

Polychaete assemblages associated with the invasive green alga *Avrainvillea amadelpha* and surrounding bare sediment patches in Hawaii

WAGNER F. MAGALHÃES^{1,2} (<http://zoobank.org/urn:lsid:zoobank.org:author:15B35B98-C1A4-4124-A191-8F4A3A5BC8B7>) AND
JULIE H. BAILEY-BROCK^{1,2,*} (<http://zoobank.org/urn:lsid:zoobank.org:author:FC91F8C4-D607-4B35-8923-C36889C5577F>)

¹ Department of Biology, University of Hawaii at Manoa, 2538 McCarthy Mall, Honolulu, Hawaii 96822, USA (wagnerfm@hawaii.edu; jbrock@hawaii.edu)

² Water Resources Research Center, University of Hawaii at Manoa, 2540 Dole Street, Honolulu, Hawaii 96822, USA

* To whom correspondence and reprint requests should be addressed. E-mail: jbrock@hawaii.edu

Abstract

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Avrainvillea amadelpha is one of the most widespread invasive green algae on Hawaii's reefs, but virtually nothing is known about its associated fauna. A total of 16 sampling stations were selected: ten stations were distributed in areas where the invasive alga occurred abundantly ('A' stations) and six stations were placed on bare sand patches ('S' stations). Three replicates of ~475 cm³ each were collected in March 2010 at each station, by hand, using a nalgene corer (11 cm in diameter by 5 cm deep). Based on the comparison between *Avrainvillea amadelpha*-dominated bottoms and the surrounding bare sediment patches, our study demonstrates that these habitats support a diverse and abundant polychaete assemblage, with 2621 individuals and 84 species collected. The species *Sphaerosyllis densopapillata* (34.14%), *Phyllochaetopterus verrilli* (8.32%), *Protocirrineris mascaratus* (5.9%), *Exogone longicornis* (4.9%) and *Syllis cornuta* (4.47%) are the dominant taxa. The non-metric multidimensional scaling clearly separated the 'A' stations from the 'S' stations. ANOSIM has shown that stations within the *a priori*-defined group 'A' are significantly dissimilar from the stations in the group 'S' ($R = 0.527$; $P = 0.1\%$). SIMPER analysis has confirmed the slight but greater dissimilarity between algae and sediment stations (average dissimilarity = 60.12) than within either algae (52.27) or sediment stations (52.04). The invasive green alga *A. amadelpha* facilitates the development of above-ground polychaete communities, but the negative effects of this invader on the infaunal communities should be further investigated.

Keywords

invasive species, seaweeds, *Avrainvillea amadelpha*, Polychaeta, Maunalua Bay

Introduction

Invasive species are considered to be one of the greatest threats to marine biodiversity (Vitousek et al., 1997) and can act by altering the physical environments in significant ways for other species (Cuddington and Hastings, 2004). Macroalgae are especially worrying invaders because they can develop into ecosystem engineers, changing food webs and spreading beyond their initial point of introduction efficiently (Thresher, 2000).

The effects of invasive algae on indigenous communities are being increasingly well-understood, particularly through studies concerning *Caulerpa* species. *Caulerpa taxifolia* has spread in temperate regions worldwide and modifies chemical and physical sediment and water properties (Gribben et al., 2013). The presence of this species is known to increase the density of epibiotic organisms by facilitating recruitment of native species (Gribben and Wright, 2006; Bulleri et al., 2010). However, it may also decrease the density of infaunal

organisms and modify the abiotic environment (Neira et al., 2005; Gribben et al., 2013). The presence of the invasive *Caulerpa racemosa* var. *cylindracea* in the Mediterranean has been proven to expand suitable habitat for polychaete worms, increasing the number of associated species (Argyrou et al., 1999; Box et al., 2010; Lorenti et al., 2011).

The green siphonous alga *Avrainvillea amadelpha* (Montagne) A. Gepp and E. Gepp, 1908 (Order Bryopsidales) has been reported since the early 1980s from the south-east shore of Oahu, Hawaii (Brostoff, 1989) and now is considered one of the most widespread invasive non-indigenous species in Maunalua Bay (Coles et al., 2002). This species proliferates in soft bottom habitats, co-occurring in areas that were once dominated by the endemic Hawaiian sea grass *Halophila hawaiiiana* (Smith et al., 2002).

Efforts to remove introduced algae from reefs in Kaneohe Bay and off Waikiki have been ongoing and have achieved some success (Smith et al., 2004). However, little effort has

been made to investigate whether the invertebrate taxa inhabiting the bottoms dominated by these invasive algae are composed of native species or introduced species.

Avrainvillea amadelpha mats typically serve as substrates for many native species of epiphytic algae (Smith et al., 2002), and this association is known to increase the diversity of associated faunal assemblages by providing food and shelter (Johnson and Scheibling, 1987; Duffy, 1990). The physical complexity of the habitat may also be increased, providing a refuge from fish predation (Coull and Wells, 1983; Dean and Connell, 1987) and greater availability of surface area for recruitment (Connor and McCoy, 1979, McGuinness and Underwood, 1986). Algal turfs have been shown to reduce impact from wave exposure (Dommasnes, 1968) and enhance communities on exposed reefs (Bailey-Brock et al., 1980).

The macrobenthic assemblages associated with invasive algae in Hawaii are scarcely known, and this study aimed to provide baseline data on the polychaete worms associated with *A. amadelpha* mats and nearby bare sediment patches prior to removal efforts.

Materials and methods

Study area and sampling design

This study was carried out on nearshore reef flats in Maunalua Bay on the south shore of Oahu, Hawaii (fig. 1). The area is predominantly composed of consolidated limestone reef flats covered by a shallow layer of fine to coarse sand. The reef flats support abundant growth of the non-indigenous algae *Gracilaria salicornia*, *Hypnea musciformis* and *Avrainvillea amadelpha* (Coles et al., 2002).

A total of 16 sampling stations were selected for this study: ten stations were distributed in areas where *Avrainvillea*

amadelpha occurs abundantly ('A' stations) and six stations were placed on bare sand patches ('S' stations; fig. 1). Three replicates of approximately 475 cm³ each were collected in March 2010 at each station, by hand, using a nalgene corer (11 cm in diameter by 5 cm deep). The *Avrainvillea amadelpha* samples ('A' stations) were composed of sediment to a depth of 5 cm and the overlying algae within the corer. The sediment samples ('S' stations) consisted of the top 5 cm of sediment.

All samples were fixed in buffered 4% formalin and Rose Bengal mixture immediately after sampling for a minimum of 48 h. Organisms were carefully removed from the crevices and branches of the algae, placed in 70% ethanol, then the sediments were elutriated over a 0.5-mm sieve and the retained infauna placed in 70% ethanol. The polychaetes were sorted, counted and identified to the lowest taxonomic level possible using compound and dissecting microscopes.

For comparative purposes, 20 samples of *Gracilaria salicornia* were collected (ten samples during the summer months and ten during the winter months of 2009) on the reef in front of the Natatorium in Waikiki on the south shore of Oahu, Hawaii. Samples were collected with a nalgene corer (11 cm in diameter by 5 cm deep). This dataset is part of an unpublished report by C. Moody, and the samples were donated and the polychaetes were later identified to species level by the authors.

Data analyses

The replicates within each station were summed, and the abundance (N), species richness (S), and Shannon–Wiener diversity index ($\log e; H'$), and Pielou's Evenness (J') were calculated for each station. nMDS ordination was constructed to produce two-dimensional ordination plots to show relationships between stations in relation to polychaete abundance and richness.

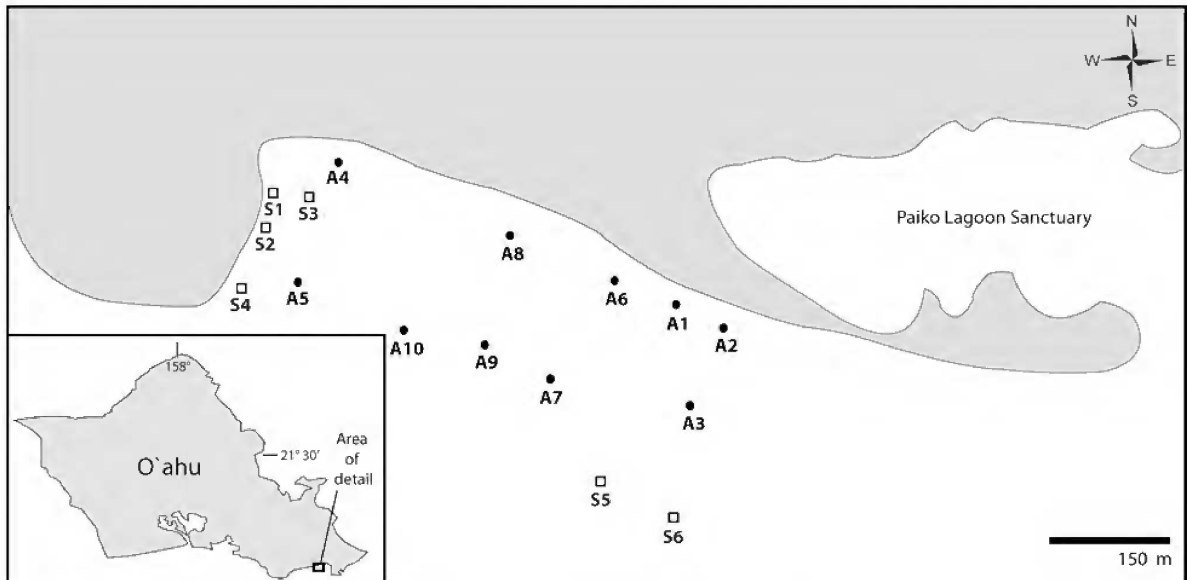


Figure 1. Map of the study area showing the algae ('A' stations; circles) and sediment stations ('S' stations; squares).

Table 1. Summary of the results from SIMPER analysis with the species that contributed to up to 60% of the similarity within each group of stations.

Species/contribution to similarity (up to 60%)	'A' stations (%)	'S' stations (%)
<i>Sphaerosyllis densopapillata</i> (Syllidae)	14.84	16.89
<i>Exogone verugeta</i> (Syllidae)	8.34	
<i>Branchiosyllis exilis</i> (Syllidae)	7.07	
<i>Armandia intermedia</i> (Opheliidae)	6.63	
<i>Lysidice</i> nr. <i>unicornis</i> (Eunicidae)	6.19	
<i>Scyphoproctus</i> sp. (Capitellidae)	5.71	
<i>Perinereis nigropunctata</i> (Nereididae)	5.12	
<i>Syllis cornuta</i> (Syllidae)	4.92	8.86
<i>Phyllodoce parva</i> (Phyllodocidae)	4.71	
<i>Lumbrineris dentata</i> (Lumbrineridae)		10.12
<i>Exogone longicornis</i> (Syllidae)		9.01
<i>Paraonella</i> sp. (Paraonidae)		8.65
<i>Westheidesyllis heterocirrata</i> (Syllidae)		6.53

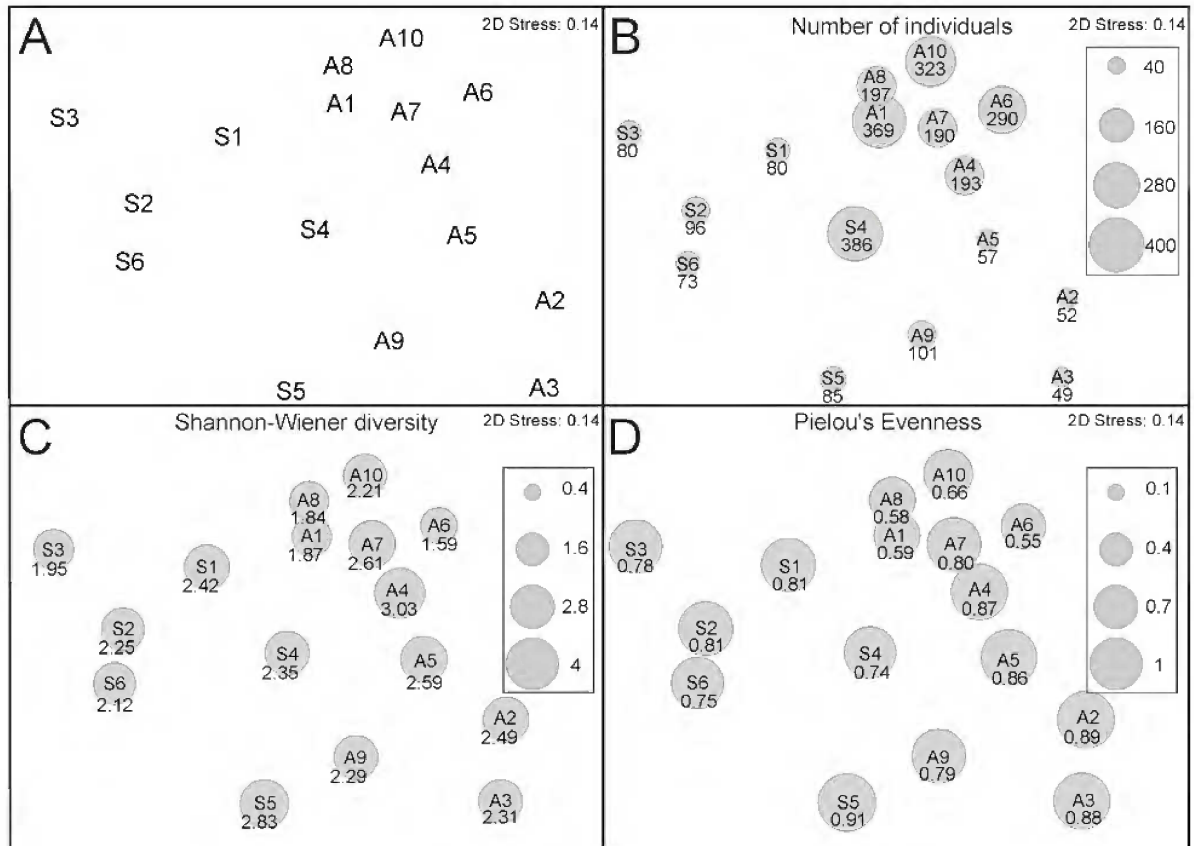


Figure 2. nMDS ordinations of polychaete assemblages: A, using data of all taxa; B, bubbles indicating abundance in number of individuals; C, bubbles indicating values of Shannon–Wiener diversity; D, bubbles indicating values of Pielou's Evenness.

An analysis of similarity (ANOSIM) was performed to test the statistical significance of the *a priori*-defined groups (i.e. 'A' stations vs. 'S' stations). Similarity percentage analysis (SIMPER) identified those taxa that explained relatively large proportions of the similarity within a group. All multivariate analyses were done using the Bray–Curtis similarity coefficient with non-standardized and fourth root transformed data using PRIMER 6.0 software.

Results and discussion

A total of 2621 polychaetes representing 84 taxa were collected. The 'A' stations had a total of 64 taxa and 1821 individuals, while the 'S' stations had a total of 47 taxa and 800 individuals. The most abundant species were *Sphaerosyllis densopapillata* (Syllidae; 34.14%), *Phyllochaetopterus verrilli* (Chaetopteridae; 8.31%), *Protocirrinis mascaratus* (Cirratulidae; 5.9%), *Exogone longicornis* (Syllidae; 4.9%) and *Syllis cornuta* (Syllidae; 4.47%). Syllid polychaetes comprised the most abundant and rich polychaete family, with 1517 individuals and 24 species. Syllids are known to be the most abundant and species-rich polychaete family associated with *Posidonia* beds in the Mediterranean (e.g. Gambi et al., 1995).

The non-metric multidimensional scaling clearly separated the 'A' stations from the 'S' stations (fig. 2). The Shannon–Weiner diversity index did not seem to explain many of the differences between the groups; however, polychaetes from the 'A' stations occurred in greater abundance compared with the 'S' stations, with exception of station S4 (fig. 2).

ANOSIM indicated that stations within the *a priori*-defined group 'A' were significantly dissimilar from stations in the group 'S' ($R = 0.527$; $P = 0.1\%$). SIMPER analyses confirmed the slight but greater dissimilarity between algae and sediment stations (average dissimilarity = 60.12) than within either algae (52.27) or sediment stations (52.04). The syllid *Sphaerosyllis densopapillata* was the most abundant species overall and explained 14.82% of the similarity within the 'A' stations and 16.89% within the 'S' stations (table 1). The other top taxa varied greatly between the types of stations (table 1). *Sphaerosyllis densopapillata* was removed from the analysis of similarity to verify the influence of this abundant species on the dissimilarity between stations. The average dissimilarity increased between algae and sediment stations (from 60.12 to 64.5) and within both algae (from 52.27 to 55.6) and sediment stations (from 52.04 to 56).

Even though there were significant differences between the stations located on *Avrainvillea amadelpha* mats and those sampled on sediments without the algae (ANOSIM), stations within the algal mats were also dissimilar. This might have been explained if other variables such as length and density of algal branches, amount and size of the sediment within the branches, human disturbance near shore, and nature of the underlying substrate were measured.

Several polychaete worms, including the tube builder *Mesochaetopterus minutus* and the syllid *Westheidesyllis heterocirrata*, were predominantly collected from the bare sediment patches. *Mesochaetopterus minutus* is a gregarious worm that forms tufts of sand-covered tubes and is mainly

found on shallow-water reef flats along O'ahu's south shore (Bailey-Brock, 1979, 1987). This species may be playing an important role in these assemblages by binding the sediments loosened by the algal removal efforts in and around their tubes. Chaetopterids can reach densities of 62,400 per m² on O'ahu's south shore, and if they are present in high densities on the outer reef flats of the area where *A. amadelpha* has been removed, they may retain the sediments that would otherwise be transported closer to the shore (Bailey-Brock, 1979). Chaetopterid mounds retain a high abundance of polychaetes but a low diversity, with only 22 species being found by Bailey-Brock (1979).

The diversity of polychaete species found in *Avrainvillea amadelpha* mats is considerably higher than that found in another invasive alga, *Gracilaria salicornia*, present in south Oahu (table 2). *Gracilaria salicornia* is low growing, less structured and has small thalli and many branches, as opposed to *A. amadelpha*. A total of 15 polychaete species have been found commonly in both invasive algae, and the syllids were the dominant family in *G. salicornia* as well (table 2). The most abundant polychaetes associated with *G. salicornia* were *Nereis jacksoni*, *Syllis cornuta* and the ctenodrilid *Raphidrilus hawaiiensis*. The ctenodrilid was originally described from those algal assemblages (Magalhães et al., 2011) and has been found in low abundance in association with *A. amadelpha* at the study site.

Avrainvillea amadelpha mats are a suitable habitat for polychaetes at this location, especially for those detritus feeders favoured by the fine sediment coating accumulated on the branches and in crevices of the alga. The presence of the macroalga *Caulerpa racemosa* has also been shown to increase the diversity and abundance of polychaetes (Argyrou et al., 1999; Box et al., 2010). Lorenti et al. (2011) also observed that polychaetes increased in percentage contribution to the total macrofaunal diversity after the introduction of *C. racemosa*.

The development of above-ground communities are usually facilitated by the presence of invasive macroalgae because of the added structure they give to previously unstructured habitats (Wonham et al., 2005; Gribben et al., 2013). This unnatural increase in diversity in previously unvegetated sediments may have detrimental effects, especially below ground. For instance, the biomass of the invasive *Caulerpa taxifolia* has been negatively associated with the abundance of infaunal organisms (Gribben et al., 2013), and modification of environmental parameters below ground by invasive species has also been noted (e.g. Neira et al., 2005).

Current efforts to remove the attached *A. amadelpha* in the area of this study may help to recover the previous ecological state of the local polychaete assemblages, since infaunal organisms have been known to recover quickly after restoration of the sedimentological characteristics of the habitat (Dernie et al., 2003). Further collections after the removal efforts will be necessary to compare with the results presented herein. This study was conducted two months before the first effort at removal of invasive alga from the area and represents important baseline information for understanding the resilience of this ecosystem.

Table 2. Taxonomic list of polychaete species organized by family found on bare sediment patches, *Avrainvillea amadelpa* and from another invasive alga *Gracilaria salicornia*.

	<i>Avrainvillea amadelpa</i>	Bare sediments	<i>Gracilaria salicornia</i>
Amphinomidae			
<i>Eurythoe</i> sp.	X	X	
<i>Linopherus microcephala</i> (Fauvel, 1932)		X	
Ampharetidae			
<i>Lysippe</i> sp.	X		
Capitellidae			
<i>Capitella jonesi</i> (Hartman, 1959)	X		
<i>Capitellethus cinctus</i> Thomassin, 1970	X		
<i>Heteromastus</i> cf. <i>filiformis</i> (Claparède, 1864)	X		
<i>Notomastus tenuis</i> Moore, 1909		X	
<i>Scyphoproctus pullielloides</i> Hartmann-Schröder, 1965	X	X	
<i>Scyphoproctus</i> sp.	X	X	
Chaetopteridae			
<i>Mesochaetopterus minutus</i> Potts, 1914		X	
<i>Phyllochaetopterus verrilli</i> Treadwell, 1943	X	X	X
Cirratulidae			
<i>Aphelochaeta</i> sp.	X		
<i>Caulleriella bioculata</i> (Keferstein, 1862)	X		
<i>Caulleriella</i> sp.	X		
<i>Cirriformia crassicolis</i> (Kinberg, 1866)	X	X	
<i>Cirriformia</i> sp.	X		
<i>Monticellina</i> nr. <i>cryptica</i> Blake, 1996	X		
<i>Protocirrineris mascaratus</i> Magalhães & Bailey-Brock, 2013	X	X	
<i>Tharyx</i> sp.	X		
<i>Timarete hawaiiensis</i> (Hartman, 1956)			X
<i>Timarete punctata</i> (Grube, 1859)			X
Cossuridae			
<i>Cossura</i> cf. <i>coasta</i> Kitamori, 1960	X		
Ctenodrilidae			
<i>Raphidrilus hawaiiensis</i> Magalhães, Bailey-Brock & Davenport, 2010	X		X
Dorvilleidae			
<i>Dorvillea</i> sp.	X		X
<i>Protodorvillea biarticulata</i> Day, 1963		X	
Eunicidae			
<i>Eunice afra</i> Peters, 1854	X	X	
<i>Eunice antennata</i> (Savigny in Lamarck, 1818)			X
<i>Lysidice</i> nr. <i>ninetta</i> Audouin & Milne-Edwards, 1833	X		
<i>Lysidice</i> nr. <i>unicornis</i> (Grube, 1840)	X	X	X
Flabelligeridae			
Flabelligeridae gen. sp.	X		

	<i>Avrainvillea amadelpha</i>	Bare sediments	<i>Gracilaria salicornia</i>
Hesionidae			
Hesionidae fragment			X
Lumbrineridae			
<i>Lumbrineris dentata</i> Hartmann-Schröder, 1965	X	X	X
<i>Lumbrineris latreilli</i> Audouin & Milne Edwards, 1834		X	
Maldanidae			
<i>Axiothella quadrimaculata</i> Augener, 1914			X
<i>Rhodine</i> sp.	X		
Nereididae			
<i>Micronereis</i> sp.	X		
<i>Neanthes arenaceodentata</i> (Moore, 1903)		X	
<i>Nereis jacksoni</i> Kinberg, 1866			X
<i>Nereis</i> sp.	X		
<i>Perinereis nigropunctata</i> (Horst, 1889)	X	X	
<i>Platynereis dumerilii</i> (Audouin & Milne Edwards, 1834)			X
Oeonidae			
<i>Arabella</i> sp.	X		
<i>Arabella iricolor</i> (Montagu, 1804)	X	X	
Opheliidae			
<i>Armandia intermedia</i> Fauvel, 1902	X	X	
<i>Polyopthalmus pictus</i> (Dujardin, 1839)	X		
Orbiniidae			
<i>Naineris</i> sp.	X	X	
<i>Questa caudicirra</i> Hartman, 1966		X	
<i>Questa retrospermatoca</i> Giere, Ebbe and Erseus, 2007	X	X	
Oweniidae			
<i>Galathowenia oculata</i> (Zachs, 1923)	X	X	
Paraonidae			
<i>Aricidea</i> sp.	X		
<i>Cirrophorus</i> sp.		X	
<i>Paraonella</i> sp.	X	X	
Phyllodocidae			
<i>Eumida</i> sp.		X	X
<i>Phyllodoce parva</i> (Hartmann-Schröder, 1965)	X	X	
Pilargidae			
<i>Synelmis</i> cf. <i>gibbsi</i> Salazar-Vallejo, 2003		X	
Protodrilidae			
<i>Protodrilus albicans</i> Jouin, 1970		X	
Sabellidae			
<i>Amphiglena mediterranea</i> (Leydig, 1851)	X	X	
<i>Branchiomma nigromaculatum</i> (Baird, 1865)	X		X
<i>Euchone</i> sp.	X		

	<i>Avrainvillea amadelpa</i>	Bare sediments	<i>Gracilaria salicornia</i>
Sigalionidae			
Sigalionidae gen. sp.		X	
Spionidae			
<i>Aonides</i> sp.	X		
<i>Laonice</i> nr. <i>cirrata</i> (M. Sars, 1851)	X		
<i>Microspio granulata</i> Blake and Kudenov, 1978		X	X
<i>Spio filicornis</i> (Müller, 1776)		X	X
Sternaspidae			
<i>Sternaspis</i> sp.	X		
Syllidae			
<i>Branchiosyllis exilis</i> (Gravier, 1900)	X	X	
<i>Brania rhopalophora</i> (Ehlers, 1897)	X	X	X
<i>Brania</i> sp.	X		X
<i>Exogone longicornis</i> Westheide, 1974	X	X	
<i>Exogone</i> sp.	X	X	X
<i>Exogone verugera</i> (Claparède, 1868)	X	X	X
<i>Grubeosyllis mediodentata</i> (Westheide, 1974)	X		
<i>Haplosyllis</i> sp.	X	X	X
<i>Myrianida pachycera</i> (Augener, 1913)	X		X
<i>Odontosyllis</i> sp.	X		
<i>Opistosyllis</i> sp.		X	
<i>Pionosyllis</i> sp.		X	
<i>Sphaerosyllis centroamericana</i> Hartmann-Schröder, 1974			X
<i>Sphaerosyllis densopapillata</i> Hartmann-Schröder, 1979	X	X	
<i>Sphaerosyllis riseri</i> Perkins, 1981	X		
<i>Sphaerosyllis</i> sp.	X		
Syllinae juv.		X	
<i>Syllis cornuta</i> Rathke, 1843	X	X	X
<i>Syllis variegata</i> Grube, 1860	X		
<i>Trypanosyllis</i> sp.	X		
<i>Typosyllis aciculata orientalis</i> Imajima & Hartman, 1964	X	X	
<i>Typosyllis crassicirrata</i> Treadwell, 1925			X
<i>Typosyllis ornata</i> Hartmann-Schröder, 1965		X	
<i>Typosyllis</i> sp.	X		X
<i>Virchowia japonica</i> Imajima & Hartman, 1964	X		
<i>Westheidesyllis heterocirrata</i> (Hartmann-Schröder, 1959)	X	X	
Terebellidae			
<i>Nicolea gracilibranchis</i> (Grube, 1878)			X
<i>Polycirrus</i> sp.	X		X
Trichobranchidae			
<i>Trichobranchus</i> nr. <i>glacialis</i> Malmgren, 1866	X		

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References

- Argyrou, M., Demetropoulos, A., and Hadjichristophorou, M. 1999. Expansion of the macroalga *Caulerpa racemosa* and changes in soft bottom macrofaunal assemblages in Moni Bay, Cyprus. *Oceanologica Acta* 22(5): 517–528.
- Bailey-Brock, J.H. 1979. Sediment trapping by chaetopteric polychaetes on a Hawaiian fringing reef. *Journal of Marine Research* 37: 643–656.
- Bailey-Brock, J.H. 1987. Phylum Annelida. Pp. 213–454 in: Devaney, D.M. and Eldredge, L.G. (eds), *Reef and shore fauna of Hawaii*. Bishop Museum Press: Hawai'i.
- Bailey-Brock, J.H., White, J.K., and Ward, L.A. 1980. Effects of algal turf and depressions as refuges on polychaete assemblages of a windward reef bench at Enewetak Atoll. *Micronesica* 16(1): 43–58.
- Box, A., Martin, D., and Deudero, S. 2010. Changes in seagrass polychaete assemblages after invasion by *Caulerpa racemosa* var. *cylindracea* (Chlorophyta: Caulerpales): community structure, trophic guilds and taxonomic distinctness. *Scientia Marina* 74(2): 317–329.
- Brostoff, W.N. 1989. *Avrainvillea amadelpha* (Codiales, Chlorophyta) from O'ahu, Hawai'i. *Pacific Science* 43: 166–169.
- Bulleri, F., Balata, D., Bertocci, I., Tamburello, L., and Benedetti-Cecchi, L. 2010. The seaweed *Caulerpa racemosa* on Mediterranean rocky reefs: from passenger to driver of ecological change. *Ecology* 91(8): 2205–2212.
- Coles, S.L., DeFelice, R.D., and Eldredge, L.G. 2002. *Nonindigenous marine species at Waikiki and Hawai'i kai, O'ahu, Hawai'i*. Bishop Museum Technical Report 25. 245 pp.
- Connor, E.F., and McCoy, E.D. 1979. The statistics and biology of the species–area relationship. *The American Naturalist* 113: 791–833.
- Coull, B.C., and Wells, J.B. 1983. Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. *Ecology* 64: 1599–1609.
- Cuddington, K., and Hastings, A. 2004. Invasive engineers. *Ecological Modelling* 178: 335–347.
- Dean, R.L., and Connell, J.H. 1987. Marine invertebrates in algal succession. II. Tests of hypothesis to explain diversity with succession. *Journal of Experimental Marine Biology and Ecology* 109: 217–247.
- Dernie, K.M., Kaiser, M.J., and Warwick, R.M. 2003. Recovery rates of benthic communities following physical disturbance. *Journal of Animal Ecology* 72: 1043–1056.
- Dommasnes, A. 1968. Variations in the meiofauna of *Corallina officinalis* L. with wave exposure. *Sarsia* 34: 117–124.
- Duffy, J.E. 1990. Amphipods on seaweeds: partners or pests? *Oecologia* 83: 267–276.
- Gambi, M.C., Giangrande, A., Martinelli, M., and Chessa, L.A. 1995. Polychaetes of a *Posidonia oceanica* bed off Sardinia (Italy) – spatio-temporal distribution and feeding guild analysis. *Scientia Marina* 59: 129–141.
- Gribben, P.E., Byers, J.E., Wright, J.T., and Glasby, T.M. 2013. Positive versus negative effects of an invasive ecosystem engineer on different components of a marine ecosystem. *Oikos* 122: 816–824.
- Gribben, P.E., and Wright, J.T. 2006. Invasive seaweed enhances recruitment of a native bivalve: roles of refuge from predation and the habitat choice of recruits. *Marine Ecology Progress Series* 318: 177–185.
- Johnson, S.C., and Scheibling, R.E. 1987. Structure and dynamics of epifaunal assemblages on intertidal macroalgae *Ascophyllum nodosum* and *Fucus vesiculosus* in Nova Scotia, Canada. *Marine Ecology Progress Series* 37: 209–227.
- Lorenti, M., Gambi, M.C., Guglielmo, R., Patti, F.P., Scipione, M.B., Zupo, V., and Buia, M.C. 2011. Soft-bottom macrofaunal assemblages in the Gulf of Salerno, Tyrrhenian Sea, Italy, an area affected by the invasion of the seaweed *Caulerpa racemosa* var. *cylindracea*. *Marine Ecology* 32(3): 320–334.
- Magalhães, W.F., Bailey-Brock, J.H., and Davenport, J.S. 2011. On the genus *Raphidrilus* Monticelli, 1910 (Polychaeta: Ctenodrilidae) with description of two new species. *Zootaxa* 2804: 1–14.
- McGuinness, K.A., and Underwood, A.J. 1986. Habitat structure and the nature of communities on intertidal boulders. *Journal of Experimental Marine Biology and Ecology* 104: 97–123.
- Neira, C., Levin, L.A., and Grosholz, E.D. 2005. Benthic macrofaunal communities of three sites in San Francisco Bay invaded by hybrid *Spartina*, with comparison to uninvaded habitats. *Marine Ecology Progress Series* 292: 111–126.
- Smith, J.E., Hunter, C.L., Conklin, E.F., Most, R., Sauvage, T., Squair, C., and Smith, C. 2004. Ecology of the invasive red alga *Gracilaria salicornia* (Rhodophyta) on O'ahu, Hawai'i. *Pacific Science* 58: 325–343.
- Smith, J.E., Hunter, C.L., and Smith, C.M. 2002. Distribution and reproductive characteristics of nonindigenous and invasive marine algae in the Hawaiian Islands. *Pacific Science* 56: 299–315.
- Thresher, R.E. 2000. Key threats from marine bioinvasions: a review of current and future issues. Pp. 24–36 in: Pederson, J. (ed.), *Marine bioinvasions. Proceedings of the First National Conference*, January 24–27, 1999. Massachusetts Institute of Technology, Sea Grant College Program: Boston.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J., and Melillo, J.M. 1997. Human domination of Earth's ecosystems. *Science* 277: 494–499.
- Wonham, M.J., O'Connor, M., and Harley, C.D.G. 2005. Positive effects of a dominant invader on introduced and native mudflat species. *Marine Ecology Progress Series* 289: 109–116.