Intertidal Mussel Bed Dynamics Report

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1 Introduction

In 2014, sea star wasting disease (SSWD) hit the Oregon Coast and caused severe declines in the ochre star *Pisaster ochraceus* in Oregon's Marine Reserves (see *Intertidal Sea Star Monitoring* for detailed analysis of this decline). The ochre star is the original keystone predator; it can promote biodiversity by eating its preferred mussel prey *Mytilus californianus*, thereby preventing mussel beds from invading the lower shore and competitively displacing a diverse array of macrophytes, their consumers, and other sessile invertebrates (Paine 1969). When SSWD caused sudden declines in the predatory ochre star, we expected 1) an increase in overall cover within the mussel beds, 2) that the mussels would become more dense toward the lower edges of the beds, and 3) that the lower limits of the beds would move down. Further, these mussel beds, once established, can become persistent alternative community states because the large size of mussels and the protection the dense bed provides reduces predation by sea stars (Paine and Trimble 2004). By comparing the time course and magnitude of this mussel take-over among sites, we can also understand whether the strength of keystone predation varied among sites before SSWD.

To track changes in mussel beds in response to *P. ochraceus* declines, ODFW Marine Reserves Program partnered with the Partnership for the Interdisciplinary Study of Coastal Oceans (PISCO) to track changes in mussel beds at intertidal sites in three Reserves and two Comparison Areas. These included yearly transects from the low to high intertidal at Cascade Head, Otter Rock and Cape Perpetua Marine Reserves and at Fogarty Creek (Otter Rock Comparison Area) and Tokatee Klootchman (Cape Perpetua Comparison Area). The goal of these mussel bed surveys was to track the changes in mussel cover, the vertical distribution of the mussel beds, and the limits of the mussel beds over time.

1.2 Research Questions

1. How has the cover of mussels changed since sea star wasting disease in each reserve and comparison area?

2. How have mussel bed limits changed since sea star wasting disease in each reserve and comparison area?

2 Methods

2.1 Data Collection

Mussel bed dynamics were surveyed annually at 5 sites (Fig. 1). The sites included three Marine Reserves, including Cape Perpetua, Otter Rock, and Cascade Head. The two Comparison Areas included Tokatee Klootchman (near Cape Perpetua) and Fogarty Creek (near Otter Rock). PISCO began the Cape Perpetua Marine Reserve, Fogarty Creek, and Tokatee Klootchman sites in 2015, and ODFW collaborated with PISCO to expand these surveys to Cascade Head and Otter Rock Marine Reserves in 2017.

Mussel cover was quantified using 0.25m^2 photoquadrats taken along 5 fixed transects spanning from below to above the mussel beds at each site (for more detail, see *Intertidal Methods*). Transects were repeated yearly in summer at each site, and we analyzed percent cover of mussels visually from photographs in the laboratory. We used surveying equipment to calculate the shore level (elevation) of each quadrat (for more detail, see *Intertidal Methods*). Between 2015 and 2020, we spent 21 days in the field and quantified 1,297 quadrats in 102 transects (Table 1).

Table 1. The number of mussel bed vertical transects and photoquadrats performed at each Marine Reserve and Comparison Area over time.

Area	Year	N Transects	N Quadrats
Cape Perpetua Marine Reserve	2015	5	76
	2016	5	63
	2017	5	66
	2018	5	62
	2019	5	64
Tokatee Klootchman Comparison Area	2015	5	42
	2016	5	48
	2017	4	40
	2018	5	46
	2019	5	53
Otter Rock Marine Reserve	2015	-	-
	2016	-	-
	2017	5	55
	2018	5	55
	2019	4	41
Fogarty Creek Comparison Area	2015	4	65
	2016	5	87
	2017	5	88
	2018	5	100
	2019	5	101
Cascade Head Marine Reserve	2015	-	-
	2016	-	-
	2017	5	56
	2018	5	45
	2019	5	44

2.2 Data Analysis

2.2.1 Data Preparation

We used JMP 15 and R, RStudio (v 1.2.5042) and the dplyr (v1.0.3) and tidyverse (v1.3.0) packages to prepare all data. Mussel cover data for each quadrat were bound together into one file, and site and shore level information were added using dplyr and tidyverse functions in R. When analyzing percent cover of mussels, we excluded quadrats below or above the shore level, outside which no mussels were seen in any year of the study at that site. This allowed us to analyze coverage only within the mussel zone rather than outside the beds.

To calculate the limits of the mussel beds over time, we used JMP 15. For each transect and year, we fit a normal distribution to the shore level of quadrats in each transect weighted by the mussel cover. This distribution was used to define the zone of the mussel bed in meters above mean lower low water; we defined the lower limit of the mussel bed as the 5th percentile of this distribution, the middle of the bed as the 50th percentile (median), and the upper limit of the bed as the 95th percentile.

2.2.2 Mussel Cover Analysis

We analyzed mussel cover over time using mixed effects generalized linear models (glmer package v1.1-23). We first averaged mussel cover among transects in each quadrat (dplyr v1.0.3) since these quadrats were not independent and we were interested in whether mussel cover changed over time in each bed as a whole. Since data collection at some sites began in 2015 (Cape Perpetua Marine Reserve, Fogarty Creek and Tokatee Klootchman) and others began in 2017 (Otter Rock Marine Reserve and Cascade Head Marine Reserve), we analyzed these 2 groups of sites separately. For each model, we tested the effects of site and year on mussel proportion cover, included transectID nested within site as a random variable, and specified binomial distributions.

2.2.3 Mussel Bed Limits Analysis

We analyzed changes in the vertical height of mussel limits in each transect over time using mixed effects generalized linear models (lme4 package v1.1-27.1). We tested the effects of year, site, and limit type (upper, middle and lower) on the vertical height of the bed limits and included transectID nested within site as a random variable.

3 Mussel Cover Results

Takeaway: Counter to our expectations after SSWD, no Marine Reserve nor Comparison Area showed increases in mussel percent cover within mussel beds.

Table 2. The mean, standard error and 95% confidence interval of the yearly percent mussel cover within mussel beds at 3 Marine Reserves and 2 Comparison Areas.

Area	Year	N Transects	Mean Mussel Cover (%)	SE Mussel Cover (%)	95% CI Mussel Cover (%)
Cape Perpetua Marine Reserve	2015	5	46.1	3.0	8.3
	2016	5	40.4	4.4	12.2
	2017	5	43.7	4.1	11.3
	2018	5	50.4	3.7	10.2
	2019	5	52.4	4.2	11.7
Tokatee Klootchman Comparison Area	2015	5	68.7	7.0	19.4
	2016	5	59.0	9.7	27.0
	2018	5	62.2	10.9	34.6
	2019	5	61.9	6.1	17.0
	2017	4	62.5	7.5	20.7
Otter Rock Marine Reserve	2017	5	51.6	8.1	22.5
	2018	5	52.2	8.8	24.5
	2019	4	50.2	11.5	36.6
Fogarty Creek Comparison Area	2015	4	74.1	5.7	18.0
	2016	5	62.4	6.2	17.3
	2017	5	63.6	7.0	19.3
	2018	5	60.1	7.9	21.9
	2019	5	63.2	7.5	20.8
Cascade Head Marine	2017	5	36.7	9.9	27.8
	2018	5	47.7	21.3	26.4
	2019	5	50.0	22.2	27.6

Table 3. Generalized linear model results testing the effects of site and year on mussel cover over time. a) Results Cape Perpetua Marine Reserve and 2 Comparison Areas from 2015-2019. b) Results for Cascade Head and Otter Rock Marine Reserve from 2017 - 2019.

a) Cape Perpetua, Tokatee Klootchman, and Fogarty Creek 2015-2019

Factor	ChiSq	df	P
Year	1.6	4	0.803
Site	5.8	2	0.054
Year*Site	3.9	8	0.863

b) Otter Rock and Cascade Head 2017-2019

Factor	ChiSq	df	P
Year	1.4	2	0.486
Site	0.2	1	0.666
Year*Site	1.9	2	0.378

3.1 Mussel Cover in Cape Perpetua Marine Reserve

Mussel cover within the beds at Cape Perpetua Marine Reserve were similar over time, only varying <12% (Fig. 1, Table 2, Table 3a). There is a slight upward trend in recent years that aligns with our hypothesis of increased mussels after sea star wasting, but the timing is surprising since the mussel predator *P. ochraceus* recovered in density at Cape Perpetua around 2017 (see Fig. 1 in *Intertidal Sea Star Monitoring Appendix)*. Mussel coverage at Cape Perpetua Marine Reserve was slightly lower but statistically similar to its Comparison Area at Tokatee Klootchman (Fig. 2, Table 3a, P = 0.470).

Tokatee Klootchman Comparison Area

Mussel coverage in Tokatee Klootchman Comparison Area showed little change since 2015 (Fig. 1, Table 2, Table 3a). The slight decline in cover from 2015-2016 was not significant (Table 3a), and is counter to expectations of increased mussel cover after SSWD.

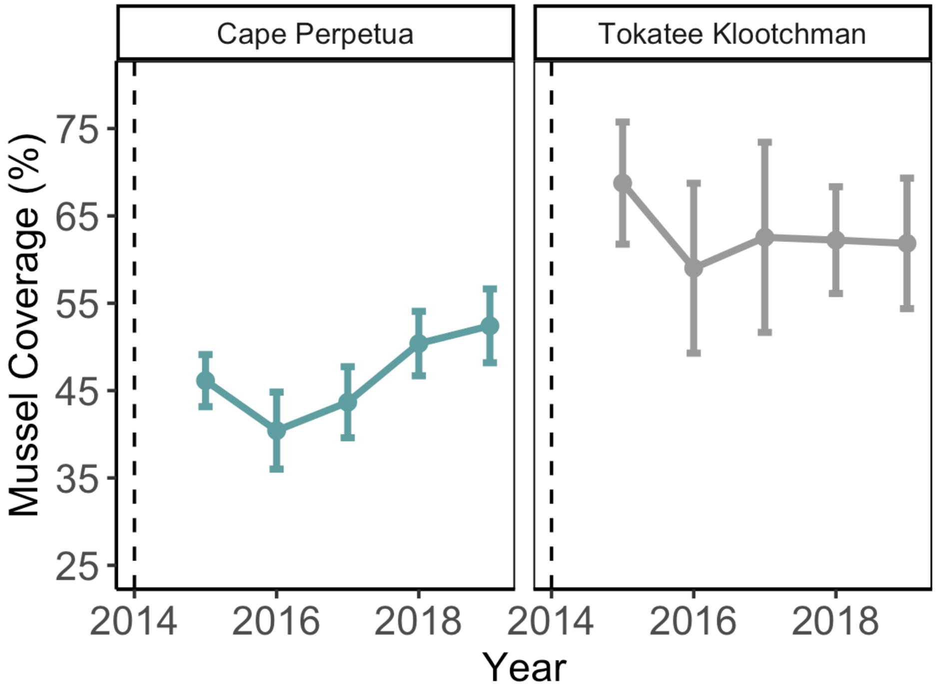

Figure 1. The percent cover (Mean ± SE) of mussels within mussel beds over time at Cape Perpetua Marine Reserve and Tokatee Klootchman Comparison Area. The dashed line in 2014 indicates the outbreak of sea star wasting disease.

3.2 Mussel Cover in Otter Rock Marine Reserve

Otter Rock Marine Reserve showed remarkably static bed coverage over time, with almost no change (Fig. 2, Table 2, Table 3b). The beds show less mussel coverage than those at Fogarty Creek Comparison Area (Fig. 2, Table 2). We have no data for mussel cover immediately after SSWD, so it is unclear whether bed coverage changed in the immediate years after the disease outbreak. Notably, these beds are unchanging from 2017 onwards despite quite low densities of the mussel predator *P. ochraceus* (see Fig. 3, *Intertidal Sea Star Monitoring*). Mean mussel coverage was consistently lower in Otter Rock Marine Reserve than Fogarty Creek Comparison Area, but 95% confidence intervals show that variation among transects was high in both areas (Table 2), suggesting that mussel bed coverage is patchy at both sites.

<u>Fogarty Creek Comparison Area</u>

Mussel coverage in Fogarty Creek Comparison Area showed little change since 2015 (Fig. 2, Table 2, Table 3a) . The slight decline in cover from 2015-2016 was not significant (Fig. 2, Table 3a), and is counter to expectations of increased mussel cover after SSWD.

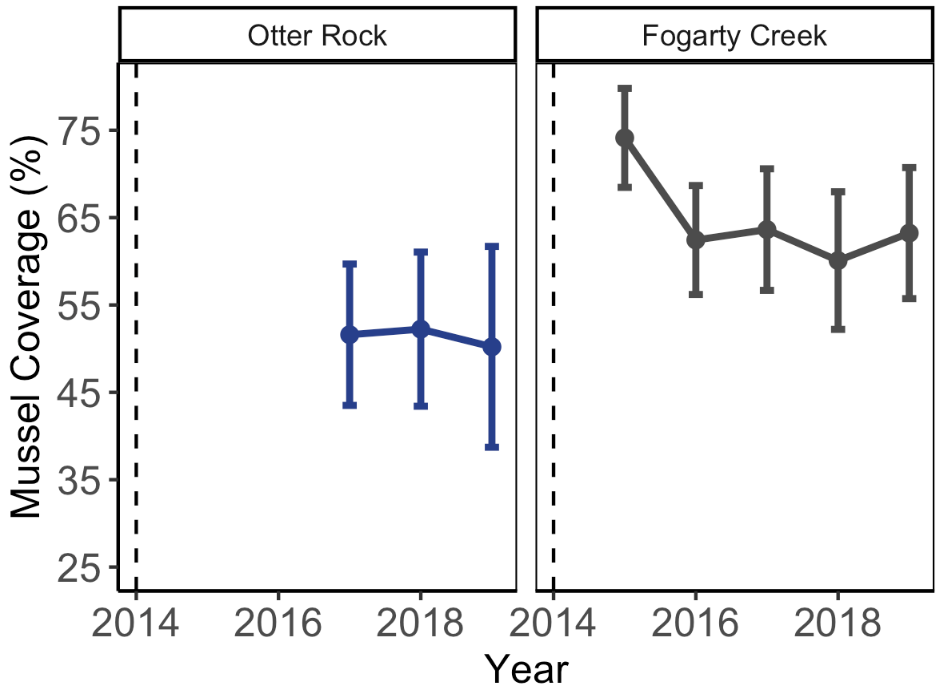

Figure 2. The percent cover (Mean ± SE) of mussels within mussel beds over time at Otter Rock Marine Reserve. The dashed line in 2014 indicates the outbreak of sea star wasting disease.

3.3 Mussel Cover in Cascade Head Marine Reserve

There was no significant change in mussel cover at Cascade Head Marine Reserve over time (Fig. 3, Table 3b). Pairwise comparisons among years showed that all years had similar mussel coverage ($P > 0.397$ for among years). This is likely due to the high variation in mussel coverage among transects at this site. Mussel cover was generally similar between Cascade Head, Otter Rock and Cape Perpetua Marine Reserves, but variability in mussel cover among transects was highest at Cascade Head, Marine Reserve (Table 2). This is likely caused by mussel beds being somewhat patchier at Cascade Head, especially in the upper part of the beds where the flat rock surface allows mussels to persist in shallow depressions and tidepools.

We have no data for mussel cover immediately after SSWD, so it is unclear whether bed coverage changed after the disease outbreak. While the direction of the trend aligns with our hypothesis that mussels should increase after SSWD, further monitoring is needed to determine whether mussel beds are changing over time. Note that there is high variability in bed coverage within this site (Table 2.)

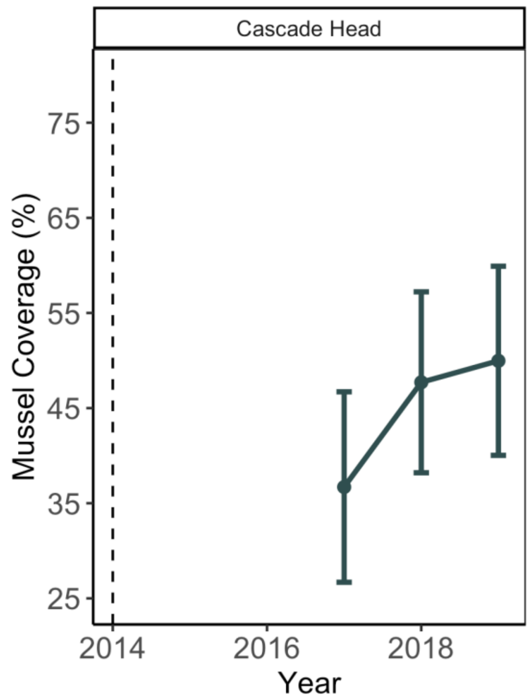

Figure 3. The percent cover (Mean ± SE) of mussels within mussel beds over time at Cascade Head Marine Reserve. The dashed line in 2014 indicates the outbreak of sea star wasting disease.

4 Mussel Bed Limits

Takeaway: Despite the expectation that mussel beds would move downward after SSWD killed the keystone predator *P. ochraceus*, we found no evidence that mussel lower, middle, nor upper limits changed since 2015 in any Marine Reserve or Comparison Area.

Takeaway: Comparing the three Marine Reserves, beds at Cape Perpetua are higher on shore, Beds at Otter Rock beds are lower on shore, and beds at Cascade Head are 'squeezed' vertically (inhabit a narrower zone). Reserve and their respective Comparison Area bed limits are generally similar to one another.

Table 4. The mean, standard error, and 95 % confidence intervals of shore heights (meters above mean lower low water) of the upper, middle and lower limit of mussel beds at 3 Marine Reserves (Cape Perpetua, Otter Rock and Cascade Head and 2 Comparison Areas).

Area	Limit Type	N Transects	Mean Shore Height	SE Shore Height	95% CI Shore Height
Cape Perpetua Marine Reserve	Upper Limit	25	3.86	0.06	0.07
	Middle of Bed		3.06	0.06	0.16
	Lower Limit		2.33	0.03	0.12
Tokatee Klootchman Comparison Area	Upper Limit	24	3.36	0.07	0.05
	Middle of Bed		2.89	0.08	0.12
	Lower Limit		1.99	0.05	0.08
Otter Rock Marine Reserve	Upper Limit	14	2.74	0.13	0.10
	Middle of Bed		1.98	0.07	0.16
	Lower Limit		1.37	0.11	0.14
Fogarty Creek Comparison Area	Upper Limit	24	3.39	0.04	0.27
	Middle of Bed		2.52	0.06	0.16
	Lower Limit		1.67	0.03	0.27
Cascade Head Marine Reserve	Upper Limit	11	3.35	0.05	0.23
	Middle of Bed		3.19	0.07	0.13
	Lower Limit		2.40	0.12	0.13

Table 5. Generalised linear model results testing the effects of year, site, and bed limit type on the shore level of mussel beds for 3 Marine Reserves (Cape Perpetua, Otter Rock and Cascade Head) and 2 Comparison Areas.

Factor	ChiSq	df	P
Year	2.7	1	0.099
Site	146.6	12	< 0.001
Limit	1950.0	10	< 0.001
Year * Limit	3.6	2	0.169
Year*Site	3.8	4	0.435
Site * Limit	69.8	8	< 0.001
Year * Site * Limit	4.8	8	0.775

4.1 Mussel Bed Limits in Cape Perpetua Marine Reserve

Mussel beds limits at Cape Perpetua have been stable since SSWD (Fig. 4, Table 4, Table 5). Interestingly, the upper limits of Cape Perpetua's mussel beds are significantly higher on shore than any other Reserve or Comparison Area (Table 4, Table 5, $P < 0.021$ for all pairwise comparisons), and the middle of the beds and the lower limits are higher on the shore than the respective limits at Otter Rock and Fogarty Creek ($P < 0.007$). Overall, Cape Perpetua's mussel beds are high on the shore.

Tokatee Klootchman Comparison Area

Similar to the Cape Perpetua Marine Reserve, mussel bed limits in Tokatee Klootchman Comparison Area did not change since SSWD (Fig. 4, Table 4, Table 5). The lower limit at Tokatee Klootchman did move vertically downward 0.54m, but the trend was not significant (Table 5). The height of the lower and middle mussel bed limits were similar to Cape Perpetua Marine Reserve ($P > 0.101$), but the upper limit is lower on shore ($P > 0.014$), likely because there is less rock topography at this site.

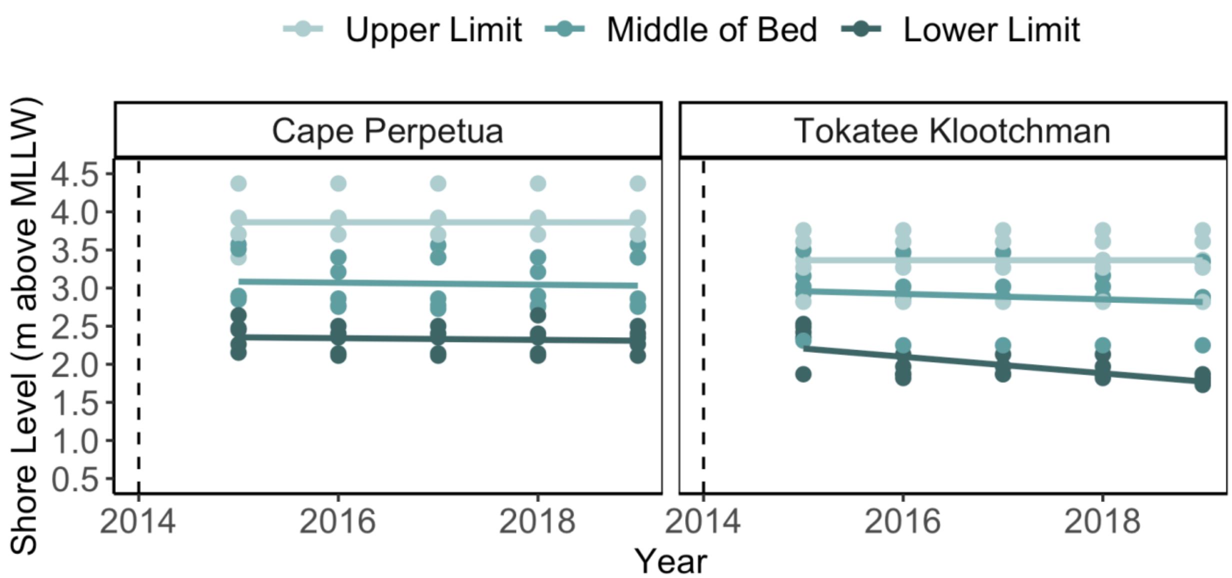

Figure 4. The height on shore of the upper, middle and lower limits of mussel beds over time at Cape Perpetua Marine Reserve and Tokatee Klootchman Comparison Area. The dashed line in 2014 indicates the outbreak of sea star wasting disease.

4.2 Mussel Bed Limits in Otter Rock Marine Reserve

Mussel beds limits at the Otter Rock Marine Reserve have remained unchanged since 2017 (Fig. 5, Table 4, Table 5), but we do not know whether they changed in the years just after sea star wasting disease. Mussel beds were markedly lower at Otter Rock than at any other area (Fig. 5, Table 4), and this was true of upper, middle and lower limits (Table 5, $P < 0.012$ for all pairwise comparisons to limits at other sites except lower limits at Fogarty Creek where $P = 0.4321$).

<u>Fogarty Creek Comparison Area</u>

Similar to the Otter Rock Marine Reserve, mussel bed limits in Fogarty Creek Comparison Area have not changed since SSWD (Fig. 5, Table 4, Table 5). Fogarty Creek had similar lower limits to the Otter Rock Marine Reserve ($P = 0.432$), but the upper limit and middle of the bed were higher than those at Otter Rock ($P > 0.012$).

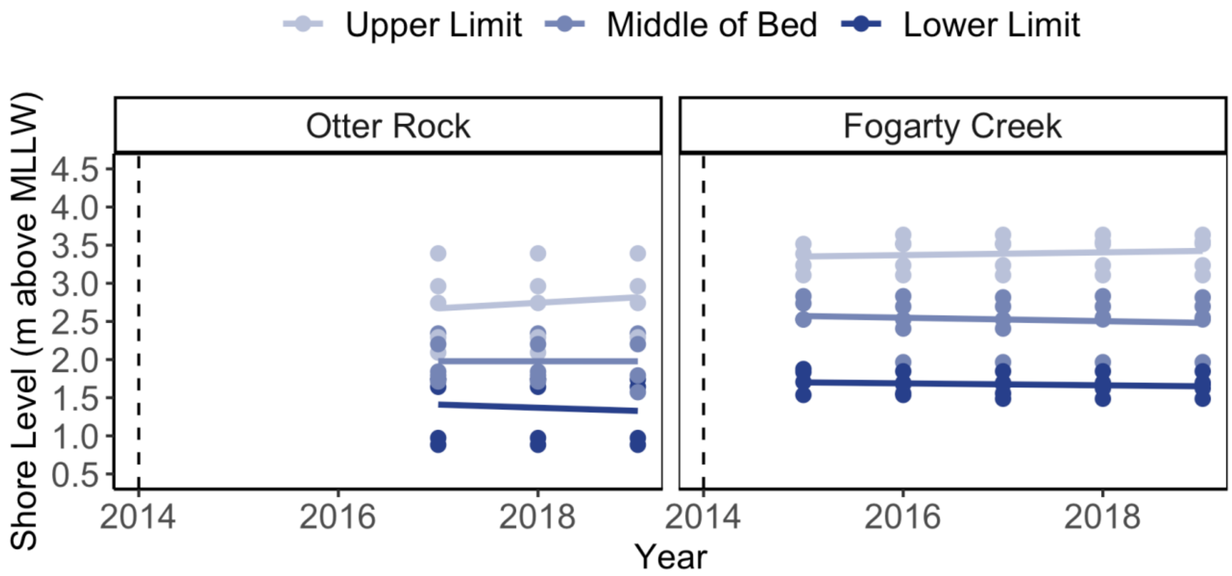

Figure 5. The height on shore of the upper, middle and lower limits of mussel beds over time at Otter Rock Marine Reserve and Fogarty Creek Comparison Area. The dashed line in 2014 indicates the outbreak of sea star wasting disease.

4.3 Mussel Bed Limits in Cascade Head Marine Reserve

Mussel bed limits have not changed over time at Cascade Head since 2017 (Fig. 6, Table 4, Table 5). However, we have no data for the years post SSWD, so it is possible that beds changed between 2014 and 2017 in the years after the disease. The lower limits and middles of the mussel beds at Cascade Head are higher on the shore than at either Otter Rock Marine Reserve or Fogarty Creek Comparison Area ($P < 0.006$), but are similar to Cape Perpetua Marine Reserve and Tokatee Klootchman Comparison Area ($P > 0.313$). However, the upper limit is lower on shore than at most of the other sites (Table 4), suggesting the mussel beds are somewhat “squeezed” at this location, and the mussels inhabit a narrower band within the intertidal zone at Cascade Head than in other areas.

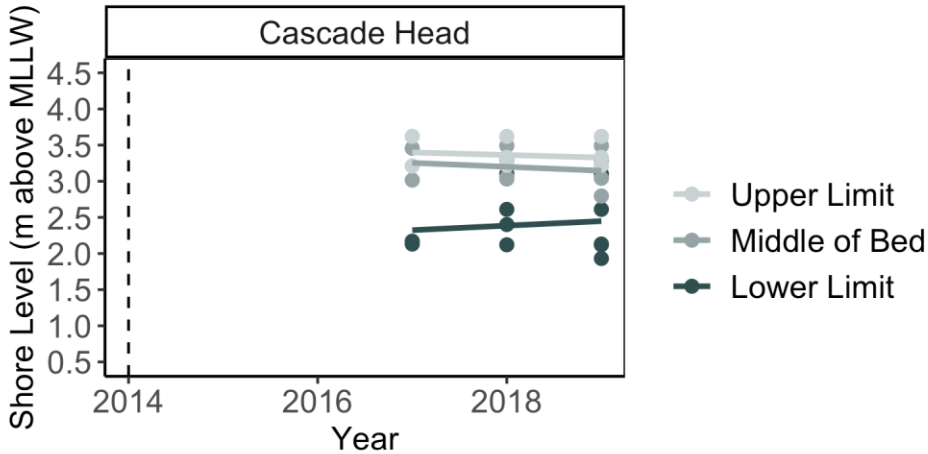

Figure 6. The height on shore of the upper, middle and lower limits of mussel beds over time at Cascade Head Marine Reserve. The dashed line in 2014 indicates the outbreak of sea star wasting disease.

5 Takeaways and Discussion

5.1 Summary of Findings

How have the 1) cover of mussels and 2) mussel bed limits changed since sea star wasting disease in each Reserve and Comparison Area?

The widespread decline in the keystone predator sea star *P. ochraceus* in Oregon did not result in increased mussel cover within beds nor seaward mussel bed movement at any Marine Reserve or associated Comparison Area. This is surprising because experimental manipulations have shown downward movement of mussel beds when *P. ochraceus* were removed (Paine 1969. Robles and Desharnais 2002, Robles et al. 2009). Indeed, the keystone predation concept was developed using experiments on the *Mytilus-Pisaster* interaction (Paine 1969). Thus, it may be that keystone predation may be generally less strong at these Oregon sites compared to the Washington (Paine 1969) and British Columbian (Robles et al. 2009) sites where this theory was developed. Alternatively, it may be that it takes multiple years of predation-free conditions for slow-growing mussels beds to respond, and sea stars have recovered too quickly for this mussel increase to take place. In particular, *P. ochraceus* densities recovered within a few years after SSWD at Cape Perpetua Marine Reserve and Tokatee Klootchman Comparison Area and seem to be recovering at Cascade Head Marine Reserve (see *Intertidal Sea Star Monitoring Appendix* for more detail).

It is well known that top-down forces like keystone-predation are contingent upon the strength of bottom-up process (Menge 2000). Thus, there may be other factors that are 'prerequisites' of strong keystone predation in the rocky intertidal. For example, the primary way that mussel beds move downward is when young mussels recruit into the low zone, then grow to form new beds over multiple years (Robles and Desharnais 2002). This mussel recruitment also can increase cover within the established beds when young recruits settle into gaps in the beds. Note that already-established adult mussels are sessile, and cannot easily move downward to take advantage of newly predator-free space. During the past 5-7 years, much of Oregon's coast, including some of the sites we cover here (Cape Perpetua Marine Reserve, Tokatee Klootchman Comparison Area, Fogarty Creek Comparison Area), have experienced anomalously low rates of mussel recruitment (B. Menge, unpublished data), which may be related to oceanographic patterns (Menge and Menge 2013). So, it is quite possible that mussel beds have not responded to sea star declines simply because mussel recruitment happened to be low at these sites just after SSWD. Indeed, PISCO sites near Cape Blanco, Oregon have had drastic changes in mussel bed movement since SSWD, and also experienced high mussel recruitment in the years after SSWD (B. Menge and S. Gravem, unpublished data). Overall, it appears that mussel beds in Marine Reserve and

Comparison Areas covered here are remarkably stable, and this may be a combined result of fairly rapid sea star recovery and low mussel recruitment since 2014.

6 References

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