

Simona Augytė\* and Frank J. Shaughnessy

# A floristic analysis of the marine algae and seagrasses between Cape Mendocino, California and Cape Blanco, Oregon, USA

**Abstract:** The biogeographic area between Cape Mendocino, California and Cape Blanco, Oregon in the USA spans over 320 km and is characterized by prominent coastal headlands. This study was a first attempt to produce a current intertidal macroalgal and seagrass species list for this understudied region with basic habitat attributes included. A total of 164 species of marine macroalgae (105 species within 16 orders in Rhodophyta, 32 species within six orders in Heterokontophyta, Phaeophyceae, and 27 species in six orders in Chlorophyta) and two species of seagrasses (Anthrophyta) were identified. The optimal habitat for most species was the rocky intertidal in the mid zone (>50%), while some species were specialists in either tidepool and/or sandy habitats (~20%). Furthermore, based on Akaike Information Criterion, our top ranking model suggests that species richness is dependent on zonation, functional grouping and site location. Based on the seven functional group classification, the leathery macrophytes and crusts were the most prevalent at the two capes exposed to higher wave action and upwelling. One near-endemic species (*Cumathamnion sympodophyllum*), one invasive species (*Sargassum muticum*), and seven new records for the region were identified.

**Keywords:** biogeography; Cape Blanco; Cape Mendocino; floristics; macroalgae.

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## Introduction

Marine biogeographic classifications of coastal ecosystems are derived primarily from the lists of benthic

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seaweeds and macroinvertebrates. Species richness in local marine communities is heavily influenced by the larger spatiotemporal species pool resulting from succession, speciation, immigration and extinction events (Dudgeon and Petraitis 2001, Gaylord et al. 2002, Witman et al. 2004, Bobadilla and Santelices 2005, Broitman and Kinlan 2006, Tuya and Haroun 2009). The radiation, or the diversification of organisms into new forms, of benthic marine biota can be gradual along a coastline where formerly continuous populations undergo reproductive isolation due to geographic or oceanographic barriers (Adey and Steneck 2001, Lindstrom 2001).

Baseline data on species distributions is necessary for monitoring shifts in coastal community composition over time in relation to anthropogenic disturbances or sea surface temperature (SST) changes (Spalding et al. 2007, Jose Cruz-Motta et al. 2010). Warming and cooling SST have been shown to change the distributional ranges of benthic marine organisms by either dividing biogeographic regions or homogenizing larger regions (Silva 1992, Barry et al. 1995, Sagarin et al. 1999, Blanchette et al. 2008). Macroalgae respond rapidly to such environmental fluctuations as they are limited by water temperature for growth and distribution, and may therefore be used as valuable bioindicators in the coastal environment (Abbott and Hollenberg 1976, Lüning 1990, Druehl 2000, Kang et al. 2011). Marine species identification is critical to managers of complex ecosystems (Hofmann and Gaines 2008) in order for them to select and monitor marine protected areas (MPAs) and delineate ecosystem based management (EBM) processes. MPAs are a management tool to reduce, prevent and/or reverse the declines in marine biodiversity and increase the productivity of near shore marine ecosystems (Lubchenco et al. 2003, Spalding et al. 2007). The choice of sites for MPAs is based on biological, social and economic criteria. Floristic data are used to identify potentially sensitive habitats, the distribution of non-native taxa and species composition, all of which can indicate whether a given system is resilient enough to maintain its function in the face of disturbance (Roberts et al. 2003, Levin et al. 2008).

The headlands of Cape Blanco, Oregon (USA) south to Cape Mendocino, California (USA) bracket approximately

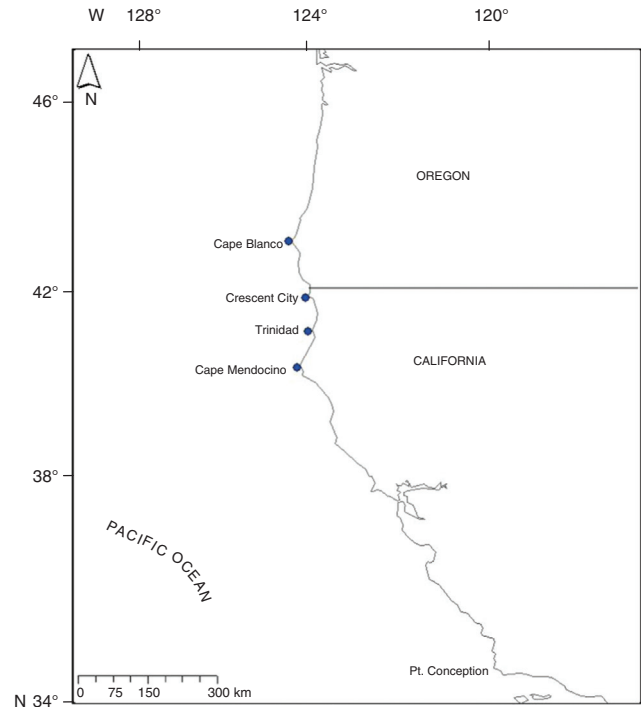
320 km of shoreline that potentially form either a discrete biogeographic unit or possibly a transition region between northern and southern seaweed floras. Existing biogeographic schemes place this segment of coastline within the Mendocinian Province bioregion, nested within a larger designation, called the Cold Temperate Northeast (NE) Pacific coast (Valentine 1966, Spalding et al. 2007, Blanchette et al. 2008). The headlands of both capes are characterized by seasonal upwelling during the spring and early summer which brings cold (10–13°C) nutrient rich waters to the surface (Magnell et al. 1990, Barth et al. 2007, Tweddle et al. 2010), consequently sustaining a diverse and productive marine ecosystem (Foster et al. 1988, Lüning 1990, Blanchette et al. 2009). Desiccation stress, sand disturbance and high wave action are some of the physical factors structuring intertidal species distribution in the NE Pacific (Waaland 1977, Littler et al. 1983, Denny 2006). It has been suggested that desiccation stress is ameliorated by early morning low tides as well as the thick fog that forms during the summer when light intensity is at its peak (Foster et al. 1988). Rocky intertidal and subtidal communities between the two capes are also heavily impacted by large sediment loads carried to the shoreline by nine rivers and numerous streams in the area (Borgeld et al. 2007) that could be driving the types of macroalgae found in the intertidal.

The region between the capes has been poorly studied relative to other adjacent regions in the NE Pacific. Previous studies (e.g., Doty 1947a,b, Dawson 1965, Abbott and Hollenberg 1976, Boyd and DeMartini 1977, Hansen 1997) have focused on one of the two states, but not exclusively on this region. Given the significance of marine floristic data in general and the lack of floristic studies that focus on the potentially important transitional region from Cape Blanco to Cape Mendocino, the main objective of this study was to produce a current species list for this area. As part of this objective, the basic habitat attributes of each species were recorded in order to allow the future comparisons of habitat attributes among bioregions.

## Materials and methods

### Site description

Four areas spanning 320 km of linear coastline (2.5 degrees latitude) in northern California and southern Oregon (Figure 1) were surveyed during the spring and summer of 2010 with preliminary sampling done in 2009. These areas were selected based upon the accessibility by foot as



**Figure 1** Map showing the four study locations.

well as the representation of different headland features and between-cape habitats. Sampling was restricted to rocky intertidal and shallow subtidal areas composed of bedrock and boulders and exposed to open ocean swells. Embayments with freshwater inputs and the subtidal were not sampled. This area of coastline is characterized by mixed semidiurnal tides; two lows and two highs of different height during one 24-h period. All the sampling was done during the lowest of the low tides ranging typically from -0.1 m to -0.6 m mean lower low water (MLLW).

The northernmost sampling point at Cape Blanco (42°50'15.39"N, 124°33'50.4"W) in Curry County is a prominent headland, and is the westernmost point in the state of Oregon. The intertidal is composed of large boulder fields, bedrock, and high cliffs intermixed with sandy patches. This area experiences early summer upwelling and has been identified as a major biogeographic boundary for zooplankton and benthic invertebrate larvae (Broitman and Kinlan 2006). The southernmost sampling location at Cape Mendocino (40°26'24.36"N, 124°24'34.2"W) in southern Humboldt County is the westernmost point in the state of California and a prominent headland with a large upwelling center on its south side. The Mattole River and Eel River provide high sediment loads to shores on the north side of this cape. The hard bottom habitat in this area is characterised by large expanses of rocky beach composed of bedrock and boulder fields, surge channels

and tidepools intermixed with long stretches of coarse sandy beaches. The two sites surveyed in between the two capes were Trinidad (41°3'33"N, 124°8'35"W) and Crescent City (41°45'21"N, 124°12'6"W) and are located in Humboldt and Del Norte counties, respectively. The beaches are composed of sand intermixed with rocky boulder fields. Surge channels are common for sites exposed to strong ocean swells, although some areas are protected by coves. The estuary, Humboldt Bay, is located about 24 km south of the town of Trinidad, which is located north of the large Eel River. Crescent City is located north of the Klamath River.

## Survey technique

Ten geographical positioning system (GPS) coordinates (NAD83 UTM zone 10N) were randomly chosen roughly within 13 km stretches of coastline around each of the four sampling areas, and five of these were surveyed based on accessibility (Table 1). A Garmin hand-held device (Garmin, Olathe, Kansas, USA) was used to place a 30 m transect line at the chosen GPS point, starting at the highest tidal height and heading west into the subtidal zone. Every species within 1.5 m on each side of the transect was recorded. The sampling intensity was consistent across all sites and each transect extended to the MLLW or lower. Basic habitat attributes were recorded for each species: intertidal zone (high, mid, low, and shallow subtidal),

substrate type (epibenthic, epilithic, epiphytic and epizoic), presence of sand, and if found in a tidepool.

Identifications were made in the field or in the laboratory when necessary. Vouchers were pressed onto acid-free herbarium paper, labeled and deposited in the Humboldt State University's Cryptogamic Herbarium. Coralline species were decalcified in a mixture of 27 ml of nitric acid in 1 l of water. This mixture was changed every 10 min until no bubbles were leaving the sample, then cross sections were made for identification (Riosmena-Rodriguez et al. 1999). Numerous taxonomic guides were used to identify specimens and recent taxonomic updates were used as sources for current nomenclature including Dawson (1965), Abbott and Hollenberg (1976), DeCew and Silva (2002), Gabrielson et al. (2004, 2006), Mondragon and Mondragon (2003), Lindstrom (2008), Guiry and Guiry (2010), Miller (2012), Sutherland et al. (2011), Wynne and Saunders (2012), Nielsen et al. (2013).

## Patterns of algal composition

Species richness was evaluated by fitting a generalized linear mixed effects (GLMER) model based on the morphology of seven functional groups, following designations by Nielsen and Navarrete (2004): articulated corallines, coralline and fleshy crusts, filaments, corticated

**Table 1** Collection information for each site and transect, including GPS coordinates, height of low tide (relative to MLLW) on the sampling date and County name.

Site	Transect	Latitude	Longitude	Tide (m)	County
Cape Blanco, OR	Lighthouse	42.841	-124.564	-0.4	Curry
	East of Lighthouse	42.839	-124.562	-0.5	
	Battle Rock, Port Orford	42.737	-124.483	-0.3	
	South of the Cape	42.833	-124.562	-0.4	
	South of Port Orford	42.716	-124.465	-0.4	
Crescent City, CA	Pebble Beach	41.757	-124.223	-0.4	Del Norte
	Point St. George	41.786	-124.256	-0.6	
	South of Point St. George	41.771	-124.244	-0.6	
	Battery Point Lighthouse	41.745	-124.202	-0.2	
	South of Jetty	41.737	-124.195	-0.6	
Trinidad, CA	Palmer's Point	41.131	-124.163	-0.5	Humboldt
	North of Luffenhotlz Beach	41.035	-124.123	-0.5	
	Houda Point	41.036	-124.121	-0.5	
	Elk Head	41.069	-124.159	-0.4	
	Martin's Creek	41.078	-124.156	-0.3	
Cape Mendocino, CA	Mussel Rock, surge channel	40.348	-124.364	-0.4	Humboldt
	Mussel Rock, urchin fields	40.418	-124.401	-0.4	
	Lost Coast	40.418	-124.400	-0.5	
	Devil's Gate	40.406	-124.391	-0.2	
	South of Mussel Rock	40.342	-124.363	-0.1	

Latitude and longitude are in the WGS-84 datum.

macrophytes, corticated foliose, leathery macrophytes, and foliose blades, along each transect at each of the four study areas. The GLMER was constructed in R software (R Development Core Team 2013) with the ‘lme4’ package (Bates et al. 2013). For predictors of species richness we looked at three categorical variables: intertidal zone, functional group and transect as fixed effects. Data from only three intertidal zones were used in the study: the high, the mid and the low. We also investigated several models with the three predictors used as random effects with and without interaction terms. Visual inspection of diagnostic residual plots did not reveal any obvious deviations from homoscedasticity or normality. We then compared several models against each other using Akaike Information Criterion (AIC), more specifically the corrected AIC (AICc), that allowed us to correct for a potential bias due to small sample size (Anderson 2008), to evaluate which parameters were important for predicting species richness. We proposed and ran 10 models and of those, evaluated three with the lowest delta AIC values.

## Results

A total of 164 species/subspecific taxa of benthic marine macroalgae (105 red, 32 brown, and 27 green algae) and two species of seagrasses were collected during this survey (Table 2). The taxa spanned six orders in Chlorophyta, six in Heterokontophyta (Phaeophyceae), and 16 in Rhodophyta. Richness was similar across the four study areas: Cape Mendocino had 90 species, Cape Blanco had 89 species, Trinidad had 83 species and Crescent City had 76 species (Figure 2). Three species were found outside of the sampling season but were included in Table 2: *Halochlorococcum porphyrae*, *Coilodesme californica* and *Petalonia fascia*. Only one known near-endemic macroalga, *Cumathamnion sympodophyllum*, was found at the Trinidad site. The invasive *Sargassum muticum* was found at the Crescent City site. Two parasitic species were found: *Goniomophyllum skottsbergii* found growing on *Cryptopleura* sp., and *Janczewskia gardneri* found growing on *Osmundea spectabilis*. Seven new records for this region were identified: *Acrochaetium densum*, *Colaconema rhizoideum*, *Lithophyllum impressum*, *Pseudolithophyllum muricatum*, *Ralfsia pacifica*, *Ulvella ramosa* and *Ulvella wittrockii*. A comparison of the zonation across the four sites revealed that taxa diversity was highest (35–56%) in the mid intertidal, and slightly lower (30–36%) in the low intertidal (Figure 3). Only 25% of species showed a preference for tidepools and 19% were found in sand-impacted habitats.

Habitat and species heterogeneity was found throughout all four study areas as these were comparable in the amounts of the following functional groups: articulated coralline, corticated foliose, corticated macrophytes, filamentous, and foliose (Table 3). However, the two capes were typified by a slight increase in the number of species belonging to the leathery macrophyte as well as coralline and fleshy crust groups and the two southern sites, Trinidad and Cape Mendocino, showed a slight increase in the abundance of species belonging to the corticated foliose and corticated macrophytes. Based on AICc values, the GLMER model with the highest support for species richness takes into account the effects of intertidal zone, functional group and transect; the latter was treated as a random variable grouped within sites (Tables 4 and 5). This model suggests that species diversity across zones is different for the seven functional groups in the individual transects used in the study design (Figure 4A–C). Comparison of confidence intervals for the logistic regression models showed significantly different mean values for the fixed variables tested as there was no overlap with the vertical dashed line, meaning the comparisons among the different parameters are significant (Figure 5).

## Discussion

The present study produced a seaweed and seagrass species list for the biogeographic unit extending from Cape Blanco, Oregon to Cape Mendocino, California, at four rocky intertidal sampling areas with basic habitat information for each species. The development of a floristic list for particular sites has rarely been undertaken between the capes (Boyd and DeMartini 1977, Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO), Coastal Biodiversity Surveys) and this study includes cryptic algae such as endophytes and parasitic species oftentimes overlooked in macroseaweed-oriented surveys. Furthermore, this work provides some of the fundamental information to be incorporated into coastal conservation and management as a tool for monitoring the effects of climate change and more localized factors on marine biota.

Given the effects the two capes have on ocean circulation and, between the capes, the significant discharge of river sediments, it was not expected that our four study areas would contain such high macroalgal diversity. Other environmental parameters could be driving the patterns observed in the structuring of intertidal communities over this 320 km of rugged coastline. A large-scale study along the NE Pacific coastline from Baja, Mexico, to Alaska,

Table 2 Marine macroalgae and seagrasses taxa between Cape Mendocino and Cape Blanco found during 2009 and 2010 at four survey locations.

Phylum/Order	Species name & authority	B	C	T	M	Zone	TP	Sand	Substrate
Chlorophyta									
Bryopsidales	<i>Bryopsis corticulans</i> Setchell			X		H	X		Epilithic
	<i>Codium fragile</i> subsp. <i>californicum</i> (J. Agardh) Maggs et. J. Kelly	X		X		M, H			Epilithic
	<i>Codium setchellii</i> N.L. Gardner		X	X	X	L			Epilithic
Cladophorales	<i>Chaetomorpha aerea</i> (Dillwyn) Kützing			X	X	H	X	X	Epilithic
	<i>Cladophora columbiana</i> Collins	X		X	X	H			Epilithic
	<i>Rhizoclonium tortuosum</i> (Dillwyn) Kützing	X		X		L, M			Epilithic, epizoic
Oltmannsiellopsidales	<i>Halochlorococcum porphyrae</i> (Setchell et N.L. Gardner) J.A. West, C.M. Smith et McBride			X		M			Endophytic in <i>Porphyra</i>
Prasiolales	<i>Prasiola meridionalis</i> Setchell et N.L. Gardner		X			S			Epilithic
Ulotrichales	<i>Acrosiphonia arcta</i> (Dillwyn) Gain	X	X	X		M, H			Epilithic
	<i>Acrosiphonia coalita</i> (Ruprecht) Scagel, Garbary, Golden et M.W. Hawkes	X		X	X	M			Epilithic
	<i>Collinsella tuberculata</i> Setchell et N.L. Gardner	X	X	X		M			Epilithic
	<i>Ulothrix flacca</i> (Dillwyn) Thuret			X		M, H			Epiphytic on <i>Fucus</i> , epilithic
	<i>Urospora penciliformis</i> (Roth) J.E. Areschoug	X		X	X	H, S		X	Epilithic
	<i>Urospora wormskioldii</i> (Mertens ex Hornemann) Rosenvinge			X		H			Epilithic
Ulvales	<i>Blidingia dawsonii</i> (Hollenberg et Abbott) Lindstrom, Hanic et Golden	X		X	X	M			Epizoic
	<i>Blidingia minima</i> (Nägeli ex Kützing) Kylin	X		X	X	M, H			Epiphytic on <i>Fucus</i> , epilithic, epizoic
	<i>Blidingia minima</i> var. <i>vexata</i> (Setchell et N.L. Gardner) J.N. Norris			X	X	H			Epilithic
	<i>Korrmannia leptoderma</i> (Kjellman) Bliding	X	X			H	X		Epiphytic on <i>Phyllospadix</i>
	<i>Ulva californica</i> Wille	X	X	X	X	L, M			Epilithic
	<i>Ulva intestinalis</i> Linnaeus	X	X	X	X	H, S			Epilithic
	<i>Ulva lactuca</i> Linnaeus	X	X	X	X	M		X	Epilithic
	<i>Ulva linza</i> Linnaeus	X	X	X	X	M, H		X	Epilithic
	<i>Ulva lobata</i> (Kützing) Harvey		X			H	X		Epilithic
	<i>Ulva stenophylla</i> Setchell et N.L. Gardner			X		L	X		Epilithic
	<i>Uvella geniculata</i> (N.L. Gardner) R. Nielsen, C.J. O'Kelly et B. Wysox	X				L			Endophytic in <i>Laminaria</i>
	<i>Uvella ramosa</i> (N.L. Gardner) R. Nielsen, C.J. O'Kelly et B. Wysox	X				L			Endophytic in <i>Mazzaella</i>
	<i>Uvella wittrockii</i> (Wille) R. Nielsen, C.J. O'Kelly et B. Wysox		X			M			Endophytic in <i>Sphacelaria</i>
Heterokontophyta (Phaeophyceae)									
Desmarestiales	<i>Desmarestia latifrons</i> (Ruprecht) Kützing	X				H		X	Epilithic
	<i>Desmarestia ligulata</i> (Stackhouse) Lamouroux	X	X	X	X	L, M	X		Epilithic
	<i>Coilodesme californica</i> (Ruprecht) Kjellman		X	X		L			Epiphytic on <i>Cystoseira</i>
	<i>Colpomenia peregrina</i> (Sauvageau) Hamel	X	X	X	X	M	X		Epilithic, epiphytic on <i>Neorhodomela</i>
Ectocarpales	<i>Ectocarpus fasciculatus</i> Harvey		X		X	L			Epiphytic on <i>Egregia</i> & <i>Cystoseira</i>
	<i>Ectocarpus siliculosus</i> (Dillwyn) Lyngbye	X				L			Epiphytic on <i>Cystoseira</i>
	<i>Elachista fucicola</i> (Velley) Areschoug	X				L			Epiphytic
	<i>Haplogloia andersonii</i> (Farlow) Levring	X	X	X	X	L, M	X		Epilithic

(Table 2 Continued)

Phylum/Order	Species name & authority	B	C	T	M	Zone	TP	Sand	Substrate
Fucales	<i>Hecatonema streblonematooides</i> (Setchell et N.L. Gardner) Loiseaux		X			L			Epiphytic on <i>Desmarestia</i>
	<i>Leathesia marina</i> (Lyngbye) Decaisne	X		X	X	M, H			Epilithic
	<i>Scytosiphon dotyi</i> M.J. Wynne			X	X	H	X		Epilithic
	<i>Scytosiphon lomentaria</i> (Lyngbye) Link			X	X	H	X		Epilithic
	<i>Soranthra ulvoidea</i> Postels et Ruprecht	X	X	X	X	M, H	X	X	Epilithic, epiphytic on <i>Odonthalia</i>
	<i>Fucus distichus</i> Linnaeus	X	X	X	X	M			Epilithic
	<i>Pelvetiopsis limitata</i> (Setchell) N.L. Gardner			X	X	H			Epilithic
	<i>Sargassum muticum</i> (Yendo) Fensholt		X		X	M		X	Epilithic
	<i>Stephanocystis osmundacea</i> (Turner) Trevisan	X	X	X	X	L	X	X	Epilithic
	<i>Alaria marginata</i> Postels et Ruprecht	X	X	X	X	L, M	X	X	Epilithic
Laminariales	<i>Costaria costata</i> (C. Agardh) D.A. Saunders	X		X	X	L	X		Epilithic
	<i>Egria menziesii</i> (Turner) Areschoug	X	X	X	X	L, M			Epilithic
	<i>Laminaria ephemera</i> Setchell			X	X	L			Epilithic
	<i>Laminaria setchellii</i> Silva	X	X	X	X	S, L	X		Epilithic
	<i>Laminaria sinclairii</i> (Harvey ex J.D. Hooker et Harvey) Farlow, Anderson et Eaton	X	X	X	X	L, M		X	Epilithic
	<i>Lessoniopsis littoralis</i> (Farlow et Setchell ex Tilden) Reinke	X		X	X	L			Epilithic
	<i>Nereocystis leutkeana</i> (Mertens) Postels et Ruprecht	X	X	X	X	L, M	X		Epilithic
	<i>Postelsia palmaeformis</i> Ruprecht	X		X		L			Epilithic
	<i>Pterygophora californica</i> Ruprecht	X	X	X	X	S			Epilithic
	<i>Saccharina sessilis</i> (C. Agardh) Kuntze	X	X	X	X	L, M	X		Epilithic
Ralfsiales	<i>Analipus japonicus</i> (Harvey) M.J. Wynne		X	X	X	M, H			Epilithic
	<i>Ralfsia pacifica</i> Hollenberg		X			M			Epilithic
	<i>Battersia racemosa</i> (Greville) Draisma, Prud'homme et H. Kawai		X	X	X	M		X	Epilithic
	<i>Phaeostrophion irregulare</i> (Setchell) N.L. Gardner	X	X	X	X	M, H	X	X	Epilithic
	<i>Acrochaetium densum</i> (K.M. Drew) Papenfuss				X	L			Epiphytic on <i>Egria</i>
	<i>Rhodochorton purpureum</i> (Lightfoot) Rosenvinge			X		S			Epilithic
	<i>Ahnfeltia fastigiata</i> (Endlicher) Makienko			X	X	L, M		X	Epilithic
	<i>Bangia</i> sp.	X				H			Epilithic
	<i>Pyropia abbotiae</i> (V. Krishnamurthy) S.C. Lindstrom		X	X	X	M			Epilithic
	<i>Pyropia californica</i> J. Agardh			X	X	L			Epilithic, epiphytic on <i>Nereocystis</i>
Sphaecelariales	<i>Pyropia conwayae</i> (S.C. Lindstrom et K.M. Cole) S.C. Lindstrom			X	X	M			Epilithic
	<i>Pyropia gardneri</i> (G.M. Smith & G.J. Hollenberg) S.C. Lindstrom	X		X		L			Epiphytic on <i>Laminaria</i>
	<i>Pyropia gardneri</i> (G.M. Smith & G.J. Hollenberg) S.C. Lindstrom	X		X		L			Epiphytic on <i>Laminaria</i>
	<i>Pyropia kanakaensis</i> (Mumford) S.C. Lindstrom			X	X	M			Epilithic
	<i>Pyropia lanceolata</i> (Setchell et Hus) S.C. Lindstrom	X	X			M			Epilithic
	<i>Pyropia perforata</i> (J. Agardh) S.C. Lindstrom			X	X	M			Epilithic
	<i>Pyropia smithii</i> (G.J. Hollenberg et I.A. Abbott) S.C. Lindstrom			X	X	M			Epilithic
	<i>Wildemania occidentalis</i> (Setchell et Hus) S.C. Lindstrom		X	X		M			Epiphytic on <i>Mastocarpus</i>
	<i>Wildemania schizophylla</i> (G.J. Hollenberg) S.C. Lindstrom	X		X		H	X	X	Epilithic
						M			Epilithic

(Table 2 Continued)

Phylum/Order	Species name & authority	B	C	T	M	Zone	TP	Sand	Substrate
Ceramilales	<i>Anithammionella spirographidis</i> (Schiffner) E.M. Wollaston				X	M			Epiphytic on <i>Ceramium</i>
	<i>Callithamnion pikeanum</i> Harvey	X	X	X	X	L, M			Epilithic
	<i>Ceramium gardneri</i> Kylin			X	X	M, H			Epilithic
	<i>Ceramium pacificum</i> (Collins) Kylin			X	X	M, H			Epilithic
	<i>Cryptopleura lobulifera</i> (J. Agardh) Kylin	X		X	X	L, M	X		Epilithic
	<i>Cryptopleura ruprechtiana</i> (J. Agardh) Kylin	X	X	X	X	L, M			Epilithic
	<i>Cryptopleura violacea</i> (J. Agardh) Kylin			X	X	L, M	X		Epilithic
	<i>Cumathamnion sympodophyllum</i> M.J. Wynne et K. Daniels			X	X	M			Epilithic
	<i>Cumathamnion decipiens</i> (J. Agardh) M.J. Wynne et G.W. Saunders	X		X	X	L, M			Epilithic
	<i>Gonimophyllum skottsbergii</i> Setchell			X	X	L			Parasitic on <i>Cryptopleura</i>
	<i>Grateloupta californica</i> Kylin			X	X	M	X	X	Epilithic
	<i>Hymenena flabelligera</i> (J. Agardh) Kylin				X	H			Epilithic
	<i>Hymenena multiloba</i> (J. Agardh) Kylin				X	L	X	X	Epilithic
	<i>Janczewska gardneri</i> Setchell et Guernsey				X	L			Parasitic on <i>Osmundea</i>
	<i>Microcladia borealis</i> Ruprecht	X	X	X	X	L			Epilithic
	<i>Microcladia coulteri</i> Harvey			X	X	L			Epilithic
	<i>Neoptilota hypnoides</i> (Harvey) Kylin	X		X	X	L			Epiphytic on <i>Cystoseira</i> stipe
	<i>Neorhodomeia larix</i> (Turner) Masuda			X	X	M			Epiphytic on corallines
	<i>Odonthalia floccosa</i> (Esper) Falkenberg	X	X	X	X	M			Epilithic
	<i>Odonthalia washingtoniensis</i> Kylin			X	X	L, M			Epilithic
<i>Osmundea spectabilis</i> (Postels et Ruprecht) K.W. Nam	X	X	X	X	L, M			Epilithic	
<i>Polyneura latissima</i> (Harvey) Kylin	X	X	X	X	L			Epilithic	
<i>Polysiphonia hendryi</i> var. <i>deliqescens</i> (G.J. Hollenberg) G.J. Hollenberg			X	X	M, H			Epilithic	
<i>Polysiphonia hendryi</i> var. <i>gardneri</i> (Kylin) G.J. Hollenberg			X	X	M, H		X	Epilithic	
<i>Polysiphonia hendryi</i> var. <i>hendryi</i> N.L. Gardner		X	X	X	M, H		X	Epilithic	
<i>Polysiphonia hendryi</i> var. <i>luxurians</i> (G.J. Hollenberg) G.J. Hollenberg	X	X	X	X	M			Epilithic	
<i>Polysiphonia paniculata</i> Montagne	X			X	M			Epilithic	
<i>Pterochondria woodii</i> (Harvey) G.J. Hollenberg	X	X		X	SS, L			Epiphytic on <i>Egregia</i>	
<i>Ptilota filicina</i> J. Agardh		X	X	X	SS, L			Epiphytic on <i>Cystoseira</i>	
<i>Tiffaniella snyderae</i> (Farlow) I.A. Abbott				X	L, M			Epilithic	
<i>Colaconema rhizoideum</i> (K.M. Drew) P.W. Gabrielson				X	L			Epiphytic on <i>Codium</i>	
<i>Bossiella chiloensis</i> (Decaisne) H.W. Johansen			X	X	M			Epilithic	
<i>Bossiella dichotoma</i> (Manza) P.C. Silva	X		X	X	M, H	X		Epilithic	
<i>Bossiella orbigniana</i> (Decaisne) P.C. Silva				X	L			Epilithic	
<i>Bossiella plumosa</i> (Manza) P.C. Silva	X		X	X	L			Epilithic	
<i>Calliarthron tuberculosum</i> (Postels et Ruprecht) E.Y. Dawson	X	X	X	X	L, M	X		Epilithic	
<i>Clathromorphum reclinatum</i> (Foslie) W.H. Adey				X	L			Epiphytic on <i>Ahnfeltiopsis</i>	
<i>Corallina chilensis</i> Decaisne	X	X	X	X	L, M	X		Epilithic	
<i>Corallina vancouveriensis</i> Yendo	X		X	X	L, M	X		Epilithic	
<i>Lithophyllum dispar</i> (Foslie) Foslie	X			X	L, M	X	X	Epilithic, epiphytic on <i>Prionitis</i> & <i>Ahnfeltiopsis</i>	

(Table 2 Continued)

Phylum/Order	Species name & authority	B	C	T	M	Zone	TP	Sand	Substrate
Erythropeltidales	<i>Lithophyllum impressum</i> Foslie	X				M			Epilithic
	<i>Melobesia medioacris</i> (Foslie) Setchell et Mason	X	X	X		SS, L	X		Epiphytic on <i>Phyllospadix</i>
	<i>Mesophyllum conchatum</i> (Setchell et Foslie) W.H. Adey			X		L			Epiphytic on <i>Bossiiella</i> & <i>Egria</i>
	<i>Pseudolithophyllum muricatum</i> (Foslie) Steneck et R.T. Paine				X	L			Epizoic
	<i>Erythrotrichia carnea</i> (Dillwyn) J. Agardh	X	X			L			Epiphytic on <i>Alaria</i>
	<i>Porphyrostromium boryanum</i> (Montagne) P.C. Silva	X	X	X		L			Epiphytic on <i>Cystoseira</i>
	<i>Smithora naidadum</i> (Anderson) G.J. Hollenberg	X				M			Epiphytic on <i>Phyllospadix</i>
	<i>Gelidium coulteri</i> Harvey				X	M			Epilithic
	<i>Ahnfeltiopsis gigartinooides</i> (J. Agardh) P.C. Silva et DeCew	X			X	M		X	Epilithic
	<i>Ahnfeltiopsis linearis</i> (C. Agardh) P.C. Silva et DeCew	X	X	X	X	L, M		X	Epilithic
	<i>Callophyllis pinnata</i> Setchell et Swezy	X	X		X	L			Epiphytic on <i>Cystoseira</i>
	<i>Callophyllis violacea</i> J. Agardh	X			X	M			Epilithic
	<i>Chondracanthus canaliculatus</i> (Harvey) Guiry	X		X	X	M, H		X	Epilithic
	<i>Chondracanthus exasperatus</i> (Harvey et J.W. Bailey) J.R. Hughey	X			X	M		X	Epilithic
	<i>Constantinea simplex</i> Setchell	X	X	X	X	L, M		X	Epilithic
Gelidiales	<i>Cryptosiphonia woodii</i> (J. Agardh) J. Agardh	X	X	X	X	M		X	Epilithic
	<i>Dilsea californica</i> (J. Agardh) Kuntze	X	X	X	X	M		X	Epilithic
	<i>Endocladia muricata</i> (Endlicher) J. Agardh	X	X	X	X	L, M		X	Epilithic
	<i>Erythrophyllum delesseriooides</i> J. Agardh	X	X	X	X	M, H			Epilithic
	<i>Farlowia conferta</i> (Setchell) I.A. Abbott	X	X	X	X	L, M			Epilithic
	<i>Farlowia mollis</i> (Harvey et Bailey) Farlow et Setchell	X	X	X	X	M, H		X	Epilithic
	<i>Gloiopeltis furcata</i> (Postels et Ruprecht) J. Agardh	X		X		M			Epilithic
	<i>Gloiosiphonia californica</i> (Farlow) J. Agardh	X			X	M			Epilithic
	<i>Gloiosiphonia verticillaris</i> Farlow	X	X			M, H		X	Epilithic
	<i>Mastocarpus jardiinii</i> (Agardh) West	X	X	X	X	M			Epilithic
	<i>Mastocarpus papillatus</i> sp. complex (Agardh) Kützing	X	X	X	X	M			Epilithic
	<i>Mazzaella flaccida</i> (Setchell et N.L. Gardner) S. Fredericq	X	X	X	X	M			Epilithic
	<i>Mazzaella linearis</i> (Setchell et N.L. Gardner) S. Fredericq	X	X	X	X	M		X	Epilithic
	<i>Mazzaella oregana</i> (Doty) J.R. Hughey, P.C. Silva et Hommersand	X	X	X	X	L			Epilithic
	<i>Mazzaella parksii</i> (Setchell et N.L. Gardner) J.R. Hughey, P.C. Silva et Hommersand	X		X	X	L, M			Epilithic
Gracilariales	<i>Mazzaella splendens</i> (Setchell et N.L. Gardner) S. Fredericq	X	X		X	L, M			Epilithic
	<i>Mazzaella volans</i> (C. Agardh) S. Fredericq	X	X	X	X	L, M			Epilithic
	<i>Pikea californica</i> Harvey	X		X	X	L, M		X	Epilithic
	<i>Pikea pinnata</i> Setchell		X	X		L			Epilithic
	<i>Gracilariopsis andersonii</i> (Grunow) E.Y. Dawson	X	X		X	M		X	Epilithic
Halymeniales	<i>Halymenia schizymeniooides</i> G.J. Hollenberg et I.A. Abbott			X	X	M, H			Epilithic
	<i>Prionitis filiformis</i> Kylin		X	X	X	M			Epilithic
	<i>Prionitis lanceolata</i> (Harvey) Harvey	X	X	X	X	L, M			Epilithic
	<i>Prionitis sternbergii</i> (C. Agardh) J. Agardh	X	X	X	X	L		X	Epilithic



(Table 2 Continued)

Phylum/Order	Species name & authority	B	C	T	M	Zone	TP	Sand	Substrate
Hildenbrandiales	<i>Hildenbrandia occidentalis</i> Setchell	X		X		L			Epilithic
	<i>Hildenbrandia rubra</i> (Sommerfelt) Meneghini	X				M			Epilithic
Nemastomatales	<i>Schizymenia pacifica</i> (Kyllin) Kylin	X		X		L	X		Epilithic
	<i>Halosaccion glandiforme</i> (S.G. Gmelin) Ruprecht	X	X	X	X	M			Epilithic, epiphytic on <i>Corallina</i>
Plocamiales	<i>Palmaria mollis</i> (Setchell et N.L. Gardner) van der Meer et Bird			X	X	M	X		Epilithic
	<i>Plocamiocolax pulvinata</i> Setchell			X	X	M			Parasitic on <i>Plocamium</i>
	<i>Plocamium oregonum</i> M.S. Doty	X		X	X	M			Epilithic
Rhodymeniales	<i>Plocamium pacificum</i> Kylin	X	X	X	X	L, M			Epilithic
	<i>Plocamium violaceum</i> Farlow		X	X	X	L, M			Epilithic
	<i>Neogastroclonium subarticulatum</i> (Turner) L. Le Gall, Dalen et G.W. Saunders			X	X	M, H			Epilithic
	<i>Rhodymenia pacifica</i> Kylin				X	L			Epilithic
Anthophyta									
Alismatales	<i>Phyllospadix scouleri</i> W. J. Hooker	X	X	X	X	L, M	X	X	Epilithic
	<i>Phyllospadix torreyi</i> S. Watson	X	X	X	X	L		X	Epilithic

B, Cape Blanco; C, Crescent City; T, Trinidad; M, Cape Mendocino. Tidal zone is indicated as S: splash, H: high, M: mid, L: low, SS: shallow subtidal. Also included are the following habitat attributes: if the species occurred in a tidepool (TP), if sand was present (Sand), and substrate type (epilithic, epiphytic, epizooic, or endophytic).

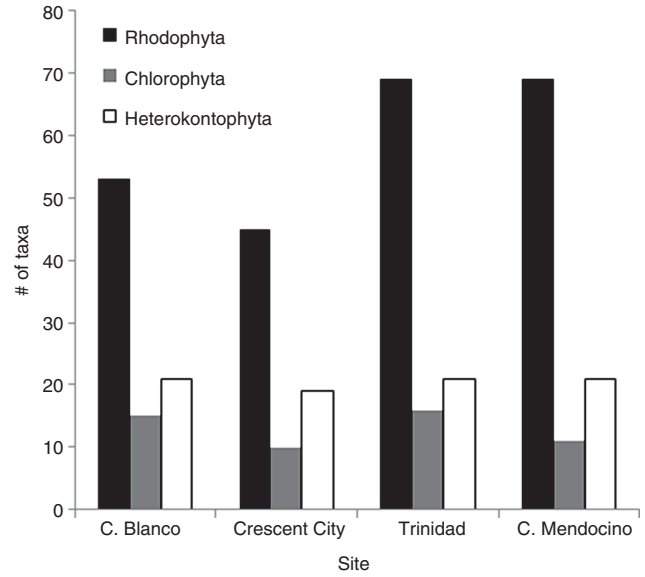


Figure 2 The number of marine macroalgal taxa found at each of the four study areas grouped into phyla.

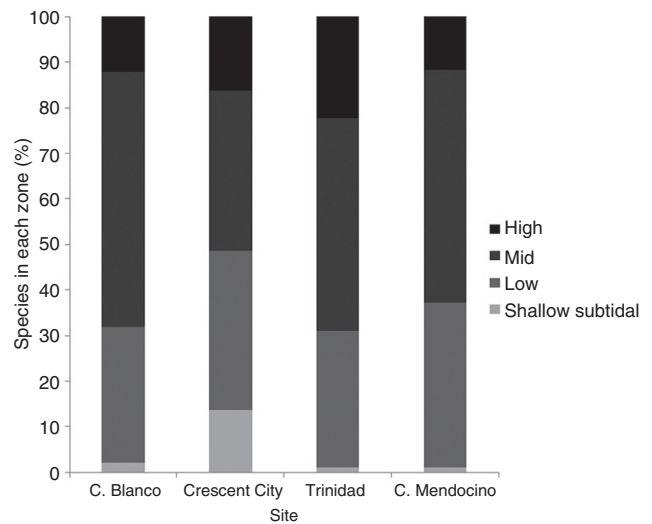


Figure 3 Marine macroalgal species percentages at each of the four study areas in each of the four zones; high, mid, low and shallow subtidal.

Table 3 Number of species in each of the seven functional groups found at each of the four study areas.

	B	C	T	M
Articulated coralline	5	4	6	6
Corticated foliose	24	21	24	23
Corticated macrophyte	17	15	25	26
Crust	5	2	3	6
Filamentous	15	12	15	15
Foliose	8	9	11	6
Leathery	13	11	10	13

B, Cape Blanco; C, Crescent City; M, Cape Mendocino; T, Trinidad.

**Table 4** Results for the top three GLMER models for species richness, a continuous variable, based on AICc values.

Model	Predictors for species richness	AICc	$\Delta$ AICc	Degrees of Freedom	Weight
1	Zone, group, transect <sup>a</sup> and site <sup>a</sup>	347.8	0.0	15	0.65
2	Zone, group, transect and site (interaction), and site <sup>a</sup>	349.1	1.3	21	0.35
3	Zone, group, site <sup>a</sup>	405.6	57.8	10	<0.001

The predictors used in the analysis were all categorical variables including zone, functional group and transect. <sup>a</sup>indicates random variable.

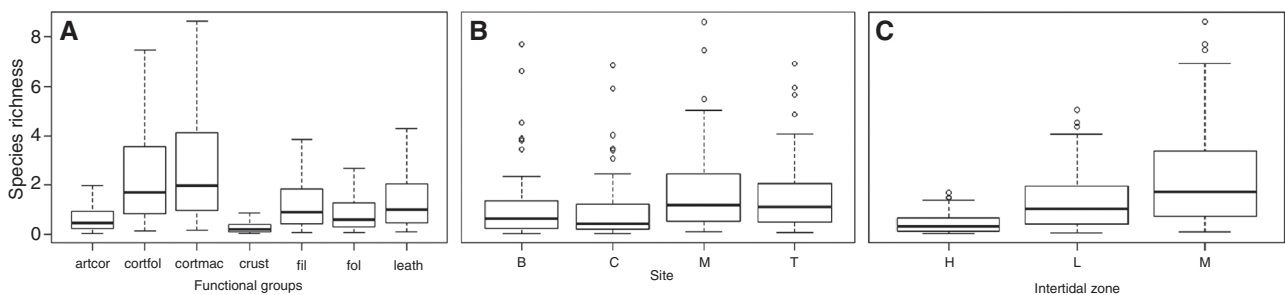
**Table 5** (A and B) Parameter estimates for the top model (model #1 in Table 4) selected based on AICc criterion.

	Estimate	Standard error
A. Fixed effects used in the model		
Intercept	-1.5910	0.2641
Zone low	1.0986	0.1873
Zone mid	1.6354	0.1776
Corticated foliose	1.3304	0.2345
Corticated macrophyte	1.4796	0.2314
Crust	-0.8329	0.3795
Filamentous	0.6712	0.2568
Foliose	0.2985	0.2757
Leathery macrophyte	0.7765	0.2524
	Variance	Standard deviation
B. Random effects used in the model		
Intercept	0.18445	0.42947
Transect 2	0.73335	0.85636
Transect 3	1.38494	1.17683

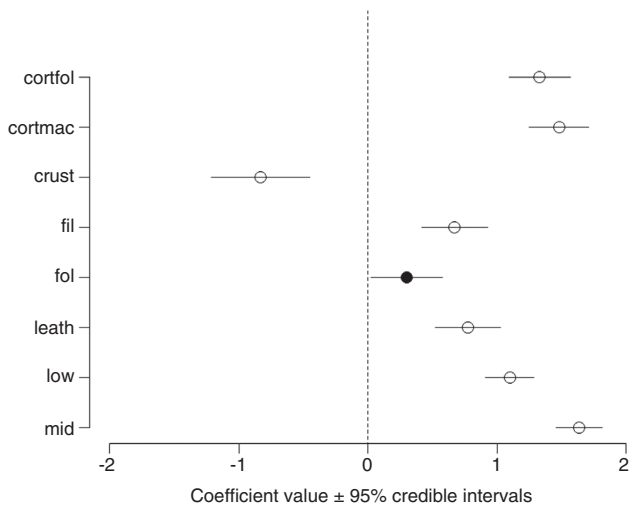
US (Blanchette et al. 2008) quantified both macroinvertebrates and macroalgae (with a few selected sites from Cape Blanco to Cape Mendocino) and found both the faunal and floral species composition to change gradually over latitude. Potentially, the gradual change in species composition could be due to the phenomenon of dispersal

of seaweed spores close to the parental population, a process that has been shown to have a strong effect on the ecological succession of the subsequent populations (Dudgeon and Petraitis 2001, Gaylord et al. 2002, Bobadilla and Santelices 2005, Broitman and Kinlan 2006). The present study used a different approach for defining a site and included smaller, often overlooked, cryptic species. All of the seven taxa previously undocumented for this region are inconspicuous; two are endophytic greens, two are epiphytic reds, and three are crustose forms (both fleshy and coralline).

In this bioregion, abrupt changes in species distributions may therefore be more common for particular lineages than at the scale of the entire flora. For example, molecular sequencing of species in the order Bangiales has revealed that *Wildemania schizophylla* has a northern limit at Cape Mendocino. Three other species, *Pyropia kanakaensis*, *Pyropia abbottiae* and *Porphyra rediviva* have their southern range limits in northern California (Lindstrom 2008). Similarly, Lindstrom et al. (2011) have shown that seven species of *Mastocarpus* Kützing occur within the bounds of the capes region and two species have range limits at Cape Mendocino, namely *M. vancouveriensis* S.C. Lindstrom, J.R. Hughey and P.T. Martone and *M. agardhii* (Setchell and N.L. Gardner) S.C. Lindstrom, J.R. Hughey and P.T. Martone. As stated in their study, *Mastocarpus* is

**Figure 4** Box plots of the best fit GLMER model for species richness with each of the predictors with standard deviation.

(A) Species richness for each of the seven functional groups; artcor: articulated corallines, cortfol: corticated foliose, cortmac: corticated macrophytes, crust: crust, fil: filamentous, fol: foliose and leath: leathery macrophytes. (B) Species richness for each of the three tidal zones; H: high, L: low and M: mid. (C) Species richness for each of the four study areas; B: Cape Blanco, C: Crescent City, M: Cape Mendocino and T: Trinidad.



**Figure 5** Plot showing the means for the eight fixed parameters based on the best fit regression model for species richness with 95% credibility intervals showing the variation in means. None of the values fall along the middle line, showing that all are significant except fol: foliose (black dot, p-value > 0.5).

known to exhibit interspecific morphological variation and is morphologically difficult to distinguish among species. Consequently, for our list of taxa, only two species of *Mastocarpus* were included.

Our mixed effects model suggests that intertidal macroalgal species richness based on functional groups was tightly coupled with the intertidal zones and transects grouped within the study areas. The intertidal zones harbour functional groups assemblages that are specific to those zones. Furthermore, based on the confidence intervals, the fitted GLMER model shows that most of the parameters were significant, except the foliose group. Highest species richness was found in the mid intertidal composed of the corticated foliose and the corticated macrophyte functional groups. Lowest species diversity was found in the low intertidal as well as the articulated coralline and fleshy crust groups. However, overall it was found that the two capes showed a slightly greater abundance of the leathery macrophyte and the crust (fleshy and coralline) groups than the non-cape study areas. Increasing wave exposure has been tightly correlated with an increase in brown algal species richness and a decrease in both the green and red algae in Japan (Nishihara and Terada 2010). In the Pacific NE, it has been reported that high wave action could account for the increase in the leathery macrophyte group as some members of Phaeophyceae, such as *Postelsia palmaeformis*, *Lessoniopsis littoralis* and *Pelvetiopsis limitata* occur only on the exposed outer coast (Waaland 1977). In addition to wave action, higher upwelling intensity has been correlated with an

increase in nutrient fluxes leading to an abundance of corticated, structurally complex algae and a decrease in ephemeral species on the Chilean coast (Broitman et al. 2001, Nielsen and Navarrete 2004). Similarly, a common coastal feature south of Cape Mendocino is a cyclonic eddy that has been reported to increase nutrient supply to the euphotic zone (Hayward and Mantyla 1990) and drive primary production and phytoplankton blooms. In our study, therefore, it was hypothesised that the Cape Blanco and Cape Mendocino sampling areas would house more structurally complex functional groups, but this was only slightly true for leathery macrophytes, as the heavily corticated group was found throughout all four sampling sites. Throughout this region, sand deposition and abrasion could also be driving a decrease in ephemeral species and selecting for corticated groups that are able to withstand periods of burial or partial scouring.

In conclusion, this study described the rocky intertidal seaweed flora from an area that has not previously been treated as a single bioregion. Species diversity was highest in the mid intertidal and the vast majority of algae were epilithic, with only a few epiphytic on other algae, epizooic on snail shells, endophytic, and parasitic on tissues of other algae. Although sediment and sand abrasion is tolerated by some macroalgae and a few have even established a niche in this environment tolerating periodic burial, most of the macroalgae sampled inhabit a rocky substrate without sediment deposition. Although the impact of the coastal headlands on setting macroalgal species boundaries is still unclear, studies suggest that the effects of the cape headlands on ocean currents in combination with the disturbance produced by sediment loads may act as a distributional barrier to the dispersal of benthic marine organisms on both the species and the gene level (Magnell et al. 1990, Barth et al. 2000, Kelly and Palumbi 2010). This issue as well as the role of dispersal of algal propagules on species reproductive success along this coastline has the potential to be resolved with further sampling and molecular work on the macroflora. Furthermore, additional intensive sampling over longer temporal scales may reveal cryptic species that were overlooked or were absent from the transects of this study.

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