

**Grazing pressure on juvenile *Nereocystis luetkeana* sporophytes: potential top-down effects of the majid crab *Pugettia producta***

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## **Abstract**

The range and distribution of *Nereocystis luetkeana* kelp forests in the San Juan Islands have changed in the past 100 years. Urchin removal experiments designed to test the paradigm of top-down control of kelp forests by urchins in the San Juan Channel showed no significant differences in macroalgal density or community composition after urchins were removed, suggesting that grazing by other invertebrates may control kelp populations. Few studies have been completed on the effects of grazing by crabs like *Pugettia producta* on kelp forest communities. A caging experiment was conducted over 15 days in the field to compare the grazing impacts of *P. producta* to those of mesograzers in the kelp forest canopy on juvenile *Nereocystis* sporophytes. Six types of blocks were suspended off the Friday Harbor Labs breakwater in triplicate. Kelps were attached to blocks with 1) two different closed cages with 13 mm and 50 mm mesh, 2) two different open cages with 13 mm and 50 mm mesh, 3) a 13 mm mesh cage with an individual *P. producta*, or 4) no cage and exposed to grazing. At the end of the experiment, the amphitoid amphipod *Peramphithoe* was the most commonly seen mesograzer associated with the blocks. Significant differences in kelp mass and area change were observed between control blocks and crab-only blocks, implying that individual *P. producta* have a much greater impact on juvenile sporophyte survival than canopy mesograzers associated with the blocks.

## **Introduction**

The rocky subtidal zones of most temperate coasts are dominated by brown macroalgae in the order Laminariales, commonly called kelps (Dayton 1985). These

algae form complex, stratified, three-dimensional habitats known as kelp forests, which are among the most productive ecosystems on the planet. One kelp species, *Macrocystis pyrifera* can grow 20 meters in 80 days (North 1971). The ecology of kelp forests has also been well studied over the past 50 years (e.g. Paine and Vadas 1969, Duggins 1980, Foster 1990); they create habitat for many culturally and economically important species, engaged in complex ecological interactions.

*Nereocystis luetkeana* (bull kelp) is a canopy-forming annual species that provides habitat for a large number of fish and invertebrate species in rocky subtidal habitats of the northeast Pacific Ocean. *N. luetkeana* ranges from the coast of Alaska south to California, growing below the lowest low tide level to 18 m depth (Carney et al. 2005). It thrives in turbulent waters, which facilitate the uptake of nutrients across the thallus surface (Hurd and Stevens 1997). Like other kelps, *N. luetkeana* alternates generations between a microscopic, haploid gametophyte and a macroscopic, diploid sporophyte (Maxwell and Miller 1996). It is the sporophyte of the kelp that is the canopy-forming stage and is most susceptible to grazing, especially at a young age (see Henriquez et al. 2011 for information on kelp gametophyte grazing).

In California and Alaska, the most commonly accepted ecological paradigm for canopy-forming kelps assumes grazing determines kelp distribution and abundance, specifically grazing by sea urchins (*Strongylocentrotus* spp.). Urchin populations are in turn controlled through predation by sea otters (*Enhydra lutris*), indirectly maintaining a diverse macroalgal assemblage (Duggins 1980, Carter et al. 2007). However, urchins are not the only grazers of kelp; other species can have significant or even population-controlling top-down effects on kelp abundance and distribution. Chenelot and Konar

(2006), for example, found that the small gastropod *Lacuna vincta*, when present in large numbers, severely impacts the growth and development of juvenile *Nereocystis*.

In the San Juan Islands of Washington State, the distribution and abundance of *N. luetkeana* forests has changed over the past 100 years. San Juan kelp beds first surveyed in 1911 showed a decrease in total area by 53% and an average decrease in density of 35% in *Nereocystis* when surveyed 95 years later, while new beds were discovered outside of historically surveyed areas (Spencer 2006). These changes could be due to pollution, lack of sporophyte recruitment, increased levels of sedimentation and decreased available rocky substrate, grazing by invertebrates, or any combination of these factors (Dobkowski 2010).

One understudied grazer is *Pugettia producta*, the northern kelp crab. *P. producta* is a large species of majid (spider) crab found from Vancouver Island south to Santa Rosalia Bay off the California coast (Rathbun 1925). *P. producta* feeds on kelps, especially *Egregia menziesii* (Ricketts and Calvin 1968, Bracken and Stachowicz 2007) and *M. pyrifera* (Andrews 1945) in California and *N. luetkeana* and *Sargassum muticum* in the northern parts of its range (Morris et al. 1980). In the winter, when many of the crab's preferred annual algal foods are not present, the crabs may feed on barnacles, hydroids, and bryozoans (Knudsen 1964). As grazers, kelp crabs have been found to have significant top-down effects on kelps like *Egregia*, where selective grazing on the thallus decreases its high surface area to volume ratio and negatively affects the kelp's ability to uptake nutrients (Bracken and Stachowicz 2007).

Kelp crabs may have potential for top-down control of *Nereocystis*. In a 1996 urchin removal study in the San Juan Channel, macroalgae, including *Nereocystis*, did

not increase in numbers over the two-year period for which urchin grazing was eliminated, implying the influence of other invertebrate grazers, including *P. producta*, on macroalgal density (Carter et al. 2007). Juvenile sporophytes used in a 2010 study by Dobkowski on bull kelp growth in current and past kelp forest sites around San Juan Island sustained extensive damage after 10 days, and it was suggested that this damage may have been caused by *P. producta* (Dobkowski, pers. comm.). The purpose of this field experiment is to determine if: (1) grazing can be a significant factor influencing the survival of juvenile *N. luetkeana* sporophytes; and (2) *P. producta* has any significant impact on *Nereocystis* in comparison to other grazers.

## **Materials and Methods**

A caging experiment was conducted in the field off the dock at Friday Harbor Labs, San Juan Island, WA. Juvenile *Nereocystis* sporophytes were enclosed in either 1) closed cages with large or small mesh, 2) open cages with large or small mesh, 3) a small mesh cage with an individual *P. producta*, or 4) no cage and exposed to grazing. Eighteen juvenile sporophytes with a pneumatocyst diameter ranging from 3.0 to 5.0 cm and stipe lengths ranging from 20.2 to 144.5 cm were collected from the dock at Friday Harbor Labs and from the drifting stipe of an adult sporophyte. Individual kelps were laid out flat, photographed, blotted, and weighed wet before being affixed to eighteen 14x19x19 cm hollow concrete blocks using methods described by Dobkowski (2010). Each kelp was assigned to one of six treatment blocks: uncaged control blocks (hereafter referred to as uncaged), caged blocks with open sides and 13 mm mesh (13 mm open), caged blocks with open sides and 50 mm mesh (50 mm open), closed caged blocks with 13 mm mesh

(13 mm closed), closed caged blocks with 50 mm mesh (50 mm closed), and closed caged blocks with 13 mm mesh and one *P. producta* inside (crab). A summary of the different blocks can be seen in Table 1. Crabs were collected from a variety of locations, and notes were taken on dimensions, sex and overall state before placement in the cages. In addition to the living juvenile kelps, sporophyte blades of roughly 300 cm<sup>2</sup> were blotted and weighed and placed in the cages with the crabs to keep them satisfied over the course of the experiment. In the caged treatments, the cage consisted of a plastic meshwork wrapped around the block and supported by steel wire, with a total height of 34 cm. The blocks were assigned to random locations off of the south FHL breakwater and suspended at a depth of 2 m below the water's surface. Kelp source and the composition, density, and approximate age of the macroalgal canopy above the blocks were recorded.

Every five days over a 15-day period, the blocks were briefly taken to the surface for observations of sporophyte and crab condition and position, cage fouling, associated animals, and other factors; diatom films were removed from the walls of caged treatments with a brush. Initial blade area, stipe length, and pneumatocyst diameter were measured from photographs using ImageJ. At the end of the 15-day period, the sporophytes were re-photographed, weighed again, and re-analyzed in ImageJ. Observations on associated animals, overall sporophyte stage, and any evidence of grazing were recorded in words and pictures. Grazing marks were compared to photographs of damage to juvenile sporophytes incurred in the lab by various grazer species, including *P. producta*.

Changes in blade area and mass were recorded and analyzed using R. Most analyses were conducted using a one-way ANOVA, with significance levels of pairwise tests determined using a Tukey Honest Significant Difference test.

**Table 1: Summary of blocks**

Block	Purpose	n
Uncaged	Shows effects of all grazers in a natural setting	3
Open 13 mm cage (13 mm open)	Accounts for shading effects of 13 mm mesh	3
Open 50 mm cage (50 mm open)	Accounts for shading effects of 50 mm mesh	3
Closed 13 mm cage (13 mm closed)	Excludes medium to large grazers	3
Closed 50 mm cage (50 mm closed)	Excludes large grazers	3
Enclosed crab (crab)	Directly demonstrates effect of <i>P. producta</i> on <i>N. luetkeana</i>	3

## Results

A significant positive correlation was found between blade area change and mass change for all treatments ( $R^2 = 0.60$ ,  $p < 0.001$ ,  $F = 82.13$ , Fig. 1). Individuals on all blocks except the crab block experienced an average net increase in mass. The uncaged control blocks showed the most growth with an average 205.5% increase in mass. In the crab block, the average mass decreased by 58.9% (Fig. 2). Significant differences in mass change were observed between the crab and 50 mm closed blocks and between the crab and uncaged blocks ( $p = 0.041$  and  $0.008$  respectively, Tukey test), and a marginal difference in mass change was observed between the crab and 13 mm open blocks ( $p = 0.079$ , Tukey test). No significant differences in mass change were observed between the 13 mm open, 50 mm open and their corresponding closed blocks (Fig. 2). Similar results

were found for treatment effects on kelp blade area. A net increase in area was seen in the uncaged (95.5%), 13 mm open (37.1%), and 50 mm closed (37.9%) blocks. The only significant difference in area change was seen between the crab and the uncaged blocks ( $p = 0.009$ , Tukey test). A marginally significant difference in area change was seen between the crab and 50 mm closed blocks, and between the crab and 13 mm open blocks ( $p = 0.085$  and  $0.087$  respectively, Tukey test). No significant differences in blade area change were observed between the open cage control blocks and their corresponding closed cage blocks (Fig. 3).

27.8% of the kelps (all three on the crab blocks, one on a 13 mm mesh open cage block, and one on a 50 mm mesh open cage block) had at least half of their blades cut off at the meristem within the first 5 days of the experiment. Within 15 days, all of the kelps on the crab blocks had no blades attached (one still had pieces of the original blades present). The 13 mm mesh open block kelp lost half of its blades, while all the blades were removed in the 50 mm open block kelp. Of the 15 kelps that still had blades, 66.7% had holes eaten through the blades, 33.3% had longitudinal or transverse tears in the blades, 53.3% had scrape marks where the meristoderm and cortex had been removed or bitten off, 73.3% had blade furling, 86.7% had bites taken out of the edges, and all had erosion and wear at the proximal ends of the blades. All kelps in the crab blocks also had the stipe cut and devoured below the pneumatocyst. Images of different damage types observed on kelps can be seen in Fig. 4.

The most common animal on the blocks after the 15-day experiment was *Pandalus danae*, found clinging to the sides of closed 13 mm mesh cages or inside the open cages and closed 50 mm mesh cages. After 5 days, one *P. danae* were present on



one block; after 10 days, they were present on 6 blocks; and by the end, they were present on all 18 blocks (fig 5). Also present were the shrimp *Heptacarpus stylus* and *H. brevisrostris*, found on all block types except the 50 mm mesh open treatment blocks, typically on the outside of the cages, or sitting on the block itself. The tube-forming amphipod *Peramphithoe* sp. (individuals observed were approx. 6 mm) was found on two kelps each from an uncaged block and a closed 50 mm mesh caged block. Two 35-mm penpoint gunnels (*Apodichthys flavidus*) and a small *Cancer oregonensis* with a carapace about 10 mm wide, were associated with the three 13 mm closed blocks. A small *Oregonia gracilis* was found inside a 50 mm closed block, and an unidentified juvenile sculpin was found inside a crab block (Table 2).

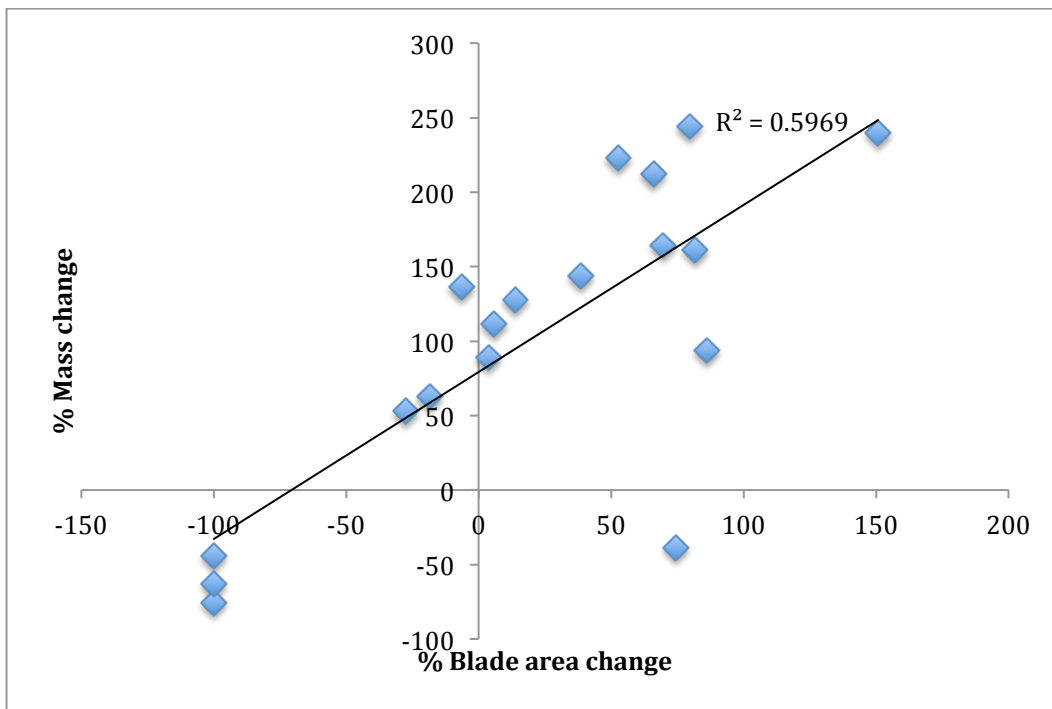


Figure 1: Percent mass change and percent blade area change in kelps across all treatments.  $p < 0.001$

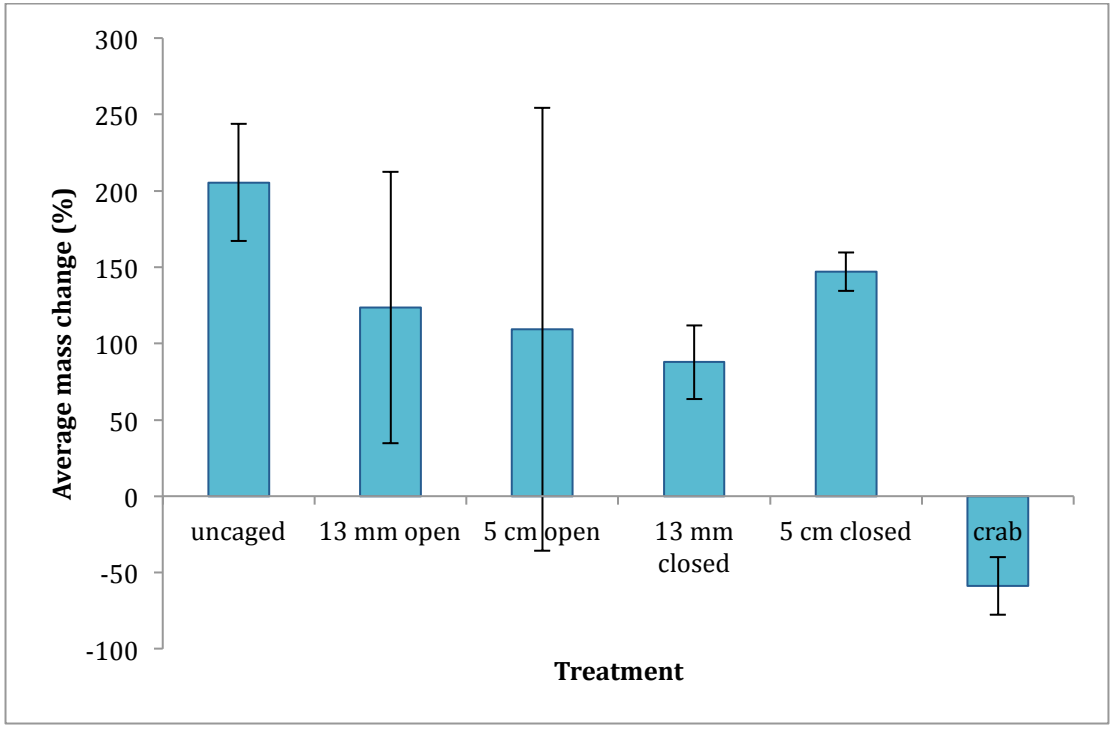


Figure 2: Average mass changes in kelps across treatments. Error bars= 1 s.d. Average mass changes were calculated by subtracting the final mass divided by the initial mass, multiplied by -100.

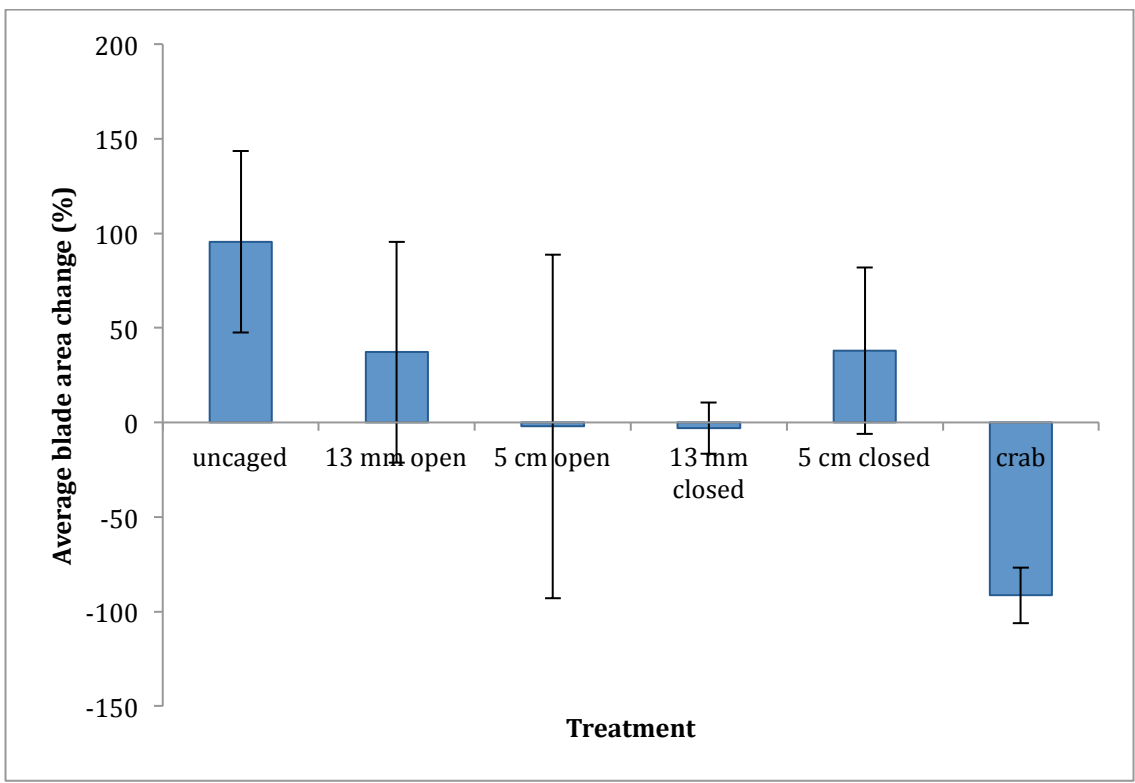


Figure 3: Average blade area changes in kelps across treatments. Error bars= 1 s.d. Average mass changes were calculated by subtracting the the final mass divided by the initial mass, multiplied by -100.

**Table 2: Animals associated with all blocks**

Kelp	Day 5 Animals	Day 10 Animals	Day 15 Animals
uncaged			<i>P. danae</i> , <i>Heptacarpus. stylus</i> , <i>Peramphithoe</i>
			<i>P. danae</i>
			<i>P. danae</i>
13 mm open		<i>P. danae</i>	<i>P. danae</i> , <i>H. stylus</i>
			<i>P. danae</i>
		<i>P. danae</i>	<i>P. danae</i>
50 mm open		<i>P. danae</i>	<i>P. danae</i>
			<i>P. danae</i>
		<i>P. danae</i>	<i>P. danae</i>
13 mm closed			<i>P. danae</i> , <i>H. stylus</i> , <i>Cancer oregonensis</i>
		<i>P. danae</i>	<i>P. danae</i> , <i>Apodichthys flavidus</i>
			<i>P. danae</i> , <i>A. flavidus</i>
50 mm closed		<i>P. danae</i>	<i>P. danae</i> , <i>Oregonia. gracilis</i>
	<i>Pandalus. danae</i>		<i>P. danae</i> , <i>Peramphithoe sp.</i>
			<i>P. danae</i> , <i>H. stylus</i>
crab			<i>P. danae</i> , <i>H. stylus</i> , <i>H. brevirostris</i>
			<i>P. danae</i>
			<i>P. danae</i> , sculpin

## Discussion

The lack of significant differences between open cage blocks of both sizes and the uncaged control blocks indicates that shading by cage mesh did not have a significant effect on mass change or blade area change; all differences in this experiment can most likely be attributed to grazing and growth uninhibited by shading.

Significant differences in average mass change and blade area change between the uncaged control blocks and the caged crab blocks suggest that *P. producta* is capable of decimating juvenile bull kelps in comparison to other grazers, like *Peramphithoe*, which may have been present in the breakwater canopy or in the water column and would have had access to the juvenile kelps. Direct comparison of grazing by caged *P. producta* to grazing by breakwater mesograzers is plausible since *P. producta* will consume

*Nereocystis* over other types of algae when given the choice (Dobkowski et al., submitted). This and the fact that juvenile sporophytes are smaller, more tender, and less encrusted with epiphytes suggests that the limited diet presented within the cages was a reasonable representation of what they would eat in the wild regardless of other available foods, and can therefore be directly compared to the other blocks without crabs.

This preference, combined with the extensive damaging capability seen in the experiment, suggests that *P. producta* can have potentially devastating effects on young generations of *Nereocystis* recruits. The canopy-forming adult sporophyte likely has the advantage of a size refuge from grazing to the point of death (Leonard 1994). Destroying large numbers of juvenile sporophytes before they reach the size refuge could have significant negative impacts on kelp forests as a whole, and could potentially determine the location and success of new and old forests. The destructive ability of kelp crabs may also be compounded by a lack of crab predators (Dobkowski et al., submitted). Sea otters, which were rare in the San Juan Archipelago before their extermination from Washington (Lance et al. 2004), are known to feed on *P. producta* (Carter et al. 2007). While urchin removal simulating sea otter predation did not increase macroalgal abundance, removal of kelp crabs and other herbivores was not attempted and could yield different results. A lack of predation by sea otters could result in an increase in crab abundance, magnifying kelp crabs' top-down effects on *Nereocystis* and other algae (Dobkowski et al., submitted).

Of the animals associated with the blocks, only *Peramphithoe* is an obligate herbivore. Little is known about the diet of *Oregonia gracilis*, but like most crabs, including *Cancer oregonensis*, *O. gracilis* has been known to scavenge dead fish in a

laboratory setting (O'Clair and O'Clair 1998). Neither species is probably responsible for any damage to the kelps in this experiment. *Pandalus danae* is not an herbivore, but feeds on soft-bodied prey like polychaetes. Little is known about the diet of the two species of *Heptacarpus* associated with the kelps, but they are thought to feed on soft-bodied prey in a fashion similar to *P. danae* (O'Clair and O'Clair 1998; Staude, pers. comm.).



**Figure 4: Principle types of damage seen in juvenile *Nereocystis*. A, superficial scraping and holes; B, amphipod furling; C, longitudinal tearing, D, bit edges and holes; E, proximal wear; F, blades severed near intercalary meristem. s = scraping, h = holes, b = bit edges. Scale bar = 1 cm.**

No polychaetes, herbivorous or otherwise, were observed in association with the blocks, so the shrimps' diets in this context remain unknown. *Apodichthys flavidus* and most local sculpin species are important predators of gammarid amphipods like *Peramphithoe*, and although some sculpins are known to eat algae either opportunistically or as a primary food source, none occur commonly in the San Juan Archipelago (Love 2011).

Based on laboratory observations of *P. producta*, the severing of blades at the meristem in the 3 crab blocks can be directly attributed to the crabs in the cages. Severed blades in the 50 mm mesh and 13 mm mesh open cage blocks could not be directly attributed to any single herbivore, however, and could either have been caused by snipping off the blade directly or by wearing into the blade tissue near the meristem, causing the blades to break off indirectly as a result of wave action. Given the paucity of animals with large snipping organs (e.g. chelipeds) associated with these treatments, the latter option seems more likely. In addition, 73.3% of the kelps with blades at the end of the experiment had either 1) holes eaten directly through the blade, or 2) the meristoderm and cortex scraped away on one side in the center or margin of the blade. These two types of damage have been shown to reduce the ability of kelp blades to withstand drag and stay attached to the thallus (Krumhansel et al. 2011). Of these kelps, 82.2% also had blades furled into tubes in the style of *Peramphithoe*, which has been shown to eat through kelp meristoderm and cortex (Cerdeira et al. 2010), leaving holes and surface scars similar to those seen in the experiment. The snail *Lacuna vincta* also damages kelp blades in this way (Krumhansel et al. 2011), but was not observed on any of the kelps used in this experiment.

Transverse and longitudinal tears on the blades were similar to those created by *P. producta* in the lab, but could not be attributed to any specific kind of grazer, as nothing with any tearing capability was observed in association with those kelps. The wear and tear on the distal portions of the blades in all kelps with blades remaining was likely due to natural microbial degradation of the blade as it grew, and cannot be attributed to any specific grazer.

These kinds of damage and their associated grazers are most likely dependent on the experimental site and positioning of the blocks in the water column. The presence of a pre-existing macroalgal canopy above the blocks on the edge of the breakwater contributed a specific community of grazers and other animals different from an experimental setup directly on the benthos. Hanging the blocks in the water column below a macroalgal canopy likely selected for smaller mesograzers and other animals with the ability to swim (e.g. *Peramphithoe*, *Heptacarpus*, *Pandalus*) or climb to the juvenile *Nereocystis* hanging from ropes. Blocks placed directly on the benthos could allow for a direct comparison of the effects of larger, more ungainly grazers like large *Pugettia producta* and *Strongylocentrotus* spp. on juvenile bull kelp.

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