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THE ROCKY INTERTIDAL BIOTA OF THE FLORIDA KEYS: FIFTY-TWO YEARS OF CHANGE AFTER STEPHENSON AND STEPHENSON (1950)

Tyler B. Smith, John Purcell, and John F. Barimo

ABSTRACT

A study of the rocky intertidal environments of the Florida Keys by Stephenson and Stephenson (1950) serves as a valuable baseline of littoral communities prior to extensive development and human population pressures. Five of the study areas originally surveyed in 1947 were resurveyed in 1999 to assess any community changes which may have occurred in the intervening 52 yrs. A more extensive sampling effort in 1999 yielded a greater number of taxa as compared to 1947 (120 vs 78). However, one intertidal zone showed a decrease in taxa richness, not all species recorded in 1947 were seen in 1999, and others had shifts in abundance or zones of occurrence. The gray zone at the high mean water mark may have experienced degradation from the deposition of seagrass, debris, or hydrophobic substances as suggested by a 79% decrease in the species that occurred there, despite an increase in the number of species found in all other zones. Harvesting, pollution, or general habitat degradation may explain the complete absence or reduced abundance of some species, particularly those considered as dominant or characteristic intertidal community members in 1947. Increased nearshore eutrophication and/or changes in grazer communities may explain an apparent upward shift of some macroalgal species and the appearance at more heavily developed sites of algal nutrient indicator species (e.g., Cladophora, Chaetomorpha, and Enteromorpha). Our results are consistent with increasing evidence that disturbances, such as eutrophication, are having a negative effect on rocky intertidal communities of the Florida Keys.

Natural and anthropogenic processes affecting communities of organisms often occur on spatial and temporal scales larger than the typical observational time of ecological measurements. Patterns of meteorological cycles, climate cycles, recruitment cycles, trends in anthropogenic impact, and their ecological effects, cannot be understood unless measurements are available at the appropriate spatial and temporal scales (Levins, 1992). The need for long-term monitoring has been recognized and steps have been taken to develop programs that accumulate and integrate long-term ecological records (e.g., the International Long Term Ecological Research Network; Sprott, 1998). However, many of these programs are less than two decades old and lack of larger spatial and temporal observations still hinder the development of future predictions of ecosystem behavior and relevant management decisions (see Glynn and Colgan, 1992; Connell et al., 1997).

Despite the paucity of long-term observations, there are alternative methods of acquiring data at scales appropriate for identifying trends in communities. For example, paleoecology and paleoclimatology are disciplines developed for the purpose of reconstructing both recent and ancient ecological environments. However, where long-term databases are absent and reconstruction from preserved materials not possible, the ecological restudy may be the only way to gain information about change. In this type of investigation, an earlier ecological study acts as a baseline for comparison, and hypotheses can be assessed about the extent and types of change that have occurred. For example, in the marine and maritime environment restudies have been used to document climate related shifts in intertidal species distributions (Sagarin et al., 1999), changes in algal community composition and distribution in the lower Florida Keys (Dawes et al., 1999), and forest habitat loss in the upper Florida Keys (Strong and Bancroft, 1994).

The Florida Keys and their rocky intertidal shorelines are the remains of coral reef and oolite buildups created during the sea level high stand of the Pleistocene approximately 120,000 yrs ago (Hoffmeister and Multer, 1968). These carbonate islands run from Soldier Key in the northeast following a southwesterly arc to the Dry Tortugas, covering a distance of about 360 km. The Middle and Lower Keys are bordered by Florida Bay on their northern and western shores, and the Florida Reef Tract and the Atlantic Ocean to the south and east. Their rocky intertidal shores support a predominantly tropical West Indian fauna, a consequence of the warm Florida Current (Stephenson and Stephenson, 1950).

Over the last half-century, the Florida Keys have undergone a variety of anthropogenically induced changes. The Overseas Railroad altered the natural exchange of estuarine and oceanic waters, the Everglades drainage into Florida Bay has been increased, deforestation has resulted in large habitat fragmentation and loss, and dredge-and-fill developments (equal to 9.6% of the total land area of the Florida Keys) have destroyed shoreline habitat, led to high turbidity and sedimentation, and otherwise degraded local water quality (compiled in Lott et al., 1996). For instance, there are indications that the nearshore waters of the Florida Keys have been experiencing more eutrophic conditions as the result of both watershed enrichment of Florida Bay and run-off and septic well leakage from the Florida Keys (Lapointe et al., 1990; Lapointe and Clark, 1992; Paul et al., 1995; Lapointe et al., 2002, Lapointe et al., 2004). Concomitant with these changes, the resident human population has increased over four-fold since the 1940s (Lott et al., 1996) and in 1999 reached nearly 90,000 (Florida State Department of Health, www.doh.state.fl.us). There has been growing concern that anthropogenic pressure on the Florida Keys has degraded many biological communities.

A survey of the Florida Keys rocky intertidal shoreline between January and February 1947, serves as a valuable record of this habitat (Stephenson and Stephenson, 1950). The Stephensons' generalized zonation scheme for the Florida Keys translates average tidal levels (i.e., supralittoral, midlittoral, and infralittoral) to more relevant and recognizable intertidal features based on rock coloration and can be used to compare zonation patterns seen in other rocky intertidal assemblages (Fig. 1).

As components of their description of the Florida Keys rocky intertidal shoreline, the Stephensons provided a partial species list of terrestrial plants, animals, and algae found within each tidal zone, an estimate of species richness for each zone, photographic and diagrammatic records of many locations, and a comparison of the characteristics of many of the locations they surveyed. Together these descriptions create a picture of the rocky intertidal communities of organisms and their habitat as they existed in 1947. We undertook a reexamination of the condition of these communities in an effort to understand the extent and types of changes that have occurred in this environment in the period from 1947 to 1999.

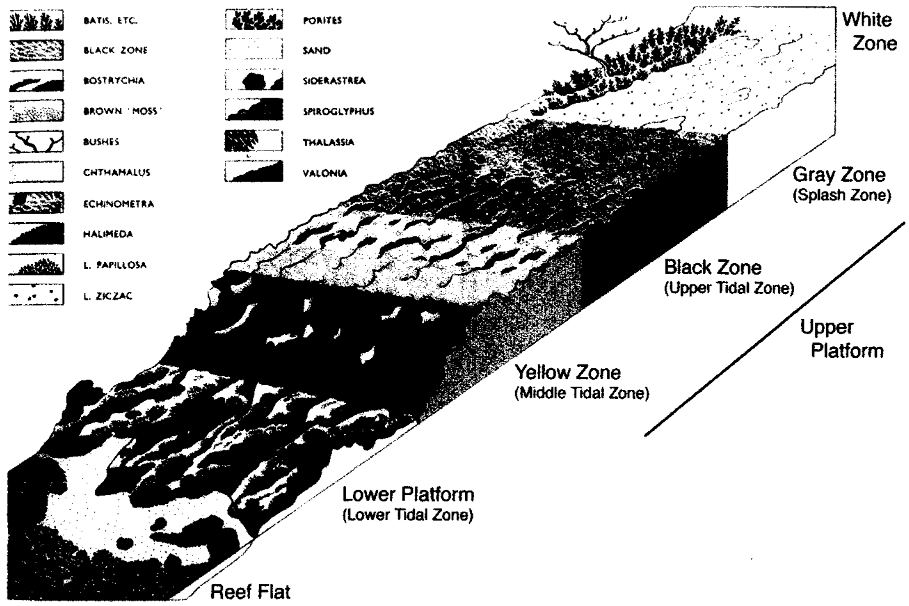


Figure 1. A modified version of the original zonation scheme for the Florida Keys rocky intertidal based on dominant rock coloration at various tidal heights from Stephenson and Stephenson (1950). Modified and reprinted and with permission from Blackwell Publishing, Inc.

Materials and Methods

Site Selection and Characteristics.—Our sampling sites replicated as closely as possible the original areas surveyed by the Stephensons in 1947. The Stephensons surveyed shorelines on Soldier, Plantation, Crawl, Vaca, and West Summerland Keys (Fig. 2) and noted the unique characteristics of the areas. All intertidal areas were documented in Stephenson and Stephenson (1950) by descriptive or photographic landmarks, a shoreline map, and a reference distance from highway mile markers or permanent structural landmarks, or some combination of the above. Thus, we were able to find the original sites surveyed in 1947 with reasonable certainty. For example, the West Summerland Key site was located from a photograph with a prominent landmark that identified the site and the orientation of sampled areas along the shoreline (Fig. 3).

Crawl Key I is the original area sampled in 1947, however, the natural rocky intertidal shoreline in this location had been commercially developed into a constricted inlet with a sloping seawall composed of loose carbonate boulders. In light of this direct alteration to Crawl Key I, a less impacted adjacent area approximately 300 m to the south (Crawl Key II) was also sampled and used in overall comparisons.

Physical Differences Between Studies.—In addition to increasing anthropogenic influences on the Florida Keys rocky intertidal between 1947 and 1999, there have been some changes in average and acute physical impacts. Sea level had increased approximately 12 cm between studies [(dynamic height at Key West, Florida)/time = 0.23 ± 0.01 cm yr^{-1}; Maul and Martin (1993)]. In addition, average air temperature had increased approximately 0.4 °C between studies [based on trend for temperature at Key West (1974–1999) = 0.14 °F per decade, using 77.1 °F and 77.8 °F as starting and ending points given in trendline; NOAA National Climactic Center, Asheville; ©2006, 1 March, 2006. Available from: http://www.ncdc.noaa.gov/oa/climate/research/cag3/y2.htm]. Unfortunately, no reliable nearshore sea surface temperature records for the Florida Keys are available for comparison. Acute hurricane impacts were somewhat different preceding the studies. A Category 3 hurricane passed over the Up-

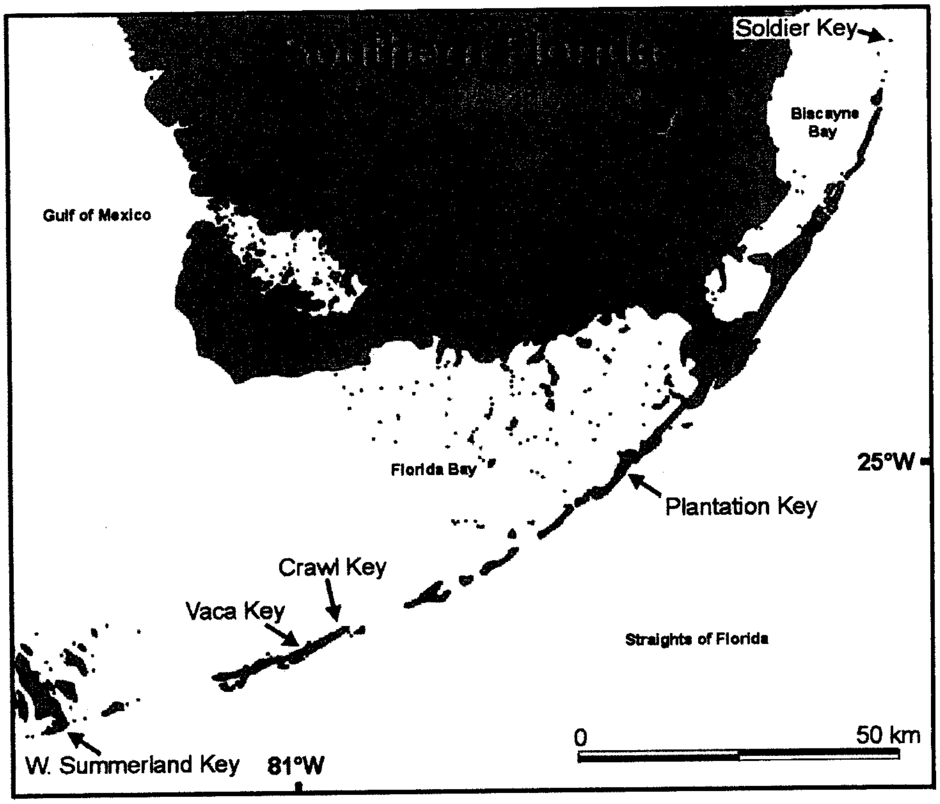
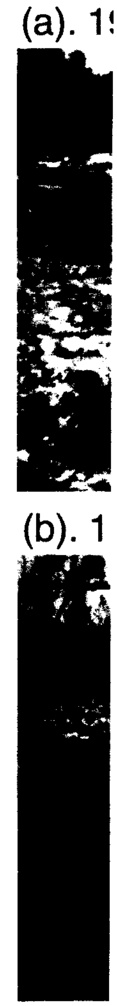


Figure 2. Map of southern Florida with sites sampled indicated by arrows and labels. Areas in black denote high human population densities.

per Florida Keys in 1945, < 2 yrs before the Stephenson's investigation (Barnes, 1998). A Category 5 storm, Hurricane Andrew, passed over the northern Upper Florida Keys in 1992 and Category 1 Hurricane Georges passed over the Lower Florida Keys in 1998 (NOAA National Climactic Data Center, Asheville; ©2006, 1 March, 2006. Available from: http://www.ncdc.noaa.gov/oa/climate/research/cag3/y2.html). While there is no information to evaluate the different impacts of these storms on the rocky intertidal biota, each study period included a recent history of storms and at least a 5 mo recovery period.

Community Sampling.—Zonation was determined using the intertidal color shift scheme developed by Stephenson and Stephenson (1950), based on collections of organisms from the five study sites. They focused on the more dominant members of the overall biota for each color zone. This bias to more common and conspicuous community members emphasizes that the 1947 sampling is probably a conservative estimate of species occurrence and richness at the sampling locations. We instead chose to sample the intertidal biota in an unbiased manner within randomly defined areas at each site surveyed in the Stephensons' original study. Transects were used to sample the flora and fauna of the white, gray, black, and yellow zones, and the inner margin of the lower platform. At three haphazardly chosen areas within each study site, 50 m transects were laid in each recognizable color zone, parallel to the trend of the shoreline. However, in sites where the extent of the shoreline available for sampling was limited, transects were laid in only those areas large enough to accommodate the full 50 m transect (e.g., Vaca Key and Crawl Key). The black and gray zones of Plantation Key were not sampled because they had been covered by an abrupt rock seawall. Transects were deployed in the approximate middle of each color zone and roughly followed the topographic complexities of the shoreline. A 0.5 × 0.5 m clear acrylic quadrat marked with 20 random points (after



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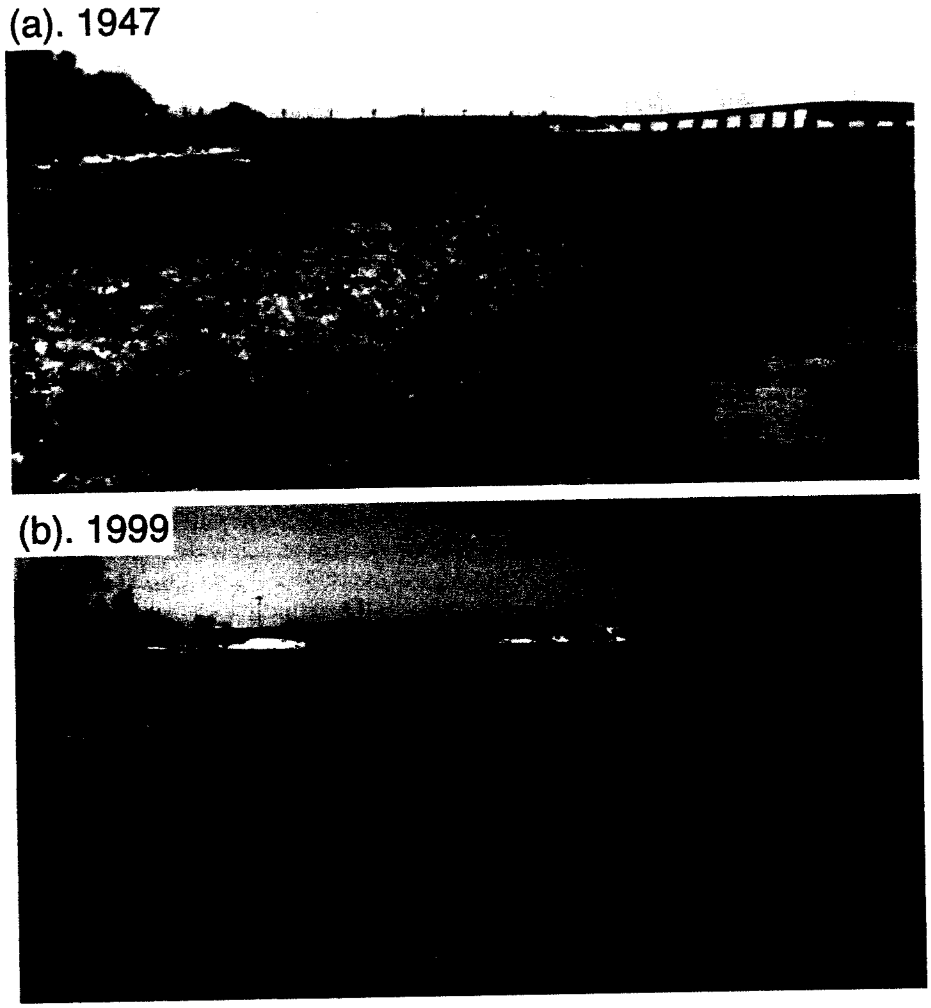

Figure 3. Photo comparison of the West Summerland Key rocky intertidal location from (A) 1947 and (B) 1999. Relocating the study sites surveyed by Stephenson and Stephenson (1950) was aided by photographic records, such as photo (A), modified and reprinted from the original manuscript with permission from Blackwell Publishing, Inc.

Lubchenco and Menge, 1978) was positioned at each of five random distances along and offset from the transect. All large, visible, motile animal taxa and bivalves present under the quadrat were counted as numbers of individuals while all other sessile animal taxa (e.g., barnacles and vermetid gastropods) and algae were recorded as percent cover based on the number of points under which they appeared. In keeping with the Stephenson and Stephenson (1950), only macroscopic algal forms, herein referred to as macroalgae, were sampled and algal films and diminutive turfs were excluded. Allochthonous organisms (e.g., seagrass, drift algae, and free sponges), which had apparently floated in from offshore areas, were recorded, but not included in community analysis in keeping with the Stephensons' analysis. Holes and crevices within the quadrats were briefly examined for the presence of cryptofauna. Representative samples of each species were collected, preserved, and transported to the laboratory for positive identification. Identification was made to the lowest possible taxonomic level, with most organisms identified to species.

White zone flora, consisting of herbaceous shrubs and trees, were surveyed with a 4 m wide belt transect extending inshore from the wrack or flotsam line, following the original procedure of Stephenson and Stephenson (1950). Belt transects were centered on the middle of each area sampled. Vascular plant species occurring within the belt transect were noted and representative portions of the plants were collected for positive identification using Wunderlin (1998). In addition, each species was categorized by its abundance in each belt transect. Categories were (1) uncommon, occurred once in a transect; (2) common, occurred more than once in a transect; and (3) dominant, was the most common species in a transect. Estimates were pooled for each key surveyed. All sampling was conducted in full daylight within 3 hrs of low tide (Table 1).

Physical Measurements.—The structure of the shoreline was characterized by its rugosity and width. Rugosity was measured as the ratio of a contour-following chain to a straight length of transect tape laid along the same path. Measurements were made perpendicular to the trend of the shoreline in the middle of each of the three transects at each site and averaged to give an estimate of the rugosity for the site. In addition, the width of each color zone was recorded along the rugosity transect. Due to time constraints, these measurements were not taken for Soldier Key and Crawl Key I.

Analyses.—The relative occurrence of taxa was compared between our study and Stephenson and Stephenson (1950) to elucidate possible changes in taxonomic composition in the 52 yrs separating the studies. Abundance data from Stephenson and Stephenson (1950) was considered qualitative and incomplete and could not be used for statistical comparisons as their primary purpose was to identify the most characteristic species of each color zone. This historic bias towards conspicuous and common biota results in a limited unidirectional comparison. Only a drop in species numbers or an absence of a common 1947 species in the 1999 data set was considered important, unless strong evidence, such as parity with the literature or clear trends with recognizable causative factors, was available to support an increase in species occurrence or abundance between the studies.

The Crawl Key II site was excluded from the overall analysis because it was not one of the Stephensons' original sites. However, we used this site for comparisons among sites within our study. Data for species presence in 1947 was taken directly from the Stephenson's paper and species names were verified and updated as necessary. Where either their or our data could not provide exact species identifications, the specimens were compared at the lowest possible taxonomic level. This allowed the most conservative estimate of change. Comparisons of taxonomic richness were made with Jaccard's Index (*Sj*), which indicates relative similarity or dissimilarity between communities (Magurran, 1988):

$$Sj = a/(a + b + c)$$

where a represents the number of elements in common between two sets of data, b represents the number of elements unique to one set, and c represents the number of elements unique to the other set.

We established criteria for separating out the 20 most common species seen in 1999 for comparison with the 20 most common species list developed by the Stephensons (Stephenson and Stephenson, 1950; p. 387). As initial criteria, species had to occur at more than one site and have a total abundance of at least 20 individuals or a coverage of at least 0.47 m^{-2} (equal to 0.5% of the sampled substrate). For terrestrial plants, the species had to occur in at least four sites. We felt this more stringent criterion was necessary to compensate for the qualitative nature of the terrestrial plant sampling. These criteria produced a list of 19 species with *Halimeda opuntia* (Linnaeus) Lamouroux, 1816 chosen as the 20[th] species. While other equally abundant and/or common species could have been included, *H. opuntia* was one of the Stephenson's original species and provided the most conservative comparison.

Taxonomic richness in each intertidal zone was compared between Stephenson and Stephenson (1950) and this study. Groups of taxa were defined as terrestrial plants, algae and

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Table 1. Characteristics of the keys sampled including position, dates of sampling, orientation, impacts, and the color zones present. Symbols: dv1-urban development in the immediate vicinity (< 10 m) of the sampling sites, dv2-urban development within 500 m of the sampling sites, HG-Hurricane Georges (1998), HA-Hurricane Andrew (1992); Oc-oceanic orientation, FB-Florida Bay orientation.

					GPS	
Site	Date(s) sampled	Impacts	Side	Site	Latitude (N)	Longitude (W)
				1	24° 39.100′	81° 18.218′
West Summerland	3/17/99	HG	Oc	2	24° 39.121′	81° 18.178′
				3	24° 39.145′	81° 18.147′
				1	24° 43.350′	81° 04.505′
Vaca	3/16/99	dv2, HG	FB	2	24° 43.461′	81° 04.645′
				3	24° 43.418′	81° 04.707′
				1	24° 44.081′	81° 00.924′
Crawl I	7/30/99	dv1, HG	FB	2	24° 44.067′	81° 00.958′
				3	24° 44.108′	81° 00.956′
				1	24° 44.052′	81° 01.125′
Crawl II	3/20/99	dv1, HG	FB	2	24° 44.048′	81° 01.123′
				3	24° 44.011′	81° 01.211′
				1	24° 58.251′	80° 33.165′
Plantation	7/22/99	dv1, HG	Oc	2	24° 58.235′	80° 33.147′
				3	24° 58.232′	80° 33.133′
				1	25° 35.445′	80° 09.677′
Soldier	8/11/99	HA	Oc	2	25° 35.382′	80° 09.549′
				3	25° 35.461′	80° 09.644′

seagrass, marine animals, and land-adapted animals following the Stephensons' scheme (p. 386). The distribution of the number of taxa found within each zone, when normalized to the total number of taxa found, was compared between studies using a Chi-square goodness of fit test at the $\alpha = 0.05$ level.

The diversity of communities of organisms at the 1999 sites was compared with both a log series index and the Margalef diversity index. The log series diversity index was chosen based on its insensitivity to sample size and abundance of the most common species, and its good discriminative ability (Magurran, 1988). Because this measure is unsuitable for communities measured as coverage, the Margalef diversity index was used for species recorded by coverage. The Margalef index also has good discriminative ability and is insensitive to the abundance of the most dominant species (Magurran, 1988).

Results

Sampled sites differed in orientation and potential natural and anthropogenic impacts (Table 1). Sites also tended to vary in the widths and rugosities of their respective color zones (Table 2), but only the West Summerland site showed a significant difference in width ($\alpha = 0.95$), a reduction of the yellow zone from 4.7 m (1947) to 1.9 m ± 0.32 SD (1999).

Taxonomic richness and diversity of the rocky intertidal differed considerably between 1947 and 1999. We recorded a total of 120 taxa compared to the 78 taxa found by the Stephensons. Analysis of the running mean of total taxa richness showed that the appearance of new taxa within our quadrats approached an asymptote, indicating the sufficiency of our sampling effort over all sites. Jaccard's Index of species similarity-dissimilarity between the two periods was 0.36 (Table 3), indicating dissimilarity between the species records. This dissimilarity was strongest within mac-

Table 2. The width (m) of the different color zones (W) and their Rugosity Indices (Rg) as recorded in 1999 compared with the widths reported in 1947 by Stephenson and Stephenson (1950). WS = West Summerland site, Vc = Vaca site, C II = Crawl Key II site, C I = Crawl Key I site, Pl = Plantation site, nz = color zone not present.

			White		Grey		Black		Yellow					
Site	Year	Site	W	Rg	W	Rg	W	Rg	W	Rg	W	Rg	Width (G+B+Y)	Width (Total)
		1	6.8	1.1	3.6	1.1	3.4	1.2	2.0	1.5	2.1	1.5		
WS	1999	2	2.9	1.0	2.0	1.0	4.2	1.4	2.1	1.4	2.3	1.3		
		3	4.8	1.0	3.6	1.2	2.3	1.3	1.5	1.3	2.2	1.4		
		Avg	4.8	1.1	3.1	1.1	3.3	1.3	1.9	1.4	2.2	1.4	8.2	15.3
	1947				4.0		4.2		4.7				12.9	
		1	nz	nz	0.8	1.3	2.2	1.4	nz	nz	3.8	0.6		
Va	1999	2	nz	nz	nz	nz	nz	nz	1.0	1.0	2.3	1.5		
		3	0.9	1.1	1.7	1.3	2.4	1.4	2.8	2.5	3.9	1.8		
		Avg	0.9	1.1	1.3	1.3	2.3	1.4	1.9	1.8	3.3	1.3	5.5	9.7
	1947				3.3		0.8		0.6				4.7	
		1	1.0	1.0	4.0	1.0	0.9	1.1	3.2	1.2	0.8	1.3		
C II	1999	2	1.0	1.0	1.8	1.1	2.6	1.2	1.1	1.8	1.0	2.0		
		3	0.9	1.1	2.1	1.4	2.3	1.3	1.5	2.0	1.0	2.0		
		Avg	1.0	1.1	2.6	1.2	1.9	1.2	1.9	1.7	0.9	1.8	6.5	8.4
C I	1947				3.6		2.2		1.3				7.3	
		1	1.7		nz	–	nz	–	13.3	–	4.0	–		
Pl	1999	2	2.0		nz	–	nz	–	7.8	–	3.1	–		
		3	2.9		nz	–	nz	–	6.9	–	2.4	–		
		Avg	2.2		nz	–	nz	–	9.3	–	3.2	–	9.3	14.7
	1947				3.9		3.5		2.2				5.7	

roalgae, with values of 0%, 0%, and 14% for filamentous cyanobacteria, Phaeophyta, and Chlorophyta, respectively. This reflects the fact that these algal taxa either did not occur in the Stephensons' species list or were rare. Overall, 24 taxa were recorded by the Stephensons but not encountered during our sampling effort (Table 4).

Of the 20 most common species in each of the two studies, 12 were common to both studies. Unique to the Stephensons' list were the maritime plants *Sesuvium portulacastrum* (L.) L., 1759 and *Batis maritima* L., 1759, the algae *Dictyosphaeria* (=*Valonia*) *ocellata* (M. Howe) J. L. Olsen-Stäjkowich, 1985, *Laurencia* spp., and the gastropods *Detracia bulloides* (Montagu, 1808), *Nerita peloranta* L., 1758, *Nodilittorina tuberculata* Menke, 1828, *Nodolittorina ziczac* (Gmelin, 1791), and *Stramonita rustica* (Lamarck, 1822). Species unique to our list were the mangroves *Avicennia germinans* (L.) Stearn, 1958, *Laguncularia racemosa* Gaertn. f., and *Rhizophora mangle* L., 1753, the alga *Hypnea musciformis* (Wulfen in Jacquin) Lamouroux, 1813, the hermit crabs *Clibinarius tricolor* (Gibbes, 1850), and *Calcinus tibicen* (Herbst, 1791) [treated as one group], the isopod *Ligia* spp., and the sponge *Chondrilla nucula* Schmidt, 1862. Species on their "20 Most Common Species" list that narrowly missed the criteria for ours were *B. maritima*, *Laurencia* spp., and *D. bulloides*. On the other hand, some species they included in their "20 Most Common Species" list were never encountered in our sampling, i.e., *D. ocellata*, *N. tuberculata*, and *S. rustica*.

Taxonomic richness across intertidal color zones tended to be higher in 1999 (Fig. 4), averaging a 30% increase, but this was likely a simple reflection of our greater sampling effort. In the gray zone, there was a 79% decrease in the number of sampled

Table 3. Species occurrence and Jaccard's Indices (*Sj*) within broad taxonomic groupings and in total between the 1999 study and Stephenson and Stephenson (1950). $Sj = a / (a+b+c)$. Values range from 0 to 1, with 1 indicating complete similarity and 0 indicating complete dissimilarity. "Cyanobacteria" refers to conspicuous filamentous cyanobacteria.

Group	Species occurrence			Jaccard's Index
	(a) 1947 and 1999	(b) 1947 only	(c) 1999 only	(*Sj*)
Vascular Plants	13	2	21	0.36
Chlorophyta	3	2	17	0.14
Rhodophyta	8	4	9	0.38
Phaeophyta	0	0	4	0.0
Cyanobacteria	0	0	1	0.0
Molluscs	20	11	10	0.49
Other Invertebrates	8	6	6	0.40
Total	52	25	68	0.36

Table 4. Taxa recorded by Stephenson and Stephenson (1950) but not encountered in the 1999 study.

Vascular plants
- *Monanthochloe littoralis* Engelm., 1859
- *Sporobolus virginicus* (L.) Kunth, 1829

Algae
- *Gelidiella pannosa* (Feldmann) Feldmann and Hamel, 1934
- *Jania capillacea* (Lamouroux, 1812)
- *Spyridia filamentosa* (Wulfen) Harvey in Hooker, 1833
- *Tellamia intricata* Batters, 1895
- *Dictyosphaeria* (*Valonia*) *ocellata* (M. Howe) Olsen-Stäjkowich, 1985
- crustose coralline algae*

Gastropods
- *Acmaea pustulata* Helbling, 1779
- *Littoraria angulifera* (Lamarck, 1822)
- *Melampus flavus* auct. non Gmelin, 1791
- *Onchidella* (*Onchidium*) *floridana* (Dall, 1885)
- *Stramonita rustica* (Lamarck, 1822)
- *Truncatella pulchella* Pfeiffer, 1839
- *Nodilittorina tuberculata* Menke, 1828°
- *Truncatella bilabiata* Pfeiffer, 1940

Other invertebrates
- *Arca barbata* (Linnaeus, 1758)
- *Arca imbricata* Bruguiere, 1789⁺
- *Bartholomea annulata* (Le Sueur, 1817)
- *Coenobita clypeatus* (Herbst, 1791)
- *Condylactis gigantea* (Weinland, 1860)
- *Cyclograpsus integer* H. Milne-Edwards, 1837
- *Pachygrapsus transversus* (Gibbes, 1850)
- *Phymanthus crucifer* (Le Sueur, 1817)

* Treated as one group by Stephenson and Stephenson (1950).
° We believe this to be the species listed as *Tectarius tuberculatus* by Stephenson and Stephenson (1950).
⁺ Listed in the Stephensons' study as the synonym *A. umbonata*.

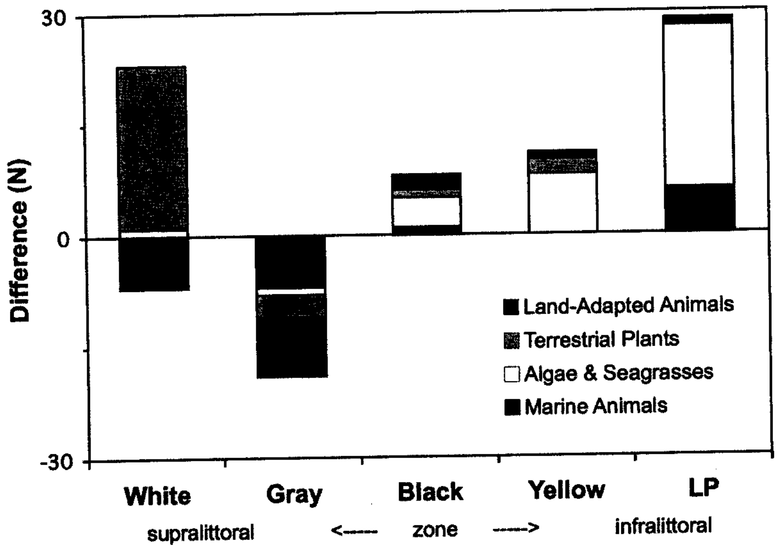

Figure 4. Comparison of the number of species (N) occurring in different intertidal color zones between 1947 and 1999. Species groupings were defined in Stephenson and Stephenson (1950, p. 386). The ordinate is the number of species occurring in a particular taxonomic grouping in a particular color zone in 1999 minus that reported by the Stephensons in 1947. Positive values indicate greater species numbers in a taxonomic group for 1999 while negative values indicate a loss of species.

taxa (28 taxa in 1947 and six taxa in 1999). A chi-square goodness of fit test showed that relative distribution of organisms in each intertidal zone was not significantly different between studies ($\chi^2 = 0.414$, $P = 0.98$).

In 1999, the distribution of algal coverage among sites was relatively homogeneous, with the exception of Soldier Key. Of the 18.75 m^2 of shoreline sampled at each site an average of 2.38 m^2 (± 1.28 SD) or 13% was covered with conspicuous algae. However, the Soldier Key algal community consisted of only two species with a coverage of 0.16 m^2 or 1%.

At some sites we found a high occurrence of algae typically associated with eutrophic habitats (Fig. 5). These included filamentous cyanobacteria (Littler and Murray, 1975; López Gappa et al., 1990), *Cladophora* spp., *Chaetomorpha* spp., *Polysiphonia* spp., and *Ulva* spp. (Reyes and Marino, 1991; Lapointe et al., 1992; Lapointe et al., 1994). None of these five eutrophic species or groups, was reported by Stephenson and Stephenson (1950). Eutrophic algal coverage as a percentage of the total algal coverage at each site was highest at Plantation Key (14%), Crawl Key I (63%), and Crawl Key II (33%). Eutrophic algal coverage as a percentage of total area sampled was also highest at Plantation (17%), Crawl Key I (12%), and Crawl Key II (20%), with up to 28% of the Lower Platform occupied by cyanobacteria at Crawl Key I.

In the 1999 survey, community characteristics differed among sites (Table 5). Taxonomic richness of the animal communities ranged from a high of 26 species at West Summerland Key to a low of five species at Crawl Key I, with an overall mean of 15.2 (± 7.4 SD) animal species per site. Abundance of species recorded as individuals also varied greatly among sites, with a high of 2083 animals at Crawl Key II and a low of 33 animals at Vaca Key (mean = 912.3 ± 818.2 SD). In most cases the most abundant

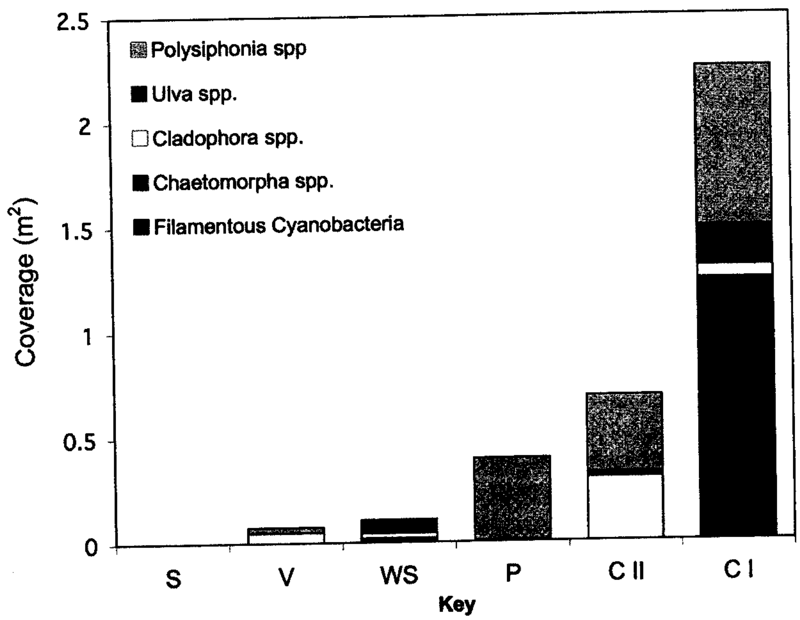

Figure 5. Comparison of the coverage of algal species or taxa associated with eutrophic environments between the sites studied in 1999 (S = Soldier Key, V = Vaca Key, WS = West Summerland Key, P = Plantation Key, C II = Crawl Key II, and C I = Crawl Key I).

animal was the gastropod *B. minima* and most variation in animal abundance was due to this species (Appendix II).

Concentrations of wrack, consisting mostly of detached seagrasses covering the substrate, were common in the upper intertidal zones of most sites. Over all sites this coverage averaged 5.0 ± 19.0 SD, 9.3 ± 29.1, and 21.6 ± 33.2 for the white, black, and gray zones, respectively. High variance was largely due to the fact that the actual vertical position of the wrack line tended to vary among sites, changing the zone that contained the greatest concentration of wrack.

Discussion

Changes in species composition of Florida Keys rocky intertidal communities between 1947 and 1999 was indicated by species reductions or absences, loss of species richness in the gray zone, and the presence of previously absent species. As mentioned above, as the result of our greater sampling effort in 1999, decreases in particular taxa and in the number of taxa in the gray zone across multiple keys are particularly strong evidence of community change. Furthermore, increased species presence in 1999 as compared to 1947 may be indicative of change in community composition where these findings parallel similar results from the literature or follow gradients of factors potentially driving species change.

The reduction in species occurring in the gray zone in 1999 may reflect a decrease in the quality of this habitat. The gray zone encapsulates the high water mark and, thus, is subject to accumulation of floating material. Hydrophobic substances are known to be deposited at the high water mark (e.g., oil, Jones et al., 1998; and tar, Butler et al., 1998) and have been implicated in habitat degradation of rocky shores

Table 5. Diversity indices and abundances of animals quantified as individuals, and of animals and plants quantified as coverage for the different sites surveyed in 1999. WS = West Summerland Site, Tot = total, Pl = plants, Ag = algae, An = animals, Ind = taxa with abundance recorded as individuals, Cov = taxa with abundance recorded as coverage in m^2, Mg = Margalef's diversity index, α = log series index.

	Taxa richness (N)				Abundance		Diversity Ind		Diversity Cov
Site	Tot	Pl	Ag	An	Ind	Cov	Mg	α	Mg
WS	60	17	18	26	1,560	2.36	3.0	3.8	23.3
Vaca	51	15	24	12	33	4.24	1.7	2.7	19.4
Crawl I	30	8	17	5	49	3.65	0.8	1.0	13.1
Crawl II	38	8	16	14	2,083	2.13	1.4	1.7	21.1
Plantation	40	5	14	21	1,009	4.04	2.3	2.9	13.6
Soldier	29	14	2	26	740	0.45	1.4	1.6	–5.0
Average	41.5	11.2	15.2	15.2	912.3	2.81	1.8	2.3	14.3

(Southward, 1982). Tar deposits were observed by us to be quite common at the sites studied. In addition, flotsam, particularly detached seagrass, had a high coverage at the study sites in 1999. While the Stephensons did not mention detached seagrass, it is likely that increasing seagrass die-offs, such as occurred in Florida Bay beginning in 1987 (Zieman et al., 1999) and seasonally in the Lower Florida Keys (Lapointe et al., 2004), have caused acute and chronic build-ups of wrack at the high tide mark with a subsequent release of nutrients upon decomposition. The movement of wrack during high water may further its impact, leading to chronic smothering, as well as eutrophication. In addition, acute seagrass wrack impacts may have been caused by the recent passage of Hurricane Georges along the Florida Keys 6 mo prior to initiation of the study and localized winter storms in 1998–1999. These storm events deposited large quantities of wrack and flotsam in the upper intertidal (T.B.S., per. obs.).

The absence or reduction of animal species at the sites studied is likely to have multiple causes ranging from harvesting, pollutants, and habitat degradation. Some of the absences may be the result of local extirpation by collectors for the curio or pet trade which has been shown to be important in structuring intertidal assemblages elsewhere (Crowe et al., 2000). This may explain the absence of *Acmaea pustulata* Helbling, 1779, *Littorina angulifera* (Lamarck, 1822), *Melampus flavus* auct. non Gmelin, 1791, *N. ziczac, N. tuberculata, S. rustica, Truncatella bilabiata* Pfeiffer, 1840, and *Coenobita clypeatus* (Herbst, 1791), as well as the loss from the "20 Most Common Species" list, indicative of a shift in dominance, of *D. bulloides, N. peloranta, N. tuberculata, N. ziczac,* and *S. rustica.* Gastropods may have value to shell collectors. By 1947 *N. peloranta* was already noted by the Stephensons as 'greatly reduced' in number due to shell harvesting (Stephenson and Stephenson, 1950, p. 388). The anomuran *C. clypeatus* is known to be sold into the pet trade (Calardo et al., 2003) and used as bait by some local fishermen (T.B.S., pers. obs.). This large hermit may also suffer from population limitation due to low gastropod shell availability, an interaction with low large gastropod abundance (Fotheringham, 1980). Lastly, *S. rustica* may also be sensitive to the antifouling biocide tributyltin, which is known to cause imposex in neogastropods elsewhere (Ellis and Pattisina, 1990; Bryan and Gibbs, 1991).

Comparison of this study with earlier studies also supports a trend of increasing encroachment of macroalgal species into the intertidal zones. This pattern was first described by Dawes et al. (1999) who compared intertidal algal abundance transects from 1964–1968 with the same transects repeated in 1995 and 1996 at the Content Keys in the western mouth of Florida Bay. Comparison of our data with those of Zischke (1973) and Stephenson and Stephenson (1950) indicate that algal species that were recorded as subtidal are now present in intertidal zones. Zischke's study at Pigeon Key, near W. Summerland Key, lists 20 species as only occurring in subtidal zones, nine of which we recorded in the intertidal. The Stephenson's study noted 16 subtidal algal species growing in "reef flat" areas adjacent to the intertidal, six of which we found growing in the intertidal. While increases in species abundances between the Stephenson's study and ours must be treated with caution for reasons mentioned above, the recognition of some of these species by the Stephensons, their appearance at multiple sites up to the yellow zone, together with literature support, is suggestive of an upward migration. The causes behind this shift are unknown but may be related to eutrophication of Florida Bay (Dawes et al., 1999; Lapointe et al., 2002) and nearshore eutrophication from development on the Florida Keys (Lapointe et al., 2004). However, in our study all intertidal zones at all keys, with the exception of Soldier Key, experienced additions of subtidal algae regardless of their orientation (i.e., oceanic or bay) or degree of human development. This may indicate that large-scale factors underlie algal zonation changes such as lowered herbivory or widespread increases in water column nutrients. Interestingly, the absence of notable algal abundance at uninhabited Soldier Key, may reflect its position at the mouth of Biscayne Bay, the most oligotrophic sector of this water body (Caccia and Boyer, 2005).

The occurrence in our quadrats of algal nutrient indicator genera may be the result of increased nutrient delivery to the intertidal at some sites. These algal species were in highest abundance at sites with the closest human development (within 10 m) and on keys with the highest human population densities (Lott et al., 1996). The appearance and high abundance of these species may be a recent phenomenon, as none of these species were noted by the Stephensons. Also, algal nutrient indicator species have appeared in Florida Bay intertidal sites in the last three decades (Dawes et al., 1999) and have appeared subtidally in association with nutrient enrichment around the world (Valiela et al., 1997), including the Florida Keys (Lapointe et al., 2004).

In summary, we found indications that change has occurred in the Florida Keys rocky intertidal environment over the 52 yrs separating the two studies. Aspects of change included the decreased abundance of plants and animals in the gray zone, the loss or decreased abundance of formerly common animal species, particularly within the gastropods, an upward shift of some subtidal algal taxa into the intertidal, and the occurrence of algae associated with eutrophic environments at most of the sites. While our results suggest anthropogenic factors are the driving force behind species composition changes, further work is needed to attribute direct causation in this often overlooked environment in the heavily studied Florida Keys.

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Literature Cited

Barnes, J. 1998. Florida hurricane history. University of North Carolina Press. 330 p.

Bryan, G. W. and P. E. Gibbs. 1991. Impacts of low concentrations of tributyltin (TBT) on marine organisms: a review. Pages 323–361 *in* M. C. Newman and A. W. McIntosh, eds. Metal ecotoxicology: concepts and applications. Lewis Publishers, Boston.

Butler, J. N., P. G. Wells, S. Johnson, and J. J. Manock. 1998. Beach tar on Bermuda: recent observations and implications for global monitoring. Mar. Poll. Bull. 36: 458–463.

Caccia, V. G. and J. N. Butler. 2005. Spatial patterning of water quality in Biscayne Bay, Florida as a function of land use and water management. Mar. Poll. Bull. 50: 1416–1429.

Calado, R., J. Jin, A. L. Rhyne, R. Araújo, and L. Narciso. 2003. Marine ornamental decapods-popular, pricey, and poorly studied. J. Crust. Biol. 23: 963–973.

Connell, J. H., T. P. Hughes, and C. C. Wallace. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol. Monogr. 67: 461–488.

Crowe, T. P., R. C. Thompson, S. Bray, and S. J. Hawkins. 2000. Impacts of anthropogenic stress on rocky intertidal communities. J. Aquatic Ecosyst. Stress and Recov. 7: 273–297.

Dawes, C. J., C. Uranowski, J. Andorfer, and B. Teasdale. 1999. Changes in the macroalga and zonation at the Content Keys, Florida. Bull. Mar. Sci. 64: 95–102.

Ellis, D. V. and L. A. Pattisina. 1990. Widespread neogastropod imposex: A biological indicator of global TBT pollution. Mar. Pollut. Bull. 21: 248–253.

Fotheringham, N. 1980. Effects of shell utilization on reproductive patterns in tropical hermit crabs. Mar. Biol. 55: 287–293.

Glynn, P. W. and M. W. Colgan. 1992. Sporadic disturbances in fluctuating coral reef environments: El Niño and coral reef development in the Eastern Pacific. Amer. Zool. 32: 707–718.

Hoffmeister, J. E. and H. G. Multer. 1968. Geology and origin of the Florida Keys. Geol. Soc. Amer. Bull. 79: 1487–1502.

Jones, D. A., J. Plaza, I. Watt, and M. Al Sanei. 1998. Long-term (1991–1995) monitoring of the intertidal biota of Saudi Arabia after the 1991 Gulf War oil spill. Mar. Pollut. Bull. 36: 472–489.

Lapointe, B. E. and M. Clark. 1992. Nutrient inputs from the watershed and coastal eutrophication in the Florida Keys. Estuaries 15: 465–476.

____________, M. M. Littler, and D. S. Littler. 1992. Modification of benthic community structure by natural eutrophication: the Belize barrier reef. Proc. 7th Int. Coral Reef Symp. 1: 323–343.

____________, D. A. Tomasko, and W. R. Matzie. 1994. Eutrophication and trophic state classification of seagrass communities in the Florida Keys. Bull. Mar. Sci. 54: 696–717.

____________, W. R. Matzie, and P. J. Barile. 2002. Biotic phase-shifts in Florida Bay and fore reef communities of the Florida Keys: linkages with historical freshwater flows and nitrogen loading from Everglades runoff. Pages 626–648 *in* J. W. Porter and K. G. Porter, eds. The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: an ecosystem sourcebook. CRC Press, Boca Raton.

____________, P. J. Barile, and W. R. Matzie. 2004. Anthropogenic nutrients enrichment of seagrass and coral reef communities in the Lower Florida Keys: discrimination of local versus regional nitrogen sources. J. Exp. Mar. Biol. Ecol. 308: 23–58.

Levins, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73: 1943–1967.

Littler, M. M. and S. N. Murray. 1975. Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. Mar. Biol. 30: 277–291.

López Gappa, J. J., A. Tablada, and N. H. Magaldi. 1990. Influence of sewage pollution on a rocky intertidal community dominated by the mytilid *Brachiodontes rodriguezi*. Mar. Ecol. Prog. Ser. 63: 163–175.

Lott, C., R. Dye, and K. M. Sullivan. 1996. Historical overview of development and natural history of the Florida Keys. Site characterization for the Florida Keys National Marine Sanctuary and environs. Vol. 3. The Preserver. Zenda, Wisconsin. 49 p.

Lubchenco, J. A. and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. Ecol. Monogr. 48: 67–94.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton. 192 p.

Maul, G. A. and D. M. Martin. 1993. Sea level rise at Key West, Florida, 1846–1992; America's longest instrument record? Geophys. Res. Let. 20: 1955–1958.

Paul, J. H., J. B. Rose, S. Jiang, C. Kellogg, and E. A. Shinn. 1995. Occurrence of fecal indicator bacteria in surface waters and the subsurface aquifer in Key Largo, Florida. Appl. Env. Microbiol. 61: 2235–2241.

Reyes, E. and M. Marino. 1991. Diel dissolved oxygen dynamics and eutrophication in a shallow well-mixed topical lagoon (Cancun, Mexico). Estuaries 14: 372–381.

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.

Southward, A. J. 1982. An ecologist's view of the implications of the observed physiological and biochemical effects of petroleum compounds on marine organisms and ecosystems. Philos. Tran. R. Soc. B 297: 241–255.

Sprott, P. 1998. The International Long Term Ecological Research Network. US LTER Network Publishing, Albuquerque. 109 p.

Stephenson, T. A. and A. Stephenson. 1950. Life between tide-marks in North America. I. The Florida Keys. J. Ecol. 38: 345–402.

Strong, A. M. and G. T. Bancroft. 1994. Patterns of deforestation and fragmentation of mangrove and deciduous seasonal forests in the upper Florida Keys. Bull. Mar. Sci. 54: 795–804.

Valiela, I., J. McClelland, J. Hauxwell, P. J. Behr, D. Hersh, and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnol. Oceanogr. 45: 1105–1118.

Wunderlin, R. P. 1998. Guide to the vascular plants of Florida. University of Florida Press, Gainesville. 806 p.

Zieman, J. C. 1999. Seagrass die-off in Florida Bay: long term trends in the abundance and growth of Turtle Grass, *Thalassia testudinum*. Estuaries 22: 460–470.

Zischke, J. A. 1973. An ecological guide to the shallow-water marine communities of Pigeon Key, Florida. St. Olaf College, Northfield. 46 p.

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Appendix I. Vascular plants found in the white zone at Crawl I, Crawl II, Plantation (Plant), Soldier, Vaca, and W. Summerland (WS) Keys in 1999. Abundance: *present, **common, ***dominant

	Location					
Species	Crawl I	Crawl II	Plant	Soldier	Vaca	WS
Acacia choriophylla Benth., (1842)						*
Anacardiaceae Pistacia simaruba L., 1753						*
Avicennia germinans (L.) Stearn, 1958		*	**	**	**	**
Batis maritima L., 1759		**		***		**
Bidens pilosa L., 1753 exotic						**
Blutaparon vermiculare (L.) Mears, 1982				**		
Blutaparon vermiculare (L.) Mears, 1982		*			**	*
Borrichia arborescens (L.) DC.	*	**		**	**	
Borrichia frutescens (L.) DC., 1836					**	
Canavalia rosea (Sw.) DC., 1825				*		
Casuarina equisetifolia L., 1759 exotic	***				**	*
Coccoloba uvifera (L.) L.	*				*	
Cocos nucifera L., 1753 exotic	**				*	
Conocarpus erectus L., 1753		**			**	**
Distichlis spicata (L.) Greene, 1887		**				*
Euphorbia heterophylla L., 1753				*		*
Fimbristylis cymosa R. Br., 1810 exotic		**				*
Heliotropium curassavicum L., 1753		*		*		*
Hymenocallis latifolia (P. Mill.) M. Roemer, 1847				*		
Ipomoea pes-caprae (L.) R. Br., 1816				**		
Laguncularia racemosa Gaertn. f., 1805		**	*	**	***	***
Melanthera nivea Small, 1903				*		
Monanthochloe littoralis Engelm., 1859		**				
Musa sp. exotic	*					
Panicum amarum Ell., 1816						*
Rhizophora mangle L., 1753	**	**	*	**	*	**
Sabal palmetto (Walt.) Lodd. ex J. A. and J. H. Schultes, 1830					*	
Salicornia bigelovii Torr., 1858	*	*		*		
Sarcocornia perennis (P. Mill.) A. J. Scott, 1978		***			**	
Serenoa repens (Bartr.) Small, 1926					*	
Sporobolus virginicus (L.) Kunth, 1829						
Suaeda linearis (Ell.) Moq., 1840		**			**	**
Suriana maritima L., 1753		**	**		**	
Thespesia populnea (L.) Soland. ex Correa, 1807 exotic			*			*
Vitex trifolia L., 1753 exotic	**					

lant), Soldier,
**dominant

Vaca	WS
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Appendix II. Algae and animal species found in each color zone for Crawl I, Plantation, Soldier, Vaca, and W. Summerland Keys combined. Values for all algal species and animal species marked with "*" are average coverage per m^2. Values for all other animal species are average number of individual m^{-2}. Total area sampled in each zone was 18.75 m^2 over all locations.

	Zone				
	White	Gray	Black	Yellow	LP
Filamentous Cyanobacteria			0.010		0.056
Chlorophyta					
Acetabularia crenulata Lamouroux, 1816					0.001
Anadyomene stellata (Wulfen) C. Argardh, 1823				0.005	
Batophora oerstedi Agardh, 1854				0.001	0.006
Bryopsis spp.				0.003	0.001
Caulerpa cupressoides (West in Vahl) C. Agardh, 1817					0.017
Caulerpa mexicana (Sonder ex Kuet.) J. Ahardh, 1849					0.001
C. racemosa (Forsskål) J. Agardh, 1873					0.003
Chaetomorpha spp.			0.001		
Cladophora spp.			0.001	0.004	0.003
Cladophoropsis sp.				0.007	0.009
Codium repens P. and H. Crouan ex Vickers, 1905					0.006
Derbesia spp.				0.009	0.003
Dictyosphaeria cavernosa (Forsskål) Børgesen, 1932				0.009	0.011
Ulva spp.				0.006	0.007
Halimeda incrassata (Ellis) Lamouroux, 1816					0.001
Halimeda opuntia (Linnaeus) Lamouroux, 1816					0.009
Halimeda tuna (Ellis and Solander) Lamouroux, 1816					0.008
Neomeris annulata Dickie, 1874				0.012	0.003
Penicillus capitatus Lamarck, 1813					0.007
Udotea conglutinata (Ellis and Solander) Lamouroux, 1816					0.001
Rhodophyta					
Acanthophora spicifera (Vahl) Børgesen, 1910					0.010
Amphiroa fragilissima (Linnaeus) Lamouroux, 1816					0.008
Bostrychia spp.	0.002		0.007	0.123	0.027
Callithamnion spp.					0.0001
Catanella caespitosa (Withering) Irvine, 1976				0.002	
Centroceras clavulatum (C. Agardh) Montagne, 1846				0.011	0.006
Ceramium spp.			0.000	0.053	0.015
Chondria spp.				0.001	
Galaxaura spp.				0.001	0.004
Herposiphonia secunda (C. Agardh) Ambronn, 1880			0.011	0.004	0.005
Hypnea cervicornis J. Agardh, 1851					0.010
Hypnea muciformis (Wulfen in Jacquin) Lamouroux, 1813					0.031
Laurencia papillosa (C. Agardh) Greville, 1830				0.007	0.006
L. intricata Lamouroux, 1813					0.001
Lophosiphonia spp.				0.011	0.003
Murrayella periclados (C. Agardh) F. Schmitz, 1893			0.001		
Polysiphonia spp.			0.004	0.019	0.039

Appendix II. Continued.

	Zone				
	White	Gray	Black	Yellow	LP
Phaeophyta					
Dictyota spp.					0.0004
Padina spp.					0.009
Sargassum spp.			0.027		0.015
Stypopodium zonale (Lamouroux) Papenfuss, 1940					0.003
Porifera					
**Chondrilla nucula* Schmidt, 1862					0.027
*Porifera Species A (orange)					0.005
*Porifera Species B (purple)					0.001
Cnidaria: Anthozoa					
**Siderastrea radians* (Pallas, 1766)					0.011
**Zoanthus sociatus* (Ellis and Solander, 1786)				0.003	0.005
Crustacea: Cirripedia					
Chthamalus angustitergum (Pilsbry) no date given			3.680	25.440	0.533
Tetraclita stalactifera (Lamarck), 1818				1.387	4.267
Crustacea: Anomuridae					
Clibanarius tricolor (Gibbes, 1850) / *Calcinus tibicen* (Herbst, 1791)				12.320	1.707
Crustacea: Decapodoa					
Geograpsus lividus H. Milne-Edwards, 1837			0.053	2.187	
Sesarma cinereum (Bosc, 1802)			0.053		
Uca spp.					0.053
Crustacea: Isopoda					
Ligia spp.	0.160	0.213	0.373	0.320	0.160
Mollusca: Gastropoda					
Batillaria minima (Gmelin, 1791)		0.160	24.800	50.347	6.133
Cantharus tinctus (Conrad, T. A., 1846)				0.053	0.053
Cenchritis muricatus (Linnaeus, 1758)	3.787		0.427		
Cerithium lutosum Menke, 1828					0.053
Columbella mercatoria (Linnaeus, 1758)					0.427
Detracia bulloides (Montagu, 1808)	5.067				
Echininus nodulosus (Pfeiffer, 1839)	0.053				
Fissurella spp.				0.053	
Lithopoma americanum (Gmelin, 1791)					0.160
Thais deltoidea (Lamarck, 1822)				0.213	0.053
Melampus coffeus (Linnaeus, 1758)	0.053				
Mitrella ocellata (Gmelin, 1791)					0.160
unidentified limpet			0.213	0.373	
Nerita peloronta Linnaeus, 1758			0.907	0.160	
Nerita tessellata Gmelin, 1791			0.640	1.760	
Nerita versicolor Gmelin, 1791			8.533	0.320	
Nodilittorina ziczac (Gmelin, 1791)	0.107		0.107	0.053	

Yellow	LP
	0.0004
	0.009
	0.015
	0.003
	0.027
	0.005
	0.001
	0.011
0.003	0.005
25.440	0.533
1.387	4.267
12.320	1.707
2.187	
	0.053
0.320	0.160
50.347	6.133
0.053	0.053
	0.053
	0.427
0.053	
	0.160
0.213	0.053
	0.160
0.373	
0.160	
1.760	
0.320	
0.053	

Appendix II. Continued.

	Zone				
	White	Gray	Black	Yellow	LP
Planaxis lineatus (E. M. da Costa, 1778)			1.067		
Siphonaria alternata Say, 1826			0.053	0.533	
Siphonaria pectinata (Linnaeus, 1758)			0.107	0.320	
**Spiroglyptus irregularis* (d'Orbigny, 1842)				0.023	0.013
Strombus pugilis Linnaeus, 1758					0.107
Tegula fasciata (Born, 1778)					0.160
Trachypollia nodulosa (C. B. Adams, 1845)					0.053
Mollusca: Polyplacophora					
Acanthopleura granulata (Gmelin, 1791)				1.493	0.213
Mollusca: Bivalvia					
Brachidontes exustus (Linnaeus, 1758)				5.760	10.720
Isognomon alatus (Gmelin, 1791)				1.333	0.213
Pinctada imbricata Roding, 1798					0.053
Echinodermata: Echinoidea					
Echinometra lucunter (Linnaeus, 1758)					0.320
Lytechinus variegatus (Leske, 1778)					0.053