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Spatial and Temporal Variation in Rocky Intertidal Communities along the Main Hawaiian Islands[1]

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Abstract: Thirteen benthic rocky intertidal communities were quantitatively assessed on Maui, Moloka'i, O'ahu, and Hawai'i Island between the years 2004 and 2007. Our goals were to test for differences in invertebrate and macroalgal abundance and composition to understand how these tropical communities are organized. Percentage cover surveys revealed a diverse intertidal system with 49 macroalgal, 1 cyanobacterial, and 31 invertebrate taxa. Shores were frequently dominated by a few macroalgae and mollusks, and at two sites these organisms were distributed in discrete vertical bands. Common intertidal taxa included the introduced alga *Acanthophora spicifera;* species in the macroalgal genera *Padina*, *Sargassum*, and *Laurencia;* turf forms of algae; and the mollusks *Siphonaria normalis*, *Nerita picea*, and species of littorine snails. Multivariate statistics found community structure to vary among sites and years, but there was lack of evidence for island-specific or substratum-specific assemblages. SIMPROF analysis revealed support for 11 different types of structure. This first description of community-level patterns at multiple intertidal sites along the Main Hawaiian Islands documents substantial spatial variation both among and within shores, as well as substantial temporal variation for select sites. These findings are in contrast to the characterization of a homogeneous tropical system and thus suggest that biotic and abiotic factors in the Main Hawaiian Islands act on a local scale to drive structure.

SYSTEMATIC MONITORING of ecological communities provides a baseline from which to measure human impacts in the long term (Murray et al. 2006) and in the short term allows for early detection and potential eradication of invasive species (Simberloff et al. 2005). In addition, large to mesoscale spatial and temporal community studies have provided much needed ecological information on how communities are formed and maintained. For example, surveys conducted over 10 to hundreds of km over multiple years have found patterns within communities related to global climate change (Barry et al. 1995, Sagarin et al. 1999), recruitment (Broitman et al. 2008), and coastal processes (Blanchette et al. 2008). Furthermore, spatial descriptions of marine communities are needed for adequate design of reserves, as efforts are made to include sites that are representative of, or unique to, specific areas (Airame et al. 2003). Intertidal habitats are model systems for examining spatial and temporal structure because physical conditions fluctuate with the tides and abundance and diversity of organisms can vary among and across shores. Also, these habitats are particularly vulnerable to human

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threats because they lie at the interface between terrestrial and subtidal habitats and thus bear the impact of both terrestrial and marine alterations. For these reasons, large to mesoscale survey efforts of benthic organisms are being conducted in temperate intertidal areas (Barry et al. 1995, Sink et al. 2005, Nakaoka et al. 2006, Blanchette et al. 2008, Broitman et al. 2008, Delaney et al. 2008). Fewer surveys have been conducted in tropical intertidal habitats, yet early investigations have characterized these habitats as homogeneous with minimal spatial or temporal variation and shores dominated by crustose algal forms, which harbor sedentary grazers (Garrity and Levings 1981, Lubchenco and Gaines 1981, Williams 1993, but see Vinueza et al. 2006).

Hawaiian nearshore habitats appear to be lush with fleshy macroalgae (McDermid 1988, Smith 1992), and these habitats are unique in part because the isolation of the archipelago has resulted in a high number of endemic species. However, Hawaiian intertidal habitats are not insulated from threats. Boat traffic and interest in aquaculture has resulted in numerous alien species introductions (Eldredge and Smith 2001, Eldredge and Carlton 2004). A total of 343 species is known to have been introduced to Hawai‘i’s waters; these include 287 species of invertebrates and 27 species of macroalgae (Eldredge and Smith 2001, Eldredge and Carlton 2004). Three species of introduced macroalgae particularly invasive in shallow-water habitats (Smith et al. 2002) are *Acanthophora spicifiera*, *Gracilaria salicornia*, and *Hypnea musciformis*, which are visually abundant in Hawai‘i’s intertidal zone along with the introduced barnacle *Chthalamus proteus* (Zabin et al. 2007*b*). The biogeographic status of a fourth nuisance alga, *Avrainvillea amaldelpha*, is unknown, but past records indicate that it was not common in shallow-water habitats. The tropical beauty of Hawaiian shores has attracted human visitation, harvesting of organisms, and development of oceanside resorts. Furthermore, sewage overflows have led to shallow-water macroalgal blooms of nuisance native and introduced species (Stimson et al. 2001, Dailer et al. 2010). However, to our knowledge there have been only a few studies that describe both the invertebrate and algal communities of intertidal habitats in Hawai‘i (Bird 2006, Zabin et al. 2007*a*). These were short-term studies that either did not involve the systematic collection of quantitative data or did not describe the algal community beyond functional form (algal forms described by Littler and Littler [1984]) at multiple sites. Thus it is difficult to assess any possible impacts to the community as a whole.

In marine environments, factors such as ocean transport (Blanchette et al. 2008), wave exposure (Bustamante and Branch 1996), and productivity (Menge et al. 1997) can explain patterns in communities across large geographic scales, and physical and biological conditions, such as predation (Bertness 1981, Menge and Lubchenco 1981), competition (Connell 1961), wave action (Bustamante and Branch 1996), and facilitation (i.e., an interaction between two organisms that benefits one organism and causes harm to neither) (Menge 2000) influence structure at local scales. The main islands in the archipelago of Hawai‘i are separated by a maximum distance of ~104 km. Current velocity and direction and wave heights are often variable and determined by wind direction (http://www.soest.hawaii.edu/hioos/oceanatlas/). These physical factors could influence the abundance and diversity of organisms among islands. Furthermore, interactions between large-scale and local-scale factors could contribute to structure among sites. Contrary to early descriptions of stasis in tropical intertidal zones, the oceanic islands of the Galápagos experience substantial temporal and spatial variability from the combined interaction of herbivory and, more prominently, the oscillation of El Niño currents (Vinueza et al. 2006). Similar synergisms could shape structure across the archipelago of Hawai‘i.

In Hawai‘i there are a variety of shore types that vary in both composition and profile. Shores can be composed of basalt or limestone substrate and may be covered with varying amounts of sand. Tidal benches can be flat, raised reef platforms; gently sloped; or cliff-like, and boulder- to cobble-sized fields are made up of dead coral heads and/or basaltic rocks (Kay 1979, Abbott 1999). These variable habitats may suit the survival of different species, resulting in unique communities. Smith (1992) found differences in macroalgal diversity among sites within a single island's intertidal habitat, and Zabin et al. (2007*b*) found that intertidal species assemblages at bench sites were more similar to each other than to those found at cobble sites. Other studies on nearshore benthic communities have found that distributions or abundances of benthic organisms can vary with island habitat (Vroom et al. 2010), depth (Littler and Doty 1975), temperature (Cox and Smith 2011), and wave exposure (Bird 2006). We might expect similar findings for the benthic intertidal community.

In addition to the large-scale variation in structure among shores, organisms in intertidal habitats are often zoned or are distributed into discrete vertical bands at a landscape level (Doty 1946, Stephenson and Stephenson 1949, Connell 1961, Benson 2002 [review]). These bands are a result of complex interactions between biotic and abiotic factors that are influenced by the fluctuating tide and wave activity (Benson 2002). Vertical distribution of organisms has been documented in a few tropical localities (Mak and Williams 1999, Bird 2006, Sibaja-Cordera 2008). The zonation pattern typically described is as follows: littorine mollusks and nerites dominate the upper littoral zone, crustose algal forms dominate midshore and in areas with high wave activity, and fleshy macroalgae generally occur lower on the shore in more-sheltered areas (Mak and Williams 1999, Sibaja-Cordera 2008). Yet in the Main Hawaiian Islands organisms experience microtides that fluctuate by a maximum of ±1 m. Because of this limited tidal range, seasonal wave activity, and often relatively flat and narrow benches, intertidal organisms are often underwater or whole shores are unaccessible for sampling. Despite the narrow intertidal zone, earlier studies have suggested that there is structure at this fine spatial scale: temperature is variable at a landscape level (Cox and Smith 2011), barnacles and mollusks compete to occupy preferential microhabitats (Zabin and Altieri 2007, Zabin 2009), and on a man-made shore algal and invertebrate functional groups occupy different thermal zones influenced by wave activity (Bird 2006). However, the intertidal community as a whole has not been quantitatively assessed at multiple locations to identify any vertical community patterns that are repeated and temporally consistent.

The research goal of this study was to describe the benthic intertidal community on several Main Hawaiian Islands to investigate whether these habitats are homogeneous systems or if these habitats harbor variability at multiple scales related to island, hard substratum type, or microtides. Specifically, we examined these data to test three hypotheses: (1) invertebrate and macroalgal abundance and composition will vary among sites, as would be predicted if biotic or abiotic factors varied among islands and shores; (2) temporal variation is limited, because physical factors have remained relatively similar during the length of the monitoring program; (3) organisms are distributed into discrete vertical bands, as would be predicted if microtidal fluctuations influenced structure at fine spatial scales. In addition, we describe the presence and abundance of alien species at our study sites.

MATERIALS AND METHODS

Site Description

Thirteen rocky intertidal sites located on the islands of Hawai‘i, Maui, Moloka‘i, and O‘ahu (Figure 1, Table 1) were sampled by an educational citizen-scientist program called OPIHI or Our Project in Hawai‘i's Intertidal during the years 2004–2007 (described in detail in Baumgartner et al. [2009]). A previous case study (Cox et al. 2012) showed that the community data collected by these trained secondary students are robust and, at the level of detail sampled, similar to those of more experienced professional researchers. Some sites were sampled multiple times within a year, and not every site was sampled each year. Sites were selected to represent a variety of rocky intertidal habitats but also had to be easily accessible by students. Each site spanned a minimum of 15 m along the coast and was at least 10 m from the top of the

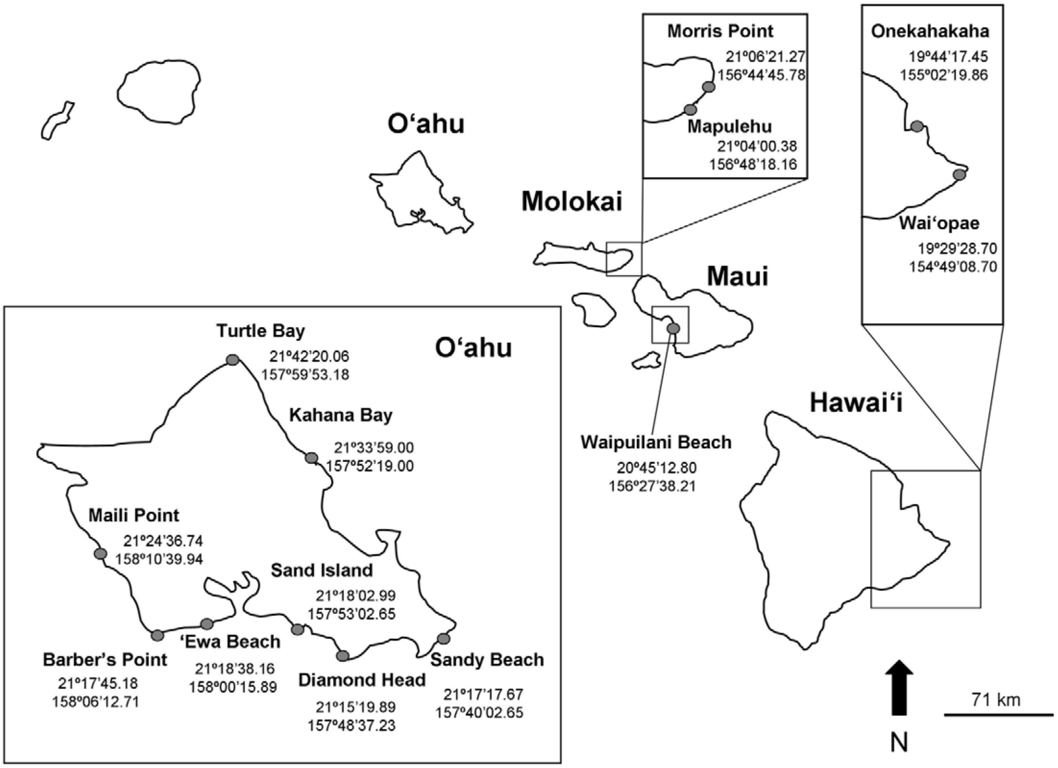

Figure 1. Location of intertidal sites sampled throughout the Main Hawaiian Islands by the citizen-scientist monitoring program, OPIHI.

littorine zone to the water's edge at mean low water.

Sites can be described as gently sloped basalt or limestone bedrock benches, bedrock surrounded by patches of sand, or boulder- to cobble-sized rocky habitats (Table 1). These shores are located on all sides of the islands, and seasonal onshore waves are common at all sites. However, some sites such as Diamond Head (DH) have offshore reefs that provide some protection. The Wai'ōpae (WOP) monitoring site is located within a Marine Life Conservation District where collection of any kind is prohibited. Species richness varies among sites (Zabin et al. 2007*a*).

OPIHI Data Collection

Trained secondary students (grades 6–12) supported by researchers sampled sites on low tides ranging from 0.0 to –0.15 m that occurred in February–June each year and collected abundance data for macroalgae and invertebrates using traditional ecological sampling methods. At each site, depending upon the number of students available and the geography of the site, three to seven transect lines were placed ~2 m apart, perpendicular to shore and extended up to 30 m. Between 5 and 12 0.25 m^2 quadrats (each with five horizontal and five vertical strings, creating 25 intercepts) were placed at evenly spaced intervals along each transect. The percentage cover of algae and invertebrates in each quadrat was sampled by one of two methods: visual estimation or point contact. Specific methods are described in detail in Baumgartner and Zabin (2006). In the visual estimation method, the grid was used as a reference to assist students in estimation of the percentage cover of

TABLE 1

Site Name, Description, Number of Times Sampled within the Month(s) for Each Year, and Sampling Method Used within Quadrat

			No. of Times Sampled in Years Month(s) Sampled Method Used (VE or PC)			
Site Name	Shore Habitat Type	Substrate Composition	2004	2005	2006	2007
Barbers Point (BP)	Bench	Limestone		3 Mar.–May VE	2 Apr.–May VE	5 May VE
Diamond Head (DH)	Bench	Limestone and basalt	2 Feb. VE, PC*	4 Feb.–Mar. VE, PC*	4 Apr. VE, PC**	4 Apr. VE, PC**
‘Ewa Beach (EB)	Bench	Limestone			2 May VE	
Kahana Bay (KB)	Sand and bedrock	Limestone	2 Feb.–Mar. VE, PC	2 Feb.–Mar. VE, PC		
Mā‘ili Point (MPT)	Bench	Limestone				2 Apr. PC
Mapulehu (M)	Silt and cobble	Basalt			2 Apr. VE, PC*	
Morris Point (MP)	Sand and bedrock	Limestone			1 May PC	
Onekahakaha (O)	Bench	Basalt				2 May PC
Sand Island (SI)	Bedrock/Cobble and sand	Basalt		2 Apr.–May VE	2 Apr.–May VE	5 May VE
$^{+}$Sandy Beach (SB)	Sand and bedrock	Basalt			2 May VE	2 Apr. VE
Turtle Bay (TB)	Bench	Limestone		3 May–June PC		
Wai‘ōpae (WOP)	Bench	Basalt				1 May PC
Waipu‘ilani Beach (WB)	Coral rubble and sand	Limestone		2 May VE, PC*	1 Apr. PC	2 Apr.–May PC

Note: VE, visual estimate; PC, point contact. The presence and number of asterisks (*) indicates the visits and the number of comparisons (*, 1; **, 2) used in method bias evaluation (see Figure 2 [e.g., data collected by VE and PC methods on the same day at DH occurred 6 times (once in 2004 and 2005 and twice in 2006 and 2007) and are used in analyses]). +, SB 2007 sampling was not included in community analyses because large waves prevented full access to the exact 2006 monitoring site.

each organism or “bare” substratum (i.e., substratum that lacked obvious macrocover) encountered. In the point-contact method students recorded the taxa or bare substratum that occurred under each of the 25 intercepts within the quadrats. The density per area (the number of individuals per quadrat) and size measurements of macroinvertebrates were not recorded. Nonetheless, the methodology applied in this study accurately represents the spatial cover of all macrobenthic organisms encountered (for discussion of techniques see Meese and Tomich [1992]).

Students were trained to identify species to the lowest taxon possible for their abilities under field conditions using the keys and characteristics described in Abbott (1999), Hoover (2002), Abbott and Huisman (2004), and Huisman et al. (2007). Some taxa were identified only to genus because identification at the species level often requires careful examination of microscopic features. Bare substratum that lacked obvious macrocover was recorded as rock or sand (if it could not be swept away by hands) along with other categorical data. Categories included “other/unknown algae”; “other/unknown invertebrates”; crustose coralline, brown crust (which includes species of *Ralfsia* and *Peyssonnelia*); cyanobacteria; and algal turf (mixture of macroalgal species 1–2 cm tall). Furthermore, taxa such as *Sargassum aquifolium* (formerly *Sargassum echinocarpum* [see Mattio et al. 2009]) and *Sargassum polyphyllum*, which have few distinguishing characteristics and can be confused by less-experienced collectors (Cox et al. 2012), were pooled by a more-experienced researcher (T.E.C.), after data collection, into a single genus (e.g., *Sargassum* spp.) or a common taxonomic or functional form group (e.g., *Galaxaura/Liagora* both are red, calcified erect forms that are dichotomously branched). If an organism was difficult to identify, students photographed it and attempted to identify the taxon at a later date.

Evaluation of Two Survey Methods

Before examination of community patterns, the appropriateness of comparing or combining percentage cover data collected from the two sampling approaches (visual estimation or point contact) within a gridded quadrat were evaluated. For eight sampling trips to three sites (DH, $n = 6$; Mapulehu (M), $n = 1$; Waipuʻilani Beach (WB), $n = 1$) over multiple years, students collected data using both visual estimation and point-contact methodologies in the 5 to 12 quadrats placed along the three to seven transect lines (Table 1). Using one of the two methods (point contact or visual estimation), students collected data in quadrats placed along a transect line, then repositioned the quadrats and resampled the same transect line using the second method.

The percentage cover of each taxon was calculated for each methodological approach by pooling the quadrat data over the entire site from the multiple transects. Data were analyzed for similarity using the statistical package PRIMER-E+ (Clarke and Warwick 2001). For each site, the percentage cover data were square-root transformed to downweight common taxa and account for the patchy nature of intertidal species. Using the Bray-Curtis index, a resemblance matrix was constructed to compare similarity between methods and among sampling visits. A nonmetric multidimensional scaling (nMDS) plot was created to visually examine for any bias that may have been introduced into the community structure estimates using these two methodological approaches. For DH, the only location visited more than once, a one-way analysis of similarity (ANOSIM) was used to examine statistical differences in estimates of community similarity that may have resulted from the two methods.

Large-Scale Community Comparisons

Before determining large-scale community patterns, the percentage cover of each taxon was calculated from the data produced from each sampling visit. Because sampling occurred between the months of February–June, a two-way ANOSIM (site × month) was used to screen the data for monthly variation. Based upon the results from that screening, monthly repeated samplings were combined to produce a year by site average of percentage cover for each taxon. These values were calculated by pooling data from all quadrats from the entire site over the multiple transect lines for each sampling visit. When two sampling methodologies were employed in one visit, the percentage cover for each taxon was calculated for each method and then averaged. Similarly, if repeated sampling occurred within the same month, the percentage cover for each taxon was calculated for each visit and then averaged to produce one percentage cover value for each taxon in the month sampled.

The statistical program Primer-E$^+$ was used to analyze and compare abundance and distribution patterns among sites and years (Clarke and Warwick 2001). A square-root transformation was performed to decrease the influence of the abundant taxa and account for the patchy nature of invertebrate species but keep the emphasis on dominant species, because earlier efforts (Cox et al. 2012) had revealed that students were best able to quantify abundant taxa. A Bray-Curtis similarity matrix among sites and years was generated. In addition, similarities among sites were compared separately by year to ensure that patterns among sites remained similar when additional sites were added to the monitoring program.

Multivariate statistics were used to investigate if assemblages varied with islands, sites, years, and hard substratum type. A PERMANOVA with 999 permutations was used to test for statistical differences in assemblages across years, sites, and islands. Islands, sites nested within islands, and year were fixed factors, and interaction terms were included in the model. Due to limited degrees of freedom, a separate one-way ANOSIM was used to investigate any statistical differences in communities at shores with differing hard substratum of either basalt, limestone, or mixed basalt and limestone. An nMDS and a cluster diagram were produced from Bray-Curtis similarities to examine community patterns. The SIMPROF routine was used to further identify significant multivariate structure, and the SIMPER routine was used to examine which species contributed to the structure observed. Certain species have narrow requirements for growth (such as corals) or are possible indicators of nutrient enrichment or herbivory levels (e.g., *A. spicifera*) (Stimson et al. 2001, Fong et al. 2003, Smith 2003), thus the results from the SIMPER routine can be used to facilitate the identification of abiotic or biotic conditions that determine structure.

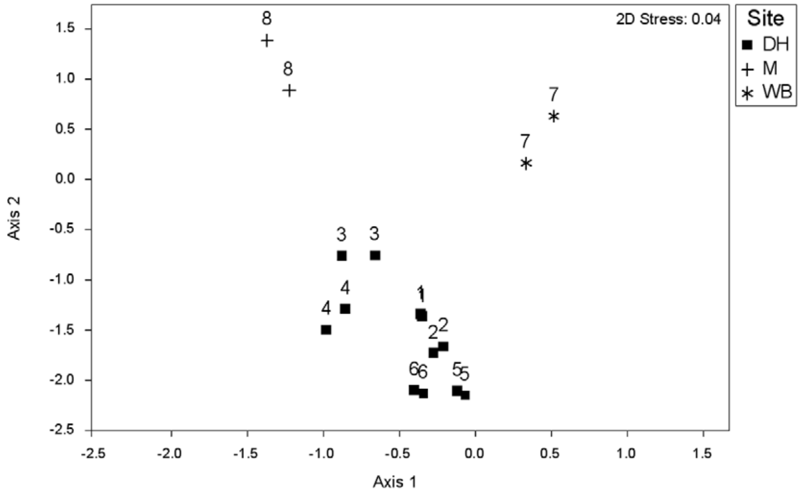

Figure 2. A nMDS plot based on Bray-Curtis similarity values generated from square-root transformed abundance data collected on the same day (same day = same number) made using two methodologies (point contact or visual estimation) at three sites sampled by trained citizen scientists from the OPIHI program. Percentage cover values for each taxon were pooled over the entire site. Note the limited variation in multidimensional space around samples collected at the same site and same day using the two methodologies.

TABLE 2

Abundance of Macroalgae and Cyanobacteria Expressed as Mean Percentage Cover (SE) by Site

Algae	BP	DH	EB	KB	MPT	M	MP	O	SI*	SB	TB	WOP	WB*
Acanthophora spicifera	**9.4 (9.1)**	**1.6 (1.0)**	**16.5**	**27.5 (22.7)**	**29.9**	**23.9**	—	—	**4.2 (1.3)**	**0.4**	**0.6**	—	**7.5 (2.3)**
Asparagopsis taxiformis	—	—	—	—	—	—	—	—	0.4 (0.4)	—	0.2	—	—
Astronema breviarticulatum	0.3 (0.4)	0.1 (0.1)	—	7.4 (2.1)	—	—	—	—	—	—	—	—	0.4 (0.5)
Avranvillea amadelpha	—	**0.1 (0.1)**	—	—	—	—	—	—	**0.1 (0.1)**	—	—	—	—
Cyanobacteria	0.3 (0.3)	1.9 (0.9)	—	—	—	31.0	—	—	4.1 (3.3)	—	—	0.3	2.2 (2.7)
Bornetella sphaerica	0.2 (0.2)	—	—	—	—	—	—	—	0.3 (0.4)	—	—	—	—
Botryocladia skottsbergii	—	—	—	—	—	—	—	—	—	—	—	—	—
Brown crust	0.5 (0.4)	—	—	—	—	—	5.4	—	0.5 (0.7)	—	—	2.3	0.7 (0.9)
Caulerpa spp.	—	—	0.1	—	—	—	—	—	—	—	—	—	—
Chaetomorpha spp.	—	—	0.3	—	—	—	—	—	—	—	—	—	0.1 (0.1)
Chnoosphora implexa	—	0.1 (0.1)	—	—	—	—	—	—	—	—	—	—	—
Cladophora/Cladophoropsis	0.4 (0.5)	0.5 (0.2)	—	—	—	34.6	3.0	—	0.1 (0.1)	—	0.9	—	0.1 (0.1)
Codium edule	0.2 (0.1)	—	—	—	—	—	—	—	0.5 (0.3)	—	—	—	—
Codium spp.	—	—	—	—	—	—	—	—	0.4 (0.5)	—	—	—	—
Colpomenia sinuosa	—	—	0.1	—	—	—	—	—	0.1 (0.1)	0.8	0.5	—	0.7 (0.6)
Crustose coralline	1.4 (1.4)	0.3 (0.1)	0.8	1.2 (1.7)	—	0.7	2.2	—	1.4 (1.2)	—	0.2	9.4	27.8 (6.4)
Dictyopteris spp.	0.1 (0.1)	0.5 (0.5)	—	—	—	—	—	—	—	—	—	—	—
Dictyosphaeria cavernosa	0.5 (0.6)	0.1 (0.1)	16.6	—	—	—	—	1.6	—	—	—	—	—
Dictyosphaeria spp.	—	—	—	—	—	—	—	—	0.2 (0.2)	—	—	—	—
Dictyosphaeria verslusyii	3.5 (0.4)	1.5 (1.5)	—	—	—	—	—	—	0.2 (0.2)	1.9	2.0	—	—
Dictyota acutiloba	0.2 (0.2)	0.4 (0.5)	11.8	—	—	—	—	0.5	—	—	—	1.2	0.3 (0.2)
Dictyota sandvicensis	—	0.3 (0.3)	—	—	6.7	0.3	—	—	—	—	—	—	0.2 (0.3)
Dictyota spp.	1.0 (1.3)	4.2 (2.5)	—	—	3.1	—	—	—	—	—	1.3	—	0.1 (0.1)
Galaxaura/Liagora	—	—	—	—	—	—	—	—	0.3 (0.3)	1.7	—	—	—
Gelid	—	0.0 (0.1)	—	—	—	—	—	—	—	3.0	—	—	0.1 (0.1)
Gracilaria salicornia	—	**0.4 (0.4)**	—	—	—	**0.2**	—	**23.8**	—	**2.7**	—	—	—
Halimeda discoidea	0.1 (0.0)	0.7 (0.7)	1.5	—	—	—	0.2	—	—	—	0.2	—	—
Hydroclathrus clathratus	—	—	—	—	—	—	—	—	—	—	0.8	—	—
Hypnea cervicornis	—	—	1.6	—	—	1.2	—	—	—	—	—	—	—
Hypnea chordacea	0.1 (0.1)	—	—	—	—	—	—	—	—	—	—	—	—
Hypnea musciformis	—	**0.3 (0.4)**	—	—	—	—	—	—	—	—	—	—	**11.9 (7.1)**
Laurencia mcdermidiae	0.1 (0.2)	0.3 (0.4)	—	—	0.8	—	—	—	—	—	—	0.2	—
Laurencia spp.	4.7 (1.6)	14.4 (4.6)	17.3	—	7.0	4.3	—	—	2.8 (3.3)	3.4	13.0	1.4	1.5 (1.1)
Lobophora variegata	—	—	—	—	—	—	—	—	0.3 (0.4)	—	—	0.9	—
Martensia spp.	—	0.1 (0.1)	—	—	—	—	—	—	—	—	—	—	—
Microdictyon setchellianum	0.1 (0.1)	0.4 (0.3)	2.1	—	—	—	—	—	—	—	14.2	—	—
Neomeris spp.	0.4 (0.2)	—	—	—	—	—	—	—	0.1 (0.1)	—	—	—	—

Other algae	0.9 (0.5)	3.9 (3.2)	—	14.6 (15.5)	33.5	—	—	5.7	4.5 (4.0)	—	6.0	0.1	0.3 (0.2)
Padina spp.	46.3 (10.0)	31.3 (2.6)	4.0	1.5 (2.1)	1.0	0.2	9.9	56.0	27.1 (11.2)	13.7	16.6	0.6	2.9 (0.5)
Pterocladiella caeruluscens	0.1 (0.1)	—	—	—	—	—	—	—	—	—	—	—	—
Pterocladiella capillacea	—	0.1 (0.1)	—	—	1.4	—	—	—	—	—	—	—	—
Sargassum spp.	5.6 (0.5)	14.4 (2.6)	9.6	3.2 (4.6)	—	2.8	—	—	1.4 (1.8)	5.7	4.3	—	7.3 (1.6)
Sphacelaria spp.	—	—	—	—	—	—	—	—	—	—	—	—	0.1 (0.1)
Trichogloea requienii	—	—	—	—	—	—	—	—	0.1 (0.1)	—	—	—	0.3 (0.4)
Turbinaria ornata	—	0.4 (0.2)	2.4	—	1.5	0.3	—	—	—	0.8	1.8	—	—
Ulva lactuca	—	—	—	0.6 (0.3)	3.8	—	—	—	—	—	—	—	16.6 (4.8)
Ulva flexuosa	—	0.5 (0.6)	—	—	—	—	—	—	—	—	—	—	—
Ulva reticulata	—	—	—	—	—	—	—	—	—	—	—	—	0.5 (0.2)
Wrangelia elegantissima	—	0.2 (0.2)	—	—	—	—	—	—	—	—	1.1	0.1	—
Turf	17.4 (8.8)	17.7 (6.2)	10.0	13.6 (19.3)	4.1	—	79.3	4.1	48.0 (13.9)	64.5	33.7	59.1	12.4 (7.7)

Note: The mean was calculated by pooling quadrat data over the entire site for each sampling. Then the percentage cover of each taxon (per site) was averaged by day, by month, by year, and then by site to produce a single mean abundance of each taxon for each site. Thus the SE is based on the number of years a site was sampled. Communities at sites with increased temporal variability have larger SEs and have been noted with an asterisk (*). Cryptogenic and invasive species are in **boldface**.

Fine-Scale Distribution and Abundance

Two sites (Barbers Point [BP] and DH) on the south shore of O‘ahu with similar habitat and substratum were selected to examine the vertical distribution of species. These locations were selected because they had been sampled consistently over multiple years and shared relatively high overall community similarity. An examination of organism distribution at these two sites could provide insight into patterns that are consistent from year to year and occur in more than one intertidal location in the Main Hawaiian Islands.

For every sampling visit to the two sites, the percentage cover of taxa was determined for each quadrat placed along the transect line. Then these percentage cover values were averaged for each 1 m distance from the water’s edge across the three to seven transect lines. With each sampling visit there were slight variations (±1 m) in transect length due to tidal changes or quadrat placement (students could sample every meter or every 1.5 m depending on a teacher-driven protocol). To account for these variations and to identify larger vertical distributional patterns, percentage cover for each taxon from each meter location were averaged into 5-m bins (0–4.9, 5.0–9.9, 10.0–14.9, 15.0–19.9, 20+). Thus the 0–4.9 m bin includes the average percentage cover of each organism that extended from the water’s edge at low tide vertically (or “up”) toward the high-tide line 4.9 m. The 5.0–9.9 m bin directly followed the 0.0–4.9 m bin and was thus located closer to the high-tide line. These bins continued “up” the shore to 30 m. The percentage cover of each organism by bin was expressed as relative taxon abundance or the percentage cover of each taxon within the bins, standardized to the pooled percentage cover for the taxon at the site. Relative taxa abundance will emphasize any change in fine-scale distribution. The relative taxon abundance for each sampling visit by bin was then averaged by year (same-day sampling with two methodologies were first averaged by day, then data were averaged by month and averaged by year). These year averages were averaged again to produce an overall site average and standard error (standard deviation divided by number of years sampled) of relative taxon abundance (%). The relative taxon abundance is presented for the dominant taxa at the site.

RESULTS

Evaluation of Two Survey Methods

Visual estimation and point-contact methods revealed similar percentage cover results (Figure 2). The community structure that resulted from each method did not differ statistically for collections that occurred at DH (one-way ANOSIM: DH, Global *R*, –0.15, *P*-value = .94). Furthermore, data collected on the same day with both methods resulted in estimates of community structure that were represented closer in multidimensional space (in the nMDS) than sampling made on a different day or at a different site. The two methods employed in one visit resulted in 86.2% similarity in community structure for data collected at M and 89.1% similarity in community structure for data collected at WB. The limited variation in community structure estimates and results by Meese and Tomich (1992) allowed us to confidently pool (compare or average) data collected using the two methodologies.

Large-Scale Community Comparisons

Monthly variation in community structure was not evident in repeated sampling (two-way ANOSIM: month, Global *R* –0.075, *P*-value = .72). Therefore we were confident in pooling the percentage cover data by year for the large-scale community comparisons.

Forty-nine macroalgal, one cyanobacterial, and 31 invertebrate taxa were recorded from the 13 intertidal sites (Tables 2, 3). Most sites were dominated by a few macroalgae and mollusks, with the exception of WOP, where coral cover was abundant. Common taxa or functional forms at other sites included species in the macroalgal genera *Padina*, *Sargassum*, *Laurencia*, and the introduced *Acanthophora spicifera;* turf forms of algae; the pulmonate limpet *Siphonaria normalis;* the nerite snail *Nerita picea;* and species of littorine snails.

Introduced or alien macroalgae were found at many intertidal sites, and these invaded sites were located on all sampled islands (Table 2). *Acanthophora spicifera* was the most common introduced species, found at 10 out of 13 sites. This species was also abundant, with greater than 10% cover at five of these sites. There were only two sites without introduced benthic species, Morris Point (MP) and WOP. *Avrainvillea amadelpha* was found at two sampled intertidal sites (Sand Island [SI] and DH), both of which were located on the island of O‘ahu. *Hypnea musciformis* was abundant at WB, and *Gracilaria salicornia* was abundant at Onekahakaha (O). Aside from *C. proteus* (which, if found, would have been recorded as “barnacle”), no other introduced benthic invertebrates were found using these methods.

The abundance and composition of taxa varied among sites and by year as evident in the cluster and nMDS plots. Despite the distinct cluster of three samplings from the one Maui site (WB) in the nMDS plot, structure did not statistically vary by island or hard substratum type (Figure 3, Table 4). Furthermore, sites by year clustered into statistically distinct communities (Figure 3).

The SIMPROF routine (999 permutations, alpha = .05) recognized 11 distinct community assemblages. Statistically recognized clusters did not reveal assemblage patterns with island or substratum type (Figure 3). The composition and abundance of organisms at M (Cluster A), WOP (Cluster C), MPT (Mā‘ili Point, Cluster D), O (Cluster E), WB 2007 (Cluster F), and EB (‘Ewa Beach, Cluster K) are statistically distinct and do not form genuine clusters with other samplings. The community structure at KB (Kahana Bay, Cluster B) is also unique because the 2004 and 2005 collections made at that site form a genuine cluster sharing 56.4% similarity. This community can be characterized by the presence and abundance of *A. spicifera*, *Astronema breviarticulatum*, barnacles, and *N. picea.* In contrast to KB, the composition and abundance of organisms at WB in 2005 and 2006 (Cluster G) were statistically distinguishable from the WB 2007 estimate (Cluster F). Forty-one percent of the overall dissimilarity was due to the decrease in abundance of *H. musciformis*,

TABLE 3

Abundance of Marine Invertebrates Expressed as Mean Percentage Cover (SE) by Site

Invertebrates	BP	DH	EB	KB	MPT	M	MP	O	SI*	SB	TB	WOP	WB*
Actinopyga mauritana	—	—	—	—	0.4	—	—	—	—	—	0.1	—	—
Anthopleura nigrescens	—	—	—	0.0 (0.1)	—	—	—	—	—	—	—	—	0.2 (0.2)
Barnacles	—	0.2 (0.1)	—	14.7 (7.2)	—	—	—	—	—	—	—	—	—
Brachidontes crebristriatus	—	—	—	3.3 (2.4)	0.5	—	—	3.1	—	—	—	—	—
Colobocentrotus atratus	—	—	—	—	0.8	—	—	—	—	—	—	—	0.4 (0.5)
Conus ebraeu	—	—	—	—	0.2	—	—	—	—	—	—	—	—
Dendropoma gregaria	3.7 (2.3)	2.0 (1.4)	5.3	—	—	—	—	—	1.3 (1.6)	—	—	—	—
Echinolittorina hawaiiensis	—	0.2 (0.1)	—	0.0 (0.1)	—	—	—	—	—	—	—	—	0.3 (0.4)
Echinometra mathaei	—	—	—	—	1.2	—	—	0.5	0.2 (0.1)	—	1.5	0.5	—
Echinometra oblonga	—	—	—	—	0.1	—	—	—	0.3 (0.3)	—	0.3	—	—
Fireworm	—	—	—	—	—	0.2	—	—	—	—	—	—	0.2 (0.2)
Holothuria cinerascens	—	—	—	—	—	—	—	—	0.1 (0.1)	—	0.6	—	—
Holothuria atra	—	0.1 (0.0)	—	—	—	—	—	—	0.2 (0.2)	—	—	—	—
Isognomon californicum	0.3 (0.1)	—	—	0.9 (1.3)	0.1	—	—	2.1	0.1 (0.1)	—	—	—	0.1 (0.1)
Isognomon perna	—	—	—	0.1 (0.2)	—	—	—	—	—	—	—	—	—
Littoraria pintado	—	0.1 (0.0)	—	0.3 (0.1)	—	—	—	—	—	—	—	—	—
Montipora capitata	—	—	—	—	—	—	—	—	—	—	—	8.5	0.2 (0.2)
Montipora flabellata	—	—	—	—	—	—	—	—	—	—	—	0.7	—
Morula granulata	0.3 (0.3)	—	—	—	—	—	—	—	0.1 (0.0)	0.4	0.1	—	—
Nerita picea	0.2 (0.1)	0.1 (0.0)	—	6.9 (5.6)	—	—	—	1.0	—	—	0.1	—	—
Ophiocoma erinaceus	—	—	—	—	—	—	—	—	—	—	—	0.1	—
Other invertebrates	—	0.1 (0.1)	—	2.5 (3.2)	0.3	—	—	1.6	0.1 (0.1)	—	—	0.1	—
Pocillopora damicornis	—	—	—	—	—	—	—	—	—	—	—	0.2	0.3 (0.3)
Pocillopora meandrina	—	—	—	—	—	—	—	—	—	—	—	1.8	0.1 (0.1)
Porites lobata	—	—	—	—	—	—	—	—	—	—	—	9.5	0.4 (0.4)
Serpulorbis	0.6 (0.7)	—	—	—	—	—	—	—	0.5 (0.6)	—	—	2.7	—
Siphonaria normalis	0.8 (0.4)	0.5 (0.3)	—	1.4 (0.7)	0.2	—	—	—	—	—	—	—	—
Spirobranchus giganteus	—	—	—	—	—	—	—	—	—	—	—	0.1	—
Sponge	0.1 (0.1)	—	—	—	—	—	—	—	—	—	—	—	—
Stomatopod	—	—	—	—	—	—	—	—	0.1 (0.0)	—	—	—	—
Unidentified coral	—	—	—	—	1.1	—	—	—	0.1 (0.1)	1.1	—	0.1	—

Note: The mean was calculated by pooling quadrat data over the entire site for each sampling. Then the percentage cover of each taxon (per site) was averaged by day, by month, by year, and then by site to produce a single mean abundance of each taxon for each site. Thus the SE is based on the number of years a site was sampled. Communities at sites with increased temporal variability have larger SEs and have been noted with an asterisk (*).

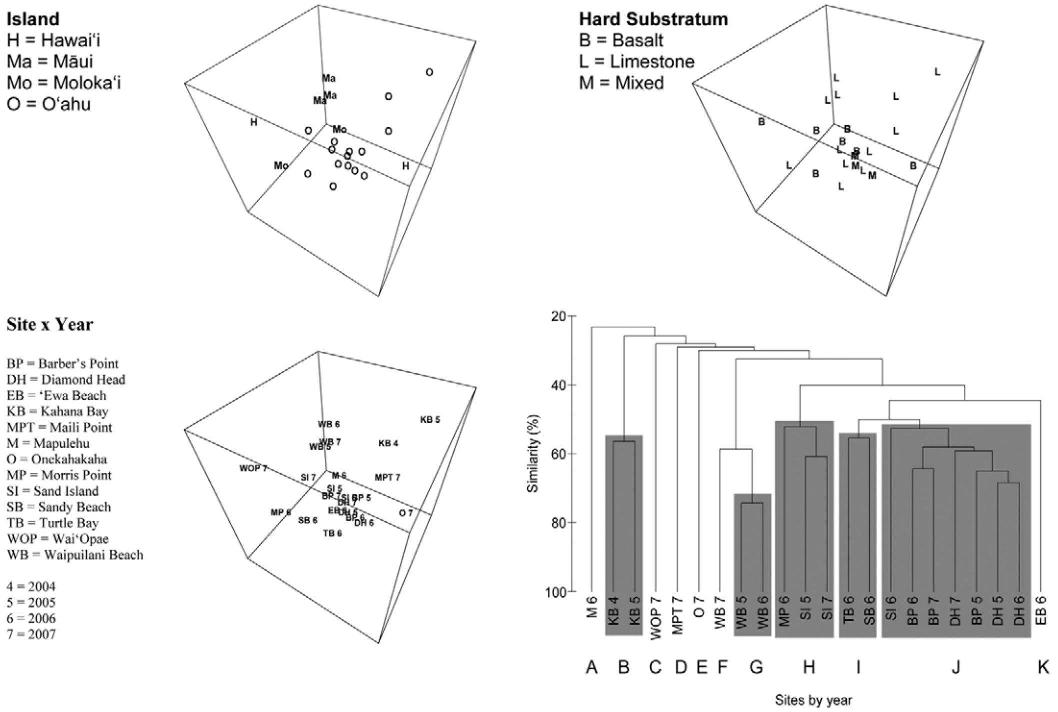

Figure 3. nMDS and cluster diagrams revealed community structure among sites and years. The data cloud in the nMDS represents the Bray-Curtis resemblance of transformed abundance values occurring at each site for every year sampled. The three plots contain the same data cloud labeled in a different manner: island location (*upper left*), hard substratum type (*upper right*), and site by year (*lower left*) (see Table 1 for abbreviations). The cluster diagram (*lower right*) shows the similarity among samplings. Letter groups (A–K) and gray boxes demonstrate indistinguishable community structure based on the results of a SIMPROF routine with 999 permutations at an alpha of .05.

TABLE 4

Results from Multivariate Statistics Revealing That Communities Vary among Sites and Year

PERMANOVA

Factors Tested	df	SS	MS	Pseudo-F	Unique Permutations	*P* (Permutations)
Island	3	14313.0	4770.8	1.5	999	.167
Year	3	4913.5	1637.8	1.4	999	.261
Site (Island)	9	41039.0	4559.9	8.5	998	.001*
Island × Year	2	16249.9	812.4	0.7	998	.523
Site (Island) × Year	5	6849.9	1370.0	2.6	998	.001*

One-way ANOSIM

	Global *R*	*P*-value
Hard substratum type	–0.009	.56

* Indicates significant findings.

the increase in turf algal forms, and the presence of *Lyngbya* that were recorded in 2007. Despite these differences in community structure the year samplings at WB are most similar to each other than to other sites.

Clusters I, J, and K include sites located on the island of O‘ahu, and these three clusters were adjoined into a single larger cluster that lacked statistical support but shared 54.7% similarity (Figure 3, Table 5). The benthic communities at BP and DH (all years), located on the south shore of O‘ahu, are statistically indistinguishable from one another and form a genuine cluster with another south-shore community, SI in 2006 (Cluster J). These sites share a similar abundance of *A. spicifera* and species from the algal genera *Padina*, *Laurencia*, and *Sargassum*. However, in 2005 and 2007 the community at SI was more similar in structure to the community at MP, which is located on the island of Moloka‘i. This cluster (H), shares 55% similarity, and 76.9% of this similarity is because of the similar abundance of turf algal forms and species from the brown alga genus *Padina*. EB is also located on the south shore of O‘ahu and, although distinct in structure, is most similar to Clusters J and I. Last, the presence and abundance of turf algal forms and species from the brown algal genera *Padina* and *Sargassum* contribute 69.3% to the similarity between TB (Turtle Bay) and SB (Sandy Beach) on the north and east shores of O‘ahu. These two sites form a genuine cluster (I) that is most similar to Cluster J.

Results from the SIMPER analyses reveal the top three taxa or functional forms with the largest proportional contribution to the dissimilarities among clusters (Table 6). The category *"Cladophora/Cladophoropsis"* and species of cyanobacteria from the genus *Lyngbya*

TABLE 5

SIMPER Results: Sites by Year with Statistically Similar Structure and Taxa That Contribute (70%) to Similarity

Clusters with More Than 1 Sample (% Similar) Taxa	Sampling Included in Cluster[a]	Island Location	% Contribution
B (56.4)	KB 4, KB 5	O‘ahu	
Acanthophora spicifera			21.9
Barnacles			20.2
Astronema breviarticulatum			15.9
Nerita picea			11.0
G (74.4)	WB 5, 6	Maui	
Crustose coralline			23.6
Ulva lactuca			19.9
Hypnea musciformis			12.6
Sargassum spp.			9.8
Acanthophora spicifera			9.5
H (55.1)	MP 6, SI 5, SI 7	Moloka‘i and O‘ahu	
Turf (mix of 1–2 cm tall species)			50.3
Padina spp.			26.6
I (55.4)	TB 6, SB 6	O‘ahu	
Turf (mix of 1–2 cm tall species)			37.8
Padina spp.			19.1
Sargassum spp.			12.4
J (64.7)	SI 6, BP 5–7, DH 5–7	O‘ahu	
Padina spp.			26.3
Turf (mix of 1–2 cm tall species)			16.1
Laurencia spp.			11.7
Sargassum spp.			11.6
Acanthophora spicifera			6.1

[a] BP, Barbers Point; DH, Diamond Head; KB, Kahana Bay; MP, Morris Point; SB, Sandy Beach; SI, Sand Island; TB, Turtle Bay; WB, Waipu‘ilani Beach; 4, 2004; 5, 2005; 6, 2006; 7, 2007.

TABLE 6

Dissimilarity Matrix among Clusters A–K and the Three Taxa with the Largest Contribution (%) to Dissimilarities

Comparisons	B	C	D	E	F	G	H	I	J	K
A	**80.1**	**88.8**	**75.1**	**95.5**	**70.1**	**74.2**	**81.4**	**78.1**	**73.0**	**63.9**
Isl (Mo)	+Cla 17.9	–Tur 18.2	–O A 14.4	+Cla 14.3	↑Cla 14.6	↑Cla 16.6	–Tur 20.0	–Tur 17.5	↓Pad 13.3	+Cla 14.6
Sub (B)	+Lyn 16.9	+Cla 9.6	+Cla 11.3	+Lyn 13.5	↑Lyn 9.9	↑Lyn 15.7	↑Cla 13.6	+Cla 11.7	↑Cla 13.0	+Lyn 13.8
	↑A.sp 6.7	+A.sp 8.0	+Lyn 10.7	↓Pad 12.2	–Tur 9.1	–U.la 10.1	↑Lyn 12.4	↑Lyn 11.3	↑Lyn 11.4	–D.ca 11.4
B		**89.5**	**71.3**	**70.3**	**66.9**	**71.5**	**76.2**	**82.3**	**71.0**	**78.7**
Isl (O)		↓Tur 17.8	↓ O A 12.7	↓Pad 20.8	↓CC 8.7	↓ CC 14.0	↓Tur 20.9	↓Tur 15.9	↓Pad 16.2	–Lau 10.9
Sub (L)		–P.lo 8.2	↓A.sp 10.1	–G.sa 14.8	↑Bar 6.7	↓U.la 11.0	↓Pad 10.4	↓Pad 9.7	–Lau 8.5	–D.ca 10.7
		–M.ca 7.8	–Lau 7.9	+A.sp 11.0	↓Tur 6.4	–H.mu 10.7	+Bar 7.1	–Lau 7.4	↓Tur 7.1	–D.ac 9.0
C			**80.2**	**85.6**	**66.2**	**71.6**	**60.7**	**68.1**	**74.8**	**78.1**
Isl (H)			↑Tur 12.0	↑Tur 18.1	↑Tur 15.8	↑Tur 19.1	+P.lo 11.3	+P.lo 8.1	↑Tur 12.5	↑Tur 11.8
Sub (B)			–A.sp 9.9	+P.lo 8.4	+P.lo 9.2	+P.lo 9.3	+M.ca 10.7	+M.ca 7.7	↓Pad 8.6	–A.sp 7.1
			↓O A 9.8	+CC 8.3	+M.ca 8.7	+M.ca 8.8	↑Tur 9.4	↑CC 7.6	+P.lo 7.7	–D.ca 7.1
D				**77.5**	**66.8**	**70.9**	**78.3**	**69.5**	**68.1**	**67.4**
Isl (O)				+A.sp 14.5	↑O A 14.0	↑O A 15.0	↑O A 12.3	↑A.sp 11.1	↑O A 11.3	+O A 13.4
Sub (L)				↑O A 11.7	↑A.sp 10.4	↑A.sp 10.4	↑A.sp 11.4	↑O A 10.6	↑A.sp 9.7	–D.ca 8.3
				↓Pad 8.7	–CC 6.3	–CC 9.2	↓Tur 9.4	↓Tur 10.1	↓Pad 9.2	–D.ac 7.0
E					**78.3**	**81.4**	**69.3**	**69.5**	**64.2**	**81.6**
Isl (H)					↑Pad 11.8	–CC 13.0	↓Tur 21.7	↓Tur 18.1	↑G.sa 10.4	–Lau 10.2
Sub (B)					+G.sa 9.6	↑Pad 12.1	+G.sa 13.1	–Lau 8.5	–Lau 9.0	–A.sp 9.9
					–CC 8.3	+G.sa 10.6	↑Pad 7.8	–Sar 7.1	–Sar 9.0	↓D.ca 8.0
F						**41.3**	**61.8**	**68.9**	**62.3**	**67.0**
Isl (Ma)						+Lyn 8.2	↓Tur 12.7	↓Tur 10.7	↓Pad 13.1	–D.ca 10.1
Sub (L)						↓H.mu 7.1	↓Pad 7.7	↓Pad 8.0	↓Lau 6.5	↓Lau 9.3
						↑Tur 7.0	+Sar 6.8	↑CC 6.2	↑CC 6.4	↓D.ac 7.5
G							**72.3**	**70.9**	**67.8**	**67.8**
Isl (Ma)							↓Tur 17.2	↓Tur 15.2	↓Pad 12.3	–D.ca 11.1
Sub (B)							+U.la 11.1	↑CC 9.8	↑CC 10.0	↓D.ac 8.8
							↑CC 9.8	–U.la 8.5	+U.la 9.3	↓Lau 8.7
H								**55.3**	**59.4**	**72.0**
Isl (O, Mo)								↓Lau 9.9	↑Tur 11.3	↓Lau 10.8
Sub (B, B)								–Sar 8.4	–Sar 9.3	↓D.ca 10.6
								–M.se 6.8	↓Lau 9.0	↑Tur 9.1
I									**49.9**	**58.7**
Isl (O)									↑Tur 12.7	↑Tur 10.8
Sub (B, L)									↑M.se 6.4	–D.ca 10.5
									↓Pad 5.1	–D.ac 8.9

J Isl (O) Sub (B, L, *M*)	**54.3** ↓D.ca 11.1 ↑Pad 10.0 ↓D.ac 9.3
K Isl (O) Sub (L)	—

Note: Symbols indicate whether a taxon is present (+), absent (–), with increased (↑) or decreased abundance (↓) at sites and years included in the cluster on the left (row). **Boldface** numbers are the dissimilarity (%) between the row (left) labeled cluster and the column labeled cluster (top). Island location (Isl) (H, Hawai‘i; Ma, Maui; Mo, Moloka‘i; O, O‘ahu) and hard substratum type (Sub) (B, basalt; L, limestone; M, mixed) of sites within clusters are specified in row. Abbreviations: A.sp, *A. spicifera;* Bar, barnacle; CC, crustose coralline forms; Cla, *Cladophora/Cladophoropsis;* D.ac, *D. acutiloba;* D.ca, *D. cavernosa;* G.sa, *G. salicornia;* H.mu, *H. musciformis;* Lau, *Laurencia;* Lyn, *Lyngbya* spp.; M.ca, *M. capitata;* M.se, *M. setchellianum;* Pad, *Padina;* P.lo, *P. lobata;* O A, other algae; Sar, *Sargassum* spp.; Tur, turf algal form; U.la, *U. lactuca.*

were always within the top three taxa with the largest proportional contribution to dissimilarity of M (Cluster A) for each community comparison. The increased abundance of turf or crustose algal forms and the presence of coral species contributed to the uniqueness of WOP (Cluster C) because these taxa occurred as the top three contributors to dissimilarity in 7 of 10 cluster comparisons. An invasive alga, *A. spicifera*, and “unknown” algal species were dominant at MPT (Cluster D) and contributed substantially to dissimilarity of MPT from nine other community clusters. Also, the introduced red alga *G. salicornia* was a top three contributor to the dissimilarity of O from five other clusters. The presence and increased abundance of *Ulva lactuca*, *Hypnea musciformis*, and crustose coralline species repeatedly (occurred within the top three 5, 2, and 6 out of 11 instances, respectively) contributed to the dissimilarity of WB 2005–2006 (Cluster G). Algal turf forms occurred as a top three contributor in 7 out of 11 comparisons of dissimilarity with Cluster H. The increased abundance and presence of species from the algal genera *Padina*, *Laurencia*, and *Sargassum* were often (7, 4, and 2 respectively out of 11 comparisons) included within the top three taxa with the largest proportional contribution to dissimilarity of Cluster J, but the decreased abundance of algal turf, increased abundance of *Microdictyon setchellianum*, and species of *Padina* contributed 24% to the dissimilarity of Cluster J from Cluster I. Cluster K had a comparatively high abundance of *Dictyosphaeria cavernosa* and *Dictyota acutiloba*.

Fine-Scale Distributions and Abundances

Taxa varied in relative abundance vertically (up the shore), and these patterns were consistent among years (Figure 4). The community at both sites revealed similar zonation of macroalgae and mollusks. The macroalgae *Sargassum* and *Laurencia* were common close to the submerged subtidal zone; *Padina* was distributed closer to the high-tide line. The vermetid *Dendropoma gregaria*, pulmonate limpet *Siphonaria normalis*, and snails *Nerita picea* and *Echinolittorina hawaiiensis* dominated the area nearest to the high-tide line.

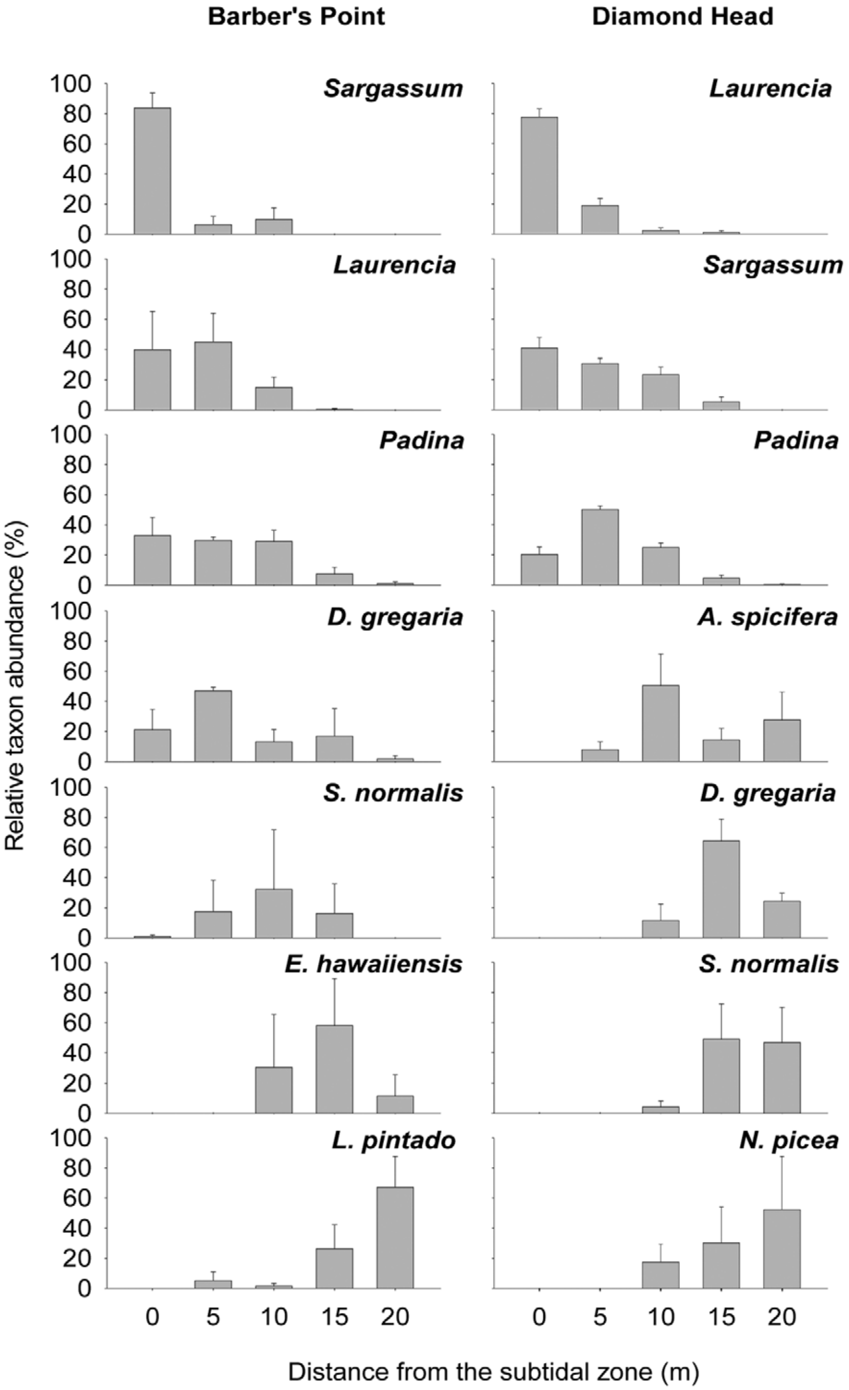

Figure 4. Relative taxon abundance (±SE) of dominant macroalgae and invertebrates at distance from the subtidal zone for two sites, BP (*left*) and DH (*right*). See Materials and Methods for data calculation. Taxa are arranged in order of distribution from offshore (*top*) to onshore (*bottom*). Macroalgae: *Padina*, *Sargassum*, *Laurencia*, *Acanthophora spicifera;* mollusks: *Dendropoma gregaria*, *Siphonaria normalis*, *Echinolittorina hawaiiensis*, *Littoraria pintado*, *Nerita picea*.

DISCUSSION

We describe the community structure of benthic organisms at 13 intertidal sites on four of the Main Hawaiian Islands. Mollusks and macroalgae dominate much of the Hawaiian intertidal, and the invasive species *Acanthophora spicifera* is common. Benthic communities were found to differ among sites and year but not with island or hard substratum type. Multivariate statistics reveal distinct community structure and 11 unique assemblages of benthic organisms. This substantial variability among sites and temporal variation for select sites by year suggests that physical or biological factors act on a local scale to shape community assemblages. Furthermore, fine-scale vertical patterns were evident at two narrow shores as would be predicted if conditions varied with the microfluctuating tides. These results are in contrast to several earlier descriptions of homogeneous tropical intertidal habitats (Garrity and Levings 1981, Lubchenco and Gaines 1981, Williams 1993, but see Vinueza et al. 2006) and are surprising given the limited tidal range.

Community structure among sites and years did not vary in a predictable manner with island, as a measure of geographic distance, or hard substratum type. Other studies examining intertidal structure have found distance (Bustamante and Branch 1996, Nakaoka et al. 2006, Blanchette et al. 2008), currents (Bustamante and Branch 1996, Blanchette et al. 2008, Broitman et al. 2008), and large-scale productivity (Menge et al. 1997) to correlate with site similarities. The Main Hawaiian Islands are within one biogeographic province with relatively little variation in sea-surface temperature, and large-scale currents bathe islands in similarly productive waters (Kay 1979, Abbott 1999). In addition, organisms had to cross vast oceanographic barriers to reach these islands (Kay 1979, Abbott 1999). Thus it is not surprising that community composition does not diverge with island or geographic distance, so high variation among sites and for some years was unexpected. Schoch and Dethier (1996) investigated temperate intertidal zones over a scale similar to that in this study and found habitat descriptor (example: bench versus cobble habitat) a good indicator of community structure. Hard substratum type could be an indicator of habitat availability because rock types may erode or form similarly, providing different types of habitats suitable for different types of organisms. Furthermore, intertidal fish assemblages are known to vary with substratum type (Yoshiyama et al. 1986, MacPherson 1994, Cox et al. 2010). However, for benthic organisms abundance and composition did not vary with substratum type. It should be noted that Banks and Skilleter (2007) cautioned that broad-scale categories of shorelines can fail to capture microhabitat and species diversity that occur at a shore.

Outlier communities (such as M, MPT, KB, WOP, WB, EB), or those that did not group with high similarity to other sites, may provide insight into local factors that override large-scale processes (Blanchette et al. 2008). Based on the species assemblages and environmental conditions at those sites we predict that local scale factors such as recruitment, predation, nutrient inputs, wave exposure, and sand scour may alter and maintain these communities. Small-scale current patterns along the south shore of O‘ahu can contribute to transmission of invertebrate larvae to different sites, and in turn these currents could determine what adult species are present or maintained at a site (Parnell 2000, Zabin 2005). Furthermore, sites are speculated to differ in levels of freshwater input, herbivory, and nutrients.

Bottom-up factors, such as nutrients, are known to contribute to the variability of tropical intertidal communities in the Galápagos (Vinueza et al. 2006) and could be driving community differences in the Main Hawaiian Islands. The communities that occurred at WB, KB, M, and MPT may be indicative of elevated nutrient inputs from different local sources. Nuisance blooms of macroalgae (*Hypnea musciformis*, *Acanthophora spicifera*, and *Ulva lactuca*) are common on the reefs off WB in Kīhei, Maui (Smith 2003), and were found at high abundance in the associated intertidal zone (this study). These blooms have been linked to localized eutrophication of coastal waters from sewage inputs from a nearby injection well (Smith 2003). This site is also the only coral-rubble habitat sampled. KB is the only sampled intertidal site that is located in a relatively clean bay, and it is situated near Kahana stream. This stream and submarine groundwater discharge drain water from the Koʻolau mountain range that surrounds the valley of Kahana (Garrison et al. 2003). An abstract reported by Zabin et al. (2007*a*) also found KB to have low species richness compared with other intertidal sites on Oʻahu. The freshwater input could account for these observed differences in community structure. *Acanthophora spicifera* was dominant at M and MPT, but these sites lack other obvious similarities. The benthic substrate at M is silt and mud with cobbles near a fishpond where edible algae are cultivated, and it sits at the base of Mapulehu Gulch. Terrestrial sedimentary input in shallow-water habitats is common on the east side of Molokaʻi, where this site is located (Bothner et al. 2006). MPT is a limestone bench on the west side of Oʻahu, located near a large drainage outlet. A homeless camp surrounds the beach, where harvesting of marine life is common and sanitation appears to be a problem (T.E.C., pers. obs.).

The community at WOP was unique in that it is free from introduced macroalgae, and corals are in high abundance. WOP also did not share high similarity with any other site. Corals are often associated with warm, low-nutrient oceanic waters where herbivory is high (Smith et al. 2001), and WOP is located within a permanent "no take" Marine Life Conservation District. Perhaps conservation efforts result in higher herbivory rates than at the other sampled sites. Also, unlike other sampled sites with few to many tide pools of various depths, the habitat at WOP can be characterized by numerous large and often deep tide pools where coral resides.

Disturbance can contribute to spatial variation and temporal variation in tropical habitats (Vinueza et al. 2006). SI 2005, 2007, and MP were community samplings with low biotic cover, dominated by turf. Turf algae are specialized for areas with high physical stress and moderate grazing pressure (Hay 1981), and it is possible that for this shore habitat type, scour and predation prevent the cover of lush macroalgae and abundance of small mollusks that occurred at other sites. Also it is plausible that boulders and sand that occur at SI are tossed in large seasonal waves, creating a disturbance that would alter the community and account for the temporal variation. Further physical measurements and experimental testing should be examined with structure to clarify factors that shape the community over these mesoscales for the Main Hawaiian Islands.

Introduced macroalgae were common in intertidal habitats, yet their impact on that type of benthic community has been little studied, and the successful invasion of these alien species at some sites and not others could account for the high spatial variability among sites. Introduced species were found at sites on all islands sampled, with *A. spicifera* being the most common alien species found. This species is known to have increased growth rates in nutrient-rich waters (Fong et al. 2003) and to be a preferred food of herbivores (Stimson et al. 2001). Its abundance at sites suggests that herbivores in the intertidal zone at certain sites are not present in high-enough numbers to limit biomass production. *Avrainvillea amadelpha* was found only at sampled sites on Oʻahu. Recent observations of this species in rocky habitats (T.E.C., pers. obs.) where not previously noted are of concern. Competition between native and introduced species is likely; it has been described in Hawaiʻi's rocky intertidal between an invasive barnacle and a native limpet (Zabin and Altieri 2007) and is suggested to occur between *A. spicifera* and native *Laurencia* species (Russell 1992). Thus, future efforts should be made to document and monitor any changes in abundance of introduced species, to quantify any impacts to the community, and to assess the feasibility of removal in rocky intertidal habitats—similar to efforts already undertaken on Hawaiʻi's reefs (Conklin and Smith 2005).

Zonation patterns on the two shores share similarities to those documented by Sibaja-Cordero (2008) in Costa Rica on a rugged island coastline and by Bird (2006) on a wave-dominated shore on Oʻahu but are very different from the patterns described by Menge and Lubchenco (1981) in Panama. In

Panama, fleshy macroalgae are limited to cracks and crevices. In our study fleshy macroalgae were common on all surfaces in the lower intertidal and were more common than what is described by others elsewhere in the tropics (Bertness 1981, Garrity and Levings 1981, Menge and Lubchenco 1981) or for a wave-dominated Hawaiian shore (Bird 2006). Bird (2006) also described a helmet urchin (*Colobocentrotus atratus*) zone above the high-tide line, which was not found at the sites included in this study. Zonation patterns of fleshy algal genera were also documented by this study, and descriptions of this level of vertical distributions are lacking for other localities.

The zonation patterns observed at two shores in Hawai‘i suggest the importance of local- to microhabitat-level interactions, in shaping communities at finer spatial scales, for even the narrowest of shores. Other studies conducted in the tropics have posited predation (Bertness 1981, Garrity and Levings 1981, Menge and Lubchenco 1981), nutrients (Vinueza et al. 2006), and temperature/desiccation (Southward 1958, Vermeij 1973, Garrity 1984) as determinants of distributions. In Hawai‘i, Cox and Smith (2011) described several species of intertidal mollusks that occur in cooler crevices near the high-tide line, but lush algal beds cover the lower shore. Hawai‘i's microtidal regimes and wave action could perhaps limit harsh conditions and account for differences in algal fine-scale distributions from those described in Panama (Menge and Lubchenco 1981). In addition, competition and partitioning are likely to alter the distributions of Hawaiian mollusks and macroalgae because these factors have been described for O‘ahu (Zabin 2009) and elsewhere in the tropics (Levings and Garrity 1983, Ortega 1985, Sutherland and Ortega 1986, Mak and Williams 1999). In Panama, neritid species differ in their tolerances to temperature, exposure, and predation and when removed, co-occurring littorines increase in size (Levings and Garrity 1983). Similarly, in Hong Kong, littorines control the abundance of biofilms and limit algal recruitment from higher zones (Mak and Williams 1999). Along with the common neritid *Nerita picea*, Hawai‘i has two common littorines in intertidal zones, *Echinolittorina hawaiiensis* and *Littoraria pintado*. *Littoraria pintado* is often found higher on the shore than *E. hawaiiensis* (Kay 1979), and this distribution was observed at Diamond Head. In addition, wave activity and subsequent lower temperatures correlated with the distributions of urchins, mollusks, and macroalgal functional groups at a wave-exposed site on O‘ahu (Bird 2006). Further fine-scale experiments and investigations are needed to discern which factors contribute to this fine-scale zonation in Hawai‘i.

The characterization of Hawaiian shores is important for conservation of intertidal habitats because it not only provides a better understanding of the ecological processes that shape these communities, but it also provides a baseline from which to measure ecological change. Eutrophication, climate change, invasions, and harvesting are likely to impact these intertidal habitats, and results from this study suggest that some sites have already been altered. Last, these findings stress the importance of local factors in shaping structure at multiple scales and clearly indicate that Hawaiian intertidal zones vary spatially and can vary temporally.

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Literature Cited

Abbott, I. A. 1999. Marine red algae of the Hawaiian Islands. Bishop Museum Press, Honolulu.

Abbott, I. A., and J. M. Huisman. 2004. Marine green and brown algae of the Hawaiian Islands. Bishop Museum Press, Honolulu.

Airame, S., J. E. Dugan, K. D. Lafferty, H. Leslie, D. A. McArdle, and R. R. Warner. 2003. Applying ecological criteria to marine reserve design: A case study from the California Channel Islands. Ecol. Appl. 13:170–184.

Banks, S. A., and G. A. Skilleter. 2007. The importance of incorporating fine-scale habitat data into the design of an intertidal marine reserve system. Biol. Conserv. 138:13–29.

Barry, J. P., C. H. Baxter, R. D. Sagarin, and S. Gilman. 1995. Climate-related, long-term faunal changes in a California rocky intertidal community. Science (Washington, D.C.) 267:672–675.

Baumgartner, E., and C. J. Zabin. 2006. Visualizing zonation patterns. Sci. Teach. 73:60–64.

Baumgartner, E., C. J. Zabin, J. K. Philippoff, T. E. Cox, and M. L. Knope. 2009. Our project in Hawaii's intertidal: Ecological monitoring provides a thematic foundation for student inquiry. Pages 191–209 *in* R. Yager, ed. Inquiry: The key to exemplary science. National Science Teachers Association, Arlington, Virginia.

Benson, K. R. 2002. The study of vertical zonation on rocky intertidal shores: A historical perspective. Integr. Comp. Biol. 42:776–779.

Bertness, M. D. 1981. Predation, physical stress, and the organization of a tropical rocky intertidal hermit crab community. Ecology 62:411–425.

Bird, C. E. 2006. Aspects of community ecology on wave-exposed rocky Hawaiian coasts. Ph.D. diss., University of Hawai'i at Mānoa, Honolulu.

Blanchette, C. A., C. M. Miner, P. T. Raimondi, D. Lohse, K. E. Heady, and B. R. Broitman. 2008. Biogeographical patterns of rocky intertidal communities along the Pacific coast of North America. J. Biogeogr. 35:1593–1607.

Bothner, M. H., R. L. Reynolds, M. A. Casso, C. D. Storlazzi, and M. E. Field. 2006. Quantity, composition, and source of sediment collected in sediment traps along the fringing coral reef off Moloka'i, Hawai'i. Mar. Pollut. Bull. 52:1034–1047.

Broitman, B. R., C. A. Blanchette, B. A. Menge, J. Lubchenco, P. A. Raimondi, C. Krenz, M. Foley, D. Lohse, and S. D. Gaines. 2008. Spatial and temporal patterns of invertebrate recruitment along the west coast of the United States. Ecol. Monogr. 78:403–421.

Bustamante, R. H., and G. M. Branch. 1996. Large scale patterns and trophic structure of southern African rocky shores: The roles of geographic variation and wave exposure. J. Biogeogr. 23:339–351.

Clarke, K. R., and R. M. Warwick. 2001. Changes in marine communities: An approach to statistical analysis and interpretation. 2nd ed. Primer-E Ltd., Plymouth, United Kingdom.

Conklin, E. J., and J. E. Smith. 2005. Abundance and spread of the invasive red algae, *Kappaphycus* spp., in Kane'ohe Bay, Hawai'i and an experimental assessment of management options. Biol. Invasions 7:1029–1039.

Connell, J. H. 1961. The influence of intraspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus.* Ecology 42:710–723.

Cox, T. E., E. Baumgartner, J. Philippoff, and K. S. Boyle. 2010. Spatial and vertical patterns in the tidepool fish assemblage on the island of O'ahu. Environ. Biol. Fishes 90:329–242.

Cox, T. E., J. Philippoff, E. Baumgartner, and C. M. Smith. 2012. Expert variability provides perspective on the strengths and weaknesses of citizen-driven intertidal monitoring program. Ecol. Appl. 22:1201–1212.

Cox, T. E., and C. M. Smith. 2011. Thermal ecology on an exposed algal reef: Infrared imagery a rapid tool to survey temperature at local spatial scales. Coral Reefs 30:1109–1120.

Dailer, M. L., R. S. Knox, J. E. Smith, M. Napier, and C. M. Smith. 2010. Using δ^{15}N values in algal tissue to map locations and potential sources of anthropogenic nutrient inputs on the island of Maui, Hawai‘i, USA. Mar. Pollut. Bull. 60:655–671.

Delaney, D. G., C. D. Sperline, C. S. Adams, and B. Leung. 2008. Marine invasive species: Validation of citizen science and implications for national monitoring networks. Biol. Invasions 10:117–128.

Doty, M. S. 1946. Critical tide factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific coast. Ecology 27:315–328.

Eldredge, L. G., and J. T. Carlton. 2004. Hawaiian marine bioinvasions: A preliminary assessment. Pac. Sci. 56:211–212.

Eldredge, L.G., and C. M. Smith, eds. 2001. A guidebook of introduced marine species in Hawaii. B. P. Bishop Museum and the University of Hawai‘i, Honolulu.

Fong, P., K. E. Boyer, K. Kamer, and K. A. Boyle. 2003. Influence of initial tissue nutrient status of tropical marine algae on response to nitrogen and phosphorus additions. Mar. Ecol. Prog. Ser. 262:111–123.

Garrison, G. H., C. R. Glenn, and G. M. McMurtry. 2003. Measurement of submarine groundwater discharge in Kahana Bay, O‘ahu, Hawai‘i. Limnol. Oceanogr. 48:920–928.

Garrity, S. D. 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. Ecology 65:559–574.

Garrity, S. D., and S. C. Levings. 1981. A predator-prey interaction between two physically and biologically constrained tropical rocky shore gastropods: Direct, indirect, and community effects. Ecol. Monogr. 51:268–286.

Hay, M. E. 1981. The functional morphology of turf-forming seaweeds: Persistence in stressful marine habitats. Ecology 62:739–750.

Hoover, J. P. 2002. Hawaii's sea creatures: A guide to Hawaii's marine invertebrates. Rev. ed. Mutual Publishing, Honolulu.

Huisman, J. M., I. A. Abbott, and C. M. Smith. 2007. Hawaiian reef plants. University of Hawai‘i Sea Grant College Program, Honolulu.

Kay, A. E. 1979. Hawaiian marine shells. Bernice P. Bishop Mus. Spec. Publ. 64 (4).

Levings, S. C., and S. D. Garrity. 1983. Diel and tidal movement of two co-occurring neritid snails: Differences in grazing patterns on a tropical rocky shore. J. Exp. Mar. Biol. Ecol. 67:261–278.

Littler, M. M., and M. S. Doty. 1975. Ecological components structuring the seaward edges of tropical Pacific reefs: The distribution, communities, and productivity of *Porolithon*. J. Ecol. 63:117–129.

Littler, M. M., and D. S. Littler. 1984. Relationships between macroalgal functional form groups and substrate stability in a sub-tropical rocky intertidal system. J. Exp. Mar. Biol. Ecol. 74:13–34.

Lubchenco, J., and S. D. Gaines. 1981. A unified approach to marine-plant interactions. I. Populations and communities. Annu. Rev. Ecol. Syst. 12:405–437.

MacPherson, E. 1994. Substrate utilization in a Mediterranean littoral fish community. Mar. Ecol. Prog. Ser. 114:211–218.

Mak, Y. M., and G. A. Williams. 1999. Littorinids control high intertidal biofilm abundance on tropical, Hong Kong rocky shores. J. Exp. Mar. Biol. Ecol. 233:81–94.

Mattio, L., C. E. Payri, and M. Verlaque. 2009. Taxonomic revision and geographic distribution of the subgenus *Sargassum* (Fucales, Phaeophyceae) in the western and central Pacific islands based on morphological and molecular analyses. J. Phycol. 45:1213–1227.

McDermid, K. J. 1988. Community ecology of some intertidal subtropical algae, and the biology and taxonomy of Hawaiian *Laurencia* (Rhodophyta). Ph.D. diss., University of Hawai‘i at Mānoa, Honolulu.

Meese, R. J., and P. A. Tomich. 1992. Dots on the rocks: A comparison of percent cover estimation methods. J. Exp. Mar. Biol. Ecol. 165:59–73.

Menge, B. 2000. Testing the relative importance of positive and negative effects on community structure. Trends Ecol. Evol. 15:45–46.

Menge, B., B. A. Daley, P. A. Wheeler, and T. Strub. 1997. Rocky intertidal oceanography: An association between community structure and nearshore phytoplankton concentration. Limnol. Oceanogr. 42:57–66.

Menge, B. A., and J. Lubchenco. 1981. Community organization in temperate and tropical rocky intertidal habitats: Prey refuges in relation to consumer prey gradients. Ecol. Monogr. 51:429–450.

Murray, S. N., R. F. Ambrose, and M. N. Dethier. 2006. Monitoring rocky shores. University of California Press, Berkeley.

Nakaoka, M., N. Ito, T. Yamamoto, T. Okuda, and T. Noda. 2006. Similarity of rocky intertidal assemblages along the Pacific coast of Japan: Effects of spatial scales and geographic distance. Ecol. Res. 21:425–435.

Ortega, S. 1985. Competitive interactions among tropical intertidal limpets. J. Exp. Mar. Biol. Ecol. 90:11–25.

Parnell, P. E. 2000. The effects of circulation, larval planktonic period, adult distribution, and pollution on benthic recruitment in Hawaiian coastal waters. Ph.D. diss., University of Hawai‘i at Mānoa, Honolulu.

Russell, D. J. 1992. The ecological invasion of Hawaiian reefs by two marine red algae, *Acanthophora spicifera* (Vahl) Boerg. and *Hypnea musciformis* (Wulfen) J. Ag., and their association with two native species, *Laurencia nidifica* J. Ag and *Hypnea cervicornis* J. Ag. ICES Mar. Sci. Symp. 194:110–125.

Sagarin, R. D., J. P. Barry, S. E. Gilman, and C. H. Baxter. 1999. Climate-related change in an intertidal community over short and long time scales. Ecol. Monogr. 69:465–490.

Schoch, G. C., and M. N. Dethier. 1996. Scaling up: The statistical linkage between organismal abundance and geomorphology on rocky intertidal shorelines. J. Exp. Mar. Biol. Ecol. 201:37–72.

Sibaja-Cordero, J. A. 2008. Vertical zonation in the rocky intertidal at Cocos Island (Isla del Coco), Costa Rica: A comparison with other tropical locations. Rev. Biol. Trop. 56:171–187.

Simberloff, D., I. M. Parker, and P. N. Windle. 2005. Introduced species policy, management, and future research needs. Front. Ecol. Environ. 3:12–20.

Sink, K. J., G. M. Branch, and J. M. Harris. 2005. Biogeographic patterns in rocky intertidal communities in KwaZulu-Natal, South Africa. Afr. J. Mar. Sci. 27:81–96.

Smith, C. M. 1992. Diversity in intertidal habitats: An assessment of the marine algae of select high islands in the Hawaiian archipelago. Pac. Sci. 46:466–479.

Smith, J. E. 2003. Factors influencing algal blooms on tropical reefs with an emphasis on herbivory, nutrients, and invasive species. Ph.D. diss., University of Hawai‘i at Mānoa, Honolulu.

Smith, J. E., C. L. Hunter, and C. M. Smith. 2002. Distribution and reproductive characteristics of nonindigenous and invasive marine algae in the Hawaiian Islands. Pac. Sci. 56:299–315.

Smith, J. E., C. M. Smith, and C. L. Hunter. 2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs 19:332–342.

Southward, A. J. 1958. A note on the temperature tolerances of some intertidal animals in relation to environmental temperatures and geographic distribution. J. Mar. Biol. Assoc. U.K. 37:49–46.

Stephenson, T. A., and A. Stephenson. 1949. The universal features of zonation between tide-marks on rocky coasts. J. Ecol. 37:289–305.

Stimson, J., S. T. Larned, and E. J. Conklin. 2001. Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalga *Dictyosphaeria cavernosa* in Kāne‘ohe Bay, Hawai‘i. Coral Reefs 19:343–357.

Sutherland, J. P., and S. Ortega. 1986. Competition conditional on recruitment and temporary escape from predators on a tropical rocky shore. J. Exp. Mar. Biol. Ecol. 95:155–166.

Vermeij, G. J. 1973. Morphological patterns in high-intertidal gastropods: Adaptive strategies and their limitations. Mar. Biol. (Berl.) 20:319–346.

Vinueza, L. R., G. M. Branch, M. L. Branch, and R. H. Bustamente. 2006. Top-down herbivory and bottomup El Niño effects on Galápagos rocky-shore communities. Ecol. Monogr. 76:111–131.

Vroom, P. S., C. A. Musburger, S. W. Cooper, J. E. Maragos, K. N. Page-Albins, and M. A. V. Timmers. 2010. Marine biological community baselines in un-impacted tropical ecosystems: Spatial and temporal analysis of reefs at Howland and Baker Islands. Biodivers. Conserv. 19:797–812.

Williams, G. A. 1993. Seasonal variation in algal species and abundance in the presence of molluscan herbivores on a tropical rocky shore. J. Exp. Mar. Biol. Ecol. 167:261–275.

Yoshiyama, R. M., C. Sassaman, and R. N. Lea. 1986. Rocky intertidal fish communities of California: Temporal and spatial variation. Environ. Biol. Fishes 17:23–40.

Zabin, C. J. 2005. Community ecology of the invasive intertidal barnacle *Chthamalus proteus* in Hawai‘i. Ph.D. diss., University of Hawai‘i at Mānoa, Honolulu.

———. 2009. Battle of the barnacle newcomers: Niche compression in invading species in Kāne‘ohe Bay, O‘ahu, Hawai‘i. Mar. Ecol. Progr. Ser. 381:175–182.

Zabin, C. J., and A. Altieri. 2007. A Hawaiian limpet facilitates recruitment of a competitively dominant invasive barnacle. Mar. Ecol. Progr. Ser. 337:175–185.

Zabin, C. J., J. S. Pearse, E. M. Danner, and E. Baumgartner. 2007*a*. Comparison of species composition in two contrasting open-coast, rocky intertidal habitats: California and Hawai‘i. Abstract. Ecological Society of America Annual Meeting, San Jose, California.

Zabin, C. J., J. Zardus, F. B. Pitombo, V. Fread, and M. G. Hadfield. 2007*b*. A tale of three seas: Consistency of natural history traits in a Caribbean-Atlantic barnacle introduced to Hawai‘i. Biol. Invasions 9:523–544.