EFFECTS OF WAVE EXPOSURE ON INTERTIDAL FUCOID ALGAE

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ABSTRACT

Two species of intertidal fucoid algae, *Pelvetia compressa* and *Hesperophycus californicus,* are commonly found along moderately wave exposed rocky intertidal regions along the California coast. Both species decrease in size and abundance going from wave-protected to wave-exposed intertidal areas. On the west end of Santa Cruz Island there is a noticeable gradient in wave exposure from Forney Cove to Frasier Point. In order to evaluate the effects of both wave exposure and tidal height on size and survival of these two species, we transplanted 20 adults and juveniles of both species from a wave-protected site (Forney) to an adjacent wave-exposed site (Frasier) at both high and low tidal heights, as well as 20 individuals of each species and age from Forney to Forney to control for transplant effects. Survival of adult *Pelvetia* was highest in the low zone at Frasier and low at both Forney and Frasier high. Survival of *Pelvetia* juveniles was extremely low at both tidal heights at Frasier. *Hesperophycus* survival at Frasier did not differ from that at Forney for either adults or juveniles. The most dramatic effect of transplantation was on plant size. All individuals transplanted to Frasier were immediately reduced in size relative to controls. These results are consistent with the idea that wave action can prevent plants from attaining large sizes in wave-swept intertidal areas.

Keywords: *Pelvetia compressa*, *Hesperophycus californicus*, Santa Cruz Island, Frasier Point, Forney Cove, wave exposure, algal size.

INTRODUCTION

Both ecologists and biogeographers have been long interested in determining the factors limiting the distributions of species in nature. Although particular species may have distributions which extend across broad geographical areas, they may be locally rare within their geographical range. This pattern holds for two marine algal species, *Hesperophycus californicus* and *Pelvetia compressa,* whose distributions both extend across broad geographic areas from northern California (and British Columbia for *Pelvetia*) to Baja, yet are distributed patchily within these broad areas. Some of the factors known to influence the local distributions of intertidal species include wave action, nutrient/food availability, rock type, and intensity of grazing/predation and competition. It is likely that some or all of these environmental factors may influence distributions depending on the particular location, however in this study we focus our attention on the effects of wave exposure.

Exposure to wave action is generally considered an important factor in the distribution and abundance of intertidal organisms (Carefoot 1977; Denny 1988; Vadas et al. 1990). In shallow marine and intertidal areas, a dramatic environmental gradient exists among shores exposed to different levels of wave action. Wave action and water movement are known to influence species size, morphology, and distribution patterns, and organisms on wave-swept shores are often much smaller than those in more wave-protected habitats (Lewis 1968; Menge 1976; Blanchette 1997). These trends occur both within species, and between sites of close proximity. Examples include mussels and seastars (Harger 1970, 1972; Paine 1976 a,b), gastropods (Kitching et al. 1966; Behrens 1972; Etter 1989; Boulding 1990; Boulding and Van Alstyne 1993), and seaweeds (Russell 1978; Schonbeck and Norton 1981; Norton 1991). Organisms living in wave-swept intertidal environments are subjected to some of the highest hydrodynamic forces on earth which scale with both the magnitude of the flow and the size of the organism (Denny et al. 1985, 1988). Dislodgment or breakage can occur when the force exceeds the strength of the organism or its attachment to the rock. Thus, survival in this environment is enhanced by features which minimize the forces that an organism experiences, and therefore minimizes its risk of being broken or torn from the rock. These features may include high attachment strength, high breaking strength, high flexibility and extensibility, small size, low drag morphology, and/or a combination of these traits (Koehl 1977, 1982; Denny et al. 1985; Holbrook et al. 1991; Gaylord et al. 1994; and Dudgeon and Johnson 1992). Most marine plants do not have a fixed morphology throughout their lifetime, and are able to modify their shape and size to suit conditions. Sub-lethal forces may break off several branches of a plant reducing its overall size. In this case, the plant's probability of survival is increased, since the size of the plant is reduced while its tenacity remains unaffected. This pattern of thallus breakage was documented in a field experiment in which the intertidal rockweed, *Fucus gardneri*, was reciprocally transplanted between wave-exposed and wave-protected sites (Blanchette 1997). Large plants from the wave-protected site were not immediately dislodged by wave action at the exposed site. They were, however, reduced in size over time as branches were pruned by wave action.

The west end of Santa Cruz Island provides an ideal setting to examine the effects of wave exposure on intertidal organisms. Frasier Point is directly exposed to the prevailing swells from the northwest and is extremely wave exposed (Figure 1). Forney Cove lies on the opposite side of this peninsula to the south and is very much protected from wave action (Apt et al. 1988; Tissot 1995). Swells from the south are more rare, and much of the wave intensity generated by a south swell is broken up by a large rocky point and therefore does not reach the intertidal area. Both *Hesperophycus* and *Pelvetia* are extremely abundant at Forney, yet are absent or extremely rare at Frasier (Apt et al. 1988). The few plants at Frasier appear extremely small and "stunted" relative to the Forney population, suggesting that wave exposure may also be a limiting factor in their ability to grow to a large size (authors' pers. obs.).

In order to examine the effects of wave exposure on the size and survival of both *Hesperophycus* and *Pelvetia,* we transplanted both species to Frasier as well as back to Forney to control for the transplant procedure. Our study attempts to address the following questions:

- How does wave exposure influence size and survival in both *Pelvetia* and *Hesperophycus*?
- Do these effects depend on plant age?
- To what degree do the size and survival of wave exposed transplants depend on tidal height?

METHODS

Study Location

This study was carried out at Frasier Point, on the western end of Santa Cruz Island. The point is a rocky (basalt) headland fully exposed to oceanic waves on the northwestern side (hereafter referred to as 'Frasier'), and the southwestern side (hereafter referred to as 'Forney') is protected from swells (Figure 1). Experimental plots were located on horizontal rock surfaces in the mid-intertidal zone and ranged from 2.2 to 3.0 m above mean lower low water (MLLW). The high-zone, wave-exposed community at Frasier was dominated by *Porphyra perforata*, *Endocladia muricata*, and the barnacles *Balanus glandula* and *Chthamalus fissus*. The most abundant herbivores were the limpets *Lottia digitalis, L. pelta, L. strigatella* and the snail *Littorina scutulata*. The high-zone, wave-protected community at Forney was dominated by *Pelvetia compressa* and *Hesperophycus californicus.* The barnacles *B. glandula* and *C. fissus* were patchily present at this site and the snails *Littorina scutulata* and *Tegula funebralis* were the most abundant grazers.

Study Organisms

Pelvetia compressa and *Hesperophycus californicus* are both common high intertidal fucoid brown algae. The thallus of *Hesperophycus californicus* is attached by a broad discoid holdfast, from which arise bilaterally branched flattened fronds with a distinct midrib. Receptacles are present

Figure 1. Western point of Santa Cruz Island. Frasier is the more wave exposed site to the north (right) and Forney is the protected cove to the south (left).

at the apices of mature plants and become swollen at the time of reproduction. Fertile plants are found in the population throughout the year. Plant growth is apical and branching is dichotomous. Reproductive structures (conceptacles) develop from cells in receptacles of higher order branches. The modular character of *Hesperophycus* means that a single plant may be reproductive throughout the year as branches reach reproductive maturity at different times. *Hesperophycus* are perennial and can reproduce for several successive years. *Pelvetia compressa* is similar in form to *Hesperophycus*, however its axes are subcylindrical rather than flattened, and lack midribs (Abbott and Hollenberg 1976). *Pelvetia* is known to occur from British Columbia to Baja California and *Hesperophycus* ranges from Santa Cruz, California to Baja California.

Transplant Experiment

To examine how plant survival is affected by size and degree of wave exposure, we transplanted *Hesperophycus* and *Pelvetia* from Forney to Frasier and recorded sizes and survival of all plants over a one-year period.

Experimental Design

We haphazardly collected equal numbers of randomly selected juvenile and mature (reproductive) plants of both species from Forney. We carefully chiseled out a solid section of the rock from beneath the holdfast of each chosen plant. Plants were used in the transplant experiment only if the adhesion of the holdfast to the section of rock remained firm during this process. We continued sampling until we had collected 240 plants. Out of this total there were 60 plants in each of four categories (juvenile *Pelvetia* [JP], adult *Pelvetia* [AP], juvenile *Hesperophycus* [JH] and adult *Hesperophycus* [AH]). The transplant technique involved gluing the sections of rock to which plants were attached into pre-chiseled holes at the transplant site using marine epoxy putty (Z spar, Kopper's Co. Los Angeles) so that the transplant was flush with the surrounding rock. In this way the plant's tenacity to the rock was maintained and the epoxy did not touch the plant or interfere with its growth. Each plant was individually marked by attaching a numbered plastic label to the putty.

The experimental design consisted of 20 plants from each of the four categories (JP, AP, JH and AH) transplanted to each of the following locations: 1) Forney high zone, 2) Frasier high zone, and 3) Frasier low zone. Because plants were collected from the high zone at Forney, transplants of plants to Forney high served as controls for the transplant procedure.

Data Collection

The transplant experiment was initiated in September 1996 and lasted approximately one year. We censused the transplants and controls every two months. For each individual we recorded survival (presence vs. absence), and size in terms of planform area. Area measurements were made by photographing each individual against a white sheet next to a ruler and analyzing plant area using an image processing program (Image 1.41, National Institute of Health). Since both *Hesperophycus* and *Pelvetia* can perennate and regrow from a holdfast, plants were recorded as missing only when the entire holdfast was dislodged.

Data Analysis

Data on survival from the transplant experiment were analyzed using a Kaplan-Meier model which calculates the proportional survival of plants in each treatment over time. Comparisons of the mean proportional change in size between transplants at Frasier and control transplants at Forney were performed using a repeated measures analysis of variance. In all cases the Mauchly criterion was used to test the assumption of sphericity. For cases in which the sphericity chi-square test was significant we based results on the Greenhouse-Geisser adjusted multivariate F tests. All statistical analyses were done using JMP software (SAS Institute 1990).

Physical Site Characteristics

As part of an ongoing study on biogeographic variation in recruitment, we have been measuring several different physical characteristics at Frasier Point. Our data include measurements of maximal wave force and seawater nutrient concentrations, both of which are detailed below.

Wave Force

To verify and quantify our initial subjective estimates of the relative wave intensity at all sites, we installed maximum wave force meters. Maximum wave force meters are designed to record the force imposed by the largest wave passing over the device during the time of deployment. The maximum wave force meters were developed by Bell and Denny (1994) and the spring tensions and attachment system have been slightly modified for use at our sites. Five large eyebolts were installed at each site, and small carabiner quick-links were used to attach wave force meters to these bolts. Eyebolts were placed in relatively open areas at each site to avoid confounding effects of the local topography. Five wave force meters were deployed at each area during each sampling date.

Nutrients

Seawater concentrations of nitrate and nitrite were measured from surf-zone seawater samples collected every two months. Five separate seawater samples were collected from each site and processed by the analytical lab at the University of California, Santa Barbara (UCSB). Nutrient concentration data were analyzed using a repeated measures ANOVA and multiple comparisons among sites were made using a Tukey HSD. All statistical analyses were performed using JMP statistical software (SAS Institute 1990).

RESULTS

Survival

The number of transplants remaining declined in all treatments over the course of the experiment (Figure 2). The putty and tag were not dislodged in any cases. The results of the Log Rank analysis of proportional survival of transplants based on species and age at both high and low Frasier sites relative to the transplant controls at Forney are shown in Table 1. Survival of adult *Hesperophycus* at Frasier high did not differ significantly from Forney plants, however survival of Frasier low adult *Hesperophycus* was significantly reduced relative to the Forney plants. Juvenile *Hesperophycus* exhibited a rapid decline at all sites and there were no significant differences between the survival of transplants at either of the Frasier sites and survival of Forney plants. Adult *Pelvetia* at Frasier low survived relatively well compared to the Forney plants, while survival of Frasier high adult *Pelvetia* dropped sharply between February and April. There were, however, no significant differences in survival of transplants at either of the Frasier sites and survival of Forney plants. Juvenile *Pelvetia* at both Frasier sites suffered the sharpest declines, and survival of transplants at both sites was significantly reduced relative to the Forney transplants.

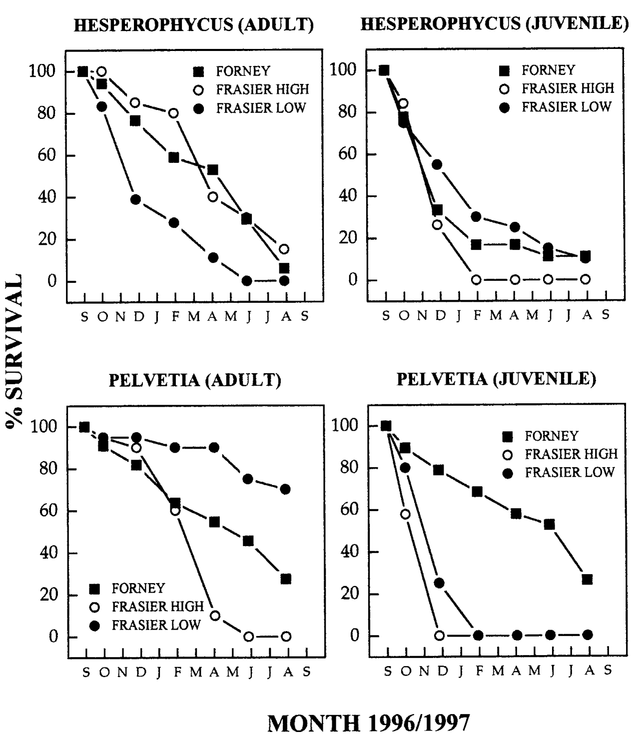

Figure 2. Percentage of transplants in each of the 3 treatments surviving over the course of the experiment. Forney transplants are represented by solid squares, transplants to Frasier high are represented by open circles and transplants to Frasier low are solid circles. Adult *Hesperophycus* are in the top left, juvenile *Hesperophycus* are in the top right, adult *Pelvetia* are in the lower left and juvenile *Pelvetia* in the lower right.

Size

The net proportional change in size of Forney transplants was positive over the course of the experiment for all species and ages (Figure 3). In contrast, both Frasier high and low transplants of all species and ages exhibited a net negative proportional change in size over the course of the study. Mean proportional change in size of transplants at both Frasier sites was reduced relative to the Forney plants and varied significantly depending on the particular species and age group (Table 2).

Adult *Hesperophycus* sharply decreased in size over time at both high and low Frasier sites relative to the Forney transplants. Sizes of transplants at Frasier high became significantly smaller than those at Forney over time, yet sizes

Table 1. Results of a LogRank test in which the proportional survival of transplants in each group was compared with the proportional survival of transplants in the same species/age group at Forney.

Species	Age	Site	Chi Square	P
Hesperophycus	Adult	High Frasier	0.1717	0.6786
		Low Frasier	9.0175	0.0027
	Juvenile	High Frasier	0.0261	0.8718
		Low Frasier	1.4558	0.2276
Pelvetia	Adult	High Frasier	1.6336	0.2012
		Low Frasier	0.0404	0.8407
	Juvenile	High Frasier	16.8238	0.0001
		Low Frasier	13.0246	0.0003

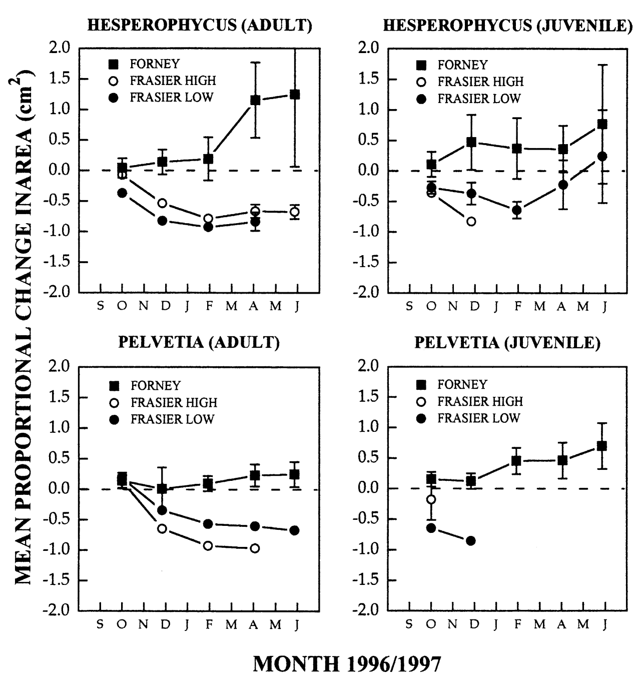

Figure 3. Proportional change in size (cm^2) for plants in each of the three treatments (relative to initial size) over the course of the experiment. Data are means ± 1 s.e.m. Treatment symbols and figure layout are as described for Figure 2.

Table 2. Results of a repeated measures analysis of variance comparing the proportional change in size of plants from each group over each time period to transplants of each species/age group at Forney. In all cases the sphericity chi-square test was significant and the results are based on the Greenhouse-Geisser adjusted multivariate F tests.

Species	Age	Site	Time	Effect	F	DF Num	DF Denom	P
Hesperophycus	Adult	High Frasier	Sep - Apr	Site	6.5478	1	15	0.0218
				Time x Site	5.908	1.5646	23.469	0.0152
		Low Frasier	Sep - Apr	Site	2.4105	1	9	0.1549
				Time x Site	1.2951	1.4308	12.877	0.2941
	Juvenile	High Frasier	Sep - Dec	Site	14.4554	1	8	0.0052
				Time x Site	1.8061	1	8	0.2158
		Low Frasier	Sep - Apr	Site	3.7385	1	5	0.111
				Time x Site	0.6721	1.9799	9.8993	0.531
Pelvetia	Adult	High Frasier	Sep - Apr	Site	2.8052	1	6	0.145
				Time x Site	3.3222	1.3215	7.9292	0.1004
		Low Frasier	Sep - Apr	Site	14.0696	1	22	0.0011
				Time x Site	4.8828	1.8722	41.189	0.014
	Juvenile	High Frasier	Sep - Oct	Site	16.6225	1	25	0.0004
				Time x Site	.	.	.	.
		Low Frasier	Sep - Dec	Site	15.7287	1	18	0.0009
				Time x Site	2.4859	1	18	0.1323

of Frasier low transplants were not reduced significantly relative to the Forney transplants over time. Juvenile *Hesperophycus* at Frasier high were significantly reduced in size relative to Forney transplants in the first sampling period, however the time X site interaction was not significant. Although the proportional change in size for juvenile *Hesperophycus* at Frasier low was reduced relative to Forney, there was no significant difference between the sites. Sizes of adult *Pelvetia* transplants at both high and low Frasier were reduced relative to Forney transplants over the period from September to April, however sizes of Frasier high transplants were not reduced significantly relative to the Forney transplants over time. Juvenile *Pelvetia* at both Frasier high and low were significantly reduced in size relative to the Forney transplants.

Wave Force

We were only able to retrieve data from the wave force meters during April and May. During the winter months the wave meters at Frasier were regularly broken and we were not able to replace them. Mean maximum wave forces at Frasier in April were 48.29 ± 6.39 Newtons, and in May were 44.89 ± 5.31 Newtons. During this time period the forces at Forney were not great enough to register any reading on the wave meters. At least 10 Newtons of force are required to register a reading on the wave meters, and so the maximum forces at Forney over this time period must have been less than 10 Newtons.

Nutrients

Concentrations of nutrients in the water (nitrate + nitrite) were variable between sites and over time (Figure 4). There were significant differences in the concentration of nitrate + nitrite in water samples collected from Frasier and Forney from February to December (site effect; $F_{1,2}$ = 49.5845, $p<0.0196$; site x date $F_{5,10}$ = 7.2435, $p<0.0041$). Nitrate + nitrite concentrations at Frasier were significantly higher than those at Forney in both February and May (Figure 4).

DISCUSSION

Effects of Wave Exposure

Our results indicate that both *Hesperophycus* and *Pelvetia* have the ability to persist for at least several months at a wave-exposed site, however the cost appears to be a reduction in size. Transplants to Frasier high and low all exhibited a net negative proportional change in size over the experimental period. These results mirror the findings of Blanchette (1997) that *Fucus gardneri* are immediately reduced in size by an increase in wave exposure by thallus tattering, in which individual blades or sections of the thallus are removed by waves while the holdfast remains attached to the rock. High occurrences of branch breakage at wave-exposed sites have also been reported for *Ascophyllum nodosum*, another fucoid seaweed which is common in the

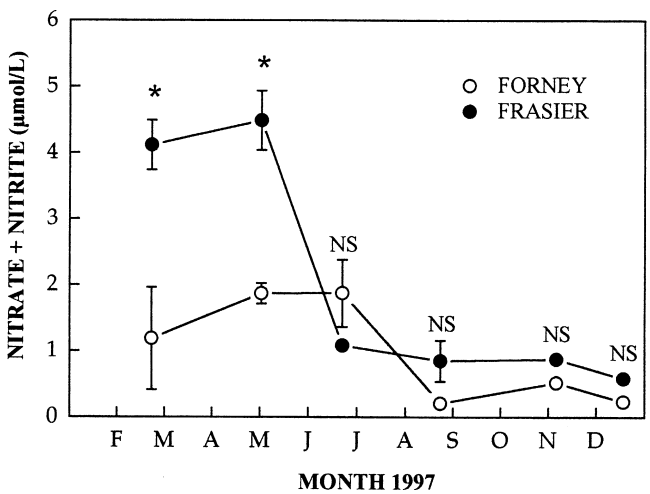

Figure 4. Concentrations of nitrate + nitrite (mg/l) in seawater samples collected at both Forney and Frasier in 1997. Data are means based on 5 samples ± 1 s.e.m.

North Atlantic (Vadas 1972; Vadas et al. 1978; and Blanchette and Gaines, unpublished data). A sub-lethal force may break off several branches of a plant reducing its overall size. In this case, the plant's probability of survival is increased, since the size of the plant is reduced while its tenacity remains unaffected. As evidenced in the transplant experiment, thallus tattering is common and seems to be an important method of size reduction. Thus several species of fucoid algae may use rapid size adjustment as a means of modifying the more traditional life history parameters of reproduction and survival, to achieve some 'optimal' size for a particular environment.

Besides increasing survivorship, tattering may have other benefits. Fracture may also be a useful mechanism of asexual reproduction and spore dispersal. Broken-off fragments may contain spores, conceptacles or gametes or may be able to re-attach to the substratum and grow (Norton et al. 1982). This method of dispersal could be important in fucoid seaweeds such as *Fucus, Hesperophycus and Pelvetia* that contain bladders or buoyant receptacles, similar to the findings of Paine (1988) that floating *Postelsia* may act as agents of long-distance dispersal. Breakage at branch points of reproductively mature receptacles could produce long distance dispersing rafts of gametes.

Effects of Age

Within a species juvenile transplants seemed to have suffered the highest mortality. This, however, is not unexpected. In a transplant study using juvenile and adult *Fucus gardneri* in Oregon by one of the authors (C. Blanchette) juvenile *Fucus* suffered the highest mortality (Blanchette, unpublished data). Kraemer and Chapman (1991) showed that hydrodynamic adaptation in *Egregia menziesii* occurs at a very early stage, and that there appear to be developmental limits to cell wall synthesis such that adult plants may not be able to adapt to a change in the force regime. Although it is difficult to determine the exact age of any of the plants used in this study, the juvenile plants were probably only several months old at most. Plants at this stage which probably suffer a relatively high rate of mortality from shading and desiccation are also small enough to suffer relatively high losses of tissue to grazers. Although survival of juveniles was low in most cases (with the exception of juvenile *Pelvetia* at Forney), the juvenile control transplants at Forney showed a positive proportional change in size, while all juveniles at Frasier were reduced to very small sizes. Juvenile *Hesperophycus* at Frasier low, however, showed a spurt of growth and increased in size in the spring of 1997 (April and June sampling periods). Interestingly, this is approximately the period of time in which the winter storm activity has died down and wave forces are much reduced. In the northeast Pacific wave heights (and therefore wave forces) are greatest in the winter months, when storms are most frequent. This seasonal variation in wave exposure can have important implications for plant size. Plants with annual life histories can take advantage of an extended lull in wave action during summer to grow and reproduce. For example, *Nereocystis luetkeana* (the bull kelp), *Postelsia palmaeformis* (the sea palm) and *Alaria fistulosa* are annual kelps that attain very large sizes in summer, and are usually ripped from the rock by heavy wave action in winter. Alternatively, perennial plants, such as *Hesperophycus* and *Pelvetia*, have meristems that remain totipotent and are able to adjust the plant's form to adapt to prevailing conditions (Norton 1991). A plant that grows beyond the optimum size during an extended calm period, such as in summer, may be pruned back to a more sustainable size in a subsequent storm. This seasonal drop in wave action is correlated with increases in size in surviving transplants of all ages, thus allowing plants to grow continually and reach large sizes (and therefore reproductive outputs) during calm periods.

Effects of Tidal Height

As mentioned earlier, both *Hesperophycus* and *Pelvetia* are commonly found in the high intertidal zone. Typically the only organisms which occur higher than these seaweeds are the barnacles *Balanus glandula* and *Chthamalus fissus* and the seaweed *Porphyra perforata* (Ricketts et al. 1939; Apt et al. 1988). Although *Hesperophycus* and *Pelvetia* were not present at Frasier, we were able to determine the approximate tidal height for the Frasier high transplants using the barnacles and other indicator organisms as references. We were also able to reference tidal height using permanently fixed bolts which had been drilled into the rock at both Frasier and Forney at specific tidal heights from a separate intertidal study. Since the vertical distributions of intertidal organisms tend to be shifted upwards at sites exposed to high wave action (Carefoot 1977) we essentially "bracketed" our transplants by tidal height by establishing a second treatment level at the upper edge of the mid-tidal zone (we refer to these as Frasier low).

As the results indicate, tidal height influenced survival of transplants only for adult *Hesperophycus* in which the

Frasier low plants suffered significantly higher mortality than the Forney controls. Although the reduced survival of the low transplants may be related to wave action by virtue of the fact that the low plants spend a higher percentage of time in water, it is difficult to say what specific factors may have contributed to their demise. Alternatively the adult *Pelvetia* at Frasier low had a much higher survival than those at Frasier high although survival did not differ significantly from the Forney controls for either treatment. The most likely explanation for the reduced survival of the high adult *Pelvetia* at Frasier is desiccation at low tide. This would also explain the enhanced survival of the low adult *Pelvetia* transplants at Frasier. Thus *Pelvetia* may be more able to cope with the increased exposure at Frasier by thallus tattering as evidenced in the reduction in size (Figure 3). Survival of all juvenile transplants was low at Frasier, and was essentially independent of tidal height.

Other Physical/Ecological Factors Influencing Size and Survival

As mentioned earlier, some of the factors known to influence the local distributions of intertidal species include wave action, nutrient/food availability, rock type, and intensity of grazing/predation and competition. This study has primarily focused on the effects of wave exposure, since this is the most obvious physical gradient spanning Frasier point. Since Frasier and Forney are located within such close proximity the general climactic and oceanic regimes are assumed to be relatively similar. Rock type is essentially the same across the point. Although the sites are in close proximity, seawater nutrient concentrations can differ between sites. As shown in Figure 4, nutrient concentrations at Frasier are significantly higher than those at Forney in the spring of 1997. Increased nutrient concentrations are known to stimulate plant growth and the availability of nutrients is one of the primary factors regulating plant growth in aquatic systems (Jackson 1977). Increased water motion has been shown to enhance both nutrient uptake (Norton et al. 1982; Parker 1963; Wheeler and North 1980) and plant growth (Norton et al. 1981; Parker 1963) in a variety of seaweeds. Although it is difficult to imagine substantial nutrient depletion for open coast seaweeds, Hanisak (1983) and Topinka and Robbins (1976) suggest that in calm-water sites, some seaweeds may be under nutrient stress. Furthermore, the addition of nitrogen has been shown to stimulate seaweed growth in some coastal waters (Chapman and Craigie 1977; Lapointe and Tenore 1981). Given that fact that nutrient concentrations at Frasier are seasonally higher than those at Forney, and Frasier is more wave exposed than Forney (favoring nutrient uptake) we would expect higher growth (greater increases in size) at Frasier. The pattern we see is essentially the opposite, suggesting that the increased wave exposure at Frasier leads to higher thallus breakage which overrides the benefits of increased growth via enhanced nutrient concentration and uptake.

Ecological factors such as competition for space and grazing can influence the sizes and morphologies of plants that are present during different seasons. Schiel and Choat (1980), Cousens and Hutchings (1983), Reed (1990), and Martinez and Santelices (1992) present evidence that sizes of seaweeds may be affected by density-dependent intra- and inter-specific competition. Since transplants in this study were all approximately uniformly spaced, it is unlikely that sizes of transplants may have been differentially affected by competition.

Levels of grazing and physical stress may also influence the size and morphology of an algal thallus within a particular life history phase. Hay (1981) has shown that algae growing in physically stressful or moderately grazed habitats tend to grow as turfs rather than spatially separated individuals. These changes in thallus morphology may be correlated with changes in size. Seasonal variations in grazing pressure have also been shown to affect plant morphology. Several annual and ephemeral high intertidal algal species have heteromorphic life histories and exist as upright morphs during the summer and as crustose or boring morphs during other seasons. The selection and continued maintenance of these different morphologies have been shown to be a function of the spatial and temporal variations in grazing (Lubchenco and Cubit 1980; Dethier 1981). The activities of grazers can also determine the points at which a plant breaks (Santelices et al. 1980). Black (1976) showed that damage by the limpet *Acmaea insessa* pruned the blades of *Egregia laevigata (menziesii)*, making it as a whole, less susceptible to removal by waves via a reduction in size, similar to the effect of wave tattering demonstrated here.

Although snail and limpet grazers were common at both Frasier and Forney, we have no evidence that sizes of transplants may have been differentially affected by grazing. The most common grazers were the limpet *Lottia digitalis* at the wave-exposed site and the snails *Tegula funebralis* and *Littorina scutulata* at the wave-protected site. Since grazers were most abundant at the protected site, effects of grazing should have been greatest there resulting in smaller plants, which is opposite to the observed pattern. Both the limpet and snail grazers seem to have little effect on adults plant but may graze heavily on recently settled spores, epiphytes, and other algae. Lubchenco (1983) found that *Littorina littorea* in New England harm young *Fucus*, but may actually benefit older *Fucus* by grazing epiphytes. We have observed *Littorina* and limpets grazing epiphytes on all the transplants, but never grazing the adult plants. The limpets probably have a larger effect on the mortality of both *Hesperophycus* and *Pelvetia* adults by bulldozing holdfasts than on the sizes of the plants by consumption.

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