The Composition and Abundance of the Algal Division Rhodophyta in a Central California Kelp Forest Located at Hopkins Marine Station

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Abstract

The spatial structure of algae within a community can be attributed to abiotic components such as substrate, relief, and light attenuation at varying depths as well as biotic factors such as herbivory from reef fishes or competition for space. These factors influence which algal species will recruit to specific regions of the kelp forest. More specifically, understanding the variability of benthic algal dynamics may provide insight into the underlying factors that control the abundance and distribution of where the species are found. Subtidal benthic algal communities in central California kelp forests are dominated by the phyletic division Rhodophyta, which is further categorized into foliose, encrusting, or geniculate species. We focus on several dominant benthic red algae in our study at Hopkins Marine Station in Monterey Bay, California. Through observational field studies using SCUBA, we sought to explore the relationship between red algal community composition with varying depth, substrate, relief, as well as other possible contributing biotic factors (invertebrate and algal abundance) though random point contact (RPC) methods in order to answer the following questions: (1) Does red algae composition change with depth? (2) Does red algae have an association with substrate? (3) Does red algae have an association with relief? With the data collected, we ran PERMANOVA tests in order to compare communities and generate a p-value, allowing us to test the significance for each of these variables. Through our analysis, we found that depth, substrate, and relief are all significantly associated in relation to the abundance of red algae. Despite the significance of our results, this study is only one of a few that examines the spatial distribution of benthic Rhodophyta in a kelp forest ecosystem. The relative scarcity of this information should encourage more surveys to be conducted in order to further distinguish ecological interactions influencing red algal compositions in temperate kelp forest ecosystems worldwide.

Introduction

Temperate kelp forests are structurally complex ecosystems with many biological and physical interactions that dictate the overall stability of its algal communities (Foster 1975b, MacArthur and MacArthur 1961). The spatial structure of algae within a community can be attributed to abiotic components such as substrate, relief, and light attenuation at varying depths as well as biotic factors, such as herbivory from reef fishes and competition for space (Reed and Foster 1984). The strengths of these interactions within the kelp forest system vary depending on geographical location as well as environmental characteristics, thus influencing which species will recruit to specific regions within the kelp forest (Foster 1975b). The structure of algal communities within temperate rocky reefs are unique.

The structure of algal communities in a giant kelp forest can be categorized into a surface
canopy layer, a smaller algal understory, and a benthic community of encrusting, foliose and turf species. The vertical stratification of algal communities creates a highly three-dimensional habitat that supports a crucial assemblage of associated invertebrates, fish, and mammals with each layer (Breda and Foster 1985). While the surface canopy and understory biomass are generally dominated by brown kelps such as *Macrocystis pyrifera*, *Pterygophora californica*, and *Cystoseira osmundacea*, the composition of benthic algal communities have been observed to vary significantly over multiple spatial scales (Reed and Foster 1984).

Benthic algal communities in central California kelp forests are dominated by the phyletic division Rhodophyta, which are categorized into foliose, encrusting, or geniculate species (Clark et al. 2004). While widely distributed spatially and with depth, red algae contribute significantly to the kelp forest ecosystem as primary producers, food for grazing herbivores, habitat, and recruitment substrate for benthic invertebrates (Breda and Foster 1985). Compositional variability in red algae communities may subsequently support diverse species associations as an essential resource base. Thus, exploration into the distribution and abundance of red algae may provide predictions regarding the structure of interacting communities.

Despite the significance of red algae in marine ecosystems, information regarding the spatial distribution of Rhodophyta is relatively scarce and limited to species lists (Breda and Foster 1985). In temperate ecosystems, the composition of algal communities may be affected by the aforementioned processes. Little work has been done to investigate the specifics of Rhodophyta community dynamics, therefore further research will increase the scientific knowledge of the interplay between specific abiotic and biotic components that structure such communities (Breda and Foster 1985).

The intent of our study is to characterize the composition and abundance of the dominant Rhodophyta species at Hopkins Marine Station. Through observational field studies using SCUBA, we sought to explore the relationship between red algal community composition with variable depth, substrate, relief, and other possible contributing biotic factors such as invertebrate abundance though random point contact (RPC) methods. We collected data on several dominant subtidal red algae categories for our investigation, along with information regarding depth, substrate, and relief. Our studies were designed to evaluate three basic questions. (1) Does red algae composition change with depth? (2) Does red algae have an association with substrate? (3) Does red algae have an association with relief? Exploration of these characteristics provide predictions as to how algae communities may be structured in a central California kelp forest, as well as how the dynamics of the community can change under variable conditions.

**Methods**

**System Description**

Investigations for this study took place along the central coast of California at Hopkins Marine Station (36°37.20′N, 121°54.18′W) located in Pacific Grove (SCCOOS). Hopkins occurs within the Lover’s Point State Marine Reserve where the take of all living marine resources is prohibited (Cal Fish and Game). Hopkins exhibits large variation in depth, substrate, and relief along the 270 meter permanent cable line (Figure 1). Point Pinos protects the cove at
Hopkins and allows the site to be generally undisturbed by swell and surge (Breda and Foster 1985). Giant kelp (*M. pyrifera*) is abundant at Hopkins, while understory kelps are relatively scarce (Breda and Foster 1985). Kelp forest ecosystems exhibit high biodiversity and productivity, therefore presenting Hopkins as an excellent site to study patterns of species associations within the kelp forest. This abiotic diversity enables us to compare the composition of red algae and the distribution of species throughout the study site.

**General Approach**

We conducted an observational field study at Hopkins over the time period of November 7 to December 3, 2013, with a total of 8 dive days. At Hopkins we conducted 22, 30-meter transects in the onshore (west) and offshore (east) direction. Each transect was 10 m apart, and perpendicular to the main cable line. On both sides of the transect tape, each diver conducted a random point contact (RPC) method in 5 meter intervals, starting at the 0 meter mark and ending at the 30 meter mark. For each 5 meter point, we recorded the depth, substrate, and relief. Because each RPC had 10 random points, we obtained 20 points of data per every 5 meters along the transect line. In total we collected 154 points of data for depth, substrate, and relief, and an overall 3080 points of data associated to the species composition. Through this method, we are able to run statistical analyses of our collected data to determine the composition of red algae at Hopkins and how it varies with respect to depth, substrate, and relief.

**Study Design**

**Data Collection**

We ran transects from the 50 to the 150 meter marks along the main cable at Hopkins. From there, we ran 30-meter transects perpendicular to the cable line in the offshore (90 degrees) direction. On the swim back to the zero meter mark, each diver recorded the depth, substrate, and relief at every 5 m (at 0, 5, 10, 15, 20, 25, and 30 meters). Perpendicular to these marks, divers laid down a 10 point RPC chain. We recorded the red algae species directly under each of the 10 points. For the ease of identification, *Rhodymenia spp.*, *Callophyllis spp.*, and *Mazzaella spp.* were not identified to the species. The remaining algae were characterized as either articulated corallines, crustose coralline, encrusting red, juvenile turf (<2 cm), filamentous red, or the following species: *Chondracanthus corymbifer*, *Cryptopleura farlowianum*, *Botryocladia pseudodichotoma*, *Prionitis lanceolata*, and *Plocamium pacifica*. With this method, we obtained 20 points of random data for 7 points along the transect. We then reeled in the tape and repeated this same method for the onshore (270 degrees) transect.

**Algal Composition vs. Depth**

To determine whether a relationship exists between the composition of red algae and depth, we recorded the depth at every 5 meter point along the transect line. This depth corresponded to all species recorded at the points along the RPC chain. Using the data collected with this method, we generated bar graphs and cluster diagrams by grouping depths into three
categories: shallow (S), ≤ 8.2m [27 ft.]; mid (M), 8.2-9.5m [28-31 ft.]; and deep (D), ≥ 9.8m [32 ft]. We ran a PERMANOVA test in order to compare communities and generate a p-value of significance for the relationship between algal species and associated depth. The p-value outcome of the PERMANOVA test is based upon permutations rather than underlying distributions (t or F test). If the p-value is <.05, we can reject the null hypothesis and accept the alternative hypothesis that there is associations between algae and the depth at which they are found.

Algal Composition vs. Substrate

Similarly, we documented the substrate at each 5 meter mark along the transect line to determine whether there is a pattern of association between algal composition and substrate. In this methodology, the substrate corresponded to the recorded species on either side of the line. The substrates were grouped as follows: sand (S); cobble (C) ≤10cm; boulder (BO), 10cm-1m; and bedrock (BR), ≥1m. We ran a PERMANOVA test between the algal composition and substrate data to generate a p-value. If it is <.05, we can reject the null hypothesis, and accept the alternative hypothesis, that there is strong associations between Rhodophyta and the underlying substrate.

Algal Composition vs. Relief

To identify if there is a relationship between algal composition and relief, we documented the relief in the same manner as depth and substrate. Each relief corresponded to our seven original 5-meter segments on the transect tape, and followed the guidelines as to ½ of a meter on either side of the transect line and ¼ meter ahead of and behind the point on the RPC chain. The relief was grouped together as follows: flat (F), 0-10 cm; shallow (S), 10cm-1m; moderate (M), 1-2m; and high (H), >2m. The PERMANOVA test between relief and Rhodophyta composition generated our significant p-value and if the p-value was found to be <.05, the null hypothesis can be reject, and we can accept the alternative that there are associations linking algae with relief.

Results

General Results

At Hopkins Marine Reserve, the statistical analysis of the PERMANOVA test allowed us to compare the abundances of red algae communities and their associations with varying depth, substrate, and relief. We found that depth, substrate, and relief all had a p-value lower than 0.05, therefore they were all statistically significant. The following species that were found at the highest abundances across all three categories (depth, substrate, and relief) were crustose coralline, invertebrates (sessile or mobile), algae (brown or green), encrusting red, articulated coralline, and Rhodymenia spp. (Figures 3, 5, 7).
Algal Composition vs. Depth

The PERMANOVA analyzing the correspondence of Rhodophyta composition and depth resulted in a p-value of 0.029, which is less than the 0.05 test, so we can reject the null hypothesis that there is no association between algae and depth (Table 1). The cluster diagram demonstrates that moderate and deep depths are composed of similar algal species as opposed to the shallower depths which contain a new spectrum of species (Figure 2). The shallow classification included a broader range of depths to account for the few transects that had an extremely shallow depth reading.

The bar graph that depicts each species and correlated depth range illustrates that the crustose coralline algae and encrusting red algae are abundant throughout all depths, while the articulated corallines, *Rhodymenia* spp., *Mazzaella* spp., and *C. corymbifera* are most strongly associated with the shallow depths (Figure 3). There is an overall higher diversity of Rhodophyta at shallower depths (Figure 3).

Algal Composition vs. Substrate

The PERMANOVA comparing Rhodophyta with the underlying substrate resulted in a p-value of 0.001. Therefore, we can reject our null hypothesis that there is no association of algae with substrate type (Table 1). The cluster diagram demonstrates that similar species are found among the sand and cobble and similar species are found associated with boulder and bedrock. Sand and boulder were found to have the most dissimilar algal compositions (Figure 4).

Sand is the least preferred substrate type of the four categories (Figure 5). *C. corymbifera* and *Mazzaella* spp. strongly prefer bedrock. Additionally, *Rhodymenia* spp., articulated corallines, encrusting corallines, and encrusting reds prefer bedrock or boulders. *Callphyllis* *spp.* demonstrates a mild preference for bedrock, however the distinction is not significant. In addition, other algae demonstrated a high preference for boulders but equal preferences for sand, cobble, and bedrock. Invertebrates also had the strongest preference for boulders and bedrock. Shell, as we predicted, was the most abundant in sand and cobble.

Algal Composition vs. Relief

The PERMANOVA test for the strengths of association regarding relief and the Rhodophyta populations generated a p-value of 0.012, which is again lower than the 0.05 test (Table 1). Therefore, we can reject our third null hypothesis that there is no association between algal composition and relief. The cluster diagram demonstrates that the algae found at medium and high reliefs are most similar (Figure 6). In addition, the flat relief exhibits the most dissimilar algal composition when compared with the three other relief categories.

Flat reliefs are the least preferred by all species of algae; most areas within this category are covered in sand and shell debris and are absent of Rhodophyta (Figure 7). *Mazzaella* *spp.* and *C. corymbifera* associate with high reliefs, while articulated corallines, encrusting reds, and *Rhodymenia* *sp.* are found throughout relatively all relief standards. Crustose corallines were more associated with intermediate reliefs.
Discussion

Analyzing the results of our study suggests red algal composition in the Hopkins kelp forest system is influenced most significantly by substrate followed by relief, then depth. We conclude that variation amongst these three factors as well as associated interactions may produce the differences we see in the community composition.

We predicted red algae would show a strong association with depth due to differences in light availability. Light attenuates with depth, the wavelengths of light that penetrate water decrease as depth increases (Lorenzen 1972). Visible light emits wavelengths between 400 and 700 nm within the electromagnetic spectrum; autotrophs utilize these same wavelengths, also known as Photosynthetically Active Radiation (PAR), to power photosynthesis (Kirk 1994). Rhodophytes flourish at multiple depths through the up-regulation or down-regulation of accessory pigments called phycobilins which increase their photosynthetic efficiency and allow them to survive in low light environments, such as beneath dense surface and understory canopies, or in highly turbid waters (Rabinowitch and Govindjee 1969). The ratios of the phycobilins, specifically phycoerythrin (PE) and phycocyanin (PC), differ between and within species; as depth increases, the ratio of PE:PC increases in Rhodophytes (Dring 1981, Payri 2001). Foliose and crustose red algae can alter their phycocyanin to phycoerythrin ratio, which allows them to be more abundant at greater depths than any other algal species in clear oceanic waters (Dring 1981, Figure 8). While we observed red algae at each measured depth, different species appeared to dominate different depths with an overall greater diversity of red algae in shallower areas. We observed a greater abundance of foliose algae, specifically *Rhodymenia* spp., *Mazzaella* spp., *Chondracanthus corymbifera* at shallow depths due to their ability to absorb light more efficiently. Their unique accessory pigments make red algae the most efficient algal group in terms of photosynthesis and depth range.

Another reason for a strong association between red algae and depth may lie in the seasonal, coastal wave exposure. Water motion acts both directly and indirectly on the subtidal red algae species at Hopkins. Surge increases in intensity in shallower areas due to the fact that less depth leaves less room for wave energy to dissipate. This increased water movement has the ability to directly remove foliose red algae species like *Chondracanthus* spp., *Rhodymenia* spp. and *Mazzaella* spp. in the shallower areas. On the other hand, we concluded articulated corallines to be abundant at shallower depths because their calcium-impregnated thalli are tolerant to strong wave exposure (Harrold et. al. 1988). Water motion indirectly impacts the species of red algae at Hopkins by thinning the *M. pyrifera* canopy, thus increasing light attenuation at deeper depths (Harrold 1987). Prior observations noted the *M. pyrifera* canopy at Hopkins to decline in size and density starting in November when wave exposure begins to increase due to winter storms (Breda and Foster 1985). Furthermore, Breda and Foster (1985) found that foliose red algal biomass overall declined when there was an increase in overstory kelp canopies.

Although foliose red algae are more vulnerable to wave exposure, we observed a high abundance at shallower depths (Figure 3). Foliose red algae are favored at exposed sites because they have rapid growth rates during short periods of low turbidity when there is increased light availability, typically in late spring and summer (Harrold et. al. 1988). These foliose red algae also have life histories (biphasic/triphasic/dormant spores) that allow them to survive harsh
winter conditions accompanied by reduced light, sand burial, and removal (Harrold et. al. 1988). Rhodymenia spp. utilize asexual reproduction by producing stolons that grow horizontally like a system of roots (Breda and Foster 1985). This spreading behavior is advantageous during the harsher winter conditions because the holdfasts can remain fastened to the rock interface, and a new thalli can be produced when favorable conditions return (Breda and Foster 1985).

Additionally, the availability of substrate is important in algal succession. When M. pyrifera and other macroalgae are torn loose from the bottom during heavy swell, new substrata is exposed for colonization (Foster 1975a). Hopkins is protected by Pt. Pinos and is generally less disturbed by swells and surge, resulting in a dense M. pyrifera surface canopy (Breda and Foster 1985). The high abundance of M. pyrifera creates a lack of unoccupied substrata at Hopkins, contributing to the absence of annual understory Heterokontophyta species such as Nereocystis luetkeana and P. californica (Breda and Foster 1985). The low density of understory brown algae provides open habitat for perennial Rhodophyta species to colonize. Furthermore, sand movement can also uncover small areas of rock, increasing available habitat for the succession of perennial benthic algae. On the other hand, sand also serves as a selecting agent. Red algae require rocky substrate for settlement, contributing to the high algal abundance we observed on bedrock and cobble. While few red algae were found interspersed in sand expanses on Diopatra ornata beds or as epiphytes on shells, only specific species, such as coralline algae, can withstand continuous burial (Foster 1975a). Thus, algal biomass is found to be consistently low in areas with high sand cover (Breda and Foster 1985).

We predict the high observed abundance on top of the reef is due to low grazing intensity. Foster (1975b) suggested that fish grazing may be reduced on top of reefs in shallow water because strong wave action deters the intensity of grazing. Similarly, Breda and Foster (1985) found that voracious kelp forest herbivores such as abalone and urchins are cryptic species that mostly dwell in cracks, thus feeding primarily on drift algae. Therefore, we ruled out grazing as a strong factor influencing Rhodophyta distribution and abundance at Hopkins. On the other hand, sessile invertebrates can outcompete red algae for space. As a recently established juvenile with small thalli, encrusting invertebrates such as bryozoans, tunicates, sponges and tube snails can epiphytically dominate the red algae species (Foster 1975b). For example, bryozoans have been observed to display selectivity and inhibition of thalli growth in Rhodymenia spp. when growing epiphytically. Furthermore, observations reveal that faster-growing red algae species avoid bryozoan overgrowth by thalli elongation above the substrate, while the slower-growing Rhodymenia spp. tended to be completely inhibited by bryozoan epiphytes (MacLean 1962).

We recognize that our broad species groups (encrusting reds, articulated corallines, and crustose corallines) may have confounded our results. We chose to group these species together for ease of underwater identification. Additionally, there are numerous species within each of these groups that can only be identified by species under a microscope or through genetic analysis. Thus, we were unable to conduct these analyses since collection of specimens is prohibited within the reserve at Hopkins. Being able to identify these species may have provided more insight into the distribution of the more common coralline species with respect to depth, substrate, and relief. For example, articulated corallines are a very speciose group. Scaling down our study may reveal species specific micro-variation, which has been shown to occur on micro-scale manipulations on glass substrata in the lab (Foster 1975b). More detailed studies on species-specific distributions can provide further insight into patterns of red algae distribution.
Many physical and biological factors play a role in structuring the assemblage of subtidal Rhodophyta communities. Throughout kelp forests, each factor varies depending on specific environmental conditions dominant in that area. In our studied kelp forest system, we found depth, relief and substrate to be the most significant contributors for algal community composition. Despite the significance of our results, this study is one of a few that examines the spatial distribution of Rhodophyta. The relative scarcity of this information should encourage additional investigations to further quantify biotic and abiotic interactions influencing red algal abundances in temperate kelp forest ecosystems. Achieving a better understanding of factors contributing to the composition and abundance of red algae communities may provide insight into the dynamics of associated trophic levels as well as how assemblages may shift in response to changing conditions.

Literature Cited


McLean, J. H. 1962. Sublittoral Ecology of Kelp Beds of the Open Coast Area near Carmel,


**Figures**

![Figure 1](image-url)  
Figure 1. Map of Hopkins Marine Reserve, depicting the permanent line that runs 270 meters along the coastline. Our study was conducted between the meter marks of 50 and 150.
Table 1. Results of the PERMANOVA analysis. Significant relationships found between algal communities and associated depth, relief, and substrate, where P(perm) is <0.05.

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Figure 2. Cluster diagram depicts the similarity of algal species found at each depth. According to the cluster, medium and deep depths had a higher crossover of species, and therefore have more similar species compositions, than those at shallow depths. There seems to be a bimodal distribution of algal species: those in the shallows differ from those at moderate to deeper depths. (S=shallow, M=mid, D=deep)
Figure 3. Bar graph illustrating the abundance of each species within each depth category. Articulated coralline algae, Mazzaella sp. and Chondracanthus corymbifera are predominantly found at shallower depths.

CRUCOR = Crustose Corallines; INV = invertebrates; ARTCOR = Articulated Corallines; SAND = sandy, no algae; SHELL = shell debris, no algae; RHODY = Rhodymenia spp.; ENCRE = encrusting (non-crustose) red algae; ALGAE = non-red algae; MAZZAE = Mazzaella spp.; JUV = juvenile red turf algae; CALLO = Calliphyllis spp.; CHONDRA = Chondracanthus corymbifera; PRION = Prionitis lanceolata; PLOCAM = Plocamium cartilagineum; BARROC = bare rock, no algae; FILAMENT = filamentous red algae; TURF = turf red algae; CRYPTO = Cryptopleura farlowianum; BOTRYO = Botryocladia pseudodichotoma
Figure 4. Cluster diagram depicting the different associations of algal communities with various substrates. The algal composition associated with sand is more similar to the composition associated with cobble, while those associated with bedrock are more similar to those found on boulders. (SA=Sand, CO=Cobble, BR=Bedrock, BO=Boulder)
Figure 5. Bar graph illustrating associations with species with the four types of substrate. From the graph, we see that crustose corallines, *Mazzaella sp.*, and *C. corymbifera* are found more frequently on bedrock and boulders. CRUCOR = crustose corallines; INV = invertebrates; ARTCOR = Articulated Corallines; SAND = sandy, no algae; SHELL = shell debris, no algae; RHODY = *Rhodymenia*; ENCRED = encrusting (non-crustose) red algae; ALGAE = non-red algae; MAZZAE = *Mazzaella*; JUV = juvenile algae we were unable to identify; CALLO = *Callophyllis*; CHONDRA = *Chondracanthus corymbifera*; PRION = *Prionitis lanceolata*; PLOCAM = *Plocamium cartilagineum*; BARROC = bare rock, no algae; FILAMENT = filamentous red algae; TURF = turf red algae; CRYPTO = *Cryptopleura farlowianum*; BOTRYO = *Botryocladia pseudodichotoma*.

Figure 6. This cluster diagram depicts the different associations of algae with varying reliefs. The communities found on flat reliefs are the most different, while the communities associated with medium and high reliefs are the most similar. (F=Flat, S=Shallow, M=Moderate, H=High)
Figure 7. This bar graph illustrates how each particular species associates with varying reliefs. Articulated corallines, *Mazzaella* sp., and crustose corallines are least often associated with flat reliefs.

CRUCOR = Crustose Corallines; INV = invertebrates; ARTCOR = Articulated Corallines; SAND = sandy, no algae; SHELL = shell debris, no algae; RHODY = *Rhodymenia*; ENCREDE = encrusting (non-crustose) red algae; ALGAE = non-red algae; MAZZAE = *Mazzaella*; JUV = juvenile algae we were unable to identify; CALLO = *Callophyllis*; CHONDRA = *Chondracanthus corymbifera*; PRION = *Prionitis lanceolata*; PLOCAM = *Plocamium cartilagineum*; BARROC = bare rock, no algae; FILAMENT = filamentous red algae; TURF = turf red algae; CRYPTO = *Cryptopleura farlowianum*; BOTRYO = *Botryocladia pseudodichotoma*
Figure 8. This image demonstrates light attenuation in the open ocean (Levine and MacNichol 1982).