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Seasonal stresses shift optimal intertidal algal habitats

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Abstract We studied how the growth, reproduction, and survival of a common intertidal rockweed (Fucus distichus) varied across its tidal elevation at 14 sites around San Juan Island, Washington, USA in spring-summer and fall-winter seasons. We also measured a suite of environmental factors including temperature, light, emersion time, slope, fetch, and herbivory. To interpret the response of Fucus we included measurements of phlorotannins and carbon storage compounds (mannitol, laminarin). Growth and reproduction exhibited parallel patterns across tidal zones and sites. Tidal zone was a significant source of variation for many Fucus response variables, whereas variation between sites was high but not generally a significant factor explaining *Fucus* growth and physiology. Unexpectedly, the tidal zone in which Fucus achieved its highest growth and reproduction switched between seasons. High zone thalli grew and reproduced better than Mid zone thalli in fall but not in spring. This result can be explained by different combinations of factors influencing Fucus in each season. In spring, longer emersion times due to daytime low tides resulted in lower growth rates higher on the shore, likely due to carbon limitation. In fall during nighttime low tides, emersion and carbon limitation stresses were minimal. Overall, fall growth was lower than spring growth, but low fall light was

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Bodega Marine Laboratory, University of California at Davis, P.O. Box 247, Bodega Bay, CA 94923-0247, USA not responsible. Instead, warmer average fall temperatures in the High zone apparently favored growth and reproduction relative to the Mid zone. In contrast, Mid zone thalli were subjected to more intense herbivory and hydrodynamic stress associated with wave exposure and steep substrata during the fall. At least for some seaweeds, living in the presumably more stressful high zone can actually confer higher integrated performance.

Introduction

Marine benthic algae are responsible for a significant fraction of the productivity of the world's oceans (Valiela 1984), supplying organic carbon to both nearshore and offshore food webs (Mann 1982; Duggins et al. 1989). Even the narrow, environmentally variable rocky intertidal zone is highly productive (Leigh et al. 1987). Seaweed growth and hence productivity are potentially limited in the field by physiological stress caused by various abiotic factors that exceed some threshold for optimal organismal function. Herbivory can also limit macroalgal biomass, and both stress and herbivory are known to influence algal distribution, abundance, chemistry, and morphology (e.g., Chapman 1989; Van Alstyne 1990; Renaud et al. 1990; Pavia et al. 1999; Dethier et al. 2005). Intertidal habitats are thought to encompass a significant stress gradient from low to high on the shore, and this is reflected in generally faster growth of thalli living lower (Schonbeck and Norton 1980; Hawkins and Hartnoll 1985, Stengel and Dring 1997). Except for high shore fucoids, most seaweeds grow better when continually submerged (Allender 1977; Edwards 1977; Schonbeck and Norton 1980). The effect of presumed gradients in intertidal stress on seaweed reproduction is poorly known. Individuals in the high intertidal zone may

have lower fertility than lower-zone thalli (Friedmann 1969, Niemeck and Mathieson 1976, Edyvean and Ford 1984). Despite the wealth of research on the physiological ecology of intertidal seaweeds in general and fucoids in particular, few studies have tested how interactions between abiotic factors might limit photosynthesis, growth, and thus, abundance (Chapman 1995). Our understanding can benefit from a more integrated approach to examining how the entire local suite of environmental factors influences algal performance (e.g., Rico 1991; Santos 1993; Malta and Verschuure 1997; Jonsson et al. 2006).

Our research addresses how the growth, survival, and reproduction of a common intertidal rockweed, Fucus distichus Linnaeus (=F. gardneri: Order Fucales, Family Fucaceae), vary among tidal elevations, sites and seasons on San Juan Island in Washington, USA. Elsewhere we describe field and laboratory manipulations of intertidal stress and herbivory (Dethier et al. 2005) and how photosynthesis (Williams and Dethier 2005), and demography (Wright et al. 2004) vary across tidal elevation and sites. Typical predictions are that higher stress accrues to individuals living higher on the shore and that photosynthesis will therefore be limited in high-zone seaweeds. However, seaweeds acclimate and adapt to their environments exquisitely but in complex ways, which can make it difficult to ascertain how environmental factors affect their performance (Middleboe et al. 2006; Hays 2007). We found that photosynthetic rates varied neither between tidal heights, despite some limitation by desiccation in the high zone, nor seasons, despite lower light in winter (Williams and Dethier 2005). We also found that recruitment and survival were not always lower in the high zone at one site (Wright et al. 2004). Herbivory and desiccation stress influence different performance indicators in experimental arenas, but few interactive effects were seen (Dethier et al. 2005).

These findings led us to test whether growth, survival, and reproduction in nature predictably and consistently vary with tidal height or with other sources of environmental variation, including herbivory. For example, we predicted that the length of the emersion period should be a critical determinant of growth because photosynthesis in air is severely limited compared to in water (Williams and Dethier 2005). However, growth can be uncoupled from photosynthesis and the light regime via stored photosynthate (Chapman and Craigie 1978; Lehvo et al. 2001), and herbivory and nutrient stress can induce the allocation of carbon to phlorotannins (Ilvessalo and Tuomi 1989; Cronin 2001; Jormalainen et al. 2003; Hemmi et al. 2005). Thus we also measured these key chemical constituents. We performed our observations at 14 field sites; this unusually large number was used in an attempt to assess the generality of the processes we studied (Foster 1990; Beck 1997), unlike most intertidal ecological research which is done at only one or a few sites. Here, we build on our previous findings and extend our research to encompass a broad range of variation in physical variables and biotic environments where *Fucus* lives, trying to build an understanding of the links between ecology, physiology, and fitness of this organism.

Methods

The species

Fucus distichus (hereafter Fucus) is very common on protected and semiprotected shorelines from Alaska to central California; it forms dense canopies in the intertidal zone, with its broad vertical distribution encompassing a presumed stress gradient (refs. above). Quantifying responses of this alga to environmental variation is relatively straightforward because of several characteristics. First, it grows in a relatively regular, dichotomous, two-dimensional manner, allowing field estimates of growth. Second, it has a simple life history, is perennial, iteroparous, and fast-growing (\sim 3 cm/month). In the Pacific Northwest, some fertile individuals can be found year round, and reproductive effort is easily quantified (Thom 1983; Ang 1991; Wright et al. 2004). Third, although fucoids often allocate substantial amounts of carbon to phlorotannins or phloroglucinol polymers (Hay and Steinberg 1992), no nitrogen-containing secondary metabolites are known. Fourth, Fucus germlings are highly susceptible to consumption by a variety of grazers (Dayton 1971; Lubchenco 1980), but adults on this coast are generally avoided by herbivores, presumably because of deterrent phlorotannins (Van Alstyne 1988). However, Littorina spp. will consume some tissue, as will Lacuna, the isopods Idotea spp., and various amphipods (Dethier 1982; Dethier et al. 2005), so herbivores can affect individual performance.

The sites

We studied *Fucus* at 14 bedrock field sites around San Juan Island, Washington (see map at http://faculty.washington. edu/mdethier/Fucus/Pages/sitemap.html). The island is at the eastern (inner) end of the Strait of Juan de Fuca; thus all sites were protected from full oceanic conditions, although they varied highly in their exposure to swell and wind waves (Table 1). Qualitative descriptors of wave exposure were made based on the maximum fetch to each site, which ranged from ca. 5 km ("low" exposure) to almost 50 km ("fairly high"). We also quantified aspect (compass heading) and local shading, and thus exposure to desiccating conditions. We controlled as much as possible for slope $(15^{\circ}-30^{\circ})$. We sampled in the High and Mid zone (ca. +1.5

 Table 1
 Sites and their associated physical variables

Site	Abbrevations	GPS: N/W	Aspect	Wave exposure	Slope (°)	Tidal h (m abo	eight ve MLL ⁷	<i>W</i>)	Relative temperature	e extremes	Est. % tin exposed a	ie nnually
						High	Mid	AM Sun	High	Mid	High	Mid
Colin's Cove South	CCS	48°32'53.57/123°00'24.11	Е	Fairly low	15	1.6	1.1	High	Hot	Mod.	56	36
Cattle Point South	CPS	48°27'06.78/122°57'40.93	SW	Fairly high	30	1.7	1.0	.pod	Hot	Hot	71	48
Davison Head	DH	48°37′18.68/123°09′04.99	WSW	Fairly low	30	1.4	0.7	.pod	Hot	Hot	38	18
Pumphouse East	PHE	48°32'45.35/123°00'27.68	MSS	Low	25	1.3	0.6	.pod	Hot	Mod.	37	16
Pumphouse West	WHA	48°32'45.68/123°00'29.61	S	Low	20	1.5	0.7	.pod	Hot	.Mod.	42	21
Reuben Tarte North	RTN	48°36'47.40/123°05'54.76	Щ	Moderate	30	1.6	1.1	High	Hot	Hot	62	41
Reuben Tarte South	RTS	48°36'45.55/123°05'51.19	SE	Moderate	30	1.5	0.7	High	Hot	Cool	52	25
Cattle Point North	CPN	48°27'06.78/122°57'40.93	NE	Fairly high	15	1.6	0.8	.pod	Mod.	Hot	66	41
Hannah Heights	НН	48°29'28.41/123°06'46.52	ENE	Fairly high	15	1.7	0.9	.pod	Mod.	Hot	52	29
Limekiln Park	LK	48°30'59.89/123°09'09.99	NE	Fairly high	20	1.8	1.1	Low	Mod.	Mod.	75	48
San Juan Co. Park	SJC	48°32'31.38/123°09'41.30	MM	Moderate	25	1.8	1.1	Low	Mod.	Cool	78	50
Willows Point	WIL	48°32'47.69/123°00'25.54	SE	Fairly low	25	1.1	0.4	High	Mod.	Cool	27	8
Colin's Cove North	CCN	48°32'53.57/123°00'24.11	MNW	Low	22	1.6	0.9	Low	Cool	Cool	57	29
Point Caution	PC	48°33′44.09/123°01′02.88	MNW	Moderate	20	1.4	0.6	Low	Cool	Cool	43	18
Temperature-stress rs imum June temperatu	ankings are from t tres (High zone) >	the TidbiTs; note that rankings 1 \cdot 29, Moderate = 25–28, Cool =	for the High <25 degree	1 zone differ fro es. Low levels (om those for t data used on	he Mid, i y in multi	n part be ple regre	cause of diff. sssions) were	erent suscepti e sampled onl	ibility to morni y at CCS (0.7 n	ng sun. Hot = 1: cool) and F	mean ((
(Inni)												

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and +0.8 m above Mean Lower-Low Water) at all 14 sites, and the Low zone (ca. +0.6 m) at two sites (data used only in multiple regressions). At each site, the High zone thalli were near the upper limit of the *Fucus* zone.

To test for the effects of tidal height, site, and season on *Fucus* response variables, individual thalli were marked in March 1999 at all 14 sites, and remeasured monthly through July (hereafter "spring" thalli). A second set was marked in September 1999 at nine sites (to make fall sampling more feasible), and remeasured monthly through January (hereafter "fall" thalli). Thalli (15–32) were randomly chosen along a 5 m horizontal transect line at each site and tidal height. To avoid tagging artifacts, thalli were located by their direction and distance from numbered putty dots on the rock.

Environmental variables

Temperature data were gathered in the High and Mid zones at each site with "Stowaway TidbiT" dataloggers (Onset Corporation, MA). We installed TidbiTs in January-February 2000 by attaching them to pieces of PVC bolted to the rock; a piece of thick flexible plastic protected the glass optical-readout points, but the sensor was exposed to the environment. Temperature (of air or water) was logged every 20 min. Algal canopies were regularly cleared away from the loggers, and data were downloaded every 3-4 months. To assess possible light limitation in the environment, near the end of each growth period we measured irradiance with a cosine PAR sensor and logged every 10 min (Li-COR Models LI-190SA and LI-1000, Lincoln, NE 68504, USA). Extinction coefficients at high tide were derived from measurements above the Fucus canopy using a spherical sensor (Li-COR Model 193SA) submersed at the water surface and at 1 m below the surface. Photosynthesis-irradiance relationships were previously derived for summer and winter (Williams and Dethier 2005), at the end of each growth period.

Herbivore densities on the surrounding rock were quantified in March, June, September, and January. At each tidal height, we counted all mobile invertebrates in five 400 cm² quadrats randomly located along the transect line. Small limpets (<1 cm) often could not be identified to species and thus were lumped into one functional group, but other taxa were quantified by species. At the same times we estimated the total algal canopy cover in each quadrat.

Fucus response variables

Survival was quantified by noting the number of remaining thalli (of the 15–32 at each site and height) on each date, and whether each thallus was completely gone, or a hold-fast or section of stipe remained. Growth was measured

non-destructively by quantifying variables that correlate closely with biomass: maximum thallus length and number of tips longer than 1 cm from the last dichotomy. The length x tips product was converted to wet biomass using linear regressions of 50 unmanipulated thalli taken from each site in March 1999 and weighed in the lab (mean $r^2 = 0.878 \pm 0.011$ SE, n = 30 collections). Wet to dry biomass conversions used regressions calculated separately for each experimental period. To compare 'maximum' growth rates over each 4-month-period among sites and tidal heights, we calculated sizes only for thalli that suffered little herbivory, i.e. did not lose length or tips from one month to the next. These undamaged thalli showed clear exponential growth, with regressions of log estimated dry biomass versus time having high r^2 values (Spring and Fall mean $r^2 = 0.961 \pm 0.002$ SE, n = 369 thalli). A growth curve was calculated for each undamaged thallus, and these values were averaged for each site, season, and tidal height. All other analyses (reproductive allocation, phlorotannins, etc.) used all surviving thalli, not just these undamaged ones.

After the final growth measurement, we collected the thalli and quantified the amount of tissue (surface area) of each lost to herbivory. Thalli were either photocopied (Spring 1999) or photographed (Fall-Winter 1999-2000) while held flat (with non-overlapping branches) between plexiglas plates. Calculations of surface area were made from these "grazed" images and again after areas of the thalli apparently lost to herbivory were shaded using NIH Image (for Macintosh). This shading involved filling holes, lost cusp-shaped chunks of wing tissue, and missing tips to estimate total "ungrazed" surface area. In addition, a subset of the thalli (49 of 521) was liberally shaded (i.e., larger tips and questionable lost dichotomies included) and surface areas again calculated, to determine the variation around our loss estimates (see "Results"). For analyses we used the conservative shading data (minimal estimates of thallus area lost to herbivory).

Reproduction was quantified in three independent ways. The population-level variable of percent thalli bearing receptacles was counted on each sampling date. For individual investment in reproduction, after harvest we counted the number of receptacles per thallus, then separated receptacles from vegetative tissue and determined the dry mass of each.

Phlorotannin content of each thallus was analyzed in a 0.35 g sample of finely-chopped tissue, frozen overnight and then ground in 70% methanol and extracted for 24 h in the dark at room temperature. Phlorotannin concentration was determined by a Folin-Denis method using phloroglucinol as a standard. We later verified that there was no difference between standards made with phloroglucinol and phlorotannin purified from *Fucus distichus* from the study population (Dethier et al. 2005).

Brown seaweeds such as Fucus spp. store carbon taken up in excess of growth demands as mannitol and laminarin, which then can support growth during times of reduced photosynthesis (Lehvo et al. 2001). We isolated mannitol by conducting three successive extractions of 0.5–0.9 g dry tissue with 50 mL of 100% ethanol at 80°C, decanting after each extraction. One mL sub-samples of the extract were evaporated, reconstituted with de-ionized water, and analyzed for mannitol using a periodate-chromotropic acid assay (Lambert and Neish 1950). To extract laminarin, the remaining algal tissue was soaked in 0.1N NaOH overnight and homogenized in a tissue grinder, after which 2N HCL was added to precipitate alginates. The supernatant containing the laminarin was assayed as glucose following the anthrone reagent method of Yemm and Willis (1954). Samples (n = 5-11 per site) were analyzed from a subset of sites, seven in summer and five in winter.

Analyses

For each season, effects of the variables Site and Tidal Height were tested using a randomized block (=site) design, analyzing the variance attributable to each for the response variables: growth (undamaged thalli only, i.e. growth with little herbivory), phlorotannin content (mg/g dry thallus), reproductive allocation (g reproductive tissue/ g thallus, and number of receptacles per thallus), and mannitol and laminarin content. Thalli averages were used in the analyses. We report exact P values and discuss results that were close to the conventional P < 0.05 cutoff for significance (Moran 2003). We did not test spring-fall differences in this block model because seasons were not replicated in a second year. Instead, Mann-Whitney nonparametric tests were performed on mean growth rates from each site in spring versus fall for each tidal height. Tukey's test for non-additivity (Underwood 1997) was performed on all analyses to assess a site x height interaction. Residuals were plotted and transformations made if indicated. Site and height differences (and their interaction) in survival were tested in a logistic regression appropriate for binomial survival states.

We explored the influence of environmental factors at each site on *Fucus* response variables using multivariate regression methods (Glanz and Slinker 1990). For this analysis, we used data from all surviving thalli to examine how the sum of the environment affected total thallus response (including tissue loss to herbivory or waves). The factors tested were: % algal canopy; average density of *Lacuna*, *Littorina* spp., limpets, and summed herbivores; tidal height, using Effective Shore Level measures from summertime TidbiT data (Harley and Helmuth 2003); wave exposure (maximum fetch); rock slope; percent time emersed daily during spring-summer (March–August); percent time emersed annually; average daily maximum temperature (June 2000); number of days April through July when the temperature exceeded 25° , 27° , and 30° (for Spring analyses); number of days over 12° and 15° October through January (for Fall analyses); and mean and s.d. daily temperature April-May 2000. First, univariate regressions were run to determine whether each individual dependent variable satisfied the assumption of normality (Wilk-Shapiro tests: P > 0.05 or W > 0.95). In preliminary analyses, factors that did not affect growth or showed high colinearity were eliminated to constrain the number of variables. Data were log-transformed or arcsine square-root transformed as necessary. After determining the appropriate scale of measurement for each dependent variable, multivariate regression models were developed using a stepwise modelbuilding algorithm and Wilk's Lambda to guide variable selection; variables left in the model were significant at the P = 0.150 level. Separate analyses were run for fall and spring data, using Type II sums of squares. Analyses were run using the general linear model procedure in SAS 9.1 (Statistical Applications Software 2004).

Results

Physical environment

Because of the timing of low tides as well as changes in atmospheric conditions during the year, seasonal changes in the types and degree of stresses experienced by intertidal algae in Washington are profound. While the total number of hours per day of exposure to air remains fairly constant throughout the year (ca. 50% of the time at our High level, 22% at the Mid), the timing of the lower low tides swings from daytime in the spring and summer to after dark in the fall and winter (Fig. 1). Thus in both zones, virtually all of the springtime emersion is during the day (leading to potentially severe desiccation, especially in the High zone), whereas all of the fall emersion is at night (so that desiccation stresses are minimal except during rare freezing conditions). Note that the Mid level is always submerged during daylight hours throughout November, December, and January, and ambient light during these months is always low (Fig. 2, see below).

The continuous recording of temperature using TidbiT dataloggers at all sites confirmed this seasonal pattern, and allowed us to rank the 14 sites by degree of temperature extremes experienced (Table 1). Detailed temperature data can be found at http://faculty.washington.edu/mdethier/ Fucus/Pages/Data.html. Maximum temperatures at all sites were seen in July, reaching a mean daily value of 36.2° in the High zone at the hottest site (DH, south-facing, Table 1) and 23.0° for the coolest (PC, north-facing). TidbiTs in the



Fig. 1 Seasonal change in the hours of aerial exposure (emersion) during the daylight versus night at the two tidal heights used in this study. Times were calculated based on the Friday Harbor Harmonic Tidal Station (Tides and Current Program, Nobeltec). High = +1.5 m above MLLW (mean lower low water), Mid = +0.8 m. Exact tidal heights at each study site are given in Table 1

Mid zones (exposed for less long) recorded cooler temperatures; during the spring growth period, maximum daily temperatures in the Mid zone were cooler by an average of 3.3° . Daily mean temperatures averaged over all sites from March to July were $12.2^{\circ} \pm 3.1^{\circ}$ in the High zone and $11.0^{\circ} \pm 2.6^{\circ}$ Mid. In the fall, Mid zone temperatures ranged from 3.8° cooler than High in September and 2.8° in October, down to no difference in December, once emersion is entirely at night (Fig. 1). A few sites (e.g. HH, Table 1) had Mid TidbiTs that were as hot or slightly hotter than the adjacent High ones in the spring, reflecting their placement on a more-horizontal or a more-south-facing surface. Temperature minima were similar at all sites (seldom below 2°C); no significant freezes occurred during the measurement period. Daily mean temperatures over the fall period were $8.3^{\circ} \pm 0.2^{\circ}$ High and $8.6^{\circ} \pm 0.3^{\circ}$ Mid.

There is a close connection between temperature extremes and severe desiccation stress. Hydration status of thalli in situ was measured near FHL on "typical" warm summer days (methods and data in Haring et al. 2002; Williams and Dethier 2005; Dethier et al. 2005). High-zone thalli exposed to air early on a sunny day in July reached values as low as 27% of their hydrated mass just before reimmersion. Mid-zone thalli, which were emersed for less long, never became quite as dried but still dropped below 50% of their hydrated mass. In each zone, thalli from the top canopy of a thick *Fucus* bed dried more rapidly than did those protected under other thalli.

Light was sufficient in both seasons for *Fucus* photosynthesis to reach net maximum rates (Pmax) for at least 5 h per day (Fig. 2a, b). Our previous results demonstrated that, due to photoacclimation, *Fucus* photosynthetic rates in winter were equivalent to summer rates, despite shorter days and lower incoming light; winter photosynthesis saturated at a lower irradiance (100 µmol photons/m²/s versus 1,000 in summer, Williams and Dethier 2005). Light transmission through the water to the *Fucus* canopy at high tide was similar in winter (January) and summer (August), with mean extinction coefficients of 0.386 and 0.373 respectively. Thus the ambient light data presented here combined with our previous results indicate that *Fucus* was never severely light limited, even in winter when light at the top of the canopy was only 135–200 µmol photons/m²/s at noon.

Fig. 2 Summer versus winter irradiance. Incoming average (+SE) photosynthetically-active radiation (PAR) at Friday Harbor Laboratories from 13 June to 8 August 1999 (summer) and 22 January-9 February 2001 (winter). Shaded areas represent the length of the daily light period when PAR exceeded the value required to achieve maximum photosynthesis. The period is slightly truncated when thalli are under water due to reduced transmission. The mid-day dip in winter was caused by a building shadow over the sensor



Survival patterns

Survival of thalli over 4 months varied among sites and tidal heights, with losses ranging from 6–83% of spring thalli and 18–87% of fall thalli. Some thalli clearly succumbed to herbivory, especially in areas where the snail *Lacuna* migrated up into the mid intertidal during the cool fall months (see below). Others vanished abruptly, especially during late-spring tides. The only significant difference in survival was that High zone thalli suffered more mortality from May to June than Mid zone thalli (P = 0.044, Table 2); at this time, severe desiccation makes thalli brittle, and waves during a rising tide can snap them at their stipe (Haring et al. 2002).

Growth

Figure 3 illustrates mean growth rates of undamaged thalli that survived through the experimental periods for all 14 spring and 9 fall sites. Of the fall sites, one (HH) had insufficient thalli present in the High zone to study this population, while a second (RTS Mid) suffered such high mortality from Lacuna that no growth rate could be calculated. Growth varied highly among sites, heights, and seasons. Average slopes of the growth curves varied by a factor of ca. 2 but did not correspond in any obvious way with siteto-site temperature differences. The striking patterns visible are that: (1) overall, growth in the fall (September–January) was much lower than in the spring (March-July) for the Mid (Mann–Whitney test, P = 0.005, df = 1) but not High zone thalli (P = 0.248, df = 1); and (2) there was a reversal among seasons in the zone where fastest growth occurred. In the spring, growth was faster in the Mid-zone thalli than in the High zone at almost all sites. Tidal height contributed significantly to the variation in growth but there was no effect of site (Table 2). In the fall, there was again a significant effect of height but the Mid zone thalli grew much slower, with no effect of site (Table 2). For growth and all other variables tested, tidal height and site were additive (i.e., non-interacting), based on Tukey's tests (P > 0.20).

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Fig. 3 Slopes of growth curves from all undamaged thalli from all sites for the spring (March–July 1999) and fall (September 1999–January 2000). Slopes are least squares means (and one s.e.). Sites (in this and subsequent figures) are arranged with the 'hottest' to the left and the 'coolest' to the right

Storage of mannitol and laminarin

Fucus stored a substantial amount of carbon (9–17% dry mass) as mannitol and laminarin (Fig. 4). Carbon storage (mannitol, laminarin, mannitol + laminarin) did not differ across tidal heights and sites (Table 2), with the exception that mannitol was significantly higher in Mid than in High zone thalli at the end of spring. The absolute difference was <1%, which is probably not biologically significant. Storage in each season was very similar; however, the major storage compound shifted from mannitol, which is readily mobilized, in spring to laminarin in fall. The presence of carbon stores corroborates that photosynthesis was not limited by light in either season (otherwise fall carbon stores should diminish), and the difference in growth between seasons cannot be explained by differential storage.

Reproduction

Many marked thalli that survived the 4-month growth periods formed receptacles (most were small and pre-reproductive when initially marked). Mean length at first reproduction was quite consistent among sites, heights, and seasons, between 8 and 12 cm. The exception was a cohort of dwarf

Table 2Probability levels from
logistic regression (survival) and
random block (=sites) analyses
of variance for *Fucus distichus*.
Interactions between site
and tidal height were tested
explicitly in the logistic
regression and with Tukey's
test for non-additivity for the
ANOVA. Subscripts are degrees
of freedom

	Spring			Fall		
	Height	Site	Interaction	Height	Site	Interaction
Survival	0.0441	0.128 ₁₃	0.667 ₁₃	0.2271	0.3237	0.792 ₇
Growth	< 0.001 _{1,13}	0.293 _{13, 13}	>0.995 _{1, 12}	$0.007_{1,7}$	0.663 _{7,7}	>0.995 _{1,6}
% Reproductive mass	0.010 _{1,13}	0.180 _{13, 13}	0.515 _{1, 12}	$0.068_{1,7}$	0.351 _{7,7}	0.184 _{1,6}
Herbivore damage	0.055 _{1,13}	0.681 _{13, 13}	$0.978_{1, 12}$	0.023 _{1,7}	0.019 _{7,7}	0.139 _{1,6}
Phlorotannins	0.007 _{1,13}	0.02813, 13	0.506 _{1,12}	$0.051_{1,7}$	0.009 _{7,7}	$0.700_{1,6}$
Mannitol	$0.768_{1, 6}$	0.014 _{6,6}	0.736 _{1,5}	$0.682_{1,4}$	0.115 _{4,4}	0.641 _{1,3}
Laminarin	0.258 _{1,6}	0.348 _{6,6}	0.537 _{1,5}	$0.687_{1,4}$	0.356 _{4,4}	0.239 _{1,3}
Total C storage	0. 450 _{1, 6}	0. 369 _{6, 6}	0.600 _{1,5}	$0.627_{1,4}$	0.575 _{4,4}	0.364 _{1,3}



Fig. 4 Mean (N = 5-11 per site) concentrations of carbon storage compounds (mannitol, laminarin) in thalli at the end of Spring (March–July) and Fall (September–January)

(2-5 cm) thalli at the top of the Fucus zone that had receptacles in September (Wright et al. 2004). There was high variation both within and among sites in the number of receptacles per thallus. In the spring, 69% of the High-zone and 84% of the Mid-zone thalli eventually reproduced, many beginning in May (but some each month); by July, the mean (SD) receptacles per thallus were 6.2 (5.4) in the High zone and 16.2 (10.1) in the Mid zone. In the fall, there were clearly fewer receptacles; some thalli initiated reproduction in each month, but by January only 40% of the High thalli and 32% of the Mid thalli had receptacles, with only 1.4 (0.9) per High thallus and 1.4 (1.1) per Mid thallus. This difference among seasons depended in part on the size of the thalli, since the fall thalli grew so much more slowly and thus fewer reached maturity. The proportion of the thallus mass that was reproductive followed similar patterns. At the end of the spring, this proportion was significantly greater in the Mid zone (mean among sites = 0.32 \pm 0.17) than the High (0.19 \pm 0.12), but did not differ among sites (Table 2). In the fall, there was far less reproductive biomass; High zone thalli had a greater proportion (0.06 ± 0.03) than Mid (0.02 ± 0.02) but site had no effect (Table 2).

Herbivore abundances

The most abundant herbivores found at all the sites included the periwinkles *Littorina scutulata* Gould and *L. sitkana* Philippi, mostly in the High zone, a guild of limpets (*Lottia digitalis* [Rathke], *L. strigatella* [Carpenter], *L. pelta* [Rathke], and *Tectura scutum* [Rathke]) especially in the High zone, and the small gastropod *Lacuna vincta* (Montagu), mostly in the Mid zone and below. All grazers were patchy on all spatial and temporal scales (among quadrats, levels, sites, and seasons: Fig. 5), so that distinguishing patterns is difficult. Isopods (*Idotea wosnesenskii* [Brandt]) and amphipods (*Ampithoe* spp.) were uncommon and are not graphed. The clearest pattern was that at a few sites (e.g., PHE, RTS) the small but voracious snail *Lacuna* moved up into the mid intertidal zone in the fall as the low tides started to fall at night; at these sites, they consumed virtually all of the *Fucus* before migrating lower again in the spring. There was also a tendency for *Littorina* and limpets to be less abundant at the more wave-exposed sites (e.g. CPS, SJC, LK: Table 1; Fig. 5).

Losses to herbivores

Laboratory and field observations revealed a variety of types of damage from herbivores. All of the gastropods (*Littorina* spp., limpets, and *Lacuna*) rasped the flat portions of the thalli, either just removing surface tissue or wearing holes all the way through. Limpets, especially small (<1 cm) individuals, often crawled up the thalli to rasp the upper portions, and appeared responsible for a surprising proportion of the damage. *Lacuna*, however, inflicted the most damage, consuming entire thalli to leave only stubs or midribs. In contrast, isopods and amphipods tended to consume the edges of thalli, removing cusps of tissue; while these crustaceans are capable (e.g., in the lab) of consuming thalli readily, their low numbers in the field meant that they had little overall impact.

Figure 6 illustrates the extent of herbivore damage at the field sites, expressed as (conservative) percent of the surface area lost from the estimated size of each thallus if it had remained undamaged (see "Methods"). Our more 'liberal' estimates of area lost were roughly 6% higher for the spring losses and almost 20% higher for the fall, reflecting the generally smaller losses in spring. Overall, most thalli lost less than 20% of their surface area, with the clear exception of sites with high Lacuna abundance (fall RTS, PHE; Fig. 5). In spring, estimated damage from herbivores was greater in the High zone (Table 2) but did not vary with site. This pattern may reflect the greater densities of both littorinids and limpets in the High zones. In fall, estimated damage was greater in the Mid zone (Table 2), clearly reflecting the greater numbers of Lacuna there. Damage also varied significantly among sites in the fall (Fig. 6), closely correlated ($r^2 = 0.86$) with among-site variation in *Lacuna* density (Fig. 5).

Phlorotannins

As with the other variables measured, levels of phlorotannins varied considerably among sites, seasons, and tidal levels (Fig. 7). The apparent large difference between overall spring and fall phlorotannin levels may be an artifact of our experimental protocol, although every attempt was made to be consistent; standard curves generated at these two times had very different slopes. Thus no conclusions are drawn about potential seasonal differences. For the spring, a twoway ANOVA showed strong effects on phlorotannins of both tidal height and site (Table 2). At most sites, Mid zone thalli had phlorotannin concentrations that were roughly equal to or higher than those of High thalli. In the fall, both **Fig. 5** Numbers of herbivores in 400 cm² quadrats at each site, height, and season. Bars are means and one SD of five quadrats during each of two censuses per season





Fig. 6 Estimates of amount of surface area lost relative to estimated total area if thalli had not been damaged by grazers (see "Methods") at the end of the experimental period. Mean and 1 SD/site, height, and season. No thalli were marked at HH High in Fall

factors again were important sources of variation, although tidal height was less so (Table 2), with Mid thalli again usually having the higher concentrations.

Environmental factors contributing to variation in *Fucus* responses

We performed step-wise multiple regressions to explore which environmental factors were associated with the variation observed in the growth (including damaged thalli), reproduction, survival, and phlorotannin content of Fucus (Table 3). The factors identified as potentially important for Fucus fitness-related attributes changed with season. In spring, the percent of time emersed during daylight was the only environmental factor significant for growth; it had a negative regression slope and explained >60% of the variation in growth. This factor was likewise significant and negative for the percent reproductive tissue, and the related factor of annual percent emersion had a negative effect on survival. The number of days when the temperature exceeded 30°C had a positive effect on the percent of thalli that were reproductive at the end of the season. Other significant factors were numbers of littorines (negative for percent reproductive) and limpets (positive for survival). No factor emerged as significant for phlorotannin concentration in spring. In fall, herbivores were the only significant factor influencing growth, phlorotannin content, and the percent reproductive thalli. Herbivores (primarily *Lacuna*) explained >60% of the variance in growth due to severe tissue loss leading to low or negative growth rates at some sites. Herbivores did not significantly affect fall survival, surprisingly, but factors associated with the hydrodynamic regime (wave exposure, slope of the substratum) and the



Fig. 7 Phlorotannin concentrations (mean and 1 SD mg/g dry tissue) in thalli from all sites and heights

number of days with temperature > 15° C (which could promote desiccation-induced loss of thalli, Haring et al. 2002) were negative predictors in the model.

Discussion

Our results are at odds with the paradigm that seaweeds living higher in the intertidal zone should have reduced

performance due to increased stress. Tidal height was a significant source of variation for many *Fucus* response variables, but *Fucus* grew better and had higher reproduction in different zones in different seasons; in fall, growth and reproduction were higher in the High zone than the Mid zone. This result was remarkably consistent across sites, particularly for growth, and also similar to the results from our demographic study conducted at a different site on San Juan Island (Wright et al. 2004). The mixed semi-diurnal tidal regime in the Pacific Northwest that results in no daytime low tides in the fall and winter (Fig. 1) appears to be the ultimate driver for this pattern.

In spring and summer, our analyses suggest that emersion time is of primary importance in determining the favorable zone for *Fucus* growth and reproduction, as indicated in our previous research (Dethier et al. 2005). Reduced performance at higher elevations can be explained by the strongly negative effect that emersion has on net daily carbon gain (Williams and Dethier 2005). High thalli are exposed to the air more than twice as long per day as Mid thalli, and mid-zone thalli therefore gain ~ 25 times more carbon each day.

In contrast, in the fall, the High zone becomes relatively more favorable for *Fucus* in this region. Several factors could lead to this seasonal switch. Thalli are submerged during daylight hours so emersion stress is no longer a factor. Herbivore damage (mostly from *Lacuna*) increases in the fall, especially in the Mid zone; the High zone provides a refuge. Thus in this season the density of specific herbivores becomes a better predictor of growth (Fig. 6; Table 3); however, even the growth of Mid-zone thalli undamaged by herbivores decreases in the fall (Fig. 3). Average fall temperatures are warmer in the High zone than

Model r² Partial r² Р Variable Predictor Spring Growth Spring daytime emersion (-)0.6257 0.6257 < 0.0001 % of mass reproductive Spring daytime emersion (-)0.4274 0.4274 < 0.0001 % of thalli reproductive Littorines (-)0.1842 0.0179 0.1842 Spring days $T > 30^{\circ}C(-)$ 0.1212 0.3054 0.0390 0.2366 0.2366 0.0064 Survival Annual % emersion (-) Limpets (+) 0.1602 0.3968 0.0125 Fall 0.6053 0.0001 Growth Lacuna (-)0.6053 Littorines (+) 0.0864 0.6918 0.0581 Phlorotannins Limpets (-)0.2908 0.2908 0.0209 % of mass reproductive Fall days $T > 12^{\circ}C(+)$ 0.4083 0.4083 0.0043 % of thalli reproductive Lacuna (-)0.3464 0.3464 0.0102 Survival Fall days T > $15^{\circ}C(-)$ 0.3169 0.3169 0.0150 Wave exposure (-)0.1768 0.4937 0.0370 Slope (-)0.1581 0.6519 0.0244

Table 3 Results of the multiple regression analysis for predictors with P < 0.05, with sign of coefficient for each predictor. The complete list of independent factors tested is given in the text

the Mid zone at most sites and are not accompanied by desiccation at this season. The positive effect of temperature on the growth of other fucoids is well-known (Strömgren 1977a, b, Strömgren 1983, Fortes and Lüning 1980, Keser et al. 2005), and we found that *Fucus* photosynthesis increases with water temperatures up to 30°C over short time periods (unpublished data). Warm days also have a positive effect on reproduction (Table 3), and because reproduction is size-dependent, it will necessarily parallel the relatively faster growth in the High zone. Finally, slightly (0.75 m) shallower High zone thalli might experience less light limitation when submerged compared to the Mid zone. Our underwater light data are not comprehensive enough to verify this, but at the low ambient light levels, it is a reasonable hypothesis.

Thus for the High zone Fucus, the positive effects on growth of lack of emersion stress in the fall and winter are probably counterbalanced by overall cooler temperatures (average of 3.9° cooler in the fall), leading to no change in growth among seasons. In the Mid zone, however, our seasonal comparisons show a large drop in growth and reproduction in fall. This is not surprising, as previous studies of seasonal fucoid growth showed generally higher rates in the spring-summer than fall-winter, although they measured only elongation (not biomass) and did not differentiate tidal heights (Mathieson et al. 1976; Niemeck and Mathieson 1976; Ang 1991). It is surprising, however, that reduced light in winter is not responsible for this result (e.g., Stengel and Dring 1997, Lehvo et al. 2001), assuming that Fucus distichus does not have an annual 'clock' (Lüning 1993). Knowledge of the photosynthetic physiology is critical in differentiating between light and temperature as causes for seasonal growth patterns, given the dependence of temperature on solar irradiance. We provided evidence that photoacclimation to low light allows Fucus to maintain the same net photosynthetic rate for equivalent daily periods in both seasons (see also Williams and Dethier 2005), and the seaweed is able to store as much photosynthate in the form of mannitol and laminarin in fall as in spring; this would not be expected under fall light limitation. We suggest instead that lower overall temperatures and perhaps increased damage from herbivory caused the reduction in fall-winter growth and reproduction, especially in the Mid zone. Although we did not monitor nutrients, the Strait of Juan de Fuca is nutrient rich and the lowest dissolved nitrogen concentrations occur during the spring-summer phytoplankton bloom (Horner et al. 1997). For example, dissolved nitrate in water samples taken quarterly around San Juan Island, including off our Lime Kiln site, averaged 18.4 µmol/ 1 ± 8.0 SD (C. Haug, Shannon Point Marine Laboratory, personal communication). Thus, nutrient limitation seems an unlikely explanation for the fall drop in growth and reproduction.

Herbivory is one of the most significant factors affecting seaweed abundance, diversity, deterrent chemistry, and (in some cases) fitness (reviewed in Introduction). Locally, grazers have significant effects on survival of germling stages of Fucus (e.g., Dayton 1971), although our studies showed highly variable impact on macroscopic stages. Across all sites and tidal heights, herbivores could explain from 9 to 61% of the variation in life-history variables: in reproduction, growth and phlorotannins in fall, and survival in the spring (Table 3). In other experiments (Dethier et al. 2005), we manipulated herbivores and found they had only limited effects on Fucus life-history variables. Most thalli suffered some tissue loss during their lives (often of "wing" tissue but sometimes of whole tips or dichotomies), but this was seldom lethal. The clear exception was seen in the sites where Lacuna migrated up into the mid intertidal zone during the fall and winter and decimated local Fucus populations. Lacuna was not predictably abundant, however, either among years or among sites, making generalizations about the role of this grazer difficult.

Our study was unusual in the number and diversity of field sites used, and thus the relatively wide variation in environmental variables examined. Although growth and reproduction varied substantially among the 14 sites, this variation was not significant, and the responses of Fucus did not fall neatly along our qualitative ranking of physical stress (Table 1). Only phlorotannin concentration varied significantly across sites in both seasons (Table 2). Grazing intensity also differed across sites but only in fall, due to Lacuna patchiness. During fall, shore slope and wave exposure of the sites emerged as negative predictors of survival, which is reasonable as sea conditions worsen (e.g. Wolcott 2007); Fucus attaches relatively poorly via a small discoid holdfast. The environments across sites might be too similar to yield important differences, although there was a $\sim 10^{\circ}$ C difference in the average daily maximum temperature across sites, which seems large enough to potentially result in measurable effects. More subtle aspects of the environment (e.g. morning sunlight, microhabitats) might be important in causing variation in growth, reproduction, and survival (Helmuth and Hofmann 2001; Harley and Helmuth 2003). There is also the potential for different factors to compensate for each other (Table 2). While our sites seemed diverse, Fucus distichus is found across a wide biogeographic range; clearer effects of the abiotic environment might be visible at larger spatial scales, as found by Fowler-Walker and Connell (2002) for kelp communities, and Scrosati and Heaven (2007) for intertidal diversity patterns.

How intertidal seaweeds respond to their stressful environment has been a major question in marine biology. Davison and Pearson (1996) define limitation stress as a reduction in growth due to inadequate supply of resources (e.g., low light, nutrients, or carbon dioxide), versus disruptive stress where growth is reduced due to damage from adverse conditions such as desiccation and/or temperature extremes. Seaweeds living high on the shore could suffer either or both types of stress. Previously, we demonstrated that limitation stress on Fucus distichus can be very high due to the great reduction in photosynthesis that occurs in air (Williams and Dethier 2005, Dethier et al. 2005). Here we have shown that the important role of limitation stress is also visible in the more integrative variables of thallus growth, reproduction, and survival, but only in summer. In summer, the proportion of the day that Fucus was emersed is the major factor explaining over half of the variation in growth rates and is also a significant factor for reproduction and survival. In contrast, temperature extremes at our 14 different sites, as quantified by dataloggers, have few direct effects on Fucus growth, i.e., high temperatures by themselves do not seem to constitute a stress and in fact had positive effects on reproduction and presumably on winter growth and survival. While the paradigm that intertidal stress increases with tidal elevation is very useful as a null hypothesis, it is becoming clear that at least for some seaweeds in some places, living in the presumably more stressful high zone can confer the highest integrated performance, depending on the specific combinations of factors operating in different seasons.

These conclusions have important implications for considering the effects of climate change on rocky intertidal seaweeds (Harley et al. 2006). First, the simple prediction that intertidal communities will shift shoreward will need closer examination (Harley 2003; Helmuth et al. 2005). For Fucus on San Juan Island, increasing temperatures are likely to increase rates of reproduction and primary production during the winter. Rising sea levels might decrease emersion stress in summer. Herbivory, which is currently important under only certain conditions, could emerge to play a stronger role in controlling Fucus, depending on how herbivores respond to changing conditions. We echo Helmuth et al. (2005) in advocating a comprehensive approach to understanding how intertidal organisms will respond to environmental variation that combines integrated measures of performance with physiologically-based mechanisms. This approach is particularly relevant for seaweeds because of their capacity to weather growth-limiting conditions through physiological acclimation and the storage of reserve nutrients and carbon.

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