Intertidal Community Dynamics Report

Oregon Department of Fish and Wildlife
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Published 2022

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Suggested Citation

Gravem S.A., B.A. Menge, L. Aylesworth. Intertidal Community Dynamics Report. 2022. Oregon Department of Fish and Wildlife Marine Resources Program. Newport, OR. https://ecologyreports.oregonmarinereserves.com/Data_Files/7.%20Collaborations/Intertidal%20Community%20Dynamics_Final.pdf

1 Introduction

The Pacific Northwest is famous for its abundance and diversity of intertidal life, and its tidepools attract tourists from all over the world. Many of Oregon's intertidal species are well-studied, and a legacy of long-term intertidal sites established by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) has enabled a fairly deep understanding of these communities and their dynamics (reviewed by Menge et al. 2019). Nowhere is this more true than in Cape Perpetua Marine Reserve, where B. Menge and colleagues have been working since the 1970s at their Strawberry Hill site. In 2015, the ODFW Marine Reserves team and PISCO began collaborating with PISCO to monitor in rocky intertidal habitats along the Oregon Coast. We integrated the Marine Reserves Otter Rock and Cascade Head into PISCO's long-term sea star surveys in 2015, and added whole-community surveys in 2017. Rocky intertidal habitat does not occur within the Redfish Rocks Marine Reserve, and the Cape Falcon Marine Reserve intertidal habitat is inaccessible, so these reserves were not included. Already-established PISCO sites at Fogarty Creek, 9.5 km north of Otter Rock Marine Reserve and Tokatee Klootchman, 4.8 km south of Cape Perpetua Marine Reserve, were also selection as Comparison Areas near their respective reserves (there was no suitable Comparison Area outside Cascade Head Marine Reserve).

The timing of the new collaboration in 2017 was intentional; the 2014 outbreak of sea star wasting disease (SSWD) in Oregon caused widespread and severe declines in the keystone predatory sea star *Pisaster ochraceus* (58-84% declines, Menge et al. 2016). According to the keystone predation hypothesis, which was developed in experiments in coastal Washington (Paine 1966, 1969, 1980), *P. ochraceus* increases the biodiversity of the intertidal community by eating the competitively-dominant and bed-forming mussel *Mytilus californianus*, thereby freeing space for other species like algae, barnacles, sea anemones and sea urchins to have space to live. Thus, decline of *P. ochraceus* due to SSWD was hypothesized to cause a widespread takeover by mussel beds, a decrease in abundance of several taxa, and an overall decline in biodiversity in the Marine Reserves and elsewhere (Menge et al. 2016). *By collaborating, we examined whether low intertidal zone community structure, key functional groups, and biodiversity varied firstly among the three Marine Reserves and two nearby Comparison Areas, and secondly over time as the repercussions of SSWD were expected to occur.*

We paired these surveys of intertidal communities with sea star population assessments and more detailed investigations of mussel bed dynamics, which we cover in detail in *Intertidal Sea Stars* and *Mussel Bed Dynamics*. Briefly, we found that SSWD caused substantial declines of *P. ochraceus* populations at all Reserves and Comparison Areas, that sea star populations rebounded quickly at Cape Perpetua Marine Reserve and are nearly recovered, that they have not recovered at Otter Rock

Marine Reserve, and that they may be recovering at Cascade Head Marine Reserve. But, despite the decline in sea stars, mussel bed cover has not substantially increased nor have beds moved seaward at any Marine Reserve nor Comparison Area. *Here, we investigate how intertidal communities vary among Marine Reserves and Comparison Areas, and whether SSWD has had discernible impact on these communities, as the keystone predation hypothesis would suggest.*

1.2 Research Questions

1. How do low zone intertidal communities vary with respect to a) community structure, b) key functional groups, and c) biodiversity among Marine Reserve and Comparison Areas?

2. How have low zone intertidal communities responded to SSWD with respect to a) community structure, b) key functional groups, and c) biodiversity in Marine Reserve and Comparison Areas?

1.3 Hypotheses

1. a) Intertidal low zone community structure should vary substantially among Marine Reserves, but Comparison Areas should be similar to their respective Marine Reserve since local oceanography is a major drive of community patterns (Menge et al. 2015).

   b) Based on established regional patterns (Menge et al. 2015) sessile intertidal invertebrates should dominate Cape Perpetua Marine Reserve, primary producers should dominate Otter Rock, and at Cascade Head both groups should coexist. .

   c) Biodiversity should be highest at Cape Perpetua, where abundant sea stars should act as keystone predators and free up space for many taxa.

2. a) Low intertidal zone community structure should change after sea star wasting disease and changes should be more drastic in areas with currently fewer sea stars (Otter Rock and perhaps Cascade Head Marine Reserves).

b) The functional groups eaten by sea stars, particularly mussels, should increase after SSWD, then decrease in areas where sea stars have begun to recover (Cape Perpetua and perhaps Cascade Head).

c) Biodiversity should decrease after SSWD, then increase where sea stars have begun to recover (Cape Perpetua and perhaps Cascade Head).

2 Methods

2.1 Data Collection

Intertidal communities were surveyed yearly since 2015 in Cape Perpetua Marine Reserve, Tokatee Klootchman and Fogarty Creek Comparison Areas and since 2017 in Otter Rock and Cascade Head Marine Reserves (Table 1, see Intertidal Methods Fig. 1 for map). To survey, we used the vertical transect method described in detail in Intertidal Methods. Briefly, we surveyed 5 vertical transects yearly at each area placed at fixed locations from the low to high intertidal, each spanning a mussel bed. Along each transect, we took photoquadrats (0.5m x 0.5m) every 0.5m and analyzed the percent cover of taxa to the lowest identifiable taxonomic level from photos (Table 2). For this report, we analyzed low intertidal zone photoquadrats only since we expect those communities in particular to be transitioning from multi-species to mussel-dominated after SSWD.

Table 1. Number of intertidal community transects surveyed in each Marine Reserve and Comparison Area between 2015 and 2019.

Area	Year	Number of Transects
Cape Perpetua Marine Reserve	2015	5
	2016	5
	2017	5
	2018	5
	2019	5
Tokatee Klootchman Comparison Area	2015	5
	2016	3
	2017	2
	2018	5
	2019	5
Otter Rock Marine Reserve	2017	5
	2018	5
	2019	5
Fogarty Creek Comparison Area	2015	4
	2016	5
	2017	5
	2018	5
	2019	5
Cascade Head Marine Reserve	2017	5
	2018	4
	2019	4

Table 2. The lowest taxon identified, functional groupings, and trophic roles of taxa surveyed in intertidal community photoquadrats.

Lowest Taxon Identified	**Functional Group**	**Trophic Role**	**Lowest Taxon Identified**	**Functional Group**	**Trophic Role**
Bare Space	Bare space	Bare Space	*Phyllospadix spp.*	Surf grass	Primary Producer
Pisaster ochraceus	*Pisaster*	Predators	Algal crusts	Algal crusts	Primary Producer
Leptasterias spp.	*Leptasterias*	Predators	Diatoms	Algal crusts	Primary Producer
Nucella canaliculata	Predatory molluscs	Predators	Other Green algae	Green algae	Primary Producer
Nucella ostrina and emarginata	Predatory molluscs	Predators	*Ulva spp.*	Green algae	Primary Producer
Mytilus spp.	Mussels	Sessile Prey	Fucoid algae	Fucoids	Primary Producer
Pollicipes polymerus	Gooseneck barnacles	Sessile Prey	Brown understory algae	Kelps	Primary Producer
Large barnacles	Large barnacles	Sessile Prey	*Egregia menziesii*	Kelps	Primary Producer
Tetraclita rubescens	Large barnacles	Sessile Prey	*Lessoniopsis littoralis*	Kelps	Primary Producer
Small barnacles	Small barnacles	Sessile Prey	Other kelps	Kelps	Primary Producer
Chitons	Herbivorous molluscs	Mobile Prey	*Postelsia palmaeformis*	Kelps	Primary Producer
Limpets	Herbivorous molluscs	Mobile Prey	*Saccharina sessilis*	Kelps	Primary Producer
Littorina spp.	Herbivorous molluscs	Mobile Prey	Articulated coralline algae	Corallines	Primary Producer
Other gastropods	Herbivorous molluscs	Mobile Prey	Coralline algae crusts	Corallines	Primary Producer
Lottia giganteus	Herbivorous molluscs	Mobile Prey	*Constantinea simplex*	Red understory algae	Primary Producer
Tegula funebralis	Herbivorous molluscs	Mobile Prey	*Cryptopleura ruprechtiana* and *Hymenena setchellii*	Red understory algae	Primary Producer
Sea urchins	Urchins	Non-prey	*Dilsea californica*	Red understory algae	Primary Producer
Anthopleura spp.	Anemones	Non-prey	*Endocladia muricata*	Red understory algae	Primary Producer
Phragmatapoma californica and Sabellidae	Worms	Non-prey	Fine branching reds	Red understory algae	Primary Producer
Worms	Worms	Non-prey	*Mastocarpus papillatus* and *M. jardinii*	Red understory algae	Primary Producer
Bryozoans	Other Inverts	Non-prey	*Mazzaella parksii*	Red understory algae	Primary Producer
Crabs	Other Inverts	Non-prey	Other red blades	Red understory algae	Primary Producer
Other echinoderms	Other Inverts	Non-prey	Other red turfs	Red understory algae	Primary Producer
Other sessile inverts	Other Inverts	Non-prey	*Pyropia spp.*	Red understory algae	Primary Producer
Sponges	Other Inverts	Non-prey	*Mazzaella flaccida* and *M. splendens*	Red canopy algae	Primary Producer
Tube worms	Other Inverts	Non-prey	*Odonthalia floccosa* and *Neorhodomela larix*	Red canopy algae	Primary Producer
Tunicates	Other Inverts	Non-prey			

2.2 Data Analysis

2.2.1 Data Preparation

We used R, RStudio (v 1.2.5042) and the dplyr (v1.0.3) and tidyverse (v1.3.0) packages to prepare the data. After joining the data from each quadrat, we first culled out data from any photo quadrats that were above the shore level of the lower limit of the mussel bed (see *Mussel Bed Dynamics* for more detail) recorded for each transect during the first sampling (either 2015 or 2017 depending on area). This ensured that we were focusing on the low zone and comparing the same quadrats over time. For all except biodiversity data (see below), we used Primer-e 7 with PERMANOVA+ add-on (Anderson et al. 2008, Clarke and Gorley 2015) to aggregate all taxa into functional groups (Table 2). We then averaged the percent cover of each functional group by transect, area and year to avoid the inherent non-independence of the typically ~2-5 quadrats that were adjacent to one another. This community structure matrix was used to analyze intertidal communities, key functional groups and biodiversity.

Community Structure Data Preparation

After investigating draftsmand and shade plots in PRIMER, we determined that common functional groups were over-dominant so we square-root transformed the matrix (Anderson, 2001). We then quantified community similarity using a Bray-Curtis resemblance matrix.

Key Functional Groups Data Preparation

In R, we used the gather() function in tidyverse to reorganize the community structure matrix into a data frame with functional group and untransformed percent cover as columns. We again averaged the percent cover of each functional group by transect, area and year before analysis.

Biodiversity Data Preparation

In PRIMER, we calculated the Shannon-Wiener Diversity Index (H'$\log_e$, Clarke and Gorley 2015) for each transect, area and year at the lowest taxonomic level rather than functional group (Table 2).

2.2.2 Analysis of Intertidal Communities Among Reserves And Comparison Areas and to Sea Star Wasting Disease

Community Structure

To determine whether intertidal community structure varied among Marine Reserves and Comparison Areas (Q1) and after SSWD (Q2), we first used non-metric multidimensional scaling (nMDS) plots to visualize community disimilarity between transects. We used vector overlays to visualize which functional groups were most associated with community separation. We then used Permutational Analysis of Variance (PERMANOVA) models to statistically test patterns in multivariate community structure (Anderson, 2001; McArdle & Anderson, 2001). We performed 3 separate PERMANOVAs; the first focused on comparing the three Marine Reserves (Cape Perpetua, Otter Rock, Cascade Head), the second compared Cape Perpetua Marine Reserve and Tokatee Klootchman Comparison Area, and the third compared Otter Rock Marine Reserve and Fogarty Creek Comparison Area. In each PERMANOVA, we tested the effects of area, year as a categorical variable, and their interactions on community structure, and included transect nested within area as a random variable to control for repeated measures within transects. We used pair-wise follow-up tests to investigate among-level differences in factors identified as significant by PERMANOVA. The percent contribution of each model term to the overall fit was determined by dividing the term's component of variation to total model variation (Anderson et al. 2008). We used similarity percentage (SIMPER) tests to identify the functional groups substantially contributing to dissimilarity among or similarity within each area and/or year (Clarke and Gorley 2015).

One important component of our analysis was determining whether communities were changing over time in response to sea star wasting disease. To visualize these changes, we overlaid yearly trajectories among areas and years using nMDS. This visualization depicts how the communities changed over time at a given location.

Key Functional Groups

To determine whether key intertidal species varied among Marine Reserves and Comparison Areas (Q1) and after SSWD (Q2), we used a mixed linear model in the lme4 package in R (v1.1 - 27.1). We first arcsine-square root transformed the abundance data (proportion cover which varies from 0 to 1), then tested the main and interactive effects of area, year, and functional group on abundance. Transect was included as a random factor nested within area to control for the repeated measures within transects. Area included all 3 Marine Reserves and the 2 Comparison Areas. For this full model, year was treated as a continuous variable since we were first interested in increases or decreases over time, and we did not have enough degrees of freedom to treat year as a category. Some functional groups were too rare to include in the models (i.e. all zeroes at a particular area and/or year), so we were only able to focus on key functional groups, include bare space, mussels, large barnacles, small barnacles, gooseneck barnacles, sea anemones, herbivorous molluscs, green algae, coralline algae, red canopy algae, and red understory algae in the models. We used the lsmeans package (v 2.30-0) to perform follow-up Tukey's tests on significant area and/or functional group terms. We visualized mean percent cover among areas, years and all functional groups using ggplot2 in R (v 3.3.3).

Since the above model was only able to detect increases or decreases over time, we further investigated temporal variation within each key functional group separately, and treated year as a category. Similar to above, we used the lme4 package in R, arcsine-square root transformed abundance of each functional group, tested main and interactive effects of area and year, included transect as a random factor nested within area, and performed follow-up Tukey's test on significant terms.

Biodiversity

To determine whether biodiversity varied among Marine Reserves and Comparison Areas (Q1) and after SSWD (Q2), We tested the effects of area and year on biodiversity of taxa to the lowest taxonomic level possible (Table 2) using a mixed linear model (lme4 package). Transect was again included as a random factor nested within area, and we performed follow-up Tukey’s tests (lsmeans package). We visualized mean biodiversity among areas and years using ggplot2.

3 Intertidal Communities Among Reserves And Comparison Areas

The three Marine Reserves we compared have distinct intertidal communities from one another, but each is similar to its respective Comparison Area (when present). As expected based on prior data and regional oceanographic patterns, Cape Perpetua Marine Reserve is dominated by sessile invertebrates (mussels, barnacles, sea anemones) while Otter Rock Marine Reserve is dominated by a diversity of algae. Cascade Head had both invertebrates (primarily mussels) and multiple groups of algae. Despite these differences, biodiversity was similar among the three Marine Reserves, and Comparison Area biodiversity did not differ from each respective Marine Reserve.

3.1 Intertidal Communities in Cape Perpetua Marine Reserve

Takeaway: Cape Perpetua has a distinct community structure from the other two Marine Reserves, and is dominated by sessile marine invertebrates including barnacles (gooseneck, small, and large barnacles), mussels and sea anemones, but has little algae. Communities are very similar to its Tokatee Klootchman Comparison Area. However, biodiversity at Cape Perpetua Marine Reserve is similar to other Marine Reserves and its Comparison Area.

3.1.1 Community Structure in Cape Perpetua Marine Reserve

Community structure at Cape Perpetua Marine Reserve was distinct from both Otter Rock and Cascade Head Marine Reserves. (Fig. 1, Table 3, $P < 0.001$ and $P = 0.044$, respectively). Among-reserve differences drove 35.7% of variation in the community data (Table 3), and among-transect variation was similarly important (38.5% of variation). Among-transect variation is likely driven by differences among transects in shore level, rock topography, wave exposure, or microhabitat features.

Our nMDS plots and SIMPER analysis suggests the separation of Cape Perpetua from Otter Rock Marine Reserve was associated with increased invertebrates, including barnacles (gooseneck, small, and large barnacles), mussels and sea anemones (Fig. 1). There was substantial overlap in community structure between Cape Perpetua and Cascade Head Marine Reserves, suggesting they share many of the same functional groups. The separation that did occur was associated with more gooseneck barnacles, sea anemones and bare space at Cape Perpetua than at Cascade Head Marine Reserve.

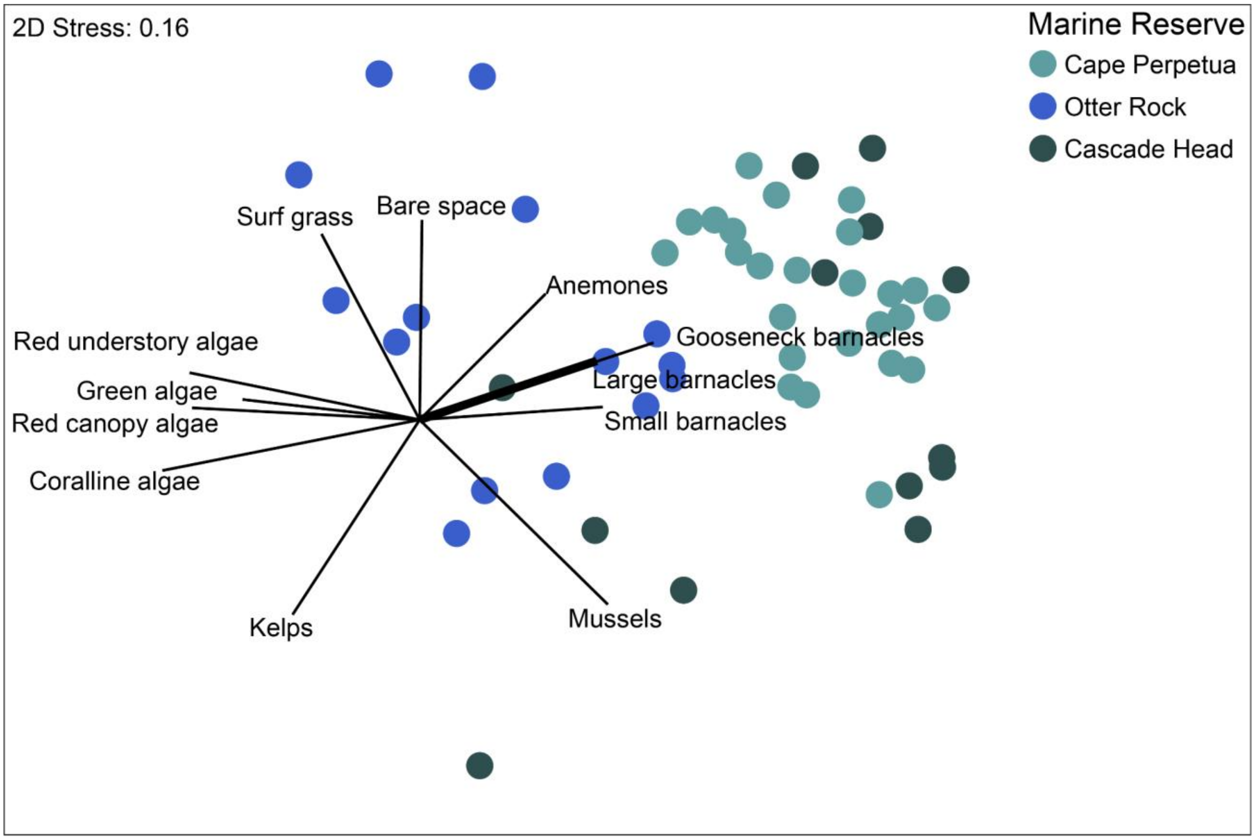

Figure 1. Non-metric multidimensional scaling (nMDS) plots depicting Bray-Curtis dissimilarity in community structure among Cape Perpetua (teal), Otter Rock (blue) and Cascade Head (dark green) Marine Reserves. Vector overlays depict functional groups most strongly contributing to data separation. Each data point represents a community at the transect level (the average of ~2-5 0.5 x 0.5m quadrats).

Table 3. PERMANOVA Results comparing community structure among the three Marine Reserves (Cape Perpetua, Otter Rock and Cascade Head) over time.

Term	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Estimate	Sq.root	% Explained
Transect [Reserve]	12	33,074	2,756	6.52	0.001	999	666.7	25.8	38.5
Reserve	2	22,460	11,230	4.70	0.001	998	619.0	24.9	35.7
Year	4	3,476	869	2.06	0.017	999	47.0	6.9	2.7
Reserve x Year	4	1,262	316	0.75	0.732	999	-23.1	-4.8	-1.3
Residual	30	12,686	423				422.9	20.6	24.4
Total	52	75,447					1,732.3		

Tokatee Klootchman Comparison Area

When comparing Cape Perpetua Marine Reserve to Tokatee Klootchman Comparison Area, we found no significant difference in community structure (Fig. 2, Table 4). Our analysis suggests that among-transect variation is much higher than among-area variation (Table 3, 44.9 % and 1.8% of the variation, respectively), suggesting these two areas are quite similar in community structure. nMDS plots (Fig. 2) and SIMPER analysis suggested that gooseneck barnacles, small barnacles, large barnacles, and surf grass were slightly more associated with Cape Perpetua Marine Reserve, while mussels and green algae were slightly more associated with Tokatee Klootchman Comparison Area.

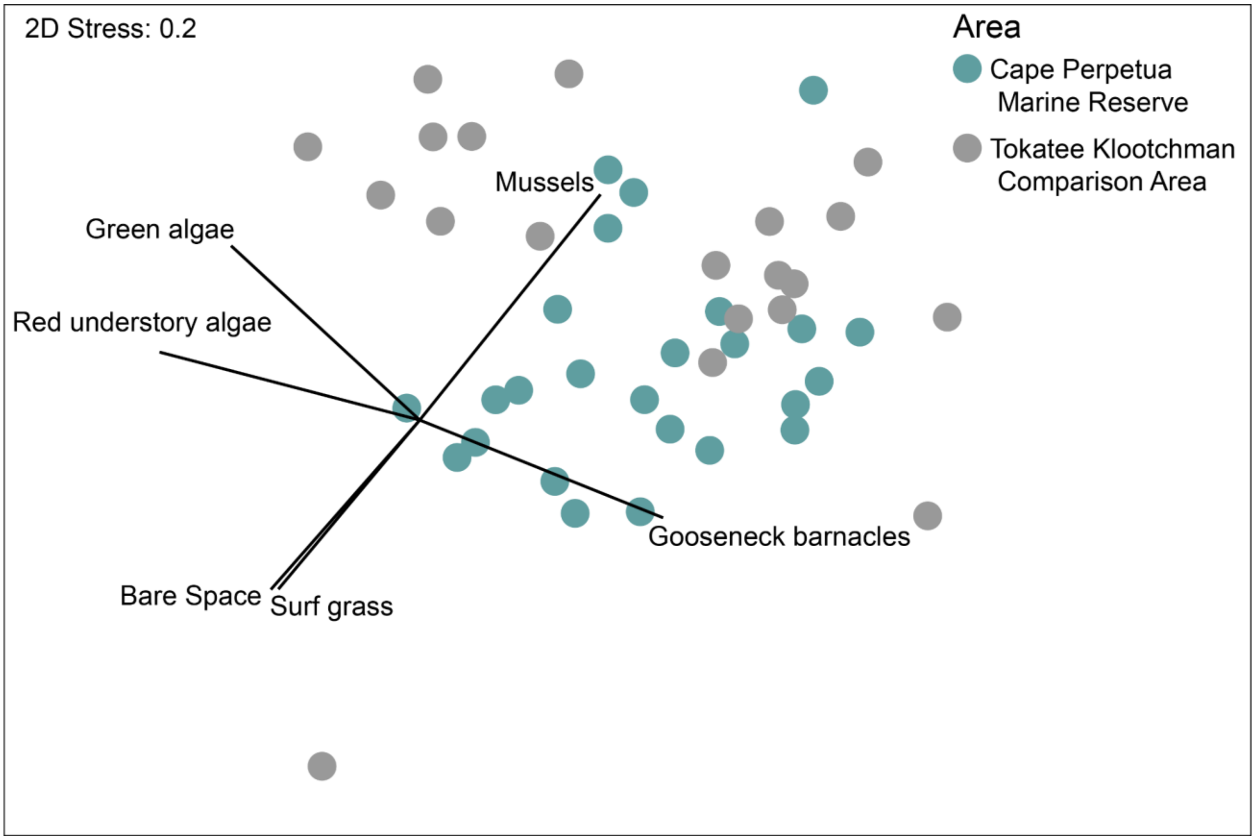

Figure 2. Non-metric multidimensional scaling (nMDS) plots depicting Bray-Curtis dissimilarity in community structure between Cape Perpetua Marine Reserve (teal) and Tokatee Klootchman Comparison Area (gray). Vector overlays depict functional groups most strongly contributing to data separation. Each data point represents a community at the transect level (the average of ~2-5 0.5 x 0.5m quadrats).

Table 4. PERMANOVA Results comparing community structure between Cape Perpetua Marine Reserve and Tokatee Klootchman Comparison Area over time.

Term	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Estimate	Sq.root	% Explained
Transect [Area]	8	18,129	2,266	4.94	0.001	997	413.1	20.3	44.9
Area	1	2,670	2,670	1.15	0.317	925	16.5	4.1	1.8
Year	4	3,060	765	1.67	0.043	999	35.0	5.9	3.8
Area x Year	4	1,776	444	0.97	0.526	998	-3.6	-1.9	-0.4
Residual	27	12,394	459				459.1	21.4	49.9
Total	44	38,373					920.0		

3.1.2 Key Functional Groups in Cape Perpetua Marine Reserve

The abundance of key functional groups varied considerably between Cape Perpetua and the other Marine Reserves (Fig. 3, Table 5, Table 6). The most abundant functional groups at Cape Perpetua Marine Reserve were all sessile invertebrates, including mussels, gooseneck barnacles, small barnacles, large barnacles, and sea anemones, in that order (Fig. 3, Table 5). Algal abundance was generally low at Cape Perpetua Marine Reserve. Surfgrass was the only primary producer that was abundant in Cape Perpetua. Among Marine Reserves, Cape Perpetua has significantly more sea anemones and large barnacles than Otter Rock, and less coralline algae (Fig. 3, Table 5, Table 6, $P < 0.042$ for all pairwise comparisons). No differences in functional group abundance were detected between Cape Perpetua Marine Reserve and Cascade Head Marine Reserve.

<u>Tokatee Klootchman Comparison Area</u>

Similar to Cape Perpetua Marine Reserve, intertidal communities were dominated by invertebrates. The most abundant functional groups at Tokatee Klootchman Comparison Area included mussels, gooseneck barnacles, green algae, small barnacles, anemones, and large barnacles, in that order (Fig. 3, Table 5). Algal abundance was also generally low. The only significant difference was increased abundance of green algae in Tokatee Klootchman compared to Cape Perpetua ($P = 0.002$).

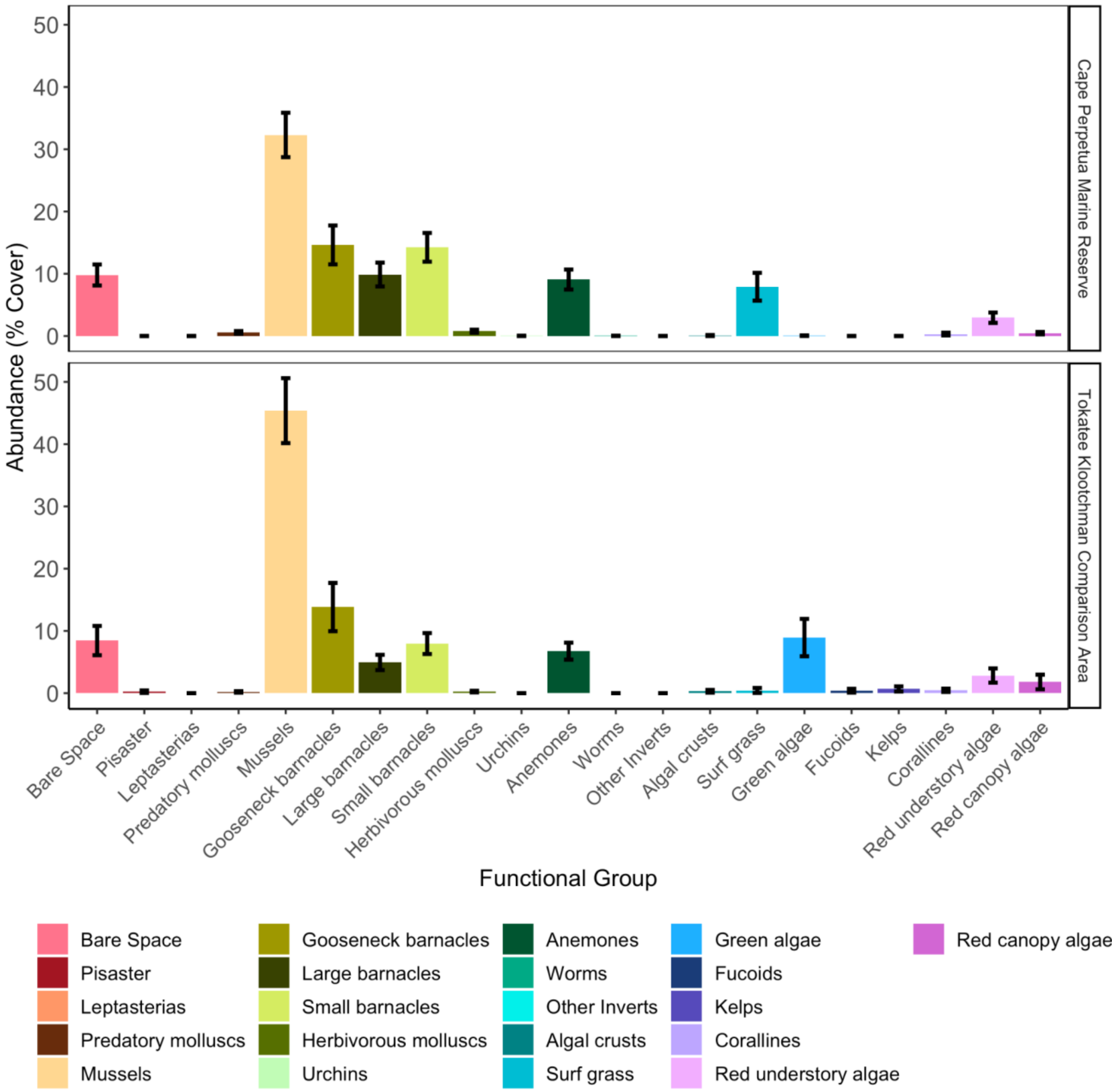

Figure 3. Average abundance (mean percent cover ± standard error) of functional groups in each transect in all years combined in Cape Perpetua Marine Reserve (top) and Tokatee Klootchman Comparison Area (bottom).

Table 5. The average abundance of functional groups (displayed as mean(standard error)). N transects is the number of transects surveyed among areas and years.

Trophic Role	Functional Group	Cape Perpetua Marine	Tokatee Klootchman Comparison	Otter Rock Marine Reserve	Fogarty Creek Comparison Area	Cascade Head Marine Reserve
Bare Space	Bare Space	9.81 (1.69)	8.45 (2.35)	8.42 (2.11)	7.31 (1.24)	8.13 (3.50)
Predators	*Pisaster ochraceus*	0.00 (0.00)	0.23 (0.20)	0.00 (0.00)	0.07 (0.04)	0.28 (0.23)
	Leptasterias spp.	0.00 (0.00)	0.00 (0.00)	0.04 (0.04)	0.00 (0.00)	0.00 (0.00)
	Predatory molluscs	0.58 (0.22)	0.20 (0.12)	0.00 (0.00)	0.07 (0.05)	0.00 (0.00)
Sessile Prey	Mussels	32.30 (3.57)	45.38 (5.22)	22.47 (5.24)	18.32 (3.46)	42.79 (10.30)
	Gooseneck barnacles	14.64 (3.12)	13.83 (3.87)	0.00 (0.00)	3.95 (1.09)	10.90 (2.89)
	Large barnacles	9.88 (1.91)	4.94 (1.23)	0.89 (0.46)	1.94 (0.77)	4.49 (1.51)
	Small barnacles	14.25 (2.31)	7.97 (1.68)	7.62 (2.43)	13.83 (3.46)	18.74 (6.52)
Mobile Prey	Herbivorous molluscs	0.78 (0.24)	0.25 (0.13)	0.11 (0.08)	0.39 (0.17)	0.21 (0.14)
Non-prey	Urchins	0.03 (0.03)	0.00 (0.00)	3.25 (1.80)	2.03 (0.88)	0.00 (0.00)
	Anemones	9.08 (1.61)	6.75 (1.36)	0.91 (0.31)	1.98 (0.44)	2.69 (1.35)
	Worms	0.03 (0.03)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
	Other Inverts	0.00 (0.00)	0.00 (0.00)	0.04 (0.04)	0.00 (0.00)	0.00 (0.00)
Primary Producer	Surf grass	7.92 (2.23)	0.43 (0.40)	13.11 (6.83)	5.12 (2.38)	0.00 (0.00)
	Algal crusts	0.08 (0.08)	0.30 (0.22)	1.02 (0.59)	0.76 (0.45)	0.23 (0.17)
	Green algae	0.06 (0.04)	8.93 (3.00)	6.51 (2.96)	0.30 (0.12)	0.26 (0.16)
	Fucoid algae	0.00 (0.00)	0.40 (0.31)	0.00 (0.00)	0.22 (0.17)	0.26 (0.26)
	Kelps	0.00 (0.00)	0.68 (0.41)	8.84 (4.81)	17.67 (3.32)	13.92 (7.37)
	Coralline algae	0.32 (0.21)	0.47 (0.27)	5.92 (1.77)	7.51 (1.31)	2.41 (1.76)
	Red understory algae	2.94 (0.83)	2.83 (1.14)	13.70 (2.89)	10.04 (1.08)	5.08 (2.55)
	Red canopy algae	0.46 (0.19)	1.80 (1.18)	12.10 (2.11)	13.23 (3.32)	0.33 (0.15)
	N Transects	**25**	**20**	**15**	**24**	**13**

Table 6. Linear mixed model results comparing the abundance (sine^{-1} square root proportion cover) of key functional groups among areas, including the three Marine Reserves (Cape Perpetua, Otter Rock and Cascade Head) and two comparison areas (Tokatee Klootchman and Fogarty Creek) over time.

Term	ChiSq	DF	F	P-value
Area	344.9	44	5.56	< 0.001
Year	0.0	1	0.22	0.879
Functional Group	1056.1	50	17.90	< 0.001
Area * Year	0.5	4	0.07	0.974
Area * Functional Group	342.7	40	5.96	< 0.001
Year * Functional Group	13.6	10	1.77	0.194
Area * Year * Functional Group	47.3	40	1.40	0.199

3.1.3 Biodiversity in Cape Perpetua Marine Reserve

Among Marine Reserves, average biodiversity over time was very similar. Though Cape Perpetua had higher taxon diversity (Fig. 4, Table 7) than Cascade Head Marine

Reserve and lower diversity than Otter Rock Marine Reserve, pairwise comparisons showed that biodiversity was not different among any Marine Reserves (Table 8, P > 0.224 for among-reserve pairwise comparisons in 2017-2019, when all area were surveyed).

Tokatee Klootchman Comparison Area

On average over time, Cape Perpetua Marine reserve also had similar biodiversity to its Comparison Area Tokatee Klootchman (Fig. 4, Table 7, Table 8, P = 0.840 for pairwise comparison).

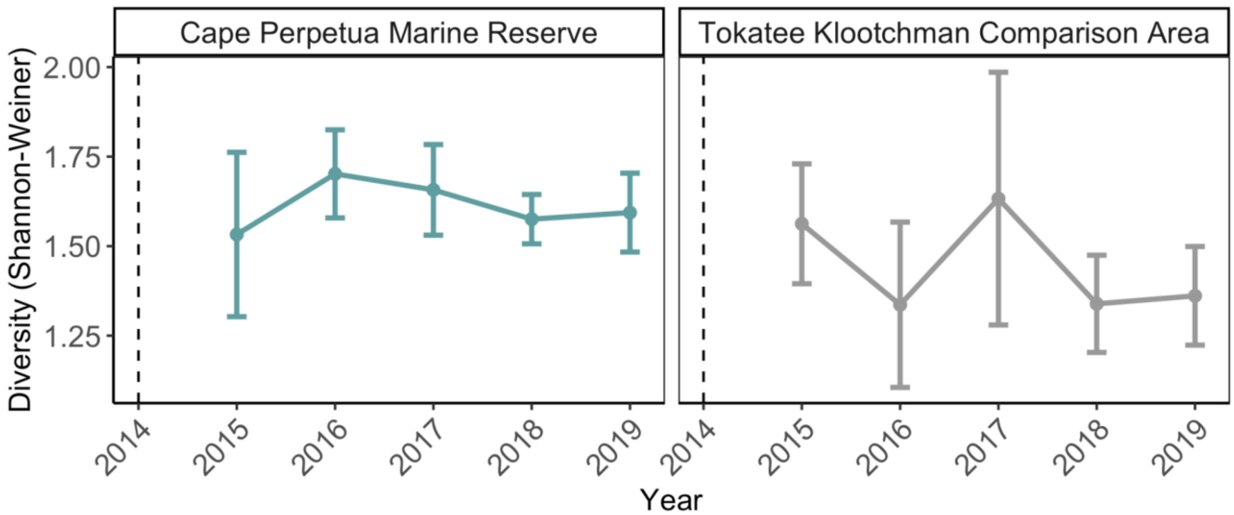

Figure 4. Average taxon biodiversity (mean Shannon-Weiner Index ± standard error) in each transect over time in Cape Perpetua Marine Reserve (teal) and Tokatee Klootchman Comparison Area (gray).

Table 7. Average species diversity (mean Shannon-Weiner index ± standard error) among the three Marine Reserves (Cape Perpetua, Otter Rock and Cascade Head) and two comparison areas (Tokatee Klootchman and Fogarty Creek).

Area	N Transects	Mean Diversity	SE
Cape Perpetua Marine Reserve	25	1.61	0.06
Tokatee Klootchman Comparison Area	20	1.43	0.08
Otter Rock Marine Reserve	15	1.68	0.11
Fogarty Creek Comparison Area	24	1.95	0.07
Cascade Head Marine Reserve	13	1.28	0.15

Table 8. Linear mixed model results comparing the species diversity (Shannon-Weiner index) among the three Marine Reserves (Cape Perpetua, Otter Rock and Cascade Head) and two comparison areas (Tokatee Klootchman and Fogarty Creek) over time.

Term	ChiSq	DF	P-value
Area	12.9	4	0.012
Year	3.0	4	0.553
Area * Year	29.2	12	0.004

3.2 Intertidal Communities in Otter Rock Marine Reserve

Takeaway: The intertidal communities at Otter Rock Marine Reserve and its Fogarty Creek Comparison Area were similar to one another, but are distinct from the other Marine Reserves. Primary producers were the dominant functional groups, including red canopy algae, surf grass, red understory algae, coralline algae and green algae. While biodiversity at Otter Rock Marine Reserve was relatively high, it was not statistically different from the other Marine Reserves nor Fogarty Creek Comparison Area.

3.2.1 Community Structure in Otter Rock Marine Reserve

Otter Rock Marine Reserve community structure was clearly distinct from both of the other Marine Reserves (Fig. 1, Table 3, $P < 0.001$ and $P = 0.022$ for Cape Perpetua and Cascade Head, respectively). Our nMDS plots and SIMPER analysis show that Otter Rock Marine Reserve was associated with more primary producers than was Cape Perpetua or Cascade Head, including red canopy algae, surf grass, red understory algae, coralline algae and green algae (Fig. 1).

Fogarty Creek Comparison Area

Community structure did not significantly differ between Otter Rock and its Comparison Area Fogarty Creek (Fig. 5, Table 9). The modest separation that did occur was due to a higher association of mussels, surf grass, and red canopy algae with Otter Rock, and more kelps and small barnacles with Fogarty Creek (Fig. 5, SIMPERS). Among-transect variation within an area was much higher than among-area variation (Table 9). Similar to the other Marine Reserves, and Comparison Areas, among-transect variation is likely driven by differences in shore level among transects, rock topography, wave exposure, or microhabitat features.

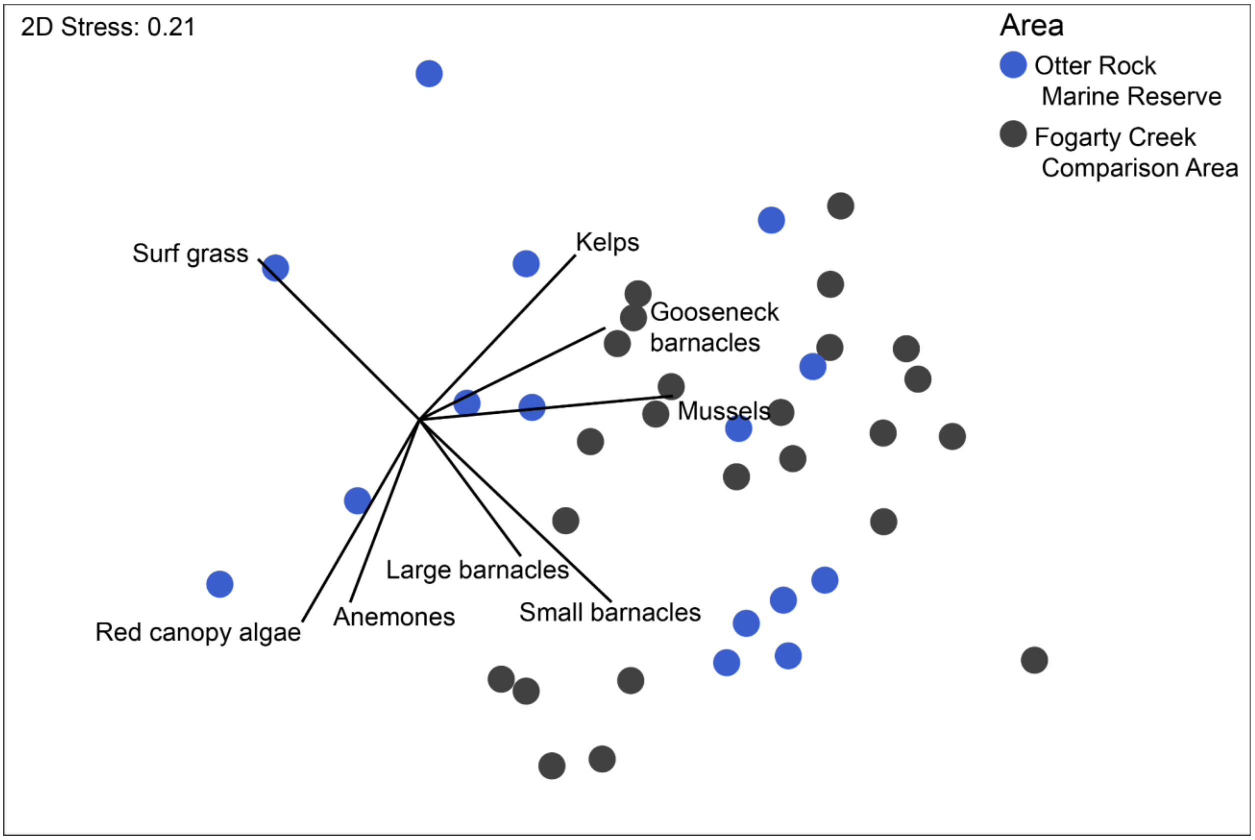

Figure 5. Non-metric multidimensional scaling (nMDS) plots depicting Bray-Curtis dissimilarity in community structure between Otter Rock Marine Reserve (blue) and Fogarty Creek Comparison Area (dark gray). Vector overlays depict functional groups most strongly contributing to data separation. Each data point represents a community at the transect level (the average of ~2-5 0.5 x 0.5m quadrats).

Table 9. PERMANOVA Results comparing community structure between Otter Rock Marine Reserve and Fogarty Creek Comparison Area over time.

Term	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Estimate	Sq.root	% Explained
Transect [Area]	8	24,327	3,041	8.36	0.001	997	690.9	26.3	58.3
Area	1	3,009	3,009	1.24	0.274	691	38.2	6.2	3.2
Year	4	2,208	552	1.52	0.095	999	26.0	5.1	2.2
Area x Year	2	1,392	696	1.91	0.063	999	66.5	8.2	5.6
Residual	23	8,364	364				363.7	19.1	30.7
Total	38	40,321					1,185.2		

3.2.2 Key Functional Groups in Otter Rock Marine Reserve

The abundance of key functional groups was clearly different in Otter Rock Marine Reserve than the other Marine Reserves (Fig. 6, Table 5, Table 6). The most abundant functional groups at Otter Rock Marine Reserve included the dominant mussels followed by a diversity of primary producers, including red understory algae, surf grass, red canopy algae, and kelps, in that order (Fig. 6, Table 5). Among Marine Reserves, Otter Rock has significantly more coralline algae but less sea anemones and large barnacles than Cape Perpetua (Fig. 6, Tables 5 & 6, $P < 0.042$ for all pairwise comparisons). Further it had more red canopy algae but fewer gooseneck barnacles than Cascade Head Marine Reserve (Fig. 6, Tables 5 & 6, $P = 0.002$ and $P = 0.004$, respectively). Other functional group differences between Otter Rock and other Marine Reserves were not significant.

Fogarty Creek Comparison Area

The abundance of key functional groups was similar between Otter Rock Marine Reserve and its Fogarty Creek Comparison Area. There were no significant differences in the abundance of any functional group between the two areas. Similar to Otter Rock Marine Reserve, intertidal communities at Fogarty Creek were dominated by mussels and diverse algae, and included mussels, kelps, small barnacles, and red canopy and understory algae, in that order (Fig. 6, Table 5).

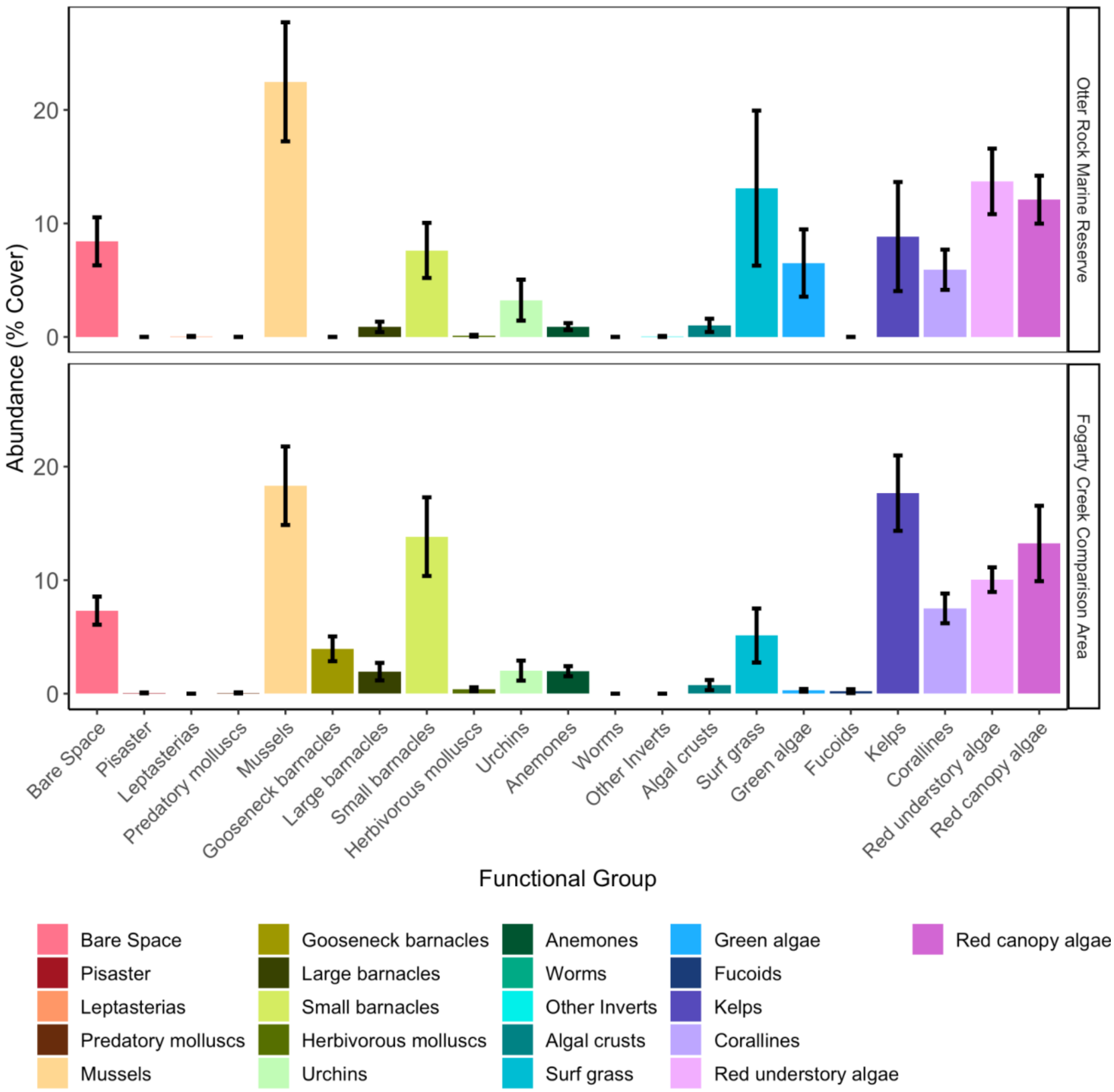

Figure 6. Average abundance (mean percent cover ± standard error) of functional groups in each transect in all years combined in Otter Rock Marine Reserve (top) and Fogarty Creek Comparison Area (bottom).

3.2.3 Biodiversity in Otter Rock Marine Reserve

While Otter Rock did have the highest average biodiversity among the Marine Reserves (Table 7), there were no statistical differences in biodiversity between Otter Rock and the other Marine Reserves (Table 8, $P > 0.224$ for all pairwise comparisons).

Fogarty Creek Comparison Area

Fogarty Creek had the highest biodiversity of any Marine Reserve or Comparison Area (Table 7). However it was not significantly higher in biodiversity than neighboring Otter Rock Marine Reserve ($P = 0.725$), nor any other Marine Reserve ($P = 0.360$ and $P = 0.102$ for Cape Perpetua and Cascade Head, respectively).

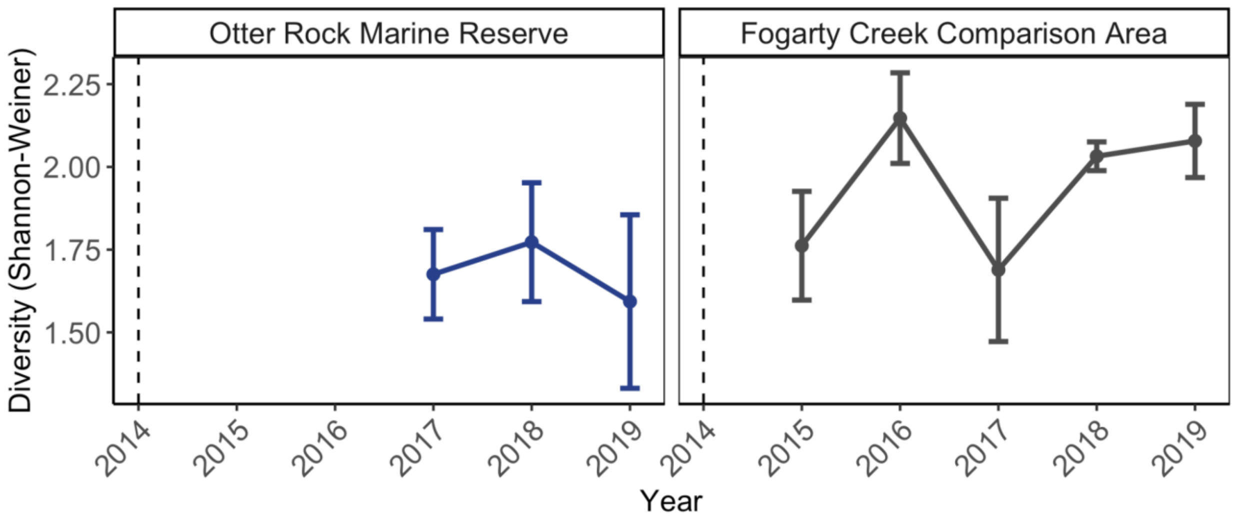

Figure 7. Average taxon biodiversity (mean Shannon-Weiner Index ± standard error) in each transect over time in Otter Rock Marine Reserve (blue) and Fogarty Creek Comparison Area (dark gray).

3.3 Intertidal Communities in Cascade Head Marine Reserve

Takeaway: Cascade Head Marine Reserve's intertidal communities are distinct from both of the other Marine Reserves, though they overlap more with Cape Perpetua than Otter Rock. Mussels were very dominant, followed by barnacles and kelps. Biodiversity was lower at Cascade Head than the other two Reserves, but this was not statistically significant.

3.3.1 Community Structure in Cascade Head Marine Reserve

Community structure at Cascade Head Marine Reserve was clearly different from Otter Rock Marine Reserve, and was distinct but had more overlap with communities at Cape Perpetua Marine Reserve (Fig. 1, Table 3, $P = 0.022$ and $P = 0.044$ for Otter Rock and Cape Perpetua, respectively). Similar to the other reserves, there was also variation in community structure within Cascade Head reserve (Table 3, transect nested in reserve term). Cascade Head Marine Reserve was associated with more mussels and kelps than both Cape Perpetua and Otter Rock Marine Reserves, and more small barnacles, and gooseneck barnacles than Otter Rock (Fig. 1, SIMPER).

3.3.2 Key Functional Groups in Cascade Head Marine Reserve

When further investigating the patterns in key functional groups at Cascade Head, we found that the most abundant functional groups included the very dominant mussels, followed by small barnacles, kelps, and gooseneck barnacles, then moderate abundance of red understory algae and large barnacles (Fig. 8, Table 5). There were no significant differences in the abundance of any functional group between Cascade Head and Cape Perpetua Marine Reserves. But Cascade Head had significantly more gooseneck barnacles and less red canopy algae than Otter Rock Marine Reserve (Fig. 8, Tables 5 & 6, $P < 0.001$ and $P = 0.004$ respectively). Other functional group differences between Cascade Head and other Marine Reserves were not significant.

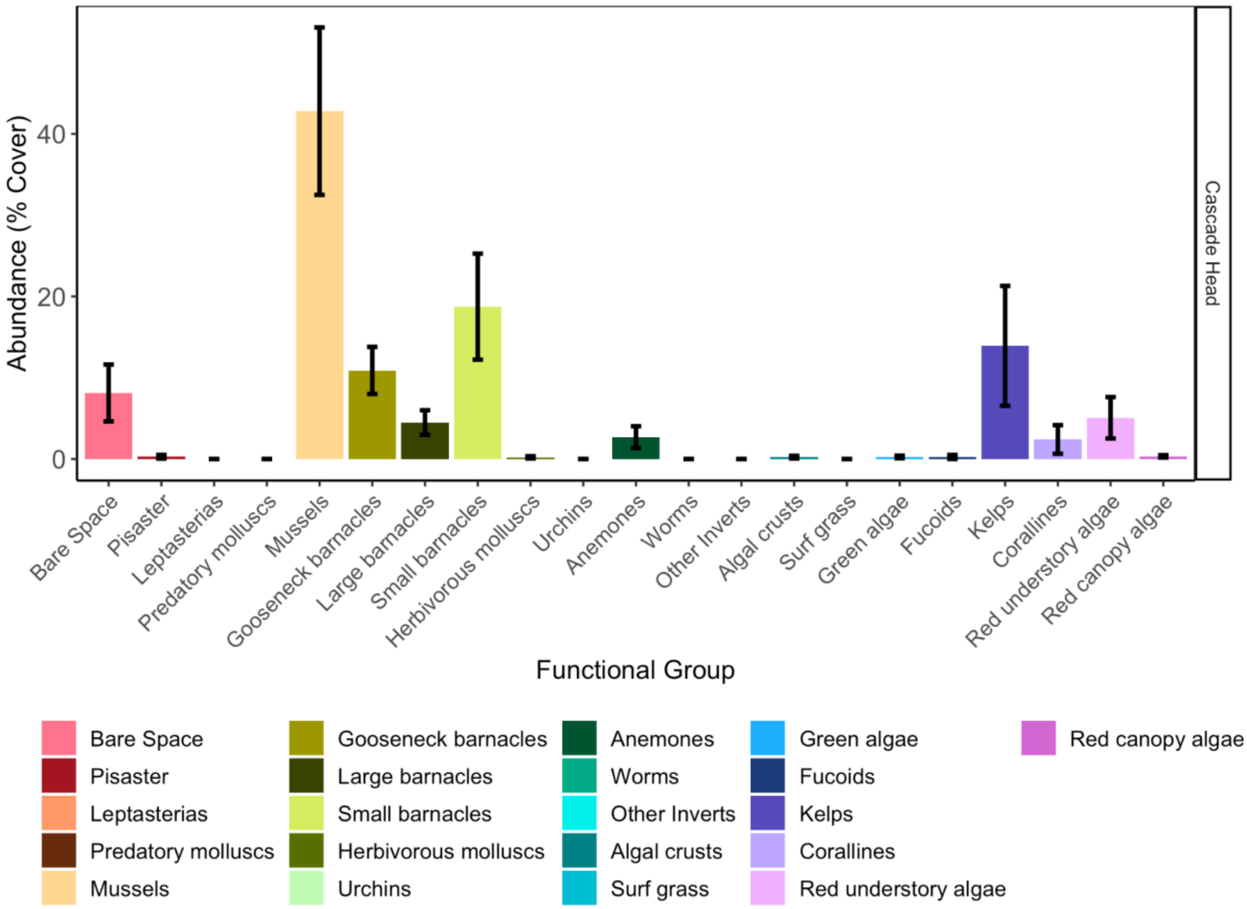

Figure 8. Average abundance (mean percent cover ± standard error) of functional groups in each transect in all years combined in Cascade Head Marine Reserve.

3.3.3 Biodiversity in Cascade Head Marine Reserve

Cascade Head has lower average taxon biodiversity compared to all other Marine Reserves and Comparison Areas (Fig. 9, Table 7). As stated above, biodiversity did not statistically differ among Marine Reserves (Table 8, > 0.224 for all pairwise comparisons).

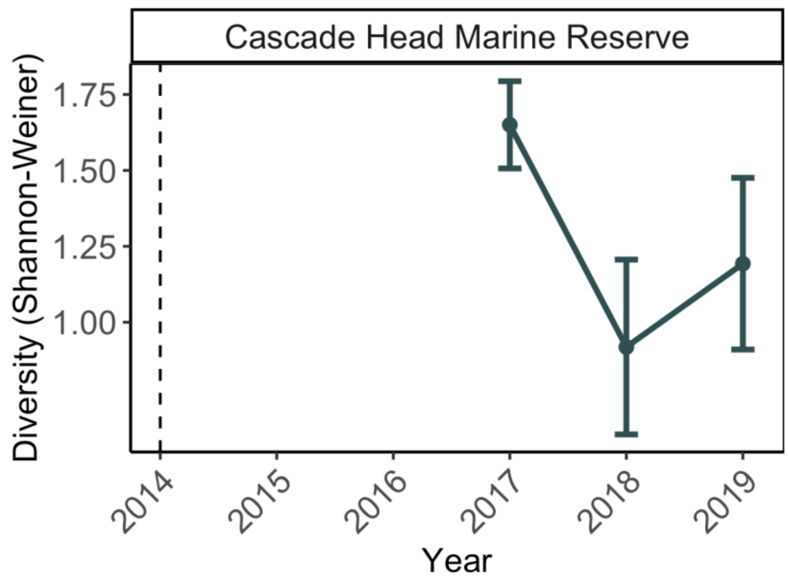

Figure 9. Average taxon biodiversity (mean Shannon-Weiner Index ± standard error) in each transect over time in Cascade Head Marine Reserve.

4 Intertidal Community Response to Sea Star Wasting Disease

Takeaway: We expected that the decline in the keystone predator *P. ochraceus* would lead to increases in mussels and other prey, declines in other functional groups, and declines in biodiversity. But in all Marine Reserves and Comparison Areas, we found either no changes or only minor changes in intertidal communities and biodiversity in the years after SSWD. Overall, the Marine Reserves were resilient to the decline of this predator, and perhaps indicate that *P. ochraceus* may not always be operating as a dominant keystone predator.

4.1 Response to SSWD in Cape Perpetua Marine Reserve

Takeaway: Despite our expectation that intertidal communities would change after SSWD in 2014, communities at Cape Perpetua Marine Reserve were mostly consistent between 2015-2019. However, there was a decrease in the prey species gooseneck barnacles in 2017, which did coincide with sea star recovery at Cape Perpetua Marine Reserve. Contrary to the keystone predation hypothesis, biodiversity did not vary, which may be linked to the rapid recovery of sea stars at this Marine Reserve. The Tokatee Klootchman Comparison Area showed a similar lack of change in intertidal communities, and also had a fairly rapid recovery of sea stars.

4.1.1 Effect of SSWD on Community Structure in Cape Perpetua Marine Reserve

Low zone community structure did not appear to respond to SSWD in Cape Perpetua Marine Reserve. Unlike the considerable differences in community structure that we detected both among and within marine reserves, variation over time was much less, with the year term accounting for <2.7% of the variation in community structure and no significant interaction between reserve and year for community structure (Table 3). When investigating trajectories of community change over time, we found that Cape Perpetua community structure was particularly consistent between 2015 and 2019, with no changes among years (Fig. 10, Table 3, $P > 0.09$ for all yearly comparisons).

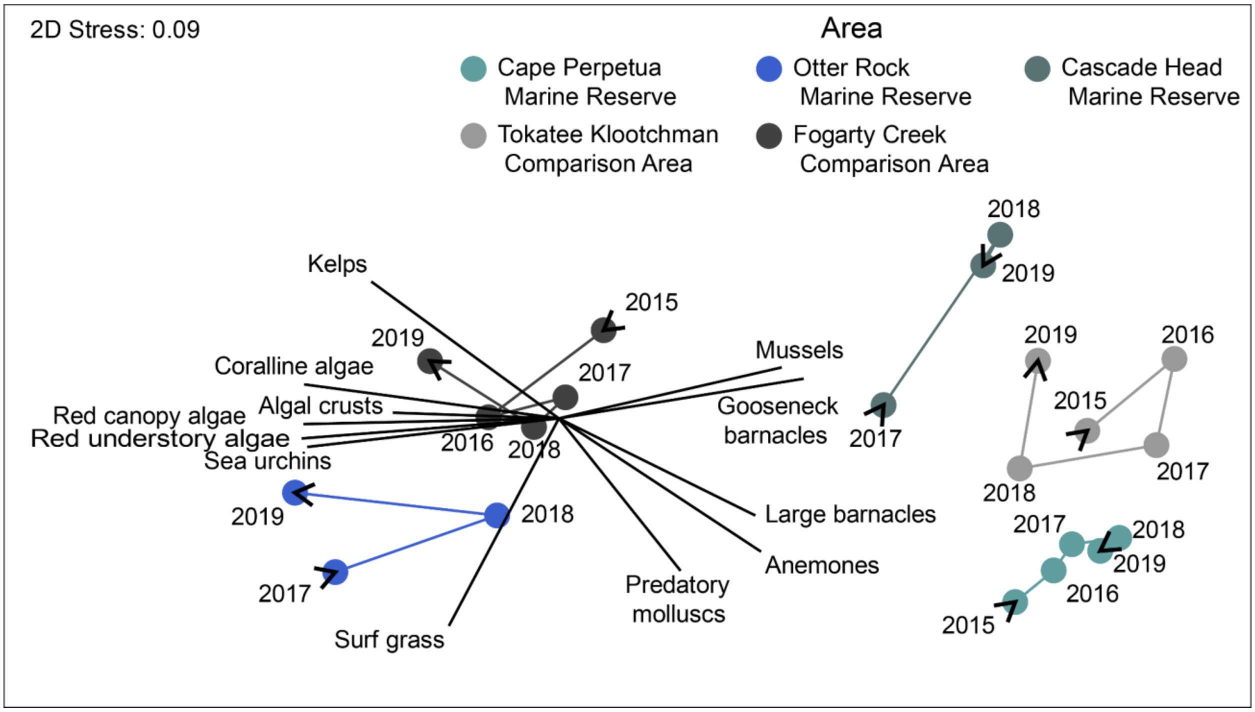

Figure 10. Non-metric multidimensional scaling (nMDS) plots depicting Bray-Curtis similarity among the three marine reserves (blues) and two comparison areas (grays). Each data point represents the centroid of community structure for each area and year, with colored vectors connecting years within each area. Black vector overlays in depict species most associated with dissimilarities among centroids.

Tokatee Klootchman Comparison Area

Similar to Cape Perpetua Marine Reserve, SSWD had no discernible effect on low zone community structure at Tokatee Klootchman Comparison Area (Table 4). The trajectory of community change at Tokatee Klootchman Comparison Area was also stable (Fig. 10), and there were no significant differences in community structure between 2015 and 2019 (Table 4, P > 0.145 for all yearly comparisons).

4.1.2 Effect of SSWD on Key Functional Groups in Cape Perpetua Marine Reserve

Our investigation into whether key functional groups responded to SSWD revealed no significant yearly variation in any Marine Reserve, Comparison Area, nor functional group (Table 6, all terms with Year $P > 0.194$). Subsequent models testing variation over area and year for each key functional group showed that the prey species gooseneck barnacles decreased between 2015 and 2017/2018 ($P = 0.054$ and $P = 0.056$, respectively) , while small barnacles increased between 2015 and 2017 ($P = 0.026$). Other functional groups did not change over time (Fig. 11).

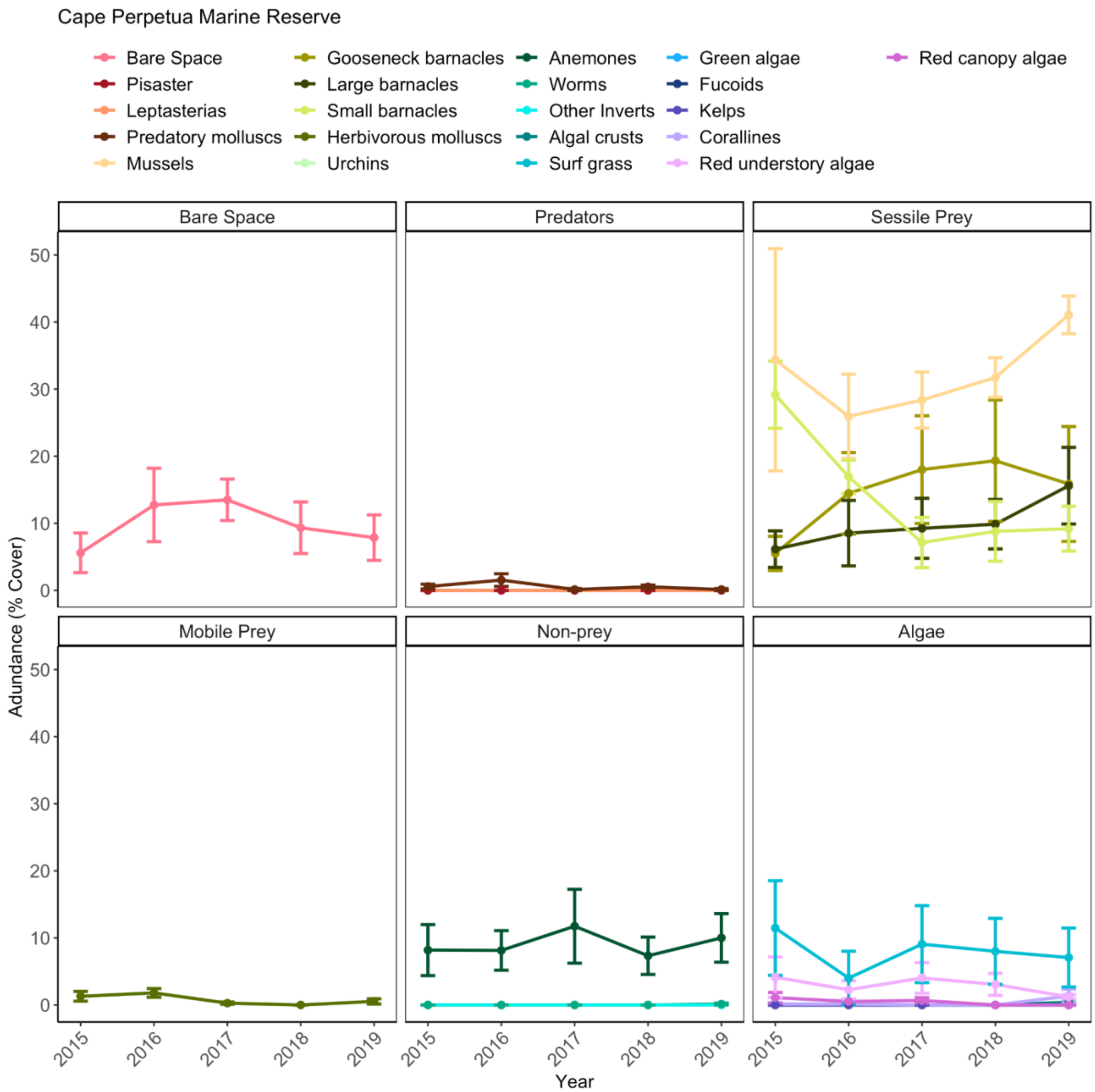

Figure 11*. Average abundance (mean percent cover ± standard error) of functional groups in each transect over time in Cape Perpetua Marine Reserve.*

Tokatee Klootchman Comparison Area

As stated above, there was no significant directional response to SSWD for any functional group nor area, including Tokatee Klootchman Comparison Area (Table 6, all terms with Year P > 0.194). Examining yearly comparisons in each key functional group (Fig. 12) showed only that green algae decreased at Tokatee Klootchman between 2016 and 2018 and 2019 (P = 0.002 and P = 0.001, respectively).

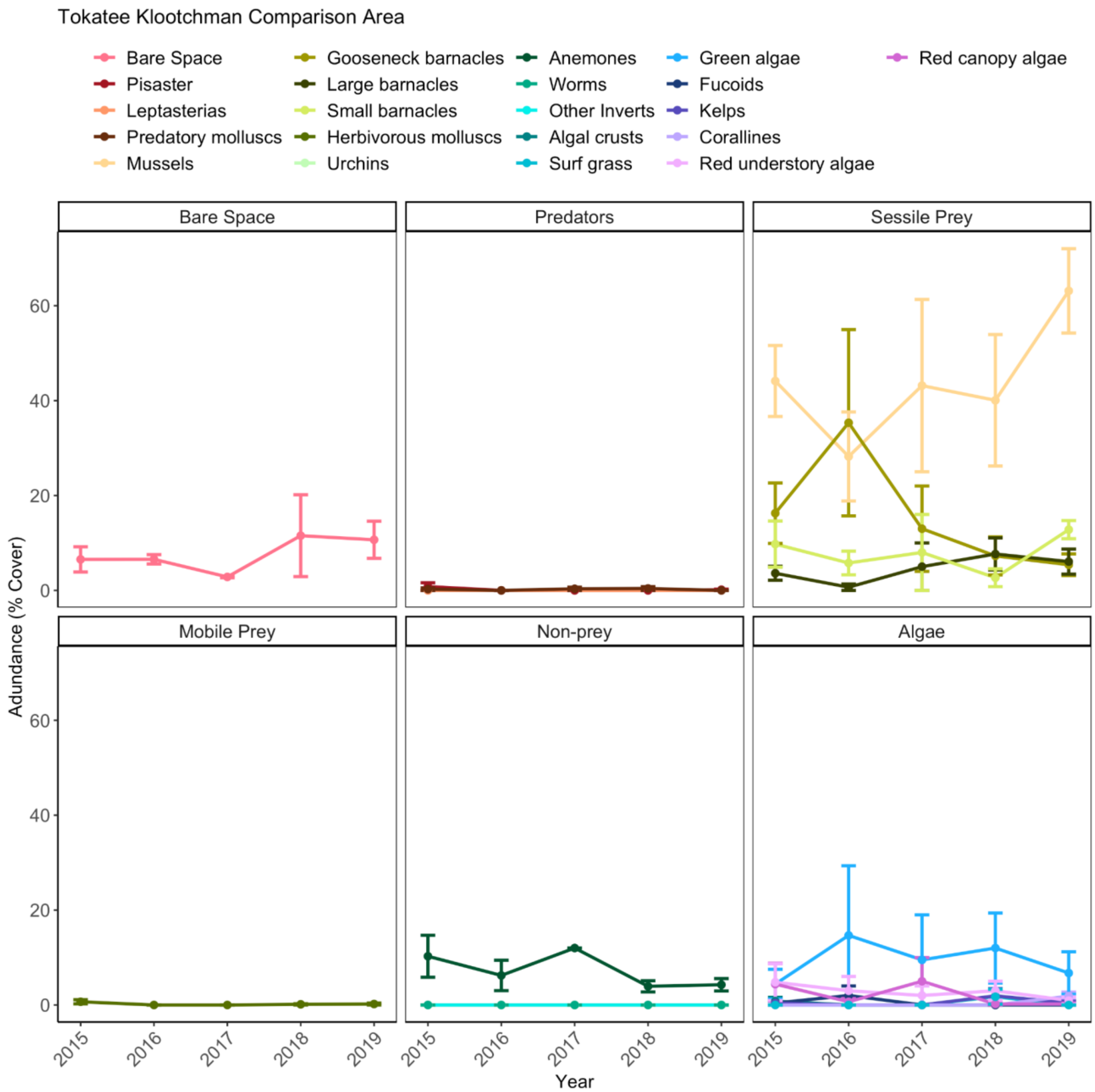

Figure 12. *Average abundance (mean percent cover ± standard error) of functional groups in each transect over time* in Tokatee Klootchman Comparison Area*.*

4.1.3 Effect of SSWD on Biodiversity in Cape Perpetua Marine Reserve

Despite our expectation that biodiversity might increase after SSWD because of the decline of the keystone predator *P. ochraceus*, we found no change in biodiversity at Cape Perpetua between 2015-2019 (Fig. 4, Table 8; P > 0.862 for all yearly comparisons).

Tokatee Klootchman Comparison Area

Similar to Cape Perpetua Marine Reserve, biodiversity at Tokatee Klootchman Comparison Area did not decrease after SSWD. Rather, biodiversity was consistent between 2015-2019 (Fig. 4, Table 8; P > 0.694 for all yearly comparisons)

4.2 Response to SSWD in Otter Rock Marine Reserve

Takeaway: Despite the continued low densities of the keystone predator *P. ochraceus* at Otter Rock Marine Reserve after SSWD, we did not detect the expected changes in community structure, changes in key functional groups, nor decreased biodiversity. However, it is possible rapid and undetected changes in communities occurred just after SSWD in 2014-2016. Intertidal communities at the Fogarty Creek Comparison Area also showed little discernible response to SSWD.

4.2.1 Effect of SSWD on Community Structure in Otter Rock Marine Reserve

Like other reserves, low zone community structure at Otter Rock was also fairly stable after the SSWD outbreak (Table 3), though we were only able to analyse data starting in 2017, three years after the disease occurred. The trajectories of community change over time showed a transition between 2017 and 2018, then a return in 2019 to a state more similar to 2017, but neither of these were significant (Fig. 10, Table 3, P = 0.085 and P = 0.272, respectively). The brief 2017-2018 change was associated with increased mussels, surf grass and kelp (Fig. 10, SIMPER).

Fogarty Creek Comparison Area

Changes in community structure over time just after SSWD were not significant at Fogarty Creek Comparison Area (Table 9). Community trajectories also show only modest change from 2015-2019 (Fig. 10, P > 0.085 for all yearly comparisons). The small changes over time were somewhat directional between 2015 and 2019 (Fig. 10, leftward along nMDS1), and were associated with decreased mussels and kelp.

4.2.2 Effect of SSWD on Key Functional Groups in Otter Rock Marine Reserve

Similar to Cape Perpetua Marine Reserve, our analyses revealed no substantial increases or decreases in key functional groups after the SSWD outbreak at Otter Rock

Marine Reserve (Table 6). Further, yearly comparisons for each functional group at Otter Rock Marine Reserve (Fig. 13) showed no differences over time.

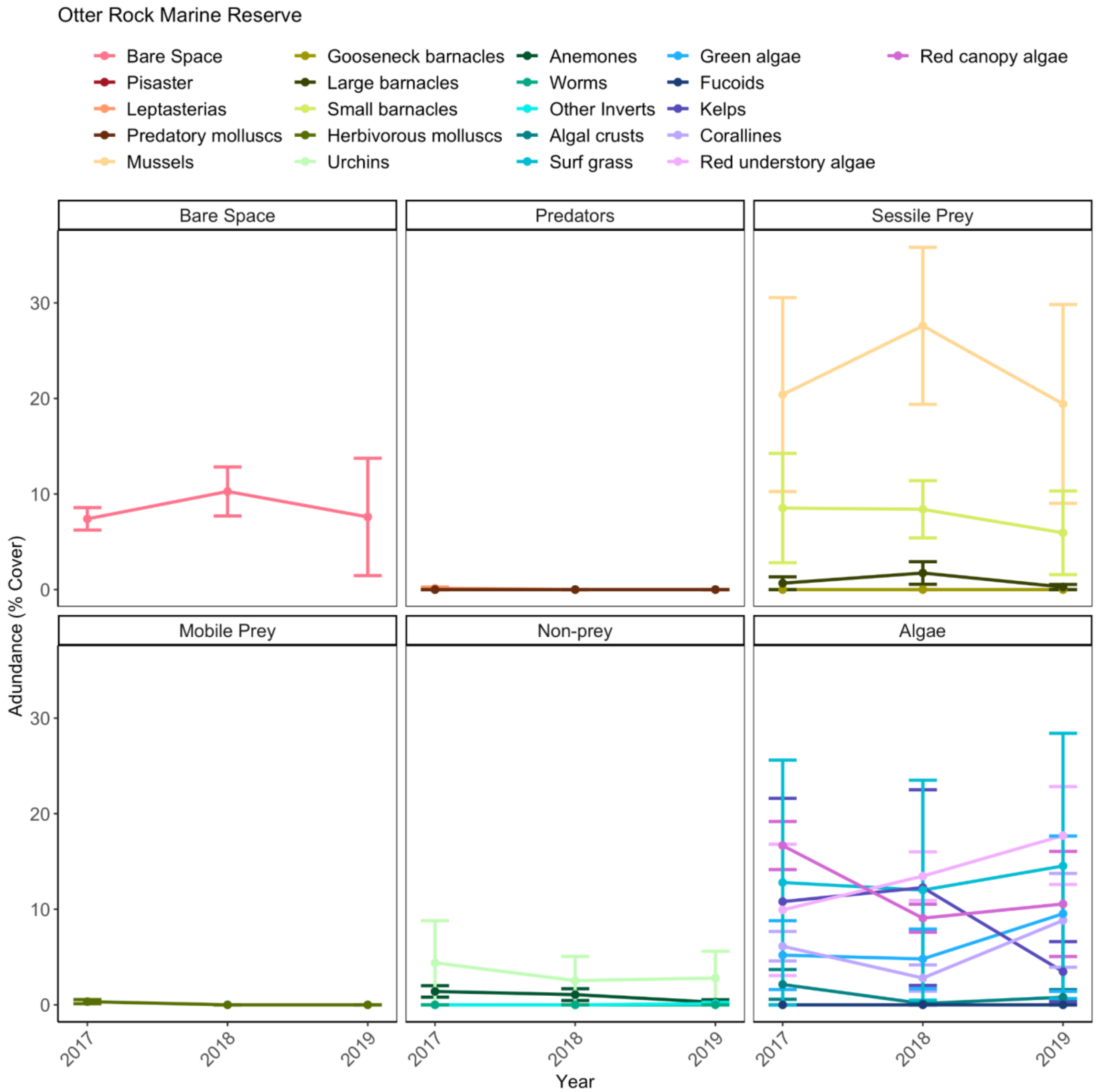

Figure 13. Average abundance (mean percent cover ± standard error) of functional groups in each transect over time in Otter Rock Marine Reserve (blue) and Fogarty Creek Comparison Area (dark gray).

Fogarty Creek Comparison Area

No increases or decreases in functional groups were found after the SSWD outbreak at Fogarty Creek (Table 6), and yearly comparisons for each functional group (Fig. 14) showed no differences among years.

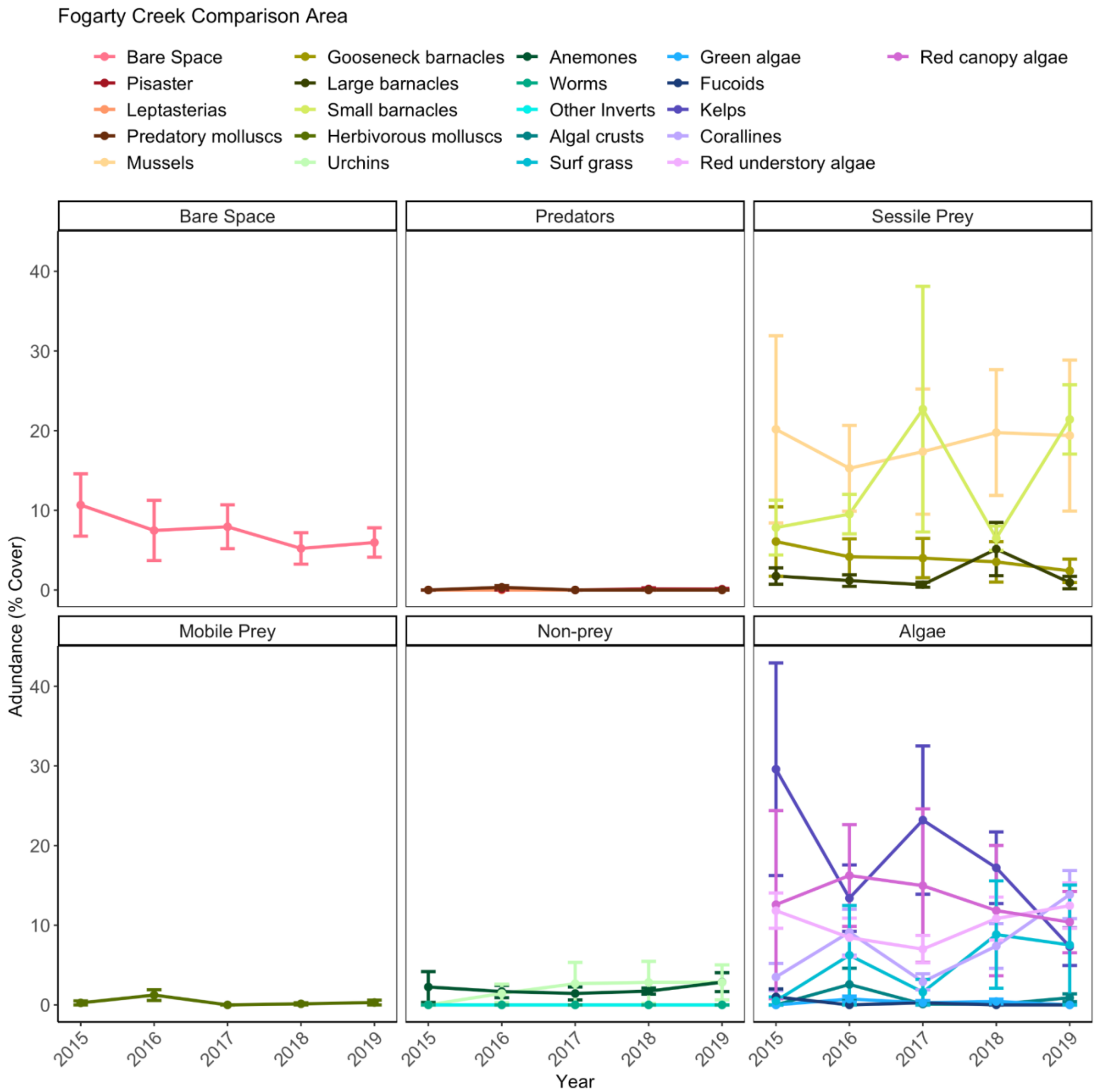

Figure 14. Average abundance (mean percent cover ± standard error) of functional groups in each transect over time in Fogarty Creek Comparison Area.

4.2.3 Effect of SSWD on Biodiversity in Otter Rock Marine Reserve

Like Cape Perpetua Marine Reserve, Otter Rock Marine Reserve did not show the expected decline in biodiversity after SSWD killed the keystone predator *P. ochraceus* (Fig. 7, Table 8; P > 0.835 for all yearly comparisons). Though it is possible that rapid changes in biodiversity occurred just after SSWD in 2014-2016 (when we have no data), there was no visual evidence of recent mussel bed expansion as of 2015 (S. Gravem pers. obs).

Fogarty Creek Comparison Area

Despite some variability in biodiversity just after SSWD in 2015-2017, biodiversity at Fogarty Creek Comparison Area did not significantly decrease after SSWD. (Fig. 7, Table 8; P > 0.073 for all yearly comparisons 2015-2019).

4.3 Response to SSWD in Cascade Head Marine Reserve

Takeaway: Three to five years after SSWD, Cascade Head Marine Reserve did not show any of the expected changes in community structure, key functional groups, or biodiversity. Like Otter Rock Marine Reserve, it is possible rapid and undetected changes in communities occurred just after SSWD in 2014-2016, but this is unclear.

4.3.1 Effect of SSWD on Community Structure in Cascade Head Marine Reserve

Again, low zone community structure at Cascade Head did not change substantially over time after the the SSWD outbreak (Table 3), though we were only able to analyse data starting in 2017, three years after the disease occurred. Visualized trajectories showed a transition between 2017 and 2018/2019, but these were not significant (Fig. 10, Table 3, P = 0.726 and P = 0.280, respectively). The modest change after 2017 was associated with increased mussels, and kelp (Fig. 10, SIMPER).

4.3.2 Effect of SSWD on Key Functional Groups in Cascade Head Marine Reserve

Like the other Marine Reserves and Comparison areas, Cascade Head Marine Reserve showed no directional change in any functional group after SSWD (Table 6). Additional yearly comparisons for each functional group at Cascade Head Marine Reserve (Fig. 15) showed no differences over time.

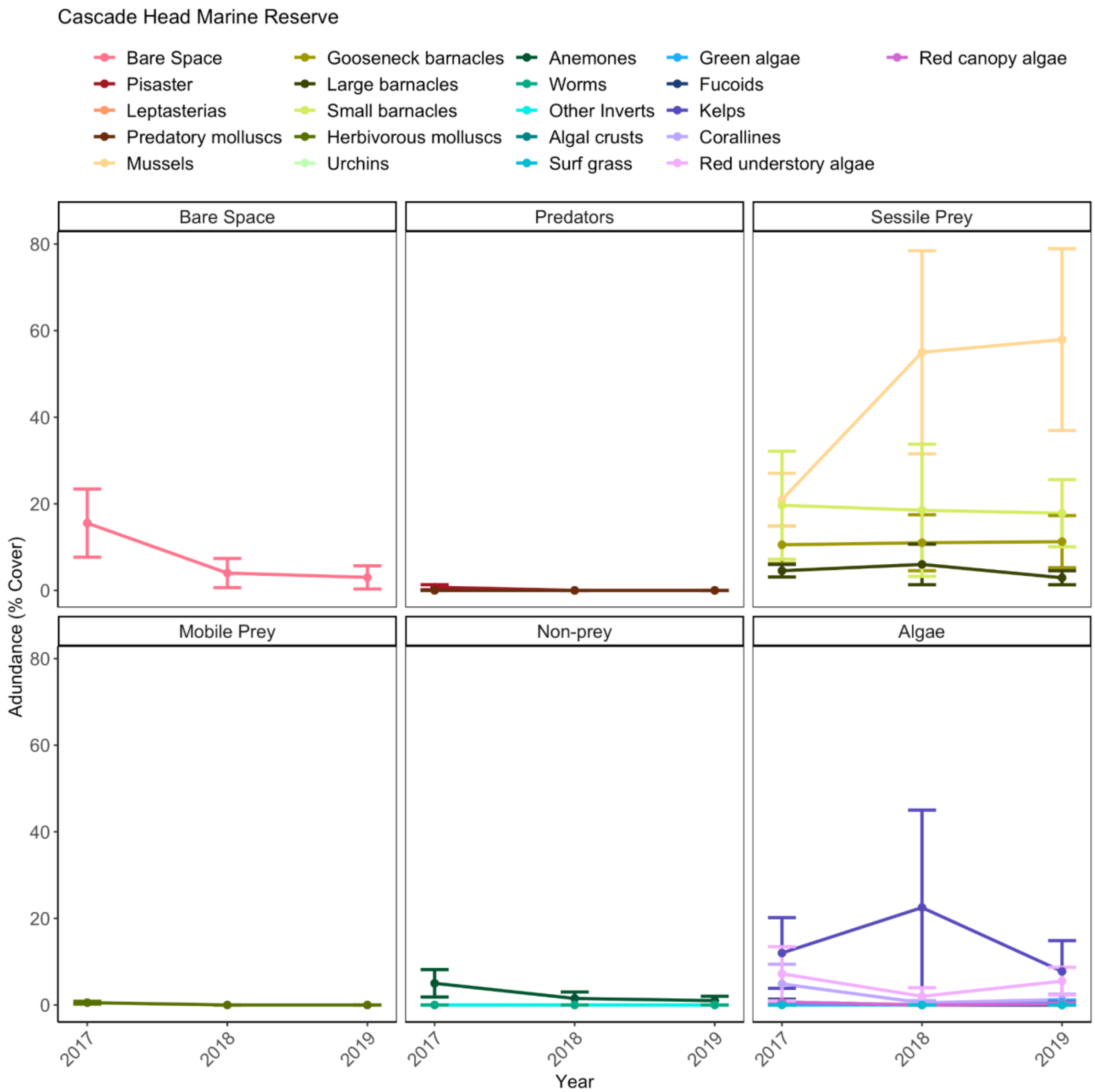

Figure 15. Average abundance (mean percent cover ± standard error) of functional groups in each transect over time in Cascade Head Marine Reserve.

4.3.3 Effect of SSWD on Biodiversity in Cascade Head Marine Reserve

Cascade Head Marine reserve showed a drop in biodiversity between 2017 and 2018 but stabilized between 2018 and 2019 (Fig. 9, Table 8; P = 0.835 and P = 0.614, respectively).

5 Takeaways and Discussion

5.1 Summary of Findings: Communities in Marine Reserves and Comparison Areas

Question 1) How do low zone intertidal communities vary with respect to a) community structure, b) key functional groups, and c) biodiversity among Marine Reserve and Comparison Areas?

Each Marine Reserve has a distinct ecological community structure in the intertidal low zone, and each likely reflects regional oceanographic features that can have strong impacts on local communities. Our finding that Cape Perpetua Marine Reserve was dominated by sessile invertebrates, that Otter Rock Marine Reserve was dominated by primary producers, and that Cascade Head was dominated by mussels, barnacles and kelps is not surprising, considering similar patterns found by Menge et al. (2015). In their study, geographic features like continental shelf width and meso-scale (10s of km) oceanographic patterns including upwelling, nutrients, and chlorophyll have profound effects on intertidal communities. Specifically, Cape Perpetua's high cover of invertebrates is likely linked to high rates of barnacle and mussel recruitment and growth, which are driven by algae blooms and very high chlorophyll concentrations at that cape, which is in turn a product of the intermittent upwelling regime and the wide continental shelf (Menge et al. 2015, Menge and Menge 2015). On the other hand, Otter Rock Marine Reserve's high cover of primary producers is likely linked to intermittent upwelling bringing high levels of nutrients to intertidal macrophytes, but the narrower continental shelf preventing invertebrates from recruiting in high densities and preventing phytoplankton blooms developing, similar to the nearby Fogarty Creek site they studied (Menge et al. 2015, Menge and Menge 2015). Menge et al. did not characterize the oceanography or shelf width of Cascade Head, but it is likely to be intermediate since the community structure at this site was intermediate to these other two Marine Reserves. Overall, the distinct communities at each Marine Reserve is likely a product of a distinct oceanographic regimes among the capes on which they are situated.

Despite our expectation that these differences in community structure would lead to differences in biodiversity, we found no biodiversity variation among reserves. Rather, many of the same species or taxa were present in all reserves, but their relative abundance changed, as described above. We had expected Cape Perpetua to have the highest biodiversity since it had the highest density of the keystone predator, but this was not the case. This suggests that either keystone predation at this site has weakened since SSWD, or that the keystone predator has a generally smaller effect on biodiversity at this site than the keystone hypothesis predicts.

Our data also show that Marine Reserves and their respective Comparison Areas had similar community structure and biodiversity, with only minor and often insignificant differences in the abundance of nearly all functional groups. Menge et al. (2015) also found that local-scale features (<10km) like species interactions and air and water temperature were somewhat less important for community structure than the meso-scale patterns described above. This may explain why communities in Marine Reserves and their respective Comparison Areas were very similar in our study. While the implementation of the Marine Reserves may protect some intertidal species like California mussels, purple sea urchins or gooseneck barnacles from being harvested by humans, no intertidal species in our study is heavily fished either commercially or recreationally. So it is not surprising that the Marine Reserves and Comparison Areas do not differ substantially. That said, it is very possible that pressure from one or more of these fisheries may increase in the future (Murray et al. 1999, Bingham et al. 2017), and the Marine Reserves may serve as an important refuge from these pressures.

5.2 Summary of Findings: Community Responses to Sea Star Wasting Disease

Question 2) How have low zone intertidal communities responded to SSWD with respect to *a) community structure, b) key functional groups, and c) biodiversity in Marine Reserve and Comparison Areas?*

To our surprise, we found no or only small changes in community structure, functional groups, and biodiversity in the the Marine Reserve and Comparison Areas following the decline in the keystone predator *Pisaster ochraceus* caused by the sea star wasting disease epidemic. At Cape Perpetua Marine Reserve, this stability is likely linked to the rapid recovery of seastars, which apparently prevented changes in mussel beds and therefore large changes in communities after SSWD (see *Intertidal Sea Stars* and *Mussel Bed Dynamics* for more). At Otter Rock and Cascade Head Marine Reserves, the lack of change in communities was more surprising, since sea star densities remain low. We only began surveying communities at these Reserves in 2017, so it is possible community changes occurred in 2014-2016, just after SSWD, and we did not detect them. However, inspection of the mussel beds in 2017 showed no evidence of recent change (S. Gravem, pers. obs), and communities at the Fogarty Creek Comparion Area also did not change substantially after 2015, so we believe it is more likely that these two Marine Reserve communities have not appreciably responded to SSWD. We did note lower biodiversity at Cascade Head Marine Reserve in 2017, which is consistent with the hypothesized decline in biodiversity after the loss of the keystone predator. But this did not coincide with increased mussel cover, so mussel takeover was not likely the driver of this decrease in biodiversity.

Overall, the three Marine Reserves and 2 Comparison Areas were remarkably resistant to community change after SSWD. We note that other sites in Oregon and California had larger shifts in mussel beds and community structure than any of the sites reported here (S. Gravem and B. Menge, unpublished data), so this lack of response does not necessarily mean *P. ochraceus* is a less effective keystone predator than Paine's studies suggest (1966, 1969, 1985). Rather, mechanisms of resistance or resilience to this event may be operating at these sites more so than others. For example, the sea star populations at Cape Perpetua Marine Reserve and Tokatee Klootchman Comparison Area were resilient to SSWS and rebounded within 2-3 years, so intertidal communities may not have had time to respond. Resistance to community change could also be increased by the presence of other predators like predatory snails (*Nucella ostrina* and *N. canaliculata*) and other sea stars (*Leptasterias* spp.), which are present at all of the areas studied here. The predators may compensate for the loss of the keystone by consuming mussels. Next, mussel recruitment must occur for mussel beds to expand and cause community change, and mussel recruitment was notably lower than usual at Cape Perpetua, Tokatee Klootchman, and Fogarty Creek in the years after SSWS (B. Menge, unpublished data). Finally, it may be that there has not been enough time for the communities to respond; Paine's seminal experiment was performed for about a decade, and these data only cover the 5 years after SSWD. PISCO is continuing this monitoring at 30 sites and is pursuing multiple studies to understand the time course of the response to SSWD. This ongoing investigation aims to uncover the mechanisms of resistance and resilience to this mortality event, and understand the generality of the keystone predation by *P. ochraceus* along the US West Coast.

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