

# Population, morphometric and biomechanical studies of three understory kelps along a hydrodynamic gradient

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**ABSTRACT:** Kelps (benthic algae in the order Laminariales) live in a highly dynamic fluid environment, and exhibit many adaptations to meet the challenges imposed by hydrodynamic forces. We examined flow effects (direct and indirect) on understory kelp population dynamics, morphology and biomechanics along gradients of current velocity and wave accelerations in the San Juan Archipelago, Washington. *Costaria costata*, *Agarum fimbriatum*, and *Laminaria complanata* all exhibited significantly higher mortalities at wave-impacted sites, but no gradient was detectable in the effects of tidal currents on survival, despite the strong tidal signal in waters of the archipelago. This pattern stands in contrast to that reported earlier for the surface-canopy bull kelp *Nereocystis luetkeana* in these waters; *N. luetkeana* mortality was strongly correlated with current, but not wave energy. The higher wave-driven mortalities of the understory species occur, even though a suite of morphological and biomechanical attributes (thallus size and thickness, holdfast area and biomass, stipe cross-sectional area, holdfast strength, blade toughness) indicate that kelps at sites characterized by high flow energy are better adapted to resist the forces imposed by waves and currents. While the forces imposed by strong currents have little effect on survival, they do have significant effects on morphology and biomechanical strength. We propose that morphological plasticity in *A. fimbriatum* and *C. costata* ameliorates the effects of both currents and waves on their survival.

**KEY WORDS:** Kelp · Hydrodynamics · Flow · Biomechanics · *Costaria costata* · *Agarum fimbriatum* · *Laminaria complanata*

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## INTRODUCTION

Any consideration of the relationship between form and function in benthic algae must, at the very least, consider the complex relationship (or synergism) between fluid dynamics and individual fitness. This is particularly true of kelps, which are benthic brown algae in the order Laminariales, that frequently live (and thrive) in the most wave- and current-swept nearshore environments. Kelp forests are a dominant nearshore feature along temperate coastlines where rocky sub-

strates provide a suitable surface for attachment, and the ecological roles and importance of these assemblages are wide-ranging and well established. The broad range of impacts that hydrodynamics have on the fitness of these common and ecologically important organisms is evident from a rich literature that examines the influence of flow on such key elements as herbivory (Blanchette 1996, Kawamata 1998, Duggins et al. 2001), nutrient uptake and gas exchange (Wheeler 1980, 1982, Raven 1997), reproduction and recruitment (Vadas et al. 1990, Pearson & Brawley 1996, Serrao et

al. 1996, Shaughnessy et al. 1996), productivity (Gerard & Mann 1979, Leigh et al. 1987, Koehl & Alberte 1988, Wheeler 1988, Glenn & Doty 1992, Hurd et al. 1996, Dayton & Oliver 1999), morphology (Neushul 1972, Koehl & Wainwright 1977, Gerard 1987, Gaylord et al. 1994, 2001, Friedland & Denny 1995, Blanchette 1997, Denny et al. 1997, Blanchette et al. 2002), and biomechanical properties (Koehl & Wainwright 1977, Armstrong 1987, Johnson & Koehl 1994, Gaylord & Denny 1997, Gaylord et al. 2001, Blanchette et al. 2002; plus, see Norton et al. 1982 and Hurd 2000 for excellent reviews). The literature is considerably thinner in its analysis of the direct or indirect relationship between flow dynamics and demographic properties of kelp populations (but see Carrington 1990, Vadas et al. 1990, Kawamata 2001, Blanchette et al. 2002). An exception to this generalization concerns the ramification of extreme flow events (storms), particularly during El Niño periods (Dayton & Tegner 1984, Dayton et al. 1984, Harris et al. 1984, Ebeling et al. 1985, Kennelly 1987a,b, Seymour et al. 1989).

Flow effects on kelps can be direct, such as the effects on nutrient uptake, or indirect, as where the flow environment determines blade morphology, which, in turn, affects blade boundary-layer dynamics and nutrient uptake. To make matters more enigmatic, both direct and indirect hydrodynamic effects may follow complex, non-linear relationships. A case in point involves the population dynamics of the common NE Pacific kelp *Nereocystis luetkeana* (Duggins et al. 2001). Found in highly energetic sites as well as sites protected from prevailing wave and current influences, *N. luetkeana* survivorship is greatly influenced by the indirect relationship between drag-induced failure and tissue damage by mesograzers (which compromises the structures of benthic attachment). Intermediate energy and variable flow regimes result in low survivorship of this plant due to extremely high grazing rates coupled with periodic high drag forces imposed on damaged kelps. At sites with low flows, herbivore damage is high but drag forces are consistently insignificant, while at highly energetic sites, herbivore damage is virtually absent. This non-linear pattern reinforces both the importance of indirect interactions as well as the importance of examining variance (or more specifically the magnitude and frequency of extreme hydrodynamic events) in addition to mean flows (Denny 1994, Eckman et al. 2003 this issue). Making the role of hydrodynamics in kelp ecology even more complex is (1) the highly variable nature of most flow environments, (2) the exposure to very different flow environments as kelps grow from their microscopic life history stage to their much larger (sometimes massive) adult size, and (3) the fact that at any given moment in time, different portions of a kelp

may exist in very different flow environments (e.g. holdfast in substrate boundary layer, and blade in freestream flow). Furthermore, kelp assemblages are typically multi-layered, with different layers exposed to different hydrodynamic regimes, and each layer potentially altering the hydrodynamic environment for other layers. In the NE Pacific, benthic algal assemblages can have up to 4 distinct canopy layers. Surface canopy kelps, such as *Macrocystis pyrifera* and *N. luetkeana*, grow through the water column, and a large fraction of their biomass and thallus surface area is found at or near the surface, where wave accelerations can produce tremendous drag forces on individuals. Understory kelps, like *Laminaria setchellii* and *Pterygophora californica*, frequently have relatively stiff stipes (up to 1 m in length), which can hold the kelp blades well off the substrate and may resist deformation in strong flows. Below this stipitate understory layer may be found another group of kelps with short flexible stipes, their blades lying on or near the substrate in any significant flow. Lastly, below all these layers may be found a diverse group of much smaller filamentous, foliose and encrusting red and brown algae in close contact with the substrate. The hydrodynamically mediated challenges to physiology, production and survival faced by algae in each of these canopy layers are likely to be very different. Superimposed upon these challenges, hydrodynamically mediated interspecific interactions may operate within and among canopy layers as well.

Much of our understanding regarding these complex interactions results from studies on surface canopy species, typically in open, exposed coastal environments. In this paper we focus on demography (specifically survival) in 3 understory species along hydrodynamic gradients in waters surrounding an island archipelago (the San Juan Islands, Washington). We also examine morphological and biomechanical attributes that we predicted would directly affect the interaction between flow and survival along this gradient. *Laminaria complanata* (Setchell et Gardner) Setchell, *Agarum fimbriatum* Harvey (short-lived, perennials), and *Costaria costata* (C. Agardh) Sanders (an annual), are among the most ubiquitous and conspicuous components of the benthic assemblage in Puget Sound and adjacent regions. *C. costata* and *A. fimbriatum* can be found (frequently together) along a broad gradient of hydrodynamic energy (waves and current). *L. complanata* is also common in northern Puget Sound. As common as these species are, their community roles and autecology are poorly understood. Vadas (1977) examined the role of polyphenolic chemical defenses in *A. fimbriatum*, and the role of these secondary compounds as deterrents to herbivory. *C. costata* has been noted as an early successional species in several stud-

ies (Duggins 1980, Maxell & Miller 1996), but none of these species received much ecological consideration prior to our earlier studies on the modification of hydrodynamics by understory species, and the consequent ramifications to recruitment, growth and survival in benthic invertebrates found within this community (Eckman et al. 1989, Duggins et al. 1990, Eckman & Duggins 1991, Duggins & Eckman 1994, 1997). In this paper, and its companion (Eckman et al. 2003), we reverse this focus and concentrate on changes in survival and morphology of kelps driven by hydrodynamic forces. We focused our research in 2 directions. First, we followed populations of these 3 species (this paper), while simultaneously measuring pertinent hydrodynamic parameters along gradients in current and wave exposure (Eckman et al. 2003). To reduce impacts of herbivory and competition as factors affecting survival, macrograzers (urchins) were removed from our study sites, and single species stands were thinned to eliminate interactions between individual kelps. The resulting experimental stands were sufficiently low in density to eliminate contact between plants, but well within the range of density commonly found in the region. Second, individuals of 2 of the 3 species of kelp were studied to examine morphological and biomechanical attributes directly affecting the survival of individuals in varying flow regimes (e.g. holdfast morphology and attachment strength, resistance to blade tearing).

Our goal in these studies is to elucidate the role that hydrodynamics plays in the population dynamics of these common and important species. We hypothesized that tidal and wave-generated forces would affect survival of these 3 species, but our experience with the kelp *Nereocystis luetkeana* (Duggins et al. 2001) prevented us from predicting whether increased hydrodynamic energy would increase or decrease survival rate. We further predicted that in the event that no relationship between hydrodynamic energy and survival existed, we would find a morphological or biomechanical attribute that acted to ameliorate the increased risk associated with increased hydrodynamic drag. However, any understanding of dynamics at this population level must ultimately integrate all the physiological and ecological factors that are influenced by the hydrodynamic environment (e.g. growth, recruitment, resistance to herbivory, etc).

This study stands apart from other work on benthic seaweeds and hydrodynamics in a number of important respects. We have attempted to integrate an analysis of hydrodynamic effects on morphological and biomechanical attributes, with an analysis of a key element of population dynamics (survival) (see Blanchette et al. 2002 for another example of this approach). The literature on the relationship between hydrodynamic

energy and seaweed form and function has thus far focused almost entirely on wave exposure, while we have attempted to differentiate between wave exposure and tidal currents (a significant source of drag in many locations) as hydrodynamic factors. Secondly, the understory subtidal assemblage we are studying, while wide-ranging and common, has received comparatively little attention from benthic ecologists. Lastly, our examination of biological attributes is coupled with an attempt to rigorously describe the hydrodynamic environment, including variation within as well as among sites.

## MATERIALS AND METHODS

**Study sites and hydrodynamic properties.** Eight study sites in the San Juan Archipelago (Fig. 1) were chosen to include a broad range of hydrodynamic regimes, incorporating variability in both tidal currents and storm-generated waves. These sites were locations of simultaneous studies of subtidal hydrodynamics (Eckman et al. 2003) and population dynamics and ecology of the surface-canopy bull kelp *Nereocystis luetkeana* (Duggins et al. 2001). Sites at Brown Island (Site B), Cantilever Point (Site C), Yellow Island (Site Y), Minnesota Reef (Site M), Reid Rocks (Site R) and Parks Bay (Site P) all were located within San Juan Channel, or smaller channels or coves connected to it. These 6 sites are sheltered by San Juan Island from strong southwesterly winds associated with fall, winter and spring storms, and therefore were expected to be

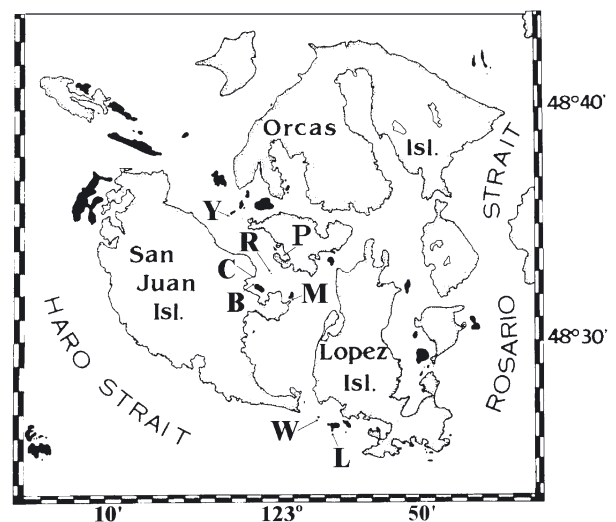


Fig. 1. Map of San Juan Archipelago showing location of 8 study sites. B: Brown Island; C: Cantilever Point; L: Long Island; M: Minnesota Reef; P: Parks Bay; Y: Yellow Island; R: Reid Rocks; W: Whale Rocks

comparatively free of large wave impacts. In contrast, sites at Whale Rocks (Site W) and Long Island (Site L) are located outside of San Juan Channel and are open to the Haro Strait and Strait of Juan de Fuca to the south and west. It was expected that these sites would experience more intense storm energy.

Six of the 8 sites (Sites B, C, L, M, W and Y — our primary sites) were the locations of most of our research, but Sites P and R were studied in a more limited fashion to expand the range of hydrodynamic environments examined. Four to 6 regions (plots) of roughly 50 to 100 m<sup>2</sup> each were defined within the 6 primary sites. Plots were created to allow studies of replicate plots of several species of kelp. Plots were established on nearly horizontal rock platforms at all sites, at depths ranging from 6.1 to 11.0 m, with most plots at depths of 7.0 to 9.2 m. As is characteristic of the shallow subtidal region in this area, these horizontal rock platforms existed within a more complex terrain of rocky shallows and steep ledges located sometimes only meters from the plots. This narrow depth range was selected to minimize variability in penetration of light and wave energy to the bottom (both considered important to kelp populations, e.g. Dayton et al. 1999).

The hydrodynamic properties of plots within each study site were assessed using a suite of identical *in situ* instrument complexes, each of which measured temperature, pressure (depth and wave signals), and current speed and direction (Eckman et al. 2003). Instruments were attached to the rock substratum using anchor bolts placed in small areas (several m<sup>2</sup>) kept clear of kelps by divers.

Measurements of current velocity were obtained approximately 20 to 30 cm above the substratum, a height that closely matches that of thalli of the 3 species of understory kelp studied (*Agarum fimbriatum*, *Costaria costata*, *Laminaria complanata*). Instruments were programmed so that temperature, pressure and flow speed were sampled at 2 Hz for 128 s every 15 min. The 2 min averages of current speed and direction, temperature, and pressure (translatable to depth) were recorded every 15 min. In addition, the instrument was programmed to examine the variance of the 2 Hz pressure fluctuations, and to record all of the high-frequency measurements of flow speed and pressure (translatable to instantaneous wave signals) if pressure fluctuations indicated an influence by waves at depth. Further details regarding design, precision, calibration, operation and use of these instruments are discussed in Eckman et al. (2003).

One to 2 instruments were deployed at each of the 6 primary sites throughout the duration of the kelp population studies (see Eckman et al. 2003 for details of these deployments). This allowed influences of storm-generated waves to be well characterized at

each site. In addition, to more fully characterize hydrodynamic variability within each site due to topographically produced variability in exposure, additional instruments were deployed within each of the 6 primary sites for a period of 1 to 3 wk (see Eckman et al. 2003, their Table 1). These additional meters were rotated among sites throughout the study period so that local spatial variability among plots in current speed was measured at all sites. The deployment of multiple meters for 1 to 3 wk within each of the primary sites ensured that much of the variability in the tidal cycle was absorbed. Therefore, flow variability both within and among sites was well characterized.

Several hydrodynamic statistics pertinent to kelp population dynamics were extracted from the instrument data. First, the 99th percentile of the 2 min average current strength is reported for each plot within each site. This statistic characterizes the maximum tidal flow to which understory plants were exposed. Second, maximum flow speeds generated by storm waves at depth are reported from each of the 6 primary sites. Data are reported for 3 intervals from fall 1995 through spring 1996. These intervals were defined by the times of retrieval and re-deployment of the instrument complexes. Recovery and re-deployment of meters was necessitated by the limited life of the instrument battery packs (~3 mo). However, since a replacement meter was deployed at the same time that each meter was retrieved, there were no gaps in coverage during the deployment period.

**Survivorship experiments.** Survivorship of 3 species of understory kelp (*Agarum fimbriatum*, *Costaria costata* and *Laminaria complanata*) was studied at the 6 primary sites (Sites B, C, L, M, W and Y). For *A. fimbriatum* and *C. costata* we measured survival rates of sporophytes that recruited naturally into replicate plots at each site. For *L. complanata*, small sporophytes (<1.0 mm total length) were outplanted to replicate plots within the 6 sites from a common, limited genetic pool of plants generated from laboratory-cultured gametophytes, and their survival was followed over time.

Plots within each site that had been cleared in late spring 1995 experienced a natural recruitment of *Costaria costata* and *Agarum fimbriatum* sporophytes. Between 26 June and 6 July 1995, numerous small *C. costata* of similar size (1 to 3 cm length) were individually marked (by marking the adjacent substrate) and mapped within 2 plots at each of the 6 sites. Neighboring plants were spaced a minimum of 1 m apart. Marking algae individually allowed us to evaluate their persistence within, or removal from, the population over time. We similarly marked individual *A. fimbriatum* within 2 plots at 5 of the primary sites (Sites B, C, L, M and Y) between 13 and 25 July 1995. There was no recruitment of *A. fimbriatum* at 6 to 11 m depth at

Whale Rocks (Site W) and, in fact, *A. fimbriatum* are rare at this site, with small populations restricted to deeper water only.

To culture *Laminaria complanata*, fertile sori were collected from a few sporophytes. Sori were mildly desiccated at 10°C for several hours to encourage spore release. Spores were released from each sorus separately, into 500 ml sterile seawater. After release, suspensions of swimming spores from all parents were mixed. This provided us with a single stock culture for each species of limited genetic diversity.

The stock culture was maintained in seawater enriched with 0.5 strength Alga-gro® medium in a vegetative gametophytic state at 8°C for several months, at an irradiance of 60  $\mu\text{E m}^{-2} \text{s}^{-1}$  and day length of 16:8 h (light:dark). The medium was changed bi-weekly, and was unialgal but not axenic. Inocula were prepared for outplanting to field sites by removing vegetative gametophytes from this stock culture and pulverizing for 45 s in a pre-cooled Waring® blender, in which the cutting blade had been replaced with a double-edged razor blade (this procedure is widely used to induce sexuality among kelp gametophytes). The filament fragments produced were then equally apportioned among 6 culture vessels, where they settled onto several hundred small (1 cm diameter) roughened plastic substrates ('discs') loosely attached to a plate in the bottom of each vessel. These cultures were then held under the same culture conditions as above for ca. 2 wk, after which time they were checked for the presence of gametangia and small (microscopic) sporophytes. Once gametangia and sporophytes were observed, all discs were outplanted to field sites over the course of ~1 wk.

Small sporophytes of *Laminaria complanata* (<1.0 mm total length) were outplanted to 2 replicate plots within all 6 primary sites in mid- to late June 1995. Discs containing small sporophytes were fixed to the substrate using epoxy. Discs were placed every meter along 2 or 3 parallel transect lines spaced 1 to 2 m apart. Prior to outplanting, all plots had been cleared of benthic macroalgae and moderate-to-large grazers (primarily sea urchins of the genus *Strongylocentrotus*). Within 1 mo of outplanting, each disk was thinned to contain a single kelp, thus establishing an even-aged, experiment-wide population of limited genetic variability. This thinning event, which occurred between 13 and 25 July 1995, signified the beginning of the outplanting survivorship experiment for *L. complanata*. Each plant was individually marked, as in the case of *Agarum fimbriatum* and *Costaria costata*.

The objective of this study was to evaluate effects of hydrodynamics on kelp survival, and we therefore attempted to eliminate (or at least greatly reduce) effects of competition (interspecific and intraspecific) and herbivory as co-variables. We removed all other

macroalgae from within plots when we began population censuses. Macroherbivores (primarily echinoids) were also removed from all plots and surrounding areas. As necessary, removals continued throughout the course of the study each time a census was conducted. Over the (almost) 2 yr that we followed the target understory populations, no obvious examples of mortality due to herbivory were observed, and all but the smallest (newly recruited) potential competitors were successfully eliminated.

*Agarum fimbriatum* and *Laminaria complanata* are perennial species with maximum life expectancies of up to 3 yr. *Costaria costata* is an annual species with very few individuals surviving after the first severe winter storms following their recruitment as sporophytes during summer. At the initiation of the survivorship study, there were 23 to 44 *A. fimbriatum* per plot. Plants were censused 7 or 8 times over the following 500 d, at intervals ranging from 40 to 90 d. We began our study of *C. costata* survival with 23 to 73 plants per plot, and censused these annual plants 6 or 7 times over the following 209 d, at intervals ranging from 13 to 45 d. We had difficulty in culturing a large number of *L. complanata* sporophytes, and plots therefore contained fewer (2 to 25) plants at initiation of the study. *L. complanata* were censused 6 or 7 times over the following 503 d, at intervals ranging from 30 to 61 d. At every census, the presence or absence of each individually numbered plant was scored.

A population census involved determination of whether an individual was present or absent, and if absent the anatomical location associated with its 'failure' (disappearance) was assigned. For example, if a holdfast and stipe, but little or no blade, remained, we noted a blade failure. If nothing at all remained we noted a holdfast failure, and if only a holdfast remained, we assigned failure to the stipe. We felt comfortable in assigning location of failure because holdfasts or holdfast-stipe combinations remain on the substrate following blade loss for periods exceeding 4 wk in *Nereocystis leutkeana* (Duggins et al. 2001). Personal observation leads us to believe the same is true for these understory species.

To compare survival of plants among plots and sites, data regarding proportion of plants surviving as a function of time were fitted to an exponential decay function, which fit empirical data well for at least the first 4 to 5 census intervals ( $r^2 \geq 0.9$  for each plot for *Agarum fimbriatum* and *Costaria costata*,  $0.74 < r^2 < 0.97$  for *Laminaria complanata*). The model used was:

$$n(t)/n_0 = \exp(-\lambda t)$$

where  $n(t)$  is the number of plants alive at time  $t$ ,  $n_0$  is the original number of plants, and  $\lambda$  is the mortality rate.  $\lambda$  was estimated by regression analysis—it is the

slope of the best linear fit of  $\ln(n[t]/n_0)$  vs  $t$ , with the intercept forced through the origin,  $\ln(n[t]/n_0) = 0$ , or  $n(t)/n_0 = 1$ , at  $t = 0$ .

Two tests were of interest *a priori*. First, we wished to test for any influence of tidal current strength on kelp mortality. Therefore, we examined the mortality rate of plants within each plot, relative to the 99th percentile of tidal current speed measured within that plot. This correlation was examined ignoring populations censused at Sites L and W, because these 2 sites are also impacted by strong wave forces (Eckman et al. 2003, see also below) that could compromise detection of any mortality–tidal current relationship. This analysis was done for *Agarum fimbriatum* and *Costaria costata* only; there were not enough *Laminaria complanata* sporophytes within most plots to permit mortality rates to be resolved at that level. Second, we wished to test for an influence of waves on kelp mortality. Because wave influences were detected at only 2 of the 6 primary sites, the appropriate test for this effect involved testing for differences among sites in the mortality rate. To improve statistical power, we pooled plants from plots within each site, and calculated a single mortality rate for each kelp species at each site. Best-fit estimates of  $\lambda$  were compared among sites using least-significant-difference (LSD) multiple comparisons tests (Sokal & Rohlf 1981). We considered it valid to combine plants from the 2 plots within each site, since we detected no impact of tidal current strength, which varies considerably between plots within sites (Eckman et al. 2003), on the kelp mortality rate (see 'Results'). This pooling within sites allowed us to compare mortality rates of *L. complanata* among sites, in addition to *A. fimbriatum* and *C. costata*.

#### Morphometric and biomechanical measurements.

To further illuminate potential hydrodynamic impacts on understory kelps, we assessed differences among sites in plant morphology and biomechanical properties, as related to patterns in flow. Similar flow-dependent variability in plant morphology has been reported for the surface-canopy plant *Nereocystis luetkeana* (Koehl & Alberte 1988, Johnson & Koehl 1994). Randomly selected *Agarum fimbriatum* and *Costaria costata*, of a full size range, were collected from most study sites between mid-August and late October 1995. Kelps were returned to the laboratory, where measurements of all parameters were immediately taken. Parameters measured were blade length, blade width, stipe length, stipe minimum diameter, stipe maximum diameter, holdfast minimum diameter, holdfast maximum diameter, blade wet weight, stipe wet weight, holdfast wet weight, holdfast dry weight, and blade cross-sectional thickness (at the center and edge of blade). Area estimates were derived from linear measurements of maximum length and width, and

assumptions regarding shape (e.g. blades were regarded as rectangles, holdfast 'footprints', and stipe cross-sectional areas were assumed to be ovals). Blade thickness was measured from tissue sections taken from midway between the stipe and the distal end of the blade. Sections were measured for cross-sectional thickness using a microscope equipped with an ocular micrometer. Midribs and meristematic regions were avoided in these thickness measurements.

Biomechanical attributes of *Agarum fimbriatum* and *Costaria costata* were evaluated in the field and the laboratory. Two attributes were chosen *a priori* because they were expected to directly impact hydrodynamic influences on plant survival. We measured the normal force required to remove a holdfast from the substrate *in situ*, and refer to this dislodgment force as holdfast 'tenacity'. We also measured the normal force required to puncture or tear a blade and refer to it as blade 'toughness'.

Holdfast tenacity was measured *in situ* for a broad size range of both *Agarum fimbriatum* and *Costaria costata* at 4 sites (*A. fimbriatum* at Sites B, C, Y, L; *C. costata* at Sites B, C, Y, W). We began by removing (and saving for later measurements in the laboratory) the blade from the stipe. A device consisting of 2 flat sheets of roughened PVC plastic (each  $10 \times 10 \times 1$  cm) was clamped tightly to the remaining stipe. A SCUBA diver then attached a recording tensometer (calibrated spring scale) to the pulling device and applied an upward force (perpendicular to the substrate) until the holdfast released from the substrate. The force required for dislodgment was recorded. We considered the upward (normal) force to be an acceptable, if not totally accurate, mimic of hydrodynamic loading, and easier to standardize than a force applied at some non-perpendicular angle. While a more lateral force might have mimicked real flow forces more accurately, the direction (bearing) of that force would probably have had a significant effect on detachment force (due to asymmetry of holdfasts), so we chose a perpendicular application of force to standardize measurements.

Blade toughness was assessed in the laboratory using a penetrometer of our own design. We collected a size range of *Agarum fimbriatum* and *Costaria costata* from 4 sites and performed all measurements on fresh material within 24 h of collection (kelps were held in circulating fresh seawater until measured). A  $5 \times 5$  cm section was cut from the mid-blade region. Thicker midrib areas were avoided. A small portion of the sample was sectioned and measured for cross-sectional thickness using a microscope equipped with an ocular micrometer. The remaining section was then sandwiched between 2 roughened, flat PVC sheets. A small (5 mm) hole had been drilled through both of the PVC sheets and, when lined up, presented a channel obscured by

only the sandwiched kelp tissue. This loaded structure was securely clamped, and the penetrometer placed lightly through the upper PVC hole until it came to rest on the algal tissue. The penetrometer consisted of a solid glass rod, 3 mm in diameter, with an end that had been rounded in a hot flame. The other end of the rod was affixed to a lightweight plastic cup which was filled with water (increasing its mass and, hence, also the force on the kelp tissue) at a constant, slow rate by supplying water through tubing from the base of an elevated reservoir kept at a constant volume. When the rod was loaded with sufficient mass, it broke through the kelp tissue. The rod was prevented from continuing its travel by a cushioned stop below the PVC sheets. We were thus able to arrest the penetrometer's movement without spilling any of the water added to the cup. Blade toughness was assessed by examining the relationship between blade thickness and total mass (water plus penetrometer assembly) required to penetrate the blade. Each individual alga in this analysis was measured 5 times, using 5 replicate blade tissue samples. Analyses were performed on the mean (of 5) values of penetration force and blade thickness.

Morphometric and biomechanical data on both *Agarum fimbriatum* and *Costaria costata* were compared among sites using either analysis of covariance (ANCOVA), to account for effects of plant size on the various attributes, or in some instances using simple ANOVA. In the latter case, either unscaled data were compared among sites, which included variance caused by differences in plant size, or ANOVA was performed on data normalized to some measure of plant size (e.g. blade width or wet weight). *A posteriori* multiple comparisons tests were made using the Bonferroni method.

It is important to note that because of practical limitations of subtidal work, we were unable to collect enough plants of both species at all sites to enable us to make the full spectrum of possible measurements and comparisons among sites. There are some unavoidable gaps in comparisons of biomechanical and morphometric attributes among sites for both species.

## RESULTS

### Hydrodynamic characteristics of sites

Although we expected *a priori* that wide uniformity in environmental (light, nutrient, hydrodynamic) conditions would occur within each site, we discovered that local topography produced substantial variability within each primary site (i.e. at scales  $\leq 10$ s of meters) in strengths of tidal currents experienced by understory kelps (Table 1; also see Eckman et al. 2003). All sites ex-

cept Sites C and P experienced occasional periods in some plots where tidal current strengths were strong ( $>30 \text{ cm s}^{-1}$ ) at heights of understory kelps. Maximum tidal currents exhibited considerable variability among plots within most sites (at most sites a range of  $\sim 2\times$ ). Site W experienced the strongest tidal currents among sites at which kelp population dynamics were studied, but currents at Site R, which lies in the middle of San Juan Channel (Fig. 1), were even stronger. Tidal flow at Site C was generally weak, and currents were virtually undetectable at Site P (Table 1).

There was considerable variability among sites in exposure to storm-generated wave energy. On several occasions during fall through early spring, instruments at Sites W and L detected significant wave energy (Eckman et al. 2003). Maximum current plus wave-generated velocities at Site W ranged from  $131$  to  $197 \text{ cm s}^{-1}$  at levels of kelps. At Site L, combined current plus wave velocities were somewhat less ( $96$  to  $151 \text{ cm s}^{-1}$ ), but were still far in excess of tidal current velocities at all sites except at Site R (Table 1).

Sites B, C, and M never experienced detectable wave activity at the depths studied. One brief instance (lasting  $<30$  min) of wave activity was detected at Site Y, and the maximum instantaneous flow speed recorded during this event (at the  $822 \text{ cm}$  depth of the sensor) was only  $54 \text{ cm s}^{-1}$ .

Instruments were not deployed throughout winter at Sites R or P, so comparable wave data there are not available. However, given their positions in San Juan Channel or adjoining, protected coves (Fig. 1), wave impacts at these sites should be minimal to undetectable.

### Kelp mortality

#### *Agarum fimbriatum*

Mortality rates of *Agarum fimbriatum* varied by  $\sim 8\times$  among plots, ranging from  $0.058$  (Site Y, Plot 2) to  $0.431 \text{ \% d}^{-1}$  (Site L, Plot 2) (Table 1). There was no obvious or detectable relationship, either monotonic or simple non-linear, between plant mortality rate and tidal current strength (Fig. 2A,  $r^2 = 0.0018$ ,  $p = 0.92$ ). The mortality rate at Site L was significantly higher (by  $\geq 54 \text{ \%}$ ) than at any of the other 4 sites at which *A. fimbriatum* recruited (Table 1). Site L was 1 of 2 sites impacted by significant storm waves, the other being Site W, where *A. fimbriatum* populations are not found within the depth range of our study. Mortality rates of *A. fimbriatum* were significantly lower at Site Y than at other sites. At all sites mortality of *A. fimbriatum* occurred primarily due to holdfast failure ( $58$  to  $72 \text{ \%}$  of cases depending on site; Table 2); breakage of the stipe was generally the second leading cause of mortality.

Table 1. *Agarum fimbriatum*, *Costaria costata* and *Laminaria complanata*. Tidal current strengths and mortality rates of kelps within and among study sites. Mean depth and 99th percentile of tidal current speed is reported along with mortality rates in each block and pooled within each site. Per-site mortality rates for each species are listed from smallest (left-most) to largest (right-most) rate. Site codes connected by a common underline are not significantly different ( $p > 0.05$ ). ND: no data; IN: insufficient numbers of plants to calculate rate

Species	Site	Block	Mean depth (cm)	99th percentile speed (cm s <sup>-1</sup> )	Per-block mortality rate (d <sup>-1</sup> × 1000) (SE)	Per-site mortality rate (d <sup>-1</sup> × 1000) (SE)	Site comparison		
<i>A. fimbriatum</i>	B	1	913	37.3	2.04 (0.07)	1.93 (0.18)	Y <u>B C M L</u>		
		2	890	35.2	1.27 (0.14)				
	C	1	913	12.4	1.66 (0.04)	2.08 (0.13)			
		2	704	27.5	2.16 (0.04)				
	L	1	ND	ND	3.10 (0.21)	3.75 (0.35)			
		2	681	34.4	4.31 (0.39)				
	M	1	847	26.5	1.89 (0.03)	2.43 (0.08)			
		2	702	37.7	2.31 (0.10)				
	Y	1	879	45.0	2.12 (0.05)	1.47 (0.02)			
		2	998	39.7	0.58 (0.02)				
	<i>C. costata</i>	B	1	882	50.0	2.52 (0.61)		3.78 (0.16)	<u>B Y C M L W</u>
			2	837	41.8	4.59 (0.23)			
C		1	681	<10	4.6 (0.29)	5.54 (0.32)			
		2	710	15.9	5.18 (0.17)				
L		1	ND	ND	13.3 (2.1)	7.01 (0.21)			
		2	681	34.4	4.06 (0.25)				
M		1	638	49.3	5.87 (0.36)	5.57 (0.36)			
		2	821	28.2	5.28 (0.16)				
W		1	787	44.8	7.55 (0.48)	7.37 (0.27)			
		2	827	80.4	7.02 (0.58)				
Y		1	888	45.4	3.88 (0.36)	3.88 (0.38)			
		2	1105	25.8	3.88 (0.28)				
<i>L. complanata</i>		B	1	913	37.3	2.74 (0.18)	Y L <u>B W</u>		
			2	ND	ND				
	C	1	ND	ND	IN				
		2	704	27.5					
	L	1	815	41.4	1.61 (0.07)				
		2	ND	ND					
	M	1	702	37.7	IN				
		2	821	28.2					
	W	1	891	73.8	3.74 (0.23)				
		2	1018	88.4					
	Y	1	ND	ND	0.645 (0.09)				
		2	930	43.7					
	(None)	P	1	688	<10				
			2	981	<10				
R		1	933	124					

### *Costaria costata*

Patterns of mortality of *Costaria costata* shared many similarities with *Agarum fimbriatum*. Mortality rates of *C. costata* varied by ~6× among plots, ranging from 0.25 (Site B, Plot 1) to 1.33 % d<sup>-1</sup> (Site L, Plot 1) (Table 1). There was no obvious or detectable relationship between plant mortality rate and tidal current strength (Fig. 2B,  $r^2 = 0.077$ ,  $p = 0.51$ ). The average mortality rates at Sites W and L, the 2 sites impacted by significant storm waves, were significantly higher (by ≥26 %) than at any other sites. Site-averaged mortality rates of *C. costata* were significantly lower at Sites B and Y

than at other sites. As was true for *A. fimbriatum*, at all sites mortality of *C. costata* occurred primarily due to holdfast failure (51 to 79 % of cases depending on site; Table 2); breakage of the stipe was generally the second leading cause of mortality.

### *Laminaria complanata*

*Laminaria complanata* was not outplanted in sufficient numbers to allow per-plot mortality rates to be calculated, nor site-averaged estimates to be made for Site M or C (only 7 plants total were present at Sites C and M at



the beginning of the census). Mortality rates of *L. complanata* were significantly higher ( $0.37\% \text{ d}^{-1}$ ) at Site W than at any other site (Table 1). Site W is the site that experiences the strongest wave-generated flows (Eckman et al. 2003). However, mortality of *L. complanata* at the other wave-impacted site (Site L) was significantly lower than at Site B. *L. complanata* mortality rates were significantly lower at Site Y than at other sites.

### Morphometric patterns

*Costaria costata* ( $n = 414$ ) and *Agarum fimbriatum* ( $n = 455$ ), collected from 8 sites, were measured for attributes we predicted might reflect morphological plasticity (or morphological divergence due to differential survival) in differing hydrodynamic regimes. Our choice of attributes was based on our *a priori* predic-

tions as to how the morphology of these kelps might vary with current or wave exposure. *A priori* we expected these attributes in the perennial *A. fimbriatum* to be especially susceptible to inputs of strong wave energy noted at Sites W and L during winter storms. In contrast, because *C. costata* is an annual that largely dies off before the advent of winter storms, we expected biomechanical or morphometric attributes to be sensitive only to the strong tidal currents exhibited at Sites R and W, or the general absence of significant tidal flows at Sites C and P. We chose attributes, such as blade surface area, stipe cross-sectional area, and holdfast dry weight, that we expected to be related to drag forces exerted on individuals, or that reflect the kelp's ability to resist breakage or dislodgment when exposed to such forces. These attributes, while numerous, are only a few of the variables that could prove to be interesting in this context.

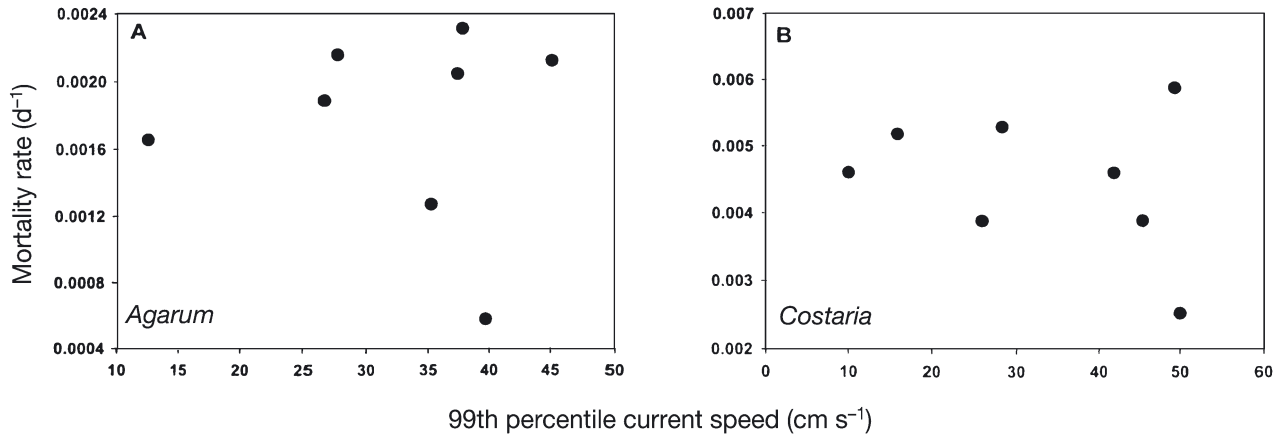


Fig. 2. (A) *Agarum fimbriatum* and (B) *Costaria costata*. Mortality rates ( $\text{d}^{-1}$ ) as functions of the 99th percentile of mean tidal current speed recorded at Sites B, C, M and Y. Data are omitted from Sites L and W as mortality rates there were impacted by storm-generated waves. (See Fig. 1 legend for site abbreviations)

Table 2. *Agarum fimbriatum* and *Costaria costata*. Sources of mortality (plant loss at blade, holdfast or stipe) at study sites.  $n$  = number of plants for which mortality source was recorded. B: Brown Island; C: Cantilever Point; L: Long Island; M: Minnesota Reef; P: Parks Bay; Y: Yellow Island; R: Reid Rocks; W: Whale Rocks

Species	Site	Mortality location (%)			n
		Blade	Holdfast	Stipe	
<i>A. fimbriatum</i>	B	4	65	31	26
	C	6	69	25	32
	L	27	58	15	33
	M	8	72	21	39
	Y	0	68	32	25
<i>C. costata</i>	B	3	79	18	33
	C	7	72	22	46
	L	8	77	15	60
	M	22	56	22	41
	W	7	51	42	57
	Y	22	56	22	32

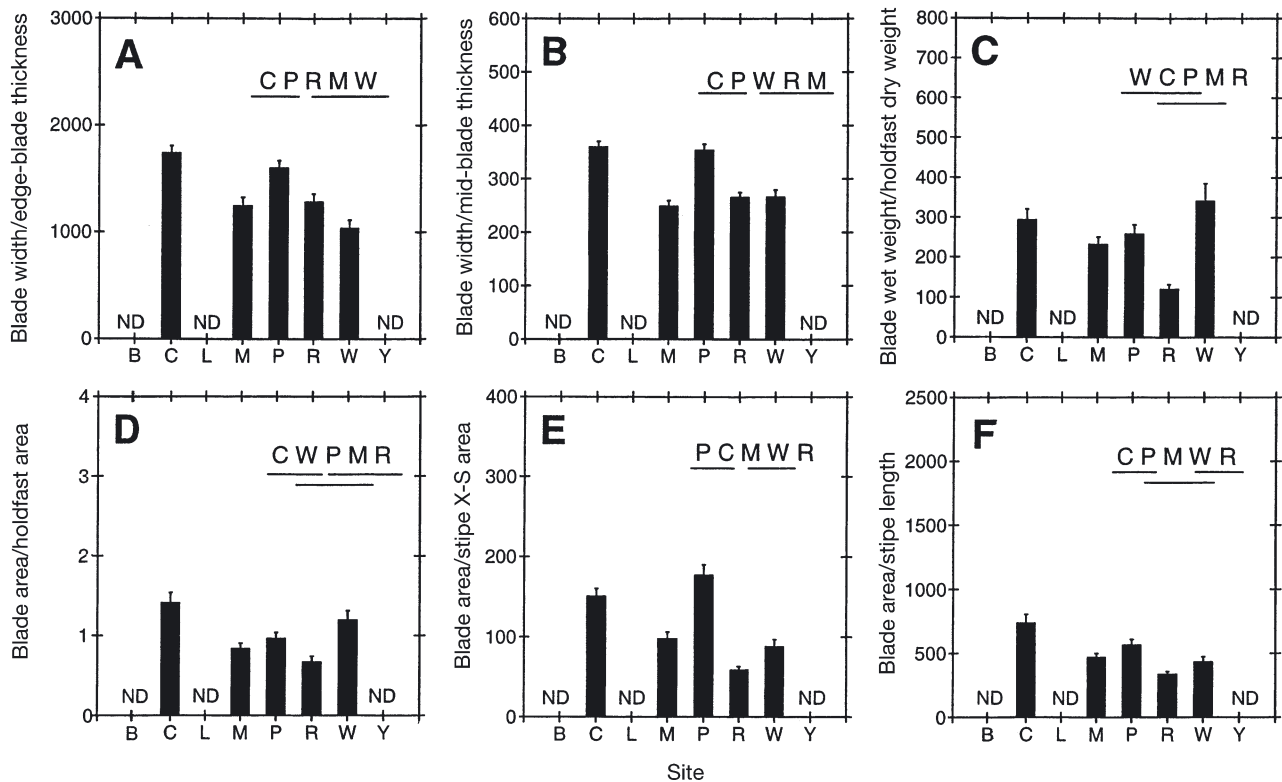


Fig. 3. *Agarum fimbriatum*. Morphological attributes (mean  $\pm$  SE) at study sites. Area in cm<sup>2</sup>, length in cm. Sites with no significant differences (p > 0.05) in Bonferonni post hoc multiple comparisons are underlined. ND = no data. (See Fig. 1 legend for site abbreviations)

### *Agarum fimbriatum*

Algal size, as measured by blade area or width, showed no differences among sites. The shape of the blade (length:width ratio) was also invariant among sites.

*Agarum fimbriatum* showed a strong pattern among sites in thickness of the blade. We measured thickness along the edge (Fig. 3A) and in the center of the blade (Fig. 3B). For both measurements, blades were significantly thinner at the weaker-flow sites (Sites C and P).

The kelp holdfast is the structure that determines how strongly the individual remains attached to the substrate. The tenacity of a holdfast could be reflected in its size or mass, but holdfast tenacity could also reflect the extent of articulation, the number of attachment points, or how strongly each attachment point adheres to the substrate. Site-specific patterns in both holdfast dry weight, scaled to total thallus wet weight, and footprint (our best estimate of the area of the holdfast–substrate interface), scaled to blade area, were obvious, if difficult to interpret, in *Agarum fimbriatum*. Significantly more massive holdfasts occurred at Site R, where currents are consistently strongest (Fig. 3C). However, holdfast mass and footprint (Fig. 3D) at Site

W (stronger current and strong wave impacts) were similar to those of plants at the lower energy sites.

*Agarum fimbriatum* have relatively short stipes (up to 7.6 cm) that are ovate in cross-section, but which are sometimes so flattened along the major axis as to be nearly strap-like. The stipe has little rigidity, and consequently the blade will usually be found lying on the substrate. Drag forces will load the stipe under tension, and stipes can bend through nearly 180° of arc in strong flows. *A. fimbriatum* stipes were significantly larger in cross-sectional area (relative to blade area) at Site R (of strongest tidal currents) than at other sites, and significantly smaller at the 2 sites with weakest flow (Sites C and P) (Fig. 3E). *A. fimbriatum* also tended to have longer stipes, relative to blade area, at sites with strong current and wave energy (Sites W and R) (Fig. 3F).

### *Costaria costata*

Algal size, as measured by blade area or blade width, showed significant differences among sites in *Costaria costata*. Blades were on average significantly larger at the weaker flow sites (Sites C and P) than at

the 2 sites characterized by strong tidal currents (Sites R and W) (Fig. 4A). Blade area is obviously important in determining drag forces on plants, but since these understory species erode from the distal end of the blade, we also looked at blade width as a longer-term reflection of total blade area (length measurements can change rapidly during periods of rapid erosion). As with blade area, blades were significantly wider at the 2 weaker-flow sites (Fig. 4B). This pattern is even more striking if one looks at the size of the 15 largest individuals observed at a site (Fig. 4C)—at Sites W and R, large *C. costata* were absent, whereas the protected sites (Sites C and P) were dominated by individuals with blade area twice as large as observed in the largest plants at Sites W and R. Individuals at protected sites were not older, since recruitment occurred at all sites at the same time. While it is possible that kelps at protected sites were growing more rapidly (we have no growth data, but do not believe there to be a significant site difference in growth rate, and a narrow depth range was chosen for the study to minimize such a possibility), the fact that we never observed any large plants at Sites W or R indicates that there was a real difference

among sites in the maximum size attained by *C. costata*. The shape of the blade varied among sites as well (Fig. 4D); at the weaker-flow sites, blades were significantly wider relative to length.

*Costaria costata* showed a strong pattern among sites in thickness of the blade. As with *Agarum fimbriatum*, we measured thickness along the edge (Fig. 4E) and in the center of the blade (Fig. 4F). For both measurements, *C. costata* blades were significantly thinner at the weaker-flow sites (Sites C and P) and significantly thicker at Site R, which has the strongest tidal currents.

Site-specific patterns in both holdfast dry weight (scaled to total thallus wet weight) and footprint, scaled to blade area, are very strong in *Costaria costata*. Holdfasts were less massive (Fig. 5A) and adhered to a smaller area of substrate (Fig. 5B) at the weaker-flow Sites C and P.

*Costaria costata* have stipes up to 24 cm in length that are ovate in cross-section and nearly circular at the stipe–holdfast junction. The *C. costata* stipe is considerably stiffer than that of *Agarum fimbriatum*, and typically holds the blade erect into the water column. *C. costata* stipes were significantly larger in cross-sectional

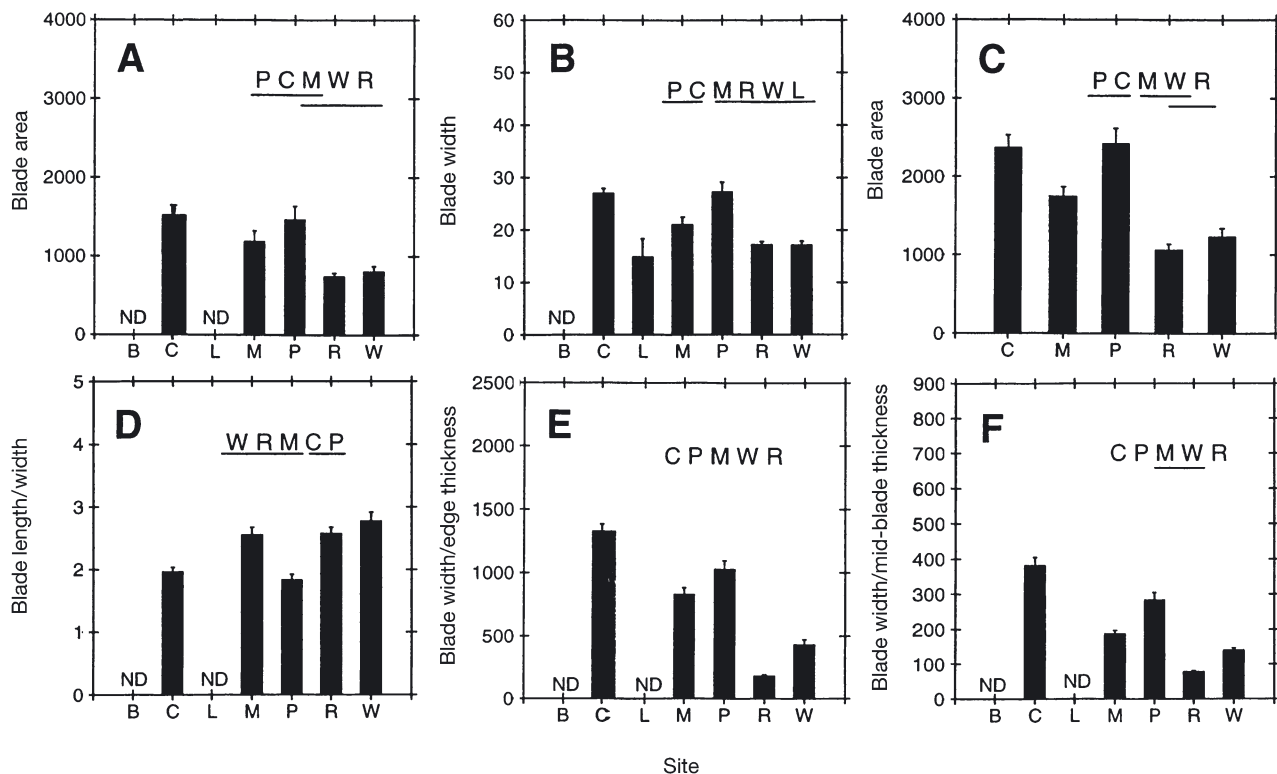


Fig. 4. *Costaria costata*. Morphological attributes (mean  $\pm$  SE) of blades at study sites. Area in cm<sup>2</sup>, length and width in cm, thickness in mm. Plots A, B, E, F include all measurements; plots C, D include only the 15 largest individuals per site. Sites with no significant differences ( $p > 0.05$ ) in Bonferroni post hoc multiple comparisons are underlined. ND = no data. (See Fig. 1 legend for site abbreviations)

area (relative to blade area) at Sites R and W (of strongest tidal currents) than at other sites, and significantly shorter at the 2 sites with weakest flow (Sites C and P) (Fig. 5C). *C. costata* also tended to have longer stipes, relative to blade area, at Site R, where currents are strongest (Fig. 5D).

### Biomechanical patterns

#### *Agarum fimbriatum*

At 3 of 4 sites (B, C and L), there was a significant linear relationship between detachment force and dry mass of the holdfast (Fig. 6A, Table 3). It was not possible to analyze these data by ANCOVA due to heterogeneity of slopes ( $p = 0.015$  for the interaction of site and holdfast mass on detachment force). However, it is obvious from Fig. 6A that detachment force is greater at Site L (one of the wave-impacted sites) than at other sites throughout the range of holdfast sizes, and that the rate of increase in detachment force with increasing holdfast size is greatest at Site L. In addition, ignoring any influence of holdfast size on detachment force,

a simple ANOVA demonstrates that mean detachment force is significantly higher at Sites L and W, the 2 wave-impacted sites (Table 3).

A very similar pattern is apparent when one considers an alternative scaling of plant size—total thallus wet mass (Fig. 6B, Table 3). At all 4 sites there was a significant linear relationship between detachment force and the thallus wet mass, but it was not possible to analyze these data by ANCOVA due to heterogeneity of slopes ( $p < 0.001$  for the interaction of site and thallus mass on detachment force). However, it is obvious from Fig. 6B that detachment force is greater at Site L than at other sites for all but the lowest thallus masses, and that the rate of increase in detachment force with increasing thallus mass is also greatest at Site L.

Another relationship further indicates the importance of wave forces to *Agarum fimbriatum* detachment force. For plants taken from Sites W and C, there were homogeneous slopes to the linear relationship between detachment force and blade width (Fig. 7A). ANCOVA shows that for a given blade, width detachment forces at the wave-impacted site (Site W) were significantly higher ( $p < 0.05$ ).

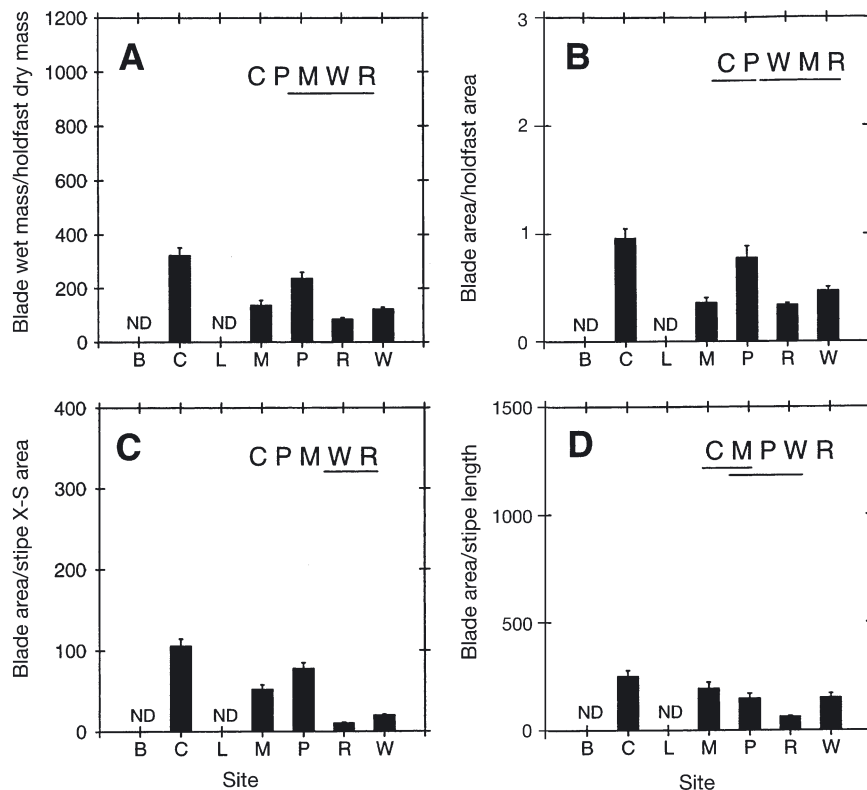


Fig. 5. *Costaria costata*. Morphological attributes (mean  $\pm$  SE) of stipes and holdfasts at study sites. Area in  $\text{cm}^2$ , length in cm. Sites with no significant differences ( $p > 0.05$ ) in Bonferroni post hoc multiple comparisons are underlined. ND = no data. (See Fig. 1 legend for site abbreviations)

The mass required for a 3 mm diameter glass rod to penetrate an *Agarum fimbriatum* blade (the so-called blade 'toughness') varied linearly with blade thickness at 4 of 5 sites (Sites C, M, P and W; Table 3). There was no clear linear relationship at Site R because there was little variance in blade thickness, all blades being relatively thick despite a wide range in thallus sizes. It was possible to perform an analysis of covariance on data from 3 sites (Sites C, P and W), because regression slopes for these sites were homogeneous (Fig. 7B, Table 3). ANCOVA indicates a highly significant ( $p < 0.001$ ) effect of site, with blade toughness (for a blade of any standard thickness) being greater at Site W (one of the wave-impacted sites) than at the other 2 sites.

#### *Costaria costata*

In marked contrast to patterns noted for *Agarum fimbriatum*, for *Costaria costata* there was no detectable relationship between detachment force and dry mass of the holdfast at 3 of 4 sites (Table 3). A significant relationship was detected only at Site C. A simple ANOVA demonstrates that detachment forces were significantly greater at Site W than at Sites B, C or L ( $p < 0.001$ ).

However, at 3 of 4 sites (Sites B, C and W), there was a significant linear relationship between detachment force and thallus wet mass (Fig. 8A, Table 3). It was not possible to analyze these data by ANCOVA due to heterogeneity of slopes ( $p = 0.017$  for the interaction of site and thallus mass on detachment force). However, it is obvious from Fig. 8A that for the full range of thallus masses, detachment force was greater at Site W (the wave-impacted site with strong tidal currents) than at Sites B and C, and the rate of increase in detachment force with increasing thallus mass was significantly greater at Site W than at Sites B and C.

The 'toughness' of a *Costaria costata* blade varied linearly with blade thickness at 4 of 5 sites (Sites M, P, R and W; Table 3). There was no clear relationship at Site C as there was little variance in blade thickness, all blades being relatively thin despite a wide range in thallus sizes. It was possible to perform ANCOVA separately on data from 2 pairs of sites with homogeneous slopes (Site P relative to W [Fig. 8B] and, separately, Site M relative to R [Fig. 8C]). ANCOVA indicates a highly significant ( $p < 0.001$ ) effect of site with blade toughness (for a blade of any standard thickness), being greater at Site W than at Site P. ANCOVA also indicates that blades are tougher at Site R than at Site M for a blade of standard thickness ( $p = 0.011$ ). Moreover, ignoring effects of blade thickness, the mean penetration forces of blades at Sites R and W were significantly greater than at the other 3 sites (Fig. 8D,  $p < 0.001$ ).

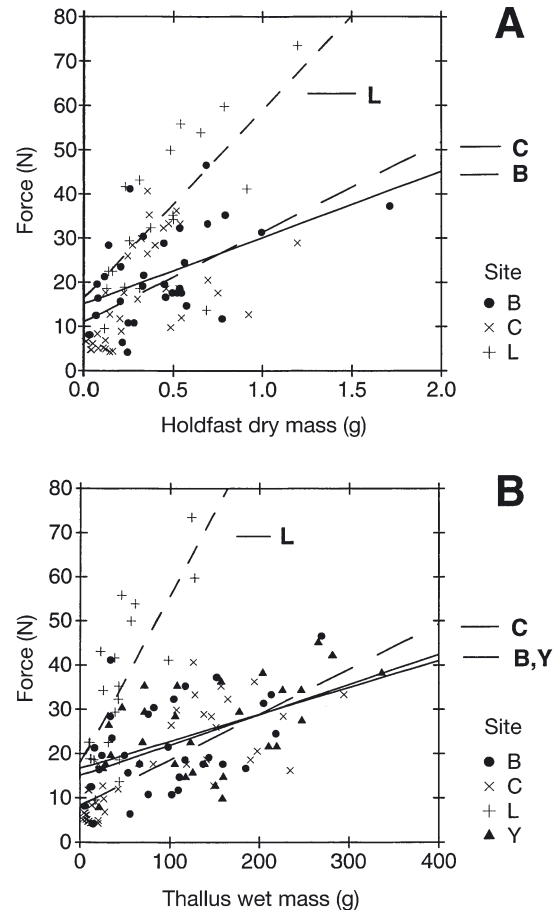


Fig. 6. *Agarum fimbriatum*. Biomechanical attributes covarying with holdfast strength at study sites. (A) Force (N) required to dislodge a holdfast versus holdfast dry mass (g). (B) Force (N) required to dislodge a holdfast versus total thallus wet mass (g). Slopes of all regression lines are highly significant ( $p < 0.001$ ), but slopes are not homogeneous. (See Fig. 1 legend for site abbreviations)

## DISCUSSION

It is worthwhile to begin by reviewing the most salient among-site comparisons that would indicate impacts of hydrodynamics on plant survival, morphology and biomechanical attributes. Strong wave-generated velocities were only detected at Sites L and W; therefore, instances in which these sites stood out may implicate wave impacts on plants. With respect to tidal currents, it is worth noting that our study sites experienced a wide range of current velocities that reflect those found in all but the most extreme habitats. As discussed above, and more fully in the accompanying paper (Eckman et al. 2003), within-site spatial variability in currents was considerable, and this variation may have contributed to some inconsistencies in our results. However, despite this vari-

Table 3. *Agarum fimbriatum* and *Costaria costata*. Relationships between biomechanical properties (holdfast detachment force [ $F_h$ , in N], blade penetration force [ $F_b$ , in N] and plant size [holdfast mass, g; thallus mass, g; blade thickness, mm]) at each site. Best-fit slopes and intercepts for each regression and simple ANOVA of mean  $F_h$  or  $F_b$  are also reported. Site codes connected by a common underline are not significantly different. ND: no data. B: Brown Island; C: Cantilever Point; L: Long Island; M: Minnesota Reef; P: Parks Bay; Y: Yellow Island; R: Reid Rocks; W: Whale Rocks

<b>Holdfast detachment force (<math>F_h</math>)</b>										
Site	Mean (SE)	$F_h = f(\text{holdfast dry mass})$				$F_h = f(\text{thallus wet mass})$				
		Slope (SE)	p	Intercept (SE)	p	Slope (SE)	p	Intercept (SE)	p	
<i>A. fimbriatum</i>										
B	23.7 (2.0)	15.0 (4.9)	0.005	15.2 (2.6)	<0.001	0.069 (0.020)	0.008	15.1 (2.8)	<0.001	
C	18.0 (1.9)	20.3 (6.5)	0.003	11.1 (2.7)	<0.001	0.108 (0.010)	<0.001	9.6 (1.2)	<0.001	
L	35.5 (4.0)	42.4 (9.9)	0.001	16.6 (5.3)	0.006	0.372 (0.078)	<0.001	17.9 (4.7)	0.001	
M	ND	ND	ND	ND	ND	ND	ND	ND	ND	
P	ND	ND	ND	ND	ND	ND	ND	ND	ND	
R	ND	ND	ND	ND	ND	ND	ND	ND	ND	
W	29.0 (1.9)	ND	ND	ND	ND	ND	ND	ND	ND	
Y	25.2 (1.8)	3.2 (5.5)	0.56	23.8 (3.0)	<0.001	0.06 (0.02)	0.015	16.7 (3.0)	<0.001	
ANOVA: <u>C B Y W L</u> ( $p < 0.001$ )										
<i>C. costata</i>										
B	20.3 (2.1)	2.74 (3.4)	0.43	18.3 (3.2)	<0.001	0.088 (0.032)	0.008	13.9 (2.94)	<0.001	
C	23.9 (1.5)	12.9 (3.6)	0.001	14.9 (3.0)	<0.001	0.127 (0.024)	<0.001	12.2 (2.7)	<0.001	
L	20.4 (2.3)	4.51 (5.5)	0.44	17.6 (4.1)	0.002	0.029 (0.206)	0.89	19.8 (4.5)	0.002	
M	ND	ND	ND	ND	ND	ND	ND	ND	ND	
P	ND	ND	ND	ND	ND	ND	ND	ND	ND	
R	ND	ND	ND	ND	ND	ND	ND	ND	ND	
W	46.7 (3.4)	17.6 (12.6)	0.18	29.6 (7.7)	0.001	0.637 (0.271)	0.03	22.7 (7.84)	0.009	
Y	ND	ND	ND	ND	ND	ND	ND	ND	ND	
ANOVA: <u>B L C W</u> ( $p < 0.001$ )										
<b>Blade penetration force (<math>F_b</math>)</b>										
Site	Mean (SE)	$F_b = f(\text{blade thickness})$								
		Slope (SE)	p	Intercept (SE)	p					
<i>A. fimbriatum</i>										
B	ND	ND	ND	ND	ND					
C	2.9 (0.08)	11.8 (2.8)	<0.001	0.48 (0.59)	0.42					
L	ND	ND	ND	ND	ND					
M	4.1 (0.2)	18.3 (2.9)	<0.001	-0.57 (0.73)	0.44					
P	2.5 (0.09)	8.89 (2.23)	<0.001	0.63 (0.47)	0.2					
R	3.7 (0.09)	4.03 (2.94)	0.18	2.57 (0.86)	0.006					
W	4.0 (0.2)	9.12 (2.46)	0.001	2.51 (0.43)	0.006					
Y	ND	ND	ND	ND	ND					
ANOVA: <u>P C R W M</u> ( $p < 0.001$ )										
<i>C. costata</i>										
B	ND	ND	ND	ND	ND					
C	2.3 (0.09)	11.3 (7.8)	0.12	0.85 (1.0)	0.43					
L	ND	ND	ND	ND	ND					
M	3.3 (0.2)	9.98 (1.15)	<0.001	0.83 (0.29)	0.009					
P	2.4 (0.2)	8.09 (0.80)	<0.001	0.57 (0.20)	0.006					
R	6.0 (0.3)	10.2 (2.5)	<0.001	2.18 (1.29)	0.1					
W	5.5 (0.2)	8.41 (0.75)	<0.001	1.70 (0.36)	<0.001					
Y	ND	ND	ND	ND	ND					
ANOVA: <u>C P M W R</u> ( $p < 0.001$ )										

ability, Site W stood out as having significantly stronger currents than did Site C. This high variability prompted us to add 2 sites: Parks Bay (Site P, having very low currents and wave exposure) and Reid Rock (Site R, having very strong currents and low wave exposure). These 2

sites are unquestionably 'end members' along the hydrodynamic gradient of current energy. Therefore, instances in which Sites W and R or Sites C and P stood out, especially relative to each other, may implicate current impacts on plants.

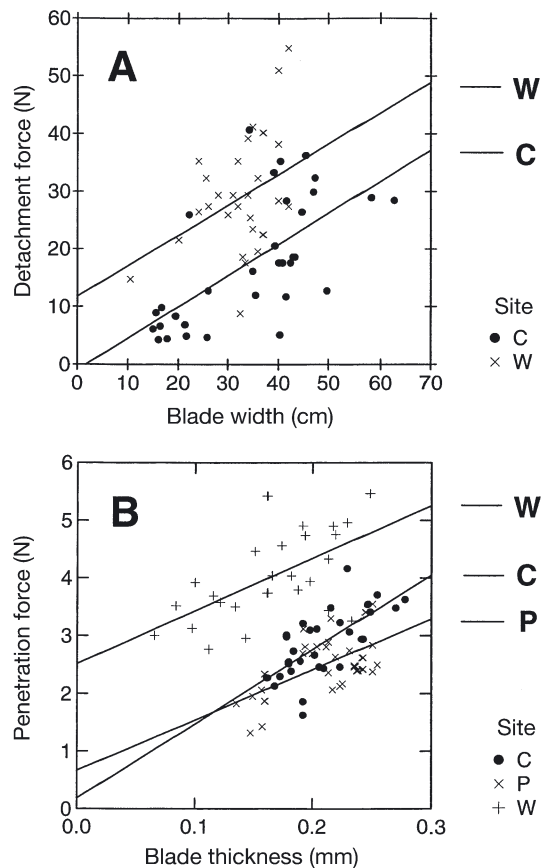


Fig. 7. *Agarum fimbriatum*. Biomechanical attributes relating (A) holdfast strength to blade width and (B) blade tissue strength to blade thickness at study sites. All slopes are significant and homogeneous. See Table 3 for results of ANCOVA. (See Fig. 1 legend for site abbreviations)

The relationship between survival and hydrodynamics in these 3 understory kelps is both interesting and enigmatic. Wave-generated velocities at our most exposed sites (Sites L and W) were less than those found at the most wave-exposed sites on open coastlines, but still exceeded maximum tidal current velocities at all sites except Site R, and appear to limit *Agarum fimbriatum*'s distribution (Duggins pers. obs.). Wave exposure clearly reduced survival in all 3 of the species we followed, and is probably responsible for 1 species (*A. fimbriatum*) being very rare at the most wave-exposed site (Site W). On the other hand, we could detect no effect on survival along the current velocity gradient in any of the 3 species. However, this result does not imply that one can dismiss the effects of current on survival. Many of the morphological and biomechanical attributes we examined in *A. fimbriatum* and *Costaria costata* varied along the current gradient in a manner parsimonious with the conclusion that an individual's resistance to hydrodynamic distur-

bance increased in habitats characterized by strong flow (cf. Blanchette et al. 2002). It is consistent with our data, and reasonable to conclude, that these morphological adaptations were in response to drag forces imposed by currents, and that such adaptations increased survival to the point where differences due to current intensity among locations are not detectable. However, any such interpretation of these data must consider the alternative possibility that strong selective pressures may have been acting to differentially remove the larger, thinner, weaker individuals from the population. Thus, it may be that over time, strong hydrodynamic forces selected against more weakly attached plants, plants with large, drag-producing thalli, or those with thinner blades. Potentially, these selective forces may even have resulted in a flow-driven shift in morphological attributes of the population at a genetic level, but for this to occur there would have to have been limited genetic exchange among meta-populations of the 2 understory species. Although the dispersal potential of released kelp spores is generally believed to be quite limited (e.g. Fredriksen et al. 1995, Forrest et al. 2000, but see Reed et al. 2000), we are less certain about the extent to which genetic exchange occurs via reproductive sporophytes that might have become detached by flow and grazing, and transported among meta-populations by the strong tidal flows in the San Juan Archipelago (e.g. see Hobday 2000). Dispersal is probably significantly more limited in understory kelps than in surface canopy species where dispersal is enhanced by structures providing floatation. Genetic differentiation could probably be swamped by the exchange of only a few individuals per generation. The only way to conclusively evaluate the alternative explanations of adaptive morphological plasticity versus selective removal would be to conduct common garden transplants to a range of sites, with individuals at dynamic sites secured in such a manner that plants survived in strong flows long enough to allow the appropriate morphology to be expressed (e.g. Shaughnessy et al. 1996, Kawamata 2001, Shaughnessy & DeWreede 2001, Blanchette et al. 2002). However, the fact that some morphometric attributes at higher-energy sites may diverge completely from values observed at low energy sites suggests that for these characteristics, individuals at one site simply never developed structures comparable to their conspecifics located elsewhere. Given the morphological plasticity that is characteristic of many marine macrophytes (see literature cited in 'Introduction'), the variability noted in our morphometric and biomechanical data is not surprising. The data are also parsimonious with the explanation that after sensing stronger flow energy, kelps respond by devoting more resources to increasing strength of attachment to the

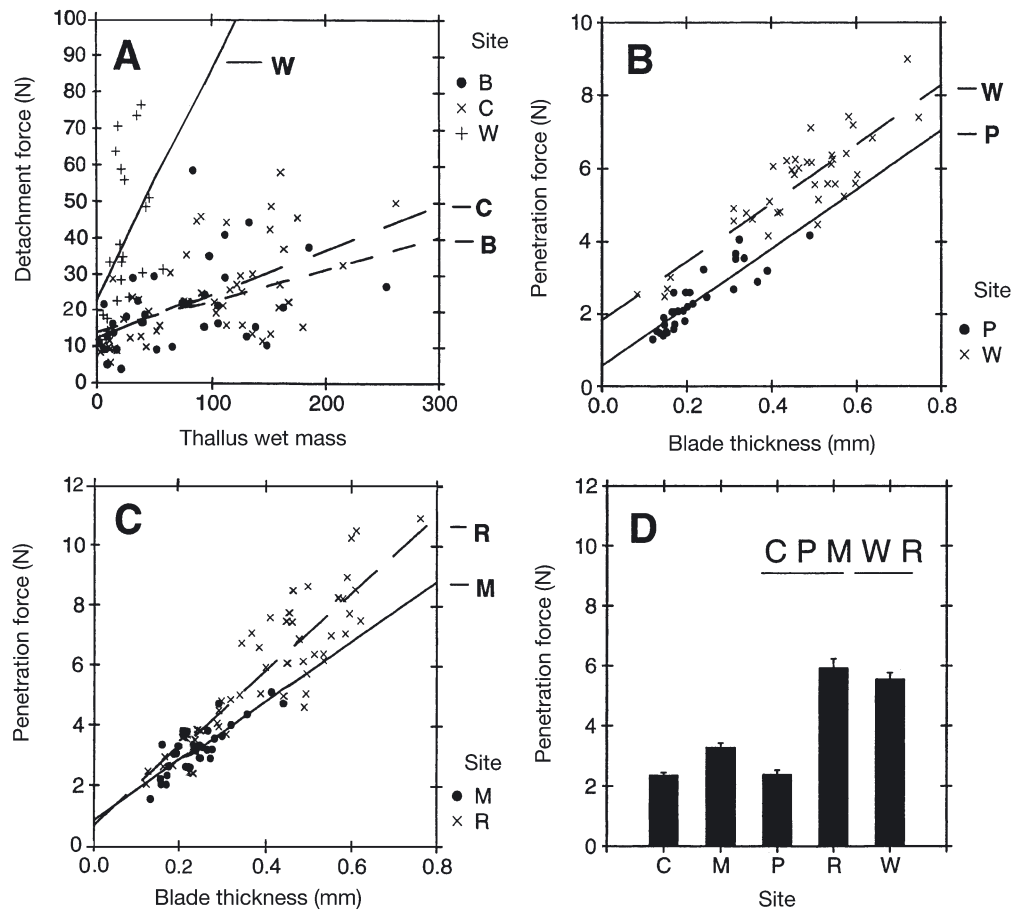


Fig. 8. *Costaria costata*. Biomechanical attributes relating (A) holdfast strength (N) to thallus wet mass (g), (B, C) blade tissue strength (N) to blade thickness (mm), and (D) mean blade tissue strength (N) compared among sites at study sites. See Table 3 for results of ANOVA and ANCOVA. Sites with no significant differences ( $p > 0.05$ ) in Bonferonni *post hoc* multiple comparisons are underlined in (D). (See Fig. 1 legend for site abbreviations)

substratum, blade toughness, or by reducing thallus surface area.

The interpretation of survival data is, on the whole, straightforward, but the justifications for our morphometric and biomechanical measurements need further discussion. First, these measurements need to be assessed in light of the observed causes of failure in *Agarum fimbriatum* and *Costaria costata*. In both these species, the leading cause of failure was holdfast dislodgment (Table 2), as was evident when a kelp disappeared between censuses without a trace of remnant holdfast or stipe (see Duggins et al. 2001 for further discussion of this assumption). We therefore measured holdfast mass and area as simple proxies for the degree of contact of the plant's anchor with the substratum. We also measured strength of holdfast attachment directly.

The stipe was the second most common location of failure (Table 2). Our choice of stipe characteristics

was perhaps more speculative. The stipe is constantly bending and exposed to tensile forces as the kelp flaps back and forth in wave accelerations, or extends in strong currents. For red algae in the genus *Mazzaella*, it is the narrow constriction between stipe and blade (where force is concentrated) where failure most frequently occurs (Shaughnessy et al. 1996, Shaughnessy & DeWreede 2001). Stipe failures were observed at all sites, and it is this structure that typically fails in the surface canopy kelp, *Nereocystis luetkeana*, particularly following even shallow excavations by grazing mollusks (Koehl & Wainwright 1977, Duggins et al. 2001). Consequently, we compared stipe length, thickness and cross-sectional area among sites to evaluate whether hydrodynamic energy had any influence on stipe morphology.

Though comparatively rare, blade failure was a gradual process, usually occurring over several censuses. Typically these failures involved a gradual ero-



sion and tattering of the blade down to the stipe. In these short (and flexible) stiped kelps, blades are frequently in contact with the substrate, and any water motion can result in substantial abrasion. Blade toughness (resistance to tearing) was assessed using a penetrometer of our own design, and such devices have been criticized. Such criticisms are justified where resistance to herbivory is being quantified (specifically by mollusks using a radula to scrape the algal surface layer). In our case, however, we feel that the penetrometer is a reasonable tool to evaluate simple resistance to penetration and tearing as a kelp blade abrades against the substrate.

Several key attributes of both *Agarum fimbriatum* and *Costaria costata* varied among sites in a manner suggesting that hydrodynamics played a key role in affecting morphological and biomechanical properties within populations. As with any field project of this nature (particularly one constrained by SCUBA limits in potentially dangerous environments), results are punctuated with some inconsistencies and enigmatic patterns (or lack of pattern). However, key patterns in this analysis are very clear. In both *A. fimbriatum* and *C. costata*, several attributes of plant morphology varied directly among sites with the intensity of the strongest tidal currents. These are discussed more fully below. Biomechanical attributes (holdfast detachment force, blade toughness) of the annual kelp *C. costata* also varied directly with tidal current strength. This relationship is logical, since plants sampled in late summer and early fall had never experienced significant wave energy, even at the sites exposed to winter storm waves (Sites L and W). In contrast, however, biomechanical attributes of the perennial kelp *A. fimbriatum* reflected variability among sites in exposure to wave energy. Plants at Sites L and W were more strongly attached to the substratum, and had tougher blades. It is obvious from these general patterns that flow energy exerts an important influence on plant structure and morphology, as well as on survival.

It is worth noting that observations and analyses for *Agarum fimbriatum* populations must be viewed as conservative. *A. fimbriatum* populations at the most energetic site (W) were very small, and there were too few individuals to use in our population dynamics study. We were able to collect enough *A. fimbriatum* from Site W for morphological and biomechanical studies, but these individuals were found in microhabitats that were slightly deeper or more protected (by local topography) from currents than individuals collected at other sites. We attempted to standardize depth for all these collections and similarly only chose kelps from the tops of broad reefs (to minimize current and wave shading effects). However, in order to find *A. fimbriatum* at Site W, we had to dive somewhat

deeper and look in areas more protected from currents. Nonetheless, in most of the *a posteriori* morphometric and biomechanical assessments for *A. fimbriatum*, Site W (the most wave-exposed site, with strong currents) grouped with Site R (the most current-exposed site). Our results for *A. fimbriatum* are thus somewhat conservative, and emergent trends more believable.

Blade shape and thickness in *Costaria costata* varied significantly along gradients in exposure to tidal currents. Blades were generally smaller and more elongate at sites with strong currents than at the more quiescent sites (Site C and P). Similar results (primarily related to wave energy) have been reported previously for *C. costata* (Bhattacharya & Druehl 1989) and other kelps (e.g. Norton 1969, Gerard & Mann 1979, Koehl & Alberte 1988, Blanchette et al. 2002), and red algae (Shaughnessy et al. 1996, Shaughnessy & DeWreede 2001). While smaller blades clearly experience reduced drag forces, the significance of more elongate blades is less obvious to us. In *Mazzaella*, reproductive capacity is related to blade length, and in this case narrow blades (at wave-exposed sites) represent an adaptation to reach reproductive length without achieving large surface area (which would result in significant drag forces) (Shaughnessy et al. 1996, Shaughnessy & DeWreede 2001). In *C. costata*, it is obvious that the answer should not lie in any ability of the thallus to grow longer than the maximum wave-orbital displacement (see Koehl 1986, 1996, 1999, Gaylord et al. 2001), as has been proposed for large seaweeds, because such displacements greatly exceed the maximum length of this small, understory kelp. In *Agarum fimbriatum*, no significant pattern in blade size or shape was observed along the exposure gradient. The trend toward thinner blades at protected sites, where kelps are not subjected to high tensile forces and abrasion against the substrate, was highly significant for both species. Building a blade of greater thickness obviously has energetic costs, particularly if the biomass is added to imbedded non-photosynthetic (medullary) tissues. Blades are almost certainly more photosynthetically efficient (per unit area) if light can penetrate the entire blade to reach chloroplasts in the lower surface of a blade lying on the substrate. A small total blade area also has negative photosynthetic ramifications, but we suggest that large blades (in *Costaria*) simply cannot survive the forces imposed in strong flows.

In both *Costaria costata* and *Agarum fimbriatum*, stipe cross-sectional areas and lengths were consistently greater at sites with stronger tidal currents. Thicker stipes should be stronger, more resistant to failure following minor damage (i.e. herbivory), and perhaps more resistant to bending (and thus more likely to keep the blade off the substrate). Patterns in stipe length (longer at exposed sites for both species)

are more problematic, but could relate to the 'steepness' of curvature of the stipe as the kelp is flattened against the substrate in strong flows. A longer stipe will bend less per unit length and may thereby be less prone to biomechanical damage.

Holdfast biomass and area (scaled to total thallus size, since larger or older individuals would be expected to have larger holdfasts) were considerably greater in *Costaria costata* at the more energetic sites. We noted that holdfasts (in both species) at exposed sites are comprised of thicker and denser branches. We are somewhat less confident in explaining the morphological pattern in *Agarum fimbriatum* with respect to holdfast morphology. At Site R (very strong currents), holdfasts had greater biomass (scaled to blade wet mass), but at Site W (wave exposure and strong currents) relative holdfast biomass was very low. Similarly, with respect to holdfast area, holdfasts at Site R were large while at Site W they were small. Although these *a posteriori* statistics for *A. fimbriatum* are somewhat confusing, it is nonetheless clear that holdfast strength of attachment to the substratum is consistently and significantly greater in both species at the more energetic sites. It is likely that the more simple measurement of holdfast mass or size was not an accurate proxy for degree or strength of attachment. At the most protected sites, we commonly observed holdfasts in both species to have long thin branches, which sometimes terminated without attaching to the substrate.

Clearly, blade toughness (resistance to penetration) would be expected to increase with blade thickness, and holdfast tenacity (resistance to dislodgment) to increase with holdfast biomass. These predictions are supported by our data and, given that blades are thicker and holdfasts (generally) more massive at energetic sites, explains, in part, how individuals are tougher and better attached at such sites. But the data (in our ANCOVA) indicate that there are additional factors operating to increase plant strength in strong flows. The linear regressions of blade toughness (penetration force) against blade thickness resulted in very different regression lines for different sites (Figs. 7B & 8B,C). In several comparisons, given a standard blade thickness, a blade from an energetic site was more resistant to penetration than one from a protected site. Such a result is consistent with the hypothesis that blades from energetic sites are built differently at the tissue level, or perhaps have different chemical compositions (see Hurd 2000, for a discussion of this issue). Similarly, when holdfast dislodgment force was regressed against holdfast biomass for *Agarum fimbriatum* (Fig. 6A), regression lines differed significantly among sites. For a given size holdfast, greater force was required to dislodge the plant at the most

energetic site. Again, tissue structure or chemical mechanisms could be hypothesized to account for these differences, but additionally in this case, the nature of the holdfast-substrate junction could be different. As mentioned above, attachments at protected sites frequently seemed tenuous. Even though holdfast failure is a major source of mortality for kelps, very little is known about the chemistry or mechanics of holdfast attachment.

We conclude by re-iterating that the survival of these 3 understory kelps in the San Juan Archipelago was greatly impacted by exposure to episodic, storm-generated waves. This result closely parallels results reported for the response of both surface canopy and understory species to storm-generated wave forces on more exposed coastlines (see references cited in the 'Introduction'), and indeed this close coupling between storms and kelp population dynamics can be considered a valid generalization, even in inland waters. Nevertheless, exceptions do occur. An example emerging from our own work in the San Juan Archipelago involves the dominant surface-canopy plant *Nereocystis luetkeana*, whose survival exhibits a complex and decidedly non-linear relationship with wave exposure and incident flow energy (Duggins et al. 2001). Our study also reinforces results reported earlier (see references cited in the 'Introduction'), which indicate that kelps respond morphologically and biomechanically to incident flow energy. It is clear from our results that understory plants respond to the regular imposition of strong tidal flows, as well as to winter storms in the case of the perennial kelp *Agarum fimbriatum*. Temporally predictable spatial variability in more tidally dominated flows can be substantial over comparatively short distances (Eckman et al. 2003) and difficult to predict *a priori*, yet plant responses to currents, even the comparatively strong ones found in the waters of the San Juan Archipelago, are apparently sufficient to ameliorate any impacts of currents on probabilities of their survival.

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