Subtidal community shifts in the western Strait of Juan de Fuca from kelp dominated systems to urchin barrens following sea star wasting disease

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Abstract

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Abstract

As the effects of climate change continue to induce environmental disturbances, it is important to understand how communities change in response. Research has established that environmental perturbations to the environment can result in community shifts. In this study, I describe shifts in kelp-dominated rocky reef systems associated with sea star wasting disease (SSWD). I used video transect data from five sites in the western Strait of Juan de Fuca collected over a 9-year period (2011-2019) to test whether community assemblages differed before and after the onset of SSWD. Results indicated significant temporal and spatial changes in community structures, with notable shifts occurring in 2016 at 4 of the 5 sites studied. Benthic communities at one site remained relatively unchanged over the study period. Marine mammal survey data indicates that sea otters (*Enhydra lutris*) are routinely present at this site, suggesting that the presence of sea otters can potentially dampen the effects of SSWD on subtidal communities.

Key Words

Sea star wasting, community ecology, kelp forest, keystone species, sea otter, urchin barren, climate change

Introduction

Shifts in marine communities occur when an ecosystem abruptly moves from one state, reinforced by a particular set of characteristics, to another (Rocha et al. 2015). Often, altered states are characterized by reduced resilience, decreased productivity, and loss of biodiversity (Carnell & Keough 2020, Rocha et al. 2015). While the theory around the topic of regime shifts has been a long standing discussion, general criteria to identify and define regime shifts has been difficult to solidify due to lack of understanding around the mechanistic drivers that induce changes as well as poor consensus around baseline states and system identity (van Putten et al. 2019, Conversi et al. 2015). However, there are two general perspectives concerning what drives shifts, the first being the "community perspective," which focuses on population ecology and changes in configurations of community assemblages, and the other the "ecosystem perspective," which focuses on how environmental perturbations affects ecosystems and the structure of their communities (Beisner 2013). Regime shifts have been documented in many marine ecosystems, including pelagic systems - often characterized by spatial shifts in single species (Conversi 2015), coral reefs - shifting from coral-dominated to algal-dominated states (Jouffray 2015, Bozec & Mumby 2015), and kelp forests that shift to urchin-dominated barrens characterized by crustose coralline algae and bare rock cover (Ling 2015, Filbee-Dexter & Scheibling, 2014). Here I adopt the community perspective to assess changes over time in high-latitude rocky reef ecosystems within the time period of two environmental disturbances - the 2013 outbreak of sea star wasting disease (SSWD) on the Pacific coast and the anomalous marine heatwave that affected the same region in 2014-15 (Rogers-Bennett & Catton 2019, Hewson et al. 2014).

Outbreaks of SSWD are known to cause widespread mortality of sea stars (Kohl 2016, Eisenlord 2016, Hewson 2014). Outbreaks have been reported over recent decades, with the first documented case described in the summer of 1978 in the Gulf of California (Pacificrockyintertidal.org, Dungan 1982). The cause of the most recent outbreak along the Pacific coast is not fully known, but the best explanation to date is provided by Hewson (2014), who links the outbreak to sea star-associated densovirus (SSaDV). This outbreak was first reported on the outer coast of British Columbia in the summer of 2013 and spread throughout the entire western coast of North America (Pacificrockyintertidal.org, Kohl 2016). Over 20 sea star species were affected, most notably the large predatory *Pycnopodia helianthoides*, or sunflower star, which showed an 80-100% decline in abundance between Alaska and California (Harvell et al. 2019). With the loss of an important mesopredator, it can be expected that cascading food web effects would potentially alter the existing community structure. A study by Burt et al (2018) examined the roles *P. helianthoides* and sea otters (*Enhydra lutris*), important predators and keystone species in this system, in controlling sea urchin abundance and kelp density on rocky reefs on the central coast of British Columbia. They found that the two predators target different urchin size classes, as indicated by an 89–98% decrease in the mean density of large urchins within 1 year of sea otters arriving at previously unoccupied sites. Consequently, the decline of *P. helianthoides* also coincided with a decrease of small and medium sized urchins. Looking specifically at urchins in the medium size class, the authors reported a 311% increase in mean density in the two years following SSWD, regardless of sea otter presence, coupled with a 30% decrease in kelp densities at the study sites. A community has greater resiliency when there is simultaneous presence of an apex predator and mesopredator; when one of these is lost, there is increased probability of a shift in community structures. In this case, the ecosystem shifted away from a kelp-dominated state toward an urchin barren (Burt et al. 2018).

Urchin barrens, which result from overgrazing of macroalgae by urchins after the loss of a top-down control (ie., predation), are associated with low primary productivity and low food-web complexity compared to the alternate state of kelp and understory algae ecosystems (Filbee-Dexter & Scheibling, 2014). A consequence of this regime shift from productive kelp-dominated rocky reefs to urchin barrens is a loss of ecosystem services typically provided by kelp forest ecosystems, including carbon storage, regulating water quality, habitat for biodiverse species assemblages and commercial species for harvest, ecotourism and recreation (Gundersen 2016).

In this study, I tested the hypothesis that SSWD altered the species-habitat associations and community structure of kelp ecosystems in the western Strait of Juan de Fuca, inducing a shift from a kelp-dominated system to an urchin barren.

Materials and Methods

Study Area

Five sites in the western Strait of Juan de Fuca, Washington have been surveyed annually by SCUBA divers every August since 2005 (Figure 1). Surveys are conducted along a 100 meter continuous transect and recorded using a forward-facing video camera with the operator swimming about one meter off the bottom of the sea floor and one meter off a vertical reef of varying heights from 3-7 meters. The 100 meter transect was videotaped in two separate 50 meter sections in opposite directions, facilitating us to divide it into two 50 meter portions, each treated as separate independent samples in the analysis for more power. Due to upgrades in video camera technology in 2011 that significantly improved the footage quality in more recent years, I restricted analyses to videos taken from 2011 to 2019.

Data Collection & Video Transect Analysis

Benthic cover was analyzed by using the open source software CoralNet (coralnet.uscd.edu, Beijbom et al., 2015). This program is an online point-count application that allows unbiased estimates of benthic cover and diversity. While CoralNet allows for automatic annotation through machine learning techniques, I chose to identify taxa manually to ensure accuracy.

Twenty evenly spaced screenshots were taken along each 50 meter video transect, for a total of 3,738 photos used for this analysis. Within CoralNet, 10 randomly distributed points in the lower 30% of the frame were sampled. Using the lower 30% of the frame focused data collection on benthos instead of open water. The video sampling was initially designed to count fish at these study sites, and hence slightly modified for the purposes of benthic data analysis.

Each screenshot was viewed and annotated with the taxon or substrate underlying each point. Eight categories of benthos were recorded: invertebrates, bare rock, algal mat, crustose coralline algae, encrusting red algae, fleshy algae (which includes kelp), other (identifiable taxon not included in list, often sand or open water), and unidentified (used when it was impossible to accurately place taxon in any above category) (Table 1). Percent cover estimates for each taxon were calculated and exported by CoralNet.

Analysis of motile taxa along each transect was conducted outside of CoralNet. Counts of individual identifiable sea stars (*Orthasterias koehleri, Dermasterias imbricata, Mediaster aequalis, Henricia leviuscula,* and *Pycnopodia helianthoides*) and urchins (*Echinoidea spp.*) were taken from the continuous video footage (Table 1). Due to varying quality of video footage, species identifications were not always possible for urchin species, which is why a higher order classification was employed.

Data Analysis

All calculations were performed in R (version 4.1.2; R Core Team 2020). The benthic data, derived from CoralNet, was adjusted to mean percent cover for each transect, while motile species were measured as absolute abundance. Bray-Curtis distance matrices were used for both types of response variables.

A hierarchical cluster analysis was conducted using Ward's minimum variance group linkage method (hclust, stats package). The analysis was based on the sea star Bray-Curtis distance matrix to separate the data into two groups with similar sets of responses. I chose to use this method instead of determining groups *a priori* as "pre-SSWD" and "post-SSWD," to avoid bias in assigning groups.

Multivariate non-metric multidimensional scaling (NMDS) ordination techniques were used to visually assess the observations that had been partitioned into groups using the cluster analysis (metaMDS, vegan package). Both motile and benthic variables were included in this analysis, with three dimensions, 300 iterations, and a minimum of 40 and maximum of 100 new runs permitted to meet the convergence criteria.

A classical indicator species analysis was conducted to identify which sea star species was most strongly associated with the two groups that were identified in the cluster analysis (multipatt, indicspecies package).

Finally, a PERMANOVA test was used to assess the statistical significance of the results (adonis2, vegan package). Restricted permutations were necessary to mitigate issues of pseudoreplication inherent to a complex study design (Hurlbert 1984). This entailed both a whole plot analysis to examine the spatial variation within the dataset, as well as a split plot analysis to examine temporal variation. The whole plot analysis restricted permutations of years, while allowing free permutation of transects among sites, while the split plot did the opposite, restricting permutations of transects and allowing free permutation of years within each site. The model used for the whole plot analysis was $Y \sim Site + Transect$, and the model for the split plot analysis was $Y \sim Transect + Year + Site{:}Year$. For all variables of interest, the F-statistic and p-value were calculated manually, with the residual as the denominator for the test statistic.

Field sampling was not conducted at site 3 in 2016 due to poor underwater visibility; to balance the data for analysis, the observations recorded at that site in 2015 were duplicated. Consequently, it should be noted that the data for that year do not represent true field data and serve only as a placeholder for the purposes of a balanced dataset.

Results

Data Summary

A quick analysis of the data was performed to get a grasp of how sea star populations varied at each site throughout the study period, plotting absolute species abundance for each year at each site (Fig. 2). This showed a general decrease in species populations at the onset of SSWD (2013-2014) and a rise in a single species in the years following. At sites 1 through 4, the resurgent species was *Orthasterias koehleri*, rainbow star, whereas at site 5, *Henricia leviuscula*, blood star, became the dominant species following the peak of SSWD.

A similar analysis was done for the benthic environment, focusing on two of the main categories contained within that dataset - fleshy algae and crustose coralline algae, with averaged percent cover for each transect plotted across years (Fig. 3). This showed a decrease in fleshy macroalgae at sites 1 through 4, whereas macroalgae at site 5 remained relatively stable. Additionally, the absolute abundance of urchins was plotted to separately assess changes in population numbers (Fig. 4). Sites 1-4 showed large increases in urchin abundance, whereas site 5 did not experience the same population spike.

Hierarchical Cluster Analysis

The hierarchical cluster analysis yielded a dendrogram, from which the two largest groups were identified for later use in analysis, referred to as Group 1 and Group 2 (Fig. 5).

NMDS

An NMDS ordination was created and visualized in two ways to examine how the observations from the whole dataset were partitioned into Group 1 and Group 2, represented by the hulls. The stress for the resultant analysis is 0.091. The first visualization (Fig. 6) illustrates the data by clustering data around centroids based on the year that observation was made. Group 1 contains observations from years 2011 to 2016, as well as six distinct points from years 2017 to 2019. Group 2 contains 3 points from 2016 with the remainder of the observations within this group coming from years 2017 to 2019. Overall, this visualization shows strong division across time, indicating temporal variation in the dataset.

The second visualization shows the data grouped by site (Fig. 7). Sites 1 through 4 all span the two groups, whereas site 5 is fully contained within Group 1. This also explains the anomalous late-year points in the first ordination. A third NMDS ordination illustrates changes in sea star abundance between sites (Fig. 8). This visualization also shows Site 5 clustering apart from the other four and reports a stress of 0.1081.

Indicator Species Analysis

The results of the indicator species analysis identified *Pycnopodia helianthoides* as the indicator species for Group 1 (Indicator Value = 0.757, p-value = 0.005). Group 2 had no indicator species.

PERMANOVA

The results of the PERMANOVA (Table 2) indicated that the differences in community composition between sites and across years was significant (p = 0.001). The majority of the variation in the dataset (51.4%) was attributed to Year.

Discussion

The analysis indicated significant spatial and temporal variation in community composition over the study period. Figure 2 shows clear changes in abundance of the five most common sea star species at the study sites. Each site exhibited a large increase of a single species following the peak of SSWD; at sites 1-4 *Orthasterias koehleri* (rainbow star) increased in abundance, whereas at site 5 this increase was seen in *Henricia leviuscula* (blood star). Shifts in motile invertebrate communities were further illustrated in Figure 4, which summarizes change in urchin abundance at each site. Again, site 5 had unique differences, with little to no increase in urchin populations compared to sites 1-4, which had very large increases. Changes in the benthic environment are demonstrated in Figure 3, which visualized changes in percent cover of fleshy algae (kelp and understory macroalgae) and crustose coralline algae. As understory macroalgae is grazed, underlying crustose coralline algae becomes exposed. Simplifying the benthic substrate categories to just these two allows for clear interpretation of changes in benthos. Sites 1 and 3 had the most severe declines of fleshy algae and, inversely, increases of crustose coralline algae. Sites 2 and 4 followed a similar but less drastic trend. Site 5, however, maintained fairly consistent coverage of fleshy algae.

Using Group 1 and Group 2 (Fig. 5) as proxies for “pre-SSWD” and “post-SSWD”, respectively, we can see from the first NMDS ordination (Fig. 6) how the dataset was divided in 2016, with observations from that year appearing in both Group 1 and Group 2. The second NMDS (Fig. 7) visualized the spatial variation in the dataset, showing sites 1 through 4 spanning the two groups, indicating that the communities at these sites experienced a shift over the study period. Site 5 on the other hand remained fully contained within Group 1, indicating that the community composition at that site remained relatively unchanged.

The results of the indicator species analysis that identified *P. helianthoides* as the indicator species for Group 1 is consistent with field observations (Harvell et al. 2019) and suggests that the use of the two groups as proxies for pre- and post-SSWD is valid. This important predator was one of the asteroid species most affected by the SSWD epidemic; the population has declined by 90% and is now classified as critically endangered (IUCN 2021). There is an increasing awareness that sea stars play an important role consuming sea urchins and as mesopredators play an important and perhaps keystone species role in the control of sea urchins, particularly smaller sea urchin size classes (Burt et al. 2018). This is particularly evident in kelp forest ecosystems where other keystone species such as apex predators like sea otters are also absent such as is the case in northern California, Oregon and parts of the Aleutian Island chain in Alaska resulting in increased vulnerability of kelp forests worldwide (Krumhansl et al. 2016; Ling et al. 2009; Rasher et al. 2020).

Differences between site 5 and the other four sites suggest other mechanisms at play. The stabilizing factor at this site is unknown, but we can hypothesize it can be attributed to the presence of sea otters, as previous marine mammal surveys and observations have documented sea otters persistently occupying this site (Hale et al. 2019). It has been documented widely throughout the north Pacific, from the Aleutian Island chain to California that sea otters are keystone species in kelp forest ecosystems providing top-down control on urchin abundances - a classic trophic cascade that occurs in nearshore rocky areas where sea otters are present, preventing overgrazing of macroalgae (Estes & Palmisano 1974; Watson & Estes 2011).

Sea otters exert profound trophic effects upon temperate rocky-reef ecosystems via consumption of invertebrate prey. In contrast to all other marine mammals, the lack of significant adipose tissue requires an extremely high metabolism and caloric supply to balance the thermoregulatory costs of living in a temperate marine environment. This translates to a voracious appetite, and sea otters are capable of consuming 20-30% of their body weight a day, with the average Northern sea otter weighing 70 (female) to 90 (male) pounds (Hale et al. 2019). The indirect effects of such strong and direct consumer-resource interactions ripple throughout the benthos, and in locations where sea otters are the primary means of regulating populations of herbivorous sea urchins such as the Aleutian Islands and parts of British Columbia, Canada, sea otter presence or absence is the difference between a diverse, productive, and healthy kelp forest or a species depauperate state of urchin-barrens (Estes & Duggins 1995; Watson & Estes 2011).

While the consumer-resource interactions driven by sea otter foraging are reasonably well understood, the notion that sea otters might mitigate some of the negative ecological effects of climate change remains uncertain, but is an idea gaining traction (Wilmers et al. 2012). Sea otters clearly cannot affect the creation or strength of a large-wave or an anomalous warm-water event, but perhaps they may limit some of the negative ecological consequences that would otherwise occur in their absence. A recent study in the Aleutian Archipelago found that in locations lacking sea otters, *Clathromorphum* spp. beds (slow-growing calcareous algae) were structurally weakened by increasing ocean acidification and thus were more susceptible to sea urchin grazing (Rasher et al. 2020). A concomitant warm-water event increased the rate at which sea urchins grazed upon the weakened algae—the net effects of the two physical variables channeled through sea urchin grazing decimated the *Clathromorphum* spp. beds. The authors argued that if sea otters had been present to regulate sea urchin abundance and behavior, such a loss could have been avoided or significantly mitigated (Rasher et al. 2020).

Another area for further exploration concerns the anomalous marine heatwave that began in early 2014 and persisted through August 2016 (Gentemann 2017). The co-occurrence of this event with SSWD, which is exacerbated by increased temperatures (Harvell 2019), confounds our ability to meaningfully attribute the shifts in community structure to a single environmental disturbance event. However, since all five study sites were in relatively close proximity, within a few kilometers of each other, it is likely that they were all similarly impacted by the temperature increases.

While these co-occurring events hinder our ability to make definitive conclusions regarding the cause of the observed shifts among benthic communities in the western Strait of Juan de Fuca, the results of this analysis show that shifts occurred, nonetheless. Understanding how benthic communities in this region respond to perturbations can help managers and others anticipate the ecological consequences of environmental disturbances and long-term change.

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Figures

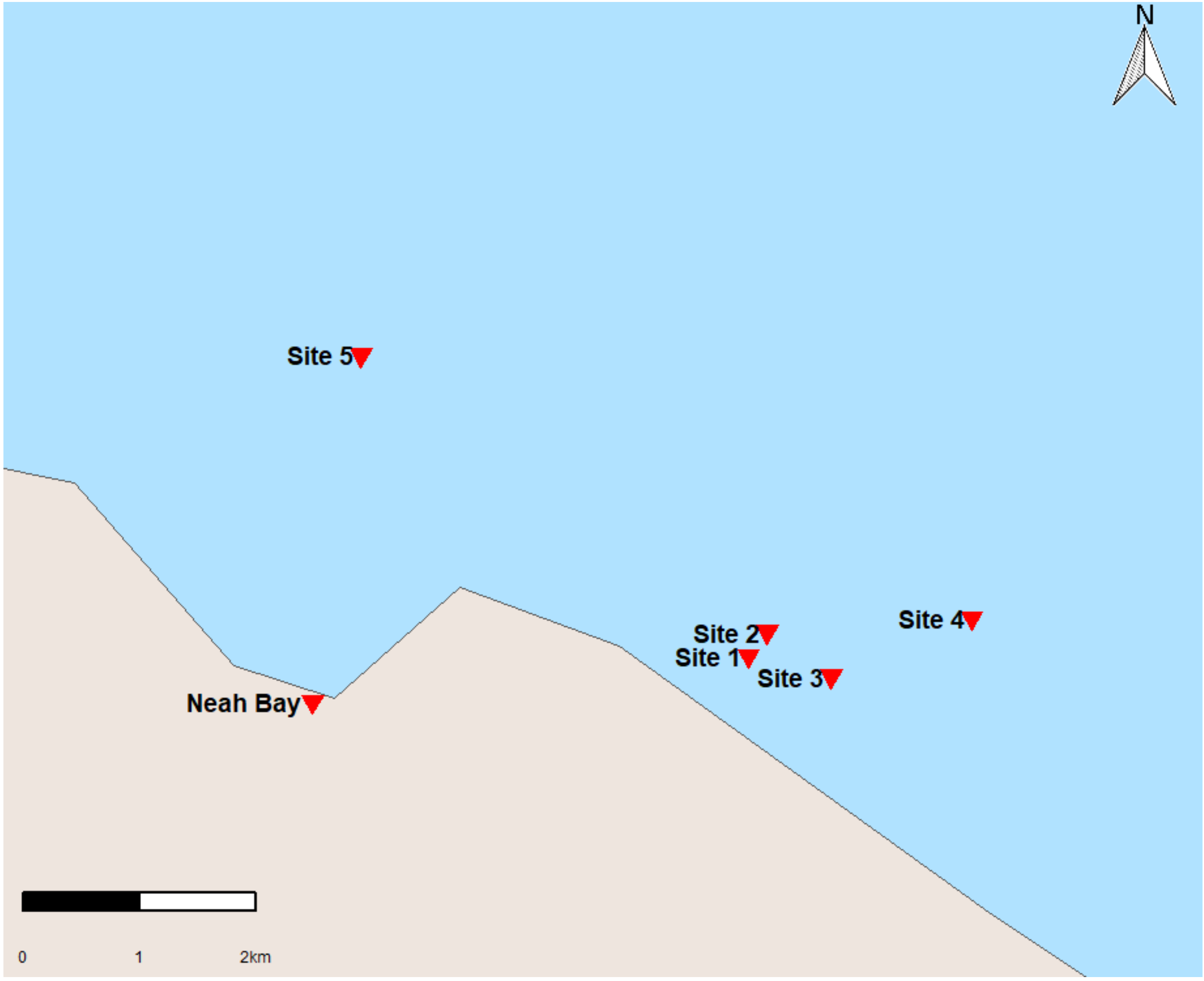


Figure 1. Five annual survey sites in Western Strait of Juan de Fuca, in the waters of Neah Bay, WA.

Figure 2. Sea star abundance at each of 5 study sites throughout the study period (2011-2019).

Figure 3. Percent cover of fleshy algae and crustose coralline algae over study period (2011-2019).

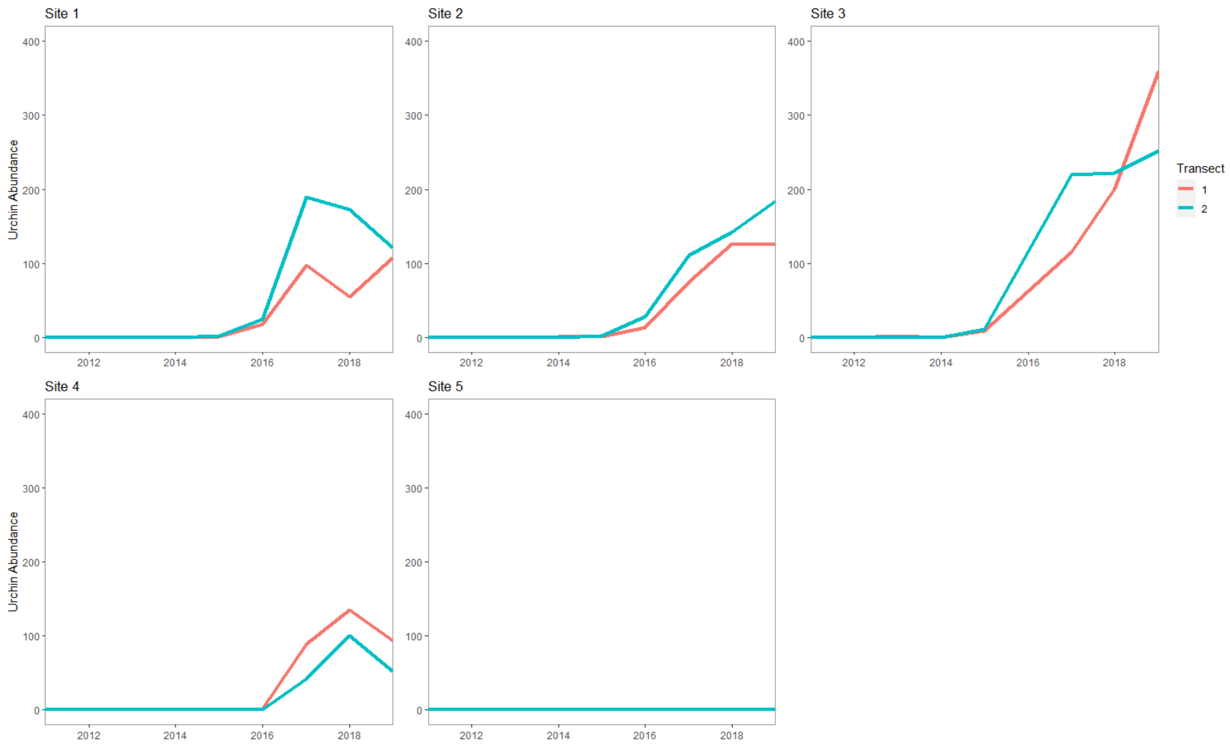


Figure 4. Sea urchin abundance over study period (2011 to 2019) at each study site. Sites 1-4 showed large increases of urchin numbers post-SSWD. Site 5, however, did not show an increase on this scale.

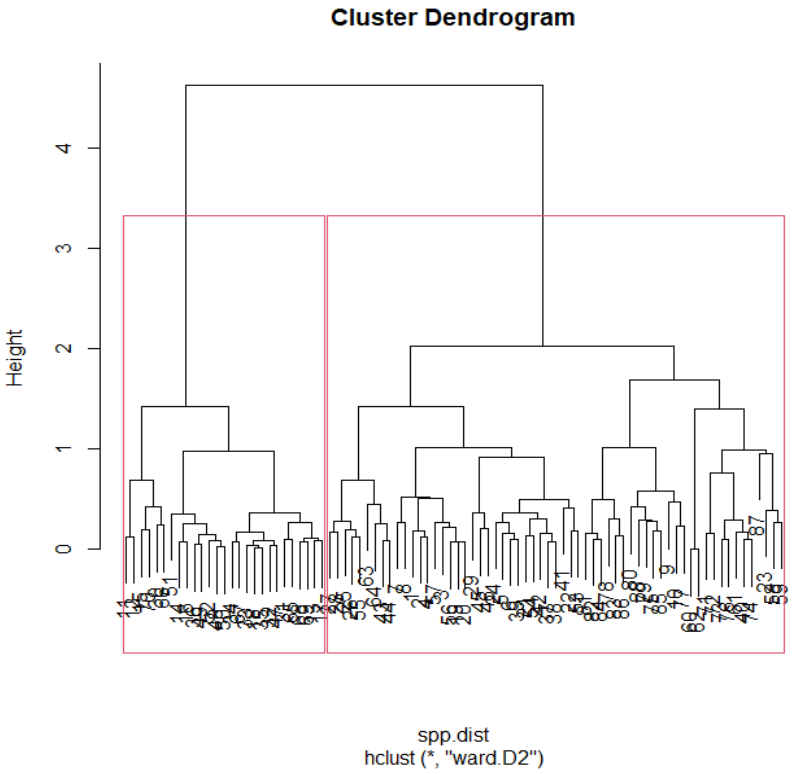


Figure 5. Dendrogram based on sea star Bray-Curtis distance matrix, indicating two distinct groups.

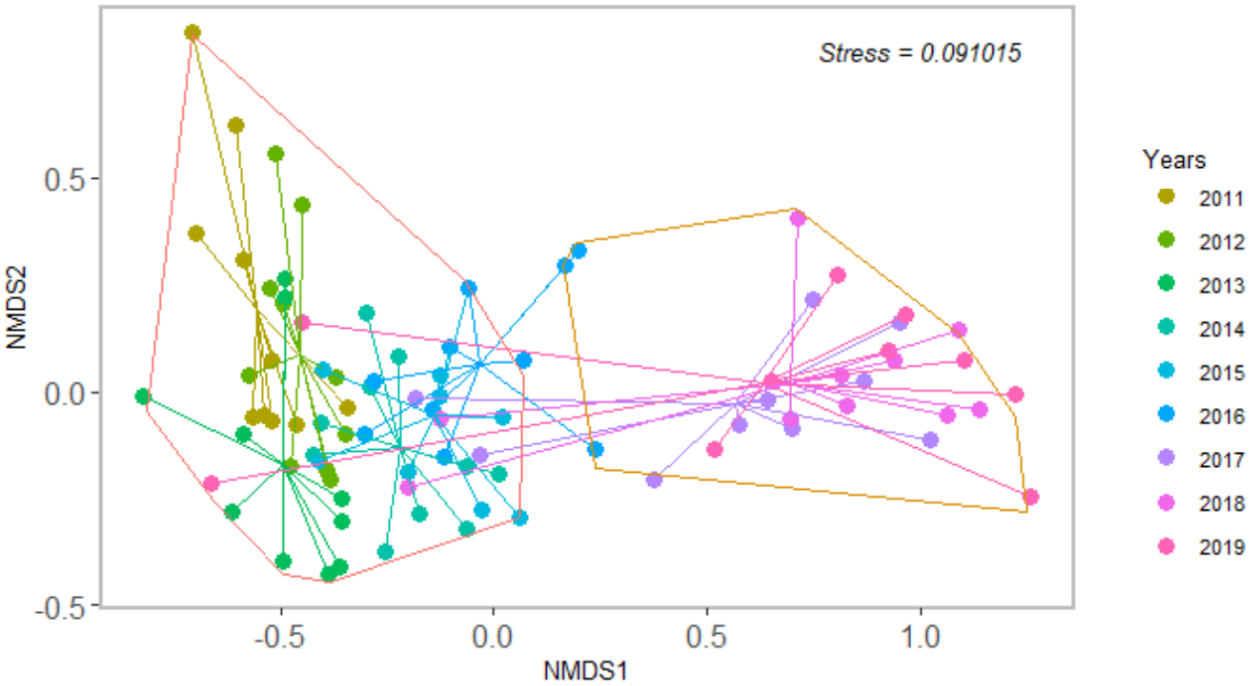


Figure 6. NMDS ordination visualizing observations by the year from which they came. The hull on the left is Group 1 and the right hull is Group 2.

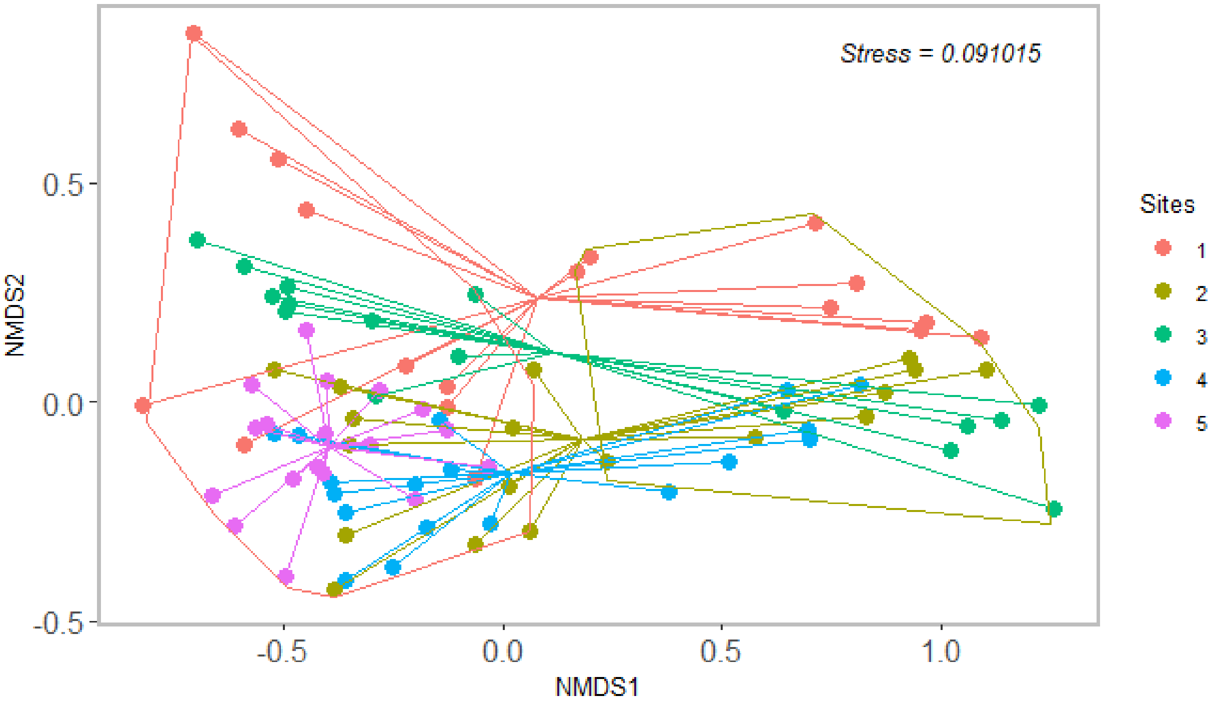


Figure 7. NMDS ordination visualizing observations by the site from which they came. Sites 1-4 span both groups, whereas site 5 is fully contained within Group 1.

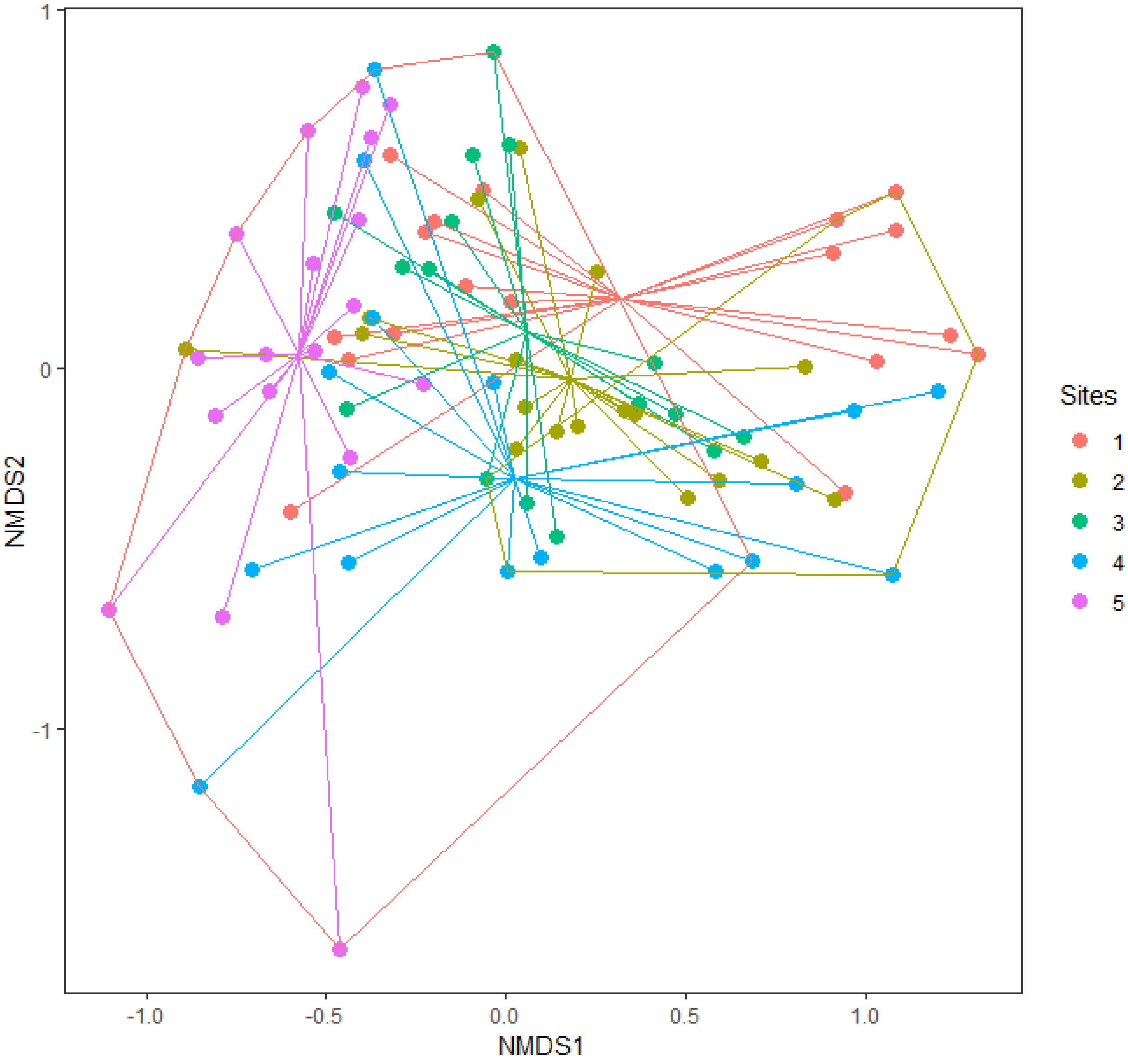
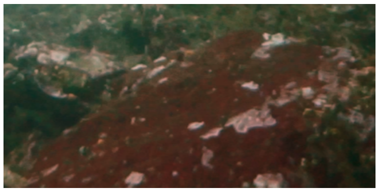
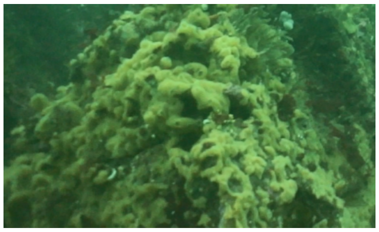


Figure 8. NMDS ordination visualizing changes in sea star abundance at each site. Sites 1-4 span across groups, whereas Site 5 is fully contained within the left hull. Stress = 0.1080555.

Tables

Table 1. Taxa identified in analysis of community assemblages.

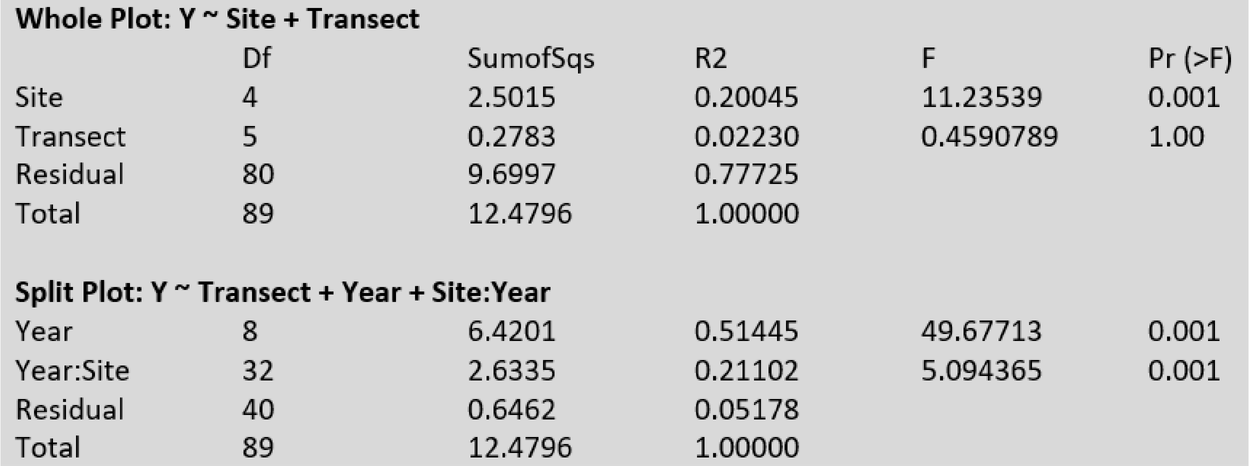
	Categories	Photo Description
Benthic Substrates (averaged percent cover)	Fleshy Algae	
	Algal Mat	
	Crustose Coralline Algae	
	Encrusted Red Algae	

	Bare Rock	
	Invertebrates	 *Metridium senile*  *Porifera*
	Other	 sand/pebbles  open water

	Unidentified	
Motile Species (absolute abundance)	*Echinoidea spp.* Sea Urchins	
	Orthasterias koehleri Rainbow Star	
	Dermasterias imbricata Leather Star	
	Mediaster aequalis Vermillion Star	

	Henricia leviuscula Blood Star	
	Pycnopodia helianthoides Sunflower Seastar	

Table 2. ANOVA table with whole plot and split plot analysis results from PERMANOVA test. The response variable for both models includes both motile taxa and benthic substrates.



Whole Plot: Y ~ Site + Transect					
	Df	SumofSqs	R2	F	Pr (>F)
Site	4	2.5015	0.20045	11.23539	0.001
Transect	5	0.2783	0.02230	0.4590789	1.00
Residual	80	9.6997	0.77725		
Total	89	12.4796	1.00000		
Split Plot: Y ~ Transect + Year + Site:Year					
Year	8	6.4201	0.51445	49.67713	0.001
Year:Site	32	2.6335	0.21102	5.094365	0.001
Residual	40	0.6462	0.05178		
Total	89	12.4796	1.00000		