). Only juveniles on articulated corallines (AC) in the exposed site and on articulated and crustose coralline algae (CC) in the protected site had sufficient sample size (>2) and thus were the only sample groups used in analyses. Thus, juvenile attachment data were used to compare the difference between juvenile attachment on AC in exposed and protected sites, and to compare the attachment between AC and CC within the protected site.

For all types and sites, juveniles primarily broke at the holdfast/substratum boundary (Figure 4.3). All holdfasts completely broke off the substratum, leaving no holdfast remnants; for this reason, holdfast break area is considered equal to the holdfast area which was originally attached. Analysis of holdfast removal data (Figure 4.4) shows that juveniles on articulated coralline algae (AC) in the exposed site required significantly more force to remove than those on AC in the protected site (p<0.001, n=23). Within the protected site, juveniles on AC required more force to remove than those on crustose coralline algae (CC; p=0.003, n=23) and had less juvenile holdfast area attached on CC than AC (p=0.008, n=23). Juveniles on CC, therefore, had weaker holdfast strength than juveniles on AC in both exposed and protected sites.

4.3.2 Site and seasonal wave-exposure effects on adults

Compared to the number of complete holdfast breaks, partial holdfast breaks occurred rarely in adult Hedophyllum sessile (Figure 4.5). As with the juveniles, adult H. sessile is removed primarily at the holdfast base (Figure 4.6). However, upon removal, either
small remnants of holdfast were left (holdfast only break) or some of the coralline algae beneath the holdfast (holdfast/substratum break) was removed as well. Both of these types of breaks were considered holdfast breaks and pooled for statistical analyses.

For complete holdfast breaks in each site, shoreward and seaward pulls were not different in removal force ($p=0.279, n=11$) or holdfast break area ($p=0.797, n=11$). These data are not shown in a figure. Shoreward and seaward pulls were pooled and used to compare force to break and break area between sites and seasons.

The force (pooled mean = 100.69 N ± 6.793 SE) required to remove $H. \text{ sessile}$ adults was consistent over sites and seasons ($p=0.355, n=13$; Figure 4.7). Holdfast break area (pooled mean = 0.0019 m$^2$ ± 0.0001 SE) was also consistent over sites and seasons, with the exception that the protected, post-storm group was significantly larger than the exposed, pre-storm group ($p=0.025, n=13$). Thus, the protected, post-storm group had a weaker holdfast attachment strength than other experimental groups (Table 4.2). There was no direct relationship between holdfast break area and the force to remove in the pre-storm sampling, but a significant relationship in the post-storm sampling (Table 4.3). Larger holdfasts support more thallus area (Figure 4.8; Table 4.4), and holdfasts at both sites support significantly less blade area in the post-storm month than in summer (Table 4.4).

Partial holdfast removal decreased the average attachment force of the remaining holdfast (Figure 4.9). However, data were variable because sample sizes were small; therefore, it can not be concluded on a statistical basis that partial removal affects the integrity of the remaining holdfast.
Even though the ANOVA showed no differences in average attachment forces between sites and seasons, there is a seasonal effect on the distribution of attachment forces within the sampled populations. There is a shift to more resistant holdfasts at both sites as a result of seasonal exposure (Figure 4.10). For simplicity, 95% confidence intervals (Table 4.5) are not shown around the estimated distributions; however, above the normalized force of 1.5, there is a seasonal effect at each site (p < 0.05).

4.4 Discussion

4.4.1 Juvenile attachment

Data presented in this chapter suggest that flow regimes and holdfast/substratum interactions are also important factors for determining juvenile survivorship and abundance. Even though there were no significant differences in substratum types available for recruitment between the sites, juveniles occur more often on articulated coralline algae than on other available substrata and this difference is more distinct in the exposed site. Previous studies on *Hedophyllum sessile* recruitment have focused on effects of grazers, specifically the chiton *Katharina tunicata*, on juvenile distributions and densities (Duggins and Dethier, 1985; Markel and DeWreede, 1998). In this study, I can not exclude grazer influence as a potential mechanism of juvenile *H. sessile* distributions since the articulated coralline algae may provide a refuge from *K. tunicata* (Markel and DeWreede, 1998).

Despite this, results here suggest that another possible mechanism for this distribution pattern is the potential attachment force that the holdfast can attain on different substrata. Significantly greater attachment force and greater strength of *H. sessile* juveniles on articulated coralline algae in the exposed site than in the protected site indicate a
biomechanical response to wave-exposure, where more hydrodynamic stress is reflected in attachment properties. In addition, juveniles of *H. sessile* on articulated coralline algae had less holdfast area yet were more firmly attached in the exposed site than in the protected site. The lack of juveniles on crustose corallines in the exposed environment, but their presence in the more protected site, could be explained by the lower force that haptera can sustain on crustose corallines. The additional force imposed on the juveniles in the more exposed site could potentially exceed the relatively low holdfast attachment force, thus removing any juveniles on the substratum in that site.

The observed differences in *H. sessile* juvenile attachment forces between sites and substrata types may be a reflection of physical mechanisms which begin acting at microscopic stages of development. Holdfasts (in Laminariales) attach by forming microscopic rhizoids from their haptera that fill in crevices on the substratum (Tovey and Moss, 1978). Thus, the greater surface roughness of articulated coralline algae may provide more interstitial areas into which rhizoids may penetrate and thus provide extra attachment force. Rougher surfaces have been shown to provide optimal settlement and growth environments for some species such as *Enteromorpha* sp (Christie and Shaw, 1968) and *Sargassum muticum* (Norton, 1983) by offering refuge from shear forces and more surface rugosity for holdfast development and attachment.

**4.4.2 Adult attachment**

In comparison to other algal taxa for which field attachment forces have been measured, *Hedophyllum sessile* has a weak attachment strength but extremely high attachment force attained by large surface area. The attachment strength of *H. sessile* is 0.07 MN·m² whereas, for example, the stipe/blade attachment strength for *Mazzaella*
linearis and M. splendens is 8-9 MN·m² (Shaughnessy et al., 1996) and for Mastocarpus papillatus is 7 MN·m² (Carrington, 1990). Despite H. sessile's low attachment strength, its overall attachment force (100.68 N) is substantially higher than other taxa which have been documented, with the exception of kelp species such as Egregia menziesii (stipe break = 89 N; Friedland and Denny, 1995). The extreme force required to remove H. sessile holdfasts is most likely correlated to the relatively large blade biomass that the holdfasts must support.

The degree to which physical selection acts for or against specific holdfast attachment forces is relative to the hydrodynamic stress imposed by drag and accelerational forces (Denny, 1988; Gaylord et al., 1994). Hydrodynamic stress is directly related to thallus size. Larger holdfasts in H. sessile support more biomass on both sampling dates and the mean biomass is lower in the post-storm sampling. The lower post-storm blade biomass may either be a result of tattering, where biomass is lost but the holdfast remains, or a result of whole thalli larger than a specific size being dislodged, as demonstrated by Gaylord et al. (1994). The latter is unlikely since then we would expect the average holdfast size to decrease after these storms, which was not observed. The most probable scenario for H. sessile is that the selection during hydrodynamic stress is specific to holdfast attachment forces (which are not necessarily correlated to holdfast size) relative to blade biomass (which progressively declines as seasonal wave-exposure increases).

Initially, it was predicted that holdfast size would be directly correlated to its removal force. Likewise, Norton et al. (1982) found that, in Macrocystis pyrifera, small holdfasts less than 2 years old were less firmly attached than those with larger holdfasts. Results from our study suggest that the relationship between size and attachment force is seasonally dependent. Within H. sessile, larger holdfast surface area does not correlate to
higher attachment force before the storm season, suggesting that the holdfast loosens as it grows and that either small holdfasts are disproportionately strong or that large holdfasts are weak. In the post-storm sampling, holdfast areas were significantly correlated to the force required to dislodge them. This indicates that events during this storm season selected against either the small, strong holdfasts or against the large, weak holdfasts.

As in the predictions by Gaylord et al. (1994), large holdfasts will be selected against because they support more biomass, but this selection is further specific for *H. sessile* to the large and loose holdfasts. After the large and loose holdfasts are dislodged, the remaining large holdfasts are less likely to be dislodged since they are more firmly attached. This is supported by evidence of a shift in the probability distribution within the populations towards more resistant holdfasts in the post-storm sampling. This dynamic indicates that biomechanical parameters measured for a population are season-specific. Population distributions may therefore fluctuate seasonally, but on an annual basis be stable by consistently having similar distributions in each season every year (Denny, 1988). Future studies should attempt to document the seasonal variation of biomechanical attributes in field populations, especially when these parameters are used to interpret demographic rates such as survival.

Extensive field sampling to establish how attachment properties vary within populations is labor intensive and destructive. The ability to predict the extent of holdfast-loosening events would be an important step towards predicting seasonal dynamics of attachment properties. However, the mechanisms which create large, loose holdfasts have not been well quantified. Loosening agents such invertebrate burrowing activities and substratum failure may be important factors.
The interactions between a kelp holdfast's invertebrate community and the growth of the holdfast has been reported (Ojeda and Santelices, 1984; McLay and Hayward, 1987), but the subsequent effects on attachment forces and survival of the kelp have been rarely documented (Tegner et al., 1995). Invertebrate communities within kelp holdfasts follow a species succession, with larger invertebrate species inhabiting larger holdfasts (McLay and Hayward, 1987).

Holdfast tunneling reduces the number of attached haptera; as a result, even though the holdfast appears large, and the biomass supported by the holdfast is also large, actual attached area may not be. In our methods for estimating holdfast area, larger burrows were accounted for, but small burrows could not be measured due to shadow effects on the images.

Substratum degradation under larger holdfasts is also responsible for loose but large holdfasts. Partial substratum failures were responsible for an average of 24% of the holdfast dislodgment occurrences and happened when bleached coralline algae were removed with the *Hedophyllum sessile* haptera. Assuming that larger holdfasts are older, coralline algae under larger holdfasts may be degraded sufficiently to increase the chance of holdfast dislodgment.

### 4.4.3 Ecological implications: recovery by juveniles after adult removal

Models on thallus dislodgment have demonstrated that removal occurs when hydrodynamically-induced force exceeds attachment forces (Gaylord et al., 1994; Friedland and Denny, 1995). Biomass loss in *Hedophyllum sessile* would ultimately reduce stress on the holdfasts. If dislodgment occurs, *H. sessile* holdfasts are the most likely location for failure and will most frequently be completely removed with no chance of regeneration. Losing part of the holdfast is a less likely occurrence and, if it happens, does not seem to weaken the remaining haptera. When adults are removed, part of the failure is at the crustose
substratum, and consequently a patch of bare rock is opened for colonization. This will most likely inhibit recolonization of this spot by *H. sessile* until coralline algae have re-established from the surrounding area. If articulated coralline algae colonize the open area, then this will enhance *H. sessile* recruitment and possibly offer a more secure attachment surface than crustose coralline algae.

### 4.4.4 Conclusion

The data presented here suggest that results from holdfast attachment field studies in one season cannot be extrapolated to another due to a complex set of dynamics. The lack of statistically significant site effects in this study could reflect that site differences in wave-exposure were not significant enough to affect attachment properties. For adult *Hedophyllum sessile*, seasonal increases in storm swells correlate to more thallus tattering and select against large, loose holdfasts. Comparison of means did not demonstrate changes in holdfast attachment forces, but comparisons of probability of dislodgment illustrated a shift towards more resistant holdfasts. The biomechanical variations which *H. sessile* juveniles display between substratum types and which adults demonstrate between seasons most likely have important ecological consequences. This is the first documentation of seasonal patterns in macroalgal attachment properties. Since an alga’s attachment is essential to its survival, this research provides motivation for future research on seasonal effects on algal attachment, and on the extent to which results from one season can be applied to other seasons.
Table 4.1 *Hedophyllum sessile* juvenile recruitment on different substrata types in May 1995, measured by % juvenile occurrence / % substratum cover. Total number of juveniles sampled in exposed site is 36, and total number in the protected site is 58.

<table>
<thead>
<tr>
<th>substratum type</th>
<th>exposed site</th>
<th>protected site</th>
</tr>
</thead>
<tbody>
<tr>
<td>articulated coralline algae</td>
<td>3.29</td>
<td>2.06</td>
</tr>
<tr>
<td>crustose coralline algae</td>
<td>0.18</td>
<td>1.72</td>
</tr>
<tr>
<td>non-calcareous encrusting red algae</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>bare rock</td>
<td>0.37</td>
<td>0.38</td>
</tr>
</tbody>
</table>
Table 4.2 *Hedophyllum sessile* holdfast attachment strengths (MN·m² ± SE) of sporophyte juveniles and adults. AC represents juveniles on articulated coralline algae and CC represents juveniles on crustose coralline algae; n is the sample size within each sample group.

<table>
<thead>
<tr>
<th>sample group</th>
<th>strength (MN·m² ± SE)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>juveniles:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>exposed, AC</td>
<td>0.023 ± 0.002</td>
<td>32</td>
</tr>
<tr>
<td>protected, AC</td>
<td>0.012 ± 0.002</td>
<td>31</td>
</tr>
<tr>
<td>protected, CC</td>
<td>0.005 ± 0.002</td>
<td>23</td>
</tr>
<tr>
<td><strong>adults:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>exposed, pre-storm</td>
<td>0.070 ± 0.011</td>
<td>17</td>
</tr>
<tr>
<td>exposed, post-storm</td>
<td>0.078 ± 0.012</td>
<td>17</td>
</tr>
<tr>
<td>protected, pre-storm</td>
<td>0.073 ± 0.015</td>
<td>17</td>
</tr>
<tr>
<td>protected, post-storm</td>
<td>0.045 ± 0.005</td>
<td>17</td>
</tr>
</tbody>
</table>
Table 4.3 Pearson correlation coefficients (R), sample sizes (n), and p-values for the correlation between adult holdfast break area and the force to remove.

<table>
<thead>
<tr>
<th>sample group</th>
<th>R</th>
<th>n</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>exposed, pre-storm</td>
<td>0.155</td>
<td>17</td>
<td>0.553</td>
</tr>
<tr>
<td>protected, pre-storm</td>
<td>0.382</td>
<td>17</td>
<td>0.131</td>
</tr>
<tr>
<td>exposed, post-storm</td>
<td>0.612</td>
<td>17</td>
<td>0.009</td>
</tr>
<tr>
<td>protected, post-storm</td>
<td>0.563</td>
<td>17</td>
<td>0.019</td>
</tr>
</tbody>
</table>
Table 4.4 Analysis of wetted blade surface area per holdfast area. Normalized blade area was calculated by the ratio between wetted blade area (m²) and holdfast area (m²). 95% confidence intervals were calculated as in Cochran (1977). Pearson correlation coefficients, R, and associated probabilities were calculated for the relationship illustrated in Figure 4.8. Post-storm samples (▲ △) have significantly (p ≤ 0.05) less blade biomass per holdfast area than pre-storm samples (● ○).

<table>
<thead>
<tr>
<th>sample group</th>
<th>normalized blade area</th>
<th>n</th>
<th>R</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>● exposed, pre-storm</td>
<td>157.07 ± 66.49</td>
<td>15</td>
<td>0.67</td>
<td>0.007</td>
</tr>
<tr>
<td>○ protected, pre-storm</td>
<td>167.91 ± 54.41</td>
<td>18</td>
<td>0.84</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>▲ exposed, post-storm</td>
<td>62.27 ± 15.19</td>
<td>21</td>
<td>0.65</td>
<td>0.001</td>
</tr>
<tr>
<td>△ protected, post-storm</td>
<td>76.98 ± 13.21</td>
<td>33</td>
<td>0.75</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Table 4.5 Coefficient values (± 95% CI) for the cumulative distributions for the probability of breaking *Hedophyllum sessile* holdfasts in exposed (E) and protected (P) sites in pre-and post-storm months. See equation (4.2) for description of the coefficients.

<table>
<thead>
<tr>
<th>coefficient</th>
<th>E, pre-storm</th>
<th>P, pre-storm</th>
<th>E, post-storm</th>
<th>P, post-storm</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a$</td>
<td>-0.38 ± 0.268</td>
<td>-0.12 ± 0.133</td>
<td>-0.07 ± 0.181</td>
<td>0.30 ± 0.160</td>
</tr>
<tr>
<td>$b$</td>
<td>-1.49 ± 0.406</td>
<td>-0.974 ± 0.187</td>
<td>-0.828 ± 0.295</td>
<td>-0.34 ± 0.200</td>
</tr>
<tr>
<td>$c$</td>
<td>0.662 ± 0.045</td>
<td>0.663 ± 0.025</td>
<td>0.612 ± 0.039</td>
<td>0.663 ± 0.032</td>
</tr>
</tbody>
</table>
Figure 4.1 Offshore wave heights between sample times. Dotted line is the daily maximum wave height and solid line represents the daily mean significant wave height as measured by the Fisheries and Oceans Canada LaPerouse Bank buoy 46206 (48° 50.1’ N, 125° 59.9’ W). Data are used with the permission by the Government of Canada, © 1997 Her Majesty in Right of Canada, Department of Fisheries and Oceans. Arrows indicate sample dates for adult attachment experiments. Dates are abbreviated by the first letter of each month, beginning in January 1996 (J 96) and ending in January 1997 (J 97).
Figure 4.2 Percent cover of substrata available for recruitment. Substratum types are abbreviated as AC= articulated coralline algae, CC=crustose coralline algae, RC = non-calcareous encrusting red algae, and BR = bare rock. Data are from exposed (shaded bars) and protected (open bars) sites, n=10, and error bars represent 95% confidence intervals. Recruitment also occurs on *Hedophyllum sessile* holdfasts, which is not shown here.
Figure 4.3 Break locations for juveniles on different substrata and at two sites. Breaks abbreviated as HO=holdfast, ST=stipe, S/BL=stipe/blade junction, and SU=substratum. Samples from the exposed site on articulated coralline algae (EXP,AC) are represented by shaded bars. Samples from the protected site are represented by open bars (for PRO, AC) and by open, hatched bars (for crustose corallines PRO,CC).
Figure 4.4 Forces (● ○ ) required to break juvenile holdfasts and the holdfast break areas (▲ △) on different substrata and at two sites. See Figure 4.3 for site and substratum abbreviations. Solid and open symbols represent exposed and protected sites, respectively. Asterisks above symbols represent groups that are significantly different: *** is different at p ≤ 0.001, and ** is 0.001 < p ≤ 0.01.
Figure 4.5 Proportion of complete holdfast breaks in adult *Hedophyllum sessile* at two sites in pre-storm and post-storm sampling dates. Exposed site data are represented by EXP. Protected site data are represented by PRO. Open bars are complete breaks and hatched bars are partial breaks.
Figure 4.6 Percent occurrence of different break locations for adults at two sites in pre- and post-storm sampling dates. Breaks are abbreviated as HO = holdfast only, H/S = holdfast and substratum, TTL HO = holdfast only + holdfast/substratum, and BL = blade. Samples from the exposed site are represented by shaded bars and those from the protected site are represented by open bars.
Figure 4.7 Forces (● ○) required to break adult holdfasts and the holdfast break areas (▲ △) at two sites in pre- and post-storm sampling dates. Solid and open symbols represent exposed (EXP) and protected (PRO) sites. Asterisks above symbols represent groups that are significantly different, 0.01 < p ≤ 0.05.
Figure 4.8 Relationship between holdfast and wetted blade surface area. Each data point represents an individual thallus sampled for holdfast attachment at exposed (● ▲) and protected (○ △) sites in pre-storm (● ○) and post-storm (▲ △) dates. Solid (exposed) and dashed (protected) lines are the regression lines for the significant, direct relationships between holdfast area and the wetted blade surface area that it supports in each sample date as noted (refer to Table 4.4 for the correlation statistics).
Figure 4.9 Changes in adult *Hedophyllum sessile* attachment force (+ SE) with successive holdfast breaks. Break numbers represent successive breaks on holdfasts which were partially dislodged. 1 = first pull, 2 and 3 = subsequent pulls on remaining holdfasts. Data from the exposed site are represented by shaded bars and those from the protected site are represented by open bars, for both in pre- and post-storm sampling dates. Sample sizes are noted above each bar.
Figure 4.10 Cumulative functions for probability of breaking. Each data point represents the observed normalized attachment forces \( f_n \) at exposed (● ▲) and protected (○ △) sites in pre-storm (● ○) and post-storm (▲ △) dates. Solid (exposed) and dashed (protected) lines are the calculated probability distributions from equation (4.2) in each sample date as noted. Equation coefficients ± 95% CI are in Table 4.5.
CHAPTER 5

Effects of morphological variation on drag forces encountered in wave-exposed sites

5.1 Introduction

Intertidal species may experience peak water velocities exceeding $14 \text{ m} \cdot \text{s}^{-1}$ (Bell and Denny, 1994), which is equivalent to wind velocities exceeding $400 \text{ m} \cdot \text{s}^{-1}$ (Vogel, 1981). Many species of macroalgae have variable morphologies that correlate with wave-exposure. For example, *Macrocystis integrifolia* has small, smooth blades in exposed sites and wide, undulate blades in sheltered sites (Hurd *et al.*, 1997). Likewise, *Hedophyllum sessile* has smooth, strap-like blades in exposed sites and wide, bullated blades in sheltered sites (Widdowson, 1965; Armstrong, 1989). Experimental evidence suggests that algal size and shape variations modify flow regimes and by doing so, effectively minimize drag or diffusion stress at wave-exposed and wave-sheltered sites, respectively (e.g. Charters *et al.*, 1969; Neushul, 1972; Wheeler, 1988; Norton *et al.*, 1982; Armstrong, 1989; Norton, 1991; Gaylord *et al.*, 1994). Thus, it is generally accepted that the forces associated with peak velocities and the macroalgal hydrodynamic requirements to minimize and resist these forces are potentially important selective factors against specific thallus shapes and sizes (e.g., Denny, 1988; Gaylord *et al.*, 1994).

At any given velocity, drag forces imposed on algal thalli are the result of the combination of friction drag (that due to skin friction) and form drag (that due to the shape and pressure wakes formed by it). For macroalgae, form drag constitutes the majority of
drag force relative to that by skin friction (Denny, 1988). Total drag force ($F_d$) is represented by the equation:

$$F_d = 0.5 \cdot \rho \cdot S_p \cdot \nu^2 \cdot C_d$$

where $\rho$ is the density of seawater, $S_p$ is projected area of thallus, $\nu$ is water velocity, and $C_d$ is the drag coefficient, also known as a shape coefficient.

Species which streamline better in flow have lower $C_d$ than species which are more bluff in shape. As velocity increases, macroalgae reconform in flow, and $C_d$ values decrease.

The rate at which a thallus conforms to flow is represented by:

$$C_d = c \cdot \nu^E$$

where $c$ is a dimensionless coefficient and $E$ is the exponent of streamlining (Vogel, 1981 and 1984). A body which does not streamline has an $E$ equal to 0, whereas a flexible body will have a negative exponent. For example, the $E$-value (between 0.5 and 4.0 m $\cdot$ s$^{-1}$) for a standard practice golf ball is approximately -0.06 (Gaylord et al., 1994) whereas the value for a reconforming, flexible alga such as *Mazzaella flaccida* (published as *Iridea flaccida*) is -0.76 (Gaylord et al., 1994).

Thallus shape and size act together to determine hydrodynamic forces on the holdfast attachment, and modifications of either of these parameters may act to minimize or maximize drag forces. Within a species, size may be the most important morphological feature to determining the magnitude of drag forces. For example, in the bladed red alga *Mastocarpus papillatus* at a given water velocity, natural ranges of shape (as measured by $C_d$) did not significantly affect hydrodynamic force whereas size (as measured by $S_p$) had a dramatic effect on forces (Carrington, 1990). Yet, when comparing hydrodynamic performance of
different species, shape may also be a significant factor determining drag forces and hence selecting for or against survival in wave-exposed sites. Dudgeon and Johnson (1992) concluded that the high dislodgment rates of *Chondrus crispus* ($C_d = 0.48$) relative to *Mastocarpus stellatus* ($C_d = 0.19$) could be attributed to differences in the species’ $C_d$ values. However, in that study, thallus projected area was significantly correlated to size, and there was a difference between species’ sizes ($C. crispus = 62.99 \text{ cm}^2 \cdot \text{g dry wt}^{-1}$; *M. stellatus* = $38.87 \text{ cm}^2 \cdot \text{g dry wt}^{-1}$); hence, size could also have contributed to the observed differential dislodgment rates. Shaughnessy et al. (1996) also determined that relative size was an important determinant of differential drag forces and dislodgment rates between *Mazzaella linearis* and *M. splendens*.

Morphological plasticity within a macroalgal species in response to wave-exposure can be dramatic, either in shape and/or size. The correlation of morphological variations to wave-exposure has been well documented (e.g., *Eisenia arborea*, Charters et al., 1969; *Macrocystis integrifolia*, Hurd et al., 1997; *Egregia menziesii*, Friedland and Denny, 1995; *Laminaria saccharina*, Gerard, 1987; *Nereocystis luetkeana*, Koehl and Alberte, 1988). However, hydrodynamic performances of morphologies within species at velocities characteristic of high wave-exposure regimes have not been well documented.

In this chapter, I document the performance of various morphologies of *Hedophyllum sessile* at velocities characteristic of low and high wave-exposures. *H. sessile* displays a strong response to wave-exposure, with dramatic morphological variations (Scagel, 1967; Abbott and Hollenberg, 1976). Morphologies in extremely protected sites consist of a single undulate blade, while those in extremely exposed sites have many, smooth, strap-like blades.
(Widdowson, 1965; Armstrong, 1989). The exposed site blades are developmentally a single blade, as there is a common meristem; however, this meristem is tattered and thus forms numerous blades, and the thallus, from a functional perspective, is multi-bladed. Furthermore, the exposed site's blades continually tatter lengthwise and crosswise throughout the winter seasons, when high wave forces are larger and more frequent (Chapter 2, Figures 2.6 - 2.8).

It has been hypothesized that the exposed site morphology is more hydrodynamically streamlined and effectively minimizes drag forces at sites of high wave-exposure, which in part reduces the risk of dislodgment (Armstrong, 1989). This hypothesis was partially supported in measurements by Armstrong (1989) which demonstrated that the more streamlined morphology generated lower speed-specific drag force between velocities of 0.5 and 2.5 m $\cdot$ s$^{-1}$. However, these conclusions were based on small sample sizes (n=3 & 4), were not extrapolated to morphological drag forces at velocities exceeding 2.5 m $\cdot$ s$^{-1}$, and did not include effects of variable thallus sizes. This chapter tests the following hypotheses:

(1) the exposed morphology reconforms more rapidly to flow than the protected morphology;
(2) at high velocities, the exposed morphology has lower $C_d$ than protected morphology; and,
(3) within the exposed morphology, lengthwise and crosswise tattering affects $C_d$ but the primary effect on total drag force is by surface area reduction.
5.2 Methods

5.2.1 Measurement of drag force

Drag forces at a range of velocities were directly measured on various morphological shapes and sizes of *Hedophyllum sessile* during July and August 1996 at Bamfield Marine Station, Vancouver Island, British Columbia.

A 1.8-meter long steel pole was held vertical in the water by a frame on the side hull of a small boat. Attached to the bottom of the pole was a double beam force transducer constructed using a similar design as in Denny (1982) except that an aluminum box beam was used instead of Plexiglas and the mounting was inverted on the pole so that the platform was facing downward. Strain gages (Showa measuring instruments, Type N11-MA-2-350-23) were wired so that the voltage output was directly proportional to the applied force. The pole and affixed transducer were positioned so that the solid beam was perpendicular to the direction of flow and submerged 1 m underwater to avoid boat wake and surface effects. The double beam transducer was calibrated before and after each series of drag experiments by hanging known masses and using the same calibration methods as in Chapter 1 for wave force recorders (equations 2.1 and 2.2; Figure 5.1).

Holdfasts were embedded in quick-set (15 minutes) anchoring cement; the cement was contained in a mold which also held a bolt to be used for attaching the entire thallus to the immersed flat platform of the transducer with a coupler nut. This ensured that the thallus orientation to flow was as it is on the shore. The boat was driven at 0.5 m · s\(^{-1}\) intervals from 0.5 - 4.0 m · s\(^{-1}\), and voltage signals from the transducer were continuously recorded by a PC-interfaced multimeter (Micronta Digital Multimeter) and stored in a DOS-based data logging
program (Appendix 2) on a Hewlett-Packard HP100 palm-top computer. At least 30 readings were sampled at each velocity. After thallus data were collected, the thallus was cut at the mold and returned to the laboratory for surface area measurements. The background drag created by the holdfast mount was then measured by repeating these procedures.

5.2.2 Velocity

Flow velocity was measured by a pitot tube mounted 0.5 m underwater, with velocities read on the boat with a deck-mounted water column. The pitot tube was constructed from a hard plastic tube, 4 mm inner diameter, which was bent at a right angle and then covered in Epoxy to protected it from shattering. Tygon tubing (inner diameter = 1 cm) was attached to the pitot tube, and fed directly into a deck-mounted, water-filled vertical column. The tube was completely filled with water and the height-rise in the water column was directly proportional to changes in water velocity. The basic principle of this design is that the water pressure (measured in N·m$^{-2}$) in the pitot tube will increase as flow velocity increases. This pressure differential will be directly reflected in the height rise in the water column. Velocity calibrations to establish water column height and velocity relationships were calculated by Bernoulli’s principles (Serway, 1982; Vogel, 1981). To correct for hydrostatic pressure effects from pitot-tube depth, static pressure ($P_s$) was measured by a static tube mounted at the same depth as the pitot-tube and calculated by:

$$P_s = P_a + (\rho \cdot g \cdot z) \quad \text{eq. 5.3}$$

where $P_a$ is absolute pressure equal to one atmosphere ($1.01 \times 10^5$ N·m$^2$), $\rho$ is water density, and $g$ is gravitational acceleration, and $z$ is the height-rise of water in the vertical water column.
The dynamic pressure ($P_0$) invested in fluid movement into the tube at each velocity was calculated by Bernoulli’s equation (Vogel, 1981):

$$P_0 = \frac{\rho v^2}{2}$$  

eq. 5.4

This equation was rewritten so that the dynamic pressure at each velocity is corrected for static pressure, and calculated for each experimental velocity ($0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0 \text{ m} \cdot \text{s}^{-1}$):

$$v = \left[2 \frac{P_o - P_s}{\rho}\right]^{1/2}$$  

eq. 5.5

$P_o$ was solved for desired experimental velocities ($v$) using $P_s$ calculated in equation (5.3). By doing so, experimental velocities are replaced by experimental dynamic pressures that must be achieved in the drag measurements. This pressure was converted to resultant change in column height ($z$) for each velocity by substituting dynamic pressure for static pressure in equation (5.3) and rewriting as:

$$z = \frac{P_o - P_a}{\rho g}$$  

eq. 5.6

By calculating $z$, experimental water velocities could be consistently attained by achieving a consistent height rise of water in a column on the boat deck.

These estimated water velocities were tested against those measured by a propeller-mounted, counter current meter (Ocean Systems, Inc.). The meter is factory-calibrated, and measures velocity by counting propeller rotations over a specified period of time. Thus, the meter measures average water velocity. The boat was driven at experimental velocities as measured by the pitot tube and vertical height-rise in the deck-mounted water column. At
each velocity, three current meter measurements, each consisting of a run of at least 2
minutes in duration, were taken. These results were compared to that expected by the pitot
tube to find the approximate error of the velocity measurements.

5.2.3 Experiments

Drag force was measured on thalli with sheltered and various exposed site
morphologies. The extremely sheltered morphology was collected near Sooke, Vancouver
Island, British Columbia, and the exposed morphology was collected near Bamfield (Figure
5.2). Various degrees of tattering in the exposed morphology were simulated by measuring
drag force on the following treatments: (1) originally collected thalli; (2) thalli with
lengthwise tears on all blades (at least twice the number of blades per holdfast); and, (3)
thalli with lengthwise and crosswise tears (Figure 5.3) where all thalli were cropped to 15
cm length, which approximates thallus length in winter (Figure 2.17). Experimental thalli
were collected, returned to seawater tables (with constant-flowing natural seawater at
Bamfield Marine Station) and measured within 48 hours.

Drag data (corrected for background drag) within each velocity were averaged. The
projected surface area was quantified by tracing the thallus outline on acetate sheets.
Outlines were scanned using a flatbed scanner and surface areas within outlines estimated to
nearest cm², using an image analysis program (Image 1.57, National Institute of Health).
Equation (5.1) was re-written as:

\[ C_d = 2 \left( \frac{F_d}{\rho \cdot S_p \cdot \nu^2} \right) \]  

and used to calculate \( C_d \) (Carrington, 1990). A power curve function was fit to equation (5.2)
using Sigma Plot (version 2.0). This relationship was used to estimate \( C_d \) at a range of
velocities exceeding 4 m • s\(^{-1}\) (Gaylord et al., 1994). In addition, drag per projected area for each morphology was calculated for the range of experimental velocities.

At each velocity for \(C_d\) and drag per projected area value, one-way ANOVA’s were performed in SYSTAT (version 5.03) to test if different morphologies have significantly different \(C_d\) values and drag per projected area. If the exposed morphology reconforms better to flow than the sheltered morphology, I expect that all exposed morphologies will have more strongly negative \(E\) values, determined by 95% confidence intervals around the power curve fit to equation (5.2). Likewise, if at high velocities the exposed morphologies minimize drag force, it is expected that all exposed morphologies will have significantly lower \(C_d\) values at 4 m • s\(^{-1}\) than the sheltered morphology and that the average extrapolated values will be different at 7 and 10 m • s\(^{-1}\). It is also predicted that within the exposed morphology tattering will affect \(C_d\) and drag forces. If so, it is expected that \(C_d\)’s and drag per surface area on average will be different. However, it is expected that the most effective mechanism of drag reduction within the exposed morphology will be by surface area reduction in the cross-wise tattered form instead of by changes in \(C_d\) values.
5.3 Results

5.3.1 Velocity

Velocities predicted by the pitot tube design were consistent with those measured by the current counter (Table 5.1). The counter errors ranged from 0.01 to 0.39 m \( \cdot \) s\(^{-1}\). In general, the counter measured average velocities slightly above that measured by the pitot tube. Thus, experimental velocities as measured by the pitot tube should be considered as approximate velocities.

5.3.2 Drag coefficients and E-values

Pre-tattered, exposed site thalli had between 5 and 8 blades which ranged from 15 to 55 cm in length. Lengthwise tatters produced 10 to 16 blades. Lengthwise and crosswise tattering produced 10 to 16 blades, with uniform lengths of 15 cm. The thalli from the sheltered site had between 1 and 2 blades which ranged from 15 to 35 cm in length.

For each thallus measured, the drag coefficient decreases with increasing velocity. Drag data are highly variable at low velocities (Figures 5.4 - 5.7); however, within each morphology tested, variation between individuals becomes less as velocity increases to 4 m \( \cdot \) s\(^{-1}\). ANOVA results for differences between morphological C\(_d\) values at each velocity are not statistically significantly different (p > 0.1). E-values were not different at the 95% confidence level (Table 5.2).

When power curve fit parameters were used to extrapolate C\(_d\) values at velocities more characteristic of exposed sites (7, 10 m \( \cdot \) s\(^{-1}\)), C\(_d\) varied from 0.003 to 0.005 (at 7 m \( \cdot \) s\(^{-1}\)) and from 0.002 to 0.003 at 10 m \( \cdot \) s\(^{-1}\) (Table 5.3). At 7 and 10 m \( \cdot \) s\(^{-1}\), the sheltered morphology, as predicted, consistently had a higher C\(_d\) than other morphologies. An increase
in number of blades by lengthwise tattering did not affect $C_d$. However, lengthwise and crosswise tattering increased $C_d$.

### 5.3.3 Drag forces

Drag per projected area in all morphologies increased with increasing velocity. Increase in number of blades was the most effective in minimizing drag forces. By $4 \text{ m} \cdot \text{s}^{-1}$, all standard errors around all average drag forces per projected area overlapped. Within each velocity, there was no statistically significant difference between any of the morphologies (ANOVA, $p > 0.1$). Seemingly streamlined morphologies generate as much drag force per unit area as the non-streamlined shapes (Figure 5.8) thus supporting results from comparing $C_d$ values.

Predicted drag forces at $7 \text{ m} \cdot \text{s}^{-1}$ on these different morphologies demonstrate that for any given projected area, the sheltered morphology generates more drag force than other morphologies (Figure 5.9). As projected area increases, the magnitude of difference between predicted drag forces for different morphologies increases. The lengthwise and crosswise tattered morphology also generates more drag than other exposed morphologies as projected area increases. However, minimization of size by lengthwise and crosswise tattering decreases drag force significantly suggesting that size-reduction, but not shape-modification, is more effective in reducing drag force.

These results indicate that the apparently more streamlined exposed morphology minimizes drag forces, which subsequently could be reflected in higher survivorship in exposed sites than if the sheltered morphology was present. Yet, the mechanism of this drag reduction is primarily from surface area minimization, not by differences generated by the thallus shape. Even though the sheltered thallus' higher $C_d$ value yields higher drag forces at
than on the other more streamlined shapes, the magnitude of the difference in force is dependent on projected area. Thus, hydrodynamic differences between morphological shape are dependent on thallus projected area.

5.4 Discussion

Original predictions that: (1) the sheltered morphology would reconform more slowly than the exposed morphology and (2) at high velocities, the exposed morphology has lower $C_d$ than the protected morphology could not be fully supported. The third prediction that lengthwise and crosswise tattering affects $C_d$ but the primary effect on total drag force is by surface area reduction was supported by non-significant differences in $C_d$ and $E$ values between tattering treatments and by drag force being most sensitive to surface area.

5.4.1 Exposed vs. sheltered morphology

Average values of $C_d$ and $E$ are typically used to predict drag forces at higher velocities (Carrington, 1990; Gaylord et al., 1994). Thus, when average values are compared, experimental predictions are supported. Extrapolations to higher velocities characteristic of exposed shores reveal that the average $C_d$ values of the sheltered and exposed morphologies become similar. Even though morphologies seem hydrodynamically similar, use of these extrapolations to higher velocities reveal that statistically non significant differences between $C_d$ and $E$ values will be reflected in different drag forces.

All morphologies have strongly negative $E$-values (-1.45 to -1.67), indicating that they all streamline quickly in flow. This passive streamlining has been shown to effectively reduce drag in many organisms such as sea anemones (Koehl, 1976; Koehl, 1977) and other
algal species (e.g. Charters et al., 1969, Carrington, 1990; Gaylord et al., 1996). These $E$-values are comparable to those measured for Hedophyllum sessile between 0.5 - 2.5 m$ \cdot$ s$^{-1}$ ($E = -1.20$; Armstrong, 1989 in Gaylord et al., 1994) and to the exposed morphology of Nereocystis luetkeana between 1.3 - 2 m$ \cdot$ s$^{-1}$ ($E = -1.11$, Koehl and Alberte, 1988 in Gaylord et al., 1994).

The initial prediction was that the sheltered morphology would have higher $C_d$ and a relatively low $E$-value. This was based on the hypothesis that the exposed morphology was a mechanism to minimize drag forces by a more streamlined shape as opposed to the more bluff shape, such as found by Armstrong (1989) for H. sessile between 0 - 2.5 m$ \cdot$ s$^{-1}$. Data here suggest that all morphologies streamline to similar magnitudes at velocities when a streamlined shape should hypothetically be of benefit. Even though predicted drag forces on each morphology are different, the natural variation within each morphology could be also sufficient to produce similar ranges of drag forces. Drag per unit surface area for all morphologies is extremely similar when water velocities reach 4 m$ \cdot$ s$^{-1}$; and, these data support the conclusion that at high velocities there are variable $C_d$ values, but the variations can not be explained by differences in these morphological shapes.

Alternate, force-reduction mechanisms by which the streamlined morphology could act are by lowering the velocities encountered and by effective minimization of accelerational forces. The exposed morphology may stack blades and lie close to the substratum whereas the sheltered morphology does not stack blades and may not be able to lie as close to the substratum. Thus, for the same thallus surface area, forms could potentially experience different velocities because they are in different positions within the benthic boundary layer; specifically, the more exposed form would be in lower velocities because it
is closer to the substratum (Koehl, 1984). This difference could not have been detected by
the method of measuring $C_d$ and $E$. Intertidal species are subjected to acceleration reaction
forces (Carstens, 1968 in Denny, 1988). These forces act on a sessile body by a pressure
differential created by a wave's accelerating water flowing around the body. This
accelerating flow creates a buoyancy force proportional to the mass of fluid displaced by the
body. The ability to compact will reduce the volume of water displaced (Koehl, 1986). For
the same structural volume, a flattened shape parallel to substratum generates lower
acceleration force than the same volume in a spherical shape (Daniel, 1983; Denny, 1988).
The more streamlined morphology may reduce accelerational forces by performing like a
flattened shape. Since acceleration forces scale with volume (Denny, 1988), any
minimization of accelerational force may be more important to reducing hydrodynamic
limitations of living in a highly wave-impacted environment than drag minimization.

5.4.2 Tattering effects

Increased blade number, but no change in blade length, affects average $C_d$ and $E$-
values. This is most likely due to blades stacking upon each other more rapidly, and thus
becoming streamlined more quickly. This result is consistent with those by Koehl and
Alberte (1988) who found that blade stacking in *Nereocystis luetkeana* was responsible for
drag reduction. However this observation is dependent on the blade length relative to the
number of blades, since the exposed morphology with short but many blades has a
hydodynamic performance similar to the sheltered morphology. In this case, pressure wakes
probably form behind the thallus, especially at lower velocities; hence, it performs as the
sheltered, bluff shape.
As previously discussed, size is a more important determinant of drag force than shape for *Hedophyllum sessile*. Thus, a potentially significant consequence of morphology may be each thallus’ structural attributes which determine tear patterns. The exposed morphology tends to initially tear lengthwise from a tissue flaw whereas the sheltered morphology tears lengthwise and crosswise along tissue undulations (personal observations). All morphologies have surface flaws yet flaws are more frequent in exposed sites (Armstrong 1987). Armstrong (1987) found that the exposed morphology is stronger and stiffer than the sheltered morphology. Thus, the sheltered morphology may be more at risk of losing significant tissue below the meristem at the base of the blade. The exposed morphology, on the other hand, may slowly tatter, first by lengthwise tatters and then by blade loss from the tips (see changes in blade length, Figures 2.17, 2.18), without losing meristematic tissue. It has been hypothesized that the loss of surface area effectively reduces drag forces but may also decrease reproductive output potential (Gaylord et al., 1994). For *H. sessile*, tattering will reduce surface area and drag forces. Yet, if meristem tissue is not lost, reproductive tissue can form from the blade bases and regrowth can happen the following growth season.

5.4.3 Conclusion

Even though experimental velocities were approximate, general conclusions can be made about patterns of reconformation by the different thallus morphologies. Variation in morphological shape in *Hedophyllum sessile* does not effectively reduce drag forces in velocities characteristic of high wave-exposure. While thalli reconform rapidly in flow from approximately 0.5 - 3.0 m·s⁻¹, the sheltered morphology generates a higher drag per projected area than the pre-tattered, exposed morphology. The tattered, exposed morphology with blades no longer than 15 cm, however, generates the most drag force. By 4 m·s⁻¹, all
morphologies generate similar drag forces. These patterns are consistent with $C_d$ values which were measured. For each morphology, there is substantial $C_d$ variation at low velocities and less at $4 \text{ m } \cdot \text{s}^{-1}$.

The most important determinant of drag force is thallus size. Even though lengthwise and crosswise tattering in the exposed morphology does not reduce $C_d$ values, it is the most effective way to reduce drag force. For $H. sessile$, advantageous consequences of the exposed morphological shape may include structural advantages for tattering without losing meristematic and reproductive tissue as well as minimizing forces imposed by wave accelerations.
**Table 5.1 Velocity measurements for drag experiments.** Predicted velocity (m·s⁻¹) is that expected from pitot tube calibrations. $P_0$ is the dynamic pressure (N·m⁻²) used to calculate the height rise in the tubing (z) associated with the velocity. Velocity measured by the counter, $n = 3$, was compared to velocities expected by pitot tube measurements.

<table>
<thead>
<tr>
<th>predicted velocity (m·s⁻¹)</th>
<th>$P_0 \times 10^5$</th>
<th>z (m)</th>
<th>counter velocity ± 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 (static pressure)</td>
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<td>0</td>
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<td>0.5</td>
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<td>4.0</td>
<td>1.088</td>
<td>0.796</td>
<td>4.09 ± 0.13</td>
</tr>
</tbody>
</table>
Table 5.2 *Hedophyllum sessile* morphological size and shape parameters. Replicate number, $n$, is the number of individuals measured and area is the average ± SE projected area. Coefficients $c$ and $E$ were fit to equation (5.2), where $C_d = c \cdot u^E$ and 95% confidence intervals of the regression calculated.

<table>
<thead>
<tr>
<th>morphology</th>
<th>n</th>
<th>area (m$^2$) ± SE</th>
<th>$c$ ± 95% CI</th>
<th>$E$ ± 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>exposed:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pre-tatter</td>
<td>10</td>
<td>0.2668 ± 0.030</td>
<td>6.24 e$^2$ ± 7.97 e$^3$</td>
<td>-1.454 ± 0.251</td>
</tr>
<tr>
<td>lengthwise</td>
<td>6</td>
<td>0.2281 ± 0.030</td>
<td>5.02 e$^2$ ± 1.37 e$^2$</td>
<td>-1.580 ± 0.193</td>
</tr>
<tr>
<td>length + crosswise</td>
<td>6</td>
<td>0.0893 ± 0.010</td>
<td>1.12 e$^1$ ± 3.81 e$^2$</td>
<td>-1.512 ± 0.414</td>
</tr>
<tr>
<td>sheltered</td>
<td>13</td>
<td>0.1912 ± 0.032</td>
<td>7.80 e$^2$ ± 1.28 e$^2$</td>
<td>-1.662 ± 0.414</td>
</tr>
</tbody>
</table>
Table 5.3 Drag coefficients for various morphologies at 4, 7, and 10 m·s\(^{-1}\). Predicted columns 7 and 10 m·s\(^{-1}\) were extrapolated from power curve fits to the measured data between 0.5 and 4 m·s\(^{-1}\).

<table>
<thead>
<tr>
<th>morphology</th>
<th>MEASURED 4 m·s(^{-1})</th>
<th>PREDICTED 7 m·s(^{-1})</th>
<th>PREDICTED 10 m·s(^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>exposed:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pre-tatter</td>
<td>0.008</td>
<td>0.003</td>
<td>0.002</td>
</tr>
<tr>
<td>lengthwise</td>
<td>0.007</td>
<td>0.003</td>
<td>0.002</td>
</tr>
<tr>
<td>length + crosswise</td>
<td>0.010</td>
<td>0.004</td>
<td>0.002</td>
</tr>
<tr>
<td>sheltered</td>
<td>0.011</td>
<td>0.005</td>
<td>0.003</td>
</tr>
</tbody>
</table>
Figure 5.1 Representative transducer calibration. Replicate calibrations were performed before and after experimental runs. Voltage output is directly proportional to applied force (FORCE = (55.051 • VOLTS) - 0.403; r²=0.996).
Figure 5.2 Map of sampling sites for exposed and sheltered morphologies of *Hedophyllum sessile*, Vancouver Island, B.C. Canada. The exposed morphology was collected at Bamfield and the sheltered morphology was collected near Sooke.
Figure 5.3 Morphological treatments in the drag experiment. *Hedophyllum sessile* thalli were attached to the double beam force transducer. (A) is exposed morphology before winter tattering occurs, n=10. (B, C) simulate winter tattering effects by increasing blade number (B; n=6) and increasing blade number with decreasing blade length (C; n=6). The sheltered morphology is represented by (D; n=13). Figure is not drawn to scale.
Figure 5.4 Exposed morphology drag coefficients. Data points represent individual thalli. The solid line is a power curve fit to the data; curve-fitting routine results are listed in Table 5.2.
Figure 5.5 Exposed, tattered lengthwise morphology drag coefficients. Data points represent individual thalli. The solid line is a power curve fit to the data; curve-fitting routine results are listed in Table 5.2.
Figure 5.6 Exposed, tattered lengthwise and crosswise morphology drag coefficients. Data points represent individual thalli. The solid line is a power curve fit to the data; curve-fitting routine results are listed in Table 5.2.
Figure 5.7 Sheltered morphology drag coefficients. Data points represent individual thalli. The solid line is a power curve fit to the data; curve-fitting routine results are listed in Table 5.2.
Figure 5.8 Drag force measured for various morphologies. Average forces per projected area (N·m⁻²) at each velocity for exposed pre-tattered (●), lengthwise tattered (▲), lengthwise and crosswise tattered (■), and sheltered (○) morphologies are not significantly different (p>0.05). Error bars are standard error of the mean.
Figure 5.9 Predicted morphological effects on drag force at 7 m·s⁻¹. Estimations used the power curve fits to drag coefficient data to predict forces at a range of projected areas. Data points represent projected areas of experimental thalli {exposed pre-tattered (●), lengthwise tattered (▲), lengthwise and crosswise tattered (■), and sheltered (○)} used in the drag experiments for which drag force was estimated.
CHAPTER 6

Validation of a physical model approach to predicting wave-induced mortality

6.1 Introduction

As demonstrated in Chapter 2, wave-exposure may affect all aspects of a species demographic parameters. Field studies on the specific effects of wave-exposure on demographic parameters such as mortality are impractical since they typically cannot isolate mechanisms of wave-exposure and their interactions with organism shape, size, and biomechanical attributes (such as strength, elasticity, flexibility). For example, as discussed in Chapter 2, specific modes by which wave-exposure affects Hedophyllum sessile’s demographics could not be defined. Instead, differences in parameters such as mortality between sites were correlated with wave-exposure, but the specific components of wave-exposure (such as maximum wave forces) can not be demonstrated to cause these differential mortality rates. Thus, because previous field studies have given limited understanding of the mechanisms by which wave-exposure interacts with organisms, recent attention in intertidal ecological studies of wave-exposure has been focused on defining physical limitations to organism survival in wave-impacted intertidal zones (e.g. Denny, 1985; Gaylord, 1994; Blanchette, 1997). Some tools used to define limitations to organism survival consist of model approaches which examine the physical mechanisms of wave-induced mortality by predicting how survival is influenced by various physical parameters which are believed to be important to organism survival.
6.1.1 Conceptual basis of physical models

These physical model approaches are based on current understanding of mechanisms of wave-organism interactions. Field studies (e.g., Charters et al., 1969; Koehl and Wainwright, 1977; Denny, 1982; Gerard, 1987; DeWreede et al., 1992; Gaylord et al., 1994), hydrodynamic theory (e.g. Vogel, 1981; Denny, 1988; and references therein), and laboratory experiments (e.g. Gaylord et al., 1994; Hurd et al., 1997) provide the foundation of knowledge for these models. Field experiments typically establish natural patterns of organism parameters relevant to the model, such as shape, size, and biomechanical properties. Hydrodynamic theory establishes the conceptual basis of models by providing information on how flow and waves interact with structures. Lab experiments which have contributed to these models consist primarily of tissue mechanical tests (such as in Denny et al., 1989), and measurements of hydrodynamically-induced forces and flow patterns on and around organisms in flume and oscillatory wave tanks (e.g. Miller et al., 1992; Gaylord et al., 1994).

The primary mortality agent of mature macroalgal forms in high wave-exposure is physical dislodgment (Dudgeon and Johnson, 1992; Gaylord et al., 1994; Blanchette, 1997). The initial wave-impact onto the shore will create a force, which compresses organisms. Yet this force is minimal in contrast to the consequent forces associated with wave-induced flows. A breaking wave creates rapid changes in instantaneous flow velocities over time and hence a high acceleration ($\geq 300 \text{ m} \cdot \text{s}^{-2}$) over organisms (Figure 6.1; Denny, 1988). The flow's peak velocity occurs after this acceleration, when acceleration is zero, and acceleration will then act once again when flow direction changes.
Hydrodynamic theory predicts that the components of wave-induced flow forces are lift, drag, and acceleration reaction forces. Furthermore, it is assumed that these components act independently and therefore have additive effects (Morison et al., 1950 in Denny, 1988). While lift forces, acting normal to flow direction, are understood to be of relatively low importance to total flow-induced force in macroalgae, the relative importances of drag and acceleration reaction forces have not been resolved. Drag force is associated with all instantaneous velocities. At a peak velocity (when acceleration is zero) and in steady flow such as in unidirectional currents, drag force will be the primary force acting on the algal attachment. However, in oscillatory flow patterns in wave-exposed sites, flow accelerating past an organism creates additional force (acceleration reaction force). In this circumstance, the acceleration reaction and drag forces act together on the alga (Figure 6.2). Limited evidence suggests that the acceleration reaction may constitute a significant portion of total hydrodynamically induced force on flexible structures (Vogel, 1984; Denny, 1985 and 1988, Gaylord, 1994; Blanchette, 1997).

These forces will most likely only dislodge macroalgae when the algal thallus is fully extended in flow, since it is at this point that the total flow-induced forces are transferred to the algal attachment. The oscillatory flow of waves cause thalli to constantly reconfigure. If the thallus is not fully extended before the wave flow changes directions, then the full force is not felt at the holdfast attachment.

6.1.2 Models and validation

Models to predict survival of macroalgae in waves are based on the above outlined principles. Commonly used model approaches are described in Denny et al. (1985), Denny (1988), Gaylord et al. (1994), and Denny (1995). The approaches are based on the
distribution of holdfast removal forces as well as on total force imposed on the algal thallus by waves, and assume that the thallus becomes fully extended in flow. Friedland and Denny (1995) designed a model for *Egregia menziesii* which includes the oscillatory component, since *E. menziesii* is a long thallus which cannot fully extend in most wave-washed environments. One commonality of all the models is that when the total wave-induced force exceeds that of the holdfast removal force (or that part of the thallus which is broken, e.g. stipe break), then the thallus (or part of the thallus such as the blade) is dislodged.

These models have elucidated mechanisms important to survival, which could not have been accomplished in field studies. For example, Gaylord *et al.* (1994) concluded that acceleration reaction forces may be as important to survival as drag forces. In this model approach, survival is predicted as a function of surface area and site wave heights, and validated by field observations of surface areas. If thallus surface areas found alive at a site are those predicted to survive for the site’s predicted wave heights, and no surface areas exceeding those are found, then the model was considered to be predictive. In this work, Gaylord *et al.* (1994) showed that models based on drag forces alone predicted that much larger surface areas should survive. Hence, the effect of drag force alone could not explain size limitation in the populations that were surveyed. Thus, this approach and its conclusions focused attention on the role of accelerational forces on survival. Yet, the observed thallus size data which were used to test and validate these models may be explained by factors other than mechanical constraints to thallus size. For example, the observed surviving surface areas could also be explained by such processes as the timing of juvenile recruitment and their subsequent growth rates whereby the observed surface areas are a function of age and growth rate. Despite the utility of this data validation approach, which has yielded
conclusions such as those by Gaylord et al. (1994), it is still unknown how well this physical model can explain macroalgal dislodgement rates and survival proportions. To date, the only test of these models with actual survival data was by Blanchette (1997) who demonstrated that, in *Fucus gardneri*, size limitation in wave-exposed sites was due to thallus tattering, not differential survivorship.

### 6.1.3 Validation procedures

The term validation implies that the model, within a designated range of applicability, possesses a satisfactory range of accuracy (e.g. Sargent, 1984 and Curry *et al.*, 1989 in Rykiel, 1996). The process of validating a model can be separated into three main components: operational, data, and conceptual validation (as reviewed by Rykiel, 1996). These components will be followed as guidelines by which this study validates a survivorship model.

Each component describes a different aspect of the model which may be of use to research and prediction. Operational validation is primarily concerned with how well the model can predict the system output and does not attempt to validate mechanisms built into the model. In this process, if the output of a model corresponds with observed data, then the model is operationally validated; however, operational validation does not evaluate the data against which the model output is compared. Data validation is the process by which the data from the real system (and its interpretation) are justified as being appropriate testers of the model predictions. Conceptual validation of a model asks if the parameters and functions within the model accurately represent relationships and processes occurring in the natural system. The conceptual bases of mechanistic models usually well represent the natural system. Additionally, because modeling is an abstraction of the real world, conceptual
validation includes the justification of why known ecological processes have been simplified in the model. A model may be operationally correct yet conceptually incorrect, and vice versa. Also, a model may be deemed operationally incorrect if the data validation is unsatisfactory.

The models in Gaylord et al. (1994) which predict thallus sizes using drag and acceleration reaction forces are operationally and conceptually valid. In this case, the field data (thallus surface areas) which were used to test model predictions were valid for the purpose of predicting optimal thallus surface area. However, I argue that, for the purpose of predicting survival, the operational validity of these models is not known because the observed, real system data used for this purpose are not valid. To achieve the aim of predicting survival, survivorship studies of different species in wave-exposed sites must be compared to physical model predictions of survival (such as in Blanchette, 1997).

This chapter's objectives are to apply a physical survivorship model to *Hedophyllum sessile*, test model assumptions, and validate the model predictions with survival values. In this way, the operational use and conceptual basis of the model for predicting survival will be assessed. Data that will be used to validate the operational use of the model are the *H. sessile* survival rates that were described in Chapter 3. There is no consistent difference between maximum wave forces experienced at each site during summer months yet more frequent differences in site maximum wave forces during other seasons (Figures 2.6 - 2.8). In the more exposed site, life expectancy is lower than in the protected site presumably due to early fall/winter storm effects on dislodgment rates (Tables 3.3 - 3.6; Figure 3.4). Thus, these populations provide adult survival patterns which could be described by organism-wave interactions.
6.2 Methods

6.2.1 Model approach

Models were constructed, following Gaylord et al. (1994), for the sites which were used in demographic analyses; these sites are fully described in Chapters 2 and 3. The model's basis is that when force exceeds holdfast attachment forces, then the holdfast is dislodged. For a given thallus surface area, survivorship (%) is estimated by:

\[
\text{SURVIVORSHIP} \% = 100 \cdot (1 - P_{\text{dislodgment}})
\]

where \( P_{\text{dislodgment}} \) is calculated as:

\[
P_{\text{dislodgment}} = \exp \left[ - \left( \frac{(a-b \cdot F_{\text{alga}})}{a-bc} \right)^{\frac{1}{b}} \right]
\]

The coefficients \( a, b, \) and \( c \) are derived from the cumulative probability distributions of holdfast removal forces calculated in equation (4.2) and listed in Table 4.5. \( F_{\text{alga}} \) is the maximum wave-induced force imposed on the holdfast attachment.

Since the relative importances of peak wave velocity and wave acceleration to the force experienced by a macroalga are not well understood, two separate estimations of the maximum wave-induced force (\( F_{\text{alga}} \)) were used. \( F_{\text{alga}} \) was estimated by predictions of (1) drag force at peak velocity (\( F_{\text{dmax}} \)), and; (2) \( F_{\text{dmax}} \) plus accelerational forces (\( F_a \)) associated with the peak wave velocity.
$F_{d\text{max}}$ was calculated by a modified standard equation for drag force, which estimates the maximum force which an organism is likely to encounter during a given time period (Gaines and Denny, 1993):

$$F_{d\text{max}} = (0.25) \cdot M_{\text{ymax}} \cdot H_m \cdot \rho \cdot C_d \cdot S_p$$  \hspace{1cm} \text{eq. 6.3}$$

where $M_{\text{ymax}}$ is the ratio of maximal wave height to site mean significant wave height, $H_m$, during a three month period, $\rho$ is seawater density (1025 kg $\cdot$ m$^3$), $C_d$ is drag coefficient, and $S_p$ is the thallus projected area. The value used for $M_{\text{ymax}}$ is 5.5 (Gaines and Denny, 1990); thus, during a three month period, the maximum wave height will be 5.5 times the site mean significant wave height. It is assumed that the maximal wave force will be a result of this maximum wave height.

The maximum wave force measured by the recorders ($F_{\text{max, recorder}}$) was used to calculate site $H_m$ (Figures 2.7, 2.8). Bell and Denny (1994) concluded that the primary force acting on the recorder is from drag force at the peak wave velocity. Thus, equation (6.3) can be applied to wave force recorder data. Four, approximately three month intervals (August - October 1995, November - February 1995/1996, August - October 1996, November - February 1996/1997) were designated for each site, based on the times when survival data were available and when storm influence on site exposure was greatest (Chapters 2 and 3). From each time interval, $F_{d\text{max, recorder}}$ was extracted from the time series data presented in Figures 2.7 and 2.8. These maximum force values were used in equation (6.3) to calculate site $H_m$ during each time interval. The drag coefficient, $C_d$, of the perforated, practice golf
ball was calculated by $C_d = 0.863 \cdot u^{-0.07}$ (Bell and Denny, 1994). The velocity ($u$) associated with $F_{\text{dmax,recorder}}$ was calculated by equation (2.6) and used to calculate the golf ball’s $C_d$. The golf ball’s projected area, $S_p$, is the ball’s cross-sectional area, equal to $1.39 \cdot 10^{-3}$ m².

*Hedophyllum sessile*, like other flexible structures, has a velocity-dependent $C_d$. The maximum $C_d$ measured (at 4 m • s⁻¹) will not be the $C_d$ at velocities beyond 4 m • s⁻¹, such as those characteristic of the exposed and protected sites. Therefore, power curve fits (Table 5.2) were used to extrapolate $C_d$ to peak velocities associated with maximum wave heights (Gaylord *et al.*, 1994). The peak wave velocity associated with each maximum height is equal to:

$$v_{\text{max}} \approx \sqrt{g \cdot 2 \cdot H_b} \quad \text{eq. 6.4}$$

which is the standard equation for peak velocity of a wave, with given height ($H_b$), breaking on a steep shore (Denny, 1988). Finally, equation (6.3) was used to calculate $F_{\text{dmax}}$ for a range of $S_p$ values.

The acceleration reaction force ($F_a$) was estimated for *H. sessile* by the standard acceleration reaction equation (Denny, 1988):

$$F_a = C_m \cdot \rho \cdot V \cdot a \quad \text{eq. 6.5}$$

where $C_m$ is the inertia coefficient, $V$ is thallus volume and $a$ is wave acceleration. It is assumed that *H. sessile* is neutrally buoyant in seawater, and therefore thallus volume was calculated as:

$$V = \frac{m_{\text{hed}}}{\rho} \quad \text{eq. 6.6}$$
Thallus mass, $m_{hed}$, was calculated for each $F_{dmax}$ model surface area by a mass to surface area relationship for which data were gathered in August 1996 during the drag force experiments in Chapter 5. $C_m$ is the inertia coefficient, and a value of 3.5 was used which is an average value measured for other morphologically similar species (Gaylord et al., 1994). Unlike $C_d$, it is reasonable to assume that $C_m$ does not change with increasing accelerations (as discussed by Gaylord et al., 1994). Accelerations accompanying peak velocities were calculated as $20 \cdot u_{max}$ (Shaughnessy et al., 1996) such that, for example, the acceleration associated with a wave of $10 \text{ m} \cdot \text{s}^{-1}$ peak velocity is $200 \text{ m} \cdot \text{s}^2$.

### 6.2.2 Model assumptions

The model assumes that the organism moves only for a short time relative to the wave period ($T$), thus allowing the thallus length ($L$) to fully extend in flow. This assumption was tested by two methods. Agreement of the two methods that the thallus would be fully extended was expected, and if there was disagreement, then model predictions should be interpreted more cautiously.

Firstly, if:

$$L < u \left(0.5 \cdot T\right)$$

then, the alga is fully extended (Vogel, 1981). Length ($L$) was calculated for ranges of $T$ (2 - 8 seconds) and average velocities, $u$, (8 - 16 m · s$^{-1}$) and compared to a conservative average *Hedophyllum sessile* length of 35 cm.

Secondly, the Keulegan-Carpenter Number ($K$) was calculated (Gaylord et al., 1994) where:
\[ K = \frac{u_{\text{max}} \cdot T}{L} \]  \hspace{1cm} \text{eq. 6.8}

If \( K > 100 \), then it can be concluded that the thallus becomes completely stretched in the flow direction. The Keulegan-Carpenter Number (\( K \)) was estimated for ranges of \( u_{\text{max}} \) (8 - 16 m \( \cdot \) s\(^{-1} \)), \( T \) (2 and 8 sec.), and \( L \) (0.075 - 0.35 m).

Models are also typically constructed using a single \( C_d \) range for a species. However, for a morphologically variable species such as \( H. \) sessile, the average \( C_d \) varies with morphology (Table 5.2). Additionally, for modeling purposes, holdfast attachment force distributions are assumed to be static. For \( H. \) sessile, attachment force distributions shift to more resistant holdfasts during winter storms (Figure 4.10), and this shift may result in time-dependent differential survival. To test if \( C_d \) variations and holdfast distributions affect survival predictions, combinations of \( C_d - velocity \) relationships and holdfast distributions were used to predict survival for a range of surface areas and \( H_m \) values for which methods are described below.

Since there was no significant site effect on holdfast attachment force distributions within season (Figure 4.10; Table 4.5), holdfast distributions were pooled for both sites within pre- (July/August) and post-storm (November) seasons. Methods for cumulative probability distributions (equations 4.1, 4.2) were used to attain these pooled distributions with the exception that actual removal force was used to rank data instead of normalized force. Percent survival using equation (6.2) was predicted at \( H_m = 1 \) m and \( H_m = 2.5 \) m using pre-storm and post-storm distribution parameters. Within each season, all average drag coefficient-velocity relationships listed in Table 5.2 were used. Experimental combinations of holdfast attachment distributions and drag coefficients were used as treatments to test the
assumptions that variations in drag coefficients and holdfast attachment distributions do not affect survival. Survival was predicted as functions of $S_p$ for all combinations of drag coefficients (sheltered, exposed no tatter, lengthwise tatter, lengthwise and crosswise tatter), holdfast attachment distributions (average pre- and post-storm), and site $H_m$ (1, 2.5 m). If, within the range of surface areas representative of those naturally found on the shore, there is no difference between each treatment’s predicted survival, then the assumption that one $C_d$ and one holdfast attachment force distribution can be used to predict survival will be supported.

6.2.3 Operational validation

Models were constructed for each experimental time interval using predictions based on drag only ($F_{d_{max}}$) and drag plus accelerational forces ($F_{d_{max}} + F_a$). It is expected that one of these approaches should yield more realistic survival values than the other. Finite survival proportions of *Hedophyllum sessile* adults were calculated for each time interval as

\[
\text{Survivorship} \, (\%) = 100 \left( \frac{N_t}{N_0} \right)
\]

Survivorship \, (\%) = 100 \left( \frac{N_t}{N_0} \right) \quad \text{eq. 6.9}

Number of individuals alive at the beginning of the interval ($N_0$) and number of adults after 3 months ($N_t$) were extracted from field data gathered by demographic methods described in Chapter 3.

For each time interval and site, actual finite survival values were plotted as a function of the average thallus surface area at the start of each time interval and compared to model predictions. X-axis error bars were constructed around the finite survival values to account
for the variation in thallus projected areas at the start of each time interval. These projected areas were gathered in August and late October 1996 during the holdfast attachment experiments (Chapter 4; Figure 4.8). These data were assumed to be representative of projected areas in August and November 1995. Data in Figure 4.8 were converted from wetted surface area to projected area by dividing wetted surface area values in half. Average projected areas ± 95% confidence intervals were then calculated. Operational validation of each model was tested by a visual goodness of fit to the field data.

6.3 Results

6.3.1 Model assumptions

For the range of lengths that *Hedophyllum sessile* attains (Figure 2.17), and an average wave period of 8 seconds, *H. sessile* will be fully extended in flow during the wash of a wave. At all wave periods, even those less than 2 seconds, and wave velocities from 8 - 16 m·s⁻¹, *H. sessile* should be fully extended before a wave changes direction (Figure 6.3). The velocities used here are most likely over-estimations of average wave velocities. Yet, between wave periods of 2 to 6 sec., it is likely that any average velocity naturally found in highly wave-exposed sites would result in $L < v (0.5T)$, equation (6.7). Additionally, at ranges of velocities with a wave period of 8 seconds, the Keulegan-Carpenter Number (K) is greater than 100 at all lengths (Figure 6.4). However, for a wave oscillation of 2 seconds, K exceeds 100 only for lengths less than 15 cm. It may be possible that wave periods in the surf environment could be as low as 2 seconds. *Hedophyllum sessile* thallus lengths vary from 12 - 27 cm throughout the year (Figure 2.17). Based on results from calculations of K,
*H. sessile* is most likely fully extended in flow, except when thallus lengths regularly exceed 15 cm (summer months), velocities are $8 \text{ m} \cdot \text{s}^{-1}$ and less, and wave periods are 2 sec. and less. These data in combination suggest that it is reasonable to assume that *H. sessile* becomes fully extended during the oscillation of wave-wash and thus flow regimes approximate those of steady flow during fall and winter months, when velocities regularly exceed $8 \text{ m} \cdot \text{s}^{-1}$ and thallus lengths are $\leq 15 \text{ cm}$.

Variations in $C_d$ and holdfast attachment forces, within the range of *H. sessile*’s naturally occurring projected areas, do not affect predicted survival at a site mean significant wave height ($H_m$) of 2.5 m (Figure 6.5). Results of survival at $H_m = 1 \text{ m}$ are not shown since they predict the same pattern except that differences between $C_d$ values and holdfast attachment forces do not appear until projected areas are much larger. Thus, a single $C_d$-velocity relationship and a single holdfast attachment force distribution can be used for predicting survival of mature *H. sessile*.

### 6.3.2 Model parameters

Drag coefficients were predicted using the $C_d$ - velocity relationship for a pre-tattered, exposed site morphology (from Table 5.2) where:

$$C_d = 0.0624 \cdot u^{-1.454}$$  \hspace{1cm} \text{eq. 6.10}

The distribution of all observed holdfast removal forces (Figure 6.6) was fit to equation (6.2) and was equal to:

$$P_{\text{dislodgment}} = \exp \left[ \left( \frac{-13.61 + 0.9402F_{\text{alga}}}{-13.61 + (0.9402 \cdot 69.39)} \right)^{-0.9402} \right]$$  \hspace{1cm} \text{eq. 6.11}
Site $H_m$ values during each 3 month interval varied from 1.66 - 2.82 m. The maximum wave heights, maximum velocities, and accelerations predicted to be associated with these $H_m$ values were estimated and shown in Table 6.1.

Thallus projected surface area ($S_p$, in m$^2$) and mass ($m$, in kg) are directly related, $n=15$, adjusted R-square=0.983, and $p<0.001$. The linear regression relationship to predict mass from thallus surface area is:

$$m_{hed} = (1.22e^{-4} \cdot S_p) + 0.002$$

**eq. 6.12**

### 6.3.3 Model results and field data

Field survival data (Table 6.2) were compared to model output for all time intervals (Figures 6.7 - 6.10). X error bars for field survival data (Figures 6.7 - 6.10) represent the range of thallus surface areas during that time, measured in August and October 1996 (extracted from data in Figure 4.8). It is assumed that these measures represent surface area variations in August and November 1995 and 1996.

In all cases, predictions using only $F_{dmax}$ were not validated. In most cases the values estimated by $F_a + F_{dmax}$ were similar to the average field survival values. When the range of field projected area values is used to evaluate $F_{dmax} + F_a$ model predictions, many field survival values can not be accurately predicted. However, overall, the average population survival is predicted better in the exposed and protected sites by $F_a + F_{dmax}$. 
6.4 Discussion

6.4.1 Operational validation of the model's ability to predict survival

Gaylord et al. (1994) concluded that $F_{d_{max}}$ alone can not describe population dislodgment rates and does not adequately explain the observed thallus sizes. Results here corroborate these conclusions. In *Hedophyllum sessile*, the observed thallus sizes are smaller in October than in August. This is most likely due to tattering and not to dislodgment of all large individuals, as discussed in Chapter 4. When wave force increases, *H. sessile* tatters by losing biomass primarily from the distal ends of the blades, which effectively reduces the thallus surface area and volume. In any event, if drag force alone were a limiting force, we would expect to see much larger individuals in these sites at all times. However, since this is not the case, other limiting factors must be selecting against individuals throughout these intervals. For the purpose of predicting survival, the use of drag forces only is rejected in support of using drag plus acceleration reaction forces.

The operational validity of this model approach using drag plus acceleration reaction forces seems to be unpredictable with model deviations from field values ranging from an overestimation of 25% (for exposed site, November - February 1995/1996) to under-estimations of 15 - 45% (for exposed and protected, August - October 1995; protected, November 1995 - February 1996; exposed, August - October 1996; protected, November 1996 - February 1997). Problems with conceptual and data validations are most likely the reasons for these deviations. Conceptual issues will be discussed in the following section (6.4.2).

The survival data used to validate the model might be improved by increasing the sample size (Table 6.2). The model's predictions are based on the distribution of holdfast
attachment forces in these populations. It is possible that, even though individuals were randomly selected, the individuals in the survival measurements were not representative of the total range of holdfast distributions. For example, if the individuals for which survival was predicted were skewed towards stronger holdfasts because the sample size was not large enough and if the model was mechanically correct, then the model would underestimate survival. It was not possible to monitor larger sample sizes in these sites because of logistical constraints during winter sampling. Likewise, the average projected thallus areas against which survival was plotted were assumed to be similar between years. Better estimates of surface area would provide more accurate data with which model predictions could be compared. In this study, it is likely that the error surrounding the mean surface area could not be reduced and that large errors reflect the range of natural variation in thallus surface areas. The most accurate surface area estimates were in November at the exposed site, whereas most variable estimates were in the protected site in both August and November and in the exposed site in August. This suggests that there is a wide range of thallus surface areas in protected sites and over time. Once tattering to an optimal size happens (such as in the exposed site in November), then surface area measurements are more predictable with less error.

6.4.2 Conceptual validation

There are numerous conceptual attributes which must be further examined in these model approaches which will ultimately affect the operational validity of the $F_{d_{\text{max}}} + F_a$ model. These include: (1) relative importances of acceleration and peak velocity to physical stress at the holdfast base, (2) effects of morphology on the inertia constant, $C_m$, (3)
estimation of acceleration and peak velocities, and (4) mechanism of mortality. These attributes will be discussed in the following paragraphs.

Relative importances of acceleration and peak velocity to physical stress at the holdfast base need to be further examined. For solid objects which do not reconfigure, accelerational forces are typically a small proportion of the total flow-induced physical force (in Denny, 1988). Because flexible structures can “trap” additional volume within their blades as they reconfigure, acceleration reaction forces may be increased and become a major proportion of total wave-induced force. This is evident in published values for the inertia coefficient, \( C_m \), of the acceleration reaction (equation 6.5), which is maximized by flexible structures (see values published in Gaylord et al., 1994).

Despite the potential importance of accelerational forces to total wave-induced force and the consequent hydrodynamic requirements that the alga must have to withstand these forces, very few studies have documented shape and size effects on the acceleration reaction. Kelp morphological characteristics which have been considered to be important morphological parameters in determining drag forces, such as blade length, number, and undulations, may thus also be determinant factors of accelerational forces. Likewise, the relative importances of these shape and size characteristics to acceleration reaction forces (in the case of acceleration, acceleration reaction forces scale with thallus volume) also need to be fully assessed.

The model assumes a similar wave breaking pattern so that acceleration is always approximately equivalent to 20 times the peak velocity and peak velocity is determined by a standard breaking wave equation (equation 6.4). This equation is based on the assumption that the wave breaks on a steep shore (plunging wave) where the full wave height breaks onto
the rock. This assumption is fully supported in the exposed site, but not in the protected site. The protected site is exposed to waves which wrap around from the exposed site, after they have broken. Thus this site also experiences surges of white water (shoaling waves) which produce less velocity than plunging waves. Nevertheless, differences between peak velocities at the sites which were measured by the wave force recorders (see discussion 2.4) are similar to the velocity differences calculated for a plunging wave. For example, the maximum velocity directly measured by the recorders was 10.6 m \cdot s^{-1} (exposed) and 8.5 m \cdot s^{-1} (protected), and peak velocities estimated for maximum wave heights within each three month time intervals were 14.1 - 16.6 m \cdot s^{-1} (exposed) and 13.5 - 14.8 m \cdot s^{-1} (protected). This suggests that the velocities calculated by equation 6.4 at both sites are appropriate estimates.

However, the relationship between peak velocity and acceleration may not be the same at both sites since the exposed site has a steeper shore than the protected site. Thus, although velocities may be appropriately estimated by the approaches used here, the magnitude of acceleration may not be estimated correctly; the protected site, for a given peak velocity, will experience lower acceleration and thus lower acceleration reaction forces. If the protected site experiences lower accelerations than those estimated in this model, these changes would then be reflected in higher predicted survival.

Analytical methods to accurately predict wave breaking patterns are not well developed. Likewise, field quantification of velocities and accelerations in the surf-zone might only yield time series subsets of the entire time series during which a field experiment is monitored. These subsets may or may not be representative of the whole time series. Additionally, field measurements of these hydrodynamic components of wave force are site-
specific. For these reasons, it is unreasonable to expect that field methods can be utilized to evaluate the relative importances of wave acceleration and velocity to subsequent physical stress on a macroalga. Controlled experiments within wave tanks or wave machines must be conducted to assess the effects of various wave patterns such as wave height, breaking point, and series (continuous wave impact vs. single wave impact) and effects of beach slope and water depth on the types of forces exerted on a thallus.

Additionally, the model assumes that dislodgment occurs instantaneously from the maximum wave impact. However, as results from Chapter 4 suggest, holdfasts loosen over time. Fatigue failure of holdfasts as a result of continuous waves below the maximum wave may also contribute to the weakening of the holdfast. This may only occur within perhaps a single set of waves, or numerous sets of waves, but nevertheless within a period of time shorter than the 3 month period measured in Chapter 4. The extent to which the fatigue failure occurs has not yet been investigated. Since fatigue failure in macroalgal tissue has been well documented (Denny et al., 1989) and since holdfasts are primarily anchored to the substratum by microscopic rhizoidal tissue (Tovey and Moss, 1978), there is no reason to assume that fatigue failure is not an important mechanism of holdfast failure.

6.4.3 Other insights gained from this model

Two other insights regarding macroalgal-wave interactions resulted from this research. Firstly, morphological shape variations (as measured by drag coefficients) did not have an effect on predicted survival in *Hedophyllum sessile*. The strap-like, bladed form of *H. sessile* has been hypothesized to be a survival advantage in wave-exposed sites by reducing drag forces (Armstrong, 1989). It has also been hypothesized that the different morphologies of *H. sessile* are due to relative degrees of desiccation and sun exposure so that
the more strap-like bladed form is found in moister and shadier sites and the undulated, bluff form found in drier and sunnier sites (Widdowson, 1965). More exposed sites are also more moist due to spray from breaking waves (Nybakken, 1986), thus this morphological pattern would also be apparent along wave-exposure gradient. Results from this study reject the first hypothesis, suggesting that drag force does not select against the sheltered morphology in the wave-exposed environment. The second hypothesis was not tested.

I suggest that the primary advantage to the more exposed morphology is in its ability to tatter lengthwise, and crosswise distally, thus maintaining meristematic and reproductive tissue. The more sheltered morphology, in contrast, tears haphazardly along undulations (personal observation) which potentially may cause a significant portion of meristematic and reproductive tissue to be lost.

6.4.4 Conclusion

The model approach designed by Denny (1985) and later applied to macroalgae (Gaylord et al., 1994) can be used to estimate macroalgal survival by using drag and acceleration reaction forces, \( F_{\text{dmax}} + F_a \). The operational ability of this model, however, has a limited range of applicability because the observer must be able to choose an appropriate wave-limited population and accurately measure surface areas and volumes. If there is a wide range of variation in these thallus attributes, predicted survival will also widely vary. However, the average prediction of survival for an average thallus area and volume needs to be compared to more extensive survival data once conceptual issues are assessed. The assumptions that, for *Hedophyllum sessile*, drag coefficients and variable holdfast force distributions do not affect survival were supported. Other conceptual questions raised here concern the mechanism and role of flow acceleration and its interaction with the macroalgal
form. These questions were not tested and must be evaluated in future studies since they will alter the applicability of this model approach.
Table 6.1 Site wave-exposure parameters for experimental times and sites. Site significant wave height ($H_m$), maximum wave height, and $u_{max}$ were estimated by equations 6.3 and 6.4, respectively. Acceleration ($a$) was estimated by $20 \cdot u_{max}$ (Shaughnessy et al., 1996).

<table>
<thead>
<tr>
<th>Sample group</th>
<th>site $H_m$ (m)</th>
<th>max. height (m)</th>
<th>$u_{max}$ (m·s$^{-1}$)</th>
<th>$a$ (m·s$^2$)</th>
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<td>11.6</td>
<td>15.09</td>
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<td>14.1</td>
<td>16.58</td>
<td>331</td>
</tr>
<tr>
<td>protected</td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Aug - Oct 1995</td>
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<td>14.1</td>
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<td>11.2</td>
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Table 6.2 Field survivorship values for adult *Hedophyllum sessile*. Data are from permanent transects described in Chapters 2 and 3.

<table>
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<tr>
<th>Sample group</th>
<th>initial n</th>
<th>final n</th>
<th>% survival</th>
<th># months</th>
</tr>
</thead>
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</tr>
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<tr>
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<td>48</td>
<td>3.4</td>
</tr>
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<td>15</td>
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<td>67</td>
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<td>6</td>
<td>60</td>
<td>2.8</td>
</tr>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aug - Oct 1995</td>
<td>38</td>
<td>24</td>
<td>63</td>
<td>3.4</td>
</tr>
<tr>
<td>Nov - Feb 1995</td>
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<td>75</td>
<td>3.4</td>
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<tr>
<td>Aug - Oct 1996</td>
<td>17</td>
<td>7</td>
<td>41</td>
<td>2.7</td>
</tr>
<tr>
<td>Nov- Feb 1996</td>
<td>10</td>
<td>9</td>
<td>90</td>
<td>2.8</td>
</tr>
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</table>
Figure 6.1 Representative illustration of flow during a wave-wash. As a wave passes through a site, flow velocities will change over time (A) until the peak velocity is reached (B). Acceleration occurs at A, and the steeper the slope, the greater the acceleration. At B, there is no acceleration. After the peak velocity is reached, acceleration occurs in the opposite direction (C). In the intertidal, these flow regimes can happen towards the shore (A-C) or seaward (D).
Figure 6.2 Illustration of wave - kelp interactions. As a single wave washes over an individual kelp, different flow induced forces which will act on the holdfast attachment. 1 = initial wave impact, 2 = reconfiguration of the thallus in resultant flow, 3 = thallus is completely extended in flow while wave is still accelerating, thus both drag ($F_d$) and acceleration reaction forces ($F_a$) act on the holdfast attachment, 4 = peak wave velocity where only flow induced force is $F_d$. 
Figure 6.3 Calculations of *Hedophyllum sessile* movement relative to wave period and velocity (equation 6.3). Data were calculated by equation 6.3 for velocities 8 (○), 10 (□), 14 (△) and 16 (▽) m·s⁻¹. Data above the horizontal dotted line at 0.35 m (*Hedophyllum sessile* thallus length) represent velocity and wave period conditions when the thallus is completely extended in flow.
Figure 6.4 Calculations of *Hedophyllum sessile* movement relative to wave period and velocity by Keulegan-Carpenter Number (K). Data were calculated in equation 6.4 for 8 (○), 10 (□), 14 (▲) and 16 (▼) m·s⁻¹ with 8 second period and 8 m·s⁻¹ with 2 second period (●). Values above the horizontal dotted line at 100 represent conditions where thallus is completely extended in flow.
Figure 6.5 Effects of variations in holdfast attachment distributions and drag coefficients on survival. Each pair of lines represent the drag coefficient for a morphology. Solid lines are for exposed morphologies and dotted lines represent the sheltered morphology. Plots for the different morphologies are labeled on the right y-axis (exposed no tatter = EXP; exposed, lengthwise tatter = EXP, L tatter; exposed, lengthwise and crosswise tatter = EXP, L + C tatter; sheltered = SHEL). The upper line of a pair is survival based on post-storm holdfast distribution and the lower line is that based on pre-storm holdfast distribution. Vertical solid line is average projected surface area in November, 1996 at both sites. Vertical dotted line is the average projected surface area in August, 1996.
Figure 6.6 Cumulative probability of holdfast dislodgment ($P_{\text{dislodgment}}$). As force increases, there is a greater probability of dislodgment. Data points represent actual data, pooled from all data gathered in Chapter 4. The solid line is the fit to equation 6.2 where $a = -13.61$, $b = -0.9402$, and $c = 69.39$. 
Figure 6.7 Predicted (lines) and actual (points) survival data for August to October, 1995. Solid lines and points are exposed site data. Dotted lines and open points are protected site data. Horizontal lines at 100 % are predictions based on drag force only and curves are those based on drag and acceleration reaction forces combined. X-axis error bars represent the 95% confidence intervals of actual projected surface areas.
Figure 6.8 Predicted (lines) and actual (points) survival data for November 1995 to February, 1996. Solid lines and points are exposed site data. Dotted lines and open points are protected site data. Horizontal lines at 100% are predictions based on drag force only and curves are those based on drag and acceleration reaction forces combined. X-axis error bars represent the 95% confidence intervals of actual projected surface areas.
Figure 6.9 Predicted (lines) and actual (points) survival data for August to October, 1996. Solid lines and points are exposed site data. Dotted lines and open points are protected site data. Horizontal lines at 100% are predictions based on drag force only and curves are those based on drag and acceleration reaction forces combined. X-axis error bars represent the 95% confidence intervals of actual projected surface areas.
Figure 6.10 Predicted (lines) and actual (points) survival data for November, 1996 to February 1997. Solid lines and points are exposed site data. Dotted lines and open points are protected site data. Horizontal lines at 100 % are predictions based on drag force only and curves are those based on drag and acceleration reaction forces combined. X-axis error bars represent the 95% confidence intervals of actual projected surface areas.
CHAPTER 7

Conclusion and recommendations for future research

7.1 General conclusion

This thesis has explored relationships between wave-exposure and *Hedophyllum sessile*’s recruitment, survival, and reproductive output. Field experiments measured *H. sessile* population parameters (such as recruitment and mortality) and their association with sites of different exposure. These experiments could not isolate mechanisms related to wave-exposure which produced the site-related demographic rates. Thus, biomechanical and physical model approaches were used to evaluate the mechanisms by which wave-exposure affects population parameters such as recruitment and adult survival. Biomechanical approaches quantified site wave-exposure differences, mechanics of juvenile and adult holdfast attachments, and thallus size and shape effects on drag forces. Offshore buoy data were directly related to wave force recordings at the study sites, thus providing a precise definition of the differences between site exposures in terms of maximum wave force throughout the experimental period. Physical model approaches evaluated the effects of variations in site wave-exposure, holdfast attachment forces, and drag forces to survival. In combination, these techniques have provided insight into the relationship between wave-exposure and demographic rates which could not have been gained if each technique was used in isolation. To my knowledge, this is one of the first ecological studies which has combined descriptive ecological techniques (e.g., demographic studies) with biomechanical experiments (e.g., holdfast attachment mechanics).
7.2 Relative importance of wave-exposure to macroalgal populations

The importance of biotic interactions to macroalgal population ecology is well documented (e.g., Dayton, 1975; Dayton et al., 1984; Paine, 1984; Dean et al., 1989; Chapman, 1990; Menge, 1991). In contrast, there are few studies documenting specific effects of wave-exposure on macroalgal demographic parameters within the range of wave-exposures that a species inhabits. Previous research suggested that *H. sessile* adult mortality occurs mainly during winter storms by physical dislodgment (Duggins and Dethier, 1984; Markel and DeWreede, 1998). Results from Chapters 3, 4, and 6 have conclusively shown that higher adult mortality occurs in sites with higher wave-exposure and with seasonally higher wave-exposure. For example, field demographic experiments presented in Chapter 3 demonstrate that life expectancy is lower in the wave-exposed site than in the protected site and that the highest adult mortality in the exposed site occurs in early fall.

Additionally, the physical mechanisms which cause dislodgment were established. High mortality is associated with loose holdfasts, relatively large thallus sizes, and early winter storms which produce high wave forces. Data presented in Chapter 4 show that the adult holdfast attachment before winter storms is more variable than after a series of storms; after storms, the remaining holdfasts are uniformly more resistant. Data suggest that holdfast weakening occurs during summer months which results in a larger proportion of loose holdfasts before early winter storm events than after storm events. Thallus size data, from Chapters 2, 4, 5, and 6, demonstrate that thalli tatter as a result of seasonal wave-exposure and that size reduction by tattering is the most effective way in which to reduce drag and acceleration reaction forces, thus also effectively increasing survival.
The biomechanical experiments yielded predictive conclusions. One important conclusion is that if early storms happen when thalli are not tattered and holdfasts are weak (i.e., in early winter dates), then there will be a greater mortality rate than if thalli are tattered and holdfasts are more firmly attached (such as in mid-winter dates). This prediction of wave-induced mortality was supported by field-studies; for example, *H. sessile* in the exposed site has a significantly lower proportion of individuals surviving to February (a mid-winter date) than those in the protected site, but this difference is due to a high mortality between early September and early October (an early winter date) and not to differential mortality in census dates between October and February.

Based on my results, recruitment densities are not affected by site wave-exposure. Successful recruitment is, however, affected by substratum type; specifically, articulated coralline algae and pre-existing *H. sessile* holdfasts provide the best substratum for recruitment. The most reasonable explanation for this is that grazers such as the chiton *Katharina tunicata* can not graze on *H. sessile* juveniles within the branches of the articulated coralline algae or in the shelter of holdfast haptera; however, they are capable of grazing on juveniles on the flat, crustose coralline algae and bare rock surfaces. The biomechanical study in Chapter 4 suggests that physical factors may also determine *H. sessile* recruitment and juvenile survival. Biomechanical surveys of *H. sessile* juvenile attachment on articulated and crustose coralline algae within the protected site demonstrate that juveniles are more firmly attached in articulated coralline algae (Chapter 4). Additionally, there is an exposure effect on juvenile attachment forces on articulated coralline algae since juveniles are more firmly attached in the exposed site.
7.3 The hypothetical compromise between reproduction and size

In the study sites, most individuals become reproductive within their first year (Chapter 3). In the exposed site, all recruits from the spring cohort grew into adult size classes and became reproductive in their first winter. In the protected site, a proportion of individuals wintered as juveniles and were not reproductive. Adult thallus tattering did not affect reproductive effort or output. In comparison to individuals in the protected site, *H. sessile* in the exposed site had lower total thallus surface areas during mid-winter months (October and December) but this was not correlated to a lower estimated reproductive output. Thus, for *H. sessile*, the hypothetical trade-off between surface area and reproductive output where minimization of surface area may increase survival but decrease reproductive output was rejected.

7.4 Recommendations for future studies

Model validation procedures in Chapter 6 demonstrate that the effects of wave-induced drag forces and holdfast attachment forces can not explain survival rates. Mortality rates in these *H. sessile* populations are related to wave-exposure. However, models which are based on drag forces at peak wave velocities relative to holdfast attachment forces predicted zero mortality for the range of thallus sizes naturally found throughout the year. Research on the relevant functional advantages or disadvantages to the survival of specific morphological shapes and sizes must focus on factors other than drag forces. Specifically, attention should focus on the role of acceleration reaction forces and holdfast fatigue failure.

Future research on wave-macroalgal interactions should focus on combining biomechanical, hydrodynamic and ecological techniques. More information is needed about the physical forces that are important to macroalgal dislodgment and their interactions with
algal shape and size. Laboratory studies do not fulfill this goal. Comprehensive experiments need to be performed in the field. In most previous studies where wave-exposure effects are documented, wave-exposure is poorly defined. In order to be more predictive, research on the relative importances of physical forces and biotic factors to macroalgal ecology along wave-exposure gradients must better specify components of wave-exposure. This study has shown that maximum wave force recorders can be used as a reliable method of defining wave-exposure.

This thesis research combined various ecological and biomechanical techniques to better understand wave-exposure effects on macroalgal populations. The data presented here document the demographic patterns related to relative degrees of wave-exposure. Additionally, experiments have illustrated the physical mechanisms (for example, holdfast attachment mechanics and the relatively low importance of drag forces) which contribute to these demographic patterns. In this way, more precise predictions about wave-macroalgal interactions and their consequent effects on macroalgal ecology, especially mortality rates, can be formulated from these experiments than would have been possible by using only demographic studies along a wave-exposure gradient. Future studies on the physical and biological interactions in the marine environment must include combinations of methods such as those utilized in this thesis.
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APPENDIX 1

Examples of column vectors for the matrix model projections

Transition matrices in Tables 3.8 - 3.11 were multiplied by column vectors over 37 iterations. Each iteration was equivalent to ~60 days, which represents field observation dates. Age intervals were 1 = 0-55 days, 2 = 55-112 days, 3 = 112 - 155 days, 4 = 155 - 209 days, 5 = 209 - 264 days, 6 = 264 - 321 days, 7 = 321 - 362 days, 8 = 362 - 425 days, 9 = 425 - 497 days, and 10 = 497 - 503 days. The gametophyte stage is represented by an approximately 60 day interval and is represented by 0.

The initial column vector to represent an April recruitment cohort in the exposed site was:

<table>
<thead>
<tr>
<th>age</th>
<th>number of individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
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</tr>
<tr>
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</tbody>
</table>
Likewise, the initial column vector to represent an April recruitment cohort in the protected site was:

<table>
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</table>

Each initial column vector was multiplied by both transition matrices for that site, and iterations thereafter were calculated in the same way (see equation 3.4). Total population size at each iteration was equal to the sum of age intervals 1 to 5 (in the exposed site) and 1 to 10 (in the protected site). Subsets of the calculated column vectors and total population sizes for transitions matrices 3.10 and 3.11, which simulate successful adult reproductive output and recruitment, are shown in the following pages. Only the first 10 iterations are shown and population numbers are rounded to the nearest whole number.
In the exposed site,

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APPENDIX 2

DOS-based, data-logging program used in the drag experiments

The following program was designed to enable a DOS-based computer to record data from a PC-interfaced multimeter. The program is written in BASIC language and was converted to an executable file using QuickBASIC (© Microsoft Corporation, 1985-1988). The program can be installed on any DOS-based computer and run on any version of DOS. Thus, it is ideal for palm-top computers for logging data in the field.

The program allows the user to designate a file name to which data are saved. Once data are collected, they are immediately shown on the screen as well as printed to that file. The user can also designate sample numbers and sampling intervals (in seconds). Data collected at each interval are separated into columns (sample number, time, AC/DC, voltage output). The file is saved as a text file and easily opened in any spreadsheet program.

I had no previous experience in writing BASIC programs. Thus, there are probably parts of the program which could either be simplified or re-arranged. However, it works extremely well for its purpose. Since the program is simply written, it is easy to follow and to modify for other purposes if necessary. Command and functional descriptions are inserted into the program in bold type and preceded by a single apostrophe ('). These descriptions do not appear on the program when it is run. Descriptions which are enclosed in quotation marks (""") appear as the program is run and are general program information and queries for the user to enter information.
1 CLS
10 PRINT " * BIOMECHANICAL ADVENTURES* "
20 PRINT " This program is designed to log voltage data from a PC interfaced multimeter."
21 PRINT " It takes about 1 sec. for any sample voltage change to register at the "
22 PRINT " multimeter (and thus computer). Therefore, this sampling method and program"
23 PRINT " are not suitable for voltage changes during a period less than 1 sec. (for"
24 PRINT " example, a wave passing over a sample). However, sampling is suitable for "
25 PRINT " measurements of drag in steady velocity. This program allows you to set "
26 PRINT " the sampling frequency and save different samples to the same file. You "
27 PRINT " can also stop sampling at any time, close a file and open a new one." 
28 PRINT " 
29 PRINT " DO YOU WANT TO CONTINUE? (enter 'y' or 'n') "
30 con$ = INKEY$
31 INPUT con$
32 IF con$ = "y" THEN GOTO 34 ELSE 33
33 IF con$ = "n" THEN GOTO 400 ELSE 29
34 CLS
35 LOCATE 1,1
40 PRINT " Once you designate the communications port that you will be using to" 
41 PRINT " hook the multimeter to, the program will open the port with instructions" 
42 PRINT " to the computer for the type of data that is being sent by the multimeter:" 
50 PRINT " This information is: " 
70 PRINT " * transmission rate: 1200 baud"
80 PRINT " * character coding: 7-bit ASCII"
90 PRINT " * parity: none"
100 PRINT " * stop bits: 2"
101 PRINT ""
102 PRINT " Data will be stored as tab delimited text to the file you have named," 
103 PRINT " and can be opened in any spreadsheet program such as Microsoft Excel." 
110 PRINT ""
120 PRINT ""
130 PRINT " DO YOU WANT TO CONTINUE? (enter 'y' or 'n') "
140 q$ = INKEY$
150 INPUT q$
160 IF q$ = "y" THEN GOTO 180 ELSE 170
170 IF q$ = "n" THEN GOTO 400 ELSE 130
180 CLS
181 LOCATE 1,1
187 PRINT "If you are using : the HP_100, enter com port 1."
188 PRINT " : the lab's HP monster, enter port 2."
189 PRINT "    : any other computer, ....check directory or guess."
190 PRINT " Enter the communications port you are using ('1' or '2')."
200 por$ = INKEY$
210 INPUT por$
220 PRINT "enter file name, including drive path"
230 INPUT file$
240 OPEN"O", #1, file$
250 PRINT "enter sampling interval (sec) 'designates sampling frequency"
260 INPUT interval 'responsible for the ability to input frequency
270 PRINT "enter sample number"
280 INPUT sample
290 ON TIMER(interval) GOSUB 10000
300 TIMER ON
310 CLS
320 LOCATE 1, 1
330 PRINT "starting time:"; TIME$
340 PRINT "press 'p' to pause sampling and choose file options" 'to pause sampling
350 starttime = TIMER
360 WHILE Timepast < 1000000
370 Timepast = TIMER - starttime
380 WEND
390 CLOSE #1
400 END

10000 'chooses port and runs program loop
10010 IF por$ = "1" THEN GOTO 10030 ELSE 10020
10020 IF por$ = "2" THEN GOTO 10040 ELSE 30200
10030 OPEN "com1:1200,N,7,2,RS,CS,DS,CD" FOR RANDOM AS #2
10040 OPEN "com2:1200,N,7,2,RS,CS,DS,CD" FOR RANDOM AS #2
10050 n$ = INKEY$
10060 IF n$ = "p" THEN GOSUB 20000 'routing to pause subroutine
10070 a$ = "D"
10080 PRINT #2, a$ 'print data to file number 2
10090 in$ = INPUT$(14, #2) 'reads 14 characters from file 2 to in$
10100 sam = sample
10200 t$ = TIME$
10300 PRINT in$; TAB(1); sam; TAB(25); t$; TAB(35); 'prints to screen
10400 PRINT #1, in$; TAB(1); sam; TAB(25); t$; TAB(35); 'prints to file
10500 CLOSE #2
10600 RETURN

19000 'subroutine gives file options: to continue, exit or close file
20000 CLS
20050 close$ = INKEY$
20100 PRINT "enter 'c' to CLOSE file and OPEN NEW file"
20200 PRINT "enter 'e' to CLOSE file and EXIT program"
20250 PRINT "enter 's' to keep current file and START NEW SAMPLE"
20300 INPUT close$
20500 IF close$ = "c" THEN 20550 ELSE GOTO 20600
20550 CLOSE #1
20551 CLOSE #2
20552 CLS
20553 LOCATE 1, 1
20554 RETURN 180
20600 IF close$ = "e" THEN 20650 ELSE GOTO 20700
20650 CLOSE #1
20651 CLOSE #2
20652 RETURN 390
20700 IF close$ = "s" THEN 20750 ELSE GOTO 20000
20750 CLOSE #2
20751 CLS
20752 LOCATE 1, 1
20753 RETURN 250

30000 'if wrong port is given,
30100 'subroutine clears screen, closes file, and sets program to re-entering data
30200 CLS
30300 CLOSE #1
30400 CLOSE #2
30500 LOCATE 1, 1
30600 PRINT "SOMETHING AMISS-----the port # you've entered is not correct"
30700 PRINT "If you are using: the HP100, enter com port 1"
30800 PRINT " : the lab's HP monster, enter port 2"
30900 PRINT " : any other computer, ....check directory or guess"
40000 GOTO 200