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Variable effects of a kelp foundation species on rocky intertidal diversity and species interactions in central California

Brent B. Hughes*

Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, California 95039, USA

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ABSTRACT

The effect of foundation species on community assemblages in physically stressful environments has received much recent attention because of the importance of foundation species in ameliorating environmental stress. Many studies have described variable effects of foundation species on community diversity at small scales, but net positive effects over large scales. *Egregia menziesii* (Turner) J.E. Areschoug is a large and robust perennial kelp that creates a structurally complex habitat on rocky shores of the Northeast Pacific. This study investigated the effects of *Egregia* sporophytes on benthic assemblages of the rocky intertidal along the central California coast. *Egregia* sporophytes strongly impacted the structure of associated communities, due to wave-driven whiplash of fronds, shading, or habitat provision. A survey of *Egregia* populations at 10 stations along 200 km of the central California coast found effects of *Egregia* density on the intertidal to be consistent among sites. Increased *Egregia* sporophyte density negatively affected algal species richness, total algal cover, and cover of the most conspicuous species of algae. However, there was a positive relationship with algal crusts, geniculate coralline algae, and sessile invertebrates. *Egregia* removal experiments at two sites within the study area experimentally tested for the effects of *Egregia* on intertidal communities. Results from Soberanes Pt. were consistent with survey results because of the negative effect of *Egregia* on algal species diversity, subcanopy layering, and cover of abundant algal species. However, removal experiments at Pigeon Pt. resulted in a positive *Egregia* effect on algal diversity and cover of abundant algal species possibly due to lower *Egregia* densities, lower wave exposure than Soberanes Pt., and stress amelioration. In the lower energy environment, *Egregia* acted as a sand trap, yet sand accumulation did not negatively impact algal diversity. Negative effects of large brown algae on benthic assemblages have been observed in temperate waters around the world for certain intertidal or subtidal kelp in wave-swept environments allowing for scouring and substrate shading. This study shows that *Egregia* and morphologically similar brown algal species can have both negative and positive effects on community diversity depending on variation in density and local environmental conditions. *Egregia* has the opposite effect on community diversity than what has been previously reported for foundation species because it negatively affects biodiversity in stressful environments, but has a positive effect in less stressful environments.

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1. Introduction

Foundation species are commonly considered to facilitate communities through a variety of processes that enhance the survivorship, abundance and diversity of local species (Dayton, 1972; Bruno et al., 2003). Foundation species are generally dominant and abundant organisms that provide a three dimensional structure to a system, thus creating habitat (Crain and Bertness, 2006), and can enhance primary productivity, ameliorate stress, and homogenize environmental variability. For example, pine trees of the North American Pacific Northwest provide habitat that benefits an entire ecosystem,

which consequently leads to greater biodiversity (Reiners et al., 1971). Likewise, in the subtidal ocean, giant kelp forests provide energy and structurally complex habitats to the benefit of many associated species, resulting in an increase in local kelp forest species diversity (Graham, 2004).

The positive effects of foundation species on the biodiversity have been described, e.g., oak and hickory forests, tropical rain forests, coral reefs, and mangroves, to name a few (Oosting, 1942; Connell, 1978; Ellison and Farnsworth, 2001; Ellison et al., 2005). Although foundation species tend to have net positive effects over large geographic scales, the effects can be positive or negative at small scales (Jones et al., 1997). For example, at the scale of a patch, the intertidal mussel *Mytilus californianus* Conrad can have negative consequences on biodiversity by competitive exclusion for space (Paine, 1966), yet across its species range, it has a net positive effect because competition is variable across large scales and the mussels

* Present address: Department of Ecology and Evolutionary Biology, Long Marine Lab, 100 Shaffer Road, University of California, Santa Cruz, California 95064, USA.
E-mail address: bbhughes@ucsc.edu.

provide habitat for small mobile organisms and substrate for opportunistic sessile organisms (Suchanek, 1992).

The direction of foundation species effects may depend on local environmental conditions, which can range from benign to harsh within a species' range (Jones et al., 1997; Bruno et al., 2003; Crain and Bertness, 2005). Foundation species generally benefit associated communities in harsh environments and have negative competitive interactions in more benign environments (Menge and Sutherland, 1987; Jones et al., 1997; Bertness et al., 1999; Bruno et al., 2003; Crain and Bertness, 2005). For example, the furoid alga *Ascophyllum nodosum* (Linnaeus) Le Jolis was found to have a net positive effect on intertidal assemblages in the high intertidal zone of the Gulf of Maine where physical stress was harsh, yet had a neutral or negative effect in the lower intertidal where physical stress was more benign (Bertness et al., 1999).

Few studies describe negative effects of foundation species on communities over large spatial scales. The morphologically similar large brown algae *Ecklonia radiata* (C. Agardh) J. Agardh, *Lessonia nigrescens* Bory de Saint-Vincent, and *Durvillaea antarctica* (Chamisso) Hariot all negatively affect local benthic species because their lack of floatation combined with high wave stress causes a sweeping motion that can remove benthic organisms (Kennelly, 1989; Santelices, 1990; Taylor and Schiel, 2005). These species have been noted to competitively remove other sessile competitors, alter recruitment of other species, and reduce herbivory. This also promotes recruitment for subsequent generations by creating space for spores to settle.

The conspicuous and perennial intertidal kelp *Egregia menziesii* (Turner) J.E. Areschoug (hereafter *Egregia*), of the northeast Pacific, has a morphology similar to *E. radiata*, *L. nigrescens*, and *D. antarctica*. The large and robust nature of *Egregia* may result in strong impacts on the structure of its associated communities, due to whiplash, shading, or habitat provision (Black, 1974; Friedland and Denny, 1995). In order to understand whether *Egregia* serves as a foundation species in the rocky intertidal and to better understand the impact it has on intertidal community dynamics, clearing experiments and geographic surveys were used to gauge the effects of *Egregia* on intertidal benthic assemblages. Results were then compared to other studies of morphologically similar large brown algae that negatively impact associated communities, as well as other foundation species that have varying community effects.

2. Materials and methods

2.1. Experimental

Two intertidal clearing experiments were used to test for variability in the effects of *Egregia* on the structure of intertidal benthic assemblages. The experimental study sites were located at Soberanes Point (E1 in Fig. 1) on the northern-most stretch of the Big Sur coastline in central California, U.S.A., and at Pigeon Point, San Mateo County, CA (E2 in Fig. 1). Field surveys of *Egregia* populations were used to compare population dynamics at the two study sites (see *Geographic sampling* methods). Both Soberanes Pt. and Pigeon Pt. had high, but unequal densities of *Egregia* (~7 and 2/m² respectively), and differed geologically and ecologically. *Egregia* populations at Pigeon Pt. differed from populations at Soberanes Pt. in sporophyte density, frond density, #fronds/plant, but not frond length (Table 1). Sporophyte and frond densities at Pigeon Pt. were less than Soberanes Pt., yet the #fronds/plant and maximum length were greater at Pigeon Pt. than Soberanes Pt., indicating that Pigeon Pt. had the more robust yet less abundant *Egregia*.

The substrate at Soberanes Pt. was quartz diorite and consisted of flat and sloping terraces that contained tide pools in the high intertidal, with intersecting tidal channels that created sloping walls in the mid to low intertidal. Soberanes Pt. had a high local kelp diversity (~14 species) with conspicuous and perennial *Egregia*

populations on flat to vertical surfaces in the mid to low intertidal. Pigeon Pt. was characterized by a sandstone conglomerate composed of rocky fragmented benches with sandy tidal channels that cut through the rock. Wave exposure was less at Pigeon Pt. than Soberanes Pt. due to the aspect of the long and flat rocky benches. The densest *Egregia* cover at both sites occurred in the late summer months (Brent Hughes, pers. obs.). Experiments ran from July 2004 to November 2005 and from April 2005 to March 2006 at Soberanes Pt. and Pigeon Pt., respectively. Experiments did not completely overlap through time because of the time demand needed to sample each site during low tide series.

Ten experimental plots (1-m×1-m in size) were established in randomly selected patches of high *Egregia* abundance (~2–7 sporophytes/m²) over the entire *Egregia* tidal range (~1 m above and below MLLW) to examine the effect of *Egregia* presence on intertidal benthic assemblages. Using a blocked design, two plots (separated far enough as to avoid creeping by *Egregia* fronds) were assigned to each of five blocks that were separated by >10 m. One plot per block was randomly selected as the removal treatment and all *Egregia* in the plot were removed, and any surrounding *Egregia* fronds that could potentially come into contact with the removal plots were cut 60 cm away from the plot. This prevented fronds from growing into the plots between the monthly sampling dates (average frond growth was ~1 cm/day). Holdfasts were not removed to avoid experimental artifacts that could arise from substrate manipulation (Kennelly, 1987). The remaining plot per block was assigned to be the *Egregia* non-removal control. Prior to setting up the *Egregia* removals, all plots were sampled using the random point contact (rpc) technique to determine the composition and % cover of benthic species by noting every layer under each point (Foster, 1975). Independent samples t-tests revealed there were no significant differences (all p-values>0.10) in cover of the main algal species, total macrophyte cover (excluding *Egregia*), sand cover, mean number of algal species or number of layers between control and removal plots at the start of each experiment, indicating there were no pre-experimental biases in treatment assignment.

Removal plots were maintained monthly for one year by counting and removing *Egregia* recruits and cutting creeping *Egregia* fronds to 60 cm away from plots. Removal and control plots were sampled again at various intervals [(2, 13, 31, 54 weeks at Soberanes Pt.) and (4, 12, 28, and 54 weeks at Pigeon Pt.)] after initial clearing to describe the succession of the benthic assemblage. Top layers were easily pulled back to reveal underlying layers. Algae were identified to species level, and all sessile invertebrates were identified to the lowest possible taxonomic level. In addition to cover, *Egregia* recruits (defined as any juvenile ≤10 cm) were counted in all removal and control plots. Recruits were removed from removal plots after counting, but not removed from control plots. The total number of recruits was minimal (3 at Pigeon Pt. and 46 at Soberanes Pt.) and their removal likely did not cause additional disturbance to plots. Sampling events were temporally spaced out enough so that recruits were not recounted on sequential sampling dates in control plots. Sessile invertebrates present in plots were also counted.

To statistically test for *Egregia* effects on the community non-*Egregia* macrophyte cover, algal species richness, and sand during the 12-month experimental period were analyzed using a repeated-measures ANOVA (SPSS Statistical Software v. 17). Treatment and date were fixed factors, “date*treatment” was also included in the model. Block was not included in the model because it was determined not to be a significant factor. The initial experimental date was not included in the model (day = 0) because only the effects of *Egregia* after removal were important to this study, and there was no bias of the data towards the removal date. All alpha levels for these analyses were set at 0.10 for this experiment to detect any differences between control and removal plots, by reducing Type II errors that fail to reject the null hypothesis (Underwood, 1997). The Greenhouse–

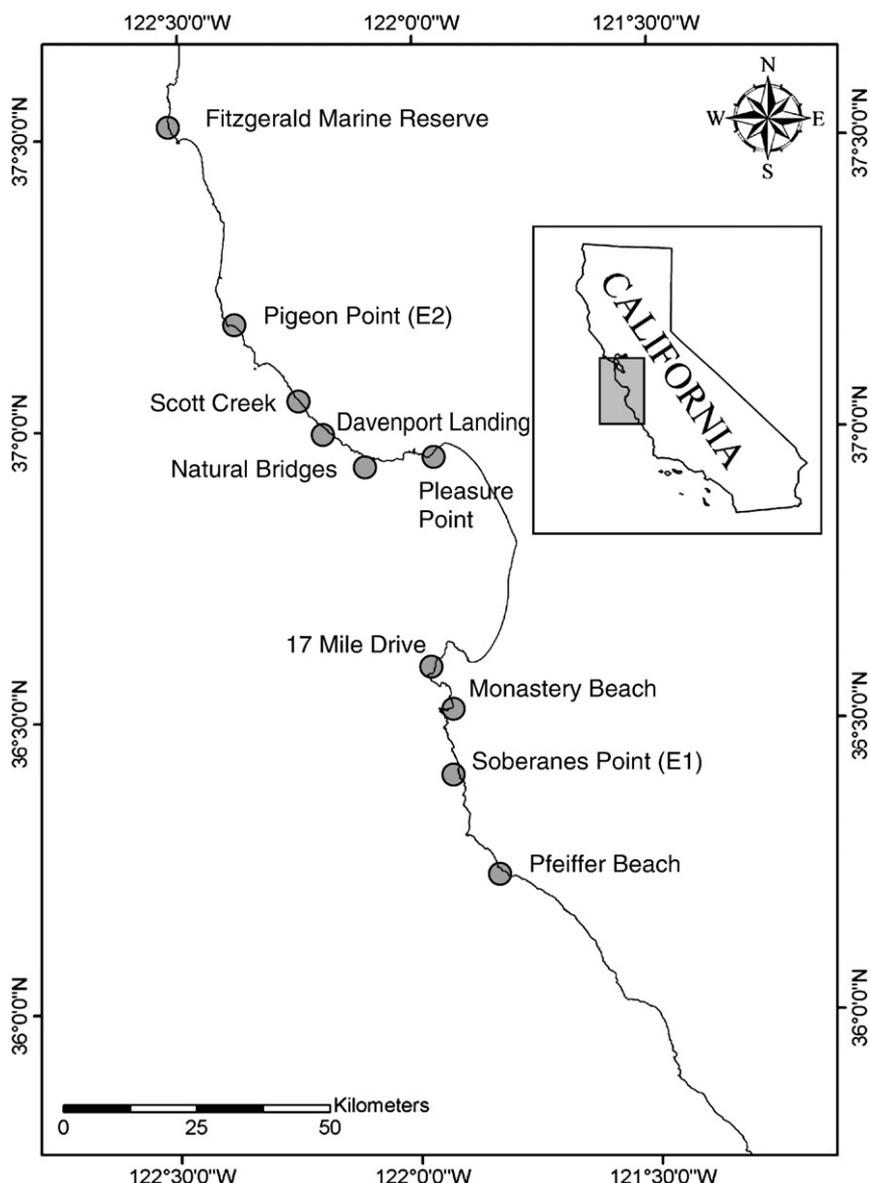


Fig. 1. Location of study sites (n = 10). (E) denotes experimental sites. Note: experimental sites were also sampled for *Geographic sampling*.

Geiser correction was used because it was the most conservative transformation (greatest reduction in degrees of freedom) to meet sphericity assumptions, and it consistently yielded the most

Table 1
Comparison of *Egrecia* populations at the two experimental sites: Soberanes Pt. and Pigeon Pt. The two populations were sampled during the winter of 2004–2005. Length was measured during June and July 2005. Plots were randomly selected.

Site		Fronds(>50 cm)/plant	Length (cm)	Sporophytes/m ²	Fronds/m ²
Soberanes Point	n	51	22	8	8
	Mean	11.1	189.8	6.5	76.1
	SD	9.11	105.27	3.42	58.84
	Min	1	75	0	0
	Max	34	420	10	183
Pigeon Point	n	57	32	31	31
	Mean	14.8	185.1	2.1	30.3
	SD	8.92	113.38	0.95	20.22
	Min	0	50	1	2
	Max	49	452	3	61

conservative results in this study. The total number of algal species was averaged from rpc data to obtain a mean for control and removal plots.

To statistically test for *Egrecia* effects on the overall benthic assemblage 12 months after *Egrecia* removal, differences in benthic community composition between control and removal plots were compared by reducing the dimensionality of the data set and investigating the species that explain most of the variance using Principal Component Analysis (PCA) (SPSS Statistical Software v. 17). Date (4 levels) (The initial experimental date was not included in the model [day = 0]) and treatments (2 levels) were combined into the within-cells correlation matrix of species cover (only species that were represented in >10% of the total rpcs were used), principal components with species that had eigenvalues less than 1.0 were discarded because they did not explain more than the original variables (Clarke and Warwick, 2001), and principal components were extracted using an unrotated factor solution. Species that had an absolute correlation (eigenvector) value less than 0.20 were also discarded. Multivariate data were non-transformed. The two significant principal components that explained the most variation and had an eigenvalue > 1 were used for analysis. These principal components

were compared between removal and control plots for the seven experimental dates using a Repeated-Measures ANOVA with date (4 levels) and treatment (2 levels) as the fixed factors, and the principal components (levels) as the dependent variable. Significant “treatment*date” interactions for individual species or groups were analyzed using an LSD multiple comparison test to examine differences in treatments among different dates.

Wave height data were also calculated to give further insight into other processes that might be affecting the intertidal assemblages. Mean daily wave height was calculated by averaging hourly data collected from the nearest monitoring buoy during the experimental period. Wave height for Soberanes Pt. came from NOAA buoy Station 46042, 27NM West of Monterey Bay, CA (http://www.ndbc.noaa.gov/station_history.php?station=46042), and data for Pigeon Pt. came from NOAA buoy Station 46012, 27NM South Southwest of San Francisco, CA (http://www.ndbc.noaa.gov/station_history.php?station=46012). Mean wave height for the two sites were compared statistically using an independent samples t-test using SPSS (Statistical Software v. 17).

2.2. Geographic sampling

To assess the generality in *Egrecia* effects on intertidal benthic assemblages, ten sites were sampled with variable wave exposure and differing geology along a ~200 km span of the central coast of California (Fig. 1). Sites were selected due to their accessibility, and the presence of conspicuous intertidal *Egrecia* populations. Popula-

tions of *Egrecia* were sampled by running a transect line through the *Egrecia* zone and randomly assigning points along the line to serve as starting points for 1 m² plots. Benthic assemblage structure was estimated using rpc and the total number of *Egrecia* sporophytes, and fronds ≥ 0.5 m were counted in the 1 m² quadrats. Various study sites were sampled between December 2004 and March 2006 during periods of low spring tides. The number of plots sampled for each site varied due to differences in the area of cover of *Egrecia* populations, although the entire *Egrecia* zone was sampled at each site on one sampling date.

To statistically test for geographic variability in the *Egrecia* effect on intertidal benthic assemblages; variability in algal species richness, intertidal macrophyte cover, and individual species and functional groups among sites were compared to #sporophytes/m² (density) and frond density (fronds/m²) using Analysis of Covariance (ANCOVA) (SPSS Statistical Software v. 17). First, regression analysis determined that sporophyte density and frond density were collinear variables. Preliminary ANCOVA testing for effects of *Egrecia* sporophyte and frond density individually on intertidal benthic assemblages determined that sporophyte density had a greater effect than frond density. Therefore, sporophyte density and the residuals from frond density were used as covariates in the final ANCOVA model, obviating any assumptions of multicollinearity. This allowed the use of two collinear variables where sporophyte density explained the majority of the variability and frond density explained some of the remaining variability not explained by sporophyte density

Table 2

Results of repeated-measures Analysis of Variance (Date and Treatment were fixed factors) at (i) Soberanes Point (SP) and (ii) Pigeon Point (PP) testing for the effects of *Egrecia* presence/absence over a 12-month period on: (a) mean algal richness, (b) total macrophyte cover, and (c) sand cover.

Effects	Source	SS	df	Mean Square	F	P
<i>(a)(i) Mean algal species richness SP</i>						
Within subjects	Date	69.08	2.54	21.21	6.63	0.004
	Date* treatment	20.28	2.54	7.99	1.95	0.161
	Error	83.40	20.31	4.11		
Between subjects	Intercept	2640.63	1	2640.63	536.17	<0.0005
	Treatment	46.23	1	46.23	9.39	0.015
	Error	39.40	8	4.93		
<i>(a)(ii) Mean algal species richness PP</i>						
Within subjects	Date	12.20	2.24	5.44	0.98	0.404
	Date* treatment	15.00	2.24	6.69	1.20	0.328
	Error	99.80	17.95	5.56		
Between subjects	Intercept	6969.60	1	6969.60	1415.15	<0.0005
	Treatment	40.00	1	40.00	8.12	0.021
	Error	39.40	8	4.93		
<i>(b)(i) Total macrophyte cover SP</i>						
Within subjects	Date	12414.20	1.48	8402.50	6.00	0.022
	Date* treatment	3522.200	1.48	2383.99	1.70	0.223
	Error	16545.60	11.82	1399.85		
Between subjects	Intercept	779526.4	1	779526.40	385.16	<0.0005
	Treatment	2496.4	1	2496.40	1.23	0.299
	Error	16191.2	8	2023.90		
<i>(b)(ii) Total macrophyte cover PP</i>						
Within subjects	Date	3104.48	1.78	1748.88	6.59	0.011
	Date* Treatment	873.88	1.78	492.29	1.86	0.194
	Error	3769.40	14.20	265.43		
Between subjects	Intercept	600985.23	1	600985.23	559.85	<0.0005
	Treatment	286.23	1	286.23	0.27	0.620
	Error	8587.80	8	1073.48		
<i>(c)(ii) Sand cover PP</i>						
Within subjects	Date	572.28	1.48	387.01	2.04	0.178
	Date* treatment	686.71	1.48	464.39	2.45	0.138
	Error	2246.93	11.83	189.94		
Between subjects	Intercept	14121.59	1	14121.59	76.98	<0.0005
	Treatment	2539.34	1	2539.34	13.84	0.006
	Error	1467.65	8	183.46		

(Underwood, 1997; Graham, 2003). Percent cover of *Egrecia* was determined not to be a good predictor variable because the mobility of fronds did not provide an accurate measure of *Egrecia* presence, and therefore was not used in the analysis.

Species that had a significant covariate*site interaction, and whose representative sites had both negative and positive slopes, were also analyzed using quantile regression to investigate general patterns in the effect of *Egrecia* sporophyte or frond density on a species' or group's cover. Other species or groups that did not have a significant covariate effect or a significant covariate*site interaction were analyzed using quantile regression analysis, as well. Quantile regression was used because of its usefulness in analyzing rates of change near the extremes of distribution due to a limiting factor, such as dense stands of *Egrecia* (Cade et al., 2005). Therefore, it only analyses the upper boundaries of the dependent variable in question. First, a linear regression was used to analyze the relationship between sporophyte or frond density and cover of the species in question. The residuals were saved and the negative residuals were discarded, the corresponding cover data from positive residuals were plotted against sporophyte density to give a better relationship between the higher values of cover and *Egrecia* density. All alpha levels for quantile regression were set at 0.05 to avoid Type I errors, and only slopes with r^2 values greater than the predetermined value of 0.200 were reported because values <0.200 do not explain enough of the total variation. Sites that had zero cover of any species or groups were left out of the regression.

3. Results

3.1. *Egrecia* effects on algal species richness

There was a significant treatment effect on mean algal richness (number of species/m²) between control and removal plots throughout the 12-month experimental period at Soberanes Pt. (Table 2ai) (Fig. 2a). The *Egrecia* removal plots were consistently higher in algal species richness than control plots throughout the experiment at Soberanes Pt. There was a sharp increase in algal species richness in *Egrecia* removal plots during the late summer and early fall 2004. Species richness decreased on the winter sampling date in *Egrecia* removal plots to a similar value as control plots. Algal species richness in *Egrecia* removal plots then increased again during summer and fall months of 2005. An LSD test comparing differences among sampling dates resulted in all dates differing significantly from October 2004, when species richness peaked in *Egrecia* removal plots. Algal richness on all sampling dates differed from the winter (February 2005) sampling date, except for the first sampling date (July 2004) and the one-year sampling date (July 2005), indicating a negative winter seasonal effect on species richness. The mean number of algal species in control plots remained relatively constant throughout the study period.

There was also a significant treatment effect on algal species richness during the 12-month experimental period at Pigeon Pt. (Table 2aii, Fig. 2b). Overall, algal species richness was significantly greater in control plots than in removal plots. Algal species richness was consistent in control plots throughout the experimental period, however there was a drop in algal species richness in control plots during the summer period. Algal species richness was equal in control and removal plots towards the end of the experiment. Initially there was a positive *Egrecia* effect on algal species richness, yet the *Egrecia* effect was not apparent at the end of the experiment. This indicated a weak positive or neutral effect of *Egrecia* on algal species richness at Pigeon Pt.

The effect of *Egrecia* sporophyte density on algal species richness was general along the central coast of California. Analysis of covariance determined there was a significant effect of adult *Egrecia* sporophyte density on algal species richness among sites (Table 3a),

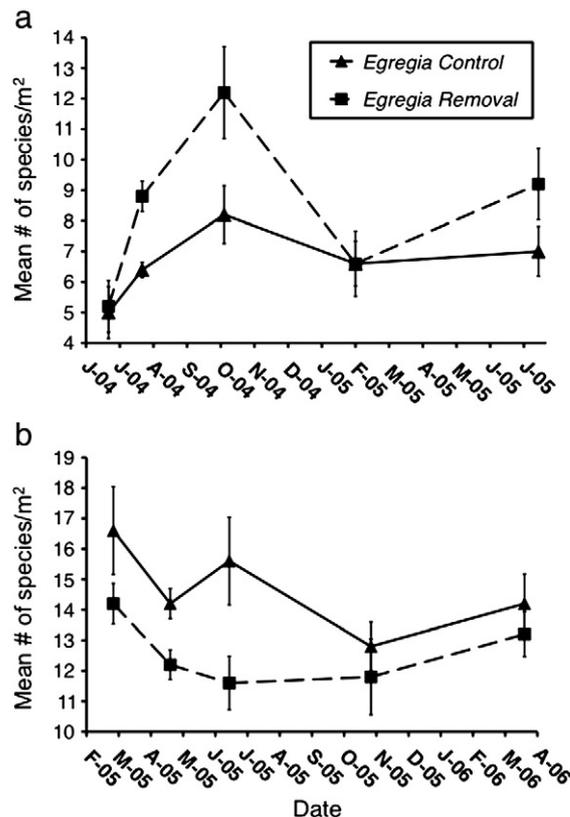


Fig. 2. Algal species richness (number of algal species m⁻² [$\bar{x} \pm SE$]) in experimental and control plots (n=5) at (a) Soberanes Pt. during the experimental period (July 2004–July 2005), and (b) Pigeon Pt. (April 2005–March 2006). The first sampling date was prior to experimental removal of *Egrecia*, and was not included in repeated-measures analysis (Table 2aii–2bii).

and regression analysis indicated that the direction of the effect was negative (Table 3b, Fig. 3a).

3.2. *Egrecia* effects on total macrophyte cover

Egrecia did not affect total macrophyte cover (excluding *Egrecia* cover) at the two experimental sites (Tables 2bi–2bii), yet there was a

Table 3 (a) Results of analysis of covariance (site = random, sporophyte density = covariate) for ten sites along the central California coast, testing for parallelism in regression slopes of the relationships between the algal species richness and sporophyte (Sporophyte# = *Egrecia* sporophytes) density among sites. (b) Regression analysis of *Egrecia* sporophyte density vs. the number of algal species.

(a)						
Source		SS	df	Mean Square	F	P
Intercept	Hypothesis	1381.28	1	1381.28	197.17	<0.0005
	Error	69.55	9.93	7.01		
Site	Hypothesis	66.47	9	7.39	2.13	0.035
	Error	305.29	88	3.47		
Sporophyte#	Hypothesis	16.43	1	16.43	4.74	0.032
	Error	305.29	88	3.47		
Site*Sporophyte#	Hypothesis	17.29	9	1.92	0.55	0.831
	Error	305.29	88	3.47		
(b)						
Slope	y-intercept	F	P	r ²	N	
-0.286	7.291	13.18	<0.0005	0.111	108	

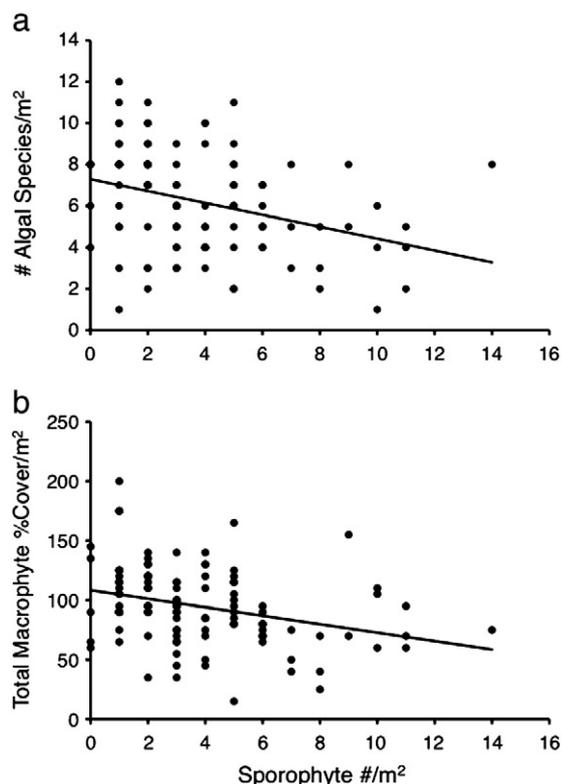


Fig. 3. Regression analysis for (a) adult *Egregia* sporophyte density vs. algal species richness (number of algal species) (Table 3b) and (b) adult *Egregia* sporophyte density vs. total macrophyte cover (Table 4b) using data from ten sites along the central California coast (Fig. 1). Regression analysis was used to visually represent results from ANCOVA analysis.

significant negative correlation between *Egregia* density and macrophyte cover when comparing across sites (Table 4a, Fig. 3b).

3.3. *Egregia* effects on sand cover

Sand was conspicuously absent from study plots at Soberanes Pt. during the duration of the experiment. However, sand was abundant

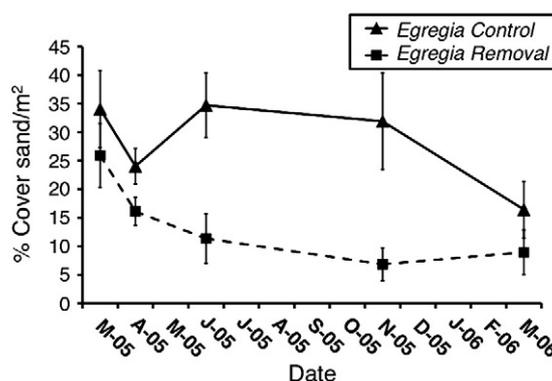


Fig. 4. Percent cover of sand (%cover m⁻² [$\bar{x} \pm SE$]) in experimental and control plots (n = 5) at Pigeon Point (April 2005–March 2006). The first sampling date was prior to experimental removal of *Egregia*, and was not included in repeated-measures analysis (Table 2cii).

at Pigeon Pt., and control plots were significantly greater in sand cover than *Egregia* removal plots (Table 2cii, Fig. 4). Geographic sampling found no general effect of *Egregia* on sand cover throughout the study area.

3.4. *Egregia* effects on community assemblages

Community assemblages shifted after removal of *Egregia* at both experimental sites (Table 5a–b), but *Egregia* removal had an opposite effect at the two study sites. At Soberanes Pt., the *Egregia* control plots were strongly associated with algal crusts, geniculate coralline algae, and robust algae, such as other kelp species, *Codium fragile* (Suringar) Hariot, and *Chondracanthus corymbiferus* (Kützing) Guiry. *Egregia* removal plots at Soberanes Pt. were strongly associated with structurally weaker algae, such as *Microcladia borealis* Ruprecht and *Gelidium coulteri* Harvey. Oppositely, *Egregia* removal plots at Pigeon Pt. were strongly correlated with algal crusts and geniculate coralline algae (Table 5b). The effects of *Egregia* on foliose algal species cover were generally negative along the central California coast (Table 5c). However, there was a positive effect on algal crusts, geniculate coralline algae, the mussel *M. californianus*, and sessile invertebrates.

3.5. Wave height analysis

Annual mean wave height was significantly greater at the Soberanes Pt. (2.13 m \pm 0.42[Standard Error]) site during its experimental period than Pigeon Pt. (1.53 m \pm 0.053[Standard Error]) (t = 8.873, df = 730, p < 0.0005). Mean wave height at Pigeon Pt. could also be lower because the study site was in a semi-protective cove.

Table 4
(a) Results of analysis of covariance (site = random, sporophyte density = covariate) for pooled data among ten sites along the central California coast, testing for parallelism in regression slopes of the relationships between total macrophyte cover and sporophyte (Sporophyte# = adult *Egregia* sporophytes) density among sites. (b) Regression analysis of adult *Egregia* sporophyte density vs. total algal cover.

(a)						
Source		SS	df	Mean Square	F	P
Intercept	Hypothesis	297120.60	1	297,120.60	143.92	<0.0005
	Error	19630.94	9.509	2064.49		
Site	Hypothesis	20015.10	9	2223.90	3.84	<0.0005
	Error	50930.03	88	578.75		
Sporophyte#	Hypothesis	3569.30	1	3569.30	6.17	0.015
	Error	50930.03	88	578.75		
Site*sporophyte#	Hypothesis	3544.72	9	393.86	0.68	0.725
	Error	50930.03	88	578.75		
(b)						
Slope	y-intercept	F	P	r ²	n	
-3.55	108.291	11.15	0.001	0.087	108	

4. Discussion

Results from the Soberanes Pt. and geographic sampling studies suggest that *Egregia* generally has a negative effect on total macrophyte cover and algal species richness. Locally, however, *Egregia* had a positive effect on algal species richness at Pigeon Pt. (Table 5). This could be due to spatial and temporal heterogeneity in abiotic factors (Jones et al., 1997; Bruno et al., 2003; Crain and Bertness, 2005). Experiments were conducted at locations that differed physically and geologically. The main abiotic factor that affects near shore communities along the central California coast is wave stress (Graham, 1997). Pigeon Pt. is semi-protected to wave disturbances due to its orientation and rock formations that dampen waves from the predominant storm direction, whereas, Soberanes Pt. faces

Table 5
 Summary of results from (a) Soberanes Point Experiment ($y = \text{Date} + \text{Treatment} + \text{Date} * \text{Treatment} + \text{error}$), (b) Pigeon Point Experiment ($y = \text{Date} + \text{Treatment} + \text{Date} * \text{Treatment} + \text{error}$), and (c) Geographic sampling ($y = \text{site} + \text{Egregia} + \text{Egregia} * \text{site} + \text{error}$), *Egregia* effect is either sporophyte density or density of frond residuals. RMA = Repeated Measures ANOVA, QR = Quantile Regression, R = Regression. Statistical results for RMA are reported in order as Treatment and Date * treatment. Statistical results from PCA are reported as the variation explained by axes whose principal components have a significant treatment or Date * treatment effect from RMA. Statistical results from ANCOVA are reported in order as Sporophyte# and Site * Sporophyte# or Frond Residuals and Site * Frond Residuals, followed by regression results. Statistical results for QR have the quantile level in parentheses.

Dependent variable	Statistical results	Significant Ind. variable(s)	Statistical test	<i>Egregia</i> effect
<i>(a) Soberanes Point</i>				
Algal species richness	Table 2ai	Treatment	RMA	–
<i>Egregia</i> recruitment	$F_{1,8} = 0.03, p = 0.864$	N/A	RMA	N/A
	$F_{2,16} = 0.04, p = 0.958$			
Subcanopy layering	$F_{1,8} = 41.43, p < 0.0005$	Treatment,	RMA	–
	$F_{8,932} = 2.94, p = 0.014$	Date * treatment		
Total algal cover	Table 2bi	N/A	RMA	N/A
<i>Mazzaella flaccida</i> (Setchell & Gardner)	$F_{1,8} = 0.36, p = 0.563$	Date * treatment	RMA	+ / – (seasonal)
	$F_{4,30} = 3.10, p = 0.033$			
<i>Microcladia borealis</i>	$F_{1,8} = 11.32, p = 0.01$	Treatment	RMA	–
	$F_{2,19} = 2.47, p = 0.103$			
<i>Gelidium coulteri</i>	$F_{1,8} = 6.76, p = 0.032$	Treatment	RMA	–
	$F_{2,19} = 1.72, p = 0.202$			
Sand	N/A	N/A	N/A	N/A
Benthic community	PC1 (19.2%)	Treatment (PC1),	PCA/RMA	Community Shift
	$F_{1,8} = 4.13, p = 0.077$	Date * treatment (PC3)		
	PC3 (11.6%)			
	$F_{2,19} = 3.48, p = 0.044$			
<i>(b) Pigeon Point</i>				
Algal species richness	Table 2aii	Treatment	RMA	+
<i>Egregia</i> recruitment	$F_{1,8} = 2.18, p = 0.178$	N/A	RMA	N/A
	$F_{1,9} = 1.90, p = 0.203$			
Subcanopy layering	$F_{1,8} = 0.63, p = 0.608$	N/A	RMA	N/A
	$F_{6,31} = 1.56, p = 0.193$			
Total algal cover	Table 2bii	N/A	RMA	N/A
<i>Odonthalia flaccosa</i> (Esper) Falkenberg	$F_{1,8} = 6.32, p = 0.036$	Treatment	RMA	+
	$F_{2,17} = 0.21, p = 0.832$			
<i>Pterosiphonia bipinnata</i>	$F_{1,8} = 6.42, p = 0.035$	Treatment	RMA	+
	$F_{2,16} = 1.28, p = 0.303$			
<i>Microcladia borealis</i>	$F_{1,8} = 29.84, p = 0.001$	Treatment	RMA	+
	$F_{2,15} = 0.80, p = 0.463$			
<i>Phaeostrophion irregulare</i> (Setchell & Gardner)	$F_{1,8} = 5.39, p = 0.049$	Treatment	RMA	+
	$F_{2,14} = 0.78, p = 0.463$			
<i>Neorhodomela larix</i> (Turner) Masuda	$F_{1,8} = 0.0, p = 0.977$	Date * treatment	RMA	+ / – (seasonal)
	$F_{2,15} = 3.6, p = 0.055$			
<i>Polysiphonia</i> sp.	$F_{1,8} = 14.13, p = 0.006$	Date * treatment	RMA	+
	$F_{2,19} = 1.086, p = 0.368$			
Sand	Table 2cii	Treatment	RMA	–
Benthic Community	PC2 (23.4%)	Treatment	PCA/RMA	Community Shift
	$F_{1,8} = 3.483, p = 0.041$			
<i>(c) Geographic sampling</i>				
Algal species richness	Table 3a–b	Sporophyte#	ANCOVA, R	–
Total algal cover	Table 4a–b	Sporophyte#	ANCOVA, R	–
<i>Cryptopleura</i> spp.	$F_{1,59} = 7.16, p = 0.010$	Sporophyte#	ANCOVA, R	–
	$F_{2,59} = 1.50, p = 0.205$			
	$F_{1,70} = 5.57, p = 0.021, r^2 = 0.075$			
<i>Mastocarpus papillatus</i> (C. Agardh) Kützing	$F_{1,21} = 5.15, p = 0.034$	Frond residuals	ANCOVA, R	–
	$F_{1,21} = 0.34, p = 0.540$			
	$F_{1,24} = 5.92, p = 0.023, r^2 = 0.205$			
<i>Prionitis lanceolata</i> (Harvey) Harvey	$F_{1,21} = 15.54, p = 0.001$	Sporophyte#,	ANCOVA, R	– / No
	$F_{1,21} = 12.04, p = 0.002$	Site * Sporophyte#		
	$F_{1,14} = 13.61, p = 0.003, r^2 = 0.511$			
<i>Corallina</i> spp.	$F_{1,77} = 1.08, p = 0.303$	Site * Frond resid.	ANCOVA, R	– / No
	$F_{7,77} = 1.81, p = 0.097$			
	$F_{1,17} = 7.21, p = 0.017, r^2 = 0.325$			
<i>Mytilus californianus</i>	$F_{1,25} = 1.38, p = 0.078$	Sporophyte#	ANCOVA, R	+
	$F_{7,77} = 0.01, p = 0.916$			
	$F_{1,28} = 5.78, p = 0.023, r^2 = 0.146$			
Algal Crust	$F_{1,28} = 5.78, p = 0.023, r^2 = 0.146$	Sporophyte#	QR(99th)	+
Geniculate Corallines	$F_{1,18} = 14.24, p = 0.001, r^2 = 0.442$	Sporophyte#	QR(99th)	+
Sessile Invertebrates	$F_{1,31} = 8.16, p = 0.008, r^2 = 0.208$	Sporophyte#	QR(90th)	+
<i>Ulva</i> spp.	$F_{1,21} = 8.1, p = 0.01, r^2 = 0.278$	Sporophyte#	QR(90th)	–
<i>Odonthalia flaccosa</i>	$F_{1,22} = 7.99, p = 0.01, r^2 = 0.267$	Sporophyte#	QR(99th)	–
<i>Chondracanthus canaliculatus</i> (Harvey) Guiry	$F_{1,5} = 10.05, p = 0.025, r^2 = 0.668$	Sporophyte#	QR(99th)	–
<i>Microcladia</i> spp.	$F_{1,24} = 8.68, p = 0.007, r^2 = 0.266$	Sporophyte#	QR(90th)	–
<i>Gastroclonium subarticulatum</i> (Turner) Kützing	$F_{1,9} = 50.23, p < 0.0005, r^2 = 0.848$	Sporophyte#	QR(99th)	–
Sand	$F_{1,9} = 0.03, p = 0.864$	N/A	ANCOVA	No
	$F_{1,9} = 0.751, p = 0.662$			

directly towards the predominant swell direction and has no buffer. Therefore, the environmental stress potential is much greater at Soberanes Pt. than Pigeon Pt. The increased wave action favors communities that are dominated by more robust algae capable of inhabiting harsh areas and consequently decreasing the overall species diversity (Connell, 1978; Sousa, 1980). This is supported by results from this study because there was less algal diversity at Soberanes Pt. than Pigeon Pt., where there was less wave stress. Increased wave activity could also increase the scouring pressure of *Egregia*, limiting the survival of species with weak attachments. It should be noted that differences in environmental stress might have been confounded due to experiments being initiated during different years and seasons. However, differences in year did not confound the result of *Egregia*'s ability to have varying effects on intertidal algal assemblages.

Previous studies investigating the effect of scouring by large brown algae on the surrounding community at wave-swept shores have consistently shown a net negative effect on community assemblages. The rocky intertidal zone of central Chile has morphologically similar flora and fauna as central California. Chile's intertidal zone is dominated by the kelp *L. nigrescens* and the kelp-like fucoid *D. antarctica*, both of which exhibit similar morphologies to *E. menziesii* (Santelices, 1990; Taylor and Schiel, 2005); *L. nigrescens* and *D. antarctica* both possess long strap-like fronds that are capable of sweeping the substrate. This sweeping motion creates an area that only permits the growth of the calcareous crust *Mesophyllum* spp., and limits the growth of *Codium dimorphum* Svedelius, *Mazzaella laminarioides* (Bory de Saint-Vincent) Fredericq, and turf-forming algae to higher regions in the intertidal (Santelices, 1990). A similar pattern of interspecific exclusion was observed in South Africa, where *Laminaria pallida* Greville created areas of barren rock between patches, freeing up space for its recruits (Velimirov and Griffiths, 1979).

Large brown algae in protected environments have different effects on community assemblages than wave-exposed environments, because wave-sheltered environments are characterized by strong desiccation, temperature and shading effects (Bertness et al., 1999). The large brown intertidal invasive alga, *Sargassum muticum* (Yendo) Fensholt, was found to have no effect on algal species composition in tidepools along the southern and central California coast (Wilson, 2001). In Washington, subtidal *S. muticum* populations were found to have a negative shading effect on associated algal communities (Britton-Simmons, 2004). The difference in effects of *S. muticum* could be due to geographic variability as well environmental variability of abiotic factors affecting tidepools and subtidal zones. *Ascophyllum nodosum* populations in the wave-protected intertidal zone of Maine were found to have varying effects on community assemblages due to amelioration of desiccation and temperature stress in the high intertidal resulting in a net positive effect and competition and shading resulting in a net negative effect in the lower intertidal (Bertness et al., 1999). *Egregia* populations at Pigeon Pt. are exposed to less wave-stress than Soberanes Pt. populations and therefore exhibit less of a whiplashing effect, which could lead to a net positive effect on the intertidal community through amelioration of desiccation and temperature stressors.

Soberanes Pt. has a granite substrate that is much more stable than the sandstone at Pigeon Pt. Sandstone is more erodible than granite and makes *Egregia* populations more susceptible to disturbances by removing entire individuals (Brent Hughes pers. obs.). Dislodged *Egregia* sporophytes were commonly observed at Pigeon Pt., but never observed at Soberanes Pt. This decrease in persistence of *Egregia* as a climax species may allow for colonization of earlier successional species (Sousa, 1980). The presence of sand could also lead to habitat amelioration by *Egregia* through the removal of sand at sites where sand is present. However, the ability to remove sand can only occur in moderate to high energy environments, where the sweeping action

of *Egregia* is greater. The presence of more sand in *Egregia* plots at Pigeon Pt. indicates that *Egregia* can act as a sand trap in low energy environments. Sand scour and accumulation can have positive effects on algal species diversity because it creates a disturbance that promotes diversity and it also deposits in low lying areas that have less desiccation and temperature stress (Littler et al., 1983; McQuaid and Dower, 1990). This result was evident at Pigeon Pt. where there was greater diversity in the *Egregia* plots where sand cover was greatest. There was also differences in community structure at each site that could also lead to differences in interactions of *Egregia* with other algal species. *Egregia* populations at Soberanes Pt. were associated with robust algae, such as *C. fragile* and coralline crusts, in contrast to *Egregia* populations at Pigeon Pt. that were associated with structurally weaker algae.

Like other morphologically similar large brown algae in wave-swept environments around the world, *Egregia* can be considered to have a net negative effect on benthic communities. These negative effects can be due to its shading of other less-dominant algal species (for examples see Black, 1974; Dayton et al., 1984; Reed and Foster, 1984; Kennelly, 1989; Connell, 2003; Clark et al., 2004). It can also have negative consequences by competitively excluding certain benthic species to grow in areas where the substrate is not swept (Velimirov and Griffiths, 1979; Santelices, 1990; Irving and Connell, 2006). It is not known if the sweeping ability is a morphological product of evolution due to the dynamic near-shore environment. However, it has two beneficial roles for the dominant species: (1) the reduction of hydrodynamic drag, and (2) sweeping of the substrate.

There are many examples in nature of organisms that display both negative and positive effects on community diversity, such as mussels, oysters, algae, and salt marsh plants (Paine, 1966; Suchanek, 1992; Bertness et al., 1999; Crain and Bertness, 2005; Kimbro and Grosholz, 2006). Salt marsh plants have been found to have varying consequences on communities over variable spatial and temporal scales (Crain and Bertness, 2005). Mussels and algae have been found to have varying effects over variable spatial scales (Paine, 1966; Suchanek, 1992; Bertness et al., 1999), and oysters have been found to have varying effects due to varying levels of disturbance (Kimbro and Grosholz, 2006). The one common factor in determining positive or negative effects of foundation species is environmental variability. Like the aforementioned organisms, populations of *Egregia* display varying consequence due to variable environmental conditions in space and time.

Many studies recognize variable effects that foundation species have on associated community assemblages, and generally conclude that foundation species have a net positive effect in harsher environments and a net negative effect in more benign environmental conditions (Jones et al., 1997; Bruno et al., 2003; Crain and Bertness, 2005). Interestingly, *Egregia* populations on the central California coast display an opposite pattern. In more benign environments *Egregia* has a net, albeit, weak positive effect, and a net negative effect in harsher wave-exposed environments (Fig. 5). Densities of *Egregia* are also higher in harsh environments, possibly leading to competitive exclusion of many other sessile organisms. This density effect has negative consequences on intertidal algal diversity and cover. However, there was a positive *Egregia* effect on sessile invertebrates, primarily mussels, barnacles and anenomes. These groups of organisms have firm attachments and may withstand the whiplash effect of *Egregia*, while benefiting from its associated defenses (i.e. whiplash) from predators (Bruno et al., 2003). *Egregia* also forms populations on sloped and at times vertical walls that can also serve as a refuge from predation (Witman and Dayton, 2001).

The effect of *Egregia*, on intertidal and subtidal communities varies during periods of high environmental stress, which can exacerbate their competitive dominance for space (Fig. 5). Investigators have recognized a lack of studies examining the effects of foundation species over large geographic ranges, yet assume that the effects of

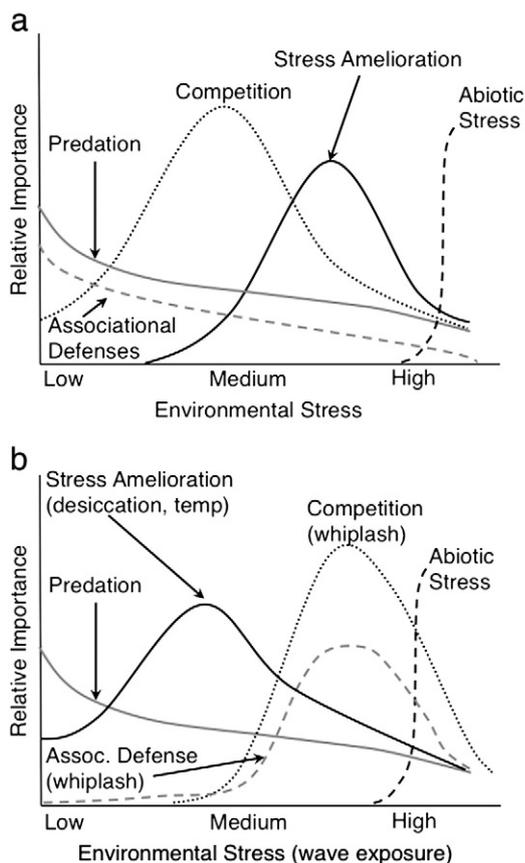


Fig. 5. The Menge–Sutherland model (Menge and Sutherland, 1987) with (a) the facilitation model included and redrawn from Bruno et al. (2003), and (b) the conceptual model of *Egregia* facilitation and competition included. The original Menge–Sutherland model included competition, predation, and abiotic stress; and the Bruno et al. (2003) model included facilitation (stress amelioration and associated defenses). The *Egregia* model was designed using results from this study.

foundation species or ecosystem engineers are generally positive over large spatial scales (Jones et al., 1997). In the case of *Egregia* along the wave-swept intertidal zone of central California, the net effect on algal species diversity and cover is negative. However, when wave energy and whiplashing effects are low the results are an overall positive effect on the intertidal community. The combination of results from this study as well as others (Menge and Sutherland, 1987; Bertness et al., 1999; Callaway et al., 2002; Helmuth et al., 2002; Bruno et al., 2003) demonstrates the necessity of considering environmental factors when looking at species interactions on scales that range from local to global.

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