

**Effects of Sea Otters on Nearshore Ecosystem Functions with  
Implications for Ecosystem Services**

by

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## **Abstract**

Sea otters are nearshore predators whose impacts have potential implications for the provision of ecosystem services on the west coast of Vancouver Island. Sea otter predation on herbivorous sea urchins can allow kelp beds to flourish. Increased kelp production can act as a food subsidy to mussels which can promote faster growth. Otters also depredate mussels, which can affect the habitat provision function of mussels and limit them to sizes that are vulnerable to other predators. In this thesis I describe two empirical studies that explore these possible effects of otters on ecosystem processes that have implications for ecosystem services.

First I investigate the impact of greater kelp productivity on carbon flow and productivity by using stable isotope analysis on kelp, water samples, and mussels in regions where otters are absent and present. I observed that mussels do not consistently assimilate higher proportions of kelp-derived carbon and do not grow faster where otters are present and kelp more abundant. This finding may be explained partly because kelp does not seem to be limiting for mussel diets where otters are absent – high observed phytoplankton biomass may dilute the kelp-derived carbon assimilated in mussel tissue.

The second study explores the impact of otters as predators of mussels by sampling mussel bed characteristics in regions along a gradient of time since otters established. Mussel bed characteristics vary predictably between regions: e.g., depth and biomass are lower in regions of comparably higher otter influence. Aggregate community biomass is also lower where otters are present, and differences in dominant species may drive differences in community structure between regions. By restricting mussels to smaller sizes, otters may also subject a greater

proportion of mussel growth to predation by seastars, potentially facilitating a greater proportion of energy flow through marine food webs.

Otter may increase secondary productivity only where primary productivity is limiting, and they seem to constrain the habitat provisioning services of mussels. This study's quantitative characterization of otter impacts on an ecosystem engineer (mussels), and the intertidal habitat they provide, complements existing studies of otter impacts on subtidal ecosystem processes that affect ecosystem services.

# Table of Contents

Abstract .....	ii
Table of Contents .....	iv
List of Tables.....	vi
List of Figures .....	vii
Acknowledgements .....	x
Dedication .....	xiii
Foreword .....	xiv
Chapter 1: Introduction .....	1
Ecosystem Services .....	1
Ecology and Ecosystem Services.....	1
Sea Otter Reintroduction and Ecology.....	3
Outline of Thesis .....	6
Chapter 2 .....	6
Chapter 3 .....	6
Summary .....	7
Chapter 2: The Importance of Kelp Derived Carbon to Mussel Growth Varies Regionally and Seasonally.....	9
Introduction .....	9
Methods.....	13
Regional Study Design.....	13
Mussel Transplants and Growth Rates.....	14
Stable Isotope Samples.....	16
Calculating Kelp Contribution .....	19
Environmental Variables.....	20
Statistical Analyses .....	22
Results .....	23
POM (>1.2 $\mu\text{m}$ ) Isotope Signature.....	23
Detritus (63-200 $\mu\text{m}$ ) Isotope Signature.....	24
Mussel Isotope Signatures.....	24
Mussel Growth .....	25
Kelp Influence on Mussel Growth .....	27
Environmental Variables.....	29
Discussion .....	33
Kelp Content in Water may not be Limiting in Either Region .....	33
Regions with Sea Otters did not Consistently have Greater Kelp Assimilation .....	34
Regions with Sea Otters did not have Greater Mussel Growth.....	35
The Importance of Kelp may Vary Seasonally .....	36
Context Dependence of Indirect Effects .....	37
Contingencies of Ecosystem Service Provisioning.....	38
Chapter 3: Mussel Bed Structure and Community Assemblages Vary Predictably with Sea Otter Occupancy Time .....	39
Introduction .....	39

Otters as Keystone Predators.....	39
Mussels as Ecosystem Engineers .....	40
Otter Predation in Mussel Beds.....	41
Methods.....	44
Regional Design .....	44
Site Description.....	45
Mussel Size Structure and Mussel Bed Depth .....	46
Biomass Estimates.....	46
Mussel Energy Flow.....	47
Statistical Analyses .....	48
Mussel Sizes Along a Sea Otter Gradient .....	49
Average Large Mussels.....	51
Mussel Bed Depths Along a Sea Otter Gradient.....	52
Mussel Bed Biomass .....	53
Community Composition.....	56
Consequences to Energy Flow .....	60
Discussion .....	62
Sea Otters Structure Mussel Beds .....	62
Mussel Size Varies with Otter Influence.....	63
Mussel Beds are Shallower where Otters have Resided Longer.....	63
Mussel and Sediment Biomass is Smaller where Otters have Resided Longer .....	64
Mussel Bed Communities Vary Between Regions of Otter Presence .....	64
Otters may Facilitate a Greater Proportion of Energy Flow from Mussels .....	67
Keystone Predation and Ecosystem Engineers .....	68
Reintroductions and Ecosystem Services.....	69
Chapter 4: Concluding Remarks .....	71
Bottom-up Impacts.....	71
Top-Down Impacts.....	71
Future Directions.....	72
Primary and Secondary Productivity.....	72
Impacts to Habitat Provision.....	73
Ecosystem Services .....	73
Closing Thoughts .....	74
Literature Cited .....	76
Appendix A.....	86
Length to Dry Weight Conversions .....	86
Appendix B .....	87
Canonical Correspondence Analysis Results.....	87

## List of Tables

Table 2.1: Locations of sites used in this study.....	14
Table 2.2: Average carbon and nitrogen isotopic signatures for kelp species, particulate organic matter (POM), detritus, and mussel pedal foot tissue in summer and winter. All isotope values are ‰. ....	17
Table 2.3: Results of Two Way Mixed Effects Models for mussel growth rates, kelp assimilation in mussel tissue, and the proportion of kelp carbon in POM and detritus .....	27
Table 2.4: ANCOVA results for the effects of the various environmental variables explored in this study on mussel growth. The only factors found to be significant were wetness and Region, in the ANCOVA including region and wetness.....	31
Table 2.5: Multiple regression results of the environmental variables and kelp contribution to diet on mussel growth rates. Wetness and temperature are found to be marginally significant. ....	33
Table 3.1: Location of Intertidal sampling sites.....	45
Table 3.2: Results from a Variance Components Analysis, looking at how important different spatial scales are for overall variance in each region. Values represent percent (%) of variance explained. ....	51
Table 3.3: Simper analysis on square root transformed data to determine the most dissimilar species in terms of biomass between regions.....	59
Table B 1: Variance explained by individual species in CCA for Barkley Sound .....	87
Table B 2: Variance explained by individual species in CCA for Kyuquot Sound.....	88
Table B3: Coordinates of species along CCA plots in Barkley Sound.....	90
Table B4: Coordinates of species along CCA plots in Kyuquot Sound.....	92

## List of Figures

Figure 1.1: A conceptual diagram of the interactions investigated in this thesis. Arrows with broken lines represent indirect interactions and solid arrows represent direct interactions. Grey arrows represent assumed interactions not investigated in this thesis. The grey box encompasses the interactions and hypothesized interactions explored in this thesis.....	8
Figure 2. 1: Map of the west coast of Vancouver Island, British Columbia Canada showing locations of the study regions.....	13
Figure 2.2: The proportion of kelp found in particulate organic matter (POM, particles above 1.2 $\mu\text{m}$ ) collected in each region for each season. These box and whisker plots indicate the median, interquartile range (box, representing the middle 50% of the data), 1.5 $\times$ interquartile range (each whisker on each side of the box, where data extend this far), and outliers (points). The figure shows medians, but statistical tests were conducted on means.....	23
Figure 2.3: The proportion of kelp found in the pelagic detrital pool in each region for each season. Refer to figure 2.2 to read the boxplots.....	24
Figure 2.4: Percent kelp-derived carbon in the diet of transplanted mussels in both Kyuquot Sound and Barkley Sound over the summer and winter. The data shown under “spring” in both cases are the same data because all transplanted mussels come from the same parent stock. The data shown for “BS spring” represent the kelp contribution to mussel diet for <i>in situ</i> mussels found in Barkley Sound that were not transplanted but collected at the same time. The broken line in both cases separate mussels found <i>in situ</i> (to the left of the line) with transplanted mussels (to the right of the line). Looking between “spring”, “summer” and “winter” mussels shows the diet trajectories of mussels originally from a common site transplanted to the different regions. Refer to figure 2.2 to read the boxplots.....	25
Figure 2.5: Size specific growth rates of mussels in the two regions in each season. Mussels growing over the course of the year (“year”) are plotted beside the seasonal growth rates for visual comparison, though this data were not used in statistical analyses. “KS” and “BS” correspond to Barkley Sound and Kyuquot Sound, respectively. Mussels grew on average 7% faster in the winter in Barkley Sound vs. the summer, and mussels grew on average 35% in the winter vs. the summer. Refer to figure 2.2 to read the boxplots.....	26
Figure 2.6: The relationship between the kelp contribution to mussel diet and mussel size-specific growth rates in each region during each season and over the year. Mussels growing over the course of both seasons are included for comparison. $R^2$ values range from 0.001 to 0.38, and P-values range from 0.9 to 0.98. ....	28
Figure 2.7: Growth rate of mussels as a function of the proportion of time mussels are wet. Regression line (growth rate = $-1.35 + 2.71 \times \text{wetness}$ , $r^2 = 0.88$ , $P = 0.02$ ) depicted for Kyuquot Sound (black). The grey trend line for Barkley Sound was nonsignificant ( $P = 0.25$ ). ....	29
Figure 2.8: Time series of mean monthly phytoplankton concentrations in each region as calculated by MODIS satellites. Points represent means and bars represent standard errors.....	30
Figure 2.9: The relationship between phytoplankton concentrations (chl $a$ ) and the relative proportion of kelp carbon assimilated by mussels (%kelp derived carbon = $123.28 - 1.01 \times \text{chl } a(\text{mg}/\text{m}^3)$ , $r^2 = 0.64$ , $P = 7.51\text{e-}05$ ). The x-axis represents a total measure of phytoplankton, and the y-axis represents the proportion of mussel diet made up of kelp. Phytoplankton is assumed to make up the proportion of mussel diet that kelp does not.....	32

Figure 3.1: The regions included in this study.....	44
Figure 3.2: Mussel size distributions in the different regions. Significant differences between regions, as found by a Tukey test, are indicated by different letters above the individual boxplots. Barkley Sound mussel sizes are largest (median = 66.5 mm, mean = 70.1 mm, sd = 27.53 mm), followed by Clayoquot Sound (median = 61.4 mm, mean = 63.5 mm, sd = 27.64 mm), followed by Cape Flattery (median = 52.0 mm, mean = 49.6 mm, sd = 19.20 mm) and Kyuquot Sound (median = 45.3 mm, mean = 45.7 mm, sd = 13.02 mm). These box and whisker plots indicate the median, interquartile range (box, representing the middle 50% of the data), 1.5 × interquartile range (each whisker, where data extend this far), and outliers (points). The figure shows medians, but statistical tests were conducted on means.....	50
Figure 3.3: The difference of live mussels from the estimated average large mussel found in Barkley Sound and Kyuquot Sound. The difference between <i>in situ</i> mussels and the average large beach cast mussel is smaller for Barkley Sound (median = -87.1 mm mean = -83.5 mm, sd = 27.5 mm) than for Kyuquot Sound (median = -83.5 mm, mean = -95.7 mm, sd = 13.0 mm). Refer to figure 3.2 to read the boxplots.....	52
Figure 3.4: Mussel bed depths in the different regions. Significant differences between regions, as found by a Tukey test, are indicated by different letters above the individual boxplots. Mussel beds in Barkley Sound (median = 12.7 cm, mean = 13.5 cm, sd = 5.87 cm) and Clayoquot Sound (median = 14 cm, mean = 13.9 cm, sd = 4.07) are deeper than mussel beds in Cape Flattery (median = 10 cm, mean = 9.7 cm, sd = 3.61 cm) and Kyuquot Sound (median = 7.75 cm, mean = 8.83 cm, sd = 2.65). Refer to figure 3.2 to read the boxplots.....	53
Figure 3.5: Biomass of mussels found in a standard 25 cm × 25 cm quadrat in Barkley Sound and Kyuquot Sound. Mussel biomass in Barkley Sound (median = 4.22 kg, mean = 5.31, sd = 2.02 kg) is higher than in Kyuquot Sound (median = 3.2 kg, mean = 3.58 kg, sd = 1.31 kg), though this difference was not found to be significant (t = -1.43, df = 4, P = 0.23). Refer to figure 3.2 to read the boxplots. ....	54
Figure 3.6: Biomass of mussel-bed associated species found in a standard 25 cm × 25 cm quadrat in Barkley Sound and Kyuquot Sound. Biomass of mussel associated species is higher in Barkley Sound (median = 1430.6 g, mean = 1531.7 g, sd = 880.6 g) than in Kyuquot Sound (median = 463.8 g, mean = 593.2 g, sd = 551.4 g). Refer to figure 3.2 to read the boxplots. ....	55
Figure 3.7: Mass of sediment found in the standard 25 cm × 25 cm quadrat in Barkley Sound and Kyuquot Sound. There is more sediment in Barkley Sound (median = 610.4 g, mean = 1068.6 g, sd = 1261.8g) than in Kyuquot Sound (median = 225.8 g, mean = 361.7 g, sd = 394.2 g). Refer to figure 3.2 to read the boxplots. ....	56
Figure 3.8: CCA plots for a) Barkley Sound and b) Kyuquot Sound. For b), as there was only one environmental variable that tracked onto a CCA axis (mussel biomass), the plot shows the first CCA axis against the unconstrained axis with the most explanatory power (CA1). Dots represent species.....	57
Figure 3.9: NMDS plot showing separation of the two regions based on invertebrate community structure. Dots represent mussel plots.....	58
Figure 3.10: The estimated biomass of the top ten most abundant (by wet biomass) morphospecies found in Barkley Sound and Kyuquot Sound.....	59
Figure 3.11: Mussel production from Barkley Sound and Kyuquot Sound estimated in calories produced over various time horizons based on observed length increases, and energy accumulation calculated based on changes in biomass. Panels are a) summer growth, b) winter growth, c) year-round growth. Black points represent energy in mussel growth from Barkley	

Sound and the black lines represent the size of escapement for mussels in Barkley Sound. Grey points represent energy from mussel growth from Kyuquot Sound and the grey lines represent the size of escapement for mussels in Kyuquot Sound. The text represents the proportion of energy in mussel growth unavailable to seastar predators on account of size escapement (black for Barkley Sound and grey for Kyuquot Sound). ..... 61

Figure A1: The fitted relationship between size and dry biomass of mussels takes an allometric form,  $y = a \times \text{length}^b$  ..... 86

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## **Dedication**

For anyone in my life who wonders why I turned to the ocean.

## Foreword

To expect the unexpected shows a thoroughly modern intellect.

Oscar Wilde

Seest thou, beside the wintry torrent's course, how the trees that yield to it save every twig, while the stiff-necked perish root and branch?

Haemon, from Sophocles' *Antigone*

# **Chapter 1: Introduction**

## **Ecosystem Services**

Ecosystem services are the ecological process that provide benefits for people (Daily 1997, MEA 2005). The Millenium Ecosystem Assessment (MEA 2005) categorized four broad categories of ecosystem services, including provisioning services (provide raw materials for goods), regulating services (maintaining conditions comfortable to humans), cultural services (catering to material and non-material benefits that are particular to cultural milieus), and supporting services (basic environmental processes on which other services depend on). One of the primary contributions of the MEA was that it demonstrated the range of benefits that natural ecosystems provide beyond what is accounted for in markets. Thinking about species and ecosystems in this way can reveal important functional roles of species as well as provide management agencies a way to manage systems to promote the provision of services (Kremen 2005). In order to properly account for the production of these services, knowledge of their production is required. Many ecosystem services (mostly those that support other services and regulate the functioning of ecosystems) both support and depend on biodiversity (Balvanera et al. 2006, but some effects of biodiversity may be due to a “sampling effect” – when diverse communities are more likely to contain the most important species as a consequence of sampling more species – and not a function of diversity *per se*, Cardinale et al. 2006) yet the ecological processes driving the provision of many ecosystem services remains rudimentary (Luck et al. 2003, Kremen 2005).

## **Ecology and Ecosystem Services**

Kremen and Ostfeld (2005) made a call to ecologists to measure and analyze ecosystem services. The four types of ecosystem services both support and depend on biodiversity, indeed many

services are directly driven by components of biodiversity (Luck et al. 2009, Kremen 2005). A meta-analysis of the role of biodiversity and ecosystem services found that biodiversity generally has a positive impact on ecosystem services, especially on supporting and regulating services (Balvanera et al 2006, but see Cardinale et al. 2006). Indeed, it is generally supporting and regulating services that are serially undervalued (Rodriguez et al. 2006). A comprehensive research program to understand the ecology of ecosystem services requires identifying the species or entities that are “ecosystem service providers” and measuring their functional contributions in the context of key environmental variables that influence the ability of these species to provide services, and measuring the spatiotemporal scale over which the provision of services operates.

Ecology is replete with contingencies, and the ability of an organism to provide ecosystem services is dependent on intra- and interspecific interactions (Salomon et al. 2010, Greenleaf and Kremen 2006), as well as environmental conditions conducive for the functioning of species that promote ecosystem services. Many research projects that aim to quantify ecosystem services selectively look at ecological functions that people benefit from. However, many species can impact ecosystem services negatively (Dunn 2010). In most cases, both positive and negative effects on ecosystem service provisioning are likely to occur, demanding the navigation of trade-offs. Thus, a full account of the impacts of a species on ecosystem services would consider the species as an ecosystem modifier (considering both potential services and disservices provided by the species). A close look at impacts on a broad set of supporting services may reveal a dramatically different picture than a narrow focus on provisioning services.

The reintroduction of sea otters off of the west coast of Vancouver Island, British Columbia provides an opportunity to study ecosystem service providers where otters provide potential

ecosystem services and disservices through their ecological role as an apex predator. Sea otters may have multiple community-level impacts that are unforeseen, demanding that we expect the unexpected.

## **Sea Otter Reintroduction and Ecology**

Sea otters were extirpated as a result of the maritime fur trade from the 18<sup>th</sup> through the early 20<sup>th</sup> centuries, and they were subsequently reintroduced to the west coast of Vancouver Island in a series of reintroductions from 1969-1972 (Nichol et al. 2005). Sea otters can deplete populations of important commercial species, but they also have important ecosystems impacts with implications for ecosystem service provision. Sea otters can release kelp from grazing pressure by urchins by significantly reducing sea urchin populations (Estes and Palmisano 1974), which has been shown to enhance shellfish growth by 2-5 fold (Duggins et al. 1989; Estes and Duggins 1995). Kelp have high tissue turnover rates, and high kelp production can lead to high concentrations of kelp derived carbon in coastal waters, which provide a food subsidy for filter feeders (Duggins et al. 1997). Sea otters are also voracious predators of a variety of marine invertebrates, including crabs, clams, snails, urchins, mussels, abalone, worms and seastars (Estes and Palmisano 1974, VanBlaricom 1988, Newsome et al. 2009). These effects – increasing nutrient availability and top-down predation – can alter people’s perceptions of sea otters and their reintroduction.

Sea otters can influence both top-down and bottom-up forces that have implications for supporting ecosystem services, and the extent of their cumulative indirect effects off of the West Coast of Vancouver Island are largely unknown (except see Morris et al. 1981, Breen et al. 1982). Kelp production may provide an important nutrient source for many shellfish. Sloughed-off kelp can provide a nutrient subsidy for filter feeders through particulate organic carbon

(POM) and dissolved organic carbon (DOM) (Mann 1973, 1988, Kaehler and Pakhomov 2006), influencing the ecosystem indirectly from the bottom-up through the otters' direct top-down impact. Otters can also have important top-down impacts on the population structure of many marine invertebrates. When otters establish in a new area, they specialize on preferred prey then generalize to a broader prey base when their preferred prey decline in abundance (Tinker et al. 2007). Through predation, otter can regulate the size structure and abundance of their prey (Estes and Palmisano 1974).

Coastal environments dominated by macrophytes, especially kelps (which have very high biomass and growth rates, Mann 1972), represent some of the most productive habitats in the world (Leigh et al. 1987). Kelp production enters nearshore food webs both directly through grazing consumption (Miller and Mann 1973) and indirectly through detrital pathways (Duggins 1988). Kelp productivity is assumed to be more important for nearshore foodwebs in winter, when phytoplankton biomass is seasonally low (Duggins 1988, Dunton and Shell 1987).

In order to quantify the contribution of kelp to benthic food webs, researchers have used stable isotope analysis to differentiate kelp versus phytoplankton as nutrient sources to a variety of organisms (Duggin et al. 1989, Bustamante and Branch 1996, Salomon et al. 2008, Tallis 2009). Stable isotope analysis is an approach to identify resources assimilated by consumers. Ratios of heavy to light isotopes of carbon and other elements such as nitrogen can act as tracers that match the tissue of a consumer to its food source (Peterson and Fry 1987). Isotopic signatures represent assimilated diets integrated over time of the tissue of the consumer (Smit 2001).

Tracking the contribution of kelp to mussel diets can provide evidence for one potential role of otters as ecosystem service providers, providing the supporting service of boosting nearshore secondary production on the west coast of Vancouver Island.

*Mytilus californianus* is a good candidate to study the impacts of increased kelp biomass on nutrient dynamics and secondary productivity because it is a dominant space-occupier and habitat-provider in mid-intertidal regions. *M. californianus* is efficient at filtering seawater and obtaining nutrients from both phytoplankton and kelp-derived production (Tallis 2009).

Mussels are also an important contributor to intertidal diversity. Mussels are competitive dominants in the intertidal region, able to outcompete other primary spaceholders (Paine 1966, Paine 1974). They form complex, multi-layered beds that provide habitat for a host of species. Over 300 species have been identified living in beds of *M. californianus* (Suchanek 1979). Mussel bed diversity has been found to increase with increasing mussel bed complexity, particularly with the sizes of mussels in the bed, the biomass of mussels in the bed, the depth of the mussel beds, and the amount of sediment that accumulated in mussel beds (Kanter 1977, Kanter 1979). Mussels can be considered ecosystem engineers in that they modify the immediate environment to facilitate the coexistence of other species. They provide physical structure that is habitat for intertidal organisms and that provides refuge from thermal and desiccation stresses (Suchanek 1979). Otters foraging within mussel beds may serve as a key source of disturbance, disrupting this habitat provisioning function of mussels through depredation. Disturbance is an important driver of ecosystem processes and community structure (Turner 2010). Mussels are also important prey sources for other predators (such as the predatory seastar *Pisaster ochraceous* and carnivorous snails in the genus *Nucella*), but they can escape predation by growing too large to handle (Paine 1976), and otter foraging can prevent mussels from achieving size escapement, promoting a greater proportion of mussel biomass to be available to these predators.

## **Outline of Thesis**

### **Chapter 2**

The first study explores if otters releasing kelp from urchin herbivory off of the west coast of Vancouver Island impact the resource dynamics and secondary production of the region. By individually tagging mussels in regions with and without otters and therefore with higher and lower biomass of kelp, I tested the influence of kelp-derived carbon on nearshore energy pathways and secondary production. Previous research has been mixed on the importance of kelp on secondary productivity. Duggins et al. (1989) found increased secondary productivity with greater kelp biomass. However, Salomon et al. (2008) found that growth rates of filter feeders were not different among regions differing in kelp biomass. The latter result was attributed to high phytoplankton productivity across regions. Nonetheless, multiple studies have found that filter feeders derive higher proportions of their diets from kelp where kelp is abundant (Dunton and Shell 1987, Duggins et al. 1989, Bustamante and Branch 1996, Salomon et al. 2008, Tallis 2009). My results show that mussel growth rates and kelp contribution to diet are not higher where otters are present, indicating that phytoplankton and kelp may not be limiting to mussels. Further, my findings suggest that high phytoplankton biomass can reduce the concentration of kelp derived carbon in the water, even in situations of high kelp productivity. These findings point to the importance of other environmental variables that can influence the ability of species to provide ecosystem services.

### **Chapter 3**

The second study in this thesis investigates the extent to which otter predation in the intertidal impacts intertidal macro and invertebrate diversity. Otters may both positively and negatively affect species that provide ecosystem services. This study quantifies how sea otters impact the

supporting services provided by mussels. I hypothesized that otters would decrease mussel bed complexity rendering mussel bed communities less diverse. Mussels support the existence of multiple species, and consequently support the fulfillment of existence values. Otters can strip mussel beds down to primary substrate (VanBlaricom 1988), and this has potential repercussions for mussel bed structure and diversity. My findings suggest that sea otters homogenize mussel beds, restricting the size of mussels and the complexity of mussel beds. This has impacts on the community of organisms in the mussel bed, but the largest impacts seem to be on the abundance of the dominant species in the mussel bed. Restricting mussels to smaller sizes also restricts mussels to fast growing size classes. Based on growth rate measurements, we investigated whether otter predation on mussels allowed for greater rates of secondary production to enter marine food webs. Our results indicate that a greater proportion of mussel production is available to seastar predators where mussels are restricted to smaller size classes, though total production may not be.

## **Summary**

The following chapters describe important potential top-down and bottom-up processes associated with sea otters that have implications for supporting ecosystem services (figure 1.1). These studies showcase important context dependencies of the provision of ecosystem services and illuminate other important disservices that ecosystem service providers can bestow to human well-being. This thesis concludes with a general discussion of the results and avenues for further research.

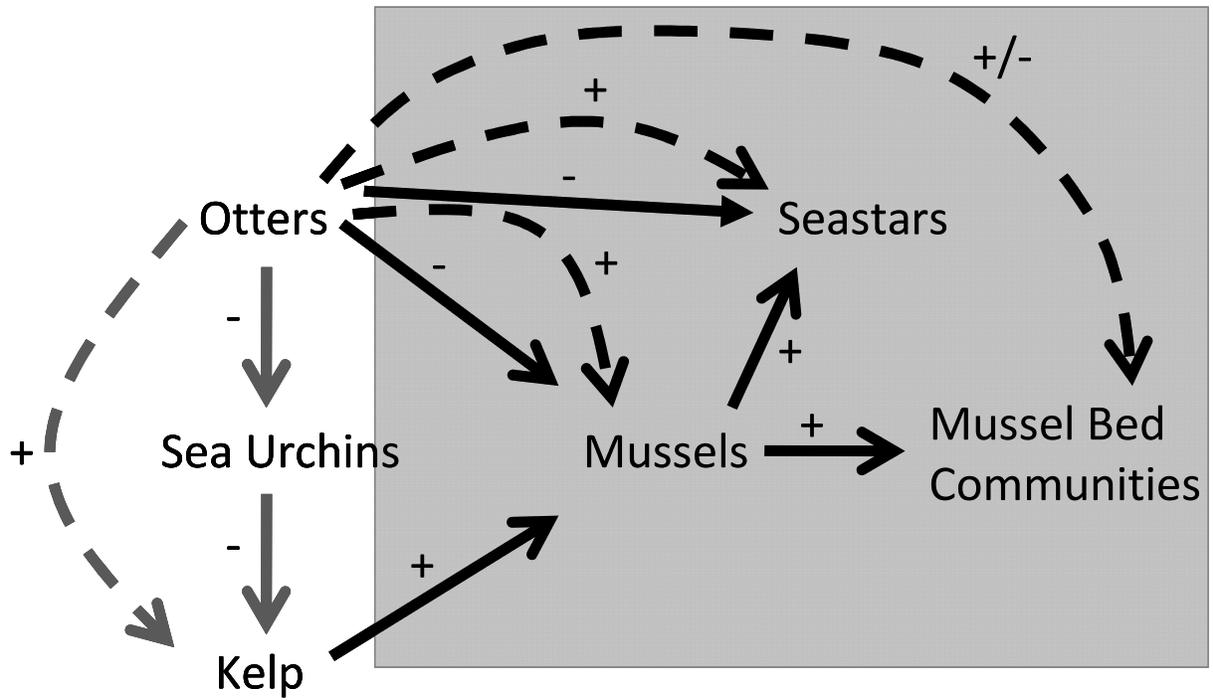


Figure 1.1: A conceptual diagram of the interactions investigated in this thesis. Arrows with broken lines represent indirect interactions and solid arrows represent direct interactions. Grey arrows represent assumed interactions not investigated in this thesis. The grey box encompasses the interactions and hypothesized interactions explored in this thesis.

## **Chapter 2: The Importance of Kelp Derived Carbon to Mussel Growth Varies Regionally and Seasonally**

### **Introduction**

Understanding the ecological processes by which species provide ecosystem services is essential if planning processes designed to account for multiple conservation objectives are to succeed (Egoh et al. 2007). Understanding the ecology of species in the context of the services they provide has revealed important functions of species that fulfill human values. For example, findings into the nuanced behavioural ecology of native pollinating bees and honey bees demonstrate the importance of uncultivated land and native pollinators in facilitating efficient pollination (Greenleaf and Kremen 2006), and research into how vertebrate diversity protects humans from Lyme disease showcases unforeseen value in various small mammals and birds (Ostfeld and LoGiudice 2003, Ostfeld et al. 2006). The reintroduction and spread of sea otters (*Enhydra lutris*) off of the West Coast of Vancouver Island, British Columbia has potential ramifications for the provision of ecosystem services. By preying upon grazers, sea otters have widespread indirect impacts on the primary production of nearshore ecosystems (Estes and Palmissano 1974), and this can translate into greater productivity at higher trophic levels (Duggins et al. 1989). In this way sea otters could be viewed as ecosystem services providers that have the potential to indirectly enhance kelp-associated marine invertebrates. This study assess whether sea otters enhance secondary production on intertidal rocky reef ecosystems.

The indirect role of sea otters and other top predators in facilitating the release of kelp-derived carbon to nearshore foodwebs has been hypothesized for decades (Mann 1973, Duggins 1988, Duggins et al 1989, Salomon et al 2008). By releasing kelp from herbivory by sea urchins, the

high primary productivity in kelp is thought to alter carbon flow in foodwebs by enhancing the availability of kelp-derived organic carbon, potentially leading to higher rates of secondary production. The contribution of kelp through particulate organic matter (POM) and dissolved organic matter (DOM) is thought to be the most important contribution to nearshore systems because of the scale of detrital production (tissue turns over 20 times per year, Duggins et al. 1997) and the large spatial extent of kelp-derived carbon in coastal waters (Kaehler et al. 2006).

The role of kelp-derived nutrients has been explored in a variety of studies, both in laboratory (Duggins 1995) and field studies (Duggins et al 1989, Bustamante and Branch 1995, Salomon 2008, Tallis 2009). The results, however, are varied. Some studies provide evidence that kelp-derived carbon magnifies invertebrate growth rates (Duggins et al 1989), while other studies report no effect on growth despite assimilation by invertebrates (Salomon et al 2008). The indirect impacts of top predators are important for understanding basic community ecology, ecosystem services (through the concept of ecosystem service providers) (Kremen 2005), and environmental management. Many studies focus on impacts that have direct impacts to ecosystem services (and often to look at provisioning services), but few have studied the indirect effect of an organism to supporting services. Here, we take advantage of a naturally expanding sea otter population on the outer coast of Vancouver Island, British Columbia, to investigate the extent to which otter presence alters carbon flow and secondary production (supporting services for broader ecosystem productivity) and how if these effects vary seasonally.

Sea otters became established off of the west coast of Vancouver Island in a series of reintroductions from 1969-1972 following the extirpation of otters by the 19<sup>th</sup> century fur trade (Nichol et al. 2005). The population and range increase of sea otters off of the west coast of Vancouver Island has led to empirical evidence of and speculation about the likely ecological

consequences of their reestablishment (Morris et al. 1981, Breen et al. 1982, Markel *in prep*). A rich history of literature provides evidence for sea otters releasing kelp from urchin herbivory in the northeast Pacific (Estes and Palmisano 1974, Duggins et al. 1989, Estes et al. 2010). One expected result is that nearshore systems will have higher secondary productivity as a result of the greater primary productivity associated with kelp release. In this sense, sea otters can be touted as providers of ecosystem services, as their role in facilitating nearshore productivity can be important. Nonetheless, as an apex predator that consumes shellfish valued by both subsistence and commercial fishers (such as sea urchins, crabs, geoducks, clams, and mussels), sea otters can also be viewed as ecosystem service detractors. Can increased productivity offset or counterbalance the loss of shellfish biomass?

To explore this issue, I examine whether increased kelp biomass leads to higher mussel growth rates. Kelps have been documented as important primary producers to nearshore ecosystems in many regions of the world, such as the Aleutian Islands (Duggins et al. 1989), South Africa (Kaehler et al. 2006), and New Zealand (Salomon et al. 2008). The idea that kelps have important community and ecosystem consequences have strong intuitive appeal given their high growth rates (some estimates are on the order of 2 feet/day for *Macrocystis pyrifera* in California (Abbot and Hollinberg 1976). Kelps have high tissue turnover rates, leading to high inputs of kelp-derived carbon sources to surrounding waters. This subsidy can affect nutrient flows and productivity, and can occur over very large spatial scales.

Previous studies have found that kelp can have an important impact on nearshore carbon dynamics, but little work has been done on the impact of seasonality on the importance of kelp carbon to nearshore ecosystems. Phytoplankton, another food source for many filter feeders, tends to follow a seasonal pattern, where it is more abundant in summer than in winter (Harris

2001). Winter storms tear up kelps, leading to senescence and degradation, and Duggins (1997), in a laboratory study found that filter feeding mussels grew faster when fed degraded kelp particles over fresh kelp particles. Degraded kelp has a lower C/N ratio than fresh kelps (probably because of the extra nitrogen added by colonizing microflora), and has lower concentrations of secondary metabolites which can deter invertebrate feeding. If degraded kelp is more important as a food source for filter feeding invertebrates than fresh kelp, then kelp is potentially more important to mussels during winter than summer. Indeed, Dunton and Schell (1987) found that a variety of marine invertebrates did depend on kelp carbon during the winter in Alaska.

Because otter presence on the west coast of Vancouver Island follows a latitudinal gradient, there are other environmental variables that could vary concurrently with the availability of kelp. Temperature, phytoplankton abundance, and wave dynamics can all influence growth rates in mussels (Menge et al. 2008), and may vary between regions of otter presence and absence. Despite these potential variations, I ask if the impact of sea otters and increased kelp biomass is great enough to be observed regardless.

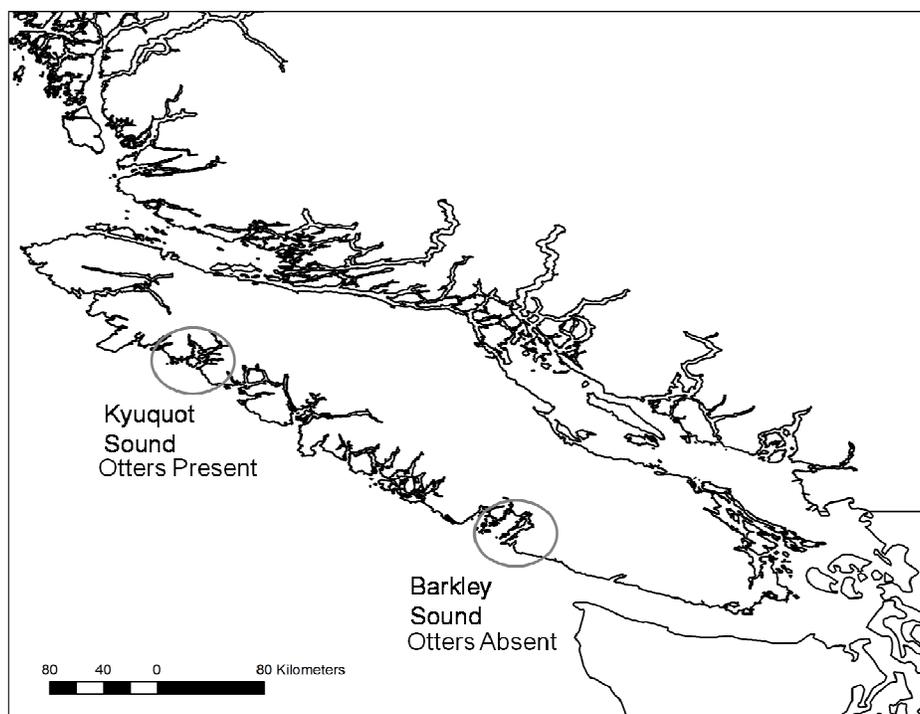
This paper aims to measure the indirect effects of sea otters on secondary production via the release of kelp-derived carbon on the west coast of Vancouver Island. Sea otters established in Kyuquot Sound during the mid to late 1980s, and populations have been growing at a rate of 15.66 – 18.6 % a year since then (Nichol et al. 2005). There are currently no otter populations in Barkley Sound, but a large proportion of that Sound is considered to be optimum habitat for expanding otter populations (Gregr et al. 2008). The hypothesis that kelp-derived carbon facilitates greater secondary production through a greater supply of nutrients is examined by testing the predictions that 1) enhanced kelp presence is associated with enriched kelp content in

nearshore waters, 2) enhanced kelp presence is associated with greater kelp synthesis in the diets of primary consumers, 3) there are higher growth rates of primary consumers in otter-present areas, and 4) the previous three predictions are particularly true in winter, when phytoplankton abundance is low and kelp is more digestible.

## Methods

### Regional Study Design

I established 5 intertidal sites nested within two regions, Kyuquot Sound and Barkley Sound, on the west coast of Vancouver Island, British Columbia, Canada (figure 2.1). I transplanted mussels at each of the five sites (Table 2.1) to measure mussel growth rates and the contribution of kelp-derived organic carbon seasonally.



**Figure 2. 1: Map of the west coast of Vancouver Island, British Columbia Canada showing locations of the study regions.**

**Table 2.1: Locations of sites used in this study**

Region	Site	Latitude	Longitude
Barkley Sound	Seppings	N 48° 50.344'	W 125° 12.446'
Barkley Sound	Helby	N 48° 51.345'	W 125° 10.245'
Barkley Sound	Diana	N 48° 50.969'	W 125° 11.319'
Barkley Sound	Sanford	N 48° 51.901'	W 125° 10.161'
Barkley Sound	Bluestone	N 48° 49.238'	W 125° 09.914'
Kyuquot Sound	KT1	N 49° 59.953'	W 127° 25.959'
Kyuquot Sound	Prop Breaker	N 49° 59.955'	W 127° 24.417'
Kyuquot Sound	Beach	N 49°59.815'	W 127°23.817'
Kyuquot Sound	TB	N 50°00.291'	W 127°24.052'
Kyuquot Sound	GDA	N 50°00.077'	W 127°23.015'

## Mussel Transplants and Growth Rates

Mussels (*Mytilus californianus*) from a common site (KT1), of approximately 50 mm were collected and transplanted to four sites (n= 49 per site) in each of Kyuquot Sound and Barkley Sound. Mussels were notched at their growing margin with a Dremel® tool in order to mark the initial size of mussels and measure growth over time (Menge et al. 2008). Transplant plots (n=5 or 8 depending on transplant technique) were established at a standard tidal height (approximately 2.35 m above chart datum in Kyuquot Sound, and 2.14 m above chart datum in Barkley Sound, see below for an explanation on the difference) in the mussel bed in each region were cleared of any primary space holder in order to transplant mussels into these plots. We attempted to standardize plot tidal heights between regions based on the amount of time mussels are submerged. Standardizing plot heights between regions was attempted by comparing heights

in a given areas against a modeled tidal cycle (using the Xtide program, Flater 2005), and finding heights in each region that correspond with equivalent submergence time. Because tidal amplitude in Kyuquot Sound was predicted to be higher than in Barkley Sound, transplants in Barkley Sound were placed lower (relative to Canadian chart datum, which approximates the lowest astronomical tide) than in Kyuquot Sound by 20 cm. The effect of wave run-up—the height that waves reach on the shore (and therefore effective tidal height)—could not be known *a priori* but was estimated after transplants were put in place.

Transplant techniques took two forms. The first included attaching mussels (n=3 per plot) to the bare substrate with Sea Goin' Marine Epoxy™ putty (n= 8 plots per site). The potential limitations of this method are that the mussels were broadly exposed to predation and artificially oriented on the substrate. The second transplant method employed vexar mesh to secure mussels (n=5 per plot) to the bedrock (n=5 plots per site). The potential limitation of this method is that the lip of the vexar mesh provided an edge at which wave forces could pull up the plot, and that the vexar could have had impacts on temperature, water motion, or sediment accumulation. Both regions are difficult to access and site visits were rare, so both methods were used to ensure that mussels would last through the growing period, increasing the probability of acquiring data on growth rates. Transplants were placed in at the end of May – early June 2009. Approximately half of the mussels remaining (some were lost over the period of time they were in the field) were collected in late August – early September 2009 while the rest were collected in late February – early March 2010. Additionally, at each site, mussels growing *in situ* surrounding our experimental plots were haphazardly chosen and notched at the same time as our initial transplant (to examine summer growth), and following our first transplant retrieval (to examine winter growth).

Mussels grow from the end of their shells, so growth was calculated by measuring the difference in length from the notch to the maximum extent of the shell. This growth increment was then standardized by the amount of time transplanted and initial mussel length using the formula:

Size specific growth = growth increment (mm)  $\times$  time (days)<sup>-1</sup>  $\times$  initial length (mm)<sup>-1</sup> (Menge et al. 2008)

Because growth in mussels is size dependent, only those mussels falling within the range of 40 to 60 mm were included in my growth analyses (Smith et al. 2009). Mussels growing *in situ* grew at rates that were not significantly different than mussels transplanted with the epoxy putty technique (Tukey Test P = 0.4608 Barkley Sound; P = 0.93654 Kyuquot Sound), however mussels growing under the vexar transplant technique grew significantly faster than *in-situ* (Barkley Sound p = 0.013, Kyuquot Sound P = 0.001) and epoxy-transplanted mussels (Barkley Sound p < 0.001, Kyuquot Sound P = 0.019). This indicates that transplant technique had an effect on mussel growth rates (though only significant for vexar transplanted mussels), but that mussels found in different regions grow at rates that are not significantly different. In light of these findings, only putty transplanted mussels and mussels found *in situ* were included in growth rate analyses. In this way we could compare mussel growth rates between regions growing over the summer (May-September), and over the fall and winter (September-March).

### **Stable Isotope Samples**

To determine the contribution of kelp carbon to mussel growth in each region, we determined the isotopic signature of 5 species of kelp (Table 2.2: n=5 samples per species) commonly occurring in the intertidal and shallow subtidal environments of each site. (*Pterygophora californica* – a subtidal species – was not taken in winter due to hazardous conditions.) Because of insufficient



Species	Kyuquot Sound Summer			Kyuquot Sound Winter		
	$\delta^{13}\text{C}(\text{SE})$	$\delta^{15}\text{N}(\text{SE})$	n	$\delta^{13}\text{C}(\text{SE})$	$\delta^{15}\text{N}(\text{SE})$	n
<i>Laminaria setchellii</i>	-15.4 (0.69)	9.03 (0.17)	5	-15.36 (0.34)	7.24 (0.24)	11
<i>Macrocystis</i>						
<i>integrifolia</i>	-13.89 (0.51)	10.00 (0.33)	5	-15.29 (0.33)	7.97 (0.46)	17
<i>Nereocystis luetkeana</i>	-16.74 (0.73)	10.1 (0.57)	5	-16.18 (0.67)	6.19 (0.33)	18
<i>Pterygophora</i>						
<i>californica</i>	-16.18 (0.92)	8.31 (0.16)	5	-	-	-
POM	-19.74 (0.13)	6.67 (0.07)	20	-18.4 (0.35)	6.13 (0.32)	14
detritus	-17.23 (0.28)	9.77 (0.26)	20	-17.67 (0.37)	7.93 (0.13)	19
Spring mussel foot	-18.50 (0.16)	8.72 (0.06)	5	-	-	-
mussel pedal foot	-18.00 (0.05)	8.76 (0.05)	62	-16.52 (0.07)	8.44 (0.07)	74

To examine kelp carbon in the water, site-specific water samples taken nearshore (approximately 100 m from shore) were filtered through standard Whatman G/F filters (1.2  $\mu\text{m}$  pore size) and zooplankton were picked off the samples. These samples are called “POM” (particulate organic matter). Vertical plankton tows at the same locations were also taken at each site and filtered through a size fraction of 63 – 200  $\mu\text{m}$ . These samples are referred to as “detritus”.

Prior to transplanting, the pedal foot tissue from five mussels were analyzed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios as a baseline for comparison between regions and over the mussel growing period. Five mussels were also taken from Barkley Sound at the time of transplant to test if early summer isotopic signatures differed between the regions.

Transplanted mussels, as well as a subset of the mussels found *in situ* were dissected, their pedal foot removed, and rinsed in deionized water. All samples for isotope analyses were dried at 60°C for 48 hours, packed into tin weight capsules and shipped to isotope laboratories for analysis. Samples were shipped to University of California Davis stable isotope facility as well as the IsoEnvironmental laboratory in Rhodes University in South Africa. Because multiple laboratories were used, a leucine amino acid standard was packaged and shipped to both laboratories to calibrate isotope data between laboratories.

No effect of transplant type was found for determining the % contribution of kelp to the diet of mussels ( $df = 2,20$ ,  $F = 0.631$ ,  $P = 0.5423$ ), so all mussels were included in analyses testing differences in kelp-derived carbon in mussels among regions.

### **Calculating Kelp Contribution**

To estimate kelp contributions to POM, detritus and mussels, a two-source mixing model was used where:

$$\% \text{ kelp}_{\text{consumer}} = ((\delta^{13}\text{C}_{\text{sample}} - \delta^{13}\text{C}_{\text{phytoplankton}} - \Delta \delta^{13}\text{C}) / (\delta^{13}\text{C}_{\text{kelp}} - \delta^{13}\text{C}_{\text{phytoplankton}})) \times 100$$

The  $\delta^{13}\text{C}_{\text{phytoplankton}}$  value used was - 23‰ in every case. This value corresponds to an offshore phytoplankton signature reported by Perry et al (1999) off of Vancouver Island, and agrees with signatures of pure phytoplankton cultures for the northeast Pacific (Duggins et al 1989). The fractionation coefficient,  $\Delta \delta^{13}\text{C}$ , was parameterized with the value of 1‰, which is a conservative measure of trophic level fractionation for marine invertebrate herbivores (Vander Zanden and Rasmussen 2001). This fractionation value leads to conservative estimates of kelp-derived carbon to mussel tissue because it effectively increases the distance between  $\delta^{13}\text{C}_{\text{sample}}$  and  $\delta^{13}\text{C}_{\text{kelp}}$  in the mixing model.

The  $\delta^{13}\text{C}_{\text{kelp}}$  value was obtained by averaging isotope values for all kelp species. Kelp values were used on a site level where possible (with the exception of Kyuquot Sound in the summer due to limited samples per site). Site to site variation (in Barkley Sound and in Kyuquot Sound winter) was not high (on the order of 1‰) where this could be compared, so I assume that site-to-site variation for Kyuquot Sound in summer may not be high either.

A concern in using simple mixing models is that it condenses all the variability of a source into a single point (Salomon et al. 2008). Furthermore, multiple potential food sources typically exist (Moore et al. 2006), and in this case phytoplankton and seven potential kelp species for mussels were identified. Here, we focused on benthic and pelagic sources of carbon (kelps and phytoplankton species) and thus reduced our end members to two sources, giving all seven kelp species equal weight (given a lack of data on relative proportions of kelps in mussel diet). If a single species contributes overwhelmingly to the diet of mussels, this may have major implications on the calculations of percent kelp-derived carbon. Due to their high growth rates and standing crop biomass, *Macrocystis integrifolia* and *Nereocystis luetkeana* likely contribute more kelp biomass to the detrital pool than any other species. However, intertidal kelps are in the closest spatial proximity to mussels, which make justifying a differential weighting of kelps difficult. Despite these drawbacks, when considering relative change in diet, isotopic mixing models can provide insight into the relative importance of kelp vs. phytoplankton, because it reflects diet composition on a common scale (% kelp-derived carbon) instead of looking at raw isotope results.

### **Environmental Variables**

Mussel growth is subject to various environmental variables, such as the amount of time that mussels are wet (which affects desiccation stress and has been used to estimate submergence

time, Blanchette et al. 2007), exposure, and water temperature. To estimate these, iButtons™ were placed in the intertidal, tracking temperature every 20 minutes. Following methods by Harley and Helmuth (2003), we were able to estimate relative exposure and effective shore level. Briefly, the method relies on recording the sudden drops in temperature (a 2° C drop was used in this study), to indicate when waves first splash a site. The modeled tide at the time of this signature is the “effective” tidal height of the plot. The difference between absolute shore level and effective shore level represents the wave run-up, and is a measure of exposure. Effective shore level has also been used to estimate submergence time (Blanchette et al. 2007), but because waves undulate (and mussels therefore would not be continuously submerged), this measure probably does not accurately measure submergence time. The Xtide tide model was used to see what proportion of time mussels were wet (termed “wetness” for convenience) given the estimate of effective shore level. Summer water temperatures were also collected in site with iButtons.

Nearshore phytoplankton concentration was estimated using daily estimates derived from the Aqua MODIS satellite which estimates chlorophyll (chl *a*) at a 1km × 1km grid cell resolution. Cloud cover can inhibit readings, but there were still approximately 44 days of readings for summer growth and 47 days of readings for winter growth. Chl *a* estimates were averaged from 5 × 5 cell grid around each site. A similar method was used by Salomon et al (2008), and found to correlate well with field measurements of chl *a*. Chl *a* estimates by MODIS have been found to correlate with field measures of chl *a* in coastal waters around the world, including the Baltic Sea (Matsamaa and Kutser 2008), Portugal (Oliveira et al. 2008), and the Strait of Georgia in British Columbia (Komick et al. 2009), and over a broad range of values (Dall’Olmo et al 2005). MODIS chlorophyll algorithms are statistically derived based on chlorophyll concentrations

ranging from 0.0008 to 90 mg/m<sup>3</sup>. Some daily readings taken for our study exceeded 100 mg/m<sup>3</sup>, likely on account of suspended sediment (SS) and coloured dissolved organic matter (CDOM) that might have artificially inflated some daily readings. Consequently, some uncertainty in the accuracy of these estimates exists. The various relationships between MODIS and *in situ* measures across the world indicate that the phytoplankton biomass data taken from MODIS, though perhaps not exact, is useful for comparative purposes nonetheless. For the purposes of this study, data were averaged over space and time (over entire growing periods), which reduced the influence of extreme values. Because MODIS estimates of chl *a* can be confounded by SS and CDOM, which can include kelp-carbon (Zheng and Tang 2007), as well as atmospheric correction issues as absorbing aerosols and nitrogen dioxide absorption (Komick et al. 2009), they should be interpreted with caution until they are verified or calibrated in these regions.

### **Statistical Analyses**

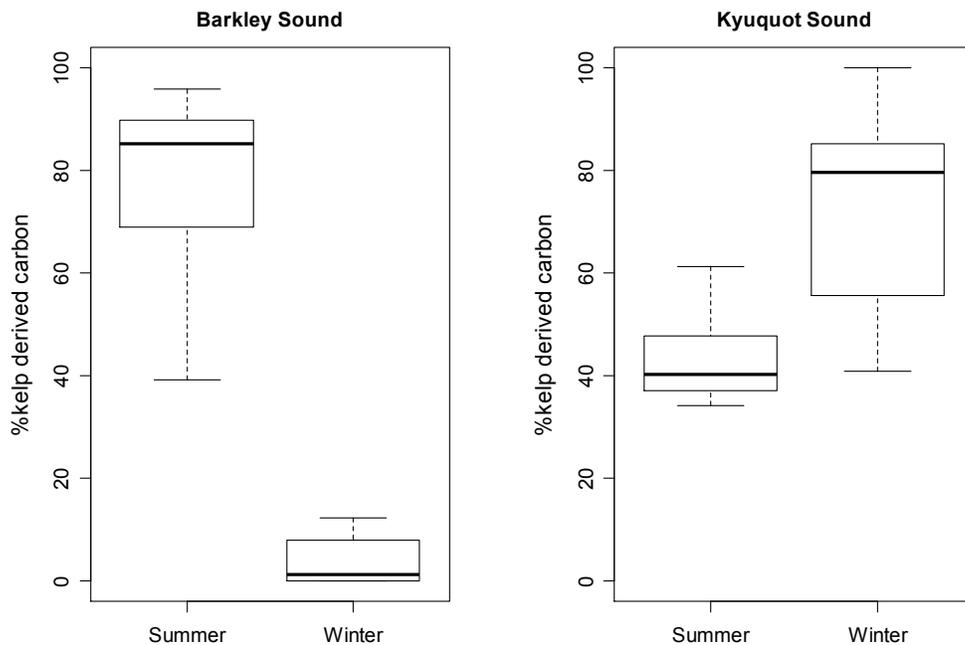
Given the hierarchical nature of our study design, linear mixed-effects models were used to test if sea otters had an effect on mussel growth rates and isotopic signatures. As such, Site was treated as a random effect whereas Region was treated as a fixed effect. Models were fit with Restricted Maximum Likelihood (REML). This method has been shown to be robust to unequal variances within and between scales and unequal sample sizes (Picquelle and Mier *in press*), and REML methods are robust to outliers (Crawley 2007). These methods assume normal distributions, so data were assessed for normality using QQ plots. Where necessary, data were  $\ln(n+1)$  transformed. In all graphs, untransformed data are presented. All hierarchical analyses were conducted using the nlme package in R (R Development Core Team 2008). To test for the

effect of environmental variables on mussel growth rates, we used ANCOVAs and multiple linear regression.

## Results

### POM (>1.2 $\mu\text{m}$ ) Isotope Signature

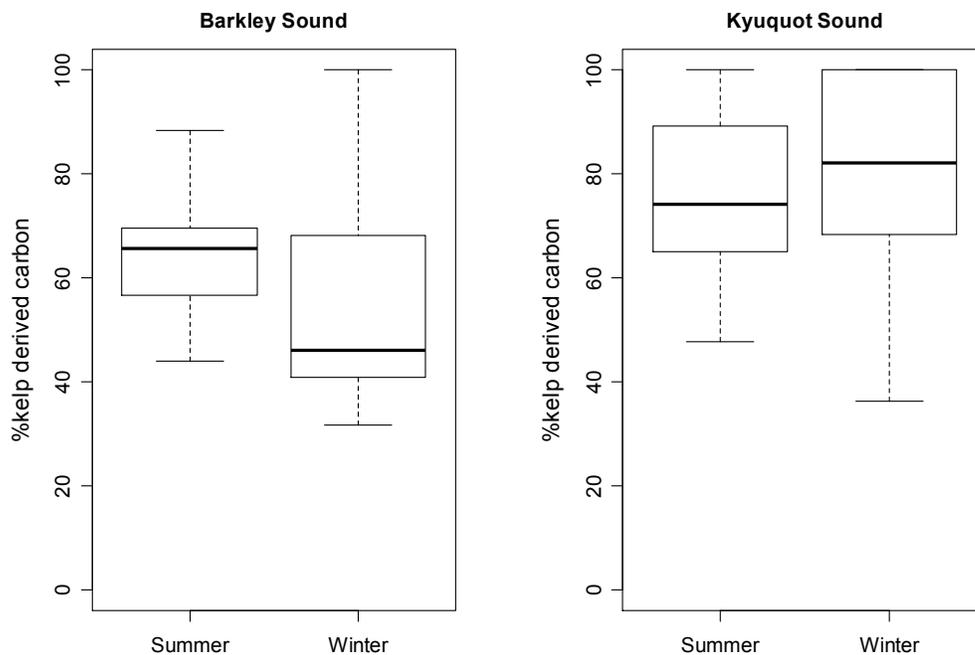
Both regions displayed considerable (but opposite) changes in kelp content of POM across seasons (figure 2.4). Particulate organic matter (POM) in Barkley Sound was composed of ~20 times more kelp in the summer compared to the winter; in contrast, POM in Kyuquot Sound had ~1.7 times more kelp in the winter relative to summer. Consequently, we found a significant effect of Season and a significant Region  $\times$  Season interaction (table 2.3).



**Figure 2.2:** The proportion of kelp found in particulate organic matter (POM, particles above 1.2  $\mu\text{m}$ ) collected in each region for each season. These box and whisker plots indicate the median, interquartile range (box, representing the middle 50% of the data), 1.5  $\times$  interquartile range (each whisker on each side of the box, where data extend this far), and outliers (points). The figure shows medians, but statistical tests were conducted on means.

## Detritus (63-200 $\mu$ m) Isotope Signature

Similar to my POM results, detritus shows a seasonal trend such that 1.2 times more kelp-derived carbon was detected in the summer in Barkley Sound relative to winter, while a higher kelp-derived carbon signature was detected in the winter of Kyuquot Sound relative to the summer (figure 2.5). This trend however, is not as pronounced as it was for POM. Season is a marginally significant factor, and there is a significant region  $\times$  season interaction (table 2.3).

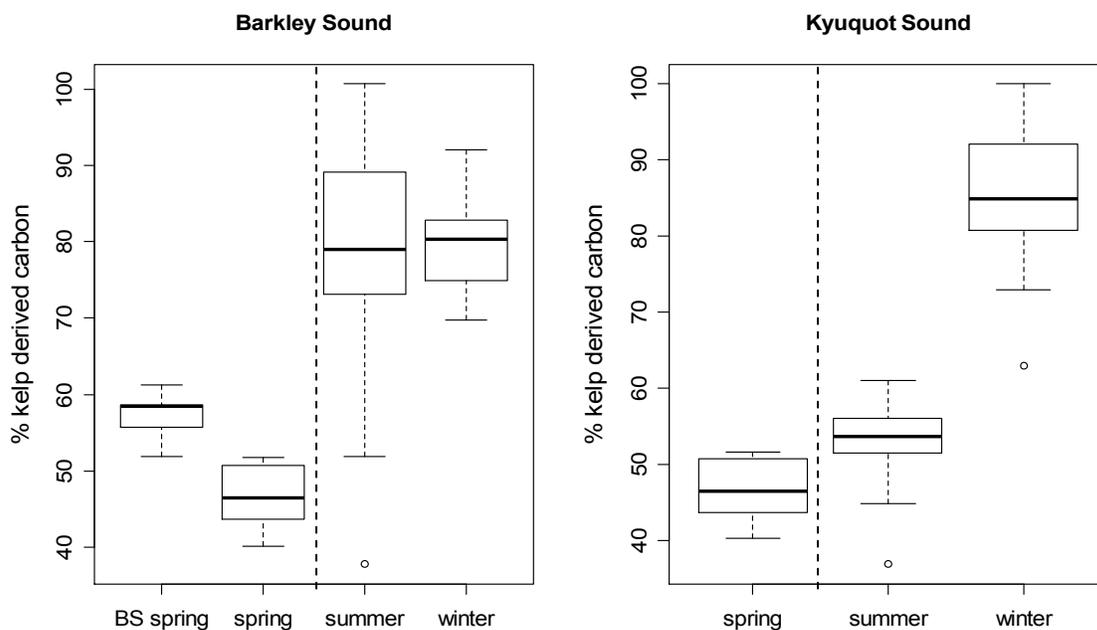


**Figure 2.3:** The proportion of kelp found in the pelagic detrital pool in each region for each season. Refer to figure 2.2 to read the boxplots.

## Mussel Isotope Signatures

Mussels from Kyuquot Sound (taken from the same site as the transplanted mussels) were relatively depleted in kelp at the time of the mussel transplant (mean 48% kelp derived carbon based on isotope-mixing model results). Nontransplanted mussels from Barkley Sound at the

same time show significantly higher kelp content than those found in Kyuquot (mean 65% kelp derived carbon,  $t = 3.98$ ,  $df = 7.36$ ,  $P = 0.004803$ ; compare the “BS spring” vs “spring” plots in figure 2.3). Transplanted mussels in Barkley Sound were more enriched in kelp relative to Kyuquot Sound in the summer but not the winter. Rather, transplanted mussels in both regions showed elevated kelp content in the winter (figure 2.3). Consequently, we detected a significant effect of Season and a Region  $\times$  Season interaction (table 2.3).

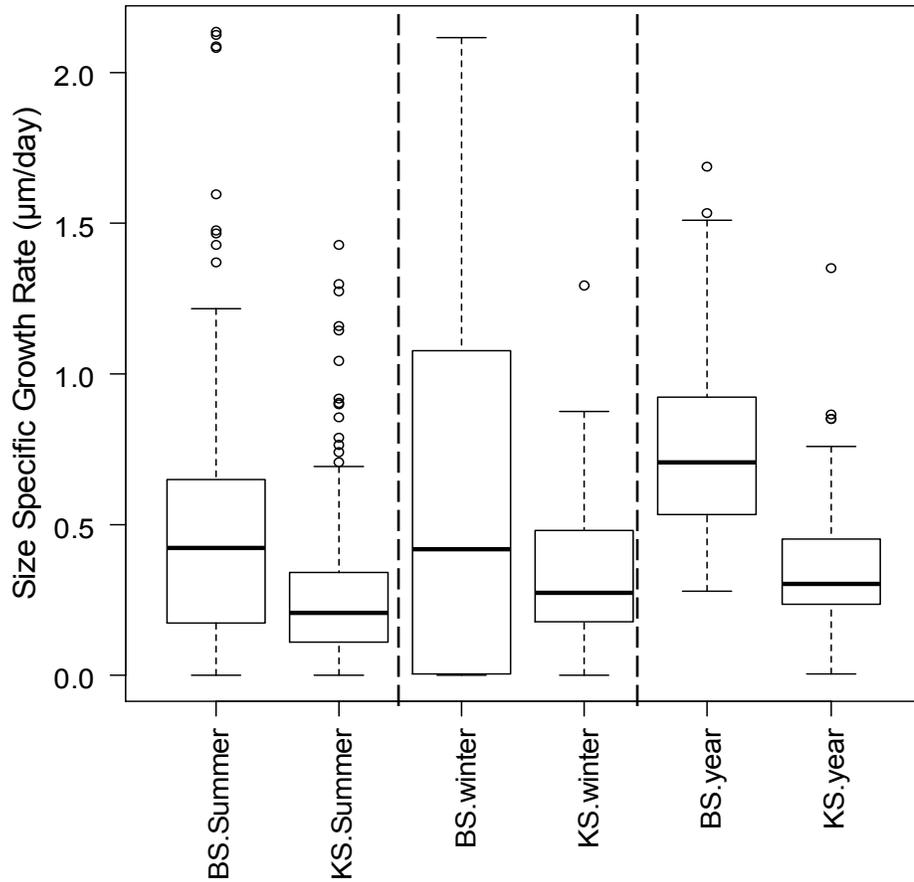


**Figure 2.4: Percent kelp-derived carbon in the diet of transplanted mussels in both Kyuquot Sound and Barkley Sound over the summer and winter. The data shown under “spring” in both cases are the same data because all transplanted mussels come from the same parent stock. The data shown for “BS spring” represent the kelp contribution to mussel diet for *in situ* mussels found in Barkley Sound that were not transplanted but collected at the same time. The broken line in both cases separate mussels found *in situ* (to the left of the line) with transplanted mussels (to the right of the line). Looking between “spring”, “summer” and “winter” mussels shows the diet trajectories of mussels originally from a common site transplanted to the different regions. Refer to figure 2.2 to read the boxplots.**

## Mussel Growth

Contrary to our predictions, mussels (epoxy and *in situ*) grew faster in Barkley Sound than in Kyuquot Sound, despite an order of magnitude more kelp recorded in Kyuquot Sound (Markel in

prep). This result is consistent between seasons. In each region, growth rates were greater in winter than in summer, though we detected considerable variation in Barkley Sound winter growth (figure 2.2). Both region and season have significant effects (table 2.3).



**Figure 2.5: Size specific growth rates of mussels in the two regions in each season. Mussels growing over the course of the year (“year”) are plotted beside the seasonal growth rates for visual comparison, though this data were not used in statistical analyses. “KS” and “BS” correspond to Barkley Sound and Kyuquot Sound, respectively. Mussels grew on average 7% faster in the winter in Barkley Sound vs. the summer, and mussels grew on average 35% in the winter vs. the summer. Refer to figure 2.2 to read the boxplots.**

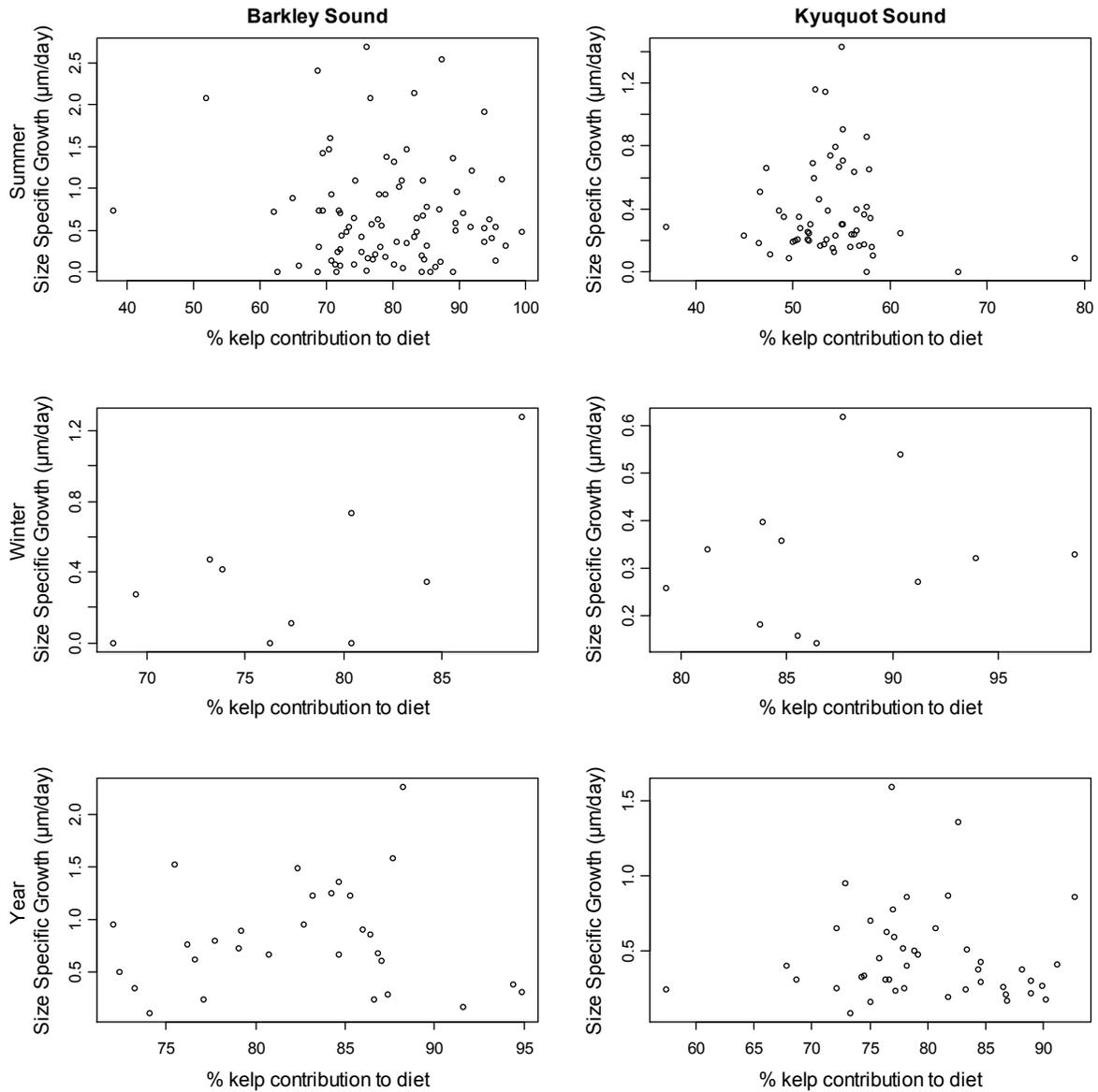
**Table 2.3: Results of Two Way Mixed Effects Models for mussel growth rates, kelp assimilation in mussel tissue, and the proportion of kelp carbon in POM and detritus**

Mussel Growth Rates	Factor	num df	den df	F-value	P-value
	Region	1	10	7.03	<b>0.02</b>
	Season	1	375	9.01	<b>0.003</b>
	Region × Season	1	375	0.55	0.45
Kelp Carbon in mussels	Factor	num df	den df	F-value	P-value
	Region	1	207	0.95	0.33
	season	2	207	183.0	<b>&lt;.0001</b>
	Region × season	2	207	141.4	<b>&lt;.0001</b>
Kelp carbon in POM	Factor	num df	den df	F-value	P-value
	Region	1	6	0.66	0.45
Kelp carbon in POM	Factor	num df	den df	F-value	P-value
	Season	1	67	6.07	<b>0.02</b>
	Region × Season	1	67	272.7	<b>&lt;.0001</b>
Kelp carbon in Detritus	Factor	num df	den df	F-value	P-value
	Region	1	7	2.88	0.13
	Season	1	57	3.74	0.06
	Region × Season	1	57	14.9	<b>0.0003</b>

### **Kelp Influence on Mussel Growth**

To test the relationship between kelp carbon and mussel growth rates within a region and season, we used mixed-effect linear regressions. Barkley Sound shows a slight but nonsignificant positive effect of kelp carbon on mussel growth in the winter ( $P = 0.09$ ,  $r^2 = 0.38$ ). However, no

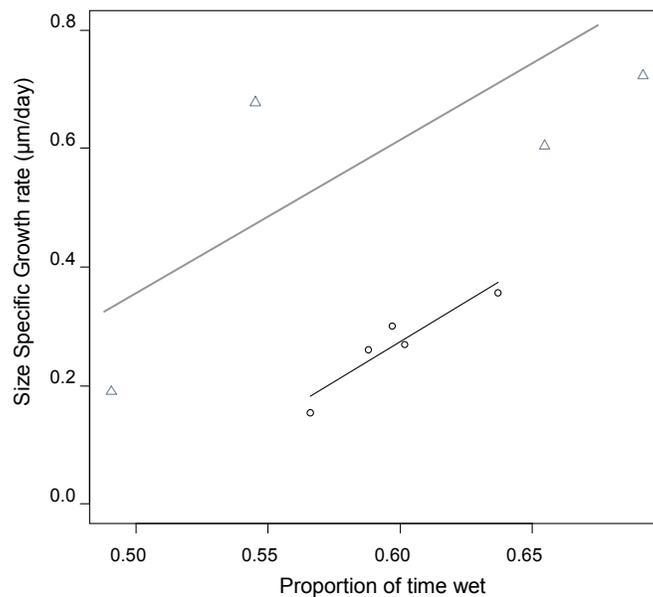
significant relationship was found in any region by season combination (P-values from 0.09 to 0.98,  $r^2$  values from 0.001 to 0.38) (figure 2.6).



**Figure 2.6: The relationship between the kelp contribution to mussel diet and mussel size-specific growth rates in each region during each season and over the year. Mussels growing over the course of both seasons are included for comparison.  $R^2$  values range from 0.001 to 0.38, and P-values range from 0.9 to 0.98.**

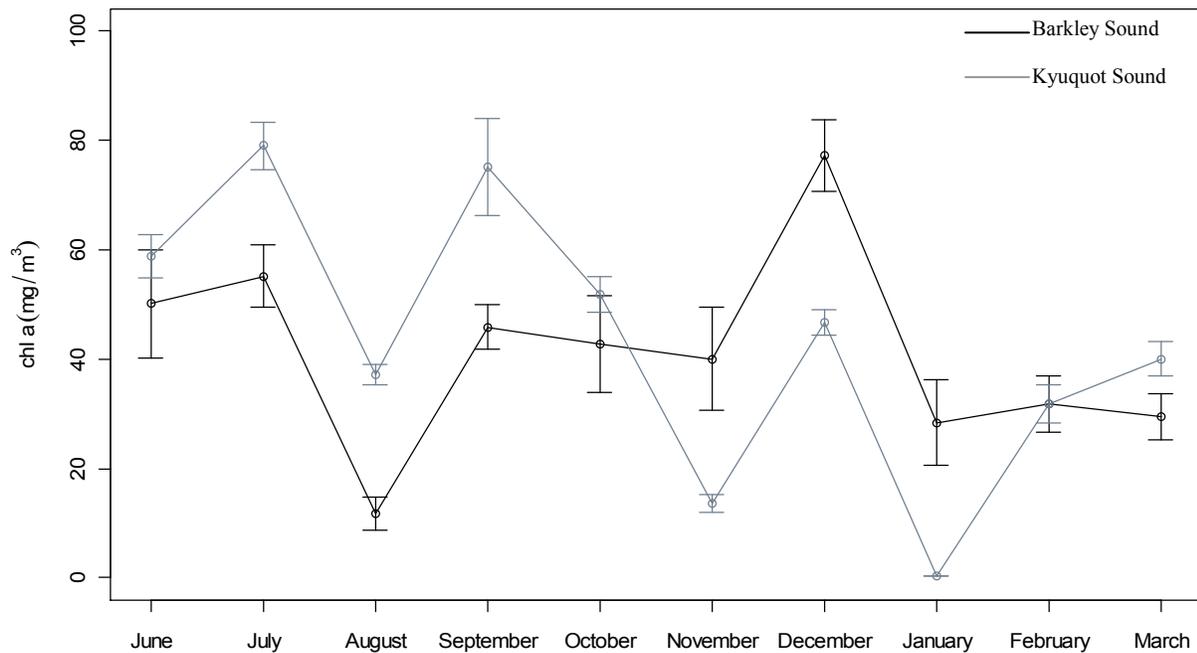
## Environmental Variables

Wave exposure (based on the iButton measures recording sudden drops in temperature) did not differ significantly between regions throughout the summer ( $t = -0.29$ ,  $df = 0.92$ ,  $P = 0.78$ ), and we found no relationship between wave exposure and mussel growth rates. Temperature was found to be significantly higher in Barkley Sound than in Kyuquot Sound (by approximately 1 °C) during summer (summer  $t = 2.75$ ,  $df = 4.75$ ,  $P = 0.04$ ). No relationship was found between temperature and growth rates however. Wetness was more variable among sites in Barkley Sound than Kyuquot Sound in the summer, and in both cases there is a trend to higher growth rates with greater wetness. A significant relationship between mussel growth rates and wetness was found in Kyuquot Sound (growth rate =  $-1.35 + 2.71 \times \text{wetness}$ ,  $r^2 = 0.88$ ,  $P = 0.02$ , figure 2.7) but not Barkley Sound ( $r^2 = 0.56$ ,  $P = 0.25$ ), though this could be a consequence of low sample size ( $n=4$  sites) as a trend is suggested.



**Figure 2.7: Growth rate of mussels as a function of the proportion of time mussels are wet. Regression line (growth rate =  $-1.35 + 2.71 \times \text{wetness}$ ,  $r^2 = 0.88$ ,  $P = 0.02$ ) depicted for Kyuquot Sound (black). The grey trend line for Barkley Sound was nonsignificant ( $P = 0.25$ ).**

Chl *a* concentration is higher in the summer in Kyuquot Sound than in Barkley Sound ( $t = -4.47$ ,  $df = 6.59$ ,  $P = 0.003$ ), though no significant difference was found in winter ( $t = -0.98$ ,  $df = 7.88$ ,  $P = 0.35$ , figure 2.8). No significant relationship, nor even a trend, was found between chl *a* concentrations and mussel growth rates. Results of ANCOVAs factoring in Region and environmental variables are presented in table 2.4. Both wetness and region are significant factors explaining mussel growth, and the ANCOVA model testing the effect of wetness and region was the only model found to be significant ( $P = 0.01$ ).



**Figure 2.8: Time series of mean monthly phytoplankton concentrations in each region as calculated by MODIS satellites. Points represent means and bars represent standard errors.**

**Table 2.4: ANCOVA results for the effects of the various environmental variables explored in this study on mussel growth. The only factors found to be significant were wetness and Region, in the ANCOVA including region and wetness.**

Temperature				
Factor	Estimate	Std. Error	t	p-value
Intercept	-0.47	1.98	-0.24	0.82
Region	-0.21	0.17	-1.19	0.27
temperature	0.07	0.14	0.51	0.62
$r^2 = 0.49$ , $F = 2.89$ , $df = 2,6$ , $p\text{-value} = 0.13$				

Wetness				
Factor	Estimate	Std. Error	t	p-value
Intercept	-0.65	0.41	-1.57	0.17
Region	-0.28	0.08	-3.62	<b>0.01</b>
Wetness	2.01	0.69	2.92	<b>0.03</b>
$r^2 = 0.78$ , $F = 10.6$ , $df = 2,6$ , $p\text{-value} = \mathbf{0.011}$				

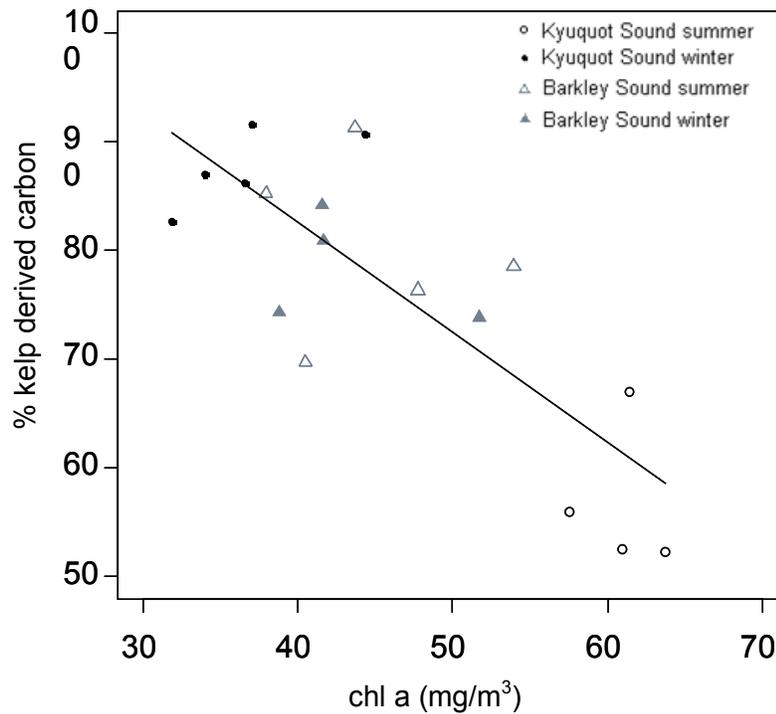
  

chl a				
Factor	Estimate	Std. Error	t	p-value
Intercept	0.14	0.50	0.27	0.8
Region	-0.44	0.19	-2.27	0.06
chl a	0.001	0.01	0.87	0.41
$r^2 = 0.56$ , $F = 43543$ , $df = 2,7$ , $p\text{-value} = 0.054$				

Exposure				
Factor	Estimate	Std. Error	t	p-value
Intercept	0.54	0.14	3.90	0.008
Region	-0.28	0.12	-2.29	0.06
Exposure	0.03	0.27	0.13	0.90
$r^2 = 0.47$ , $F = 2.63$ , $df = 2,6$ , $p\text{-value} = 0.15$				

At a site scale, I found a significant negative effect of chl *a* on the proportion of kelp carbon assimilated by mussels (figure 2.9). Specifically, pelagic phytoplankton concentrations appear to drive down the proportion of carbon in mussel tissue originally photosynthesized by kelp ( $r^2 = 0.63$ ,  $P = 7.51e-05$ ). Seasonal differences of phytoplankton concentrations and kelp-derived carbon in Kyuquot Sound seems to drive this relationship (kelp contribution to diet =  $123.28 - 1.01 \times \text{chl } a(\text{mg}/\text{m}^3)$ ).



**Figure 2.9: The relationship between phytoplankton concentrations (chl *a*) and the relative proportion of kelp carbon assimilated by mussels ( $\% \text{kelp derived carbon} = 123.28 - 1.01 \times \text{chl } a(\text{mg/m}^3)$ ,  $r^2 = 0.64$ ,  $P = 7.51\text{e-}05$ ). The x-axis represents a total measure of phytoplankton, and the y-axis represents the proportion of mussel diet made up of kelp. Phytoplankton is assumed to make up the proportion of mussel diet that kelp does not.**

All environmental variables were included in an additive model to explore how environmental variables explain the differences in summer growth rates of mussels. Wetness as well as temperature are the only two factors that are detected to be marginally significant, but the model itself was not found to be significant ( $P = 0.13$ ,  $r^2 = 0.95$ , table 2.5).

**Table 2.5: Multiple regression results of the environmental variables and kelp contribution to diet on mussel growth rates. Wetness and temperature are found to be marginally significant.**

Factor	Estimate	Std. Error	t	p-value
Intercept	-2.88	1.06	-2.71	0.11
Ch a	-0.02	0.011	-2.10	0.17
Temperature	0.25	0.08	3.16	0.09
Exposure	-0.26	0.17	-1.52	0.26
Wetness	3.34	0.85	3.93	0.06
% Kelp contribution to diet	-0.01	0.01	-1.48	0.27

$r^2 = 0.95$ ,  $F = 7.21$ ,  $df = 5,2$ ,  $p\text{-value} = 0.13$

## Discussion

Kyuquot Sound has higher kelp biomass than Barkley Sound (Markel and Martone, unpublished). The logic of the oft-cited paper by Duggins et al. (1989) would suggest that with increased kelp biomass, there would be more kelp derived detritus in the water, leading to higher rates of kelp assimilation by mussels and faster growth rates. The results of this study did not clearly conform to this explanation, and potential reasons why are presented below.

### Kelp Content in Water may not be Limiting in Either Region

Contrary to our initial predictions, kelp contribution to POM was not consistently higher in Kyuquot Sound than Barkley Sound (figure 2.4). Kelp content in detritus was consistently higher in Kyuquot Sound than Barkley Sound (but region was found to only be a marginally significant factor) and higher in the summer in Barkley Sound than the winter (figure 2.5). Water in Barkley Sound seems to have higher proportions of kelp in the summer than winter, and this seasonal trend is opposite in Kyuquot Sound. The proportion of kelp in POM is only relatively low in the winter of Barkley Sound (<16%), but the proportion of kelp in detritus is constantly high (>30% in all cases). This could indicate that kelp is found in high abundance in either region, during summer and winter. However, kelp content is expressed as percentages here, which can be misleading. Data on actual amounts of kelp and phytoplankton (as might be

provided by incorporating the percent of kelp to data on biomass estimates of POM) would better represent potential food availability, as low proportions of kelp can still be high absolute amounts for filter feeders.

### **Regions with Sea Otters did not Consistently have Greater Kelp Assimilation**

Mussel diets were not consistently enriched in kelp carbon in the region with sea otters and greater attached kelp biomass. The findings here differ from the findings of Duggins et al. (1989) and Salomon et al. (2008), who found that mussel diets are more enriched in kelp carbon where kelp biomass is higher. Though the phrase “lower” and “higher” proportions of kelp derived carbon are used here, mussels are constantly deriving much of their nutrients from kelp (>50% in almost every case, as estimated in this study). The high contribution of kelp to mussel diets indicates that kelp is always important for mussels, regardless of the presence of otters. Our findings that winter diets of mussels are consistently higher in kelp carbon do agree with the findings of Dunton and Schell (1987) and Tallis (2009), who found that mussel diets are more kelp-derived under winter conditions. Higher kelp assimilation in winter could be explained by seasonally lower phytoplankton abundances and greater digestibility of kelp-derived detritus.

Though kelp carbon may not be limiting in either region, very high concentrations of phytoplankton potentially dilute kelp-derived carbon in the water. Though there may be more kelp-derived carbon in the waters where sea otters are present, effectively there may be proportionally less kelp-derived carbon in the water when phytoplankton concentrations are high (this study’s results indicate low kelp-derived carbon in the waters of Kyuquot Sound in the summer while chl *a* measures are high). If this explanation holds, then the relative availability of kelp detritus vs. phytoplankton seems to govern the diet composition of mussels as well, as mussel diets are composed of a lower proportion of kelp where chl *a* values are high (figure 2.9).

The pattern in figure 2.9 depends on the uncertainty inherent in MODIS satellite-derived estimates of chl *a*.

Until the validity of MODIS data on chl *a* for nearshore west coast of Vancouver Island waters can be verified, the relationship between phytoplankton and kelp derived carbon can only be hypothesized. MODIS data are subject to other coloured particles (such as kelp) in the water, and areas of high kelp biomass can be expected to show high chl *a* values as a result of high proportions of kelp and kelp detritus in the water. However, the finding that there is a negative relationship between chl *a* and kelp-derived carbon in mussel tissue and water provides some evidence that the MODIS data for chl *a* are reflecting contributions of something other than kelp.

### **Regions with Sea Otters did not have Greater Mussel Growth**

As suggested by Salomon et al. (2008), our mussels may not to be food-limited. Although kelp beds are much more extensive in Kyuquot Sound, mussel growth rates are consistently lower there than in Barkley Sound. This finding might be due largely to Barkley Sound being warmer. Consistent with the explanation that food is not limiting, mussel growth rates were not significantly higher in summer than in winter in Barkley Sound, despite a greater abundance of kelp-derived carbon in POM and detritus (figures 2.2, 2.4 & 2.5). These findings contrast with those of Duggins et al. (1989), who found higher mussel growth rates where kelp biomass is high, but they align with those of Salomon et al. (2008) who found that filter feeder growth rates were not dependent on high kelp biomass.

Water temperature has previously been shown to be important for mussel growth (Menge et al. 2008), and Barkley Sound—with consistently higher water temperatures than Kyuquot Sound—also had higher mussel growth. Interestingly, within a region water temperature did not influence

growth rates, and region was not found to be a significant factor explaining growth rates in a ANCOVA model exploring the effects of temperature on growth rate (table 2.4), but temperature was marginally significant in a multiple regression model (table 2.5). The difference in effects of temperature between and within regions may be due to temperature varying for different reasons within than between regions, such as if food is carried in currents of cool water within a region, but temperature differences between regions may still account for differences in growth between regions.

### **The Importance of Kelp may Vary Seasonally**

Surprisingly, I found that mussels grow faster in winter than summer, regardless of region. The amount of kelp carbon may drive the observation of faster winter growth, as the amount of kelp derived carbon in mussel diets is higher in winter than the summer in both regions. Many kelps senesce during winter months, and winter storms can rip up attached kelp, leading to a high production of kelp particles in the water (Duggins et al. 1997). The difference in the proportion of kelp-derived carbon in mussel diets between seasons is higher in Kyuquot Sound than in Barkley Sound, and this corresponds with a greater difference in growth rates between seasons in Kyuquot Sound (mussels grew on average 7% faster in the winter in Barkley Sound vs. the summer, and mussels grew on average 35% in the winter vs. the summer). Within seasons, no statistically significant relationship was found between the amount of kelp in mussel diets and mussel growth rates, though a trend is suggested during the winter in both regions (figure 2.6) which suggests a more prominent role of kelp for mussel diet and growth during winter than summer.

An alternative hypothesis to differences in growth rates between seasons is that differences in wetness between seasons lead to differences in growth rates. Wetness corresponds to decreased

time subject to thermal and desiccation stress (Petes et al. 2008), potentially increased feeding time, and has been attributed to increased mussel growth rates (Blanchette et al. 2007). Even with low sample sizes, a relationship between wetness and mussel growth rates in the summer in Kyuquot Sound exists and one is suggested for Barkley Sound (though no significance was found) (Fig. 2.7). Wetness was also found to be marginally significant as an explanatory variable for summer mussel growth (table 2.6). Winter wave heights are generally higher than summer wave heights (which would decrease the effective sea level), and seasonal tidal cycles are such that a given rocky reef at a specific tidal height is submerged for longer periods of time in the winter than in the summer.

### **Context Dependence of Indirect Effects**

The oft-cited finding of Duggins et al. (1989)—that areas with sea otters and high kelp biomass have higher invertebrate filter feeder growth rates—was not conclusively found in this study. Two main points are important to consider in the context of this study: oceanography might modulate the proportion of kelp in nearshore waters, and the type of organism selected to measure secondary productivity likely influenced our results.

High phytoplankton biomass may effectively dilute the proportion of kelp in the water, and other oceanographic factors may also influence the availability of kelp. Kyuquot Sound may have stronger, more frequent upwelling events in summer (indicated by the high chl *a* readings) and if this causes kelp rich water to be transported offshore more frequently, it may also lead to lower proportions of kelp in the water. Accordingly, even though Kyuquot Sound has more extensive kelp beds, mussels are assimilating less kelp in the summers compared to Barkley Sound.

The other important caveat is that mussels seem to consume kelp even when there are relatively low quantities of detrital kelp in the water. Mussels may selectively filter kelp POM and DOM out of the water. Multiple studies in different regions of the Pacific coast of North America have found *M. californianus* to derive much of their carbon from kelp (California, Gilbane 2005; Washington, Tallis 2009). Repeating a similar study examining the growth rates of other filter feeders may provide different results.

### **Contingencies of Ecosystem Service Provisioning**

This study demonstrates a situation where oceanographic context drives the arbitration of ecosystem services. The release of kelp from herbivory by otters is often touted as a predictable ecological interaction (Estes et al. 2010), but the impacts of kelp on secondary production seem to depend on phytoplankton dynamics which in turn are driven by oceanographic processes such as currents, seafloor bathymetry, strength of upwelling and relaxation events. In the study of ecosystem service providers, it is not enough to understand what species provide what services, but under what conditions do certain species provide certain ecosystem services. This study indicates that the importance of kelp as a food source for mussels may not be dependent on the presence of otters, and environmental factors can mediate the importance of otters as supporting secondary productivity. There are a variety of ecosystem services that sea otters impact (some perhaps positively), and navigating the tradeoffs between multiple ecosystem services requires a comprehensive research program that accounts for the values identified by interest groups on the west coast of Vancouver Island.

# **Chapter 3: Mussel Bed Structure and Community Assemblages Vary Predictably with Sea Otter Occupancy Time**

## **Introduction**

The idea that communities and ecosystems are heavily impacted by a few species within a larger web of species interactions has important implications for an understanding of community ecology in general and issues of conservation specifically (Menge et al. 1994). Where only a few species have impacts on the larger community, some have argued for the focus of ecologists to direct their work on these species and for the allocation of conservation funds to be directed towards these species (Walker 1991, Soulé 1985). Additionally, these species seem to be prime candidates to study as ecosystem service providers (Kremen et al. 2005), because they likely have impacts on ecosystem processes with implications towards the provision of ecosystem services (for better or worse). This study examines how sea otter (*Enhydra lutris*) predation on the California mussel (*Mytilus californianus*) affects the ecosystem processes of habitat creation and energy flow.

## **Otters as Keystone Predators**

The capacity of predators to structure communities and affect ecological processes has been documented in a variety of systems (mussel dominated rocky intertidal zones, Paine 1966; sea otter dominated nearshore systems, Estes and Palmisano 1974; fish dominated pelagic systems, Power 1990; nematode dominated soil communities Preisser 2003; wolf dominated mountain forests, Hebblewhite et al. 2005). Meta-analytic reviews of trophic cascades (Shurin et al. 2002, Borer et al. 2005) indicate that strong cascades occur in marine environments where there are

mobile vertebrate predators with high mass-specific metabolic rates. Sea otters (*Enhydra lutris*) fit these requirements and have been shown to have strong top-down impacts in a variety of studies (Estes and Palmisano 1974 Duggins et al. 1989, Estes and Duggins 1995, Anthony et al. 2008). Most effects of otters have been documented through their impacts on kelps through predation on urchins (Estes and Palmisano 1974). The impacts of kelp release include increased primary productivity (Duggins et al. 1989), but also impacts to physical habitat provision (Graham 2004), which can attract avian predators to forage for invertebrates in the kelp (Irons et al. 1986) and lead to high densities of rockfish that can limit recruitment of invertebrates through predation of larvae (Gaines and Roughgarden 1987). These indirect impacts of otters on other biological interactions and nutrient processes are all consequences of a trophic cascade. Here, we examine the indirect consequences of otter predation in intertidal communities through direct impacts on an ecosystem engineer.

## **Mussels as Ecosystem Engineers**

In marine rocky intertidal communities, *Mytilus californianus* is a competitively dominant species, able to outcompete other sessile organisms that attach to primary substrate (Paine 1974). Within a range of tidal heights that are not too stressful environmentally (high intertidal heights lead to desiccation) or low enough that the ochre star *Pisaster ochraceous* eliminates them through predation, they are the dominant species (Harley and Helmuth 2003, Robles et al. 1995). *M. californianus* smothers other primary space occupiers, changing diversity at local scales (Paine 1966). But communities dominated by these mussels are far from monocultures, as mussels facilitate secondary space occupiers to grow and survive by providing habitat for a variety of marine invertebrates (Suchanek 1979). A mussel network provides succor in a hostile environment: decreasing stress from desiccation and temperature (Smith 2006) and from

physical wave forces (O'Donnell 2008), as well as providing refuge from some predators (Witman 1985).

In mussel communities, diversity has been shown to be related to the complexity of the mussel bed (Kanter 1977) and positively correlated to mussel bed thickness, mussel biomass, and amount of sediment trapped within a bed (Straughan and Kanter 1977, Straughan 1978, Smith et al. 2006). In this way *M. californianus* is considered an ecosystem engineer, providing a strong role in structuring communities by providing physical structure. Keystone species can also be considered ecosystem engineers, but I refer to ecosystem engineers here as providers of physical structure that modulate the availability of resources (autogenic ecosystem engineers, Jones et al. 1994), and have very strong per-population interaction strength (Wood et al. 2010).

Mussels are also important mid-trophic level species, providing energy and nutrients to a variety of predators, including large predators like sea otters and humans, mid-sized predators like sea stars and oystercatchers, and small predators like whelks (Asmus 1987). Mussels can also escape predation from mid-sized and small predators through size escapement (Paine 1976). Thus mussels can have varying impacts to ecological processes, with implications to supporting ecosystem services: large mussels and deep, dense mussel beds can potentially provide habitat for other organisms (they create more complex habitat matrices) but when mussels reach a size that allows them to escape predation, they trap nutrients and energy and prevent these from reaching higher trophic levels.

### **Otter Predation in Mussel Beds**

Otters are well known for their predatory impacts on sea urchins (Estes and Palmisano 1974) as well as abalone (Johnson et al. 2009). When these prey sources decline in abundance, otters

broaden their prey base, consuming a wide variety of invertebrates (Tinker et al. 2008; Ostfeld 1982; Estes and Duggins 1995b, but some studies, such as Breen et al. 1982, also suggest that otters eat a wide variety of prey soon after colonizing a new area). But this broad prey base can also narrow as prey species serially decline through predation (by otters or other predators such as humans, Salomon et al. 2007). As prey sources are serially depleted, search and handling time for depleted prey increases, which can increase the per-capita impact of otters on their remaining prey (Wootton 2002, Salomon 2007).

Otters are known to forage in intertidal mussel beds, stripping mussel beds to the bare bedrock (Doroff and DeGange 1994). As primary otter prey declines, otters (especially female otters and pups, VanBlaricom 1988) can turn to mussel beds as a stable food supply (VanBlaricom 1988). Otters tend to work from edges of mussel beds, stripping mussels off in clumps. They discard small mussels or swallow them whole, while cracking open large mussels with rocks. In this way, they may not eat all mussels in a bed, but because they either eat or discard mussels to deep waters (where they are susceptible to subtidal predators and siltation), they kill or at least remove mussels from beds (VanBlaricom 1988), acting as agents of disturbance. Research on community impacts of predation in mussel beds by smaller predators have shown how the patches created by these predators can increase diversity by creating small scale variability in the intertidal environment (Paine 1966, Wootton 1992). Because otters are large mobile predators that mussels cannot escape from through size, sea otter impacts to mussel beds are potentially extensive across space and can lead to a large scale homogenization of mussel beds.

Whereas studies examining the effects of predators on structuring communities and effecting ecological processes have focused on negative direct interactions, there have been a paucity of studies looking into how the facilitative aspects of ecosystem engineers are affected by strong

top-down predation (Bruno et al. 2003), especially in aquatic communities (Halpern et al. 2006). Mussels are important facilitators of intertidal communities, and impacts to mussel beds can have important community-level consequences (Smith et al. 2006). Situations in which other organisms promote the establishment of mussels (such as cordgrass beds providing wave shelter for mussels to establish) have been termed “facilitation cascades” (Altieri et al. 2007), to indicate facilitative interactions promote further facilitation. The process examined in this study examines how predation can indirectly hinder facilitation in an impending cascade – in which one predatory interaction (otters on mussels) impedes the facilitative functions of the prey.

Given the evidence for the wide variety of prey that otters consume, coupled with the evidence that otters consume mussels, the impacts that otter predation has on mussel beds may increase over time. I addressed this possibility by sampling along the outer coast of British Columbia and Washington, where the extirpation and subsequent reintroductions and range expansions of sea otters creates a natural experiment in which sites differ in their exposure to sea otter predation. Sites were chosen in regions as a function of sea otter occupancy time. These regions include Kyuquot Sound (otters present since the mid-late 1980’s, Nichol et al. 2005), Cape Flattery (otters present since 1990, Lance et al. 2004), Clayoquot Sound (otters present since about 2001, Nichol et al. 2005), and Barkley Sound (otters not yet established, Gregr et al. 2008). This checkerboard design allows me to study the effect of sea otter influence using a space for time substitution without having any other large environmental gradients (e.g., latitude) biasing the results.

I hypothesize that the magnitude of change to mussel beds increases with sea otter occupancy time because otters prey increasingly on mussels as preferred food choices become scarce. I predict that mussel sizes will be smaller, mussel-bed depths will decrease and mussel bed

biomass will decrease in regions of increased otter influence. As a consequence of changes to mussel bed characteristics, I hypothesize that mussel bed communities will change in composition and decrease in biomass as well. Finally, because of the presumed smaller mussel size, I hypothesize that more secondary production in the form of the proportion of energy in mussel production will be available to mid-sized mussel consumers where otters are present compared to where they are absent.

## Methods

### Regional Design

This study was conducted on the west coast of Vancouver Island and the northwest coast of Washington state (figure 3.1, site locations in table 3.1).

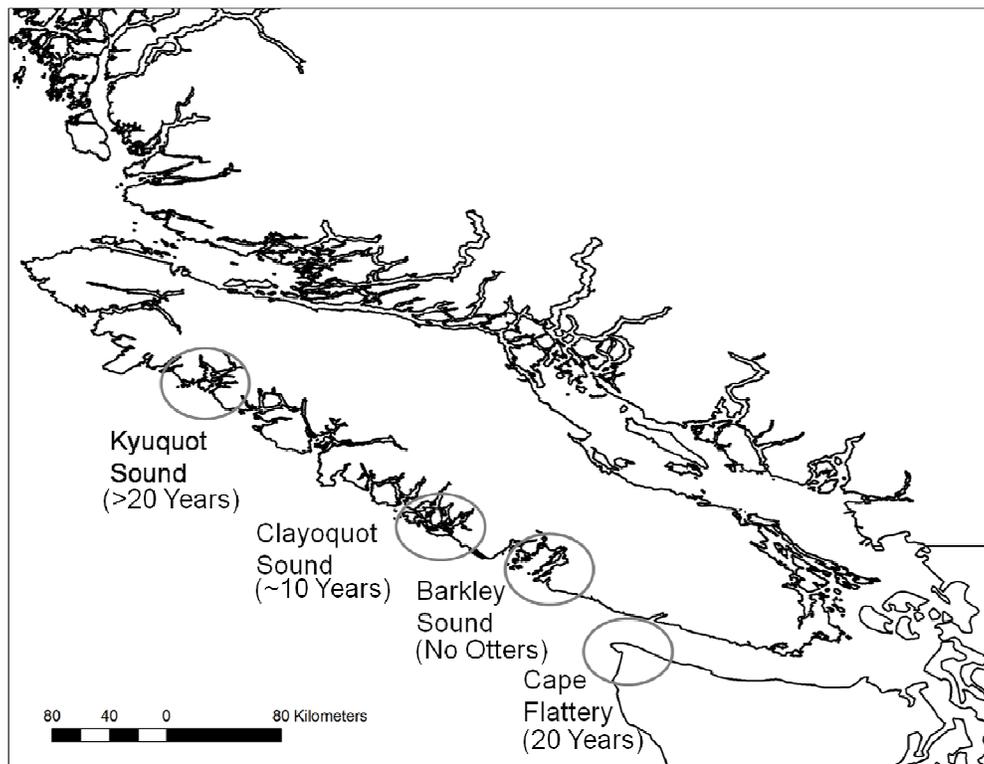


Figure 3.1: The regions included in this study.

**Table 3.1: Location of Intertidal sampling sites**

Region	Site	Latitude	Longitude
Barkley Sound	Seppings	N 48° 50.344'	W 125° 12.446'
Barkley Sound	Helby	N 48° 51.345'	W 125° 10.245'
Barkley Sound	Diana	N 48° 50.969'	W 125° 11.319'
Barkley Sound	Sanford	N 48° 51.901'	W 125° 10.161'
Barkley Sound	Bluestone	N 48° 49.238'	W 125° 09.914'
Clayoquot Sound	La Croix islets (LAC)	N 49°09.038'	W 126°00.019'
Clayoquot Sound	Blunden	N 49° 11.400'	W 126°03.724'
Clayoquot Sound	Bartlet	N 49°13.068'	W 126°05.567'
Kyuquot Sound	KT1	N 49° 59.953'	W 127° 25.959'
Kyuquot Sound	PB	N 49° 59.955'	W 127° 24.417'
Kyuquot Sound	Beach	N 49°59.815'	W 127°23.817'
Kyuquot Sound	TB	N 50°00.291'	W 127°24.052'
Kyuquot Sound	GDA	N 50°00.077'	W 127°23.015'
Cape Flattery	Shi Shi	N 48°16.594'	W 124°40.904'
Cape Flattery	Makkah	N 48° 17.841'	W 124° 40.362'
Cape Flattery	Chibadehl Rocks	N 48°23.390'	W 124°39.895'

## Site Description

All sites were chosen based on similar observed conditions of wave exposure, slope, and species composition. Sites were characterized by having *Balanus glandula* barnacles in the upper intertidal, a mid-intertidal band dominated by *Mytilus californianus*, *Pollicipes polymerus* and *Semibalanus cariosus*, and a lower intertidal band dominated by three kelp species; *Saccharina sessile*, *Laminarea setchellii*, *Egregia menziesii*, the predator *Pisaster ochraceous* and grazer *Katharina tunicata*. Sites in Barkley Sound include Sanford island (for mussel sizes and energy analysis only), Seppings island (for energy analysis only), Diana island, Helby island, and Bluestone Point. Sites in Clayoquot Sound include Bartlet island, Blunden island, and the La Croix islets (LAC). Sites in Cape Flattery include Shi Shi beach, Makaw Bay, and Chibedehl rocks. Sites in Kyuquot Sound include sites named Beach, GDA, TB (for energy analysis only), Prop Breaker, and KT1 (for energy analysis only).

## **Mussel Size Structure and Mussel Bed Depth**

At each site, ten 25 × 25cm plots were randomly chosen at the middle and lower extent of the mussel bed. In each plot, 15-50 mussels were chosen at random and measured along its longest linear dimension. A knitting needle was plunged into each mussel bed plot perpendicular to the ground until it hit the bedrock and the length of the needle was measured. In order to compare the size distribution of mussels to an estimate of mussel size potential, the largest 30 mussel shells were collected from beaches in Barkley Sound and Kyuquot Sound and the size distributions of *in situ* mussels were compared against the average large mussel shells.

## **Biomass Estimates**

In the two extreme regions of otter establishment (Kyuquot Sound and Barkley Sound), ten 25 × 25cm plots were dug out of the lower and mid mussel beds at three sites in each region. Mussels were separated from all mussel associated species and sediment, and mussels and aggregate mussel community biomass were weighed in the field. Mussel associated species were collected, fixed in formalin and preserved in a series of ethanol treatments (Smith et al. 2008) to be sorted and identified later in the lab. A random 16 oz subsample was taken from each plot and sorted to the lowest taxonomic class possible (henceforth called morphospecies). The weight of each morphospecies was recorded and the proportion of weight of each species group was multiplied by the total weight of the plot's mussel associated species to calculate an estimate of the species group for the plot. Where vertebrate fish were found, total lengths were estimated in the field while individual biomass was estimated based on published length-weight relationships for similar species (with similar morphology, Sawyer 1967, Ozen et al. 2009).

## Mussel Energy Flow

To compare energy from mussel productivity available to mid-sized predators in each region, I estimated sizes at which mussels escape seastar predation, calculated the energy available in the biomass resulting from mussel growth, and compared the proportion of this energy that is available to seastars between Barkley Sound and Kyuquot Sound. The sizes at which mussels escape seastar predation was determined by conducting surveys using ten randomly placed 1 × 1m quadrats on the lower limit of the mussel bed to count and measure the density and axial length of *Pisaster ochraceus*. Plots of size by percentile of *P. ochraceus* size were created to determine the size where there is a sharp change in slope between percentile and size. The sharp change in the slope indicates the size at which there is a rapid decrease in the population at a given size. For Barkley Sound, this occurred with *P. ochraceus* of size 22 cm (95<sup>th</sup> percentile), and for Kyuquot Sound this occurred with *P. ochraceus* of size 16 cm (97<sup>th</sup> percentile). These sizes were then compared to Paine's (1976) findings of the largest mussels available for *P. ochraceus* foraging. The resulting threshold size was then used to identify what proportion of secondary productivity was available to seastar predators and what proportion was not.

Mussel growth was determined by tracking growth rates in the field over different time periods. This was accomplished by scoring the growing edge of mussels with a Dremel® tool. Scoring mussels this way allowed us to mark the initial size of the mussels and measure the difference in growth over time (Menge et al. 2004). A range of mussel sizes were collected, dissected, and their soft tissue dried at 60 degrees for 48 hours. A relationship was fit between total length and dry weight according to an allometric relationship of the form  $m=a(\text{length})^b$ , where  $m$  is dry weight,  $a$  is length and  $b$  is a scaling factor. Dry weights of the mussels at their initial lengths and final lengths were estimated based on the allometric relationship (see Appendix A). Biomass of

the initial length was subtracted from biomass of the final length to generate an estimate of the biomass resulting from growth. A constant energy term of 4600 cal/g was applied to calculate the energy in the yearly growth of mussels from Barkley Sound and Kyuquot Sound (Paine 1971). The proportion of energy in mussels above the threshold size of mussels was assumed to be unavailable to seastar predators.

## **Statistical Analyses**

To test the effects of region on mussel bed characteristics, I used nested mixed effects models fit with Unequal Variance Restricted Maximum Likelihood (REML). These models have been found to be robust to unequal sample sizes and unequal within group variances (Picquelle and Mier in press). REML is less sensitive to outliers than maximum likelihoods and allows for degrees of freedom to be used up when analyzing fixed effects (Regions, in the case of this study), thereby allowing variance components to be estimated without being affected by fixed effects (Crawley 2007). Data were assessed for approximate normality using Q-Q plots. For analyses without nested structure (energetic analysis and ideal large mussels), Welch's t-tests were used to account for unequal variances among groups (on ranked data where normality was not met) (Ruxton 2006). Variance Components Analysis was completed on mussel size to see how variance within different regions was distributed among different levels of the nested design. Mixed effect models and variance components analyses were run using the nlme package in R (R Development Core Team 2008).

To test if mussel bed characteristics affect mussel-bed community assemblages, we use Canonical Correspondence Analysis (CCA). We used CCA rather than Redundancy Analysis (RDA) because RDA assumes linear relationships between species abundances and

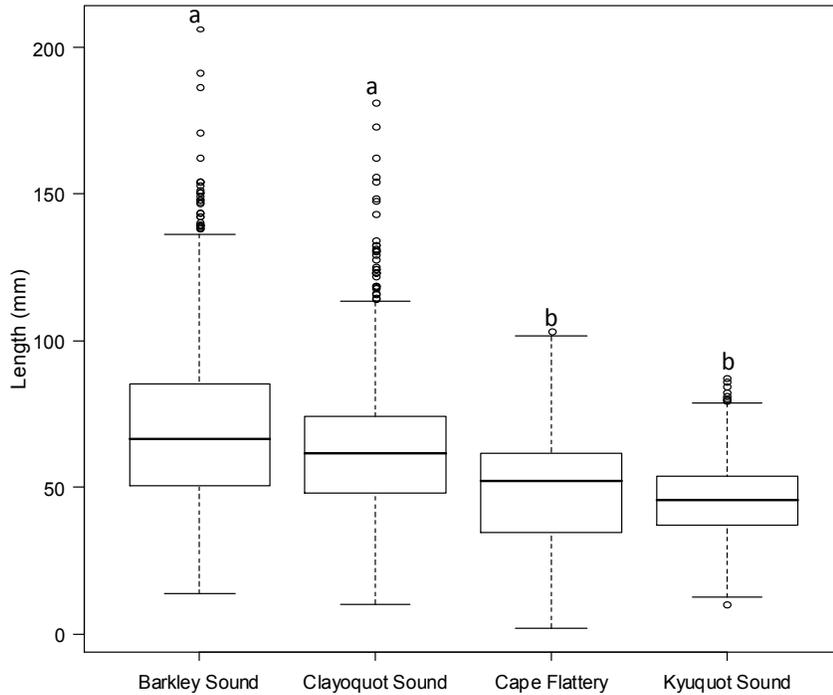
environmental variables, something not found in the data. CCA is a hybrid of Correspondence Analysis and multiple regression, and examines how environmental gradients explain biological communities. The value of the “explained inertia” in CCA is the sum of the eigenvalues of the constrained axes. A strict measure of the goodness of fit of CCA is elusive, but the proportion of explained inertia has been used by ecologists to suggest goodness of fit (Pélissier et al. 2003). In order to examine the strength of evidence for alternative environmental variables in structuring community assemblages, forward selection based on Akaike’s Information Criterion (AIC) were used to build the best fitting and most parsimonious CCA models in each Region. All statistics were computed with the R software. The CCAs were analyzed using the vegan package for R (Oksanen et al. 2010).

In order to analyze the differences in community composition between an otter present and otter absent region, nonmetric multidimensional scaling (NMDS) methods were used to graphically assess community differences, and a nested ANOSIM was conducted to see how communities differed between sites and regions. SIMPER analyses were conducted to see which species contributed most to differences between regions. NMDS, ANOSIM and SIMPER analyses were conducted with PRIMER 6.

### **Mussel Sizes Along a Sea Otter Gradient**

Mussel sizes were largest in Barkley Sound, where otters are not present, intermediate in Clayoquot Sound and Cape Flattery, and smallest in Kyuquot Sound (Fig. 3.2). There is a significant difference in mussel sizes among regions ( $df = 3,9$ ,  $F = 28.05$ ,  $P = 0.0001$ ), and mussels from Barkley Sound and Clayoquot Sound are larger than mussels from Kyuquot Sound and Cape Flattery (figure 3.2). Variation in mussel size generally decreases with sea otter

occupancy time. Mussels sizes tend to decrease along the otter gradient and become constrained to a narrower size range (figure 3.2).



**Figure 3.2: Mussel size distributions in the different regions. Significant differences between regions, as found by a Tukey test, are indicated by different letters above the individual boxplots. Barkley Sound mussel sizes are largest (median = 66.5 mm, mean = 70.1 mm, sd = 27.53 mm), followed by Clayoquot Sound (median = 61.4 mm, mean = 63.5 mm, sd = 27.64 mm), followed by Cape Flattery (median = 52.0 mm, mean = 49.6 mm, sd = 19.20 mm) and Kyuquot Sound (median = 45.3 mm, mean = 45.7 mm, sd = 13.02 mm). These box and whisker plots indicate the median, interquartile range (box, representing the middle 50% of the data), 1.5 × interquartile range (each whisker, where data extend this far), and outliers (points). The figure shows medians, but statistical tests were conducted on means.**

Variance Component Analysis reveals that differences among sites accounts for more of the variance in mussel sizes where otters have relatively higher influence, while most of the variation in mussel sizes can be attributed to the scale of the plot (25 cm × 25 cm) where otters have relatively lower influence (table 3.2).

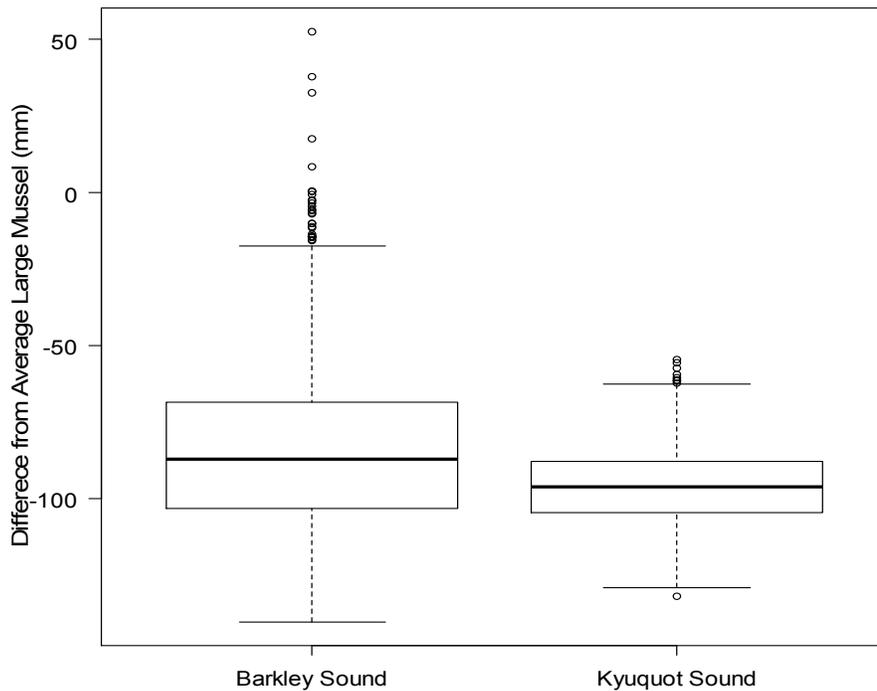
**Table 3.2: Results from a Variance Components Analysis, looking at how important different spatial scales are for overall variance in each region. Values represent percent (%) of variance explained.**

Region	Site	Plot	Error
Barkley Sound	0.86	21.6	77.5
Clayoquot Sound	3.97	21.4	74.6
Cape Flattery	2.49	5.15	92.3
Kyuquot Sound	8.21	3.18	96.8

### Average Large Mussels

The large beach-cast shells collected in Barkley Sound are larger (median = 151.2 mm, mean = 153.6 mm) than the shells collected in Kyuquot Sound (median = 138.5 mm, mean = 141.4 mm). I found a significant effect of region on the mean and variance of large mussel shells collected ( $t = 3.92$ ,  $df = 52.5$ ,  $P = 0.0001$ ;  $F = 0.35$ ,  $df = 29,29$ ,  $P = 0.006$ ).

However, in Kyuquot Sound, current mussels are not attaining the sizes of beach-cast mussels. There are some mussels in Barkley Sound that have a positive difference from the average large mussel, while this was not found in the Kyuquot mussels (figure 3.3). The difference between *in situ* mussels and the average large beach cast mussels are significantly different between Barkley Sound and Kyuquot Sound ( $t = -3.99$ ,  $df = 5$ ,  $P = 0.01$ ), and the variance between these two populations is significantly different ( $F = 4.47$ ,  $df = 1367, 1017$ ,  $P < 2.2 \times 10^{-16}$ ).

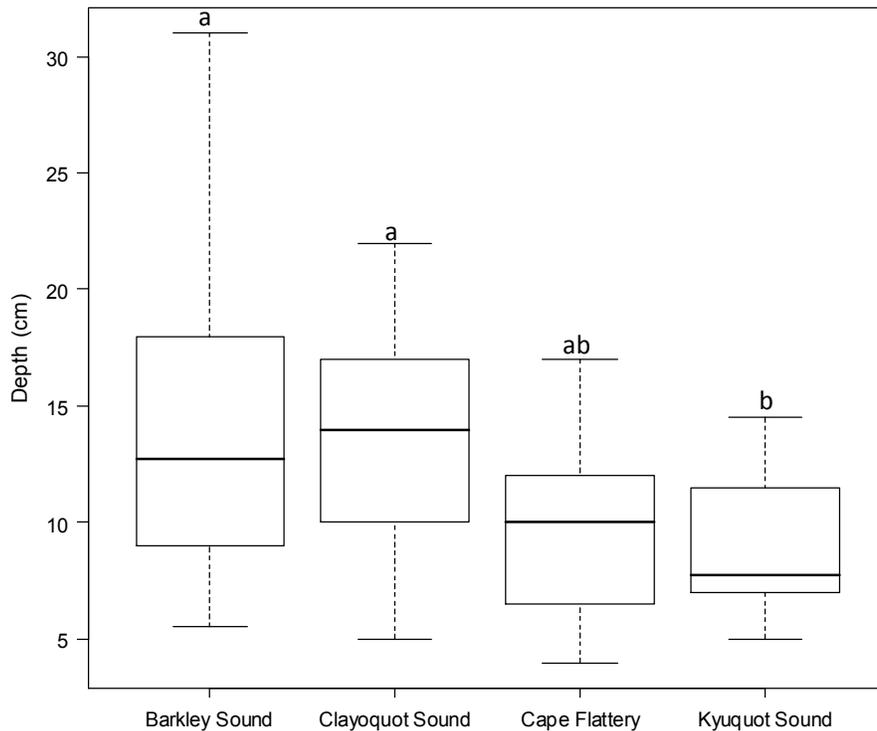


**Figure 3. 3: The difference of live mussels from the estimated average large mussel found in Barkley Sound and Kyuquot Sound. The difference between *in situ* mussels and the average large beach cast mussel is smaller for Barkley Sound (median = -87.1 mm mean = -83.5 mm, sd = 27.5 mm) than for Kyuquot Sound (median = -83.5 mm, mean = -95.7 mm, sd = 13.0 mm). Refer to figure 3.2 to read the boxplots.**

### Mussel Bed Depths Along a Sea Otter Gradient

The depths of mussel beds decreases along a gradient of increasing sea otter influence (figure 3.4). Mussel bed depths are significant different among regions (df = 3,8, F= 9.06, P = 0.006) specifically between Kyuquot Sound and Barkley / Clayoquot Sounds (P <0.001) (figure 3.4).

The variation of depths in mussel beds in the different regions also show that variability decreases along a gradient of increasing sea otter influence. Similar to mussel sizes, depths of mussel beds tend to decrease in magnitude and range across the gradient of sea otter influence (figure 3.4).

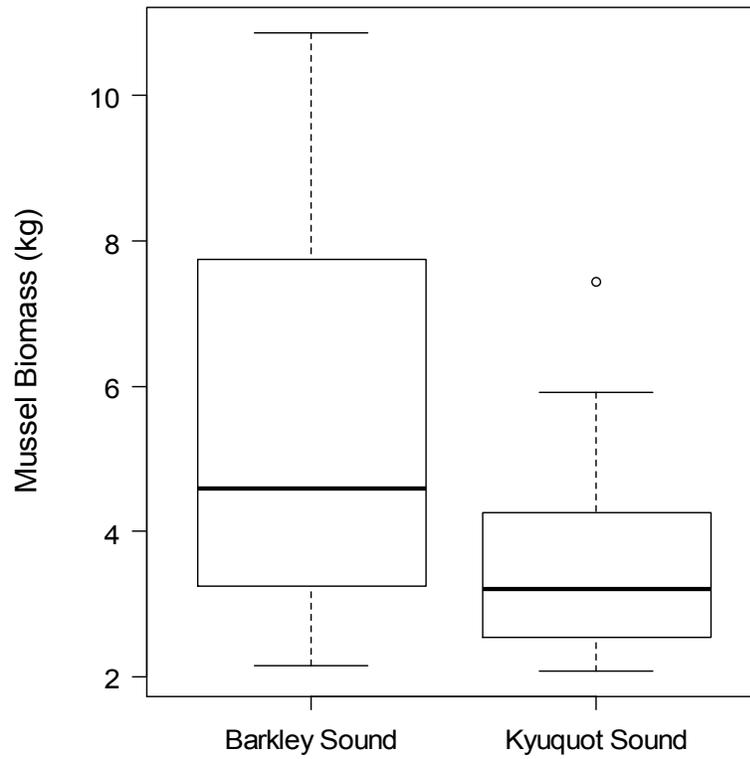


**Figure 3. 4: Mussel bed depths in the different regions. Significant differences between regions, as found by a Tukey test, are indicated by different letters above the individual boxplots. Mussel beds in Barkley Sound (median = 12.7 cm, mean = 13.5 cm, sd = 5.87 cm) and Clayoquot Sound (median = 14 cm, mean = 13.9 cm, sd = 4.07) are deeper than mussel beds in Cape Flattery (median = 10 cm, mean = 9.7 cm, sd = 3.61 cm) and Kyuquot Sound (median = 7.75 cm, mean = 8.83 cm, sd = 2.65). Refer to figure 3.2 to read the boxplots.**

## Mussel Bed Biomass

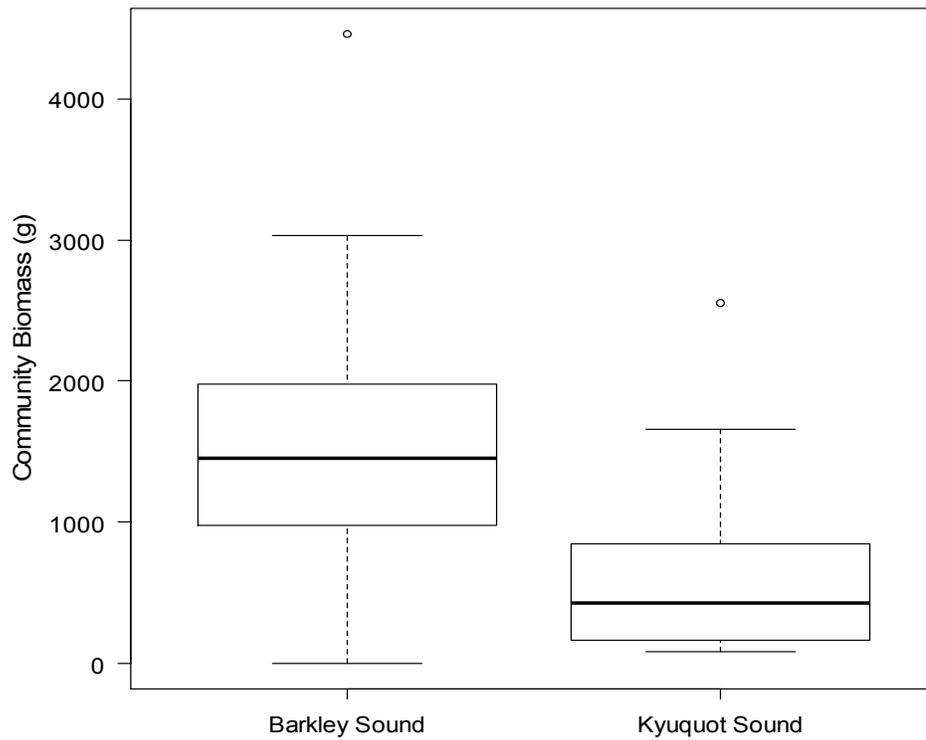
The biomass of mussels in Barkley Sound is higher than in Kyuquot Sound (figure 3.5).

However, this observed difference between regions is not significant ( $t = -1.43$ ,  $df = 4$ ,  $P = 0.23$ ).



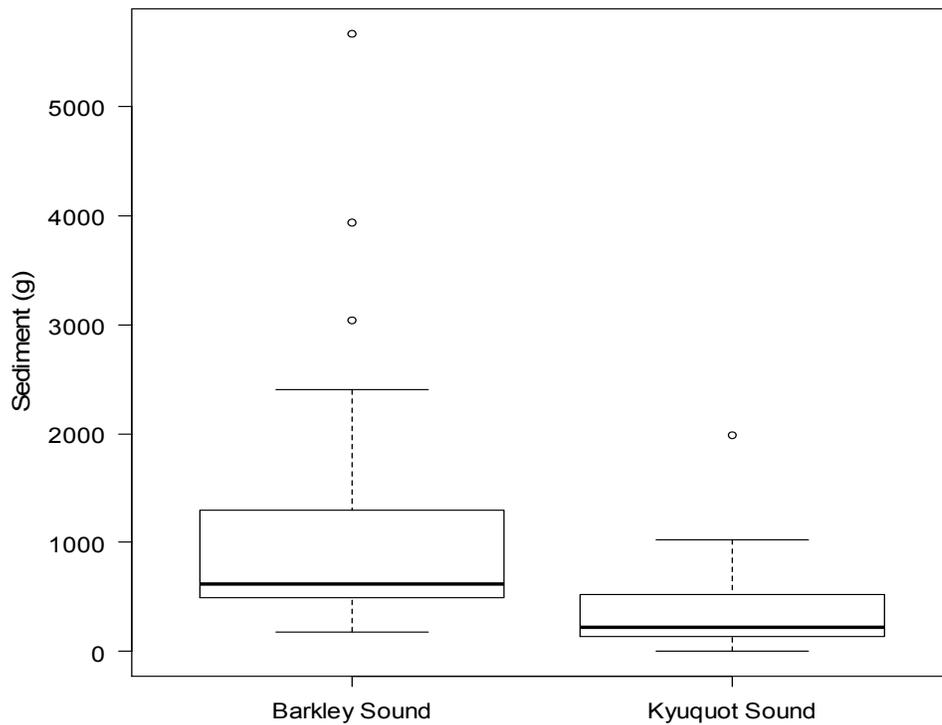
**Figure 3. 5: Biomass of mussels found in a standard 25 cm × 25 cm quadrat in Barkley Sound and Kyuquot Sound. Mussel biomass in Barkley Sound (median = 4.22 kg, mean = 5.31, sd = 2.02 kg) is higher than in Kyuquot Sound (median = 3.2 kg, mean = 3.58 kg, sd = 1.31 kg), though this difference was not found to be significant ( $t = -1.43$ ,  $df = 4$ ,  $P = 0.23$ ). Refer to figure 3.2 to read the boxplots.**

The mass of the others species in mussel beds are higher in Barkley Sound than in Kyuquot Sound (figure 3.6), and this difference between regions is significant ( $t = -3.86$ ,  $df = 4$ ,  $P = 0.018$ ).



**Figure 3. 6: Biomass of mussel-bed associated species found in a standard 25 cm × 25 cm quadrat in Barkley Sound and Kyuquot Sound. Biomass of mussel associated species is higher in Barkley Sound (median = 1430.6 g, mean = 1531.7 g, sd = 880.6 g) than in Kyuquot Sound (median = 463.8 g, mean = 593.2 g, sd = 551.4 g). Refer to figure 3.2 to read the boxplots.**

There is also significantly more debris and shell remains (sediment) in Barkley Sound than in Kyuquot Sound ( $t = -2.88$ ,  $df = 4$ ,  $P = 0.045$ ) (figure 3.7).

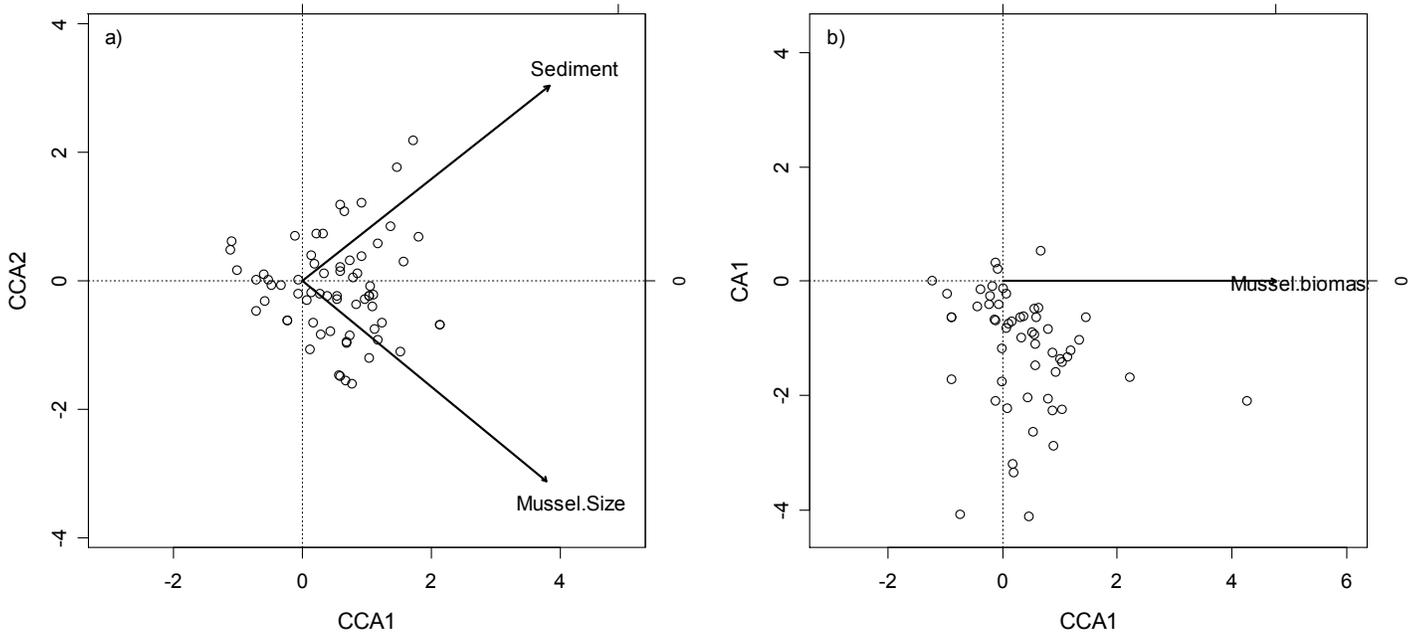


**Figure 3. 7: Mass of sediment found in the standard 25 cm × 25 cm quadrat in Barkley Sound and Kyuquot Sound. There is more sediment in Barkley Sound (median = 610.4 g, mean = 1068.6 g, sd = 1261.8g) than in Kyuquot Sound (median = 225.8 g, mean = 361.7 g, sd = 394.2 g). Refer to figure 3.2 to read the boxplots.**

## Community Composition

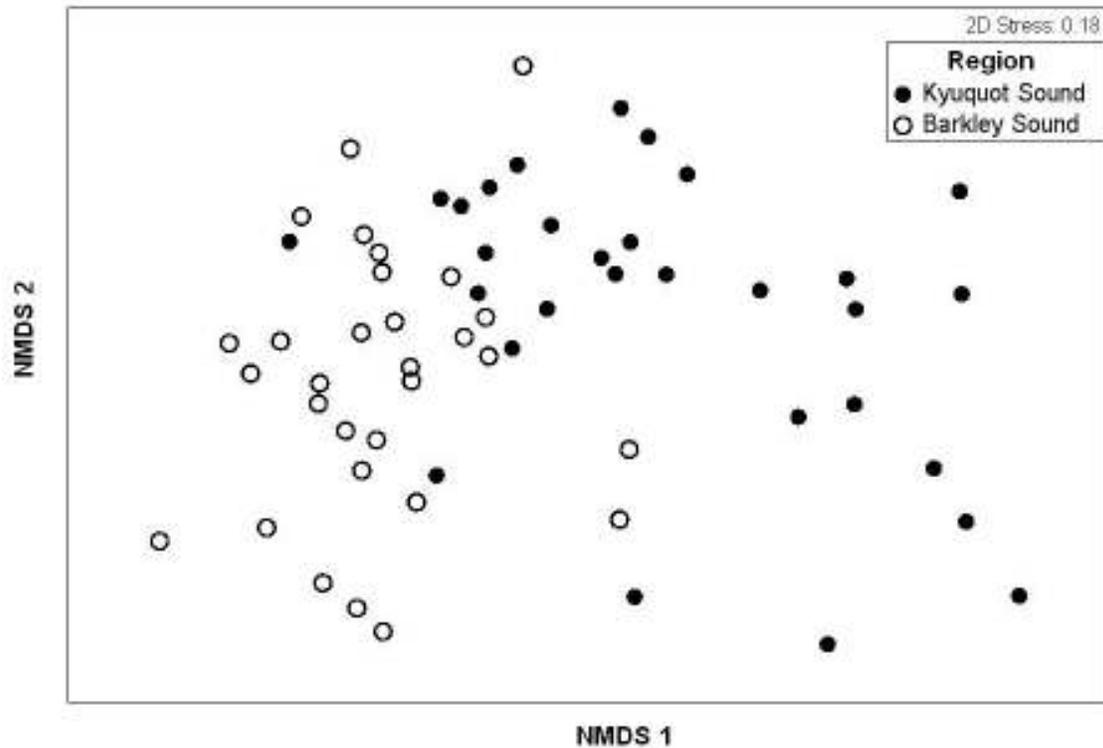
Forward selection procedures for constructing CCA models in each region show that some characteristic of mussel beds can help explain the composition of communities within each region. In Barkley Sound, average mussel size and amount of sediment and shell debris were used to create the most parsimonious model. The CCA results indicate that these constraining variables account for 24.9% of the inertia of the model. Including the variables of mussel biomass per plot and depth did not decrease AIC values (they are highly correlated with average mussel size) and were unused. In Kyuquot Sound, the most parsimonious model included only mussel biomass per plot. This constraining variable accounts for 10.70% of the inertia in the

data. Figure 3.8 shows the CCA plots for Barkley sound (a) and Kyuquot Sound (b). To locate individual species in each graph, see Appendix B.



**Figure 3. 8: CCA plots for a) Barkley Sound and b) Kyuquot Sound. For b), as there was only one environmental variable that tracked onto a CCA axis (mussel biomass), the plot shows the first CCA axis against the unconstrained axis with the most explanatory power (CA1). Dots represent species.**

Viewing an NMDS output, the mussel bed communities form separate clusters based on region, though there is some overlap (figure 3.9). The mussel-bed biomass data were square-root transformed to downplay the importance of dominant species in each plot. The NMDS output shows greater variability between plots in Kyuquot Sound than Barkley Sound. A nested ANOSIM analysis indicates separation between regions ( $R = 0.63$ ), with marginal significance ( $P = 0.1$ ). Sites within regions are more clustered than regions ( $R = 0.186$ ), and this level of similarity between sites is significant ( $P = 0.001$ ).

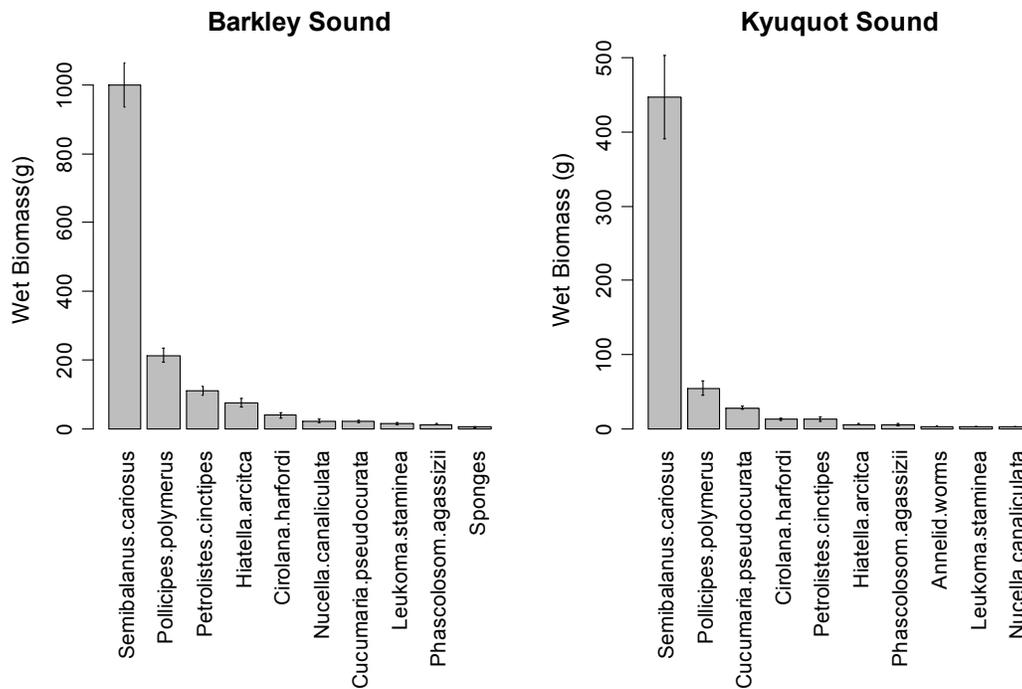


**Figure 3.9: NMDS plot showing separation of the two regions based on invertebrate community structure. Dots represent mussel plots.**

A SIMPER analysis was used to determine which species were most responsible for the difference in invertebrate community structure between regions. The species accounting for the largest portions of the variation between regions (summing to 75% of total variation) are shown in table 3.3. All species (except *Nucella ostrina*) included in this table are included in the ten most abundant species found in each region (figure 3.10). All species (except for *Cucumaria pseudocurata* and Annelid worms) have higher biomass in Barkley Sound. The inertia (variance) explained by mussel bed characteristics (according to CCA) for these species in Barkley Sound ranges from 12% to 50% and in Kyuquot Sound is from 0.4% to 28% (see appendix for the variance of CCA explained by individual species). These results indicate that mussel bed structure accounts for greater variance in the abundance of dominant species in Barkley Sound than Kyuquot Sound.

**Table 3.3: Simper analysis on square root transformed data to determine the most dissimilar species in terms of biomass between regions.**

Species	Average Biomass (square root (g)) Kyuquot Sound	Average Biomass (square root (g)) Barkley Sound	Average Dissimilarity	Dissimilarity/SD	Contribution (%) to Dissimilarity	Cummulative (%) of Dissimilarity
<i>Semibalanus cariosus</i>	17.62	30.33	11.73	1.43	23.23	23.23
<i>Pollicipes polymerus</i>	5.41	12.77	6.96	1.45	13.78	37.01
<i>Petrolistes cinctipes</i>	2.45	8.93	4.83	1.62	9.56	46.57
<i>Hiatella arcitca</i>	1.99	7.36	3.7	1.62	7.32	53.89
<i>Cucumaria pseudocurata</i>	4.98	3.65	2.45	1.45	4.86	58.75
<i>Cirolana harfordi</i>	3.2	5.09	2.17	1.24	4.3	63.05
<i>Nucella canaliculata</i>	1.1	3.75	2.05	1.41	4.05	67.1
<i>Leukoma staminea</i>	1.18	2.66	1.72	1.06	3.4	70.5
<i>Phascolosom agassizii</i>	1.6	2.72	1.71	1.26	3.38	73.88
<i>Nucella ostrina</i>	0.73	1.6	0.97	1.07	1.93	75.81



**Figure 3. 10: The estimated biomass of the top ten most abundant (by wet biomass) morphospecies found in Barkley Sound and Kyuquot Sound.**

## Consequences to Energy Flow

Converting growth rates in each region to energy suggests that there is a greater production of energy in mussels in Barkley Sound than in Kyuquot Sound (figure 3.11), but that the proportion of energy unavailable to seastars is also higher in Barkley Sound than in Kyuquot Sound in summer (12.5% in Barkley Sound and 2.3% in Kyuquot Sound), winter (8.2% in Barkley Sound and 2.8% in Kyuquot Sound) and a year growth cycle (9.6% in Barkley Sound and 0.9% in Kyuquot Sound). Alternatively, there is a greater proportion of energy available to seastars in Kyuquot Sound than in Barkley Sound. Barkley Sound contains larger mussels, and the amount of energy in mussel growth seems higher in larger mussels (figure 3.11). Using proportion of energy at each site as a replicate in each region, there is a significant difference between region for the summer (Welch's  $t$  on ranked data = 3.9158,  $df = 7.958$ ,  $P = 0.002245$ ), no significant difference between regions for the fall and winter ( $t = 1.3527$ ,  $df = 6.955$ ,  $P = 0.1092$ ), and no significant difference between regions for a full year of growth ( $t = 0.889$ ,  $df = 6.482$ ,  $P = 0.2029$ ).

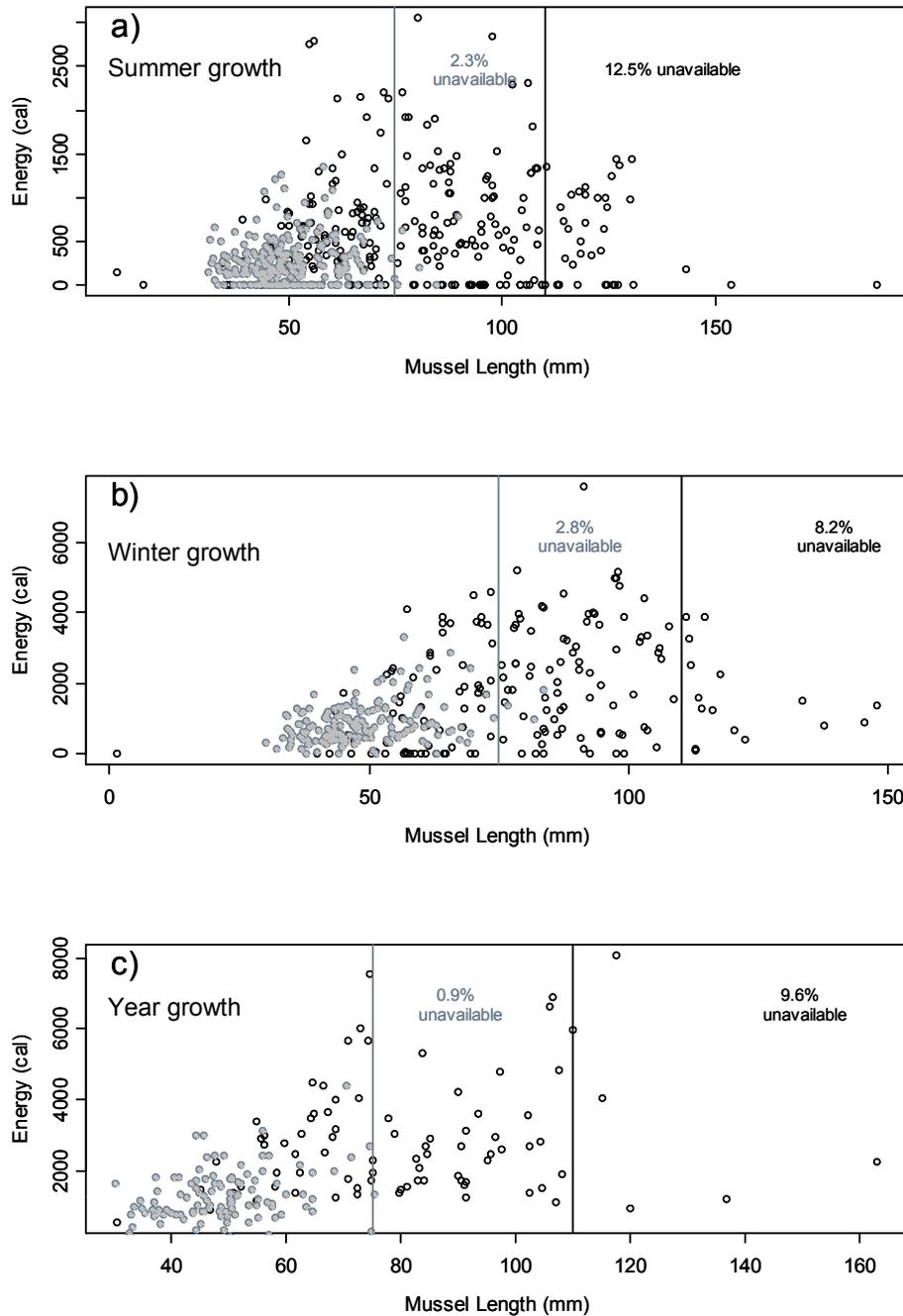


Figure 3. 11: Mussel production from Barkley Sound and Kyuquot Sound estimated in calories produced over various time horizons based on observed length increases, and energy accumulation calculated based on changes in biomass. Panels are a) summer growth, b) winter growth, c) year-round growth. Black points represent energy in mussel growth from Barkley Sound and the black lines represent the size of escapement for mussels in Barkley Sound. Grey points represent energy from mussel growth from Kyuquot Sound and the grey lines represent the size of escapement for mussels in Kyuquot Sound. The text represents the proportion of energy in mussel growth unavailable to seastar predators on account of size escapement (black for Barkley Sound and grey for Kyuquot Sound).

## Discussion

### Sea Otters Structure Mussel Beds

This study provides strong evidence that sea otters are structuring mussel beds. The data on large mussel shells collected on beaches show that mussels once attained large sizes in Kyuquot Sound although live mussels are small. Something is currently preventing the mussels from reaching these larger sizes that were previously attainable. Beach cast mussels were heavily eroded, which could signify that they have been dead a long time (and potentially predate what limits mussels from reaching large sizes), and living large mussels in Kyuquot Sound were observed in deep crevices that could be refuges from sea otters (Singh, *personal observation*). The consistency of declines in mussel bed structure along a gradient of otter influence indicates a systematic disturbance in mussel beds caused by sea otter foraging. Other types of disturbance in mussel beds (logs, wave action) tend to be patchy within mussel beds and more variable between mussel beds in a region (Guichard et al. 2003, Denny 1995, Dayton 1971). Damage to mussel beds by logs and waves can be quite sporadic in time (depending on the abundance of logs in the water from forestry practices) and mussels lean in towards the gap, to “cure” the edge of beds to prevent future damage from abiotic stresses (Paine and Levin 1981).

Sea otters, by contrast, systematically enlarge gaps in the mussel beds. Otters dislodge clumps of mussels from beds and enlarge the resulting gaps in subsequent foraging trips (VanBlaricom 1988). On some occasions, the gaps that otters create in mussel beds are expanded by wave action; otter predation can facilitate mussel mortality by waves (VanBlaricom 1988). Otters are known to eat mussels at high tide by diving and also by foraging on land at low tide (VanBlaricom 1988, Estes 1980, Harrold and Hardin 1986). Otters forage on mussels on the west coast of Vancouver Island (DFO 2007) and Washington State (VanBlaircom 1988, Laidre and

Jameson 2006). If sea otters increasingly turn to mussels for food as other prey decline, impacts to mussel beds should increase.

### **Mussel Size Varies with Otter Influence**

The data on mussel sizes support our hypothesis that mussels will be smaller in regions with higher otter influence. Coupled with this finding is the result that mussel size-ranges also decrease in areas of longer otter influence. Given that mussels are able to grow to large sizes (>100 mm), this phenomenon could occur from disturbance events removing large individuals while recruitment continues to supply small mussels (Hunt and Scheibling 2001). The consistent decrease in size and variation in size with increased duration of otters could be a result of increased frequency, duration, and/or prevalence of disturbance from mussel predation.

Initial otters into a region preferentially prey on abalone and sea urchins (Breen et al 1982), and switch to other prey items as abalone and urchins become rare. In food-poor environments, otter diets are more variable across individuals (Tinker et al. 2007)—variation that can be passed from mother to pup (Estes et al. 2003). The lack of significant difference in the mussel sizes between Barkley Sound and Clayoquot Sound could be due to the short time that otters have had to alter mussel beds in Clayoquot Sound. The lack of a statistical difference between Cape Flattery and Kyuquot Sound, where otters have been present for ~20 and >20 years respectively, may be due to otter diets stabilizing and mussel size distributions reaching equilibrium with otter predation.

### **Mussel Beds are Shallower where Otters have Resided Longer**

Duration of otter influence also correlates with mussel bed depth. Mussel bed depth can be quite variable even within a mussel bed, due to abiotic stressors such as wave exposure (Hammond and Griffiths 2004) and the layering behaviour of mussels. Mussel bed depth depends on both the

sizes of mussels and their layering, and differences in layering behaviour might contribute to variation in depths of mussel beds. Our inter-region findings are significant despite such potential variation. If sufficiently frequent, disturbance events by sea otters that strip mussels from bedrock will eventually affect mussel bed depth.

### **Mussel and Sediment Biomass is Smaller where Otters have Resided Longer**

Given that mussels are larger, and there is a trend of deeper mussel beds where otters are absent, it is unsurprising that mussel biomass and amount of sediment is also higher where otters are absent (figure 3.5 & 3.7). We did not find significant differences in mussel biomass between regions, but this may be a result of small sample size ( $n = 3$  sites)—much of the difference between regions was driven by one site in Barkley Sound (Helby). Though this study only has data of mussel biomass and sediment accumulation in the two extreme regions of otter influence, the positive relationship found between these variables leads us to assume that they will also follow the gradient of otter influence. All of the structural characteristics of mussel beds measured in this study tend to decrease with increased sea otter occupancy time.

### **Mussel Bed Communities Vary Between Regions of Otter Presence**

On a regional basis, biomass of mussel associated species decreases from otter present to otter absent areas. Biomass of individual morphospecies in each region was variable, but total biomass of mussel-associated species was much higher in the otter absent region (figure 3.6). Previous studies have found that mussel bed diversity and abundance responds to the same structural characteristics of mussel beds that we measured in this study (mussel size, mussel bed depth, mussel biomass, and amount of sediment). This study cannot determine differences in diversity

on a fine scale because not all organisms were sorted to species. Some large species groupings such as annelids and sponges were not refined further than this coarse grouping.

The results indicate that mussel bed characteristics correlate with community composition. Possible causal explanations for this correlation include dampening stresses and providing resources to species. Larger mussels provide more space for epibionts to occupy, older mussels allow more time for epibiont colonization, sediment provides substrate for species and collects food, and deeper beds provide shelter from wave action, fluctuating temperatures, and desiccation stress (Smith 2006; Straughan and Kanter 1977). None of these mechanistic variables were measured in this study, but structural characteristics were used to assess how mussel beds structure communities.

In Barkley Sound, we found that mussel size and the amount of sediments in mussel beds were important in explaining the variation in mussel bed diversity between plots. This was not the case in Kyuquot Sound, where only mussel biomass was found to explain variation in mussel bed community structure (figure 3.8). The variation in mussel size, sediment, and mussel bed depth is significantly reduced in Kyuquot Sound, which can explain why mussel bed characteristics explained less of the variation in mussel bed communities in Kyuquot Sound than in Barkley Sound. Mussel biomass does explain 10.7% of the variance in communities in Kyuquot Sound, but it is only a rough proxy of the variables that are expected to structure communities (including secondary substrate area, depth, and volumetric density of mussels).

Mussel communities tend to be different between regions, though an ANOSIM analysis indicates only marginal significance ( $P = 0.1$ ; this may be an issue of low sampling, as a pseudoreplicated test on plots in the regions has  $P = 0.001$ ). There could be true regional differences in species

pools, as some species northern limits may occur south of Kyoquot Sound, but the range of intertidal organisms on Vancouver Island is poorly documented. The species contributing the most dissimilarity to mussel bed diversity between regions (as identified by the SIMPER analysis) strongly overlap with the dominant species found in both regions (figure 3.10). These species are barnacles (*Semibalanus cariosus* and *Pollicipes polymerus*) that attach and grow on mussel shells, clams (*Hiatella arcitca* and *Leukoma staminea*) that usually burrow, and free-living decapods, echinoderms, isopods, gastropods, and sipunculid worms (*Petrolistes cincitipes*, *Cucumaria pseudocurata*, *Cirolana harfordi*, *Nucella canaliculata*, *Nucella ostrina*, and *Phascolosom agassizii*) that could be subject to wave dynamics (Sousa et al. 2009). Wave exposure was not found to be different between regions (see chapter 2), so these regional differences likely did not influence differences in community structure.

Previous studies of predation in mussel beds have found predators to increase diversity in intertidal habitats by creating patchy, heterogeneous mussel beds (Paine 1966). In these studies mussels could escape predation by growing too large to eat, and the predators forage in patches. The mechanisms of limited spatial foraging and size refuges likely contributed to this phenomenon of increasing diversity. Otters are large mobile predators that can affect the entire mussel bed and therefore the amount of habitat available to mussel-associated species, and there is no size refuge for mussels. Plot-to-plot variation in mussel size decreases with greater sea otter influence (table 3.2); this phenomenon can be attributed to otters homogenizing mussel-bed structure.

## Otters may Facilitate a Greater Proportion of Energy Flow from Mussels

Based on the methods of this study, a greater proportion of secondary production is available to predatory seastars where mussels are constrained to smaller size classes. Statistically significant results were only found for mussels grown over the summer, but in every case (summer, winter, and year round) the pattern of greater proportions of productivity available to *P. ochraceous* is present in every time period. The lack of significance found between two of the three time periods might be a result of the small sample sizes (n = 5 sites in each case), but is likely driven by other variability present.

The size of *P. ochraceous* found between the regions was drastically different, and consequently the size of the largest mussels that can be consumed by these smaller *P. ochraceous* is also starkly different. In Kyuquot Sound, smaller mussels co-occur with smaller *P. ochraceous* individuals, so size escapement by mussels can occur at lower sizes. *P. ochraceous* is a size indeterminate predator, and is able to shrink to accommodate food availability (Robles et al. 2009), and this may explain why seastars in Kyuquot Sound are smaller than in Barkley Sound. Conversely, this difference in *P. ochraceous* sizes might be a result of otter predation, as otters do feed on seastars (Morris et al. 1981). This points to an unforeseen interaction between otter predation on mussels as well as otter predation on seastars, and how this potentially conserves size escapement and the retention of energy. However, the ecological relevance of the differences in the proportion of energy available to seastars found in this study is dependent on food limitations on seastars. The higher mussel biomass in Barkley Sound than in Kyuquot Sound may negate this finding. Though a smaller proportion of mussel productivity is available to seastars where mussels reach larger sizes, ~90% (or more) of mussel production is still

available to seastar predators in every case estimated in this study, which suggests high energy flow up trophic levels regardless of the presence of sea otters.

These findings also point to the sensitivity of these kinds of results to the selection of predatory escapement. In this study, the size of *P. ochraceous* chosen was a very large (97<sup>th</sup> and 95<sup>rd</sup> percentile for Kyuquot and Barkley Sound, respectively), which may overestimate the availability of mussels to these predators. The reality of size refuges in mussels has also been questioned. Robles et al. (2009) found that under high densities, *P. ochraceous* attack very large mussels, which could indicate a lack of any size refuge. These findings were only observed where densities of *P. ochraceous* were experimentally inflated however, so attacks on large mussels may not occur naturally. The size at which mussels escape predation will depend on the predator in question as well as the size of predators in question. This study may also underestimate the proportion of energy unavailable to seastars, because other types of prey refuges can limit seastar predation. Small mussels found under other mussels in a bed may be of an edible size but protected from predation because it is not exposed.

### **Keystone Predation and Ecosystem Engineers**

The line of inquiry of this study builds on and integrates concepts of facilitation by ecosystem engineers and trophic cascades. By investigating how a keystone predator interacts with a mid-trophic ecosystem engineer, this study demonstrates how negative interactions (predation) can hinder the efficacy of positive interactions (facilitation through habitat formation) through an impeding cascade. It also suggests (though admittedly much less conclusively) that the promotion and limitation of different indirect positive interactions can trade off, in this case

limiting habitat for mussel-associated species while possibly promoting energy flow up trophic levels (but note the problems listed above for the results of promoting energy flow).

## **Reintroductions and Ecosystem Services**

Sea otters were intentionally reintroduced to BC, WA, OR and CA in the late 1960s. Their impacts on ecosystem services were not used as justification, but current programs to rewild areas of the world are often (but not solely) premised on conservation, ecological and management ethics that invoke ecosystem processes and services (Donlan et al. 2006; Beschta and Ripple 2009). The species that are reintroduced and managed for recovery are *de facto* treated as ecosystem service providers, but viewing the environment through the lens of ecosystem service providers generally focuses on positive interactions between humans and nonhumans, and is an anthropocentric view of human-ecological systems. Human values are fickle and context dependent. Many candidates for rewilding are apex predators (Donlan et al. 2006; Wilson 2004), and apex predators often have dramatic ecosystem impacts (Terborgh and Estes 2010). These changes can, and mostly will, create conflicts between values held by different interest groups that apply to different ecological contexts.

Species and ecological processes help fulfill existence values for some people (many of whom are conservation biologists and ecologists). This study demonstrates, while staying within the relatively small universe of conservation values, how otter reestablishment (fulfilling existence value), can limit the abundance of intertidal invertebrates (opposing other existence values) by introducing keystone predation (fulfilling existence values of ecological processes) that impede the habitat forming nature of intertidal mussels (opposing other existence values of ecological process). More broadly, otters have impacted the subsistence and commercial food sources of

coastal peoples (Salomon 2008; Fanshawe et al. 2003), but they have potential beneficial impacts to productivity and nutrient cycling (Duggins et al. 1989, this study). Viewing species as agents of ecosystem change (rather than just ecosystem service providers) is likely to be more helpful in studying how wildlife reintroductions affect people.

The indirect impacts of sea otters on nearshore ecosystems are numerous and wide reaching. The impacts explored in this study indicate an impact of otters on the ecosystem processes of habitat provision and energy flow. These functions have implications for the supporting ecosystem services of habitat provision and energy flows for species of interest (for existence values, commercial purposes, among others). These processes/services are diffuse and difficult to connect to particular human values. The complexities are even more apparent with the realization that there can be stark tradeoffs between the provision of different ecosystem services (Chan et al. 2006). Quantifying the contribution of different species to supporting services and human well-being has been accomplished for particular interactions that are tightly coupled to material human benefits (e.g. pollination, pest control, freshwater provision), but what is lacking is an understanding of how species with effects that are loosely and diffusely coupled to human values contribute to supporting ecosystem services.

## **Chapter 4: Concluding Remarks**

The provision of ecosystem services by organisms is dependent on species identity and environmental conditions (Kremen 2005). More importantly, ecological functions of ecosystem services providers can be broader than those functions that provide ecosystem services. In this study, evidence is presented to suggest that phytoplankton production might mediate the ability of otters to subsidize mussel growth through enhanced kelp biomass, and otters can inhibit the ability of mussels to provide habitat.

### **Bottom-up Impacts**

Contrary to our initial hypothesis, secondary production was not dependent on the presence of otters and high kelp biomass, as high concentrations of phytoplankton may dilute the concentration of kelp and reduce its assimilation by filter feeders. Given this, kelp seems to be more important for filter feeders in winter than summer. My results point to the importance of environmental context when assessing the importance of species function for the provision of ecosystem services (Salomon et al. 2008, Salomon et al. 2010). Yet, the interesting result was that kelp seemed to play an important role in mussel diets, regardless of the presence of otters. The hypothesis that otters provide ecosystem services by facilitating kelp production is premised on the assumption that kelp is limiting in the system to begin with. Where this is not the case (such as for the quantity of food for filter feeders), the extra kelp biomass allowed to establish may be largely redundant.

### **Top-Down Impacts**

Sea otters limit the habitat provision role of mussels for a community of organisms. The findings of this thesis largely support the initial hypotheses regarding the interaction between otters and

mussels. Otters are important marine predators with a diverse prey base that includes mussels (Tinker et al. 2007, Newsome et al. 2009). Interestingly, the biggest differences in community composition (based on our analyses) seem to be changes in dominant species. Mussel bed structure still explains variation in mussel bed communities where mussel bed structure is reduced, so mussels can still retain their habitat provisioning function even when mussels are constrained to small sizes and shallow beds.

The hypothesis that otters promote greater energy flow through marine food webs by limiting sizes of mussels was supported, with important caveats. Otters have population impacts on a variety of marine invertebrates, and otters may be limiting the sizes of the seastars that depredate mussel at the same time as impacting mussel size structure, therefore retaining some of the size escapement of mussels at smaller sizes (Paine 1976). The importance of the results on energy flow from secondary production may not be ecologically relevant because high proportions of secondary production are available to seastars regardless of region and seastars may not be food limited.

## **Future Directions**

### **Primary and Secondary Productivity**

A comprehensive study into primary productivity, estimating biomass of primary producers across seasons on the west coast of Vancouver Island would help tease apart the extent to which nutrient dynamics in nearshore environments mediate the role of kelp detritus in nearshore food webs. Field surveys have shown the west coast of Vancouver Island to be highly productive (Harris 2001), but the region is remote and replicating such studies across time can be difficult. The new MERIS satellite can calculate chl *a* measures on a very small spatial scale (300 m) and

can accurately detect high concentrations of phytoplankton (Gower et al. 2004). As well, a more thorough account of the primary drivers of mussel growth (density, temperature, wetness, food availability) would help identify what factors are controlling secondary productivity along the west coast of Vancouver Island (see Menge 2008 and Blanchette et al. 2007). Including other species in an analysis of impacts to secondary productivity would also provide a more complete understanding of how secondary productivity is affected by changes in primary productivity. For example, grazers, which target the biomass of kelp and drift kelp without necessarily relying on POM and DOM, might benefit from the greater kelp biomass in the presence of otters to a greater extent than filter feeders (Duggin 1988).

### **Impacts to Habitat Provision**

To better understand how otters affect mussel bed structure and energy dynamics of mussel beds, research might be conducted to better understand how mussel beds change over time. Using data on growth rates of mussels for different sizes of mussels, dynamic models of mussel bed matrices can be built to explore the development of mussel bed structure and the consequences to biodiversity and energy flow from secondary producers to higher trophic levels (Ardisson and Bourgete 1991, Guinez and Castilla 1999).

### **Ecosystem Services**

Ecosystem services are varied and numerous. This thesis has not comprehensively looked at indirect effects of otters on nearshore ecosystems. The release of kelp from urchin herbivory has implications beyond nutrient dynamics. Kelp provides vertical structure in the water column, which can provide habitat for a variety of nearshore subtidal communities, including fish and invertebrates (Arkema et al. 2009). Additionally, kelp can have impacts on the hydrodynamics of

nearshore systems, dampening wave intensity (Duggins 1988). This has implications for larval retention. Otter predation on other marine invertebrates could have other positive and negative impacts to important ecosystem services. Otters are charismatic marine mammals that have been shown to contribute substantially to Californian ecotourism (Aldrich et al. 2001, Loomis 2006). There are a variety of ecosystem consequences with implications to ecosystem services involving the regulation of populations and other coastal processes. Valuing these services also poses a significant research challenge as many of the impacts of otters on coastal ecosystem services are supporting and regulating services. These services are notoriously difficult to assess for valuation, but production function approaches, where processes contribute to final products with concrete human values, can be developed to see how otter impacts on nearshore systems affect human values (Barbier 2006).

## **Closing Thoughts**

Species with known and hypothesized community consequences are clear candidates to study how individual species impact the provision of ecosystem services. These species are important to study for the contributions they make to ecosystem services, but they may also negatively impact the provision of other ecosystem services. In no way has this thesis comprehensively explored sea otters as ecosystem service providers or detractors. Understanding the provision of ecosystem services is dependent on the species, the particular ecosystem service, and the environmental context. Which species performs what ecosystem services under what environmental conditions is highly specific, and the number of unstudied combinations points to the scale of research that still confronts ecologists trying to understand the ecology behind ecosystem services. The number of combinations also showcases the overwhelming uncertainty confronted by management agencies trying to plan for ecosystem services. The question then

becomes: under what conditions does a study of the ecological underpinnings of ecosystem services most likely provide important information for management agencies? All research is motivated by values (McMullin 1982, Allen et al. 2001, Callicott et al. 1999), and ecologists left to their own devices will study those aspects of ecosystem services that reflect their values. Studies exploring services that are important in a management context should be motivated by values that are important for the given management context.

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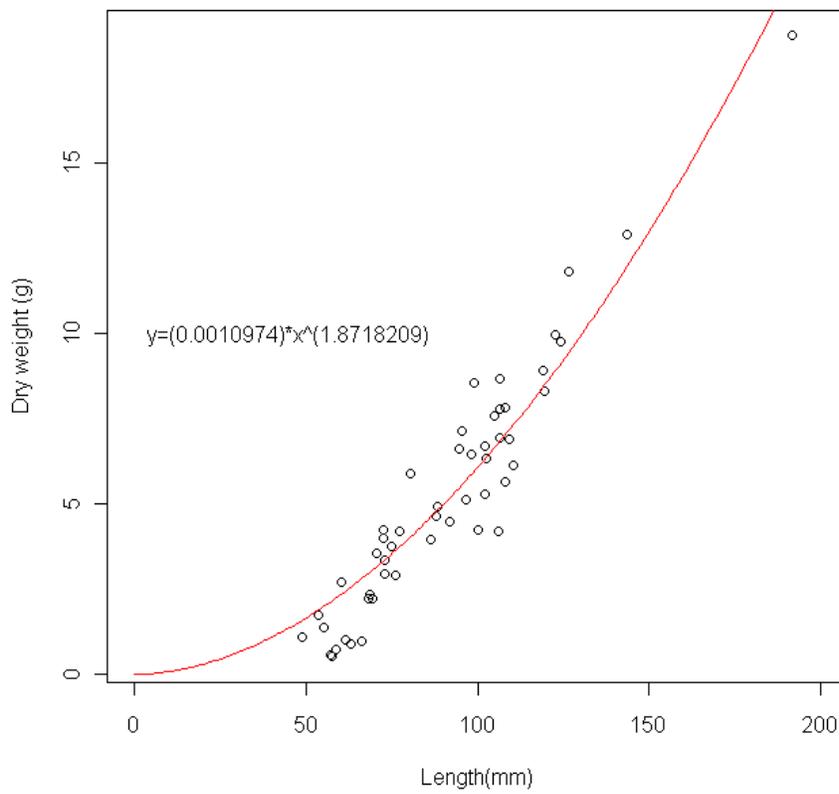
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## Appendix A

### Length to Dry Weight Conversions



**Figure A1:** The fitted relationship between size and dry biomass of mussels takes an allometric form,  $y = a \times \text{length}^b$

## Appendix B

### Canonical Correspondence Analysis Results

**Table B 1: Variance explained by individual species in CCA for Barkley Sound**

Barkley Sound	Variance explained by CCA (%)
<i>Cirolana harfordi</i>	50.3495
<i>Idotea wosnesenenkii</i>	32.1067
Amphipod	3.0823
<i>Petrolistes cinctipes</i>	38.0008
<i>Amphissa versicolor</i>	46.2838
<i>Nucella canaliculata</i>	45.7755
<i>Nucella ostrina</i>	3.8337
<i>Homalopoma baculum</i>	33.2372
<i>Styidium eschrichtii</i>	8.3989
<i>Onoba carpenteri</i>	33.9235
<i>Amphissa versicolor</i>	10.0362
<i>Lirobittium latifilosum</i>	23.5042
<i>Lirobittium interfossum</i>	22.4137
<i>Lirobittium purpureum</i>	12.9503
<i>Lirobittium esuriens</i>	85.7133
<i>Evalea tenuisculata</i>	27.1469
<i>Lirularia sp</i>	29.7739
<i>Homalopoma sp</i>	33.8304
<i>Lacuna sp</i>	5.7854
<i>Lottia digitalis</i>	17.9255
<i>Lottia paradigitalis</i>	3.7871
<i>Phascolosom agassizii</i>	23.6487
<i>Cucumaria pseudocurata</i>	31.5512
<i>Hiatella arcitca</i>	22.6129
<i>Leukoma staminea</i>	24.6938
<i>Pollicipes polymerus</i>	29.7552
<i>Semibalanus cariosus</i>	11.9326
<i>Balanus glandula</i>	2.8609
<i>Chthamalus dalli</i>	21.1353
Sponges	9.8045
Annelid worms	5.6232
<i>Katherina tunicata</i>	21.3364
Platyhelminthine worm	4.4332
Nematodes/Nemertian	12.1905
Hydroid	0.8315

Barkley Sound	Variance explained by CCA (%)
<i>Ocinobrina</i> sp.	22.7145
<i>Alia tuberosa</i>	33.9528
Hermit crab	8.8984
Hermit crab shell	9.1857
sea grass	1.0152
<i>Pisaste ochraceous</i>	17.6991
Hard coral	24.2829
<i>Mopalia</i> sp	14.3438
Articulated corraline	60.9122
<i>Ceratostoma</i> sp	8.6401
<i>Lottia pelta/persona</i>	13.9979
Crab eggs	10.9013
<i>Chlorostoma funebris</i>	7.4203
Staphilinidae	5.5829
<i>Littorina</i> sp.	13.0379
<i>Xiphister mucosus</i>	1.7473
<i>Granulina margeritula</i>	31.4846
<i>Onchedella borealis</i>	12.2557
<i>Nucella</i> eggs	3.1096
Small Chiton	5.0543
Foraminiferan	5.7391
Mesostigmatid mite	3.9816
Anenome	22.6601
Red algae	1.6092
<i>Leptasterias</i> sp	0.9460
<i>Amphissa columbiana</i>	4.7211
<i>Porphyra</i> sp	1.3896
<i>Hydractina</i> sp	1.3896
<i>Melanella thersites</i>	17.1367
Brittle star	17.1367
<i>Gobiesox maeandricus</i>	20.8092

**Table B 2: Variance explained by individual species in CCA for Kyuquot Sound**

Kyuquot Sound	Variance explained by CCA (%)
<i>Cirolana harfordi</i>	27.8000
<i>Idotea wosnesenenkii</i>	0.0003
Amphipod	0.0869
<i>Petrolistes cinctipes</i>	12.5000
<i>Amphissa versicolor</i>	1.5000
<i>Nucella canaliculata</i>	2.8700
<i>Nucella ostrina</i>	1.4900

Kyuquot Sound	Variance explained by CCA (%)
<i>Homalopoma baculum</i>	27.5000
<i>Stylidium eschrichtii</i>	17.7000
<i>Onoba carpenteri</i>	12.0000
<i>Amphissa versicolor</i>	0.0620
<i>Lirobittium latifilosum</i>	0.2880
<i>Lirobittium interfossum</i>	0.0471
<i>Lirobittium purpureum</i>	4.4300
<i>Lirobittium esuriens</i>	8.2900
<i>Evalea tenuisculata</i>	0.9380
<i>Lirularia</i> sp	6.2700
<i>Homalopoma</i> sp	1.3400
<i>Lottia digitalis</i>	8.6600
<i>Lottia paradigitalis</i>	19.6000
<i>Phascolosom agassizii</i>	28.2000
<i>Cucumaria pseudocurata</i>	13.2000
<i>Hiatella arcitca</i>	0.4000
<i>Leukoma staminea</i>	10.1000
<i>Pollicipes polymerus</i>	5.8700
<i>Semibalanus cariosus</i>	12.9000
<i>Balanus glandula</i>	0.5530
<i>Chthamalus dalli</i>	0.0101
Sponges	0.3330
Annelid worms	6.4700
<i>Katherina tunicate</i>	0.2930
Platyhelminthine.worm	4.2100
Nematodes/Nemertian	1.8600
Hydroid	10.9000
<i>Ocinobrina</i> sp	0.0617
<i>Alia tuberosa</i>	0.1470
<i>Pisaster ochraceous</i>	0.9010
Hard coral	5.7000
<i>Mopalia</i> sp	1.3100
Articulated corraline	2.7600
<i>Lottia pelta/persona</i>	2.3000
Crab eggs	1.6700
<i>Chlorostoma funebris</i>	3.5400
Staphilinidae	0.6100
<i>Onchedella borealis</i>	0.9460
<i>Nucella</i> eggs	0.7290
<i>Calliostoma ligatum</i>	3.3000
Small Chiton	0.0001
Echiuran worm	0.5020

Kyuquot Sound	Variance explained by CCA (%)
Foraminiferan	0.0750
Mesostigmatid.mite	0.2560
Anenome	3.4700
Red algae	8.2000
<i>Ulva</i> sp	0.2440
Dipteran	1.5500
<i>Onoba dinora</i>	0.0013
<i>Clinocardium nuttallii</i>	1.6700

**Table B3: Coordinates of species along CCA plots in Barkley Sound**

Barkley Sound	CCA1	CCA2
<i>Cirolana harfordi</i>	0.79619777	0.05353612
<i>Idotea wosnesenenkii</i>	0.91540081	1.22921257
Amphipod	0.06986777	-0.3027922
<i>Petrolistes cinctipes</i>	0.38908357	-0.23342887
<i>Amphissa versicolor</i>	1.72893341	2.1898061
<i>Nucella canaliculata</i>	0.59545684	0.22352247
<i>Nucella ostrina</i>	0.26777358	-0.18879989
<i>Homalopoma baculum</i>	1.2327989	-0.64033381
<i>Stylidium eschrichtii</i>	0.84889045	0.12934121
<i>Onoba carpenteri</i>	0.91911827	0.393072
<i>Amphissa versicolor</i>	0.77410621	-1.59403042
<i>Lirobittium latifilosum</i>	1.03683602	-0.23247543
<i>Lirobittium interfossum</i>	1.10348812	-0.20771159
<i>Lirobittium purpureum</i>	0.83202475	-0.36941634
<i>Lirobittium esuriens</i>	1.36501595	0.85408187
<i>Evalea tenuisculata</i>	1.09093294	-0.40239071
<i>Lirularia</i> sp	1.57188873	0.31115535
<i>Homalopoma</i> sp	1.47753466	1.77353129
<i>Lacun</i> sp	0.69352496	-0.95446896
<i>Lottia digitalis</i>	-0.53232083	0.02847284
<i>Lottia paradigitalis</i>	-0.06371078	-0.20063379
<i>Phascolosom agassizii</i>	0.54509896	-0.22645603
<i>Cucumaria pseudocurata</i>	0.54468103	-0.28270602
<i>Hiatella arcitca</i>	0.34489861	0.11892277
<i>Leukoma staminea</i>	0.74066601	0.32309084
<i>Pollicipes polymerus</i>	-0.47961817	-0.05445049
<i>Semibalanus cariosus</i>	-0.06730118	0.02860192
<i>Balanus glandula</i>	0.13212618	0.39980856
<i>Chthamalus dalli</i>	1.16701292	-0.91376519
Sponges	0.32640457	0.73363436

Barkley Sound	CCA1	CCA2
Annelid worms	0.18917032	0.27826081
<i>Katherina tunicata</i>	0.73669316	-0.84388188
Platyhelminthine worm	-0.70464626	0.02835766
Nematodes/Nemertian	-1.08722012	0.62552881
Hydroid	0.13364491	-0.17893989
<i>Ocinobrina</i> sp.	1.12193808	-0.7445153
<i>Alia tuberosa</i>	0.97903689	-0.28465865
Hermit crab	0.57093029	-1.46742755
Hermit crab shell	0.67182809	-1.54905704
sea grass	-0.33160208	-0.0676419
<i>Pisaste ochraceous</i>	0.12094315	-1.05728303
Hard coral	0.58243643	1.19533673
<i>Mopalia</i> sp	0.65287105	1.08976174
Articulated corraline	1.17944141	0.58150758
<i>Ceratostoma</i> sp	0.58549509	-1.47089655
<i>Lottia pelta/persona</i>	0.58521513	0.15680642
Crab eggs	0.22854975	0.73092563
<i>Chlorostoma funebris</i>	1.05170672	-0.07823068
Staphilinidae	0.43902063	-0.77877827
<i>Littorina</i> sp.	1.03216722	-0.23158993
<i>Xiphister mucosus</i>	-0.71872379	-0.459216
<i>Granulina margaritula</i>	1.80805091	0.69155715
<i>Onchedella borealis</i>	-1.01388367	0.16554731
<i>Nucella</i> eggs	-0.59488232	0.09688524
Small Chiton	-1.11625313	0.48970782
Foraminiferan	0.68579867	-0.94885677
Mesostigmatid mite	0.17832201	-0.64520227
Anenome	1.51383209	-1.1010601
Red algae	-0.1098744	0.70489069
<i>Leptasterias</i> sp	-0.58399678	-0.30543234
<i>Amphissa columbiana</i>	0.28853165	-0.83061368
<i>Porphyra</i> sp	-0.23226418	-0.60776987
<i>Hydractina</i> sp	-0.23226418	-0.60776987
<i>Melanella thersites</i>	2.14123031	-0.67063605
Brittle star	2.14123031	-0.67063605
<i>Gobiesox maeandricus</i>	1.03196038	-1.18870762

**Table B4: Coordinates of species along CCA plots in Kyuquot Sound**

Kyuquot Sound	CCA1	CA1
<i>Cirolana harfordi</i>	0.62566	-0.46404
<i>Idotea wosnesenenkii</i>	-0.0092	-1.7577
Amphipod	0.05829	-0.21496
<i>Petrolistes cinctipes</i>	0.92013	-1.59476
<i>Amphissa versicolor</i>	0.6532	0.521409
<i>Nucella canaliculata</i>	0.32277	-0.98298
<i>Nucella ostrina</i>	0.53499	-2.64516
<i>Homalopoma baculum</i>	1.32872	-1.02931
<i>Stylidium eschrichtii</i>	2.21894	-1.68507
<i>Onoba carpenteri</i>	0.87596	-1.24917
<i>Amphissa versicolor</i>	0.24147	-4.95565
<i>Lirobittium latifilosum</i>	-0.1355	-0.67609
<i>Lirobittium interfossum</i>	0.08916	-2.22106
<i>Lirobittium purpureum</i>	0.56265	-1.46649
<i>Lirobittium esuriens</i>	1.0383	-2.2374
<i>Evalea tenuisculata</i>	-0.1205	-0.69702
<i>Lirularia</i> sp	0.99423	-1.35419
<i>Homalopoma</i> sp	1.13656	-1.32586
<i>Lottia digitalis</i>	0.51993	-0.89716
<i>Lottia paradigitalis</i>	0.7928	-0.84059
<i>Phascolosom agassizii</i>	1.44585	-0.62935
<i>Cucumaria pseudocurata</i>	0.55779	-0.92915
<i>Hiatella arcitca</i>	-0.0765	-0.40814
<i>Leukoma staminea</i>	0.55749	-0.47269
<i>Pollicipes polymerus</i>	-0.2273	-0.263
<i>Semibalanus cariosus</i>	-0.0875	0.209826
<i>Balanus glandula</i>	0.43969	-2.04185
<i>Chthamalus dalli</i>	0.06148	-0.81863
Sponges	0.44681	-4.11647
Annelid worms	0.57013	-1.09363
<i>Katherina tunicate</i>	0.10028	-0.74942
Platyhelminthine.worm	0.78816	-2.05196
Nematodes/Nemertian	-0.3927	-0.15098
Hydroid	4.2666	-2.10103
<i>Ocinobrina</i> sp	0.17749	-3.20651
<i>Alia tuberosa</i>	-0.1177	-2.09124
<i>Pisaster ochraceous</i>	-0.7523	-4.08988
Hard coral	-0.8973	-1.72323
<i>Mopalia</i> sp	1.17963	-1.213

Kyuquot Sound	CCA1	CA1
<i>Articulated corraline</i>	-0.4513	-0.44501
<i>Lottia pelta/persona</i>	0.59176	-0.6256
<i>Crab eggs</i>	-0.9037	-0.62938
<i>Chlorostoma funebris</i>	0.88834	-2.87868
Staphilinidae	-0.2401	-0.41483
<i>Onchedella borealis</i>	0.15378	-0.70425
<i>Nucella eggs</i>	0.36435	-0.605
<i>Calliostoma ligatum</i>	1.04604	-1.41818
Small Chiton	0.0019	-0.12461
Echiuran worm	0.29681	-0.62578
Foraminiferan	0.18707	-3.35926
Mesostigmatid.mite	-0.1743	-0.09651
Anenome	0.87735	-2.2661
Red algae	-1.2285	0.007281
<i>Ulva</i> sp	-0.1197	0.324799
Dipteran	-0.9709	-0.22813
<i>Onoba dinora</i>	-0.0176	-1.18201
<i>Clinocardium nuttallii</i>	-0.9037	-0.62938