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Ecological consequences of morphological variability in a habitat-forming alga

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ECOLOGICAL CONSEQUENCES OF MORPHOLOGICAL VARIABILITY IN A
HABITAT-FORMING ALGA

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories

and the Department of Marine Sciences

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Jennifer Piper Jorve

December 2008

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SAN JOSE STATE UNIVERSITY

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ECOLOGICAL CONSEQUENCES OF MORPHOLOGICAL

VARIABILITY IN A HABITAT-FORMING ALGA

by Jennifer Piper Jorve

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ABSTRACT

ECOLOGICAL CONSEQUENCES OF MORPHOLOGICAL VARIABILITY IN A HABITAT-FORMING ALGA

by Jennifer Piper Jorve

Habitat-forming species often help ameliorate stressful environmental conditions. This study addressed the cascading effect of morphological variability in the intertidal red alga *Mastocarpus* spp. on sub-canopy microclimate and macroinvertebrate distribution and abundance at seven central California sites. Replicate 10 cm diameter cores were sampled for the morphological variables frond density, length, surface area, and dry biomass; environmental variables temperature, humidity, and irradiance; and invertebrate species richness, abundance, and prominent individual species. Principal components analysis (PCA) transformed the data, and analysis of covariance (ANCOVA) determined within- versus among-site variability. Morphological “size” and “shape” created distinct microclimates ranging from hot and dry to cool and wet, while morphological “turfiness” created light to dark microclimates. Significant associations occurred between morphology, microclimate, and invertebrates. All significant associations between microclimate and invertebrates revealed a cascading effect of morphology on microclimate on invertebrates. *Mastocarpus* spp. morphological variability created distinct microclimates usually associated with multi-species assemblages.

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INTRODUCTION

Stress is ubiquitous to all organisms and affects individuals, populations, communities, and ecosystems, dictating community structure, where organisms live, survivorship rates, physiology, and form. Stress is ultimately the factor driving species evolution (Darwin 1962, Brown and Lomolino 1998, Futuyma 1998) and can be defined as “a fitness reduction of an individual or population in response to an extrinsic factor” (Bruno and Bertness 2001). For sessile organisms, the manner in which they respond to environmental stress is key to their survival because these organisms cannot flee and must acclimate, tolerate, or perish (Newell 1979, Raffaelli and Hawkins 1996). In some environments, inhabitants change morphology (i.e. phenotypic plasticity; Denny et al. 1985, Denny 1988, Carrington 1990, Bell 1995, Trussell 1997, Pelt et al. 2004) and density (e.g., see self-thinning review by Scrosati 2005, Scrosati 2006) in response to stressful *in situ* conditions. For example, algae inhabiting the intertidal zone may increase thallus thickness to retain moisture and decrease desiccation (Bell 1995), or decrease size with increased wave exposure to reduce the chance of dislodgement (Denny 1985, Carrington 1990, Blanchette 1997). Spatial variability in stressful environments and organismal density, therefore, can result in morphological variability in sessile organisms over small to large spatial scales.

Researchers of terrestrial and marine biological systems have examined phenotypic plasticity as a mechanism by which species respond to shifting environmental conditions (Kettlewell 1965, Trussell 1997, Madigosky 2004, Pelt et al. 2004). Such within-species responses to environmental stress can be conspicuous in the marine

intertidal zone, where it is necessary for organisms to withstand daily variability in environmental stressors such as emersion, desiccation, wave exposure, ultraviolet radiation, and wind velocity (Newell 1979, Raffaelli and Hawkins 1996, Rai and Gaur 2001). The ability of attached organisms to respond physically to stress can enhance individual survivorship (Dudgeon and Johnson 1992, Blanchette 1997, Trussell 1997) and result in morphological variability (e.g. with intertidal algae; Armstrong 1987, Carrington 1990, Bell 1995, Kubler and Dudgeon 1996). For example, the maximum size of intertidal marine flora and fauna can be regulated by the degree of wave exposure (Denny 1985, 1988), the shape of individuals can be dictated by water flow patterns (Armstrong 1987), and the thickness or robustness of individual thalli can vary as a function of desiccation stress (Kubler and Dudgeon 1996). All of these morphological characteristics are dictated by the environmental conditions in which the organism inhabits, and the physiological ability of the organism to respond.

Habitat-forming species are inherently sessile and morphologically complex and can play an important role in regulating and determining community structure (Dayton 1972, Bruno et al. 2002). In large-scale terrestrial and subtidal marine systems, the impact of habitat-forming species on their communities can be conspicuous (North 1971, Harper 1977, Foster and Schiel 1985, Lowman and Rinker 2004, Gurevitch et al. 2006). Trees provide shelter, food, and shade, decrease temperature and wind velocity, and increase moisture under the canopy (Harper 1977, Lowman and Rinker 2004, Gurevitch et al. 2006). Kelps provide nutrients, food, and shade, while reducing current velocity and sedimentation within the kelp forest, subsequently decreasing sand abrasion for kelp

forest species (North 1971, Gerard 1984, Reed and Foster 1984, Foster and Schiel 1985, Jackson 1998, Clark et al. 2004). Similarly, intertidal habitat-forming species facilitate recruitment of community species by providing shelter (Wieters 2005), decreasing irradiance to the substrate lessening thermal stress (Dayton 1975, Holbrook et al. 1991, Burnaford 2004), and providing food and variable caloric value to associated herbivores (Himmelman and Carefoot 1975, Littler and Littler 1984, Blanchette 1996). These functions may be especially important in the intertidal zone as organisms experience stress of terrestrial and marine origin, yet are fundamentally marine.

Models of single-stand tree colonies predict that irradiance to the forest floor will differ with density of trees and morphology of canopy (Pelt et al. 2004). Density of canopy foliage is a result of tree type, number of branches, length of branches, number of leaves per branch, the dimensions of the leaves, and a number of other morphological characteristics (Harper 1977, Pelt et al. 2004). In subtidal kelp systems, irradiance changes spatially and temporally under subtidal canopies of *Macrocystis pyrifera* (Gerard 1984). In combination with secondary canopy species such as *Pterygophora californica*, *M. pyrifera* can reduce light at the substrate to 3% of surface influx (Reed and Foster 1984, Clark et al. 2004). Canopy-forming species also change flow velocities as shown for stands of *M. pyrifera* (Jackson 1998) and the intertidal genus *Fucus* spp. (Serrao et al. 1996). Additionally, they provide protection from dislodgement, grazing, and desiccation of *Silvetia compressa* propagules, as with the intertidal, habitat-forming turf species *Endocladia muricata* and *Mastocarpus papillatus* (Johnson and Brawley 1998). Removal of intertidal canopy-forming algae, such as *Ascophyllum nodosum*, caused

bleaching and mortality of red algal turf species *Chondrus crispus*, *Gelidium pusillum*, *Gelidium latifolium*, and *Corallina officinalis*, due to a combination of desiccation, and increased temperature and irradiance, indicating that canopy-forming species limit the effects of emersion (Jenkins et al. 1999). Therefore, temporal and spatial variability of environmental stressors due to morphological variation in intertidal, habitat-forming algae may incite a response in associated flora and fauna (Wieters 2005).

Mastocarpus papillatus is one of the most common habitat-forming intertidal algae on the Pacific coast of North America (Abbott and Hollenberg 1976) and exhibits extreme morphological variation within and among populations (Abbott and Hollenberg 1976, Carrington 1990). It is ubiquitous on rocky intertidal shores from Baja California, Mexico to Alaska, extending through multiple climate zones, within the mid to high rocky intertidal zone (Abbott and Hollenberg 1976). Growth strategies range from densely aggregated fronds to solitary individuals, forming patches of varying size and growing to heights of up to 15 cm (Abbott and Hollenberg 1976). Smaller, thinner individuals are typical of wave-exposed sites, whereas larger, blade-like individuals are characteristic of wave-protected sites (Carrington 1990, J. Jorve, Personal Observation). This morphological gradient also occurs with increased intertidal height, with smaller individuals lower in the intertidal and larger individuals higher (J. Jorve, personal observation). Morphological variability, however, also can be patchy at small spatial scales (J. Jorve, personal observation).

Mastocarpus spp. has a heteromorphic, alternation-of-generations life history, and can reproduce sexually and asexually (Abbott and Hollenberg 1976, Polanshek and West

1977, West et al. 1978, Avila and Alveal 1987, Zupan and West 1988). Dioecious, upright, gametophytic blades alternate with tetrasporophytic, non-calcareous, perennial crusts, and all life history stages can be apomictic (Polanshek and West 1977, West et al. 1978, Zupan and West 1988). Female gametophytes are characterized by swollen papillae on the thalli, whereas thalli of the male gametophytes lack papillae (Smith 1944, Abbott and Hollenberg 1976). Gametophyte thalli represent the life history phase with the greatest morphological variability (Carrington 1990) and potential to alter the intertidal microclimate. Numerous gametophyte thalli can arise from individual gametophytic crusts, which can be isolated or densely aggregated dependent on the reproductive strategy used (i.e., sexual or asexual reproduction, Zupan and West 1988). In dense aggregations it may be impossible to identify genetically distinct individuals, however, thalli only centimeters apart can be morphologically distinct (Fig. 1). The overall goal of this study was to determine the ecological and microclimate consequences of spatial variability in *Mastocarpus* spp. morphology.

I quantified the magnitude of effect that morphological variability in a habitat-forming species had on the corresponding physical and biological community. Although the focal species was *Mastocarpus papillatus*, thalli of the congener *Mastocarpus jardinii* were sometimes studied because the morphological distinction between these two species is ambiguous and they can overlap continuously in their spatial distribution. Additionally, *M. papillatus* and *M. jardinii* are now thought to be part of a species complex that is highly variable in morphology, such that they cannot be identified in situ but only differentiated with genetic analysis (Lindstrom 2008). The only other researcher

Figure 1. Distinct morphologies of *Mastocarpus* spp. within the same 10 cm diameter core.

that has investigated the ecological consequences of morphological variability with a single intertidal algal taxon found the mussel *Perumytilus purpuratus* had greater recruitment to substrate below shorter turf comprised of the red algal species *Gelidium chilense*, than longer turf of the same species (Wieters 2005). The study found that longer turf correlated with colder waters and nutrient-rich upwelling zones, but did not describe the mechanism linking greater recruitment of *P. purpuratus* below shorter *G. chilense* turf. As such, this is the first direct test of environmental and community consequences of morphological variability in marine algae. Specifically, I (1) quantified the effect of *Mastocarpus* spp. morphological variability on the underlying microclimate,

(2) determined whether this relationship was general, or varied temporally or latitudinally, and (3) identified subsequent changes in macrofauna associated with varying morphologies of *Mastocarpus* spp.

OBJECTIVES

The main goal of this study was to determine whether morphological variability affected sub-canopy microclimate, and whether this association was general in central California or site-specific. If the effect of morphology on microclimate were general, then a single slope for each morphological characteristic would best explain sub-canopy microclimate conditions. However, if this relationship were site-specific, then the effect of morphology on microclimate would vary spatially. Such site-specific trends could be explained by latitude of the site, and time, total emersion time, and ambient conditions at the time of data collection. For my study, multiple sites were chosen within a wide latitudinal range as this was thought to be the driving factor if interactive effects were present. Latitudinal variability could be determined by changes in wave exposure, ambient climate conditions, and possibly morphological variability in *Mastocarpus* spp. Therefore, significant differences in slopes of the morphology: microclimate association would suggest that site-specific differences inherent with latitudinal variability might account for observed variability in the magnitude of morphological effects on sub-canopy microclimate.

METHODS

Data Collection

In determining the strength of the effect of morphological variability on sub-canopy microclimate, scale was considered both within sites and among latitudes. Therefore, 8 study sites were chosen along the central California coast from roughly 39°N to 35°N latitude to test for within- versus among-site differences in the morphology: microclimate association (Fig. 2). Each site was chosen for its accessibility, moderate to abundant presence of *Mastocarpus* spp., and varying wave exposures to

Figure 2. Proposed 8 study sites along the central California coast.

encompass morphological variability occurring in heterogeneous site conditions. At each site, a 50-meter tape was laid parallel with the water through the center of the local *Mastocarpus* spp. distribution. At random positions along the meter tape, a second meter tape was laid perpendicular through the horizontal distribution of *Mastocarpus* spp. Twenty-eight to 34 replicate, 10-cm diameter (80 cm²) Polyvinyl Chloride (PVC) cores were placed randomly along a second 15-meter tape in order to represent the horizontal breadth of the local population (one core per vertical transect). A core size of 10 cm diameter was chosen by noting size of aggregation of similar morphologies, or size of a single, large individual, and matching core size accordingly.

Four variables were used to quantify morphological variability in *Mastocarpus* spp.: dry biomass, frond surface area, density, and frond length. These variables were chosen as they depicted small-scale characteristics relevant to microclimate; biomass per area reflected the quantity of algal material present, whereas surface area, length, and density reflected the manner in which material was distributed. Three environmental variables were measured: irradiance, temperature, and humidity. Ultraviolet (UV) radiation was not chosen as an environmental variable because the methodology was too difficult for data collected in a short period of time. Temperature and humidity measurements represented desiccation stress, and irradiance was chosen as it can inhibit photosynthesis at lesser levels, yet cause physiological stress at greater levels.

In each core, irradiance was determined using a Biospherical Instruments Inc. QSP Scalar Irradiance Sensor, and temperature and humidity were measured using DS1923 Hygrochron iButtons. Mean irradiance, temperature, and humidity were

determined from the streaming data. Accuracy of the Irradiance Sensor was +/- 7%, whereas accuracy of the iButton was +/- 0.5°C, +/- 0.04% humidity. iButtons were placed at the substrate within the center of the core for sub-canopy readings, and adjacent to the core on bare rock for ambient conditions for roughly 1.5 hours. Light readings were recorded above the core canopy for an ambient reading for 10 seconds, and below the center of the canopy for 10 seconds to detect changes in understory microclimate. After all environmental data were collected, all macroalgae and macroinvertebrates were removed from the core and placed in separate, labeled bags for further analysis in the lab. This resulted in several dependent microclimate variables per core: mean percent ambient temperature, humidity, and irradiance. Percentage of ambient temperature, humidity, and irradiance were calculated using averages of each environmental reading with the following formula: $\frac{sub - canopy}{ambient} * 100$.

With the algal collections, frond density (number of fronds collected in a core area of 80 cm²), mean frond length, wet and dry biomass, and total surface area were determined. Frond density per core was counted manually, and mean frond length was measured using calipers to within 1 mm for 10 randomly selected individuals per core. Frond surface area was determined using scanned images of wet fronds, transformed to black and white, and imported to the program Image J, which determined total frond surface area by counting the number of black pixels (versus white) and scaling this measurement to square centimeters. This surface area calculation was then doubled to account for the surface area on each side of the frond. After removing, preserving, and storing all invertebrates in ethanol within each sample into labeled vials, wet

Mastocarpus spp. biomass was measured by first rinsing the sample in fresh water, draining the algae, and weighing it using a metric scale to ± 0.1 grams. The samples were then placed into separate, labeled mesh pouches and dried on a light box for 72 hours, after which the sample was re-weighed for dry biomass to ± 0.1 grams. This resulted in independent morphological variables: mean surface area (cm^2), mean dry biomass (g), mean length (cm), and mean density ($\#/\text{cm}^2$). Invertebrates collected in each core were identified to lowest taxonomic level and counted (Morris et al. 1980). These data resulted in species richness, and abundance per species for subsequent statistical analysis.

Principal Components Analysis

Morphological variables and microclimate variables were assumed to be highly correlated within their subset of data, so correlation analysis was performed. If the variables were significantly correlated, data were transformed using Principal Components Analysis (PCA) to account for relationships amongst the variables and accurately detect natural variability in the population (error). This analysis resulted in 4 morphological principal components (PCMORPH1-PCMORPH4) and 3 microclimate principal components (PCMICRO1-PCMICRO3). Correlation analysis indicated that only 2 of 6 animal variables were highly correlated amongst each other (i.e., *Littorina* spp. and abundance; $r = 0.893$, $p < 0.001$), therefore PCA was not used to reduce the faunal data. Hypotheses were tested using principal component scores instead of untransformed, highly correlated variables to account for variability associated with the

correlations. These scores more accurately represented the morphological combinations and microclimate conditions found in nature as depicted in the data.

Independence Tests

To detect whether individual cores were collected unknowingly along a morphological gradient, data were tested for independence within a sampling site using regression analysis. PCMORPH1-4 were regressed against plot number (corresponding to the order in which data were collected) to detect trends in morphological variability along the transect tape. Potential independence issues occurred in only 3 of 64 comparisons, the strongest of which was only a weak effect for PCMORPH1 at Rancho Marino Reserve on November 11, 2007 ($p = 0.006$, $r^2 = 0.223$, $\beta = 0.0338$). These few minor issues will be considered further in the discussion and interpretation of results, where appropriate.

Analysis of Covariance

Data were analyzed using an Analysis of Covariance (ANCOVA) to discern differences in morphological, environmental, and macroinvertebrate trends within and among sites. The General Linear Model (GLM) in the form of a regression was not sufficient in defining the relationship between morphological characters and environmental data, and environmental data and invertebrate assemblage as these relationships varied among sites. Therefore, an ANCOVA allowed for a simultaneous test of Hypothesis I (spatial variability in microclimate was correlated with

morphological variability in overlying *Mastocarpus* spp. canopies) as a covariate effect and Hypothesis II (there was no effect of temporal or spatial scale on the morphology: microclimate association) as a covariate x location interaction. Specifically, location (or SITE) was a random factor, morphological characters (PCMORPH1-4) were independent covariates, and environmental data (PCMICRO1-3) were dependent variables. Significant results in the main factors of SITE and PCMORPH, and the interaction of SITE x PCMORPH, tested for the effects of 1) site on sub-canopy microclimate (differences in y-intercept), 2) morphology on sub-canopy microclimate (slope of the relationship did not equal zero), and 3) that the relationship between morphology and microclimate varied among sites (slopes did not equal zero and were not statistically similar among sites, Fig. 3).

Significance of the SITE x PCMORPH interaction was most critical as it depicted the influence of site and morphology combined. Sampling at multiple sites resulted in a confounding effect of time, as each location was sampled on a different date. Therefore, the SITE x PCMORPH interaction could have been due to either geographic or temporal effects. In addition to sampling multiple sites a single time within central California to determine spatial variability, three sites at the northern end (Bodega Marine Lab), mid (Pigeon Point), and southern end (Rancho Marino Reserve) of the study latitudinal range were sampled seasonally throughout a one-year period to determine if there was significant temporal variability in the morphology: microclimate association when space was held constant. Sampling three sites through time allowed for detection of the influence of ambient climate conditions on the morphology: microclimate association.

Figure 3. Results of significant ANCOVAs: a) if the general relationship of morphology and microclimate was significant (covariate), b) if both the general relationship of morphology and microclimate was significant (covariate) as well as the factor SITE, which indicated differences in ambient temperature depending on location, c) if both the interaction of SITE x PCMORPH and the factor SITE were significant, the relationship of morphology and microclimate varied among sites and ambient conditions differed, and d) if nothing was significant the slope of the relationship between morphology and microclimate was equal to zero.

The within-site sampling method and analysis was the same as used for multiple sites, however, the random factors in the ANCOVA analysis were SITE and SEASON, and the

interaction terms used were SITE x PCMORPH1-4, SEASON x PCMORPH1-4, and SITE x SEASON x PCMORPH1-4. Significance of any of the interaction terms would indicate a need to assess the ANCOVA using the full data set with respect to time (if any of the SEASON x PCMORPH1-4 interactions were significant), latitude (if any of the SITE x PCMORPH1-4 interactions were significant), or both time and latitude simultaneously (if any of the SITE x SEASON x PCMORPH1-4 interactions were significant). These sites were chosen for the seasonal temporal sampling due to their broad distribution of *Mastocarpus* spp., location within the latitudinal extent of the study range, and because they were typical of open coast environments in which *Mastocarpus* spp. inhabits.

The seasonal analysis indicated that there were no general effects of site or season on the morphology: microclimate association (Table 1). Consequently, all data were

Table 1. Significance of interaction terms in seasonal ANCOVA analysis. NS = Not Significant, $\alpha = 0.10$.

Seasonal Effects on Morphology:Microclimate			
	PCMICO1	PCMICO2	PCMICO3
SEASON*PCMORPH1	NS	NS	p = 0.084
SEASON*PCMORPH2	p = 0.088	NS	NS
SEASON*PCMORPH3	p = 0.052	NS	NS
SEASON*PCMORPH4	p = 0.019	NS	NS
SITE*SEASON*PCMORPH1	NS	NS	p = 0.048
SITE*SEASON*PCMORPH2	NS	NS	NS
SITE*SEASON*PCMORPH3	NS	NS	p = 0.035
SITE*SEASON*PCMORPH4	NS	NS	NS

included in a single analysis and treated as individual sampling events regardless of time or space. The few variables with marginal seasonal effects were explained with caution in the discussion. Significant results from these ANCOVAs were analyzed as follows (refer to Figure 3): (1) If only the covariate (PCMORPH1-4) was significant a general relationship of morphology and microclimate occurred regardless of space or time; (2) If both the covariate (PCMORPH1-4) and SITE were significant, ambient conditions varied depending on latitude but the morphology: microclimate association was constant; (3) If any of the interaction terms were significant, then regardless of whether the general covariate was significant, a series of subsequent analyses were performed to ascertain trends in the variable morphology: microclimate association slopes. First, regression analyses were performed to extract the slope (β), the standard error of β , and r^2 of the morphology: microclimate relationship. β and r^2 for each site/date were then regressed against latitude, and the following conditions at the time of collection: time of day, ambient temperature, ambient humidity, ambient PAR, and total emersion time to help explain differences in the slopes of the morphology: microclimate association (See OBJECTIVES section).

Invertebrate species richness per core, abundance per core, and abundance of prevalent individual species (*Chlorostoma funebris*, *Lottia* spp., *Littorina* spp., and *Musculus pygmaeus*) per core were analyzed for differences within and among sites in variable microclimates under differing morphologies of *Mastocarpus* spp. Species richness data included the four taxa *Chlorostoma funebris*, *Lottia* spp., *Littorina* spp., and *Musculus pygmaeus* and any other macroinvertebrate found within the sample cores

of *Mastocarpus* spp. Using an ANCOVA similar to the above methodology, the relationship between changes in sub-canopy microclimate that were significantly affected by morphology and invertebrate species data among sites was determined, with microclimate principal components as the independent variable, and invertebrate species as the dependent variable. A second ANCOVA also was conducted using morphological principal components as the independent variable, and invertebrate species as the dependent variable, again with SITE as the random factor. Only those microclimate principal components that were significantly affected by *Mastocarpus* spp. morphology, and morphological principal components that significantly affected sub-canopy microclimate were considered, although all were included in the ANCOVA to account for all of the variability associated with microclimate and morphological data.

Lastly, to test whether there was a cascading effect of morphological variability on sub-canopy microclimate that affected macroinvertebrate distribution, I used the residuals data from the general morphology: microclimate ANCOVAs to isolate the singular effects of microclimate. As the original microclimate data was comprised of two components; the shared contribution of the morphology: microclimate association and the singular effects of microclimate, it was necessary to isolate these parts to determine how microclimate alone affected macroinvertebrates. Using ANCOVA with the reduced (residuals) PCMICRO1-3 data as the covariate, SITE as the random factor, and the macroinvertebrates as the dependent variables, comparisons were made between significant results of the original microclimate: invertebrate analysis and the reduced microclimate: invertebrate analysis. If all significant results from the general

microclimate:invertebrate analysis remained, then both the morphology:microclimate association and microclimate alone affected macroinvertebrates. However, if all significant results from the general microclimate:invertebrate analysis were insignificant in the residuals analysis, the effect of morphological variability on microclimate affected macroinvertebrate assemblages. This analysis tested Objective III, whether variable morphologies with distinct microclimates affect sub-canopy macroinvertebrate assemblages.

The software SPSS v. 11 was used for all ANCOVAs and regressions. $\alpha = 0.10$ was chosen as the critical value in determining significance for all statistical tests. This value was inflated to equal $\beta = 0.10$, so the probability of Type I and Type II errors was equal. G*Power was used to determine the minimum number of samples needed to detect a significant interaction, therefore a difference in the morphology:microclimate association among sites. The parameters used for G*Power were: $\alpha = 0.10$; $\beta = 0.10$; number of groups = 8; and a 'medium', minimum detectable effect size = 0.25 (Cohen 1988). It was presumed that there would be a minimum number of 8 sample sites for this study, therefore, the estimated sample size of 32 cores per site per sampling date would be conservative. The eighth site (Sea Ranch) was visited twice for data collection, however, there was not a sufficient amount of *Mastocarpus* spp. at either time, therefore only 7 sites were visited in total during this experiment.

RESULTS

Principal Components Analysis

As expected, correlation analysis indicated that morphological variables were highly correlated (Table 2a) as were microclimate variables (Table 2b). Principal

Table 2. Results of correlation analysis for morphological variables (Table 2a) and microclimate variables (Table 2b). Pearson's correlation coefficients (r) are listed, * indicate significant correlations, and $\alpha = 0.10$.

a) Morphological Correlations				
	Surface Area	Dry Biomass	Length	Density
Surface Area	1	-	-	-
Dry Biomass	0.155*	1	-	-
Length	0.211*	0.318*	1	-
Density	0.096*	-0.066	-0.120*	1

b) Microclimate Correlations			
	% Ambient Temp	% Ambient Hum	% Ambient PAR
% Ambient Temperature	1	-	-
% Ambient Humidity	-0.709*	1	-
% Ambient PAR	0.014	-0.143*	1

components analysis resulted in 4 morphological principal component variables (PCMORPH1-4) and 3 microclimate principal component variables (PCMICRO1-3, Table 3), which were used in all ANCOVA analyses. The first morphological PC explained 37% of the variability in *Mastocarpus* spp. morphology, driven by the morphological variables surface area, dry biomass, and length. PCMORPH1 described the size of thalli in a core, namely as PCMORPH1 increased size of thalli in a core increased. The second most important PC explained 27% of the variability in

morphology, driven by density and surface area. PCMORPH2 described the “turfiness” of the core sample, or as PCMORPH2 increased algae were more turf-like. PCMORPH3 explained 20% of morphological variability in *Mastocarpus* spp., and was characterized by increasing biomass and density and decreasing surface area. Low values of PCMORPH3 were morphologically ‘blade-like’, while high values were morphologically “stick-like.” Lastly, PCMORPH4 explained 16% of morphological variability in the dataset and was driven mainly by increasing length, with lesser influence of decreasing dry biomass and surface area. As this was the final principal component, it was considered the leftovers of the analysis (Table 3a).

Three principal components resulted from the microclimate PCA. PCMICRO1 explained 58% of the variability in microclimate data and was characterized by increasing percentage ambient temperature, and decreasing percentage ambient humidity. Lesser values of PCMICRO1 indicated cool and wet sub-canopy microclimates, whereas greater values indicated hot and dry sub-canopy microclimates. Thirty-three percent of the variability was explained by PCMICRO2, which was driven by increasing percent ambient PAR. Therefore, greater PCMICRO2 values indicated increased light microclimates and lesser values indicated dark microclimates. PCMICRO3, which explained 9% of the variability in microclimate data, was the final principal component of the microclimate PCA and was considered the leftovers of the analysis (Table 3b).

Three principal components resulted from the microclimate PCA. PCMICRO1 explained 58% of the variability in microclimate data and was characterized by increasing percentage ambient temperature, and decreasing percentage ambient humidity.

Table 3. Principal components analysis (PCA) eigenvectors (loadings) and percent of total variance explained for morphological variables (Table 3a) and microclimate variables (Table 3b). Loadings above 0.5 were considered highly important, loadings above 0.2 were considered moderately important, and loadings below 0.2 were considered unimportant in characterizing the principal components.

a) Morphological PCA				
	PC 1	PC 2	PC 3	PC 4
Surface Area	0.547	0.562	-0.569	-0.246
Dry Biomass	0.729	-0.076	0.535	-0.421
Length	0.780	-0.114	-0.001	0.616
Density	-0.189	0.866	0.417	0.204
Variance Explained (%)	36.854	27.103	19.582	16.461

b) Microclimate PCA			
	PC 1	PC 2	PC 3
% Ambient Temperature	-0.910	0.198	0.365
% Ambient Humidity	0.928	0.001	0.372
% Ambient PAR	0.182	0.980	-0.074
Variance Explained (%)	57.421	33.345	9.235

Lesser values of PCMICRO1 indicated cool and wet sub-canopy microclimates, whereas greater values indicated hot and dry sub-canopy microclimates. Thirty-three percent of the variability was explained by PCMICRO2, which was driven by increasing percent ambient PAR. Therefore, greater PCMICRO2 values indicated increased light microclimates and lesser values indicated dark microclimates. PCMICRO3, which explained 9% of the variability in microclimate data, was the final principal component of the microclimate PCA and was considered the leftovers of the analysis (Table 3b).

Morphology: Microclimate Association Analysis of Covariance

In the general ANCOVA analyses, which tested for among-site versus within-site effects of the morphology: microclimate association, it was important to determine interaction effects before determining main effects. Significant interactions were found for 2 of 12 possible interactions (Table 4). (Detailed information on all morphology: microclimate associations including ANCOVA tables, scatterplots of significant associations, slope distribution histograms, and scatterplots of slope analyses can be found in Appendix I.) For the PCMICRO1 analysis, the only significant interaction was SITE x PCMORPH1. This indicated that among-site variability was great and the strength of the relationship of PCMORPH1 on PCMICRO1

Table 4. PCMORPH1-4:PCMICRO1-3 ANCOVA results.
* Indicates significant results where seasonal analysis implies interactive effects. NS = Not Significant, $\alpha = 0.10$.

General ANCOVA Results			
	PCMICRO1	PCMICRO2	PCMICRO3
SITE	p = 0.038	NS	NS
PCMORPH1	NS	p = 0.045	NS
PCMORPH2	NS	NS	NS
PCMORPH3	NS	p = 0.041	NS
PCMORPH4	NS	p = 0.023	NS
SITE x PCMORPH1	p = 0.039	NS	p = 0.068*
SITE x PCMORPH2	NS	NS	NS
SITE x PCMORPH3	NS	NS	NS
SITE x PCMORPH4	NS	NS	NS

was site-specific. There also was a significant effect of SITE, simply indicating that PCMICRO1 varied as a function of site regardless of any morphological variables.

For the PCMICRO2 analysis, PCMORPH1, PCMORPH3, and PCMORPH4 were significant covariates in the analysis (Table 4). This indicated that these three morphological PCs significantly predicted PCMICRO2 generally across all sites and dates. For PCMICRO2, within site variability drove all relationships with PCMORPH1, 3, and 4.

The PCMICRO3 ANCOVA indicated that the interaction term SITE x PCMORPH1 was the only significant factor (Table 4). Significance of solely the interaction term indicated that among-site variability was great, and the strength of the relationship between PCMORPH1 and PCMICRO3 was site-specific. PCMICRO3 also had significant seasonal effects for both the interaction terms SEASON x PCMORPH1, and SITE x SEASON x PCMORPH1, indicating a high amount of temporal and spatial variability in the effect of morphology on microclimate (Table 1).

Given that analyses indicated both general and among-site differences, and there were weak if any seasonal effects (Table 1), it was important to explore the among-site variability in the strength of the associations. As interaction terms were significant for 2 of 3 ANCOVA analyses, further analysis to uncover trends in the site-specific significance was necessary. Site-specific slopes (β) for each of the significant morphology: microclimate interaction term relationships were determined, and these slopes were used in regression analysis with the following variables: latitude, time of day, total emersion time, and percentage ambient temperature, humidity, and PAR. Regression analysis indicated that latitude, time of day, emersion time, and ambient temperature never explained differences in the slope of the morphology: microclimate

association among sites ($p > 0.10$ for all analyses), however, ambient humidity ($p = 0.034$, $r^2 = 0.284$, $\beta = -0.029$) and ambient PAR ($p = 0.008$, $r^2 = 0.401$, $\beta = 0.001$) significantly explained differences in site-specific slopes of the morphology: microclimate association.

In general, both relationships with interactive effects (PCMORPH1:PCMICRO1, PCMORPH1:PCMICRO3) had normal distributions of morphology: microclimate slopes centered on zero, although there was an outlier in the PCMORPH1:PCMIRO1 slope data, and data were skewed right in the PCMORPH1:PCMICRO3 slope analysis. This indicated that effects could be positive or negative, depending on SITE. Analysis of the slopes of these relationships indicated that: none of the explanatory variables significantly explained trends in the site-specific slopes on the PCMORPH1:PCMICRO1 relationship; but ambient humidity and ambient PAR significantly explained trends in the site-specific slopes on the PCMORPH1:PCMICRO3 relationship.

Invertebrates Analysis of Covariance

PC Microclimate variables were used in ANCOVA with the dependent variables animal richness, abundance, and the organisms *Chlorostoma funebris* (formerly *Tegula funebris*), *Lottia* spp., *Littorina* spp., and *Musculus pygmaeus* (Table 5). The factor SITE was significant for all microclimate: invertebrate ANCOVAs, indicating that the relative abundance of invertebrates differed among sites. (Detailed information on all microclimate: invertebrate associations including ANCOVA tables, scatterplots of

Table 5. PCMICRO1-3:Invertebrate ANCOVA results. NS = Not Significant, $\alpha = 0.10$.

Microclimate:Invertebrate ANCOVA Results						
	Richness	Abundance	<i>C. funebris</i>	<i>Lottia</i> spp.	<i>Littorina</i> spp.	<i>M. pygmaeus</i>
SITE	p < 0.001	p < 0.001	p < 0.001	p < 0.001	p < 0.001	p < 0.001
PCMICRO1	NS	NS	NS	NS	NS	p < 0.001
PCMICRO2	p = 0.032	NS	NS	NS	NS	NS
PCMICRO3	NS	NS	NS	NS	NS	p < 0.001
SITE x PCMICRO1	NS	p = 0.045	NS	NS	p = 0.088	p < 0.001
SITE x PCMICRO2	NS	NS	NS	p = 0.073	NS	NS
SITE x PCMICRO3	NS	NS	NS	p = 0.047	NS	p < 0.001

significant associations, slope distribution histograms, and scatterplots of slope analyses can be found in Appendix II.) In the animal richness analysis the covariate PCMICRO2 was significant, while none of the interaction terms were significant, indicating that the relationship between PCMICRO2 and richness was general for all sites and dates.

Additionally, for the animal abundance analysis, the interaction term between SITE x PCMICRO1 was significant, however, none of the covariates were significant.

Therefore, the effect of PCMICRO1 on animal abundance was site-specific.

Four prominent individual species were analyzed for trends among sites. First, there were no significant covariate or interaction terms for the analysis of the effect of PCMICRO1-3 on *Chlorostoma funebris* (Table 5). Second, the interaction terms SITE

x PCMICRO2, and SITE x PCMICRO3 were significant in the *Lottia* spp. analysis, whereas none of the covariates were significant. This indicated that the effects of PCMICRO2 and PCMICRO3 on *Lottia* spp. were site-specific. Third, the interaction term SITE x PCMICRO1 was significant in the analysis on *Littorina* spp., indicating that the effect of PCMICRO1 on *Littorina* spp. was site-specific. Lastly, the interaction terms SITE x PCMICRO1, and SITE x PCMICRO3 were significant in the *Musculus pygmaeus* analysis. However, the covariates PCMICRO1 and PCMICRO3 also were significant, which indicated that although there were general relationships for the two covariates, the strength of the relationship was site-specific. This appeared to be due to *M. pygmaeus* data generally clustered on zero with few outliers that created a general trend.

Interaction terms were significant for several ANCOVA analyses (PCMICRO1:Abundance, PCMICRO2:*Lottia* spp., PCMICRO3:*Lottia* spp., PCMICRO1:*Littorina* spp., PCMICRO1:*Musculus pygmaeus*, PCMICRO3:*Musculus pygmaeus*, Table 5), therefore, further analysis to discover trends in the site-specific significance was necessary. Site-specific slopes (β) for each of the significant microclimate:invertebrate interaction term relationships were determined, and these slopes were used in regression analysis with the following variables: latitude, time of day, total emersion time, and percent ambient temperature, humidity and PAR. Regression analysis indicated that latitude and ambient temperature never helped to explain differences in the slope of the microclimate:invertebrate association among sites ($p > 0.10$ for all analyses), however, time of day, emersion time, and ambient humidity and

PAR significantly explained differences in site-specific slopes of the microclimate:invertebrate relationship.

Slopes of the microclimate:invertebrate relationships were generally zero with multiple sites displaying positive or negative slopes. The distribution of slopes was most likely non-normal due to the patchy distribution of mobile invertebrates in the intertidal system. Analysis of the slopes of these relationships indicated that: the explanatory variables time of day ($p = 0.075$, $r^2 = 0.210$, $\beta = -2.352$), ambient humidity ($p = 0.025$, $r^2 = 0.311$, $\beta = 0.711$), and ambient PAR ($p = 0.024$, $r^2 = 0.313$, $\beta = -0.011$) significantly explained trends in the site-specific slopes on the PCMICRO1:Abundance relationship; none of the explanatory variables significantly explained trends in the site-specific slopes on the PCMICRO2:*Lottia* spp. relationship nor the PCMICRO3:*Lottia* spp. relationship; emersion time significantly explained trends in the site-specific slopes on the PCMICRO1:*Littorina* spp. relationship ($p = 0.057$, $r^2 = 0.236$, $\beta = 2.313$); ambient PAR significantly explained trends in the site-specific slopes on the PCMICRO1:*Musculus pygmaeus* relationship ($p = 0.059$, $r^2 = 0.231$, $\beta = -0.009$); whereas none of the explanatory variables significantly explained trends in the site-specific slopes of the PCMICRO3:*Musculus pygmaeus* relationship.

To determine whether morphological variability would better explain trends in invertebrate distribution, a second ANCOVA was performed using PCMORPH1-4 on the same 6 invertebrate variables (Table 6). Results were significant for 4 of 6 variables, indicating that within- and among-site variability were high. (Detailed information on all morphology:invertebrate associations including ANCOVA tables, scatterplots of

Morphology:Invertebrate ANCOVA Results						
	Richness	Abundance	<i>Chlorostoma funnebralis</i>	<i>Lottia spp.</i>	<i>Littorina spp.</i>	<i>Musculus pygmaeus</i>
SITE	0.003	<0.001	NS	NS	<0.001	NS
PCMORPH1	NS	NS	0.077	NS	0.005	0.018
PCMORPH2	NS	0.007	0.002	NS	0.051	<0.001
PCMORPH3	NS	<0.001	0.001	NS	<0.001	0.019
PCMORPH4	NS	NS	NS	NS	0.019	0.077
SITE x PCMORPH1	NS	0.023	NS	NS	<0.001	NS
SITE x PCMORPH2	NS	0.008	0.047	NS	<0.001	NS
SITE x PCMORPH3	NS	<0.001	NS	NS	<0.001	NS
SITE x PCMORPH4	NS	0.001	NS	NS	<0.001	NS

Table 6. PCMORPH1-4:Invertebrate ANCOVA results. NS = Not Significant, $\alpha = 0.10$.

significant associations, slope distribution histograms, and scatterplots of slope analyses can be found in Appendix III.) In the animal richness analysis only SITE was significant, therefore, relative animal richness varied among sites. For the animal abundance analysis, all of the interaction terms between SITE x PCMORPH1-4 were significant, and

the factor SITE, and the covariates PCMORPH2 and PCMORPH3 were significant. Therefore, the effects of PCMORPH1 and PCMORPH4 on animal abundance varied among sites. As both the covariates and interaction terms were significant for PCMORPH2 and PCMORPH3, among-site variability drove these associations, however, site-specific data were centered mainly on zero and overlapped in a consistent manner to create a general trend. The significance of the factor SITE indicated solely that the relative animal abundance at each site varied.

Four prominent individual species were analyzed for trends among sites. First, the covariates PCMORPH1-3 and the interaction SITE x PCMORPH2 were significant for the analysis on *Chlorostoma funebris* (Table 6). Within-site variability in PCMORPH1 and PCMORPH3 affected these morphology:invertebrate relationships, which were general across all sites in central California. However, as both the covariate and the interaction were significant for PCMORPH2, among-site variability affected the association, however site-specific data overlapped in a consistent manner to form a general trend. Second, none of the morphological factors explained within- or among-site variability in *Lottia* spp. Third, all factors were significant in the analysis on *Littorina* spp., indicating a high amount of variability in the effect of morphology on *Littorina* spp. Both covariate and interaction terms were significant for all four PCMORPHs, indicating among-site variability affected the relationships between morphology and *Littorina* spp., however, data centered around zero with consistent overlapping of site-specific relationships created overall general trends. Significance of the factor SITE indicated that the relative abundance of *Littorina* spp. varied depending

on location. Lastly, all four covariates were significant in the *Musculus pygmaeus* analysis, indicating that there was a general effect of all morphological PCMORPHs on *M. pygmaeus* that was consistent within all sites in central California.

Slopes of the morphology:invertebrate relationships were generally zero with multiple sites displaying positive or negative slopes. Slopes were most likely non-normal due to the patchy distribution of mobile invertebrates in the intertidal system. Analyzing the slopes of these relationships indicated that: the explanatory variables ambient humidity ($p = 0.071$, $r^2 = 0.214$, $\beta = -0.432$) and ambient PAR ($p = 0.047$, $r^2 = 0.253$, $\beta = 0.007$) significantly explained trends in the site-specific slopes of the PCMORPH1:Abundance relationship; ambient PAR significantly explained trends in the site-specific slopes of the PCMORPH2:Abundance relationship ($p = 0.058$, $r^2 = 0.233$, $\beta = -0.014$); time of day ($p = 0.098$, $r^2 = 0.183$, $\beta = 3.080$) and emersion time ($p = 0.085$, $r^2 = 0.197$, $\beta = -5.843$) significantly explained trends in the site-specific slopes of the PCMORPH3:Abundance relationship; none of the explanatory variables significantly explained trends in the site-specific slopes of the PCMORPH4:Abundance relationship nor the PCMORPH2:*C. funebris* relationship ($p > 0.10$ for all regression analyses); ambient PAR significantly explained trends in the site-specific slopes of the PCMORPH1:*Littorina* spp. relationship ($p = 0.038$, $r^2 = 0.272$, $\beta = 0.007$); latitude significantly explained trends in the site-specific slopes of the PCMORPH2:*Littorina* spp. relationship ($p = 0.079$, $r^2 = 0.493$, $\beta = 2.503$); time of day ($p = 0.033$, $r^2 = 0.287$, $\beta = 3.314$) and emersion time ($p = 0.059$, $r^2 = 0.232$, $\beta = -5.456$) significantly explained trends in the site-specific slopes of the PCMORPH3:*Littorina* spp. relationship; and

latitude significantly explained trends in the site-specific slopes of the PCMORPH4:*Littorina* spp. relationship ($p = 0.072$, $r^2 = 0.508$, $\beta = -7.047$). The response of invertebrates to morphological variability in *Mastocarpus* spp. was more variable, as the majority of terms in a given analysis were either greatly significant or greatly insignificant, than the response of invertebrates to sub-canopy microclimate where the distinction between significant within- (covariate) versus among- (interaction) site variability in predicting invertebrate response was more consistent.

To determine whether morphological variability affecting microclimate in turn affected invertebrate species distributions, comparisons were made between significant results of the microclimate:invertebrate relationships, and the reduced-microclimate:invertebrate relationships. As all results that were significant in the microclimate:invertebrate analyses (Table 5) were no longer significant in the reduced-microclimate:invertebrate analyses, the effects of microclimate on macroinvertebrate distribution were due solely to the cascading effect of morphological variability on microclimate (Table 7). Therefore, *Chlorostoma funebris* distribution was affected

Table 7. Summary of invertebrate ANCOVAs. Underlined text indicates those invertebrates that are associated with microclimate that is affected by morphological variability in *Mastocarpus* spp.

Combined ANCOVA Results				
	<i>C. funebris</i>	<i>Lottia</i> spp.	<i>Littorina</i> spp.	<i>M. pygmaeus</i>
Morphology	Yes	No	Yes	Yes
Microclimate	No	<u>Yes</u>	<u>Yes</u>	<u>Yes</u>

solely by morphological variability in *Mastocarpus* spp., but invertebrate richness and abundance, and the species *Lottia* spp., *Littorina* spp., and *Musculus pygmaeus* were associated with cascading effects of morphological variability on microclimate.

Specifically, variability in *Mastocarpus* spp. size created microclimates that ranged from hot and dry, to cool and wet, which affected the distribution of invertebrate abundance, *Littorina* spp., and *M. pygmaeus*. Morphological size and turfiness affected irradiance sub-canopy, and both species richness and *Lottia* spp. distribution were affected by morphologically induced changes in sub-canopy irradiance.

DISCUSSION

Morphological variability in *Mastocarpus* spp. significantly altered sub-canopy microclimate, the affects of which were both broad-scale and localized. Variability in morphology occurred year-round, and the morphology: microclimate association was not generally affected by seasonal fluctuations in local climate conditions or inter-seasonal shifting morphologies. This association also elicited a response in invertebrate species present within this latitudinal spread of central California, where microclimate that was significantly altered by morphological variability explained trends in species composition (richness and abundance) and single species responses (*Chlorostoma funebris*, *Lottia* spp., *Littorina* spp., and *Musculus pygmaeus*). Invertebrate species responded more variably to morphological variation in *Mastocarpus* spp. than to sub-canopy microclimate; however, both factors combined explain trends in all invertebrate species and assemblages investigated.

Morphology: Microclimate Association

Morphological variability in *Mastocarpus* spp. created two distinct microclimates: microclimates that ranged from cooler and wetter to hotter and dryer than ambient conditions (PCMICRO1), and microclimates that ranged from darker to equal to that of ambient light conditions (PCMICRO2, Table 3b). Trends in the morphology: microclimate association were site-specific with regards to PCMICRO1, but were general across all sites with regards to PCMICRO2 (Table 4). Therefore, the effect that morphological variability had on irradiance (PCMICRO2) reaching the substrate was

universal within central California; however, the effect of morphology creating cool and wet to hot and dry microclimates (PCMICRO1) varied as a function of location.

Changes in size alone (surface area, length, and dry biomass; PCMORPH1) caused sub-canopy microclimate to fluctuate between stress amelioration (cooler and wetter microclimates than ambient conditions) and stress enhancement (hotter and dryer microclimates than ambient conditions). The direction and magnitude of this association fluctuated among sites, indicating that in some areas, patches of smaller sized fronds of *Mastocarpus* spp. created cool and wet microclimates whereas patches of larger sized fronds created hot and dry microclimates. In these instances, the interstitial space between smaller individuals may trap cooler, humid air more efficiently than their hydrophilic counterparts of larger size (Hay 1981, Bell 1995, Scrosati and DeWreede 1998). As larger individuals can inherently hold more water in their tissue, the moist air may be drawn from the sub-canopy into the thalli (Bell 1995). Without the aid of moisture to keep the environment cool, sub-canopy air temperature may increase more rapidly (i.e., differences in specific heat of dry air vs. humid air). In areas characterized by negative slopes, smaller individuals can ameliorate ambient conditions to 58% of ambient temperature and 160% of ambient humidity, whereas larger individuals can alter ambient conditions to 136% of ambient temperature and 79% of ambient humidity sub-canopy.

Conversely, some sites exhibited opposite effects of morphology on microclimate: smaller sized *Mastocarpus* spp. patches created more hot and dry microclimates, whereas larger sized patches created cool and wet microclimates. This relationship followed the

terrestrial paradigm that larger canopies ameliorate the effects of stressful ambient conditions to the understory by blocking exposure to light, heat, wind, UV radiation, and so forth, more than their smaller counterparts (Harper 1977, Lowman and Rinker 2004, Gurevitch et al. 2006). Larger *Mastocarpus* spp. individuals can ameliorate ambient conditions to 60% of ambient temperature and 190% of ambient humidity, whereas smaller individuals alter ambient conditions to 106% of ambient temperature and 113% of ambient humidity sub-canopy. The variability in the effect of size on temperature and humidity indicated that external factors may help to explain the shifting relationship; however, as none of the explanatory variables explained trends in the slopes, it was difficult to explain the among-site variability. Significance of the factor SITE indicated that ambient conditions varied as a function of site; however, neither ambient temperature, humidity, nor PAR explained changes in the slopes in the effect of size on sub-canopy temperature and humidity.

The size of *Mastocarpus* spp. also had an effect on sub-canopy irradiance. This effect was consistent within central California; as the size of thalli in the core increased, irradiance decreased. The magnitude of this effect ranged from 85% of ambient irradiance sub-canopy under small-sized individuals to 1% ambient irradiance sub-canopy under large-sized *Mastocarpus* spp. However, the amount of variability in irradiance for smaller sized *Mastocarpus* spp. (PCMORPH1) indicated there might be a size threshold near the principal component score of zero. Therefore, light is able to reach the substrate for negative scores of PCMORPH1, but once the threshold is reached, the amount of irradiance incident to the substrate for positive scores of PCMORPH1 is

near zero. This threshold is most likely the size of *Mastocarpus* spp. at which the thalli shift from standing erect, to falling over and blanketing the substrate (J. Jorve, personal observation). Similar trends have been found in terrestrial systems, where increases in Leaf Area Index (LAI) of forest canopies, or the amount of material covering a known surface area, caused subsequent decreases in PAR transmittance to the substrate (Monsi and Saeki 1953 in Parker 1995). In addition, leaf distribution has a large effect on sub-canopy light transmission, with horizontally oriented leaves (planophilic) causing the most drastic reduction in PAR transmission (de Wit 1965 in Parker 1995). Therefore, as the thalli of *Mastocarpus* spp. reached the size at which they lay prostrate to the substrate, or planophilic, light transmission to the substrate was severely reduced.

PCMORPH3 also significantly affected sub-canopy irradiance consistently within central California. Negative principal component scores for this morphological term indicated a shift from “blade-like” patches of *Mastocarpus* spp. at lesser values of PCMORPH3 to “stick-like” patches of *Mastocarpus* spp. at greater values of PCMORPH3. Greater surface area, lesser dry biomass, and lesser densities characterized “blade-like” patches whereas “stick-like” cores had lesser surface area, greater dry biomass, and greater density (Table 3a). The “stick-like” *Mastocarpus* spp. were characteristic of the species *M. jardinii*, whereas the “blade-like” *Mastocarpus* spp. were more like the species *M. papillatus*, although not all species were categorized in PCMORPH3 according to this manner. The amount of irradiance reaching the substrate increased as morphologies shifted from “blade-like” patches of *Mastocarpus* spp. to “stick-like” patches of *Mastocarpus* spp. within central California (Fig. 6). However, the

amount of variability in irradiance near PCMORPH3 scores of zero indicated that the lesser density “blade-like” patches and the greater density “stick-like” patches both reduced sub-canopy irradiance to almost zero (roughly 2% ambient PAR), but the patches with intermediate levels of “blade-like” or “stick-like” fronds intercepted variable amounts of irradiance (with sub-canopy irradiance ranging from 2% to 85% ambient PAR). This pattern was most likely due to the fact that greater densities of the “stick-like” fronds blocked irradiance from reaching the substrate (Scrosati and DeWreede 1998), and the patches with larger “blade-like” fronds lay prostrate to the substrate, blanketing the area and blocking irradiance (de Wit 1965 in Parker 1995). The intermediate patches were not dense enough, or large and heavy enough to do either, allowing light to reach the substrate.

Lastly, the general association PCMORPH4:PCMICRO2 as well as the site specific association PCMORPH1:PCMICRO3 were significant in the analyses (Table 4), however, due to issues of independence and seasonality, in addition to the fact that PCMORPH4 and PCMICRO3 were considered the “leftovers” of the PCA, these variables were not considered.

Response of Invertebrates to Morphology: Microclimate Association

Morphological variability in *Mastocarpus* spp. created within- and among-site variability in sub-canopy microclimates. Single species and invertebrate assemblage data indicated that both morphological and microclimate variability significantly affected invertebrate distribution within- and among-sites (Tables 5, 6). Decreasing temperature

and increasing humidity (PCMICRO1) had solely site-specific effects on invertebrate abundance and abundance of *Littorina* spp. and *Musculus pygmaeus*. The relationship between decreasing temperature and increasing humidity on invertebrate abundance was generally negative, where a greater number of individuals were found in more hot and dry microclimates. Analyses on the site-specific slopes indicated that time of day, ambient humidity, and ambient PAR explained trends in the site-specific slopes, therefore, changing daily conditions may affect the association between microclimate and abundance. Data for *Littorina* spp. displayed similar trends. Because *Littorina* spp. and abundance were correlated ($r = 0.893$, $p < 0.001$), both results were most likely driven by the snail's natural history and ecological niche, indicating that their ability to withstand the stressful conditions of the higher intertidal zone where hot and dry microclimates prevail drove these relationships (Morris et al. 1980). Emersion time, however, significantly explained site-specific slopes of the association such that negative slopes (greater light, greater abundance of *Littorina* spp.) were associated with lesser total emersion time, and positive slopes (lesser light, lesser abundance of *Littorina* spp.) with greater emersion time, indicating that the duration of tolerance to hot and dry conditions affected their abundances. In addition, as the factor DATE was significant, the sampling dates with the four greatest abundances of *Littorina* spp. were the four samples collected at Pigeon Point, which could be strongly affecting the association.

Musculus pygmaeus displayed the opposite general trend: cooler and more humid microclimates had greater amounts of *M. pygmaeus*. This mussel attaches to the holdfast and blades of the intertidal turf alga *Endocladia muricata*, an alga that also is found in the

mid to high intertidal zone, and in patchy conjunction with *Mastocarpus* spp. (Glynn 1964, 1965, Foster et al. 1988, 1991). Samples of *Mastocarpus* spp. could have been next to patches of *E. muricata*, and in some cases *E. muricata* was found within the sample (however, a very small portion of the total core biomass). The *E. muricata* - *M. pygmaeus* association is patchy in distribution as *M. pygmaeus* recruits live closely to the adults (Glynn 1964), which could account for the distribution of the slopes to be close to the positive side of zero. In general, *M. pygmaeus* abundance was most likely highly influenced by *E. muricata*, and not a direct association to sub-canopy microclimate created by *Mastocarpus* spp.

Sub-canopy irradiance levels influenced species richness and the limpet *Lottia* spp., however, the effect of irradiance on richness was general in central California and site-specific for *Lottia* spp. (PCMICRO2). Although there was a significant general trend in the effect of irradiance on species richness, the increased amount of variability in the data at lesser irradiance levels indicated that there was a threshold level of irradiance (between principal component scores of -1 and 2 for PCMICRO2) up to which some amount of irradiance was tolerable, but after which irradiance levels were great enough such that only extremely light-tolerant species were able to inhabit those microclimates. Irradiance affected the limpet *Lottia* spp. differently among sites. Slopes were generally centered on zero, therefore the magnitude of the effect of irradiance on *Lottia* spp. was not strong. The positive effect irradiance had on *Lottia* spp. abundance may have been due to the fact that their food source, microalgae, may be more abundant in cores where light reached the substrate (Harley 2002). Conversely, increased irradiance had a

negative effect on limpet abundance in other areas, which may have been due to increased environmental stress on *Lottia* spp. Again, the significant associations between PCMICRO3 and invertebrates, and PCMORPH4 and invertebrates, were not considered, as these factors were the “leftovers” of the PCA.

Morphological variability in *Mastocarpus* spp. affected total species abundance, and the single species *Chlorostoma funebris*, *Littorina* spp., and *Musculus pygmaeus* (Table 6). Species abundance and the periwinkle snail *Littorina* spp. had similar responses to morphological variability, with site-specific effects significant for all four morphological principal components. This similar response together with the strong correlation between abundance and *Littorina* spp. ($r = 0.893$, $p < 0.001$) indicated that *Littorina* spp. affected the relationship between morphology and abundance of invertebrates. The presence of *Littorina* spp. with all *Mastocarpus* spp. morphologies demonstrated a strong relationship between the alga *Mastocarpus* spp. and *Littorina* spp. Both taxa are typical inhabitants of the mid to high intertidal zone, and although *Littorina* spp. abundances were generally unaffected by removal of habitat-forming species (Foster et al. 2003), the fact that all morphologies of *Mastocarpus* spp. affected their distribution indicated connectivity between the taxa.

The effects of size (PCMORPH1), “turfiness” (PCMORPH2), and “shape” (PCMORPH3) on *Littorina* spp. were all site-specific. Firstly, differences in the effect of *Mastocarpus* spp. size on *Littorina* spp. could be attributed to ambient irradiance conditions, such that slight increases in PAR explained the shift from greater abundance of *Littorina* spp. under smaller sized morphologies, to lesser abundances under larger

sized morphologies of *Mastocarpus* spp. As PAR increased and ambient conditions became more stressful, the snails may associate with the larger sized morphologies that tended to lay prostrate and blanket the substrate, blocking direct contact from UV radiation, therefore, ameliorating body temperatures (Burnaford 2004). As total species abundance and *Littorina* spp. abundance had the same slopes in the ambient PAR analysis, this again indicated that total species abundance was affected almost completely by *Littorina* spp.

Secondly, the effect of “turfiness” on *Littorina* spp. could be predicted by latitude; as latitude increased *Littorina* spp. shifted from greater abundances under more sparse turfs, to greater abundances under more densely packed turfs of *Mastocarpus* spp. Increased substrate area within the low-density turfs could have created more space for a greater abundance of mobile macroinvertebrates such as *Littorina* spp. in lower latitudes (Kelaher 2002). Conversely, reduced desiccation stress associated with high-density algal stands could account for the greater invertebrate abundance in greater density stands at higher latitudes (Scrosati and DeWreede 1998). Additionally, *Littorina* spp. were found nestled between the papillae of *Mastocarpus* spp. (J. Jorve, personal observation) therefore, the greater density could have created more niches in the fronds for the snails (Levin and Hay 1996).

Lastly, the site-specific effects of shape on *Littorina* spp. were explained by both time of day and emersion time. Specifically, as time of day increased (moving from morning to afternoon) more *Littorina* spp. shifted from “blade-like” to “stick-like” morphologies of *Mastocarpus* spp., and as emersion time increased, *Littorina* spp. shifted

from “stick-like” to “blade-like” morphologies. Therefore, *Littorina* spp. were found in greater abundances during the morning immediately following emersion under “blade-like” morphologies, and in greater abundances during the afternoon after prolonged emersion under “stick-like” morphologies. Mobile macroinvertebrates generally do not migrate during emersion periods (Newell 1979, Raffaelli and Hawkins 1996); however, *Littorina* spp. do migrate on wet substratum, moving to cover as exposure time increases (C.D.G. Harley, personal communication). Additionally, both of these explanatory variables (time of day and exposure time) significantly predicted the differing effects of shape on total species abundance with extremely similar slopes, reaffirming that abundance was mostly affected by *Littorina* spp.

The distribution of *Chlorostoma funebris* was significantly explained by *Mastocarpus* spp. “size”, “shape”, and “turfiness.” *Chlorostoma funebris* was the largest, most abundant grazer encountered, found almost exclusively attached to hard substrate and rarely directly on the alga itself. As size of *Mastocarpus* spp. increased, *C. funebris* abundance decreased. As this trend was consistent in central California, it was most likely due to the fact that larger fronds took up more space, crowding out these larger snails. The large amount of variability in this relationship for negative values of “size” (PCMORPH1) indicated that this trend might in fact be non-linear; as morphology transitioned from small to large sized fronds, *C. funebris* were rapidly crowded out from the substrate, at which point few were found sub-canopy.

Similarly, morphological “shape” of *Mastocarpus* spp. had non-linear effects on *C. funebris*. Although analyses indicated that as morphologies shifted from “blade-

like” to “stick-like” *C. funebris* abundance decreased, the large amount of variability associated with zero principal component scores indicated a range of possible abundances of *C. funebris* under intermediate shape morphologies, whereas both “blade-like” and “stick-like” morphologies were associated with low abundances of *C. funebris*. This was also most likely due to lack of space under the greater surface area of “blade-like” morphologies and the high-density “stick-like” morphologies. Algal material distribution was less inhibitory under intermediate shapes, allowing for the high variability in *C. funebris* distribution, most likely associated with the patchy distribution of intertidal organisms, in addition to fractal dimensions and variability of the substrate (reviews in Pickett and White 1985, Gee and Warwick 1994).

ANCOVA indicated variability in the effect of “turfiness” on *C. funebris*, however, most sites had positive slopes of the PCMORPH2:*C. funebris* relationship. Therefore, as density and surface area increased to form a more tightly packed turf, snail abundance increased. This relationship is contrary to the effects of size and shape on *C. funebris*, where greater surface area and density generally meant less space for snails to inhabit. However, increased habitat complexity and greater protection from wave exposure could account for this difference. As turf algae are characteristic in stressful environments, the interstitial spaces between the fronds of *Mastocarpus* spp. could provide refuge for the larger snails from the harsh conditions of the intertidal zone (Hay 1981, Scrosati and DeWreede 1998).

Trends in the effect of *Mastocarpus* spp. morphological variability on *Musculus pygmaeus* were general across all sites, however, data indicated that these trends were in

fact non-linear and more patchily distributed. As previously mentioned, *M. pygmaeus* are associated with the algal turf *Endocladia muricata*, which occurs in tandem with *Mastocarpus* spp. (Glynn 1964, 1965, Foster et al. 1988, 1991). Therefore, the direct effect of *Mastocarpus* spp. morphology was most likely minimal, and these general trends in the effect of morphological variability on *M. pygmaeus* were probably due to the proximity of *E. muricata* within or near the *Mastocarpus* spp. cores. The effects of PCMORPH1:PCMICRO3 on *M. pygmaeus* were not considered ecologically important as PCMICRO3 was the leftovers of the PCA microclimate analysis, and *M. pygmaeus* was probably more directly linked to adjacent effects of the alga *Endocladia muricata*.

As the reduced-microclimate:invertebrate analyses indicated, all of the significant microclimate:invertebrate results were due to the cascading effect of morphological variability on microclimate, which in turn affected invertebrate distribution (Table 7). These refuges from the stressful conditions of the intertidal zone created by morphologically induced microclimate, although variable, could ameliorate the effects of intertidal stressors. As *Mastocarpus* spp. is a cosmopolitan species on the Pacific coast of North America (Abbott and Hollenberg 1976), the association between morphological variability in this alga and the sub-canopy microclimate it creates could affect the distribution and abundance of associated invertebrates throughout this latitudinal extent as well.

CONCLUSIONS

Morphological variability in a single genera can create habitat variability usually associated with diverse, multi-species assemblages (Foster et al. 1988, 1991, Stachowicz et al. In Press). Thalli of *Mastocarpus* spp. were found from 1 to 25 cm long, with 2 to 63 fronds per 10 cm²; an order of magnitude in range for both types of biomass distribution. Shorter lengths, normally corresponding with greater densities, are consistent with most turf species in the rocky intertidal zone, mid-range lengths with mid-range densities are typical of the foliose reds, whereas the longer lengths and lesser densities are what are usually attributed to canopy-forming species (Foster et al. 1988, 1991). All of these lengths can be encountered in a single 10-cm diameter area, creating variability in habitat structure in a single alga, which could encompass the range of habitats necessary to support diverse and abundant invertebrate assemblages (Taylor and Cole 1994).

With climate change rapidly becoming a topic that scientists have to consider in all facets of ecological modeling, species with small latitudinal distributions and distinct biogeographic boundaries may be more susceptible to rapidly shifting environmental conditions. It may become pertinent for management strategies to target those species that serve a variety of ecological functions, inhabit a wide range of environments (i.e. wave exposed to wave protected sites), span a large latitudinal gradient, and are economically valuable and sustainable to harvest. *Mastocarpus* spp. encompasses all of these characteristics, ameliorates rapidly shifting environmental conditions in the highly stressful intertidal zone, and is host to a large diversity of invertebrate species that range

in distribution and abundance. Although most of the effects of morphology, microclimate, and invertebrate interactions were influenced by location, environmental amelioration existed in some capacity throughout central California, and possibly throughout the entirety of its range along the Pacific coast of North America.

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APPENDIX I. MORPHOLOGY:MICROCLIMATE DATA

Tables, scatterplots and histograms of the effect of Mastocarpus spp. morphological variability on sub-canopy microclimate.

Table 1. ANCOVA table for PCMORPH1-4:PCMICRO1.

ANCOVA Results for PCMICRO1					
	SS	DF	MS	F	P
SITE	13.013	15	.868	1.764	.038
PCMORPH1	1.213	1	1.213	2.465	.117
PCMORPH2	.306	1	.306	.622	.431
PCMORPH3	.366	1	.366	.743	.389
PCMORPH4	.018	1	.018	.036	.849
SITE x PCMORPH1	12.939	15	.863	1.754	.039
SITE x PCMORPH2	9.440	15	.629	1.279	.211
SITE x PCMORPH3	8.080	15	.539	1.095	.359
SITE x PCMORPH4	9.381	15	.625	1.271	.217
Error	200.690	408	.492		

Table 2. ANCOVA table for PCMORPH1-4:PCMICRO2.

ANCOVA Results for PCMICRO2					
	SS	DF	MS	F	P
SITE	7.990	15	.533	.870	.599
PCMORPH1	2.487	1	2.487	4.059	.045
PCMORPH2	.454	1	.454	.741	.390
PCMORPH3	2.581	1	2.581	4.213	.041
PCMORPH4	3.171	7.348	3.171	5.176	.023
SITE x PCMORPH1	7.348	15	.490	.800	.678
SITE x PCMORPH2	5.834	15	.389	.635	.846
SITE x PCMORPH3	6.834	15	.456	.744	.740
SITE x PCMORPH4	11.742	15	.783	1.278	.212
Error	249.928	408	.613		

Table 3. ANCOVA table for PCMORPH1-4:PCMICRO3.

ANCOVA Results for PCMICRO3					
	SS	DF	MS	F	P
SITE	16.377	15	1.092	1.335	.178
PCMORPH1	2.152	1	2.152	2.631	.106
PCMORPH2	.817	1	.817	.999	.318
PCMORPH3	.006	1	.006	.008	.930
PCMORPH4	.241	1	.241	.296	.587
SITE x PCMORPH1	19.737	15	1.316	1.609	.068
SITE x PCMORPH2	14.093	15	.940	1.149	.310
SITE x PCMORPH3	15.106	15	1.007	1.231	.245
SITE x PCMORPH4	7.326	15	.488	.597	.878
Error	333.734	408	.818		

Table 4. Results of regression analysis using individual sampling SITE slopes for each of the morphology:microclimate associations (PCMORPH1-4:PCMICRO1-3) regressed against possible explanatory variables latitude, time of day, emersion time, and ambient conditions. NS = Not Significant, $\alpha = 0.10$.

Beta Analysis of ANCOVA Results		
	PCMORPH1:PCMICRO1	PCMORPH1:PCMICRO3
Latitude	NS	NS
Time of Day	NS	NS
Emersion Time	NS	NS
Ambient Temperature	NS	NS
Ambient Humidity	NS	$p = 0.034$ $r^2 = 0.284$ $\beta = -0.029$
Ambient PAR	NS	$p = 0.008$ $r^2 = 0.401$ $\beta = 0.001$

Figure 1. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMOPRH1:PCMICRO1. Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 2. Scatterplot of general trend for PCMOPRH1:PCMICRO2 ($p < 0.001$, $r^2 = 0.071$, $\beta = -0.261$).

Figure 3. Scatterplot of general trend for PCMORPH3:PCMICRO2 ($p < 0.001$, $r^2 = 0.025$, $\beta = 0.155$).

Figure 4. Scatterplot of general trend for PCMICRO2:PCMORPH4 ($p = 0.009$, $r^2 = 0.014$, $\beta = 0.115$).

Figure 5. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMICRO3:PCMORPH1. Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 6. PCMORPH1:PCMICRO1 β frequency distribution.

Figure 7. PCMORPH1:PCMICRO3 β frequency distribution.

Figure 8. Scatterplot of the PCMORPH1:PCMICRO3 slopes of each SITE regressed against significant explanatory variables (analysis of β). Errors bars are standard error of β ($p = 0.034$, $r^2 = 0.284$, $\beta = -0.029$).

Figure 9. Scatterplot of the PCMORPH1:PCMICRO3 slopes of each SITE regressed against significant explanatory variables (analysis of β). Errors bars are standard error of β ($p = 0.008$, $r^2 = 0.401$, $\beta = 0.001$).

APPENDIX II. MICROCLIMATE:INVERTEBRATE DATA

Scatterplots and histograms of the effect of sub-canopy microclimate variability on macroinvertebrate distributions.

Table 1. ANCOVA table for PCMICRO1-3:Richness.

ANCOVA Results for Species Richness					
	SS	DF	MS	F	P
SITE	104.382	15	6.959	3.354	<.001
PCMICRO1	.549	1	.549	.264	.607
PCMICRO2	9.620	1	9.620	4.637	.032
PCMICRO3	.009	1	.009	.004	.949
SITE x PCMICRO1	31.003	15	2.067	.996	.458
SITE x PCMICRO2	30.415	15	2.028	.977	.478
SITE x PCMICRO3	21.872	15	1.452	.700	.785
Error	896.282	432	2.075		

Table 2. ANCOVA table for PCMICRO1-3:Abundance.

ANCOVA Results for Species Abundance					
	SS	DF	MS	F	P
SITE	150785.778	15	10052.385	9.888	<.001
PCMICRO1	1059.526	1	1059.526	1.042	.308
PCMICRO2	.010	1	.010	<.001	.998
PCMICRO3	1211.899	1	1211.899	1.192	.276
SITE x PCMICRO1	26215.489	15	1747.699	1.719	.045
SITE x PCMICRO2	4367.975	15	291.198	.286	.996
SITE x PCMICRO3	21161.665	15	1410.778	1.388	.149
Error	439181.102	432	1016.623		

Table 3. ANCOVA table for PCMICRO1-3:*C. funebris*.

ANCOVA Results for <i>Chlorostoma funebris</i>					
	SS	DF	MS	F	P
SITE	1750.582	15	116.705	3.701	<.001
PCMICRO1	15.640	1	15.640	.496	.482
PCMICRO2	32.796	1	32.796	1.040	.308
PCMICRO3	8.141	1	8.141	.258	.612
SITE x PCMICRO1	547.683	15	36.512	1.158	.302
SITE x PCMICRO2	590.423	15	39.362	1.248	.232
SITE x PCMICRO3	436.243	15	29.083	.922	.539
Error	13620.945	432	31.530		

Table 4. ANCOVA table for PCMICRO1-3:*Lottia* spp.

ANCOVA Results for <i>Lottia</i> spp.					
	SS	DF	MS	F	P
SITE	294.102	15	19.607	3.960	<.001
PCMICRO1	10.354	1	10.354	2.091	.149
PCMICRO2	1.649	1	1.649	.333	.564
PCMICRO3	.003	1	.003	.001	.981
SITE x PCMICRO1	76.696	15	5.113	1.033	.420
SITE x PCMICRO2	118.086	15	7.872	1.590	.073
SITE x PCMICRO3	126.611	15	8.441	1.705	.047
Error	2139.093	432	4.952		

Table 5. ANCOVA table for PCMICRO1-3:*Littorina* spp.

ANCOVA Results for <i>Littorina</i> spp.					
	SS	DF	MS	F	P
SITE	119808.924	15	7987.262	11.309	<.001
PCMICRO1	786.627	1	786.627	1.114	.292
PCMICRO2	243.197	1	243.197	.344	.558
PCMICRO3	1041.256	1	1041.256	1.474	.225
SITE x PCMICRO1	16290.447	15	1086.030	1.538	.088
SITE x PCMICRO2	3116.698	15	207.780	.294	.996
SITE x PCMICRO3	11058.182	15	737.212	1.044	.408
Error	305100.021	432	706.250		

Table 6. ANCOVA table for PCMICRO1-3:*M. pygmaeus*.

ANCOVA Results for <i>Musculus pygmaeus</i>					
	SS	DF	MS	F	P
SITE	19716.931	15	1314.462	5.730	<.001
PCMICRO1	3522.252	1	3522.252	15.355	<.001
PCMICRO2	10.986	1	10.986	.048	.827
PCMICRO3	4515.796	1	4515.796	19.686	<.001
SITE x PCMICRO1	14517.596	15	967.840	4.219	<.001
SITE x PCMICRO2	192.561	15	12.837	.056	1.000
SITE x PCMICRO3	13241.986	15	882.799	3.848	<.001
Error	99098.734	432	229.395		

Table 7. Results of regression analysis using individual sampling SITE slopes for each of the significant interaction PCMICRO1-3:Invertebrate associations regressed against possible explanatory variables latitude, time of day, emersion time, and ambient conditions. NS = Not Significant, $\alpha = 0.10$.

Analysis of Betas of Significant Interactions in Microclimate:Invertebrate ANCOVA Results						
	PCMICRO1: Abundance	PCMICRO2: <i>Lottia</i> spp.	PCMICRO3: <i>Lottia</i> spp.	PCMICRO1: <i>Littorina</i> spp.	PCMICRO1: <i>M. pygmaeus</i>	PCMICRO3: <i>M. pygmaeus</i>
Latitude	NS	NS	NS	NS	NS	NS
Time of Day	$p = 0.075$ $r^2 = 0.210$ $\beta = -2.352$	NS	NS	NS	NS	NS
Emersion Time	NS	NS	NS	$p = 0.057$ $r^2 = 0.236$ $\beta = 2.313$	NS	NS
Ambient Temperature	NS	NS	NS	NS	NS	NS
Ambient Humidity	$p = 0.025$ $r^2 = 0.311$ $\beta = 0.711$	NS	NS	NS	NS	NS
Ambient PAR	$p = 0.024$ $r^2 = 0.313$ $\beta = -0.011$	NS	NS	NS	$p = 0.059$ $r^2 = 0.231$ $\beta = -0.009$	NS

Figure 1. Scatterplot of PCMICRO2:Richness with regression line indicating the significant general trend for the entire dataset ($p = 0.032$, $r^2 = 0.002$, $\beta = 0.032$).

Figure 2. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMICRO1:Abundance. Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 3. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMICRO2:*Lottia* spp. Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 4. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMICRO3:*Lottia* spp. Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 5. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMICRO1:*Littorina* spp. Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 6. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMICRO1:*M. pygmaeus*. The black dashed line indicates the significant general trend of PCMICRO1:*M. pygmaeus* for the entire dataset ($p < 0.001$, $r^2 = 0.005$, $\beta = -1.154$). Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 7. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMICRO3:*M. pygmaeus*. The black dashed line indicates the significant general trend of PCMICRO3:*M. pygmaeus* for the entire dataset ($p < 0.001$, $r^2 = 0.001$, $\beta = -0.391$). Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 8. PCMICRO1: Abundance β frequency distribution.

Figure 9. PCMICRO2:*Lottia* spp. β frequency distribution.

Figure 10. PCMICRO3:*Lottia* spp. β frequency distribution.

Figure 11. PCMICRO1:*Littorina* spp. β frequency distribution.

Figure 12. PCMICRO1:*M. pygmaeus* β frequency distribution.

Figure 13. PCMICRO3:*M. pygmaeus* β frequency distribution.

Figure 14. Scatterplot of the PCMICRO1:Abundance slopes of each SITE regressed against significant explanatory variables (analysis of β). Errors bars are standard error of β ($p = 0.075$, $r^2 = 0.210$, $\beta = -2.352$).

Figure 15. Scatterplot of the PCMICRO1:Abundance slopes of each SITE regressed against significant explanatory variables (analysis of β). Errors bars are standard error of β ($p = 0.025$, $r^2 = 0.311$, $\beta = 0.711$).

Figure 16. Scatterplot of the PCMICRO1:Abundance slopes of each SITE regressed against significant explanatory variables (analysis of β). Errors bars are standard error of β ($p = 0.024$, $r^2 = 0.313$, $\beta = -0.011$).

Figure 17. Scatterplot of the PCMICRO1:*Littorina* spp. slopes of each SITE regressed against significant explanatory variables (analysis of β). Errors bars are standard error of β ($p = 0.057$, $r^2 = 0.236$, $\beta = 2.313$).

Figure 18. Scatterplot of the PCMICRO1:*M. pygmaeus* slopes of each SITE regressed against significant explanatory variables (analysis of β). Errors bars are standard error of β ($p = 0.059$, $r^2 = 0.231$, $\beta = -0.009$).

APPENDIX III. MORPHOLOGY:INVERTEBRATE DATA

Scatterplots and histograms of the effect of Mastocarpus spp. morphological variability on macroinvertebrate distributions.

Table 1. ANCOVA table for PCMORPH1-4:Richness.

ANCOVA Results for Species Richness					
	SS	DF	MS	F	P
SITE	72.597	15	4.840	2.363	.003
PCMORPH1	2.313	1	2.313	1.129	.289
PCMORPH2	.072	1	.072	.035	.851
PCMORPH3	.001	1	.001	<.001	.994
PCMORPH4	.538	1	.538	.263	.608
SITE x PCMORPH1	42.875	15	2.858	1.396	.145
SITE x PCMORPH2	31.461	15	2.097	1.024	.429
SITE x PCMORPH3	33.448	15	2.230	1.089	.364
SITE x PCMORPH4	24.461	15	1.631	.796	.682
Error	845.823	413	2.048		

Table 2. ANCOVA table for PCMORPH1-4:Abundance.

ANCOVA Results for Species Abundance					
	SS	DF	MS	F	P
SITE	116309.944	15	7753.996	6.615	<.001
PCMORPH1	1063.570	1	1063.570	.907	.341
PCMORPH2	8675.769	1	8675.769	7.401	.007
PCMORPH3	18427.884	1	18427.884	15.721	<.001
PCMORPH4	1881.065	1	1881.065	1.605	.206
SITE x PCMORPH1	33222.323	15	2214.822	1.889	.023
SITE x PCMORPH2	37660.281	15	2510.685	2.142	.008
SITE x PCMORPH3	61159.375	15	4077.292	3.478	<.001
SITE x PCMORPH4	44349.564	15	2956.638	2.522	.001
Error	484123.149	413	1172.211		

Table 3. ANCOVA table for PCMORPH1-4: *C. funebris*.

<i>ANCOVA Results for Chlorostoma funebris</i>					
	SS	DF	MS	F	P
SITE	594.222	15	39.615	1.302	.197
PCMORPH1	95.865	1	95.865	3.151	.077
PCMORPH2	294.881	1	294.881	9.693	.002
PCMORPH3	353.736	1	353.736	11.628	.001
PCMORPH4	2.044	1	2.044	.067	.796
SITE x PCMORPH1	680.811	15	45.387	1.492	.104
SITE x PCMORPH2	779.260	15	51.951	1.708	.047
SITE x PCMORPH3	559.372	15	37.291	1.226	.249
SITE x PCMORPH4	247.922	15	16.528	.543	.916
Error	12564.353	413	30.422		

Table 4. ANCOVA table for PCMORPH1-4:*Lottia* spp.

ANCOVA Results for <i>Lottia</i> spp.					
	SS	DF	MS	F	P
SITE	91.010	15	6.067	1.163	.112
PCMORPH1	2.875	1	2.875	.551	.458
PCMORPH2	1.603	1	1.603	.307	.580
PCMORPH3	.300	1	.300	.058	.810
PCMORPH4	3.180	1	3.180	.610	.435
SITE x PCMORPH1	78.171	15	5.211	.999	.455
SITE x PCMORPH2	59.130	15	3.942	.756	.727
SITE x PCMORPH3	69.919	15	4.661	.894	.572
SITE x PCMORPH4	43.750	15	2.917	.559	.905
Error	2154.035	413	5.216		

Table 5. ANCOVA table for PCMORPH1-4:*Littorina* spp.

ANCOVA Results for <i>Littorina</i> spp.					
	SS	DF	MS	F	P
SITE	112934.492	15	7528.966	9.808	<.001
PCMORPH1	6065.724	1	6065.724	7.901	.005
PCMORPH2	2939.712	1	2939.712	3.829	.051
PCMORPH3	11593.021	1	11593.021	20.312	<.001
PCMORPH4	4228.949	1	4228.949	5.509	.019
SITE x PCMORPH1	34448.896	15	2296.593	2.992	<.001
SITE x PCMORPH2	38629.726	15	2575.315	3.355	<.001
SITE x PCMORPH3	60907.364	15	4060.491	5.289	<.001
SITE x PCMORPH4	48257.647	15	3217.176	4.191	<.001
Error	317047.356	413	767.669		

Table 6. ANCOVA table for PCMORPH1-4:*M. pygmaeus*.

ANCOVA Results for <i>Musculus pygmaeus</i>					
	SS	DF	MS	F	P
SITE	4361.606	15	290.774	1.169	.293
PCMORPH1	1411.432	1	1411.432	5.674	.018
PCMORPH2	3812.482	1	3812.482	15.327	<.001
PCMORPH3	1379.283	1	1379.283	5.545	.019
PCMORPH4	784.268	1	784.268	3.153	.077
SITE x PCMORPH1	3402.397	15	226.826	.912	.551
SITE x PCMORPH2	4252.685	15	283.512	1.140	.318
SITE x PCMORPH3	3065.727	15	204.382	.822	.654
SITE x PCMORPH4	2896.328	15	193.089	.776	.704
Error	102732.224	413	248.746		

Table 7. Results of regression analysis using individual sampling SITE slopes for each of the significant interaction PCMORPH1-4:Invertebrate associations regressed against possible explanatory variables latitude, time of day, emersion time, and ambient conditions. NS = Not Significant, $\alpha = 0.10$.

Analysis of Betas of PCMORPH:Abundance ANCOVA Results				
	PCMORPH1: Abundance	PCMORPH2: Abundance	PCMORPH3: Abundance	PCMORPH4: Abundance
Latitude	NS	NS	NS	NS
Time of Day	NS	NS	p = 0.098 r ² = 0.183 β = 3.080	NS
Emersion Time	NS	NS	p = 0.085 r ² = 0.197 β = -5.843	NS
Ambient Temperature	NS	NS	NS	NS
Ambient Humidity	p = 0.071 r ² = 0.214 β = -0.432	NS	NS	NS
Ambient PAR	p = 0.047 r ² = 0.253 β = 0.007	p = 0.058 r ² = 0.233 β = -0.014	NS	NS

Table 8. Results of regression analysis using individual sampling SITE slopes for each of the significant interaction PCMORPH1-4:Invertebrate associations regressed against possible explanatory variables latitude, time of day, emersion time, and ambient conditions. NS = Not Significant, $\alpha = 0.10$.

Analysis of Betas of PCMORPH: <i>Littorina</i> spp. ANCOVA Results				
	PCMORPH1: <i>Littorina</i> spp.	PCMORPH2: <i>Littorina</i> spp.	PCMORPH3: <i>Littorina</i> spp.	PCMORPH4: <i>Littorina</i> spp.
Latitude	NS	p = 0.079 r ² = 0.493 β = 2.503	NS	p = 0.072 r ² = 0.508 β = -7.047
Time of Day	NS	NS	p = 0.033 r ² = 0.287 β = 3.314	NS
Emersion Time	NS	NS	p = 0.059 r ² = 0.232 β = -5.456	NS
Ambient Temperature	NS	NS	NS	NS
Ambient Humidity	NS	NS	NS	NS
Ambient PAR	p = 0.038 r ² = 0.272 β = 0.007	NS	NS	NS

Figure 1. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMORPH1:Abundance. Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 2. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMORPH2:Abundance. The black dashed line indicates the significant general trend of PCMORPH2:Abundance for the entire dataset ($p = 0.007$, $r^2 = 0.034$, $\beta = -8.869$). Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 3. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMORPH3:Abundance. The black dashed line indicates the significant general trend of PCMORPH3:Abundance for the entire dataset ($p < 0.001$, $r^2 = 0.003$, $\beta = 2.759$). Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 4. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMORPH4:Abundance. Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 5. Scatterplot of the significant general trend of PCMORPH1:*C. funebris* for the entire dataset ($p = 0.077$, $r^2 = 0.011$, $\beta = -0.623$).

Figure 6. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMORPH2:*C. funebris*. The black dashed line indicates the significant general trend of PCMORPH2:*C. funebris* for the entire dataset ($p = 0.002$, $r^2 < 0.001$, $\beta = -0.121$). Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 7. Scatterplot of the significant general trend of PCMORPH3:*C. funebris* for the entire dataset ($p = 0.011$, $r^2 < 0.001$, $\beta = -0.046$).

Figure 8. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMORPH1:*Littorina* spp. The black dashed line indicates the significant general trend of PCMORPH1:*Littorina* spp. for the entire dataset ($p = 0.005$, $r^2 = 0.004$, $\beta = -8.728$). Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 9. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMORPH2:*Littorina* spp. The black dashed line indicates the significant general trend of PCMORPH2:*Littorina* spp. for the entire dataset ($p = 0.051$, $r^2 = 0.021$, $\beta = -6.258$). Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 10. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMORPH3:*Littorina* spp. The black dashed line indicates the significant general trend of PCMORPH3:*Littorina* spp. for the entire dataset ($p < 0.001$, $r^2 = 0.001$, $\beta = -1.650$). Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 11. Scatterplots of individual sampling dates with their corresponding regression slopes for PCMORPH4:*Littorina* spp. The black dashed line indicates the significant general trend of PCMORPH4:*Littorina* spp. for the entire dataset ($p = 0.019$, $r^2 = 0.001$, $\beta = -1.170$). Blue indicates samples collected at Bodega Bay, red indicates samples collected at Pigeon Point, green indicates samples collected at Rancho Marino Reserve, and yellow indicates samples collected at all other sites. Stars indicate samples collected in winter, squares indicate samples collected in spring, circles indicate samples collected in summer, and diamonds indicate samples collected in fall.

Figure 12. Scatterplot of the significant general trend of PCMORPH1:*M. pygmaeus* for the entire dataset ($p = 0.018$, $r^2 = 0.015$, $\beta = 1.999$).

Figure 13. Scatterplot of the significant general trend of PCMORPH2:*M. pygmaeus* for the entire dataset ($p < 0.001$, $r^2 = 0.016$, $\beta = -2.057$).

Figure 14. Scatterplot of the significant general trend of PCMORPH3:*M. pygmaeus* for the entire dataset ($p = 0.019$, $r^2 = 0.064$, $\beta = 4.155$).

Figure 15. Scatterplot of the significant general trend of PCMORPH4:*M. pygmaeus* for the entire dataset ($p = 0.077$, $r^2 = 0.027$, $\beta = -2.689$).

Figure 16. PCMORPH1: Abundance β frequency distribution.

Figure 17. PC MORPH2: Abundance β frequency distribution.

Figure 18. PCMORPH3:Abundance β frequency distribution.

Figure 19. PC MORPH4: Abundance β frequency distribution.

Figure 20. PC MORPH2:C. funebris β frequency distribution.

Figure 21. PC MORPH1: *Littorina* spp. β frequency distribution.

Figure 22. PCMorPH2:*Littorina* spp. β frequency distribution.

Figure 23. PC MORPH3: *Littorina* spp. β frequency distribution.

Figure 24. PCMorPH4:*Littorina* spp. β frequency distribution.

Figure 25. Scatterplot of the PCMORPH1:Abundance slopes of each SITE regressed against significant explanatory variables (analysis of β). Errors bars are standard error of β ($p = 0.071$, $r^2 = 0.214$, $\beta = -0.432$).

Figure 26. Scatterplot of the PCMORPH1:Abundance slopes of each SITE regressed against significant explanatory variables (analysis of β). Errors bars are standard error of β ($p = 0.047$, $r^2 = 0.253$, $\beta = 0.007$).

Figure 27. Scatterplot of the PCMORPH2:Abundance slopes of each SITE regressed against significant explanatory variables (analysis of β). Errors bars are standard error of β ($p = 0.058$, $r^2 = 0.233$, $\beta = -0.014$).

Figure 28. Scatterplot of the PCMORPH3:Abundance slopes of each SITE regressed against significant explanatory variables (analysis of β). Errors bars are standard error of β ($p = 0.098$, $r^2 = 0.183$, $\beta = 3.080$).

Figure 29. Scatterplot of the PCMORPH3:Abundance slopes of each SITE regressed against significant explanatory variables (analysis of β). Errors bars are standard error of β ($p = 0.085$, $r^2 = 0.197$, $\beta = -5.843$).

Figure 30. Scatterplot of the PC MORPH1:*Littorina* spp. slopes of each SITE regressed against significant explanatory variables (analysis of β). Errors bars are standard error of β ($p = 0.038$, $r^2 = 0.272$, $\beta = 0.007$).

Figure 31. Scatterplot of the PCMORPH2:*Littorina* spp. slopes of each SITE regressed against significant explanatory variables (analysis of β , $p = 0.079$, $r^2 = 0.493$, $\beta = 2.503$).

Figure 32. Scatterplot of the PC MORPH3:*Littorina* spp. slopes of each SITE regressed against significant explanatory variables (analysis of β). Errors bars are standard error of β ($p = 0.033$, $r^2 = 0.287$, $\beta = 3.314$).

Figure 33. Scatterplot of the PCMORPH3:*Littorina* spp. slopes of each SITE regressed against significant explanatory variables (analysis of β). Errors bars are standard error of β ($p = 0.059$, $r^2 = 0.232$, $\beta = -5.456$).

Figure 34. Scatterplot of the PCMORPH4:*Littorina* spp. slopes of each SITE regressed against significant explanatory variables (analysis of β , $p = 0.072$, $r^2 = 0.508$, $\beta = -7.047$).