

# The Effects Of Multiple Predators On the Size Structure of Red Urchin Populations in British Columbia

An undergraduate Directed Studies (BISC 498) research project  
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## Introduction

Predator-prey body size relationships influence trophic structure, transfer efficiency, and interaction strength within a food web (Jonsson and Ebenman 1998). Size distributions of both predators and prey are an important component to the population dynamics of a community. Knowledge of the strength of predatory interactions within a food web can provide insight to the relationships between the sizes of prey and their predators. Predators are generally larger than the size their prey and predator size is often positively correlated to prey size (Vezina 1985, Warren and Lawton 1987, Cohen et al. 1993). The relative body size of a predator and its prey largely contribute to the ecology and evolutionary consequences of predator-prey relationships. This is most defined in systems involving size-dependent predators. These predators are effective agents of selection among prey species that differ in body size or growth rate. Size dependent predators therefore influence the structure of prey populations by diminishing prey species of a preferred size (Kerfoot and Peterson 1980). Prey species that can reach a large size through embellishments of the exoskeleton can often attain a size refuge from predators (Sousa 1992). Thus, the risk of predation may be lower for larger prey compared to smaller individuals. The risk of an individual prey being consumed may also depend on the size- structure of the predator population, as larger predators generally have the ability to handle and consume larger prey (Sousa 1992).

The level and mode of predation on sea urchins can significantly impact the structure of marine communities because community structure is drastically different in the presence and absence of kelp beds. Three species of sea urchins inhabit coastal British Columbia including the green urchin (*Strongylocentrotus droebachiensis*), purple urchin (*Strongylocentrotus purpuratus*), and red urchin (*Strongylocentrotus franciscanus*). However, I found that red urchins are by far the most abundant species, accounting for 89% and 93% of all urchins sampled on the Central Coast and Haida Gwaii respectively. Urchins are important determinants in shaping nearshore benthic community structure because of their imperative ability to excessively graze fleshy macroalgae (Kitching and Ebling 1961, North 1971, Mann 1977, Vadas 1977). Persistently large sea urchin populations can be attained when urchin density and biomass are not reduced by external controls such as predation (Byrnes et al. 2013). Absence or removal of important predators can cause outbreaks of urchin populations that result in extensive barren seafloor landscapes due to overgrazing (Estes and Palmisano 1974, Breen and Mann 1976, Duggins 1980). Barren areas consisting of minimal life as a consequence of sea urchins released from predation pressure represents an iconic example of a trophic cascade in ecology.

The most influential predator of sea urchins in British Columbia is undoubtedly the sea otter (*Enhydra lutris*) (Estes and Duggins 1995, Estes et al. 1998). Sea otters are apex predators that are capable of inducing prominent ecosystem-level effects across almost all the nearshore marine communities they inhabit (Duggins et al. 1989, Estes 1990, Estes and Duggins 1995, Estes and Palmisano 1974, Garshelis et al. 1986). In order to maintain a high metabolism requiring up to 30% of their body mass per day, otters consume an extensive amount of benthic invertebrates, including urchins (Costa 1978, Riedman and Estes 1990). Sea otters are size-selective predators that can limit the size, distribution, density and abundance of their prey (Estes et al. 1989, Watson 2000). As they move into a new rocky habitat, sea otters nonrandomly select large, calorically rich, and easily captured sea urchins first (Kvitek and Oliver 1988). Kelp-dominated systems

generally result from sea otter predation, as the removal of herbivores significantly reduces grazing pressure (Estes and Duggins 1995). Therefore, the sea otter can play an important role in kelp forests by limiting sea urchin size and abundance to levels below those at which destructive grazing can occur. However, maritime fur trade hunting in the early 20th century drove otters to local extinction. In BC, sea otters have begun to recover along Vancouver Island and the Central Coast. While their range continues to expand, they have not yet made to Haida Gwaii. The recovery and growth of sea otter populations provides a unique opportunity to examine the drastic changes they bring to nearshore communities. In addition, more common urchin predators may be present in sufficient numbers to regulate urchin populations where otters have not yet begun to recover and are worth investigating (Nelson and Vance 1979, Tegner 1980).

*Pycnopodia helianthoides* are an abundant starfish on BC's coast and are considered the only important predator of urchins other than sea otters in this area (Duggins 1983). Other species such as the gastropod *Fusitriton oregonensis*, wolf eels, and lithoid crabs are known to consume urchins, but are not considered significant predators (Duggins 1983). The nature of *Pycnopodia* predation on sea urchins is very different than that of sea otters. *Pycnopodia* exists in a dynamic equilibrium with its prey, opposed to otters that decimate urchin populations. Thus, while otters affect nearshore kelp beds by eliminating nearly all sea urchins and other important benthic herbivores, *Pycnopodia* impose a considerably different effect. This difference in predation may change the size frequency distribution of red urchin populations in the absence of otters in BC. In similar coastal systems, size-limited predators such as the spiny lobster (*Panulirus interruptus*) and the California sheephead fish (*Semicossyphus pulcher*) have been identified as important predators that influence urchin populations (Tegner and Levin 1983, Cowen 1983). Tegner and Dayton (1981) attributed these predators to the bimodal size frequency distribution observed for the red sea urchin populations. The bimodal structure has been largely explained by the ability of large red urchins to reach a size refuge from size-limited predators, while small urchins seek refuge

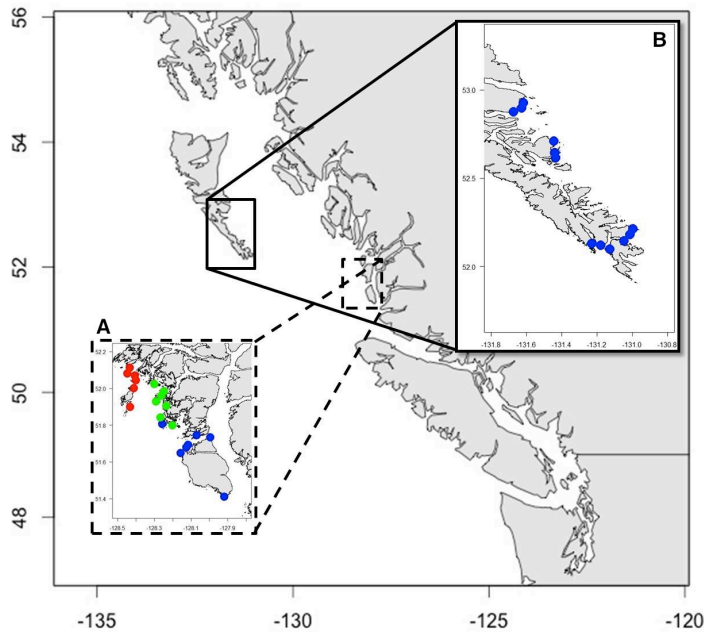
under the large spines of adult urchins. *Pycnopodia* are potentially also size-limited predators and its size-selective nature may effectively influence the size frequency distribution of red urchins where otters have not yet recovered in BC.

This paper assesses the influence of sea otter versus *Pycnopodia* predation on the size frequency distribution of red sea urchin populations along the Central Coast and Haida Gwaii in British Columbia. My hypothesis was that, in the absence of sea otters, *Pycnopodia* could effectively influence the size frequency distribution of red urchins in BC. Furthermore, I predicted that *Pycnopodia* predation is responsible for the observed bimodal size frequency distribution of red urchins in the absence of otters, consistent with that of other size-limited predators of red urchins in similar marine systems. To examine how changing predation pressures might affect urchin population size frequency distributions, I analyzed and compared data from several study sites varying from low to high otter occupation time (0-33 years since recover) along the Central Coast and Haida Gwaii. Size-frequency data is presented and hypotheses are proposed to explain the observed population structures and natural controls of red and purple urchin populations.

## Methods

### *Study Sites*

Surveys were conducted in two locations on the West Coast of British Columbia at sites where otters have been present for up to 33 years since recovery and areas where they still have not recovered (Fig. 1). Study sites within each area ranged from 4-15 m in depth. Urchin and *Pycnopodia* size data were collected from 12 sites in 3 regions located on the east and 1 region on the west side of Haida Gwaii where otters have not yet returned since local extinction. All sites within Haida Gwaii were located within the Gwaii Haanas National Park Reserve. Sea urchin and *Pycnopodia* size data were also collected from 20 sites along the Central Coast following a gradient of low to high otter occupation time (0-33 years).



**Figure 1. Locations where surveys were conducted on the Central Coast (A) and Haida Gwaii (B). Blue dots represent low otter occupation time (0-2 years), green dots represent intermediate otter occupation time (3-8 years), and red dots represent high otter occupation time (17-33 years).**

### *Urchin Quadrats*

Size and abundance data of *Strongylocentrotus franciscanus* were collected during June and July of 2013 in 1 x 1 m quadrats along the Central Coast of BC (n = 18 per site) and Haida Gwaii (n = 10 per site). Divers randomly placed quadrats through the depth range at each site (4-15m). Densities of red urchins were estimated by counting all urchins within each quadrat. Sizes of urchins within each quadrat were measured as the test maximum diameter to the nearest centimeter using calipers.

### *Pycnopodia Transects*

Belt transects were used for *Pycnopodia helianthoides*, as they are much larger and more variably distributed than could be accurately captured in 1x1m quadrats. During June and July of 2013 six replicate horizontal belt transects 30 m in length and 2 m in width (1 m on either side of central line) were surveyed at each

site. *Pycnopodia* were surveyed along 3 transects at each of the 2 depth ranges (shallow: 5-8 m and deep: 10-13 m below chart datum). Shallower transects were generally within kelp forest habitat, and deeper transects were generally just outside the extent of kelp beds and over rocky reefs typically dominated by red sea urchins. Densities of *Pycnopodia* were estimated by counting all *Pycnopodia* within each transect area. *Pycnopodia* size was measured with a ruler as the maximum arm-to-arm diameter and recorded to the nearest centimetre.

### *Data Analysis*

All data analyses were conducted using R Statistical Software. Red urchin size frequency distributions were determined in order to examine changes in the size structure of the populations when otters are present as apex predators and when otters are absent or have only recently arrived so that *Pycnopodia* act as influential mesopredators. Urchin and *Pycnopodia* size frequency distributions in Haida Gwaii were determined by pooling data for each across all sites, since I had no prior expectation of variation in urchin predators among sites in Haida Gwaii. Pooling was done in this way because Haida Gwaii does not have otters at any site and can therefore be used as a reference to compare with the Central Coast. Only 19 of the 20 sites were used from the Central Coast data set because one of the sites was insufficient for data analysis, as only one urchin was recorded. Size frequency distributions of urchin and *Pycnopodia* populations at the Central Coast sites were determined along a gradient of otter occupation time separated into the three categories of low (0-2 years), intermediate (3-8 years), and high (17-33 years). Probability density, which refers to the relative likelihood of an urchin or *Pycnopodia* to be a given size, was used to describe size frequency distributions. Histograms displaying actual frequencies were not used due to differential sampling efforts across sites.

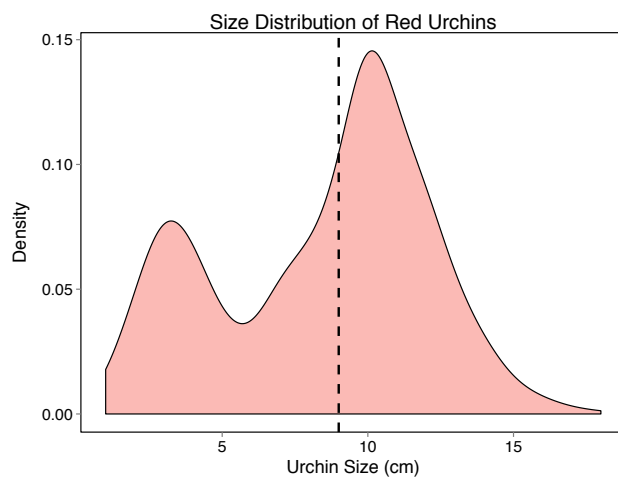
The median urchin size was determined for all Haida Gwaii sites pooled together as well as for all of the Central Coast sites pooled together. The same process was

completed for *Pycnopodia*. The Central Coast median urchin and *Pycnopodia* size was then determined separately for each category of otter occupation time. The Central Coast median urchin size for each site was plotted against otter occupation time in order to determine how urchin size changes with the length of time otters have been present in an area. The same process was completed for *Pycnopodia* at the Central Coast sites. The total biomass of *Pycnopodia* was calculated for each site using a length-weight regression method (Trebilco et al. 2013) and was plotted against otter occupation time in order to determine *Pycnopodia* predation pressure in Haida Gwaii and each category of otter occupation time on the Central Coast.

## Results

### *Haida Gwaii urchin size data with absence of otters*

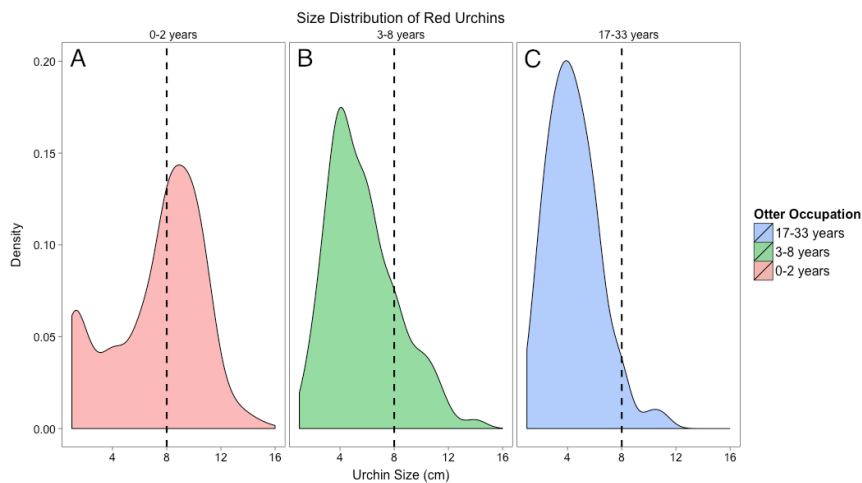
The red urchin size frequency distribution for Haida Gwaii was distinctly bimodal with the first peak consisting of small urchins about 3 cm in size and the second higher peak consisted of large urchins about 11 cm in size (Fig. 2). The depression between the two peaks consisted of intermediate sized urchins about 5-7 cm test diameter. The overall median urchin size in Haida Gwaii was 9 cm.



**Figure 2. Haida Gwaii red urchin test diameter size frequency distribution. The overall urchin median size of 9cm is represented by the dotted line.**

*Central Coast urchin size data with recovering otters*

The red urchin size frequency distributions for the Central Coast shared similar unimodal size structures for intermediate and high otter occupation sites (Fig. 3B and C). In addition, the intermediate and high otter occupation unimodal size frequency distributions illustrated a distinct absence of large urchins as well as a lack of very small urchins. Similar to the sites in Haida Gwaii where otters have not yet recovered, a characteristic bimodal population size structure with peaks around 1.5 and 9 cm test diameter was produced for low otter occupation sites (Fig. 3A). The second peak was much higher than the first and the depression between the two peaks was from about 3 to 6 cm test diameter. The overall median urchin size for all sites across all otter occupation times was 8 cm test diameter. The median urchin size for low, intermediate, and high otter occupation was 8.2 cm, 4.8 cm, and 4.3 cm respectively. Site-level analyses of red urchin median size by otter occupation time highlights the rapid nonlinear decrease in urchin size with otter occupation time (Fig. 4).



**Figure 3. Central Coast red urchin test diameter size frequency distribution separated by otter occupation time. The overall urchin median size of 8cm is represented by the dotted line.**



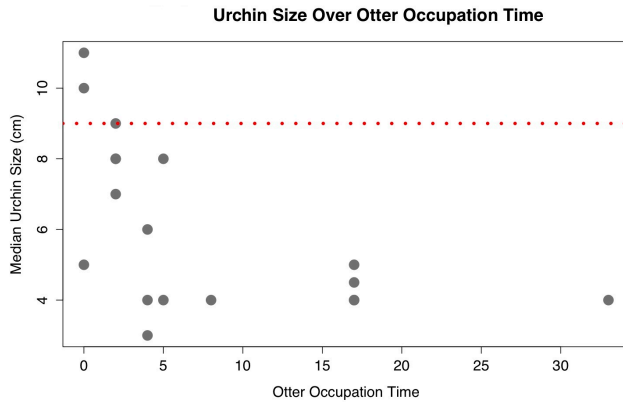


Figure 4. Central Coast median urchin test diameter along a gradient of otter occupation time. Haida Gwaii median urchin test diameter is represented by the dotted line.

*Size structure of the predator Pycnopodia*

The *Pycnopodia* size frequency distribution for Haida Gwaii demonstrated a unimodal size structure heavily skewed to the right with the largest individual measured at 72 cm (Fig. 5). The overall median *Pycnopodia* size in Haida Gwaii was 19 cm. The average *Pycnopodia* biomass across all sites in Haida Gwaii was 14136g (Fig. 8)

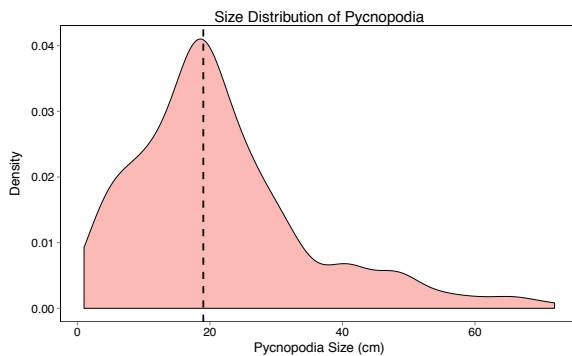


Figure 5. Haida Gwaii *Pycnopodia* size frequency distribution. The overall *Pycnopodia* median size of 19cm is represented by the dotted line.

The *Pycnopodia* size frequency distributions for the Central Coast were unimodal size structures for sites within all three categories of otter occupation time (Fig. 6). While high and intermediate otter occupation time shared similar size frequency distributions (Fig. 6B and C), sites with low otter occupation time

demonstrated a higher proportion of *Pycnopodia* in the 50-70 cm size range (Fig. 6). The overall median *Pycnopodia* size for all sites across all otter occupation times was 24 cm. The median size for low, intermediate, and high otter occupation time was 27.6 cm, 26.9 cm, and 19 cm respectively. The average *Pycnopodia* biomass was 33020g, 15280g, and 10991g for the low, intermediate, and high categories respectively (Fig. 8). As rough categories of otter occupation, it appears as though median *Pycnopodia* size on the Central Coast decreases as otter occupation time increases, but a site-level analysis suggests that factors other than otter occupation time may be important in governing *Pycnopodia* size (Fig. 7).

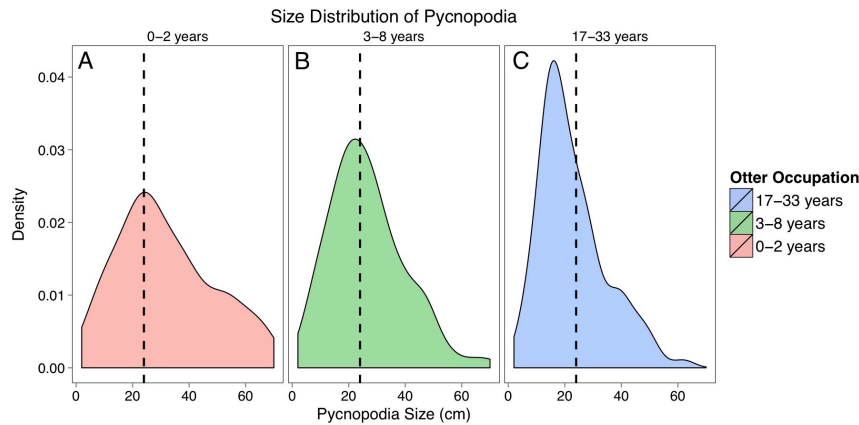


Figure 6. Central Coast *Pycnopodia* size frequency distribution separated by otter occupation time. The overall *Pycnopodia* median size of 24cm is represented by the dotted line.

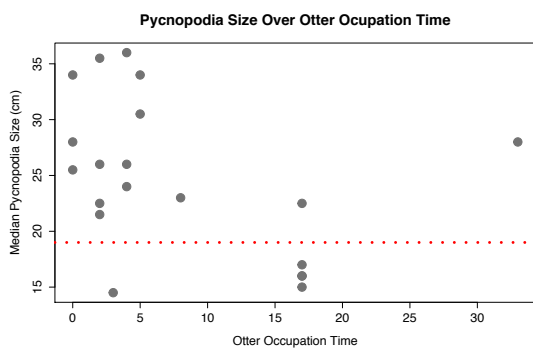


Figure 7. Central Coast median *Pycnopodia* size along a gradient of otter occupation time. Haida Gwaii median *Pycnopodia* size is represented by the dotted line

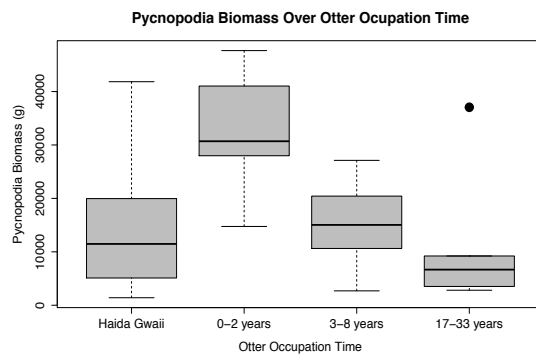


Figure 8. Total biomass of *Pycnopodia* calculated per site and grouped together for Haida Gwaii and into otter occupation time categories for the Central Coast.

## Discussion

In the absence of otters, *Pycnopodia* are thought to be one of the only important predators of urchins in BC (Mauzey et al., 1968, Tegner and Dayton 1977, Duggins 1983). Urchins are known to be a significant prey source for *Pycnopodia* (Mauzey et al. 1968), consisting of over 65% of *Pycnopodia* diet in some areas (Duggins, 1983). Most of the urchins sampled on the Central Coast were 8 cm in test diameter. For low otter occupancy time the median urchin size was only slightly lower (Fig. 3A), demonstrating that most of the 8 cm urchins were located at the sites where otters have been present for 2 years or less. In addition to an increased number of large urchins at low otter sites, there were also an increased number of small sized urchins compared to intermediate and high otter occupancy sites (Fig. 3A). The distinctive bimodal size frequency distribution for 0-2 years otter occupation time and Haida Gwaii strongly suggests that *Pycnopodia* may be capable of influencing the size structure red sea urchin populations.

The first mode may be attributed to protection of juvenile urchins from *Pycnopodia* predation by the spine canopy provided by large adults. Tegner and Dayton (1977) found that even as juveniles became too large to reside under the spines, they remained clustered close to the adults and suggested that the most important aspect of this relationship might be a potential refuge from predators for juveniles afforded by the spine canopy. Therefore, the spine canopy of adults would seem to be an effective refuge for juveniles in the specific case of predation by *Pycnopodia*. An alternative, although not mutually exclusive, hypothesis is that smaller urchins are not energetically worth the effort to process and digest (Tegner and Levin 1983).

The second mode may be prevalent because large adult red urchins are potentially able to attain a size refuge from predation (Moitza 1979, Tegner and Dayton 1981, Duggins 1983, Tegner and Levin 1983). Sea urchins have been well

documented to express defensive responses to predatory sea stars, including *Pycnopodia* (Jensen 1966, Mauzey et al. 1968; Rosenthal and Chess 1972, Dayton 1975, Phillips 1978, Moitza et al. 1979) and under some circumstances they may quite effectively reduce predation (Jensen 1966, Rosenthal and Chess 1972, Dayton et al. 1977). Duggins (1983) found that red urchins even lose their escape response from *Pycnopodia* once they reach their size refuge. The second peak is likely much larger than the first despite intense predation on intermediate sized urchins because urchin growth rates slow down as they increase in size, resulting in many year classes being grouped together in the second peak, whereas the first peak consists mostly of the first year class (Tegner and Dayton 1981).

Once urchins reach an intermediate size, they are no longer sheltered by the spine canopy and may become particularly vulnerable to *Pycnopodia* predation. In addition, urchins may become less cryptic in absence of sea otters (Tegner and Dayton 1981), making them more vulnerable to *Pycnopodia* predation. *Pycnopodia* are known to target intermediate sized urchins from about 4 to 8 cm (Duggins 1983, Tegner and Dayton 1981), which approximately corresponds with the observed size classes within the depression between the peaks of the bimodal size structure in Haida Gwaii. The depression in the size frequency represents the range of prey sizes a predator can consume and can be referred to as the predation window (Claessen et al. 2002). The predation window denotes an important link between prey mortality and predator size distribution as well as predator growth rate with size distribution of prey (Wilbur 1988, Rice et al. 1997, Classen et al 2002). The depression in the bimodal distribution matching the predation window of *Pycnopodia* suggests that mortality of intermediate sized urchins and the bimodal size structure in Haida Gwaii and low otters sites on the Central Coast are likely attributed to *Pycnopodia* predation.

The Haida Gwaii archipelago has been uninhabited by sea otters since their extirpation by the nineteenth century from overhunting (Estes 1990). For this reason, the sites located in Haida Gwaii serve as a reference to compare with the

Central Coast sites where otters are either absent or have only been present for a short period of time. The Haida Gwaii red urchin size frequency distribution shared many similar properties with that of the red urchin population structures at low otter occupation sites on the Central Coast. Both Haida Gwaii and low otter occupation Central Coast urchin populations are strongly bimodal in the presence of *Pycnopodia*. In each bimodal pattern, the first peak consists of smaller urchins whereas the second peak is higher and consists of urchins of a larger size class. Consistent with the Haida Gwaii populations, the depression between the two peaks of the low otter occupation Central Coast size structure falls within the *Pycnopodia* predation window. The Haida Gwaii populations also shared a very similar median with the low otter occupation Central Coast populations. This evidence suggests that *Pycnopodia* may have the same potential to influence the size structure of urchin populations on the Central Coast as they do in Haida Gwaii.

The Haida Gwaii urchin population size structure, however, is not completely comparable to that of the Central Coast populations with low otter occupation time. In particular, the first mode of the Haida Gwaii urchin population consists of urchins about 3 cm test diameter and the second mode consists of urchins about 11 cm test diameter, whereas the first and second mode of the Central Coast populations consist of urchins about 1.5 and 9 cm test diameter respectively. A myriad of possibilities exist that could contribute to this difference in size, such as ocean currents, difference in productivity and nutrients, or other biological and ecological processes. One major contributing factor however may be that otters are completely absent at the Haida Gwaii sites but have been present for up to 2 years at some of the Central Coast sites categorized as low otter occupation time. Any presence of otters in an area, even if its only up to 2 years, may be sufficient time to remove enough large urchins from the population to decrease the size of urchins in the peaks of the bimodal size frequency distribution. Perhaps if the sites on the Central Coast with only complete absence of otters (0 years since recovery) were analyzed separately, the peaks in urchin size would be more comparable to those of the Haida Gwaii populations. An additional hypothesis considering the first peak is that the

width may be variable since it depends on the timing of sampling in relation to when settlement took place and could be expected to vary with predator density and habitat structure (Tegner and Lavin 1983).

Sea otter size-selective predation may be responsible for the absence of larger urchins in populations where otters have been present for 3 years or longer. Sea otters have the ability to alter the abundance and size structure of urchin populations through size-selective predation (Estes and Palmisano 1974, Kvitek and Oliver 1988, Estes et al. 1989, Laidre and Jameson 2006). As sea otters move into a new habitat they nonrandomly consume urchins by quickly and easily selecting the largest ones first, reducing sea urchins to a sparse population of smaller individuals. The urchin size frequency distributions suggest that when otters have been present for at least 3 years, urchins are about half the size of urchins in areas where otters have been present for 2 years or less. The median urchin size was drastically greater (Fig. 3B and C), indicating that there were proportionately fewer 8 cm urchins at these sites. This suggests that shortly after otters return, urchin populations experience a decrease in larger sized individuals. Comparing median urchin size on the Central Coast across the gradient of otter occupation time clearly illustrates the drastic nonlinear drop in median urchin size after about 3 years of otter occupation time (Fig. 4).

The removal of large urchins by sea otters may account for the absence of small urchins seen at the intermediate and high otter occupation time sites as well. Small red urchins may rely on the spine canopy provided by large adult red urchins for recruitment and protection (Moitza 1979, Tegner and Dayton 1981, Duggins 1983, Tegner and Levin 1983). With the removal of large adults from the population, the spine canopy is no longer available, which may leave larvae without suitable habitat for recruitment as well as leave small urchins exposed and vulnerable to predation or other sources of mortality. Additionally, there may be a reduced amount of larvae produced as the result of less large reproductive adult urchins left in the population. Areas where sea otters have been present for 3 years

or longer are also associated with thick kelp forests. Kelp may prevent urchin larvae from successful recruitment due large kelps wave-driven whiplash and sweeping motion (Vásquez 1992, Konar 2000, Tamaki et al. 2009, Filbee-Dexter and Scheibling 2014).

### *Pycnopodia*

The overall median *Pycnopodia* size for the Haida Gwaii populations (19cm) was smaller than the median *Pycnopodia* size for the Central Coast populations (24 cm) (Fig. 6). It was expected that the Central Coast populations with low otter occupation time would share similar properties with the Haida Gwaii populations, as otters have not yet returned to Haida Gwaii since their extirpation. In contrast, the Haida Gwaii *Pycnopodia* populations shared the same median size (19 cm) with the Central Coast populations where otters have been present for 17 years or longer. Figure 8 illustrates the decrease in *Pycnopodia* predation pressure with increasing otter occupation time for the Central Coast sites. Haida Gwaii, however, is not consistent in this trend. This may be due to the much larger urchin size in Haida Gwaii compared to the Central Coast. The second peak of the Central Coast bimodal urchin population consists of about 9 cm urchins where otters have been present for 0-2 years, whereas the second peak of the Haida Gwaii bimodal urchin population consists of about 11 cm urchins. *Pycnopodia* may not be able to successfully consume as many urchins in Haida Gwaii because considerably more urchins may be able to reach a size refuge from *Pycnopodia* predation. The smaller median could also be attributed to factors such as oceanographic processes, density dependence and competition, or a potentially higher recruitment of *Pycnopodia* in Haida Gwaii.

The most frequent size of *Pycnopodia* on the Central Coast was 24 cm and the median size appears to decrease with otter occupation time (Fig. 6 and Fig. 7). However, the median size between all sites is not considerably different. The median *Pycnopodia* size was largest (27.6 cm) when otters are present for 2 years or less. In addition, there is an abundance of noticeably larger *Pycnopodia* about 50-70

cm when otters are present for 2 years or less. This abundance of large *Pycnopodia* may be because of the increased abundance of vulnerable intermediate sized urchins that fall within the predation window of *Pycnopodia* at low otter occupation sites. With more of the ideal intermediate sized urchins available for *Pycnopodia* to consume, *Pycnopodia* are potentially able to reach a larger size.

## Conclusion

Size-selective predators can clearly impact community composition by influencing the size structure of prey populations. The nature of the *Pycnopodia*-urchin interaction is distinctly different from that of the once abundantly distributed sea otter. Along British Columbia's coastline, as in other nearshore marine systems, urchins control the abundance, distribution, and ultimately productivity of benthic algae. While the effects of sea otter predation are predictable, rapid, and dramatic, this urchin predator has only begun to recover in few areas along BC's coastline. Large *Pycnopodia* capable of consuming sea urchins are abundant on the Central Coast and Haida Gwaii and are considered the only important urchin predator other than otters. Unlike the rare sea otter, which decimates urchin populations and establishes an alternative steady state, this starfish predator appears to coexist with its preferred prey. The depressions in the observed bimodal size frequency distributions for red urchin populations at sites where otters are absent or have only just begun to recover consist of urchins within the *Pycnopodia* predation window. Red urchins have been documented to reach a size refuge from *Pycnopodia* and the spines of large red urchins are known to provide protection for juveniles. Evidence suggests that this predatory interaction may ultimately be responsible for the observed bimodal size frequency distribution of red urchins. While this applies to only one of the three urchin species present, red urchins account for the large majority of the total urchin population in along the Central Coast and Haida Gwaii.



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