

Whelk predators exhibit limited population responses and community effects following disease-driven declines of the keystone predator *Pisaster ochraceus*

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ABSTRACT: The recent outbreak of sea star wasting disease (SSWD) along the US West Coast, which has decimated the intertidal keystone predator *Pisaster ochraceus*, is predicted to change community structure by reducing predatory control of the competitively dominant mussel *Mytilus californianus*. However, keystone species effects can be variable, and the role of other predators without the keystone predator is not well understood. We were interested in the effects of subordinate whelk predators (*Nucella ostrina*, *N. canaliculata*) on prey following SSWD, and whelk population responses to declines of their predator and competitor *P. ochraceus*. We hypothesized that whelks would limit *M. californianus* establishment by reducing prey species facilitating its recruitment. We also predicted that whelk populations would increase and shift downshore with reduced predation threat. We addressed our questions using a whelk removal experiment started before the SSWD outbreak peak, and surveys of whelk distribution, abundance, and size structure. In the absence of *P. ochraceus*, whelks weakly facilitated, rather than limited, the establishment of the competitively dominant mussel but had few effects on other prey abundance. One year after SSWD onset, surveys indicated no change in whelk vertical distributions but revealed diverging patterns in abundance of whelk species. Whelk size structure shifted to smaller individuals, indicating a potentially lagged population response. Our results suggest that subordinate predators may not have strong short-term impacts on prey communities after keystone species decline. However, poor prey recruitment may have limited any whelk effects and population changes. Our study provides important context for understanding community dynamics following one of the largest marine disease outbreaks recorded.

KEY WORDS: Sea star wasting disease · SSWD · Rocky intertidal · Oregon · Subordinate predators · *Nucella* · *Mytilus* · Mesopredator release

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INTRODUCTION

Top predators often exert strong effects on prey that can cascade to lower trophic levels. As a result, the loss of top predators has coincided with changes to community structure with implications for conservation (Sergio et al. 2006, Ritchie & Johnson 2009), community stability (Rooney et al. 2006), ecosystem processes (Estes et al. 2011), and the delivery of ecosystem services (Estes et al. 2011, Karp & Daily 2014,

Atwood et al. 2015). Large community shifts have been observed in many ecosystems when top predators are removed, for example following otter extirpation in Alaska (Estes & Palmisano 1974), after the removal of wolves in Yellowstone National Park, USA (Ripple et al. 2001), in lakes with the removal of largemouth bass (Carpenter et al. 2001), and in rocky reefs following the disease-driven loss of *Pycnopoida helianthoides* (Schultz et al. 2016). These effects might be particularly strong if the top predator is a

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keystone species, whose preferential consumption of the competitively dominant prey results in a community impact disproportionate to keystone abundance (Paine 1969, Power et al. 1996, Menge & Sanford 2013). However, the broader effects of top predator loss and trophic cascades can also be mediated by the interplay of other abiotic (Wootton et al. 1996, Pace et al. 1999, Borer et al. 2005) and biotic processes (Shurin & Seabloom 2005, Finke & Denno 2005), such as resource supply and the number of basal species (Brose et al. 2005), and top predator loss does not always lead to large community effects (Polis et al. 2000). Given that top predators may be more vulnerable to extinction and population decline than lower trophic levels (Duffy 2003, Borrvall & Ebenman 2006, Sanders et al. 2013), it is particularly important to understand what factors and ecosystem characteristics alter the outcomes of top predator loss.

In systems with 3 trophic levels, subordinate predators may be able to compensate and maintain community structure following keystone species loss, particularly if they consume the same prey species. In the presence of a top predator, subordinate predators typically have weak effects on dominant prey species and limited ability to control community structure (Robles & Robb 1993, Menge et al. 1994). However, following the loss of a top predator, subordinate predators can compensate, increasing in abundance (as in mesopredator release, see Crooks & Soulé 1999, Prugh et al. 2009), body size (Menge et al. 1994), and effect (Navarrete & Menge 1996, Navarrete et al. 2000). In the context of intraguild predation, subordinate (or intermediate) predators can be especially responsive to the loss of the top predator because they are released not only from competition for the shared prey resource but also from the threat of consumption. As a result, subordinate predators can maintain trophic cascades by minimizing the effects of top predator loss.

Here, we tested the response of subordinate predators following disease-driven declines in a rocky intertidal keystone predator, the sea star *Pisaster ochraceus*. Since 2013, sea stars along the US West Coast have experienced drastic declines as the result of sea star wasting disease (SSWD) (www.seastarwasting.org). SSWD involves a sea star-associated densovirus (SSaDV) (Hewson et al. 2014), and the disease causes sea stars to undergo a progression of symptoms that include abnormally twisted arms, lesions, inability to maintain body turgor, loss of arms, and death. Previous outbreaks of the disease in the 1970s and 1980s in New England and California were localized and tended to affect a single species (Hewson et al. 2014,

Montecino-Latorre et al. 2016). The current outbreak of SSWD is unprecedented in its spatial and temporal extent and has affected at least 20 sea star species in the northeast Pacific (Hewson et al. 2014). SSWD symptoms appeared along the Oregon coast in April 2014 (prevalence was <1%), with peak disease prevalence of 60–80% observed by mid-summer 2014. By the start of 2015, disease prevalence had declined to 25% or less, but the density of *P. ochraceus* adults had declined 2- to 9-fold, and predation rate on mussels was significantly lower than the long-term average (Menge et al. 2016).

P. ochraceus was the first identified keystone species (Paine 1969), and it can exert strong effects on rocky intertidal community structure by preferentially consuming the competitively dominant mussel *Mytilus californianus* (Paine 1966, 1974). Rocky intertidal communities display strong patterns of biological zonation across a short tidal elevational range. On the US West Coast, the high zone is dominated by furoid algae and barnacles, the mid-zone by mussels, and the low zone by algae and surfgrass. While the upper limit of a mussel bed is determined largely by environmental stress (Menge & Branch 2001), Paine's (1966, 1969, 1974) experiments indicate that the lower extent of the mussel bed can be set by *P. ochraceus*, which consumes all *M. californianus* within its foraging range. By excluding mussels from the low zone, *P. ochraceus* can promote the establishment of a diverse low zone community dominated by macrophyte and invertebrate species. Since the original research by Paine, several studies have experimentally supported this keystone effect in other intertidal locations (Menge et al. 1994, Robles et al. 1995, Menge & Sanford 2013). However, exceptions exist, and several other factors can influence the strength of predation by *P. ochraceus* on *M. californianus*, such as temperature (Sanford 1999, Pincebourde et al. 2008), wave exposure (Menge et al. 1994), and mussel recruitment (Menge et al. 1994). In these contexts, the community effects of *P. ochraceus* loss would be less acute.

In other cases, the presence of other predators in the intertidal food web may be able to limit the impacts of *P. ochraceus* declines. *P. ochraceus* co-occurs with several subordinate predator species that could exhibit compensatory responses in its relative absence, including the gastropod whelks *Nucella canaliculata* and *N. ostrina* and the smaller sea star *Leptasterias* spp. Both whelk species are consumed by *P. ochraceus* (Navarrete et al. 2000) and share multiple prey species with the keystone predator. However, because whelks do not generally feed on the domi-

nant *M. californianus* along Oregon rocky intertidal shores (Sanford et al. 2003), they would not be able to exert compensatory effects via the mechanism of direct consumption. Instead, whelks could limit *M. californianus* establishment in the low zone through consumption of early- and mid-successional species. *M. californianus* avoids recruitment to bare rock, and prefers to recruit to areas with adult *M. californianus* (Paine 1974), the mid-successional mussel *M. trossulus* (Petersen 1984), filamentous algae such as *Endocladia muricata* (Paine 1974), and barnacles such as *Balanus glandula* and *Chthamalus dalli* (Berlow 1997, Gouhier et al. 2011, Menge et al. 2011). If subordinate predators influence the low zone abundance of these species, it is possible that they may prevent *M. californianus* recruitment and eventual mussel bed establishment. However, once recruited, *M. californianus* faces spatial competition from the other prey species (i.e. the interaction shifts from facilitative to competitive), and consumption of prey species by subordinate predators may reduce competition (see Navarrete & Menge 1996).

Following the SSWD-driven decline in the key-stone predator *P. ochraceus*, we explored: (1) the impact of subordinate whelk predators on prey community structure, and (2) their population-level responses to presumed reductions in competition and consumptive pressure. We used a combination of surveys and an experimental manipulation to assess changes in whelk populations and their potential impacts on prey community structure in the context of SSWD (before and after peak disease prevalence). We hypothesized that whelks would exert negative effects on *M. californianus* in the absence of *P. ochraceus* by limiting recruitment-facilitating species. An alternative hypothesis was that if *M. californianus* were able to recruit, whelks could facilitate the recruits by consuming spatial competitors. We also hypothesized that subordinate predators would increase in population abundance because of reduced predation and more resources. These conditions could also change mean whelk length, but hypotheses might reflect changes in reproductive success, which would shift the mean length to smaller; increased growth or survival of existing individuals, which would increase the mean length; or a combination of both factors. Previous research indicated that whelks became larger in the absence of *P. ochraceus* (Navarrete & Menge 1996), so we hypothesized that the same would occur following SSWD. Finally, we predicted that whelk predators would shift their spatial distribution lower on the shore in order to utilize resources in an area previously dominated by *P. ochraceus*.

MATERIALS AND METHODS

Study system

Our study used 4 sites along the Oregon coast: Strawberry Hill (44.250° N, 124.115° W) and Yachats Beach (44.319° N, 124.109° W), located on Cape Perpetua, and Fogarty Creek (44.837° N, 124.0587° W) and Boiler Bay (44.832° N, 124.061° W) located on Cape Foulweather (Fig. 1). Cape Perpetua is a rocky headland adjacent to a wide continental shelf offshore that promotes retention of propagules such as larvae and phytoplankton (Menge et al. 2015). As a result, Cape Perpetua intertidal sites are characterized by high phytoplankton productivity and high recruitment of invertebrates (Menge et al. 1997, 2004, 2015). Cape Foulweather, in contrast, is characterized by a narrower offshore continental shelf, which leads to reduced larval retention, lower inver-

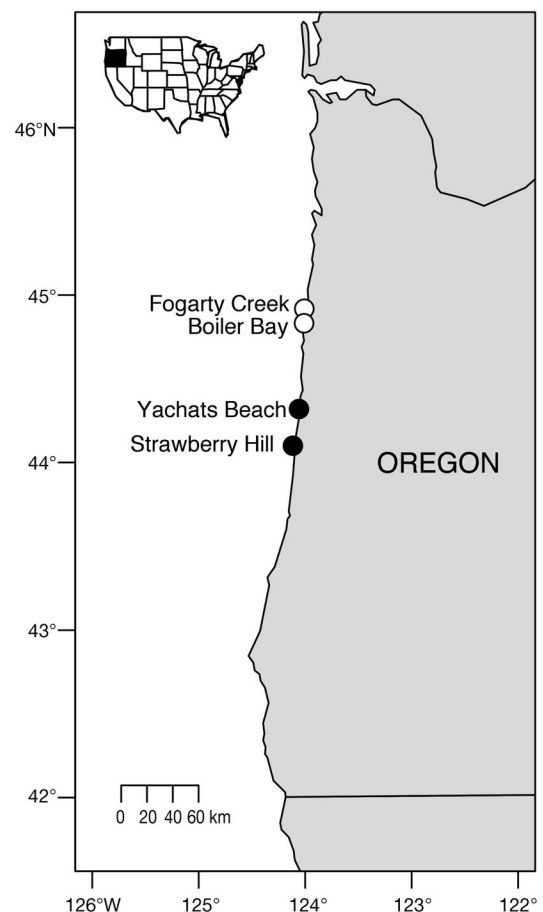


Fig. 1. Study sites in Oregon (USA). Black symbols indicate sites where both surveys and experiments were conducted, while white symbols show sites with only surveys. Fogarty Creek and Boiler Bay sites are on Cape Foulweather, while Yachats Beach and Strawberry Hill sites are on Cape Perpetua

tebrate abundance, and high macrophyte abundance. Prior to the onset of SSWD, densities of *Pisaster ochraceus* at the site scale were as high as 8 ind. m⁻² at Cape Perpetua and 4 ind. m⁻² at Cape Foulweather (Menge et al. 2016).

Subordinate predator removal experiment

To assess the effects of subordinate predators in the context of low keystone predation, we conducted a factorial removal experiment at 2 intertidal sites located on Cape Perpetua, Oregon (Strawberry Hill and Yachats Beach, see Fig. 1). We predicted that whelk predators would affect establishment of the dominant mussel, *Mytilus californianus*, by consuming the mid-successional prey species that facilitate its recruitment. Hence, we chose to follow prey dynamics from a mid-successional stage by placing plots where cover of the mussel *M. trossulus* and several barnacle species were high. Because observations showed that all predators aggregated at these dense prey patches, this mid-successional community is where we expected to see the greatest effects of subordinate predators on the prey community following SSWD. We originally examined the effects of 2 groups of subordinate predators, viz. gastropod whelks *Nucella canaliculata* and *N. ostrina* (W) and the smaller sea stars *Leptasterias* spp. (L), in a factorial design including 4 treatments: +W+L, -W+L, +W-L, and -W-L. However, *Leptasterias* spp. were rare in our plots, and treatments were combined to include control (+W) and whelk removal (-W) treatments only (see 'Data analysis' below). We note that our experiment tested the effects of subordinate predators at reduced *P. ochraceus* densities, rather than comparing their effects in the presence or absence of *P. ochraceus*.

We followed prey community structure over time in 10 replicate plots within each site at the upper edge of the low zone. The main treatment plots were 0.25 m² in size, and corners were marked with stainless steel lag screws. Each main plot was surrounded by 4 additional subplots adjacent to each plot side that acted as a buffer against predator reinvasion into the main plot. As tidal conditions permitted, we monitored plots either bi-weekly or monthly from experimental initiation in June 2014 through May 2015. At each monitoring, we counted the total number of each subordinate predator species (*N. canaliculata*, *N. ostrina*, and *Leptasterias* spp.), as well as any less common predators, such as the whelk *N. lamellosa*. When possible, we conducted a full monitoring with

counts and removals of predators in the main plot, the 4 adjacent subplots, and in the corners between subplots. On some occasions, particularly during winter months with limited site access, we only monitored the main plots. Based on short-term estimates from 2 removal plots at the Yachats Beach site in the summer of 2014, whelk reinvasion rates were 4 to 10% d⁻¹, although this is likely an overestimate of reinvasion at Strawberry Hill, where there are fewer whelks, and in the winter months, when whelk numbers decline. All removal of whelks and *Leptasterias* spp. was conducted using forceps, and removed predators were relocated away from the plot area. In plots without removals, we mimicked the use of forceps (by scraping the substrate lightly) while counting subordinate predators to limit the possibility that the physical action of predator removal would influence our results. Although SSWD caused declines in *P. ochraceus* densities, it did not extirpate the species entirely from our sites. We recorded and relocated any *P. ochraceus* within each plot, as well as any adult and juvenile *P. ochraceus* from a 3 m radius around each plot.

Photo analysis of prey communities

We monitored changes in prey community structure across experimental treatments over time photographically. On each monitoring visit, we photographed each plot, including a quadrat to provide a grid for estimating cover of prey species. Photo analysis was conducted at 4 time points: June 2014, September 2014, February 2015, and May 2015. Percent cover of *M. californianus* and several groups of mid-successional prey species including *M. trossulus* and the barnacles *Balanus glandula*, *Semibalanus cariosus*, *Chthamalus dalli*, *Pollicipes polymerus*, and *B. nubilus* were visually estimated from the photographs as a metric of abundance (e.g. Dethier et al. 1993). *Mytilus* recruits less than ~5 mm long were too small to be identified to species and these were termed 'mussel recruits.' *M. californianus* generally forms characteristic ridges on the shell at ~10 mm in length while *M. trossulus* remain relatively smooth at all sizes, so larger individuals could be distinguished. Recently metamorphosed barnacle recruits were also not identifiable to species and were categorized as 'barnacle recruits.'

Because other low intertidal zone organisms were likely to respond to variation in the abundance of mussels and barnacles, we quantified the abundance of macrophytes, anemones (*Anthopleura elegantissima*

and *A. xanthogrammica*), and sponges. Macrophytes were sorted into functional groups including crusts, turf-forming algae, and canopy-forming algae and surfgrasses. Overall, the cover of macrophytes was low in our plots throughout the experiment. We also quantified the abundance of non-focal mobile invertebrates including sea urchins (*Strongylocentrotus purpuratus*), chitons (e.g. *Katharina tunicata*, *Tonicella lineata*, *Mopalia* spp.), and limpets (*Lottia* spp.).

Surveys of subordinate predator distribution

Under reduced keystone predation, we predicted that whelk predators would shift toward foraging lower down on the shore in response to reduced consumptive pressure and increased resource density. We tested for changes in the vertical distribution of whelks from April to September of 2014 (before and after peak SSWD incidence in *P. ochraceus*) and in January and July of 2015 (when incidence of SSWD was low and adult sea star densities had been fully reduced) using vertical transect surveys. In our surveys, we quantified the density of whelks, *Leptasterias* spp., and any *P. ochraceus* within 5 intertidal zones at 4 sites. These zones were defined by ecological community type rather than absolute tide height, and included (from low to high on the shore): the upper algal zone dominated by algae and barnacles, the lower edge of the mussel bed, the middle section of mussel bed, the upper edge of the mussel bed, and the high zone dominated by barnacles and furoid algae. In some cases where *M. trossulus* was abundant within the upper algal zone, we conducted additional quadrats to target this zone specifically.

At each of 4 sites (Boiler Bay, Fogarty Creek, Strawberry Hill, and Yachats Beach, see Fig. 1), we conducted surveys using 5 replicate transect lines that ran vertically along the shore. These transect lines were marked at both ends with stainless steel lag screw. Within each transect, we measured density in one 0.25 m² quadrat within each of the 5 ecological zones, recording the distance of each quadrat along the transect line for consistency over temporally repeated sampling. Because we expected to see the greatest changes due to SSWD in the ecological zones at lower heights where *P. ochraceus* had previously been abundant, we measured predator density in additional quadrats in the upper algal zone and the lower edge of the mussel bed. This was done using a horizontal transect line that ran perpendicular from the low point of each vertical transect line described above forming an inverted 'T' shape (see Fig. S1 in

the Supplement at www.int-res.com/articles/suppl/m570p015_supp.pdf). Along each of the 5 replicate horizontal transect lines, we included 4 quadrats in the upper algal zone and 4 in the lower edge of the mussel bed. Surveys were mostly conducted during morning low tides and, when possible, we attempted to finish all 4 sites within a single tide series (~1 wk). We recorded the tidal height of each quadrat in July 2015 relative to Mean Lower Low Water (MLLW) using a laser level and stadia rod to measure the height of each plot above reference measurements at the water line in centimeters (Pincebourde et al. 2008).

Whelk size distributions and abundance

With *P. ochraceus* at low densities, whelks were presumably relieved from both competitive and consumptive pressure. Thus, we predicted that whelks would become more abundant and that size structure might shift as a result of greater food resources, less predation, and potential for increased reproductive success. We measured whelk size distributions at the same 4 sites used in the vertical abundance surveys. We haphazardly placed 0.0625 m² quadrats in the intertidal and extracted all whelks in the quadrat, taking care to include small individuals. Whelks were sorted by species and measured with calipers to the nearest millimeter. This sampling was done in a semi-stratified pattern vertically along the shore within areas of intermediate wave exposure until we had at least 200 individuals of each species at each site. Size distribution surveys were conducted in July in 2014 and 2015. When possible, all counts were conducted in a single day at each site in order to minimize the chance of repeatedly counting the same individuals.

Data analysis

In our experimental subordinate predator removals, *Leptasterias* spp. abundance was very low in all treatment plots (0 in most plots). We used ANOVAs and post hoc tests to determine whether (1) removals of only *Leptasterias* spp. (-L+W) were different from the no-removal treatment (+L+W), and (2) removals of only whelks (-W+L) were different from removals of both predators (-W-L) to test for an underlying *Leptasterias* treatment effect. The cumulative number of *Leptasterias* did not differ between the treatments in these comparisons (linear contrasts: *Leptasterias* removal vs. control in May 2015, $p = 0.877$). Because *Leptasterias* were so uncommon and had no effects,

we combined treatments (at the replicate level) to make a +whelks (i.e. +W+L and +W–L) and a –whelks (–W+L and –W–L) comparison.

To test the effects of whelks on prey species, we used linear mixed effects models to analyze the change in percent cover of each prey species using the 'nlme' package in R (Pinheiro et al. 2014). Models included a random effect for plot to account for repeated measurements over time. Percent cover data were converted to change in percent cover from experimental initiation in order to account for initial among-plot differences in cover. For some prey species (*M. californianus*, *P. polymerus*, and *S. cariosus*), we used logit-transformed change in percent cover data to improve normality prior to analysis. In all tests, we examined plots of residuals for assumptions of normality, homogeneity of variance, and independence of error terms. The final model for each prey species was determined by removing non-significant terms from a full model (which included treatment, time, site, and all interactions) and comparing the models with and without dropped terms using likelihood ratio tests (LRTs). We also used LRTs to determine if adding a weighted variance structure was necessary in cases where plots of residuals revealed heterogeneity of variance. Time was treated as a categorical variable because of non-linear relationships with change in percent cover and because there were only 3 points over which change in cover was measured. We made post hoc comparisons using the 'phia' package in R (De Rosario-Martinez 2015) using p-values obtained from a Holm-Bonferroni sequential correction.

To determine whether population abundances of each whelk species had changed from 2014 to 2015, we used negative binomial regression for survey count data, which were overdispersed, in the 'MASS' package (Venables & Ripley 2002) in R. In this case, a full model included a site \times year interaction, which was dropped if non-significant. Because more surveys were done in 2014 than in 2015, analyses compared data from all surveys and from surveys conducted only in July 2014 and July 2015. Since results were similar, we present the analysis of all survey data. To assess spatial changes in subordinate predator distributions, we ordered quadrats by measured tide height and analyzed differences in the cumulative distributions of whelk counts between the 2 years using 2-sample Kolmogorov-Smirnov tests with p-values bootstrapped using the package 'Matching' (Sekhon 2011) in R. For these tests, we used only time-matched survey data to minimize distributional changes due to season.

Whelk size distributions were normal and were analyzed using ANOVAs, which included terms for site, year, and site \times year. For *N. ostrina*, the site \times year interaction was not significant, so we used a Type II sums of squares ANOVA, as data were unbalanced. Pairwise contrasts of interest were examined using the 'phia' package. Significance was assessed at $\alpha = 0.05$ for all analyses. All analyses were performed using R version 3.3.1 (R Core Team 2014) and RStudio version 0.98.1085 (RStudio Team 2014).

RESULTS

Whelk removal experiment

The whelk removal treatments reduced the cumulative presence of whelks relative to controls once the experiment was initiated (see Fig. S2, Table S1 in the Supplement). Including the 0.5 m buffer surrounding each plot, we recorded and removed 31 929 whelks from removal plots and recorded 41 050 whelks in control plots over 11 mo. Overall, the total cover of all sessile organisms dropped from $87.7 \pm 7.4\%$ (SD) in June 2014 to $44 \pm 14.7\%$ cover on average in May 2015. These changes in total cover varied with site, time, and treatment (generalized linear mixed model [GLMM], 3-way interaction, $p = 0.023$).

We predicted that the cover of *Mytilus californianus* would be negatively influenced by whelks due to limited facilitation of mussel recruitment. However, by the final monitoring point, *M. californianus* cover was 2.11 \times higher when whelks were present than absent, although cover remained low in plots overall. The change from the initial cover was 33% larger in the control treatment, where more whelks were present, than in the whelk removal (Fig. 2A,B; GLMM treatment, $p = 0.043$; Tables S2 & S3 in the Supplement). Further, *M. californianus* cover increased over time in both treatments. The effect of time on the change in cover varied with site (GLMM site \times time interaction: $p = 0.0038$), with greater change in cover occurring at Strawberry Hill than at Yachats Beach by May 2015 ($p = 0.017$).

We expected that whelk presence would reduce cover of the remaining subdominant prey species, but whelk presence had mixed effects on prey. Change in cover for the barnacle *Balanus glandula* varied with site, treatment, and time (Fig. 2E,F; Tables S2 & S3; GLMM site \times time \times treatment interaction, $p = 0.011$). However, this interaction appeared to be driven by especially high recruitment at Yachats Beach in whelk removal treatments in September of 2014 (Fig. 2F). For

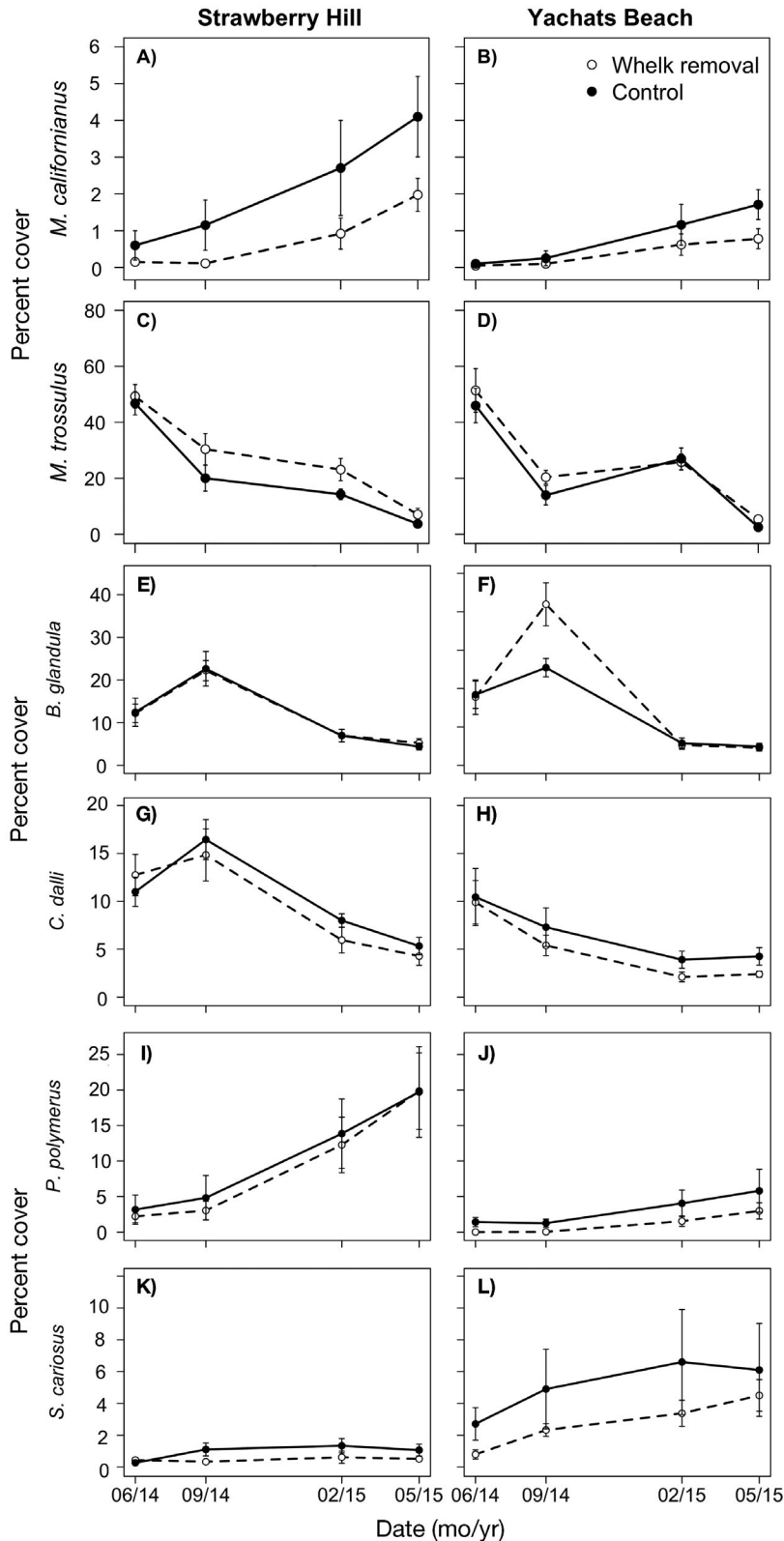


Fig. 2. Percent cover of (A, B) the dominant mussel *Mytilus californianus* and (C–L) subdominant species over time for whelk removals (dashed lines) and controls (solid line) at Strawberry Hill and Yachats Beach, Oregon. (C, D) Mussel *M. trossulus*; barnacles (E, F) *Balanus glandula*, (G, H) *Chthamalus dalli*, (I, J) *Pollicipes polymerus*, and (K, L) *Semibalanus cariosus*. Error bars are 1 SE

the rest of the prey species, changes in percent cover varied with site and time but not with treatment. For example, the change in percent cover for the mid-successional mussel *M. trossulus* became more negative over each time point (Fig. 2C,D; Tables S2 & S3; GLMM site \times time interaction, $p = 0.00018$); except for February 2015 at Yachats Beach, where it became less negative relative to starting values. Similar results were obtained for the barnacles *Chthamalus dalli* (GLMM, site \times time, $p < 0.0001$; Fig. 2G,H) and *Pollicipes polymerus* (GLMM, site \times time, $p = 0.00029$; Fig. 2I,J), where the effect of time depended on site. The barnacle *Semibalanus cariosus* also differed in abundance with site (more abundant at Yachats Beach: GLMM, site effect, $p = 0.0028$), and increased over time (Fig. 2K,L; contrasts: September 2014 vs. February 2015, $p = 0.04$, September 2014 vs. May 2015, $p = 0.0029$; Tables S2 & S3).

Whelk density surveys

In whelk surveys, abundance of *Nucella canaliculata* decreased over time with mean (\pm SE) densities of 18.98 ± 2.42 ind. m^{-2} in 2014 and 11.32 ± 1.76 ind. m^{-2} in 2015, but the effect of time was suggestive rather than significant (Fig. 3A; generalized linear model [GLM], date, $p = 0.062$; Table S4 in the Supplement). When excluding quadrats in the *M. trossulus* zone, which often led to aggregations of whelks in 2014 but not in 2015, there was no clear decrease in *N. canaliculata* over time (GLM, time, $p = 0.302$; Table S4). Only within the quadrats in the *M. trossulus* zone did densities of *N. canaliculata* decrease in 2015 relative to 2014 (GLM, year, $p = 0.013$). In contrast, *N. ostrina* abundance increased over time, with mean densities of 70.57 ± 5.04 ind. m^{-2} in 2014 versus 76.29 ± 6.93 ind. m^{-2} in 2015 (Fig. 3B; GLM, time effect with all dates included, $p = 0.0094$; Table S5 in the Supplement).

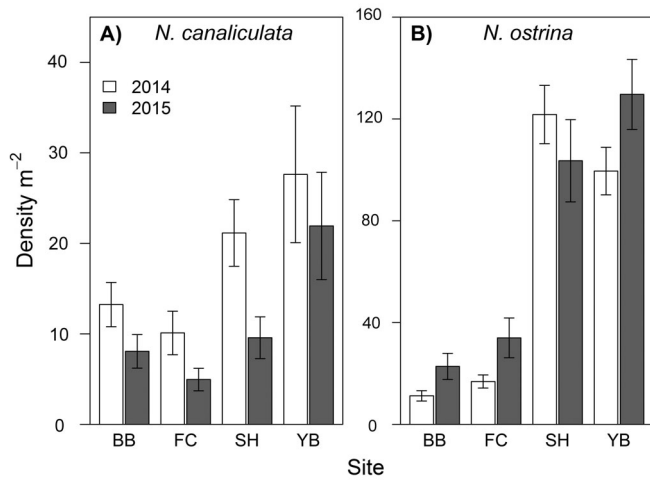


Fig. 3. Abundance at 4 survey sites of (A) *Nucella canaliculata* and (B) *N. ostrina* in 2014 (grey bars) and 2015 (white bars). Error bars are 1 SE. Fogarty Creek (FC) and Boiler Bay (BB) are sites on Cape Foulweather, Yachats Beach (YB) and Strawberry Hill (SH) are on Cape Perpetua (see Fig. 1). Data include quadrats from the *Mytilus trossulus* zone

Whelk size structure

We had hypothesized that, as shown in previous experiments (Navarrete & Menge 1996), mean whelk body lengths would increase in the absence of *Pisaster ochraceus*. However, mean length of both species decreased in 2015 relative to 2014. *N. canaliculata* was 2 mm smaller in 2015 than 2014, but this effect depended on site (Fig. 4; ANOVA, site \times year interaction, $F_{3,39} = 6.41$, $p = 0.0003$; Table 1), with length decreasing at all sites except Boiler Bay (contrast: 2014–2015 = 0.933, $df = 1$, $p = 0.07$; Table 2). For *N. ostrina*, mean body length also decreased by 2 mm from 2014 to 2015, and this effect was consistent across sites (Fig. 4; ANOVA: year, $F_{1,39} = 230.85$, $p < 0.0001$; Tables 3 & 4).

Whelk spatial patterns

We had hypothesized that whelk populations would shift lower on the shore in the absence of *P. ochraceus*, thus shifting the distribution of whelks across tide height between years. In general, our results did not support this hypothesis. The cumulative distributions across tidal elevation did not differ (non-significant 2-sample K-S tests, Table 5; Figs. S3 & S4 in the Supplement) for either species at most sites from 2014 to 2015, suggesting no downward shift in whelk populations. However, at Strawberry Hill the distribution of *N. canaliculata* moved down-shore in 2015 (K-S test, $D = 0.1574$, $p = 0.046$; Fig. S3).

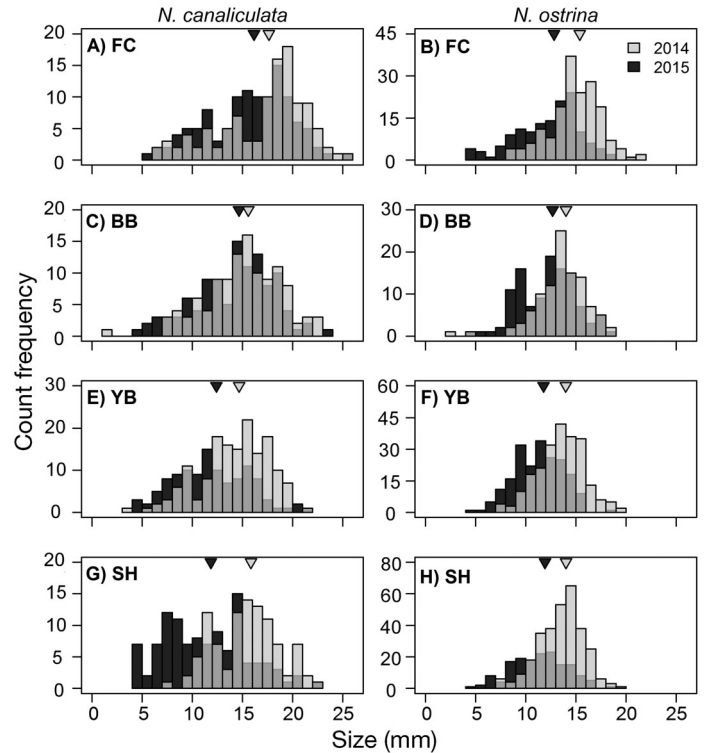


Fig. 4. Size distributions from 2014 and 2015 surveys for *Nucella canaliculata* and *N. ostrina* at (A, B) Fogarty Creek (FC), (C, D) Boiler Bay (BB), (E, F) Yachats Beach (YB), and (G, H) Strawberry Hill (SH). FC and BB are sites on Cape Foulweather, YB and SH are on Cape Perpetua (see Fig. 1). The 2 distributions are superimposed, with the region of overlap appearing as a medium grey color. Triangles at the top of each plot indicate the means for 2014 (light grey) and 2015 (dark grey)

DISCUSSION

Whelks had few direct effects on prey species in our study following declines in the keystone predator *Pisaster ochraceus* due to SSWD in Oregon. In fact, of the non-dominant prey species, only the abundance of *Balanus glandula* was affected by whelk presence. However, our results suggest that whelks facilitated establishment of the competitively dominant prey species *Mytilus californianus*. Thus, in the short-term

Table 1. Two-way ANOVA testing the effect of site and year on *Nucella canaliculata* body length. $R^2 = 0.1736$; **bold font** indicates significance at $\alpha = 0.05$

	df	SS	MS	F	p
Site	3	1530	511.2	34.3639	<0.0001
Year	1	1050	1052.83	70.7738	<0.0001
Site \times Year	3	286	95.43	6.4153	0.0003
Residuals	919	13671	14.88		

Table 2. Differences in *Nucella canaliculata* size (mm) by year. Tests of interaction contrasts from 'phia' package in R. p-values were adjusted using a Holm's correction (**bold** font indicates significance). The null hypothesis was that there would be no differences in sizes between years. BB: Boiler Bay, CF: Cape Foulweather, FC: Fogarty Creek, YB: Yachats Beach, CP: Cape Perpetua, SH: Strawberry Hill (see Fig. 1)

Site (Cape)	Estimate (2014–2015)	df	SS	F	p
BB (CF)	0.9332	1	48.8	3.2771	0.0706
FC (CF)	1.4779	1	122.7	8.2505	0.0083
YB (CP)	2.2660	1	336.5	22.6196	<0.0001
SH (CP)	3.9939	1	831.2	55.8726	<0.0001
Residuals		919	13671.0		

Table 3. Two-way ANOVA of the effect of site and year on *Nucella ostrina* body length. Type II sums of squares were used because data were unbalanced and there was no significant interaction. $R^2 = 0.1651$; **bold** font indicates significance at $\alpha = 0.05$

	df	SS	F	p
Site	3	339	17.044	<0.0001
Year	1	1530	230.845	<0.0001
Residuals	1410	9350		

at least, whelks in Oregon were unable to limit mussel establishment following the loss of a keystone predator. This result is in contrast to our original hypothesis that whelk predation may strengthen when the keystone *P. ochraceus* is removed (as seen by Menge et al. 1994, Navarrete & Menge 1996). We also found that whelks demonstrated distinct population-level differences during the emergence (2014) and persistence (2015) of SSWD. While whelk distributions showed almost no shifts across tidal elevation, population size structures shifted towards smaller individuals. Further, abundances of *Nucella ostrina* increased over time, whereas *N. canaliculata*

Table 4. Differences in *Nucella ostrina* size (mm) by year. Tests of interaction contrasts from 'phia' package in R. p-values were adjusted using a Holm's correction (**bold** font indicates significance at $\alpha = 0.05$). The null hypothesis was that there would be no differences in sizes between year. Site abbreviations as in Table 2

Site (Cape)	Estimate (2014–2015)	df	SS	F	p
BB (CF)	1.3343	1	96.3	14.599	0.0001
FC (CF)	2.5590	1	504.0	76.377	<0.0001
YB (CP)	2.2057	1	518.6	78.601	<0.0001
SH (CP)	2.0984	1	458.1	69.427	<0.0001
Residuals		1409	9297.2		

Table 5. Results from 2-sample Kolmogorov-Smirnov tests with bootstrapped p-values. The null hypothesis is that the whelk distributions (ordered over tidal elevation) from 2014 and 2015 are from the same empirical distribution function (EDF). The test statistic, D , is the maximum difference in value between the 2 EDFs. The alternative hypothesis is that the 2014 EDF is stochastically larger than the EDF from 2015 (i.e. it would lie below and to the right of the 2015 EDF) if whelks had shifted distributions towards lower tide heights in 2015. Result are from July 2014 and 2015 surveys only because of uneven sampling across years when all dates are included. Site abbreviations as in Table 2. **bold** font indicates significance at $\alpha = 0.05$

Species	Site (Cape)	D	p
<i>Nucella canaliculata</i>	FC (CF)	0.0769	0.474
	BB (CF)	0.1538	0.103
	YB (CP)	0.1029	0.371
	SH (CP)	0.1574	0.046
<i>N. ostrina</i>	FC (CF)	0.0615	0.603
	BB (CF)	0.0000	1.000
	YB (CP)	0.0882	0.527
	SH (CP)	0.0901	0.429

abundance patterns were driven by the presence of patches of the small mussel *M. trossulus*.

In conjunction with broader community predictions for the loss of *P. ochraceus* (Paine 1969), cover of the competitive dominant *M. californianus* increased in plots over time, though it remained low overall. Our finding that whelks promoted establishment of the competitive dominant *M. californianus* (i.e. cover of the mussel was higher in +W treatments) has been previously observed (Navarrete & Menge 1996, Berlow 1997, Wootton 2002), and may depend on a few factors. First, Oregon whelks do not typically consume *M. californianus*, particularly at large mussel size classes (Sanford et al. 2003). As a result, the direct effects of whelks are minimal, limiting their potential impact (as hypothesized for Oregon by Sanford et al. 2003). Instead, whelks consume several species that are spatial competitors of *M. californianus*, including the mussel *M. trossulus*, which also acts as an important settlement substratum for *M. californianus* (Paine 1974, Petersen 1984). However, we found no effect of whelk predation on *M. trossulus*, so the mechanism causing the indirect positive effect of whelks on *M. californianus* remains unclear in our study. Given that facilitation of *M. californianus* by whelks has been observed several times before, further research on the mechanism is warranted.

Generally, previous research suggests that the positive effect of whelks on *M. californianus* depends on timing and patterns of whelk predation (Navarrete & Menge 1996). Whelk predation must be weak enough so that whelks do not entirely eliminate patches of the mussel *M. trossulus* before late summer, allowing for *M. californianus* to recruit. Further, continued whelk predation on *M. trossulus* after the recruitment of *M. californianus* would reduce competition for *M. californianus* recruits as they grow (i.e. it could switch from a primarily negative interaction—predation—to include facilitation indirectly by reducing competition). This effect would occur for new *M. californianus* recruits, but adults already established in 2014 would also benefit from reduced competition as whelks consumed *M. trossulus*. Anecdotally, our 2014 data were consistent with this pattern; regardless of whelk presence, patches of adult *M. trossulus* were able to persist in the upper low zone through the winter and grow to large size (probably due to low sea star densities), but evidence of whelk predation on patches continued throughout that time period following recruitment of *M. californianus*.

In contrast to expectations that whelks are important predators of prey other than *M. californianus*, we saw few effects on other species. Dayton (1971) noted that whelks ate all *B. glandula* in experimental enclosures within 10 d in the San Juan Islands and consumed all *Mytilus* < 30 cm when allowed to feed in areas where *P. ochraceus* was experimentally excluded. In Oregon, whelks were able to limit increases in *M. trossulus* following *P. ochraceus* removal (Menge et al. 1994, Navarrete 1996). We propose several explanations for why we obtained different results. (1) We observed relatively rapid reinvasion of our removal treatments by whelks, so removal treatments reduced but did not eliminate whelk predation. Thus, although the cumulative impact of whelks over time was reduced, it is possible that our treatments were not sufficiently effective to reveal actual differences between removals and controls. However, our methods were similar to previous studies using manual removals of whelks within a similarly sized plot area (Navarrete & Menge 1996). We also observed that as the experiment progressed, most whelks reinvading removal plots were very small (~5 mm in size), suggesting that treatments effectively excluded larger individuals with the greatest impacts. (2) It is possible that differences would have emerged on longer timeframes had we extended the experiment beyond 11 mo. However, our experiment ran as long as previous studies that had shown whelk effects (Menge et al. 1994, Navarrete &

Menge 1996), so this explanation is not convincing either. (3) Most likely, recruitment (or survival of recruits over winter) of *M. trossulus* was anomalously low in 2014–2015, leading to near-absence of *M. trossulus* beds in 2015 (Fig. 5). Prior experiments have shown that the effects of *P. ochraceus* on whelks are primarily competitive and are mediated through reduction of *M. trossulus* (Navarrete et al. 2000). Previous removals of *P. ochraceus* at the Strawberry Hill site led to high colonization by *M. trossulus*, which were eventually controlled by whelks (Menge et al. 1994). In 2015, low *M. trossulus* abundances in the absence of *P. ochraceus* were unexpected and without precedent (B. Menge pers. obs.). In over 30 yr of research at these sites, *P. ochraceus* had typically consumed all *M. trossulus* within the low intertidal zone by summer's end. We do not know why either the recruitment or survival of *M. trossulus* was poor, but it likely affected the strength of whelk predation and compensation because the absence of sea stars did not increase access to valuable prey.

Low abundances of *M. trossulus* could limit the ability of the dominant mussel *M. californianus* to establish in the low zone by minimizing recruitment substrate (Paine 1974). However, we found that *M. californianus* cover increased, perhaps because both adults and recruits had reduced spatial competition from *M. trossulus* (with bare space increasing over time at both sites in both treatments). This result suggests that the environmental drivers of prey recruitment may have modified the role of whelks following SSWD (Fig. 6). *P. ochraceus* is only a keystone species when prey recruitment is high (Menge et al. 1994); likewise, low prey recruitment may limit the compensatory capacity of other predators without the keystone predator.

Limited whelk effects on prey communities could have also been driven by trait-mediated indirect interactions by the remaining *P. ochraceus* at our sites. Whelks, though rarely consumed by *P. ochraceus* (Sanford 1999), may still exhibit marked responses to its presence. Research in southern California found that whelks grew less and changed their feeding preferences in the presence of cues from *P. ochraceus* in a laboratory setting (Gosnell & Gaines 2012). Further, whelk responses to predators were non-linear with predator density, suggesting that predator presence may be more important than density (Gosnell & Gaines 2012). With approximately 20% of the *P. ochraceus* population remaining at each site, predator cues therefore may have been strong enough to retain a behaviorally mediated cascade in whelk predators. However, long-term obser-

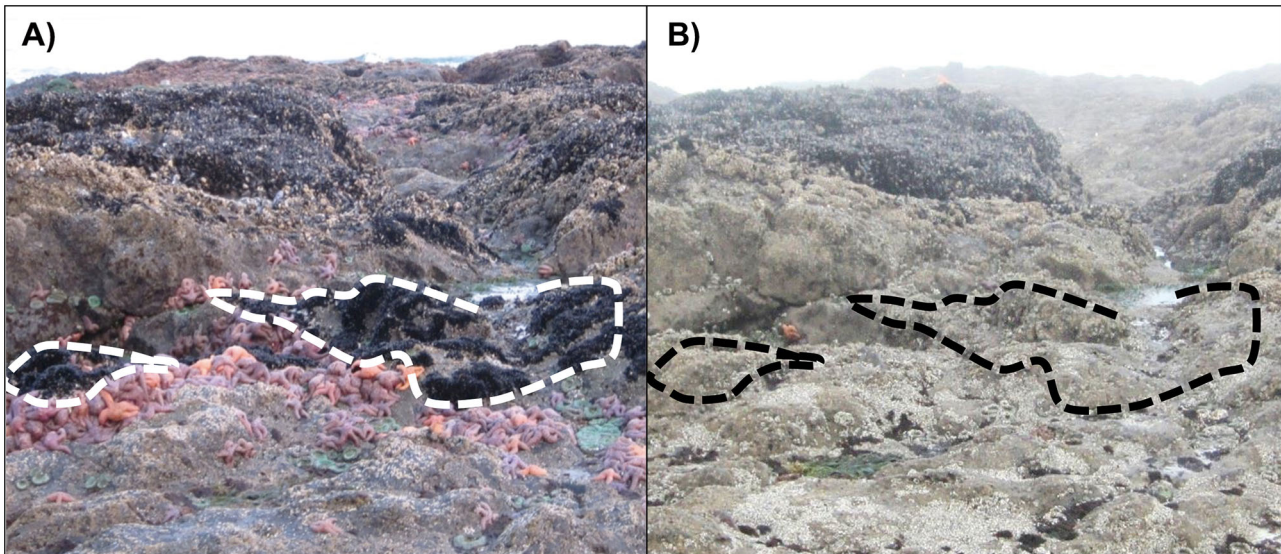


Fig. 5. Photograph of the Strawberry Hill site in (A) 2013 and (B) 2015. In 2013, there is a visible aggregation of *Pisaster ochraceus* feeding on mussels *Mytilus trossulus*, which form the black beds outlined with the dashed line. In 2015, few sea stars are visible, and there are no beds of *M. trossulus*. The space formerly occupied by the beds is indicated with the dashed area

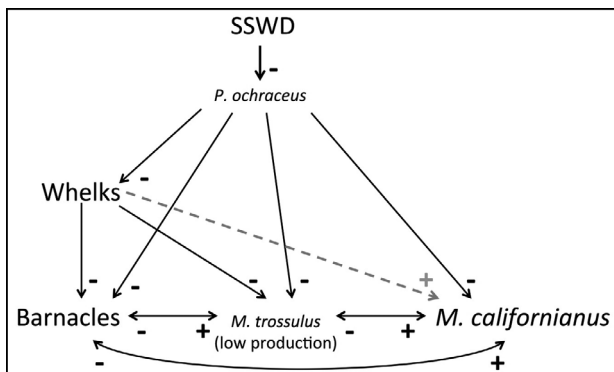


Fig. 6. Interaction web indicating the hypothesized effects of both sea star wasting disease (SSWD) and low *Mytilus trossulus* production. The web shows little effect of whelks on barnacles and *M. trossulus* (at low abundances) as well as the presence of an indirect positive effect of whelks on *M. californianus* (grey dashed arrow). The mechanism of this indirect positive effect is unclear given the limited effects of whelks on the spatial competitors of *M. californianus* adults and recruits. Dashes (-) and crosses (+) indicate negative and positive effects, respectively; arrows show the direction of the interaction(s), with double-sided arrows indicating reciprocal interactions

variations at our sites indicate that prior to the onset of SSWD, whelks were typically extremely abundant at Strawberry Hill and Yachats Beach and preyed heavily on *M. trossulus*, even when sea stars were present in high abundance and in close proximity (B. Menge pers. obs.). While trait-mediated effects of sea stars on whelks cannot be ruled out in our study, prior observations are not consistent with such an effect.

Our study did not include factorial treatments to look at effects of whelks in the presence and absence of *P. ochraceus*. Previous studies using this factorial approach have found that whelks have negligible effects in the presence of *P. ochraceus*, but they are important in the absence of the keystone (Navarrete & Menge 1996). Given the high disease incidence and the highly reduced density of adult *P. ochraceus*, we determined that such factorial manipulations were not advisable. We did, however, remove all sea stars found within or near our experimental plots, which should isolate the impacts of whelks from those of sea stars. Nonetheless, our results do differ from previous work, but were consistent at both study sites. This underscores the need for further study of what factors determine the outcome of whelk interactions with the prey community both with and without *P. ochraceus* and in the context of variable prey production.

Community dynamics implications

Subordinate consumers in other systems have also shown mixed responses to the loss of a keystone. In a long-term study tracking the removal of kangaroo rats from experimental enclosures in an arid system, Brown et al. (2001) found that other granivores in the system were unable to consume as much energy as the kangaroo rat identified as a keystone species. This lack of compensation persisted until a novel species of granivore colonized the enclosures from nearby areas

and assumed the keystone role. In other systems, however, subordinate predators can be important following top predator loss. The whelk *N. lapillus* displayed compensatory predation and delayed community changes when common eiders *Somateria mollissima*, which may act as keystone predators, were excluded from a rocky intertidal system in New Brunswick, Canada (Hamilton 2000). In the California Channel Islands, removal of the spiny lobster *Panulirus interruptus* induced a transition from a red algal turf assemblage to one dominated by *M. californianus*, but a whelk species that consumed *M. californianus* increased its predation on mussels when lobsters were removed (Robles & Robb 1993). Further, the transition to mussel bed required the loss of both lobsters and whelks, indicating support for diffuse predation by whelks through compensatory foraging shifts, although whelks were not able to control mussel populations entirely (Robles & Robb 1993).

In our study, *N. ostrina* increased in abundance while *N. canaliculata* remained at similar densities following the decline of *P. ochraceus*. These surveys are observational, following the ‘natural experiment’ of sea star wasting, so changes cannot be attributed directly to the disease. In other studies, whelk densities have increased following *P. ochraceus* removal (Menge et al. 1994, Navarrete & Menge 1996). We also found few elevational distribution changes in whelks between years. It is well known that whelks alter their elevational distribution seasonally and in response to wave action (Menge 1978), temperature (Hayford et al. 2015), and the presence of predators (Trussell et al. 2003). In other systems, subordinate species have altered their spatial distribution in response to release from a top predator (see examples in Ritchie & Johnson 2009). In our study, poor recruitment of *M. trossulus* could have limited vertical elevation shifts because the mussels are a preferred food item of *N. canaliculata*, and, without them, whelks would have less impetus to move into the low zone to forage. In 2014, we found the highest numbers of whelks aggregating around patches of *M. trossulus* in the low zone, with little aggregation occurring in 2015. Low *M. trossulus* abundance could also reduce population abundance of whelks. The converse of this trend occurred at sites in southern Oregon, where unusually high recruitment of *M. trossulus* following SSWD in 2015 resulted in large increases in *N. canaliculata* densities (B. Menge pers. obs.).

We found that the population size structure of both whelk species shifted towards smaller individuals. This could indicate several contrasting mechanisms for change in whelk populations. It could, for ex-

ample, indicate that whelks experienced increased reproductive success in 2015, thus increasing the number of small individuals. Increased survival of whelk recruits seems possible given that abundance of small prey (e.g. recent barnacle recruits and adults) was unusually high in the low intertidal during the study period. Alternatively, with the recruitment failure of *M. trossulus* at our sites, it is possible that growth rates of juvenile whelks were poor, and as a result the juvenile cohort was smaller in July 2015 than at the same time the previous year. In *N. ostrina*, smaller hatchlings grow more slowly than larger ones; if food resources were limited, it could reduce maternal investment in egg organic content and lead to smaller juveniles in the next year (Moran & Emlet 2001). In any case, our findings contrast with previous research showing increases in individual sizes of *N. canaliculata* following removal of *P. ochraceus* (Menge et al. 1994, Navarrete & Menge 1996). Whelk populations can also experience high mortality rates in response to environmental stress (Connell 1972), which we did not measure but could have affected size structure. It is also possible that the low abundance of *M. trossulus* could have limited the abundance of larger adult whelks, particularly of *N. canaliculata*, or caused them to retreat to deep within the mussel bed.

Conclusions

As the unprecedented outbreak of SSWD continues at low levels in 2017 along the US West Coast, there are opportunities for future research to inform our understanding of both the ecological consequences of the disease and of intertidal community dynamics following keystone predator loss. Evidence from the 2014–2015 outbreak of SSWD along the Oregon coast indicates that predation by *P. ochraceus* on *M. californianus*, as determined from predation rate experiments involving mussel transplants, was dramatically lower in 2014 than the mean value for 1990 to 2013 at our sites (Strawberry Hill: –15.15×, Yachats Beach: –6.4×, see Menge et al. 2016). The progression of the disease and the rate of *P. ochraceus* population recovery will be central for determining the community outcomes of SSWD, but in addition, it is critical to understand what factors may moderate the effects of keystone predator declines. Comparisons between whelk population and intertidal community changes in California, where whelks feed on *M. californianus* readily, and Oregon, where they do not, would be particularly powerful at clarifying the role of whelk predators.

Overall, we found that, in a 1 yr study, whelks exhibited a limited capacity to influence prey community structure when populations of the keystone predator were reduced by 80% in Oregon during a natural disease outbreak. This weak effect contrasted to prior experimental results, and seems likely to have resulted from unusual and unprecedented conditions, particularly the near absence of *M. trossulus* recruitment at our sites. Secondly, although we found that the presence of whelks facilitated the dominant mussel *M. californianus*, the effect was relatively small and the mechanism was not the same as previously observed (Navarrete & Menge 1996). The extent to which the reduced impact of a keystone predator persists and its longer-term consequences on intertidal community structure are worth continued investigation.

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