

The non-native turf-forming alga *Caulacanthus ustulatus* displaces space-occupants but increases diversity

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Abstract Non-indigenous seaweeds can be found in coastal habitats worldwide yet the ecological effects of only ~6 % of macroalgal introductions have been studied. The turf-forming red alga *Caulacanthus ustulatus*, a putative introduction from Asia, was discovered in southern California in 1999, yet has received very little attention despite being common in rocky intertidal habitats in the region. The purpose of this study was to evaluate the potential effects of *Caulacanthus* on native invertebrate and seaweed community composition. Macrofaunal, meiofaunal, and macroalgal community structure and diversity were compared between patches with (non-native) and without *Caulacanthus* (native) in the upper intertidal zone at 5 locations in southern California. *Caulacanthus* appears to displace macro invertebrates, such as barnacles, limpets, and periwinkles, while facilitating a more diverse array of meiofauna and macroalgae. This is likely due to the formation of a novel turf habitat in the upper zone where turfs are uncommon in this region naturally; algal turfs can increase habitat

complexity, trap sediment, and maintain moisture during low tide which likely benefits meiofauna and seaweeds by providing food, habitat, or refuge from desiccation stress. Subsequent comparisons of invertebrate and seaweed assemblages were conducted in native and non-native patches at one site in the upper intertidal zone as well as in the middle intertidal zone where a native turf zone exists. Despite differences in community composition in the upper intertidal zone, no differences were observed in the middle zone, providing support that the novel turf created by *Caulacanthus* in the upper zone drives community differences.

Keywords Non-native seaweeds · Exotic or introduced species · Rocky intertidal ecology · Non-native species impacts · Novel turf forming hypothesis

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Introduction

The introduction of non-native species is considered to be the second biggest threat, behind habitat destruction, to global biodiversity and ecosystem functioning (Vitousek and Walker 1989; D'Antonio and Vitousek 1992; Mack et al. 2000). Through the effects of biological interactions and habitat alteration, invasions can decrease native species abundances (Race

1982; Delibes et al. 2004; Carlsson and Lacoursiere 2005) and diversity (Meiners et al. 2001; Wikstrom and Kautsky 2004; Hejda et al. 2009) and alter community structure (Posey 1988; Stimpson et al. 2001; Britton-Simmons 2004). Although significant work has documented these changes, a majority of studies are concentrated in terrestrial ecosystems, while the ecological effects of non-indigenous marine species, particularly seaweeds, are less understood (Grosholz 2002; Murray et al. 2006). Recent reviews (Schaffelke and Hewitt 2007; Williams and Smith 2007) of the global distribution and impacts of non-native species of seaweeds reveal that only approximately 6 % of exotic seaweeds have been studied to determine their ecological impacts, with most studies concentrated on a small list of notorious species that have had multiple introductions worldwide.

Recently, increased emphasis has been placed on the effect of non-native seaweeds on ecosystem functioning and community composition and diversity. For example, a handful of studies have examined the role that exotic seaweeds have on herbivores and food webs (e.g. Britton-Simmons 2004; Davis et al. 2005; Sumi and Scheibling 2005; Wikstrom et al. 2006; Navarro 2009; Vogt 2010). Community level changes (biodiversity and community structure) resulting from the presence of non-native seaweeds have been studied with increasing frequency, but still constitute a major research gap (Schaffelke and Hewitt 2007; Williams and Smith 2007). Approximately 65 studies have examined community diversity and assemblage impacts by non-native seaweeds, but are limited to only 12 seaweed species, such as the green algae *Caulerpa taxifolia* (Vahl) C. Agardh and *C. racemosa* (Forsskål) J. Agardh (Piazzi and Cinelli 2001, 2003; Piazzi et al. 2003; Balata et al. 2004; Piazzi and Ceccherelli 2006; York et al. 2006), *Codium fragile* ssp. *fragile* (Suringar) Hariot (previously ssp. *tomentosoides* [van Goor] Silva; Schmidt and Scheibling 2006; Drouin et al. 2011), or the brown alga *Sargassum muticum* (Yendo) Fensholt (e.g. Britton-Simmons 2004; Sánchez et al. 2005; Buschbaum et al. 2006; Strong et al. 2006). The impacts of non-native seaweeds on community structure are inconsistent with over half exhibiting negative impacts on specific species or taxonomic groups (e.g. Ceccherelli and Cinelli 1997; Williams and Grosholz 2002; Casas et al. 2004). For example, the presence of *C. taxifolia* in the Mediterranean Sea and

southern California has resulted in decreased abundances of seagrasses (Ceccherelli and Cinelli 1997; Williams and Grosholz 2002) and the presence of the non-native red alga *Grateloupia turuturu* (Yamada) in Rhode Island, USA, has resulted in a large decrease in macrophyte biomass (Janiak and Whitlatch 2012). Alternatively, the presence of introduced seaweeds can result in no community changes (Trowbridge 2001) or, in some cases, facilitation of certain taxa (Dumay et al. 2002; Schmidt and Scheibling 2006; Byers et al. 2012). For example, the presence of *Gracilaria vermiculophylla* in mudflats in the southeastern USA has resulted in increased abundances of epifauna and a new addition to the detrital food web (Byers et al. 2012). However, these types of impacts are generally complex and include numerous indirect effects that can be difficult to study. For instance, *S. muticum* in Washington can indirectly impact the abundance of sea urchins through shading of native kelps, thus reducing the food source of urchins (Britton-Simmons 2004). Furthermore, although a non-native seaweed may be unpalatable or not used as a food source by native herbivores, the presence of a non-native seaweed can support a high abundances of epiphytes that can act as a food source for consumers thus increasing herbivore abundance or diversity (Sánchez et al. 2005; Williams and Smith 2007).

Along the coast of southern California, USA, there has been an increase in the prevalence of non-native seaweeds over the past several decades, including *S. muticum*, *S. horneri* (Turner) C. Agardh, *Undaria pinnatifida* (Harvey) Suringar, and *Lomentaria hokkaidensis* Yendo, among a list of others (Bullard and Murray 2003; Whiteside et al. 2007; Miller et al. 2011). In 1999, the turf-forming, red alga *Caulacanthus ustulatus* (Mertens ex Turner) Kützinger (synonyms *C. okamurae*, *Feldmannophycus okamurae*) was first encountered in southern California rocky intertidal habitats (Miller et al. 2011). This putative introduction from Asia is found in the upper to mid-shore habitat growing within barnacle patches, mixed within middle intertidal red algal turf zones, and epiphytic on mussels and rockweeds. This species is found in several locations along the California coastline, but is a relatively major component of local intertidal assemblages in southern California rocky shore habitats, mostly along the Palos Verdes Peninsula in Los Angeles County and south (Whiteside et al. 2007). This species has also been a suspected invader

in other locations globally, including the Atlantic coast of France (Rueness and Rueness 2000), the western Mediterranean Sea (Zentos et al. 2010), Alaska (Ruiz et al. 2006), and the Netherlands (Stegenga et al. 2006). As with most non-native seaweeds, little is known about the ecology of southern Californian non-native seaweeds, despite some being present in the region for several decades (e.g. *S. muticum* since the 1970s). The goal of this study was to examine whether community assemblages are affected by the presence of the non-native red alga *Caulacanthus* by comparing biodiversity and community structure inside non-native patches dominated by *Caulacanthus* with native patches where the alga was absent or rare.

Methods

Community effects: upper intertidal zone

To test if the non-native alga *Caulacanthus ustulatus* affects the community structure of the upper-intertidal zone in southern California waters, we sampled macroinvertebrates, meiofauna, and macroalgae in native and non-native patches at five locations in November 2010 to April 2011. Three sites were located in Orange County, including Dana Point (DPT), Shaw's Cove (SHC) and Corona del Mar (CDM), and two sites along the Palos Verdes Peninsula in Los Angeles County at Pt. Fermin (PTF proper) and Pt. Fermin North (PTN, located ~2.5 km north of PTF). All sites were characterized by gently sloping bedrock and are exposed to relatively similar oceanographic conditions.

The upper intertidal zone at each site was characterized by interspersed patches of native barnacle communities (*Chthamalus* spp. and *Balanus glandula* Darwin, 1854) and non-native *Caulacanthus* turfs. While *Caulacanthus* can inhabit a crevice/crack microhabitat that is not typically utilized by barnacles, we focused our sampling on flat rock faces where barnacles and limpets typically reside, that were at the same intertidal level, and that were facing in the same general direction to the shoreline; there were no indications that *Caulacanthus* was present on the flat surface due to differences in microhabitats as compared to native patches. Monitoring of *Caulacanthus* in fixed plots over time (Smith unpublished) suggests

that barnacle dominated plots without *Caulacanthus* can be overtaken; equally some plots that were initially high in *Caulacanthus* were observed to be nearly free of *Caulacanthus* over time. Several ($n = 10\text{--}15$ for each) 400 cm² quadrats (large plots) were randomly placed within *Caulacanthus* patches (defined as >75 % *Caulacanthus* cover) and in adjacent areas without *Caulacanthus* (defined as <10 % *Caulacanthus* cover). All macroinvertebrates visible to the naked eye were counted and the presence of macroalgae recorded within each of the quadrats. Subplots (13.7 cm², $n = 7\text{--}10$ per site) were then sampled to examine all invertebrate species, particularly targeting the meiofaunal assemblages but with macroinvertebrates also quantified. Within *Caulacanthus* patches, core samples within the algal turf were collected, taken to the laboratory, and all invertebrates counted and identified at higher taxonomic levels (typically class or order) under a dissecting scope (to 10X). In non-*Caulacanthus* patches where an algal turf was absent and consisted of mostly bare rock, limpets, and barnacles, invertebrate assemblages were recorded in subplots in the field using field scopes (to 10X, $n = 10$ per site). Additionally, the amount of sediment trapped within collected *Caulacanthus* core samples was measured; no sediment was detectable within native patches.

Three data sets, macrofauna abundance and macroalgal presence in large plots and macro- and meiofauna abundance in subplots, were compared among sites and between native and non-native patches using multi-variate techniques (PRIMER). As we were testing the effect of *Caulacanthus* on macroalgal community assemblages, the presence of *Caulacanthus* was excluded from the macroalgal analysis. A resemblance matrix was calculated using a Bray-Curtis similarity and was used to create multi-dimensional scaling (MDS) plots. A Two-Factor Analysis of Similarities (ANOSIM) was used to determine significant differences in community structure among sites and between native and non-native patches for each data set. A similarities Percentage (SIMPER) test was used to determine which species are contributing most to dissimilarities between patches. Species richness (S) and Shannon-Wiener's (H') index was calculated for invertebrate abundances in large plots (macrofauna) and subplots (macro- and meiofauna) and macroalgal presence (except H') and compared among sites and between patches using a

General Linear Model Two-Factor ANOVA (Adjusted Sum of Squares to account for unbalanced design). For macroalgae, species richness was determined without inclusion of *Caulacanthus*. The mean S and H' were calculated per patch at each site ($n = 5$) and differences between native and non-native patches examined using a Paired T test (native and non-native paired within each site).

Community effects: upper and middle intertidal turf comparisons

Differences observed in community assemblages between upper shore native and non-native patches (see results) were hypothesized to be attributable to physical conditions facilitated by the presence of the turf forming *Caulacanthus*, which accumulated sand and likely reduced desiccation stress through trapping of water during low tide. To determine the role of the turf in differences in community structure, we examined community assemblage differences in both the upper intertidal zone where a native turf is absent and in the middle intertidal zone where a native algal turf is present. The community structure of macroinvertebrates, meiofauna, and macroalgae was compared in native and non-native patches in the upper and middle intertidal zones at one site, Corona del Mar, in February 2012. Ten 400 cm² quadrats were established in the upper zone in non-native *Caulacanthus* patches (>40 % *Caulacanthus* cover) with five additional plots located in native barnacle patches (<5 % *Caulacanthus* cover). In the middle intertidal turf zone (typically articulated corallines where *Caulacanthus* can grow intertwined with other turf formers), twelve plots were established in non-native patches (>40 % *Caulacanthus* cover) and six plots in native algae turfs (<5 % *Caulacanthus* cover). Sampling of biota in large and subplots was conducted as previously described except core turf samples were also collected from the native plots in the middle intertidal zone.

The abundance of macroinvertebrates and meiofauna and the presence of macroalgal were analyzed using similar multi-variate analyses on three data sets as previously discussed. A two factor Analysis of Similarities (ANOSIM) was used to determine significant differences in community structure between zones and between native and non-native patches for each data set. In addition, ANOSIM analyses were conducted on the zones individually. A Similarities

Percentage (SIMPER) test was used to determine which species are contributing most to dissimilarities between patches. S and H' was calculated for each data set (except H' for macroalgal data) and compared among zones and between patches using a General Linear Model Two-Factor ANOVA (Adjusted Sum of Squares to account for unbalanced design). Additional T tests were conducted on diversity within each zone separately, comparing native and non-native patches.

Results

Community effects: upper intertidal zone

Macroinvertebrate community structure and diversity within large plots varied markedly among sites with clear differentiation between patches with and without the non-native *Caulacanthus*. An Analysis of Similarities (ANOSIM) revealed significant differences in community structure (Fig. 1a) both between native and non-native patches and among sites (Table 1). Dissimilarity in community composition between patches was driven primarily by high densities in native patches of the barnacle species *Chthamalus* spp., the limpet *Lottia scabra* Gould, 1846, and the periwinkle snail *Littorina* spp. (Table 2), compared to non-native patches. When examining the community structure between patches with and without *Caulacanthus* using mean abundances per site, similar patterns were observed (Fig. 1b) with significant differences between patches (Table 1). The species driving dissimilarity were limited primarily to the barnacle *Chthamalus* spp. (Native mean = 464.8 ± 129.7 , non-native mean = 10.4 ± 3.4 , ~81 % dissimilarity contribution) and the periwinkle *Littorina* spp. (Native mean = 78.9 ± 35.6 , non-native mean = 10.3 ± 3.8 , ~11 % dissimilarity contribution).

Mean (\pm SE) macroinvertebrate richness in patches with *Caulacanthus* was $3.2 (\pm 0.25)$; Table 3) while richness in native patches without *Caulacanthus* was elevated (4.1 ± 0.26). Individual sites significantly varied in their degree of difference (Table 3) but richness was consistently and significantly higher in native patches without *Caulacanthus* (Table 4). With mean species richness per patch per site, richness was also significantly higher in native patches (Table 4). In contrast, mean H' was similar in non-native ($0.71 \pm$

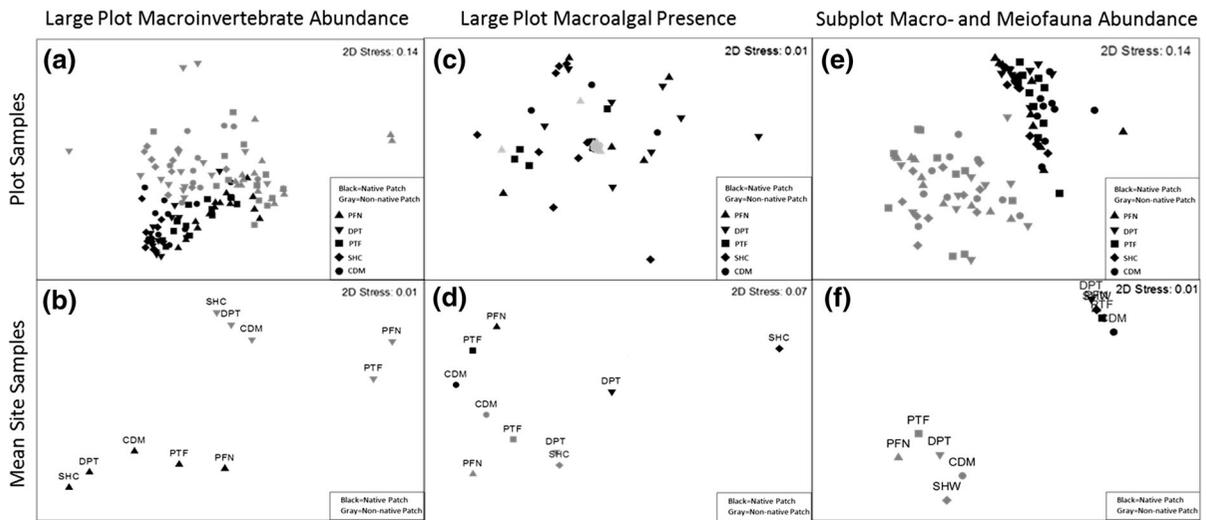


Fig. 1 Multidimensional scaling (MDS) plot presenting the similarity in community composition for three data sets: macroinvertebrate abundance in large plots (a, b), macroalgal presence in large plots (c, d), and macro- and meiofauna abundance in subplots (e, f). Presented are MDS plots for plot samples (upper graphs) and mean site samples (lower graphs) from five sites in both native patches (black) and non-native

patches with *Caulacanthus* (gray). Analysis of similarities (ANOSIM) tests reveal significant differences for all analyses; upper graphs with significant patch and site factors and lower graphs with a significant patch factor (see Table 1). For macroalgae, *Caulacanthus* presence was not included in the analyses

Table 1 Analysis of Similarities (ANOSIM) results (Global R and p value) for two studies comparing: (a) the effects of *Caulacanthus* on upper intertidal zone communities at five

sites, and (b) the effects of *Caulacanthus* in the upper and middle intertidal zones at one site

(a) Upper intertidal zone effects	Two-factor ANOSIM results				ANOSIM results	
	Patch		Site		Patch	
	Global R	p value	Global R	p value	Global R	p value
Large plot macro invertebrate abundance	0.520	0.001	0.270	0.001	0.896	0.008
Large plot macro algal presence	0.283	0.001	0.168	0.001	0.406	0.008
Subplot macro- and meiofauna abundance	0.888	0.001	0.216	0.001	1.000	0.008

(b) Upper and middle intertidal comparisons	Two-factor ANOSIM results				ANOSIM results			
	Patch		Zone		Patch: upper zone		Patch: middle zone	
	Global R	p value	Global R	p value	Global R	p value	Global R	p value
Large plot macroinvertebrate abundance	0.051	0.210	0.220	0.003	0.308	0.028	0.005	0.477
Large plot macroalgal presence	0.187	0.002	0.152	0.007	0.345	0.019	0.093	0.165
Subplot macro- and meiofauna abundance	0.209	0.027	0.332	0.001	0.449	0.006	0.050	0.281

(a) Results for two-factor ANOSIM analyses using plot data comparing native and non-native patches at five sites, and results for a one-factor ANOSIM (patch only) analyses using mean site data for the three data sets. (b) Results for two-factor (patch and zone) ANOSIM analyses and individual one-factor ANOSIM (patch) analyses for the upper and middle intertidal zones individually for three data sets

0.06; Table 3) and native patches (0.63 ± 0.05) (Table 4). Equally, mean H' between patch types at each site was similar (Table 4).

Community analyses of macroalgal presence (*Caulacanthus* excluded; Fig. 1c) also exhibited significant differences between patches and among sites

Table 2 Similarities percentages (SIMPER) results for community effects studies for the upper intertidal zone for each data set

Data set	Species	Native	Non-native	~Dissimilarity (%)
Large plot macroinvertebrate abundance	<i>Chthamalus</i> spp	451.5 (63.3)	9.9 (2.5)	65
	<i>Lottia scabra</i>	14.4 (1.8)	3.5 (0.7)	12
	<i>Littorina</i> spp	69.8 (11.7)	9.4 (2.1)	11
Large plot macroalgal presence	<i>Ulva californica</i>	0.19 (0.05)	0.84 (0.05)	31
	<i>Pseudolithoderma nigrum</i>	0.24 (0.05)	0.22 (0.05)	13
	<i>Gelidium pusillum</i>	0.00 (0.00)	0.25 (0.06)	10
	Ralfsiaceae	0.16 (0.05)	0.08 (0.03)	7
	<i>Chondracanthus canaliculatus</i>	0.02 (0.02)	0.22 (0.05)	7
Subplot macro- and meiofauna abundance	Cirripidea	57.9 (7.5)	0.9 (0.6)	46
	Ostracod (Taxa B)	0.0 (0.0)	19.7 (4.8)	14
	Copepods	0.0 (0.0)	11.1 (1.9)	11
	Gastropods	7.0 (1.0)	2.8 (0.6)	7

Means (± 1 SE) and the percent contribution to dissimilarities between native and non-native patches. Upper intertidal zone effects means are pairwise comparisons for native and non-native patches with all sites combined

(Table 1), with very little differentiation in *Caulacanthus* plots among sites. Differences in macroalgal communities in patches with and without *Caulacanthus* were driven by the higher frequency of fleshy seaweeds (*Ulva*, *Gelidium*, and *Chondracanthus*; Table 2) in non-native *Caulacanthus* patches while native patches were more frequented by encrusting algae (*Pseudolithoderma* and *Ralfsiaceae*). When examining the community structure between patches with and without *Caulacanthus* using mean abundances per site, similar patterns were observed (Fig. 1d) with significant differences between patches (Table 1). The species driving dissimilarity included a higher frequency of *Ulva* (Native mean = 0.19 ± 0.07 , non-native mean = 0.85 ± 0.08 , ~28 % dissimilarity contribution) and *Gelidium* (Native mean = 0.0 ± 0.0 , non-native mean = 0.25 ± 0.09 , ~11 % dissimilarity contribution) in non-native patches and a higher frequency of *Pseudolithoderma* (Native mean = 0.24 ± 0.11 , non-native mean = 0.23 ± 0.12 , ~10 % dissimilarity contribution) in native patches.

Macroalgae were more species rich in *Caulacanthus* patches (mean = 2.4 ± 0.2) than in patches without *Caulacanthus* (0.8 ± 0.14) with richness significantly higher in non-native patches at all sites (Tables 3, 4); the site factor and interaction term were not significant. Mean species richness per patch within sites was also found to be significantly higher in patches with *Caulacanthus* (Table 4).

Macro and meiofauna community structure in subplots (Fig. 1e) was significantly different between native and non-native patches and among sites (Table 1). Dissimilarity between native and non-native patches was driven primarily by high abundances of Cirripedia barnacles and gastropods (mostly periwinkles and limpets) in native patches and ostracods (Taxa B—two clear groups of ostracod taxa were separated as Taxa A and B) and copepods in non-native patches (Table 2). Using mean data per patch within a site revealed similar patterns (Fig. 1f; Table 1) with similar species drivers.

Mean subplot invertebrate richness in patches with *Caulacanthus* was markedly higher (mean 6.5 ± 0.97 ; Table 3) than in native patches without *Caulacanthus* (1.9 ± 0.10). Similar patterns were observed for H' (non-native mean = 1.3 ± 0.007 , native mean = 0.3 ± 0.05). Subplot species richness and H' were consistently higher in non-native patches at all sites (Table 3). A two-factor ANOVA revealed significant differences for all factors for taxa richness (Table 4) while H' was similar among sites but significantly different between patches with the interaction term also significant. Using mean data per patch for each site, both S and H' were significantly higher in non-native patches (Table 4).

While no measurable sediment was found in native patches, mean sediment accumulation in non-native *Caulacanthus* turfs was $\sim 165 \text{ cm}^3 \text{ m}^{-2}$ (± 24.7).

Table 3 Mean (± 1 SE) species richness (S) and Shannon-Weiner Index (H') (except macroalgal presence) for the three data sets in native patches without *Caulacanthus* and non-native patches with *Caulacanthus* present

Study	Site	Patch	Macroinvertebrate		Macroalgae	Meiofauna		
			S	H'	S	S	H'	
(a) Upper intertidal zone effects	DPT	Native	4.9 (0.31)	0.61 (0.11)	0.7 (0.23)	1.9 (0.18)	0.22 (0.06)	
		Non-native	3.7 (0.41)	0.70 (0.10)	2.3 (0.19)	5.8 (0.61)	1.37 (0.12)	
	SHC	Native	3.4 (0.37)	0.52 (0.04)	0.3 (0.15)	2.3 (0.21)	0.50 (0.06)	
		Non-native	2.6 (0.37)	0.54 (0.13)	2.0 (0.26)	5.0 (0.42)	1.19 (0.08)	
	CDM	Native	4.4 (0.43)	0.61 (0.09)	1.0 (0.26)	1.7 (0.15)	0.22 (0.07)	
		Non-native	3.8 (0.49)	0.85 (0.12)	2.2 (0.20)	5.7 (0.45)	1.27 (0.11)	
	PTF	Native	4.0 (0.34)	0.63 (0.10)	0.9 (0.24)	1.9 (0.10)	0.26 (0.07)	
		Non-native	3.8 (0.49)	0.63 (0.15)	3.2 (0.44)	5.6 (0.40)	1.13 (0.16)	
	PFN	Native	3.7 (0.25)	0.80 (0.09)	1.1 (0.25)	1.8 (0.20)	0.30 (0.09)	
		Non-native	3.1 (0.43)	0.81 (0.13)	2.2 (0.45)	10.3 (0.75)	1.55 (0.10)	
	All sites	Native	4.1 (0.26)	0.63 (0.05)	0.8 (0.14)	1.9 (0.10)	0.30 (0.05)	
		Non-native	3.2 (0.25)	0.71 (0.06)	2.4 (0.20)	6.5 (0.97)	1.30 (0.07)	
	(b) Upper and middle intertidal comparisons	High zone	Native	5.8 (0.37)	0.80 (0.19)	2.0 (0.64)	1.6 (0.41)	0.41 (0.11)
			Non-native	5.2 (0.33)	1.17 (0.05)	4.4 (0.50)	4.2 (0.66)	1.19 (0.16)
Mid zone		Native	6.0 (0.80)	1.23 (0.09)	6.8 (0.52)	6.6 (0.95)	0.86 (0.20)	
		Non-native	4.6 (0.57)	1.13 (0.09)	5.6 (0.53)	5.7 (0.78)	1.12 (0.13)	

(a) Upper intertidal zone effects for each site and for all sites combined (using mean per patch within a site), and (b) for upper and middle intertidal turf comparisons

Sediment accumulation varied significantly among sites and between patches (Two Factor ANOVA, 4th root transformation; presence of *Caulacanthus* $df = 1$, $F = 1,379$, $p < 0.001$; site $df = 4$, $F = 4.4$, $p = 0.003$; S X C $df = 4$, $F = 4.44$, $p = 0.03$).

Community effects: upper and middle intertidal turf comparisons

Macro invertebrate community structure in large plots was similar between patches but was significantly different between zones (Table 1). When analyzing zones separately, community assemblages were significantly different in the upper intertidal zone, but were similar in the middle intertidal zone (Table 1; Fig. 2a, b). Differences in the upper intertidal zone were driven by high abundances of barnacles, periwinkles, and limpets (Table 5).

Macroinvertebrate S and H' did not vary between patches or between zones (Tables 3, 4). Within zones separately, S and H' were similar in native and non-native patches for both the upper and middle intertidal zones (Table 4).

Community structure of macroalgae (based on presence, but with *Caulacanthus* removed) was significantly different between patches and zones (Table 1). Within zones, community structure was significantly different in the upper intertidal, but not in the middle intertidal zone (Table 1; Fig. 2c, d). Differences in the upper intertidal zone were driven primarily by the higher frequency of *Gelidium*, *Ulva*, and *Corallina*, and lower frequency of encrusting corallines in non-native patches (Table 5).

Macroalgal richness (Table 3) was similar between patches, but significantly different for the zone and interaction factors (Table 4); the interaction term was likely significant as richness was significantly higher in the non-native patches in the high intertidal zone, while it ranked higher in the native patches (but not significantly) in the middle intertidal zone (Tables 3, 4).

Subplot invertebrate (macro- and meiofauna) community structure was significantly different between native and non-native patches and among zones (Table 1). Within each zone separately, an ANOSIM revealed significant differences between patches in the

Table 4 Analysis of Variance (ANOVA) and T-test results (df, F- or T-stat. and p value) for two studies comparing: (a) the effects of *Caulacanthus* on upper intertidal zone communities at five sites, and (b) the effects of *Caulacanthus* in the upper and middle intertidal turf zone at one site

Study	Data set	Two-factor ANOVA						Paired T test				
		Patch			Site			Patch X Site				
		df	F	p value	df	F	p value	df	F	p value	T	p value
(a) Upper intertidal zone effects	Macroinvertebrate richness	1	13.92	<0.001	4	3.85	0.006	4	0.36	0.838	6.39	0.003
	Macroinvertebrate H'	1	1.01	0.316	4	1.67	0.163	4	0.32	0.864	-1.67	0.170
	Macroalgae richness	1	68.24	<0.001	4	2.09	0.087	4	1.13	0.344	-7.99	0.001
	Meiofauna richness	1	320.00	<0.001	4	13.20	<0.001	4	15.80	<0.001	-4.51	0.011
	Meiofauna H'	1	265.00	<0.001	4	1.70	0.159	4	2.70	<0.001	-9.80	0.001
Two-factor ANOVA												
(b) Upper and middle intertidal turf comparisons	Macroinvertebrate richness	1	2.37	0.135	1	0.24	0.631	1	0.29	0.593	1.21	0.258
	Macroinvertebrate H'	1	2.33	0.138	1	2.46	0.127	1	3.69	0.064	-1.88	0.133
	Macroalgae richness	1	0.74	0.398	1	29.08	<0.001	1	11.08	0.002	-4.06	0.002
	Meiofauna richness	1	0.42	0.520	1	17.35	0.000	1	5.90	0.022	-3.36	0.006
	Meiofauna H'	1	8.11	0.008	1	1.73	0.199	1	2.94	0.097	-3.94	0.002
Two-factor ANOVA												
(a) Results for two-factor (patch, site, patch X site) ANOVA analyses using plot data at five sites and results from a Paired T test (native and non-native paired within a site) using mean site data for richness and Shannon-Weiner diversity index for the three data sets (except H' with macroalgal presence data).	Zone	df	F	p value	df	F	p value	df	F	p value	T	p value
	Patch	1	2.37	0.135	1	0.24	0.631	1	0.29	0.593	1.21	0.258
	Site	4	1.01	0.316	4	1.67	0.163	4	0.32	0.864	-1.67	0.170
	Patch X Zone	4	2.09	0.087	4	1.13	0.344	4	15.80	<0.001	-4.51	0.011
	Patch X Site	4	13.20	<0.001	4	1.70	0.159	4	2.70	<0.001	-9.80	0.001
(b) Results for two-factor (patch, site, patch X site) ANOVA analyses using plot data at five sites and results from a Paired T test (native and non-native paired within a site) using mean site data for richness and Shannon-Weiner diversity index for the three data sets (except H' with macroalgal presence data).	Zone	df	F	p value	df	F	p value	df	F	p value	T	p value
	Patch	1	2.37	0.135	1	0.24	0.631	1	0.29	0.593	1.21	0.258
	Site	4	1.01	0.316	4	1.67	0.163	4	0.32	0.864	-1.67	0.170
	Patch X Zone	4	2.09	0.087	4	1.13	0.344	4	15.80	<0.001	-4.51	0.011
	Patch X Site	4	13.20	<0.001	4	1.70	0.159	4	2.70	<0.001	-9.80	0.001

(a) Results for two-factor (patch, site, patch X site) ANOVA analyses using plot data at five sites and results from a Paired T test (native and non-native paired within a site) using mean site data for richness and Shannon-Weiner diversity index for the three data sets (except H' with macroalgal presence data). (b) Results for two-factor (patch, site, patch X site) ANOVA analyses and individual T tests for the upper and middle intertidal zones separately for richness and Shannon-Weiner diversity index for three data sets (except H' with macroalgal presence data)

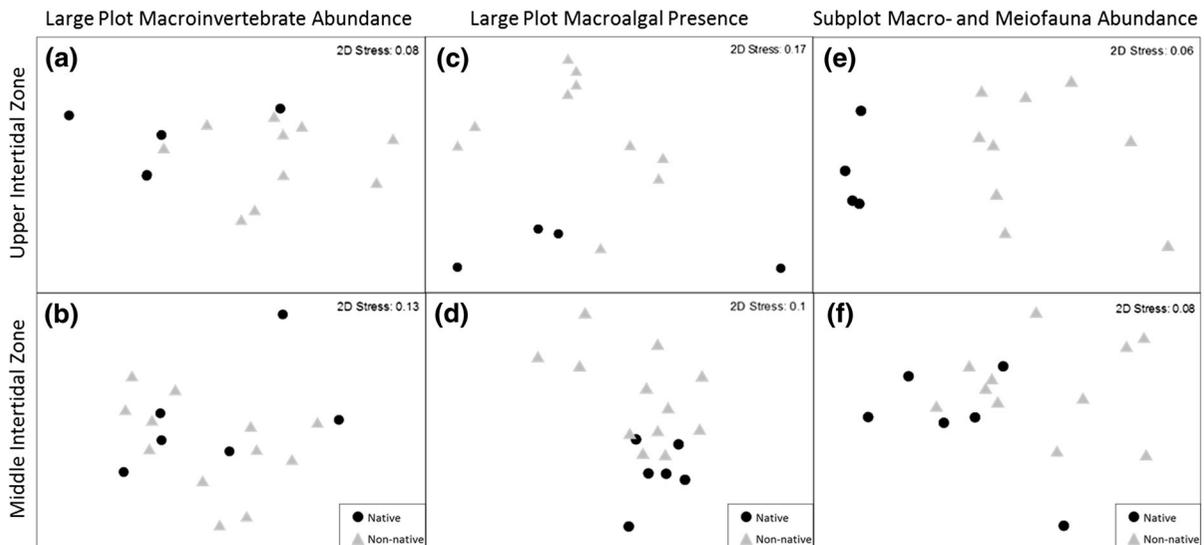


Fig. 2 Multidimensional scaling (MDS) plot presenting the similarity in community composition for three data sets: macro invertebrate abundance in large plots (a, b), macroalgal presence in large plots (c, d), and macro- and meiofauna abundance in subplots (e, f). Presented are MDS plots for upper intertidal zone samples (upper graphs) and middle intertidal zone samples (lower graphs) in both native patches (black) and non-native patches with *Caulacanthus* (gray). Analysis of similarities (ANOSIM) tests

reveal significant differences for all two-factor analyses except the patch factor in macro invertebrate abundance data. Significant differences were also observed between patches for all upper intertidal zone ANOSIM analyses while no differences were observed in middle intertidal communities (see Table 1). In c, e and f, MDS plots focused on subset of samples to better depict differences; some samples, matching the same separation patterns, caused remaining samples to clump together

high zone, but not in the middle zone (Table 1; Fig. 2e, f). Differences in the high zone patches were driven by higher abundances of barnacles and gastropods (mostly periwinkles and limpets) in the native patches and higher abundances of ostracods (Taxa B) and isopods in the non-native patches (Table 5).

Diversity (S and H') of meiofauna was ca. three-fold higher in non-native patches than native patches in the high zone (Table 3), but similar in the middle intertidal zone. A two-factor ANOVA revealed significant differences in richness for the zone factor and interaction term, while H' exhibited a significant difference for the patch factor only (Table 4). Within zones, diversity (S and H') was significantly higher in the upper intertidal non-native patches, while no difference was observed in the middle zone (Table 4).

No measurable sediment was found in native patches in the upper intertidal zone compared to $\sim 230 \text{ cm}^3 \text{ m}^{-2}$ (± 29) in non-native patches. In contrast, native turf patches in the middle intertidal zone had more sediment accumulation ($\sim 560 \text{ cm}^3 \text{ m}^{-2} \pm 254$) than non-native *Caulacanthus* turfs ($\sim 368 \text{ cm}^3 \text{ m}^{-2} \pm 124$). Because of this pattern, two-factor ANOVA analyses revealed a significant interaction term (4th root transformed,

presence of *Caulacanthus* $df = 1$, $F = 27.3$, $p < 0.001$; site $df = 4$, $F = 54.7$, $p < 0.001$; S X C $df = 4$, $F = 45.8$, $p < 0.001$).

Discussion

The non-native seaweed *Caulacanthus ustulatus* appears to be invasive in southern California, USA as it has resulted in significant alterations of the community composition of the upper rocky intertidal zone. Non-native *Caulacanthus* patches tend to have a lower diversity of macro-invertebrates, with a decrease in the abundance of barnacles, limpets, and periwinkle snails. *Caulacanthus* growing in the upper intertidal zone can be found both in cracks and crevices as well as on flat surfaces normally inhabited by barnacles and limpets. This species appears to display a unique creeping growth form, receding and advancing in multiple directions, sometimes dying in older growth areas. We focused our sampling on flat surfaces where *Caulacanthus* appears to be overgrowing the barnacle and limpet habitat, possibly smothering barnacles and inhibiting filter feeding. We

Table 5 Similarities percentages (SIMPER) results for community effects studies for upper and middle intertidal zone comparisons for each data set

Intertidal zone	Data set	Species	Native	Non-native	~Dissimilarity (%)
Upper	Large plot macroinvertebrate abundance	<i>Chthamalus</i> spp	235.6 (123.0)	16.3 (9.0)	65
		<i>Littorina</i> spp	28.6 (19.4)	6.6 (4.4)	14
	Large plot macroalgal presence	<i>Gelidium</i> spp.	0.0 (0.0)	0.7 (0.2)	14
		<i>Ulva californica</i>	0.0 (0.0)	0.7 (0.2)	13
		<i>Corallina pinnatifolia</i>	0.2 (0.2)	0.7 (0.2)	12
		Crustose Coralline	0.6 (0.2)	0.4 (0.2)	10
		Ralfsiaceae	0.4 (0.2)	0.5 (0.2)	10
		<i>Pseudolithoderma nigrum</i>	0.2 (0.2)	0.4 (0.2)	9
	Subplot Macro- and meiofauna abundance	Cirripidea	11.0 (4.4)	0.0 (0.0)	41
		Gastropods	2.8 (1.0)	2.6 (1.4)	15
		Ostracod Taxa B	0.0 (0.0)	3.2 (1.7)	11
		Isopods	0.0 (0.0)	1.8 (0.5)	11
	Middle	Large plot macroinvertebrate abundance	<i>Chthamalus</i> spp	9.8 (4.5)	9.9 (5.2)
<i>Lottia scabra/conus</i>			4.7 (2.2)	7.6 (2.1)	21
<i>Spirorbis</i> spp.			3.2 (3.2)	0.0 (0.0)	9
<i>Nuttalina</i> spp.			2.3 (0.7)	2.0 (0.7)	9
Large plot macroalgal presence		<i>Centrocerus clavulatum</i>	0.8 (0.2)	0.2 (0.1)	13
		<i>Chondracanthus canaliculatus</i>	0.7 (0.2)	0.4 (0.1)	10
		<i>Pseudolithoderma nigrum</i>	0.3 (0.2)	0.5 (0.2)	9
		<i>Gelidium</i> spp.	0.3 (0.2)	0.5 (0.2)	9
Subplot macro- and meiofauna abundance		Gastropods	75.3 (27.0)	24.3 (6.7)	58
		Sipunculids	11.5 (8.2)	3.5 (1.3)	15

Means (± 1 SE) and the percent contribution to dissimilarities between native and non-native patches. Upper and middle intertidal comparisons are reported for each zone separately

observed on multiple occasions dead barnacle tests within the turf. *Caulacanthus* can also be observed in other portions of the rocky intertidal habitat, growing over rockweeds and on mussels. Periwinkles can live on and crawl over *Caulacanthus* turfs, but the decline in the small snail in non-native patches suggests they avoid the turf, possibly due to their preference for feeding on diatoms and microalgal film (Chow 1987) that grows on *Caulacanthus*-free rock surfaces. Although periwinkle species in the region can consume macroalgae, there is little evidence that they readily consume red algae, which are often chemically defended.

Upper intertidal zone patches dominated by *Caulacanthus* also contain a different and more diverse assemblage of seaweeds with *Caulacanthus* patches having more fleshy seaweeds, while native patches

have few seaweeds, usually only the encrusting variety. The subplot sampling, intended to target meiofaunal assemblages, also differed markedly with native patches dominated by adult and juvenile barnacles and limpets while the non-native patches contained a higher variety of turf inhabiting meiofauna. The patterns observed suggest that the novel turf that *Caulacanthus* forms in the upper intertidal zone, where native turfs are rare in this region, creates a refuge for seaweeds and meiofauna to inhabit. Turf forming algae, such as *Caulacanthus*, have a high water-holding capacity during low tide (Hay 1981), which may decrease desiccation stress allowing seaweeds and other organisms inhabiting the turf to thrive in the upper intertidal zone where they normally cannot exist. In addition to reducing desiccation stress, *Caulacanthus* turfs trap sediment that is otherwise

absent in native patches, which can provide food and habitat for turf inhabiting meiofauna. Although some meiofauna can partially depend on barnacle test presence, many meiofauna are benefitted by the presence of turf forming algae that increases habitat complexity (Hicks 1980; Gibbons and Griffiths 1986; Gibbons 1988). Comparisons of meiofauna along a gradient of intertidal microhabitats (barnacles, rock, turfs, fleshy seaweeds) reveal peak densities within algal turfs, particularly when sediment is trapped in the turf (Gibbons and Griffiths 1986); increases in nematodes, foraminifera, and copepods were also found to be correlated with sand and algal turf, rather than algal biomass (Gibbons and Griffiths 1986). Additionally, meiofaunal ostracods have been shown to be more abundant and diverse in turf assemblages, likely due to the heterogeneity of the turf algae habitat and accumulation of sediment (Frame et al. 2007). Meiofauna can also obtain refuge from predators in turf forming algae (Coull and Wells 1983) as the turfs provide an increase in habitat complexity, reducing predator capture rates.

To examine the novel turf forming hypothesis of *Caulacanthus* in the upper intertidal zone on southern California rocky shore, we conducted a subsequent study that compared community assemblages in native and non-native patches in the middle intertidal zone where a native turf naturally exists. The middle intertidal zone of southern California is dominated by turf forming algae, consisting primarily of articulated corallines (e.g. *Corallina*), small red algae (e.g. *Chondracanthus*, *Gelidium*), and filamentous-like algae (e.g. *Ceramium*, *Polysiphonia*, *Centrocerus*, *Cladophora*); *Caulacanthus* is typically growing within this turf and rarely observed growing on its own. Community composition, in general, was similar in middle intertidal native and non-native turf patches, suggesting *Caulacanthus* is not impacting native assemblages in this zone. In the middle intertidal zone, a native turf is present and *Caulacanthus* is not providing a novel habitat as it does in the upper intertidal zone.

The ecological impact of non-native species of seaweeds has been greatly understudied. Recently, there has been an increase in research on the ecological impacts of exotic seaweeds, particularly in regards to their impacts on native species abundances, diversity, and community composition (e.g. Ceccherelli and Cinelli 1997; Williams and Grosholz 2002; Schmidt

and Scheibling 2006; Byers et al. 2012; Janiak and Whitlatch 2012). The effects of non-native seaweeds on native community assemblages have been mixed, but with a majority of studies exhibiting negative impacts. For example, non-native *Caulerpa taxifolia* in the Mediterranean Sea has caused declines in algal cover (Balata et al. 2004), epifauna richness (Bellan-Santini et al. 1996), seaweed biomass (Boudouresque et al. 1992), and seagrass density (Ceccherelli and Cinelli 1997). Additionally, *Fucus evanescens* C Agardh in the NE Atlantic has resulted in decreases in epiflora biomass (Schueller and Peters 1994) and epiphyte biomass and richness (Wikstrom and Kautsky 2004). Alternatively, *Undaria pinnatifida* in the New Zealand region had no detectable impact on native seaweed cover or epiflora composition (Wear and Gardner 1999; Valentine and Johnson 2005). In addition, the presence of *Gracilaria vermiculophylla* (Ohmi) Papenfuss increased epifaunal abundance (Thomsen 2010; Byers et al. 2012) and filamentous algae richness and biomass (Thomsen et al. 2006) in various locations globally.

Complicating the understanding of the effects of non-native seaweeds is that the impacts can vary spatially. In some locations there may be a negative impact while the same effects may not be observed in other locations. *Sargassum muticum* impacts appear to vary greatly among regions; for example, kelp (Ambrose and Nelson 1982) and seaweed abundance (DeWreede 1983; Britton-Simmons 2004) are detrimentally impacted by *S. muticum* in the NE Pacific, but other studies suggest no impact or a positive change on seaweeds on other continents (e.g. Forrest and Taylor 2002; Wernberg et al. 2004; Olabarria et al. 2009). Even within a region, the effects of *S. muticum* can vary depending on habitat. In the NE Pacific, negative effects were observed in the subtidal zone by Ambrose and Nelson (1982) and Britton-Simmons (2004) yet no effects were observed in intertidal pools (Wilson 2001; Smith unpublished data). Our results suggest that impacts also can vary within different zones of an intertidal habitat as *Caulacanthus* exhibited significant effects in the higher intertidal zone but not in the middle zone.

Equally, non-native seaweeds can have contrasting effects on different sets of taxa within a particular location, such as observed in our study. In the upper intertidal zone, *Caulacanthus* negatively affected macroinvertebrates, but facilitated an increase in the

abundance and diversity of seaweeds and meiofauna. Sánchez et al. (2005) also showed contrasting results; the presence of *S. muticum* caused a decrease in seaweed biomass, but only with the fleshy seaweed functional group, while overall seaweed diversity did not change. Here, epiphytic opportunistic algae benefited from *S. muticum* due to its pattern of having a diverse epiphytic assemblage (Sánchez et al. 2005). In addition, Argyrou et al. (1999) found that the replacement of native seagrass in Cyprus by the non-native *Caulerpa racemosa* resulted in concurrent increases in polychaetes, bivalves, and echinoderms while gastropods and crustaceans decreased in abundance. These results highlight that the impacts of non-native seaweeds should be examined across multiple types of taxa as effects can be complex.

Despite taxa-specific responses or variations among localities or habitats, it is clear that the introduction of non-native seaweeds can alter native communities and remain a threat to normal community assemblage composition. In addition, non-native seaweeds may have multiple indirect effects on normal ecological functioning through alteration of community assemblages, changes in abundances of functional group or feeding guilds, or modifications of environmental conditions. While many of the studies speculate on possible reasons for community changes, the driving forces for community assemblage changes by non-native seaweeds remain a knowledge gap. In our study, the impacts of *Caulacanthus* in the upper intertidal zone appear to be driven by the novel creation of a turf, which rarely exists in that particular zone in this region. Habitat alteration also has been suggested as driving forces in other studies (e.g. Bellan-Santini et al. 1996; Relini et al. 2000; York et al. 2006; Vásquez-Luis et al. 2009). In other scenarios, changes in taxa or community composition may be driven by competition between native organisms and non-native seaweeds (Williams and Grosholz 2002; Levin et al. 2002; Scheibling and Gagnon 2006; White and Shurin 2011), alterations of abiotic conditions (Tippets 2002; Strong et al. 2006), or indirect effects on epiphytic communities (Wikstrom and Kautsky 2004; Sánchez et al. 2005). As with our study, further experimental work needs to be conducted to examine the validity of these hypotheses.

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