

**MORPHOLOGY OF THE  
FOOLISH MUSSEL (*Mytilus trossulus*):  
VARIATION AND DEFENSE**

by

BriAnne Addison  
BSc, Simon Fraser University 2002

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF  
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

In the  
Department  
of  
Biological Sciences

© BriAnne Addison 2004

SIMON FRASER UNIVERSITY

FALL 2004

All rights reserved. This work may not be  
reproduced in whole or in part, by photocopy  
or other means, without permission of the author.

APPROVAL

Name: BriAnne Addison

Degree: Master of Science

Title of Thesis:

Morphology of the foolish mussel (*Mytilus trossulus*): Variation and defense

Examining Committee:

Chair: Dr. R. Nicholson

---

Dr. R. Ydenberg, Professor  
Department of Biological Sciences, S.F.U.

---

Dr. R. Butler, Adjunct Professor, Department of Biological  
Sciences, S.F.U. and Research Scientist, Canadian Wildlife  
Service

---

Dr. E. Elle, Assistant Professor  
Department of Biological Sciences, S.F.U.

---

Dr. J. Marliave, Vice President  
Marine Science, Vancouver Aquarium

---

Dr. E.B. Hartwick, Associate Professor  
Department of Biological Sciences, S.F.U.  
Public Examiner

---

November 19, 2004  
Date Approved

# SIMON FRASER UNIVERSITY



## PARTIAL COPYRIGHT LICENCE

The author, whose copyright is declared on the title page of this work, has granted to Simon Fraser University the right to lend this thesis, project or extended essay to users of the Simon Fraser University Library, and to make partial or single copies only for such users or in response to a request from the library of any other university, or other educational institution, on its own behalf or for one of its users.

The author has further granted permission to Simon Fraser University to keep or make a digital copy for use in its circulating collection.

The author has further agreed that permission for multiple copying of this work for scholarly purposes may be granted by either the author or the Dean of Graduate Studies.

It is understood that copying or publication of this work for financial gain shall not be allowed without the author's written permission.\

Permission for public performance, or limited permission for private scholarly use, of any multimedia materials forming part of this work, may have been granted by the author. This information may be found on the separately catalogued multimedia material and in the signed Partial Copyright Licence.

The original Partial Copyright Licence attesting to these terms, and signed by this author, may be found in the original bound copy of this work, retained in the Simon Fraser University Archive.

W. A. C. Bennett Library  
Simon Fraser University  
Burnaby, BC, Canada

## ABSTRACT

Mussels (*Mytilus spp.*) are dominant members of the rocky intertidal ecosystem, where interactions with predators and competitors are well documented. However, little is known about how variation in defensive morphological traits of mussels affects the outcome of interactions, or how predation affects the variation observed. In this thesis, I show that morphological diversity in foolish mussels (*M. trossulus*) in Howe Sound, British Columbia, is potentially important to interactions with mussel predators of the rocky intertidal community. Byssal attachment strength is positively related to the presence of crab and seaduck predators, but variation in several other morphological features is not easily attributable to predators. In addition, I experimentally demonstrate that seastars preferentially consume mussels with uneven shell margins and small crabs preferentially consume thinner-shelled mussels. However, large crabs either have no preference, or consume more thick-shelled mussels. Finally, I review the concepts of keystone species and trait-mediated indirect interactions, and make the case that trait-mediated interactions impact the structure and dynamics of the Howe Sound rocky intertidal community.

## ACKNOWLEDGEMENTS

Rob Butler deserves thanks for entrusting me with this project. His enthusiasm and encouragement were wonderful and absolutely necessary. The rest of my committee, Ron Ydenberg, Elizabeth Elle, and Jeff Marliave have challenged me to think about experimental design from concept, to implementation, to analysis. Brian Hartwick also helped me ensure that my cage design would stand up to the physical rigors of the marine environment. Statistical advice from Carl Schwartz, Laura Cowen, and Barry Smith was immensely helpful. Bob Elner was happy to discuss analysis and results, with humor. Rob and Barry sat through, rather, endured, practice runs of my thesis presentation. And thanks, again, to my committee for allowing me the freedom to pursue all of my academic interests.

Thanks so much to Christine Heaven and Mark Hipfner for your help with midnight field work. It was wet and cold, and I had no idea it would be so challenging to pull mussels and seastars off rocks in the dark. Rudi Kovanic, Rod McVicar and Nelson Riley drove boats and tended dives. Kristine Hanssmann and Brianna Newton also helped with field work. Larissa Addison and Peter Addison helped me build my experimental cages on a Saturday when Larissa probably had something better to do. Mark helped me put those cages in the water; he thought the whole process was a disaster, but it worked. Ian Gordon took one for the sake of science when a crab pinched him while helping me measure it. Christine, Kristine, Lans Kabba and Justin Look helped with lab work. Shucking mussels is smelly work.

Judy Higham makes sure we can all afford to eat. I don't think she knows how important this is to all of us. Connie Smith helps us all with permits and technical logistics, whether she likes it or not. Thanks Connie, for your humorous email sign-offs.

I received funding for my stipend and thesis research from an Environment Canada Science Horizons grant and the Centre for Wildlife Ecology.

There are many people who may be peripheral to a thesis, but are still instrumental in its completion. Thanks to all the grrrls (Kristen Gorman, Allison Henderson, Dana Seaman, Tawna Morgan, Sarah Jamieson, Jeanine Bond, Erin Barley, and everyone else, you know who you are) for Ethiopian food, guitar, and bouldering. Thanks to Andrea Pomeroy, my Butler/Ydenberg lab sib, for various advice. Thanks to Jim Dale for talking shop. Thanks to Alejandro Frid for talking about water. Thanks to Mark for Triangle Island and more.

# TABLE OF CONTENTS

<b>Approval</b> .....	<b>ii</b>
<b>Abstract</b> .....	<b>iii</b>
<b>Acknowledgements</b> .....	<b>iv</b>
<b>Table of Contents</b> .....	<b>vi</b>
<b>List of Figures</b> .....	<b>viii</b>
<b>List of Tables</b> .....	<b>x</b>
<b>Chapter One. A Recipe for Mussels</b> .....	<b>1</b>
The Mussel .....	2
Mussel Predators.....	3
The Howe Sound Rocky Intertidal Ecosystem.....	5
Objectives of the Thesis .....	7
<b>Chapter Two. Morphological Variation of Foolish Mussels (<i>Mytilus trossulus</i>) in Howe Sound, British Columbia</b> .....	<b>9</b>
Introduction .....	9
Methods.....	12
Collection Methods .....	12
Predator and Environmental Landscape Assessment.....	12
Mussel Morphology .....	13
Statistical Analysis.....	13
Results .....	15
Predator-Environment Associations.....	15
Mussel Morphology .....	15
Discussion .....	15
<b>Chapter Three. Picky Eaters: Do Morphological Traits of Mussels Defend them Against their Predators?</b> .....	<b>26</b>
Introduction .....	26
Methods.....	28
Mussel Morphology .....	29
Predation Experiment.....	30
Statistical Analysis.....	31
Results .....	32
Mussel Morphology .....	32
Predation Experiment.....	32
Discussion .....	33
Mussel Morphology .....	34
Predation Experiment.....	35

<b>Chapter Four. The Keystone Concept and Trait-mediated Indirect Interactions: A New View of the Rocky Intertidal Community .....</b>	<b>46</b>
Density-mediated Indirect Interactions .....	47
Trait-mediated Indirect Interactions .....	48
A New View of the Rocky Intertidal .....	49
Conclusion.....	52
<b>Reference List.....</b>	<b>56</b>
<b>Appendix I .....</b>	<b>63</b>



## LIST OF FIGURES

Figure 2.1: Howe Sound, British Columbia. Collection sites were north end of Batchelor Cove (NB), Copper Cove (CC), Millers Landing (ML), Tunstall Bay (TB), Bowen Bay (BB), and Popham Island (PI), and are indicated with dots. ....	20
Figure 2.2: Byssal attachment strength is stronger in areas of crab or seaduck predation relative to areas without. ....	25
Figure 3.1: Cage setup (a) and field setup (b). Each of 12 cages had crab, seastar, and control predator treatments. The cages were hung from a midwater line to prevent disturbance by other predators and surf. ....	38
Figure 3.2: Shell thickness (n=30 per location) and shell evenness (n=10) indices of Batchelor Cove intertidal and Popham Island fouling community mussels. Batchelor Cove mussels were thicker and less tightly closing compared to Popham Island mussels. ....	40
Figure 3.3: Adductor size measures of Batchelor Cove intertidal (n=30) and Popham Island fouling (n=30) community mussels. Batchelor Cove mussels; adductors were larger in diameter and proportional dry mass than Popham Island mussels'. ....	41
Figure 3.4: Mean (and 95% confidence intervals) count of the number of mussels remaining from each of the two morphotypes for each predator treatment. Letters connect means not significantly different (Tukey-Kramer, alpha=0.05). ....	42
Figure 3.5: The mean (and 95% confidence intervals) size of mussels remaining for each morphotype after predator treatments. Letters connect means not significantly different (Tukey-Kramer alpha=0.05). ....	43
Figure 3.6: The relationship between crab carapace width and proportion Popham Island mussels remaining is described by the line $\text{Log}(\text{PI}:\text{NB}) = -6.41 + 0.05 \text{ carapace width}$ . Larger crabs ate more Batchelor Cove mussels, leaving a greater proportion of Popham Island mussels. ....	45
Figure 4.1: TMIIIs can be described as consisting of an initiator (I), a transmitter (T) and a receiver (R), and additionally 1) the initial ecological relationship between I and T 2) the action of I that affects T, 3) The trait of T that is altered 4) the initial ecological relationship between T and R and 5) the effect on R, which could be positive or negative. ....	54
Figure 4.2: An interaction web for the Howe Sound rocky intertidal community. Solid arrows indicate direct ecological interactions with arrows pointing in the direction of energy flow. The double-headed solid arrow indicates a competitive interaction; mussels and barnacles	

compete for settlement substrate, and when very close, for phytoplankton food. Dashed lines indicate demonstrated or possible induction of trait modification. Numbered dotted lines indicate proposed indirect interactions. 1) Induction of mussel's defenses by crabs or seastars may facilitate predation by the other. 2) Induction of stronger byssal attachments by crabs may make mussels less profitable, or unexploitable by seaducks. 3) The removal of mussels by seaducks may induce riskier high intertidal foraging by seastars, making them more available to gulls. .... 55

## LIST OF TABLES

Table 2.1: Summary of mussel collections and site characteristics. Substrate types were classified as bedrock (br), boulders (bo), or cobble (co). .....	21
Table 2.2: Ordinal logistic regression and likelihood ratio tests of effects of substrate and exposure on presence of seaduck, seastar and crab predators. Seaduck and crab presence is strongly associated with the substrate type of the habitat. ....	22
Table 2.3: Mean residual values of byssal strength, shell thickness, muscle tissue, adductor diameter, maintenance tissue, and gonad tissue, and shell shape ratios for each site $\times$ quadrat combination. Values with 95% CI that overlap zero, or the grand mean are grey, those which are less than the grand mean are in black, greater than the grand mean are in white. Habitat (co=cobble, br=bedrock, bo=boulder) and predator (0=absent, 1=present) characteristics are listed below.....	23
Table 2.4: Results of ANOVAs testing the importance of substrate, exposure, littoral height and the presence of predators in predicting morphological characteristics of mussels. Dashes indicate that the predator was not included in the model because there was not a specific prediction with regards to the presence of the predator for the morphological trait. <i>P</i> -values larger than 0.05 are denoted as non-significant. Only byssal strength varies among predator regimes.....	24
Table 3.1: Morphological features measured in mussels collected at Popham Island (fouling) and Batchelor Cove (intertidal), British Columbia in October 2003.....	39
Table 3.2: F-table for fixed effects of split-plot ANOVA. ....	44

## CHAPTER ONE. A RECIPE FOR MUSSELS

The evolution of anti-predator strategies is a major topic of interest in evolutionary ecology (i.e. DeWitt et al. 2000, Trussell 2000, Walker and Bell 2000). Anti-predator strategies can include behavioural, morphological, or physiological traits that prevent consumption, or make individual prey less profitable to potential predators. Predators and prey interact *directly*: predators reduce prey numbers, prey defense mechanisms incite new foraging methods by predators, and predators induce alterations to prey traits. These density and trait changes have *indirect* effects on other members of the community.

Much of what we know about density mediated indirect interactions (reviewed in Chapter 4) has come from the rocky intertidal ecosystem. Mussels are important members of the rocky intertidal community, out-competing other benthic members for space, and serving as a food base for predators. The density interactions of mussels and their predators are well documented (see below and Chapter 4), but little is known about how the traits of individual mussels alter the predator-prey interactions in this system.

This thesis is concerned with the ecological causes and consequences of morphological variation of the marine mussel *Mytilus trossulus*, with specific attention paid to predation. In this chapter I will give background on the ecology of mussels and their seastar, crab, and seaduck predators, and then outline the objectives of the remaining chapters of this thesis.

## ***The Mussel***

Foolish mussels (*Mytilus trossulus*), also called bay mussels or blue mussels, are part of the *M. edulis* complex, which includes blue mussels (*M. edulis*) and Mediterranean mussels (*M. galloprovincialis*). These species are remarkably similar, distinguished by subtle shell morphology differences, and genetic differences (McDonald et al. 1991, Martel et al. 2000). The foolish mussel is native to the Pacific Northwest, and dominates the hard substrate shoreline of the inner coast of British Columbia (BC). On the outer coast of Vancouver Island the larger, competitively dominant *M. californianus* covers most of the intertidal zone, and *M. trossulus* is found only in a narrow band above and in less exposed areas (Blaylock 1981), that *M. californianus* is excluded from due to physiological limits (Seed and Suchanek 1992). *M. galloprovincialis* was introduced to the California coast in discharged ballast waters. This species occasionally hybridizes with *M. trossulus*, and is rarely found as far north as BC (Springer 2003).

Reproduction and development of mussels is outlined in detail by Strathmann (1987). Mussels are broadcast spawners, and usually release sperm and eggs into the water synchronously in the spring and fall, but mussels in Howe Sound appear ripe to spawn year-round (pers. obs.). After fertilization, the veliger larvae live planktonically for several weeks, feeding on nanoplankton. The veliger then metamorphoses into a pediveliger, developing a foot on which it can move around, and settles on available hard substrate. Upon settling, the larvae metamorphose into juveniles, called spat, and develop a shell. Spat may still move around and resettle by casting byssal threads into the currents to sail short distances before forming a more permanent attachment to the

substrate. A mature mussel can still move after settlement by using its foot and byssal attachments to pull itself to new locations (Ricketts et al. 1985).

Mussels are filter feeders, taking water through the open gape across the gills, and sorting desired food particles, such as cyanobacteria, green algae and diatoms, inside the body and expelling unwanted particles as pseudofaeces (Bayne et al. 1976). Nutrients and minerals are then divided between general maintenance tissue such as digestive and respiratory tissue, gonad tissue, adductor and byssal retractor muscle tissue, and shell.

### ***Mussel Predators***

The primary defense of a mussel against its predators is its bivalved shell. The shell protects the mussels from predators with various modes of attack, as well as protecting it from environmental hazards such as desiccation and crushing by driftwood and rocks. Mussel predators have evolved strategies for attacking their shell-armoured prey, but certain features of the mussel and its shell could make some individuals more vulnerable to attack than others. The foraging strategy and hypothesized defense against each of the important Howe Sound mussel predators is outlined in this section.

The primary predators of mussels are seastars. On the British Columbia coast, *Pisaster ochraceous*, the ochre seastar, is the most abundant intertidal seastar, and is considered keystone in the sheltered rocky shores where foolish mussels predominate (Paine 1966, Menge 1976). The seastar makes settlement patches available on the substrate by foraging on mussels in dense intertidal beds. The low intertidal is impacted most by seastar predation, as this predator needs long stretches of time to digest its prey before the tide recedes. Seastars usually attack their prey by clamping over the posterior

edge of the mussel and prying the shells apart with steady force until the valves are separated enough for the seastar to extrude its cardiac stomach into the shell and digest the contents (Mauzey 1966, Mauzy et al. 1968, Norberg and Tedengren 1995). Mussels with strong adductor muscles should be less vulnerable to predation by seastars because opening them will take longer, or be impossible. Also, shells that do not close evenly might be more vulnerable to predation because small gaps in the shell allow the seastar to extrude its stomach into unopened shells. Norberg and Tedengren (1995) observed that seastars that were not initially successful at prying shells open would attempt to extrude their stomachs into the small shell opening at the byssal attachment site. Ochre seastar predation can be identified by vertical trails of bare rock and whole, intact mussel shells with splayed valves.

The importance of crabs as mussel predators is not well known on the BC coast. Shore crabs (*Hemigrapsus oregonensis*, *H. nudus*) probably consume spat and small immature mussels, but do not grow large enough to be significant predators on adult mussels. Red-rock crabs (*Cancer productus*) are the likely crab predator of larger mussels, though they prey primarily on clams. Crabs consume mussels by pulling the mussel off the substrate so that it can grasp it and crush the shell (Elner 1978). Red rock crabs use cyclic loading to crush the shells of prey (Boulding and Labarbera 1986). They then eat the flesh from the broken shell fragments, leaving behind shell fragments indicative of their activity. Mussels that are strongly attached to the substrate by byssal threads may be less vulnerable to crab predation. Thick, strong shells may also defend mussels against crab predation, as thicker shells withstand stronger crushing forces and more cycles of loading force.

Thousands of molluscivorous seaducks winter in Howe Sound and the BC coast generally. Surf scoters (*Melanitta perspicillata*) are the most abundant waterbird in Howe Sound between the months of October and March (Lacroix 2001, B. Addison unpublished data). Barrow's goldeneye (*Bucephala islandica*) are also abundant, and white-winged scoters (*M. fusca*), black scoters (*M. nigra*), and long-tailed ducks (*Clangula hyemalis*) occur regularly (Lacroix 2001, B. Addison unpublished data). Seaducks are gregarious foragers; large flocks can denude a 100 m stretch of shoreline mussel bed in less than a week (R. Kovanic pers. comm.). Seaducks pull mussels off the substrate and swallow them whole, leaving only byssal threads in a large bare patch (Lacroix 2001). Recolonization of these patches is initially by adult mussels moving into the newly available substrate and subsequently by spat. Patches take about one year to recover from seaduck predation, allowing the ducks to "farm" the same sites every winter (Lacroix 2001).

### ***The Howe Sound Rocky Intertidal Ecosystem***

Howe Sound is a deep fjord estuary with extremely high productivity and 15-25‰ salinity levels (Harding 1992), making it excellent mussel habitat. Wave exposure in the Sound is generally lower than other regions of BC, but winter inflow and outflow (called "Squamish" locally) winds do cause some variation in exposure levels throughout the Sound. The shoreline substrate is variable including basaltic bedrock substrate, granite boulders, cobble and pebble, silty mud, and sand. Bull kelp forests and eelgrass, as well as rocky and artificial reefs are all present in the subtidal region within the Sound. Species richness and species identity of the intertidal zone varies from site to site.



Mussels are present in the intertidal zone throughout the Sound, however, in the past several sites heavily impacted by heavy metal contamination from mining activities had no mussel beds (Levings and McDaniel 1976).

The mussel band lies between about 1.5 and 4.1 m above chart datum in unexposed areas, and extends to the upper extent of the intertidal zone in more exposed locations, about 5 m in height. The intertidal area below 2.8 m intertidal height is heavily depredated by seastars, though evidence of seastar predation extends to the top of the mussel band in areas where crevices provide seastars a low tide refuge. Crab predation is also evident across the entire mussel band. Seaducks remove large stretches of mussel bed over the winter in Howe Sound, resulting in unusual population dynamics for the mussels in the Sound. Recolonization of the substrate by spat is extremely fast (days to weeks) in some sites, and extremely slow (months) in others (Lacroix 2001, pers. obs.).

Barnacles and algae are also important members of the intertidal zone, and are generally found in bands above and below the mussel band, respectively. Mussels are dominant space competitors and seem to exclude barnacles from the mid-lower intertidal zone (Dayton 1971, Paine 1974). Mussel beds often cover barnacles previously settled there. Barnacles also foul mussels, an interaction that is generally bad for the mussel, and possibly the barnacle too. Fouling barnacles compete with their mussel hosts for food (Buschbaum 2001), and fouled mussels are more susceptible to crab predation (Enderlein et al. 2003), though they may be less appealing to molluscivorous ducks. The physiological intolerance of mussels to desiccation prevents them from colonizing the upper intertidal in most areas, making the space available to barnacles (Seed and Suchanek 1992, Ricketts et al. 1985). The increased predation pressure on mussels in the

lower intertidal opens up space for algal species that might otherwise be suffocated by mussels (Seed and Suchanek 1992, Paine 1974, Dayton 1971, Dayton 1975). Mussels are absent from the subtidal in Howe Sound, presumably due to predation. In areas, such as Britannia Beach, that are recovering from heavy metal contamination, mussel beds extend into the subtidal because mussels have recovered more quickly than their predators (J. Marliave pers. comm.).

### ***Objectives of the Thesis***

Past studies of morphological variation in mussels have focussed on distinguishing species of *Mytilus* (Innes and Bates 1999, Caceres-Martinez et al. 2003). In the second chapter of this thesis, I measured morphological traits of foolish mussels at several sites in Howe Sound to document the range of morphological variation at this small regional scale. If predators are important in the ecology of mussels, and mussels are able to respond to predators, small scale variation in defense traits should be observable. Moreover, trade-offs in tissue allocation should cause variation in other traits of mussels. Shell growth rate is limited by the availability and uptake of minerals in seawater, and so internal shell volume limits growth and allocation to internal tissues. For example, larger adductor muscles help defend mussels against seastars, but the larger attachment area taken up by the adductor muscle reduces the amount of internal shell volume that can be allocated to gonad tissue, and shunts resources from gonad development to adductor growth. In chapter two I test the hypothesis that defense traits of mussels are associated with the type of predation they are exposed to, and whether tissue allocation is traded-off.

Allocation to defense tissue is not important if it doesn't affect the survival of the bearer of the defense trait. In the third chapter of this thesis, I experimentally measured differential predation on two distinct morphologies of mussels by crab and seastar predators. This experimental test of defensive traits shows that allocation to defense tissues does result in higher survival, however, there is also evidence that defense traits may be traded off against one another. The results also illustrate how the selectivity of predators can influence the variability in morphology that is observed in the field. Initially, experimental mussel beds had highly heterogeneous morphology within them. After predation had taken place, the predators had removed all of the individuals that were poorly defended, leaving behind a more morphologically homogeneous mussel bed.

The fourth chapter briefly reviews density-mediated and trait-mediated indirect interactions, and places the findings of the thesis in the broader context of the rocky intertidal community. Predation and competition interactions provide for many density-mediated indirect interactions (DMIIs) such as keystone predation (Paine 1966, Menge 1976), and trophic cascades (Strong 1992). Many rocky intertidal organisms are morphologically, physiologically, and behaviourally plastic providing for many possible trait-mediated indirect interactions (TMIIIs). Further studies of the rocky intertidal community framed in the context of possible TMIIIs will contribute to understanding and models of community ecology and population dynamics.

## **CHAPTER TWO.**

# **MORPHOLOGICAL VARIATION OF FOOLISH MUSSELS (*Mytilus trossulus*) IN HOWE SOUND, BRITISH COLUMBIA**

### ***Introduction***

Variation among individuals of the same species is generated through a combination of factors. Three factors contribute to the degree of variation observed in nature: genetic variability, phenotypic plasticity, and selective survival. Genetic variability is the consequence of evolutionary processes such as genetic drift, and selective survival over long (evolutionary) periods of time. Phenotypic plasticity is the ability of an organism to alter its phenotype according to immediate (ecological timescale) environmental needs. Selective survival can occur at an ecological timescale when predators are selective, preferentially consuming one phenotype over another. Interactions between marine mussels and their predators and competitors are well documented (Chapter 1 and 4 for review), but it is not clear how morphology contributes to or alters these interactions, and vice versa. It is likely that mussels respond to their predators (ie Leonard et al. 1999), and that variation in morphology affects interactions with predators (Chapter 3). To determine the relative contributions of the local marine environment and predators on phenotype, it is necessary to examine the relationship between morphology, and environmental and predator gradients.

The nature of tides generates environmental gradients from top to bottom of the intertidal zone that are extreme and unique. Exposure to desiccation, mechanical wave force, and heat and freezing vary across the intertidal, as well as between sites. These

environmental gradients, which I will call the environmental landscape, have known effects on the morphology of mussels; mussels in areas with high mechanical wave force have stronger byssal attachments and thicker shells (Blaylock 1981, Carrington 2002, Hunt and Scheibling 2001). There are also predator gradients across the intertidal and between sites, and across time. For example, seastars are higher in abundance in the low intertidal, and gull predation is greater in the high intertidal; seaduck predation occurs only during the day in the winter. Gradients across space and time in the numbers of predators create peaks and valleys in the level of danger (*sensu* Lank and Ydenberg 2003), termed the predator landscape (Butler et al. 2003).

In Howe Sound, British Columbia, foolish mussels (*Mytilus trossulus*) dominate the intertidal zone. Howe Sound is extremely productive, generating conditions that support growth of filter-feeding bivalves year-round. The predator landscape is largely generated by three important mussel predators in the Sound: ochre seastars (*Pisaster ochraceus*), red-rock crabs (*Cancer productus*), and wintering surf scoters (*Melanitta perspicillata*). Wave exposure gradients are not as varied as on the outer coast of British Columbia, but are present due to the numerous islands, inlets, and alternating inflow and outflow winds of the Sound. Shoreline substrate is also varied throughout the Sound; mud, sand, cobble, boulder, and bedrock substrates are all present. If mussel morphology is associated with environment and predator landscapes on a local scale, there is potential for vastly different morphologies to be present in the same region. This heterogeneity may have consequences for interactions between mussels and other community members, if mussel morphology affects predation rates. If predators play an important role in the

generation of mussel morphological heterogeneity, specific trait values should be attributable to differences in the specific predator landscape.

In this chapter, I investigate the effects of predator presence on the morphology of mussels. I expect that mussel populations in sites within the Howe Sound region will have distinct phenotypes, and the characteristics of each of those populations will match those predicted by local predator landscapes. For predators that exert low but long term predation pressure, I expect observed mussel traits to defend mussels against their predators, as mussels have an opportunity to respond plastically, and the predators likely forage selectively, first consuming undefended mussels. For example, crabs handle mussel prey by pulling them off the substrate and then crushing them (Elnor 1978), and they seem to prefer mussels fouled with barnacles, probably because it allows them to get a better grip (Enderlein et al. 2003, Wahl et al. 1997). Therefore, I predict that mussels in areas with crab predators will have thick, rounder shells and strong byssal attachments and fewer fouling barnacles, compared with areas where crabs are absent. *Pisaster* seastars forage by prying apart the valves of their bivalve prey and extruding their stomach for digestion. Mussels in areas of high seastar predation will have larger adductor muscles, and thinner shells that close more tightly. Mussels do not have an opportunity to respond to the presence of seaduck predators, and these predators are likely to choose prey that are easier to handle, and so seaducks should choose mussels with weaker byssal attachments, thinner shells, and fewer fouling barnacles. There should be no relationship between predators and maintenance tissue allocation because maintenance tissue plays no role in selectivity of or defense against predators. Furthermore, it is likely that there is some minimum amount of maintenance tissue

required, and allocation to extra maintenance tissue would be at the expense of allocation to reproductive and defense tissues, and so not favoured.

## ***Methods***

### **Collection Methods**

Mussels were collected in Howe Sound, British Columbia from six sites in the lower basin of the Sound (Fig 2.1), chosen for contrasting predator and environment landscapes. Collection sites were the north side of Batchelor Cove (NB, 1 February 2003) and Copper Cove (CC, 2 February 2003) in West Vancouver, Bowen Bay (BB, 28 January 2003), Miller's Landing (ML, 29 January 2003), and Tunstall Bay (TB, 30 January 2003) located on Bowen Island, and Popham Island (PI, 15 January 2003) on the west side of the south peninsula of the island, near the Vancouver Aquarium field station. Five random samples were collected by throwing a 900 cm<sup>2</sup> quadrat behind my back in the vicinity of the mussel bed. Five mussels in each quadrat were randomly selected for testing byssal strength by throwing a coin in the quadrat. The mussel was then attached to a 2.5 kg spring scale with a battery clamp, and the force required to remove the mussel from the substrate recorded. Subsequently, all of the mussels in the quadrat were collected and frozen in ziploc bags.

### **Predator and Environmental Landscape Assessment**

During mussel collections, substrate and evidence of mussel predation was recorded at each quadrat location, as well as the slope angle and distance to the waterline, using an abney level and 30m measuring tape, for calculation of intertidal height. Each of the mussel predators has distinct foraging modes that leave tell-tale evidence of their

presence. Crabs leave broken shells, seastars leave empty but intact shells and bare, linear, vertical patches, and seaducks leave byssal threads in bare patches (pers obs., Lacroix 2001). The presence of dead or live crabs and seastars corroborated other evidence of predation. All sites were surveyed again in the spring for evidence of predation, particularly by wintering seaducks, and exposure was classified as either low or medium based on observed wind and wave action. Predator presence/absence classification was confirmed with high tide diving surveys at three of the sites (TB, ML, and NB, Appendix I for survey summaries).

### **Mussel Morphology**

I randomly drew quadrats from each collection site, and mussels from each quadrat, for morphological analyses (see Table 1 for n values). Barnacles on each shell were counted. I measured shell length (L), depth (D) and height (H), and adductor attachment diameter with vernier callipers to the nearest 0.1 mm. Gonads were scored for development on a scale of 0 to 3, and for colour (white, very light orange, light orange, or orange). Gonad, muscle, and digestive/respiratory (maintenance) tissue were dissected out of the shell and dried at about 60°C for two days and then separately weighed to the nearest 0.0001g.

### **Statistical Analysis**

Three shell shape variables were calculated as D/L, H/L and D/H. Shell volume was calculated as  $\pi/2 \times L \times D \times H$ . Since I am primarily interested in morphology, not size, of mussels, I regressed adductor diameter against shell length, and muscle, gonad,



maintenance tissue, and shell dry mass and byssal strength against shell volume, and the residuals were used in further analyses. Barnacle count was log transformed due to non-normality.

I performed logistic regressions to characterize the foraging habitat of the different predators, using substrate and exposure as predictors for each of the three predators. Where predators are strongly associated with specific habitats, it is not possible to disassociate the effect of predators from the effect of habitat in my study.

Simple logistic or linear regression was also used to test for associations between substrate and slope angle and substrate and exposure that would allow elimination of some habitat covariates in ANOVA used to determine whether there was an effect of predators on mussel morphological traits. I performed an ANOVA for each morphological trait to test if predator presence predicted morphological traits of mussels. For each ANOVA, I included each predator that was predicted to have an effect on the morphological trait (see introduction), and substrate, exposure, and littoral height (environmental) predictors. Slope angle was strongly associated with substrate type ( $\chi^2 = 148.29$ ,  $DF = 2$ ,  $P < 0.001$ ), so slope angle was eliminated as an environment predictor in the predator effect ANOVAs, as substrate can be considered an umbrella variable for slope and likely other, unmeasured, environment variables. Each quadrat was treated as an independent replicate with a unique set of predators and environment variables. I did not nest quadrat into site because my sampling scheme did not obtain enough replicates of the possible predator combinations across different sites. Seastars were only absent from one site in the Sound.

## ***Results***

### **Predator-Environment Associations**

The six sites had variable substrate types, slopes, and mussel predators (Table 2.1). Environment features are related to predators present (Table 2.2). Seaducks foraged exclusively on steep, bedrock substrates ( $\chi^2 = 33.69, P < 0.001$ ), crabs foraged exclusively on shallow sloped, cobble and boulder substrates ( $\chi^2 = 22.41, P < 0.001$ ), and seastars foraged in all environment types ( $\chi^2 = 3.56, P = 0.31$ ), and at five out of the six sites.

### **Mussel Morphology**

All the measured morphological features varied between sites, and even within sites (Table 2.3). The combinations of environment and predator characteristics of each site result in differences for which a pattern is not obvious. I could not detect an effect of predators, or measured environment variables on shell shape or thickness, or soft tissue allocation. As predicted, maintenance tissue allocation did not vary by predation. Byssal strength does appear to vary by predation (Table 2.4), as well as exposure and substrate. Byssal attachments are stronger where crabs are present (Fig. 2.2) and where ducks are present, compared to where they are absent.

## ***Discussion***

Variation, while widespread even in the relatively small geographic region of Howe Sound, cannot be attributed to any one factor or set of factors. As predicted, crab presence is associated with stronger byssal attachments, but contrary to prediction, duck

presence is also associated with stronger byssal attachment. Predators are not significant predictors of other defensive morphological features. Mussels in higher exposure areas had lower barnacle loads, but level of barnacle fouling was not related to predation by ducks or crabs. Maintenance tissue did not vary by predator or environment landscapes.

In this system, two processes are likely to generate the relationship between predators and byssal attachment strength: phenotypic plasticity and selective predation. Phenotypic plasticity, an organism's phenotypic response to its local environment, can include alterations to behavioural, physiological, morphological or life-history characteristics (Tollrian and Harvell 1999). Marine and freshwater molluscs have been studied for phenotypic plasticity, and particular attention has been paid to how the physical environment alters an individual's growth trajectory (Parsons 1997, Johnson and Black 1998, Johnson and Black 2000), or shell morphology (Boulding et al. 1999, Blaylock 1981). The biotic environment affects molluscs as well; lab experiments on gastropod and bivalve molluscs have shown that predator presence can affect behaviour (Phillips 1977, Geller 1982, Edelaar 2000, Keppel and Scrosati 2004), such as foraging or avoidance behaviour, and shell morphology (Palmer 1985, Palmer 1990, Leonard et al. 1999), such as thickness and shape. Predators can also affect observed phenotype distributions by selectively consuming prey items of a particular phenotype (Richards et al. 1999, Reed and Janzen 1999). If a trait value is initially heterogeneous in a patch, and then a predator consumes all the individuals with trait values that are easier to consume or are more profitable, the patch will become homogeneous for the trait value that is less profitable and it is this trait value that will be observed. My study does not distinguish

which of these two processes are at work, since the predicted relationships between predators and morphology are the same for both processes (but see Chapter 3).

Byssal attachment is made stronger by thickening byssal threads, producing more byssal threads, or increasing the amount or strength of byssal glue (Carrington 2002). Crabs can both induce stronger byssal attachments (Coté 1995, Leonard et al. 1999, Reimer and Tedengren 1997), and should select out mussels with weaker attachments while foraging. The stronger byssal attachments observed where crabs are present could be due to these processes, as well as the influence of physical environmental variables that are autocorrelated with the presence of crabs, such as substrate type, slope angle, and possibly food availability and competition with conspecifics. It is puzzling that seaducks would choose to feed where byssal attachment is relatively strong, however this could also be due to autocorrelation with substrate type and exposure. Alternatively, the relative strength of byssal attachments in areas where ducks forage could be due to the ducks removing mussels with weaker byssal attachments, increasing the mean attachment strength measured. It is further possible that mussels detect that they are likely to be depredated by seaducks, and increase byssal attachment strength, but there is no obvious mechanism by which this could occur.

As expected, maintenance tissue, relative to mussel volume, varied little across the Sound. This is because interior shell space is limited, and we expect mussels to allocate as much space as possible to reproductive and defensive tissue, but be constrained to a required minimum amount of maintenance tissue. Food conditions in Howe Sound could support growth year-round (Harding 1992), so seasonal energy storage or gut atrophy is unlikely to be necessary. There was no detectable effect of

habitat or predators on shell thickness, shell shape, or muscle tissue. The absence of effect of seastars on any of these traits might be due to the prevalence of this predator across the entire range of *M. trossulus*. Of the sites I studied in Howe Sound, only one small area was absent of *Pisaster* seastars (Batchelor Cove). The prevalence of seastars might result in undefended mussels being removed quickly, so that they are not observed in the population. Alternatively, if seastars are rarely absent, and maintaining plasticity of seastar defense traits is costly, mussels should always defend against seastars. Furthermore, there may be trade-offs between seastar defense and physical environmental requirements, and reproduction, such as need to allocate resources to fast reproduction (see below).

Few studies have attempted to quantify variation in soft tissue allocation of mussels across environmental gradients (but see Innes and Bates 1999), even though there is almost certainly phenotypic flexibility in these traits. I detected no effect of predators on shell thickness or shape, or adductor size, but these traits have previously been shown to be flexible in the presence of predators (Leonard et al. 1999, Smith and Jennings 2000, Reimer and Harms-Ringdahl 2001, Reimer and Tedengren 1996), and individual mussels should also be able to manipulate their barnacle load by altering shell cleaning behaviour (Theisen 1972). My study may have had insufficient power because of sample sizes to detect a significant relationship between predators and morphology.

The characterization of phenotypic variation in marine mussels on regional scales has focussed on shell morphology. California mussels (*Mytilus californianus*) have both ribbed and unribbed morphs (Caceres-Martinez et al. 2003), as well as shell shape varying across exposure gradients (Blaylock 1981). Blue mussels (*Mytilus edulis*) are

also reported to have varying shell shape (Seed 1968) and byssal attachments (Carrington 2002) across exposure gradients. Despite the fact that I could not attribute morphological variation in many traits to specific environmental, or predator causes, variation is evident. In a landscape of selective predators, this variation is certain to have consequences for prey survival, as well as predator preferences (Chapter 3) and distribution. Other traits, such as habitat selection, and timing of reproduction might also be important ways for mussels to mitigate danger and ensure reproduction. Mussels may fill safer environments first, and then settle in the more dangerous areas of the Sound. The intensity of seaduck predation over the winter may favour earlier reproduction in mussels in the Sound. I observed that sometimes even very small mussels were in advanced stages of gonad development. While such traits are not site specific, they are possible ways for mussels within the region of Howe Sound to respond to predation danger.

Future field investigations of mussel response to predators should take an experimental approach. Paired predator exclosures on sites of contrasting substrate and exposure would enable a more powerful investigation of predator effects, and interactions between predators and environment, where trade-offs might complicate the predicted morphological outcomes. This would also make it possible to distinguish between phenotypic plasticity and selective predation effects on variation in morphology.

Figure 2.1: Howe Sound, British Columbia. Collection sites were north end of Batchelor Cove (NB), Copper Cove (CC), Millers Landing (ML), Tunstall Bay (TB), Bowen Bay (BB), and Popham Island (PI), and are indicated with dots.

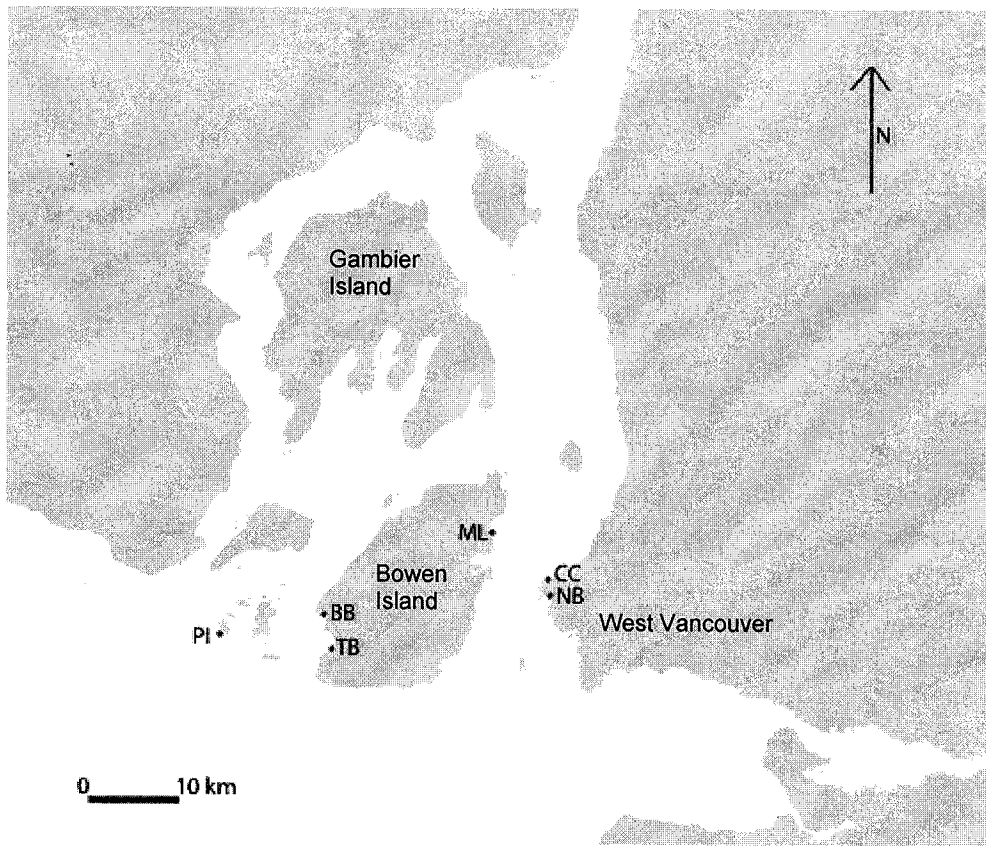


Table 2.1: Summary of mussel collections and site characteristics. Substrate types were classified as bedrock (br), boulders (bo), or cobble (co).

Site	Collection Date	Quadrat #	Intertidal Height (m)	Mussels Dissected	Slope Angle (°)	Substrate	Predation Type
PI	15-Jan	1	4.47	15	31	br	Seaduck, Seastar
		2	4.45		25	br	Seaduck, Seastar
		3	5.32	15	25	br	Seaduck, Seastar
		4	5.72		25	br	Seaduck, Seastar
		5	4.85	5	14	br	Seaduck, Seastar
BB	28-Jan	1	4.93	5	29	br	Seaduck, Seastar
		2	4.99	5	29	br	Seaduck, Seastar
		3	4.48		34	br	Seaduck, Seastar
		4	4.61		34	br	Seaduck, Seastar
		5	5.06	5	45	br	Seaduck, Seastar
ML	29-Jan	1	5.49	5	20	br	Seastar
		2	4.33	5	13	co	Seastar, Crab
		3	4.00		13	co	Seastar, Crab
		4	4.84		13	co	Seastar, Crab
		5	4.66	5	13	co	Seastar, Crab
TB	30-Jan	1	4.09	5	13	co	Seastar
		2	4.04	5	13	bo	Seastar
		3	5.01		13	bo	Seastar
		4	5.54	5	13	bo	Seastar
		5	5.91		13	bo	Seastar
NB	1-Feb	1	3.59	5	21	br	Seaduck
		2	3.18	5	12	bo	Crab
		3	3.41	5	12	bo	Crab
		4	3.79	5	15	bo	Crab
		5	4.07		15	co	Crab
CC	2-Feb	1	3.17	5	10	co	Crab, Seastar
		2	3.37		10	bo	Crab, Seastar
		3	3.56		10	bo	Crab, Seastar
		4	4.07	5	10	co	Crab, Seastar
		5	3.79	5	10	co	Crab, Seastar



Table 2.2: Ordinal logistic regression and likelihood ratio tests of effects of substrate and exposure on presence of seaduck, seastar and crab predators. Seaduck and crab presence is strongly associated with the substrate type of the habitat.

	Full Model		Substrate		Exposure	
	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>
Seaduck	33.69	<0.001	21.81	<0.001	1.14	0.29
Seastar	3.56	0.31	1.54	0.46	1.14	0.29
Crab	22.41	<0.001	15.97	<0.001	0	1.0

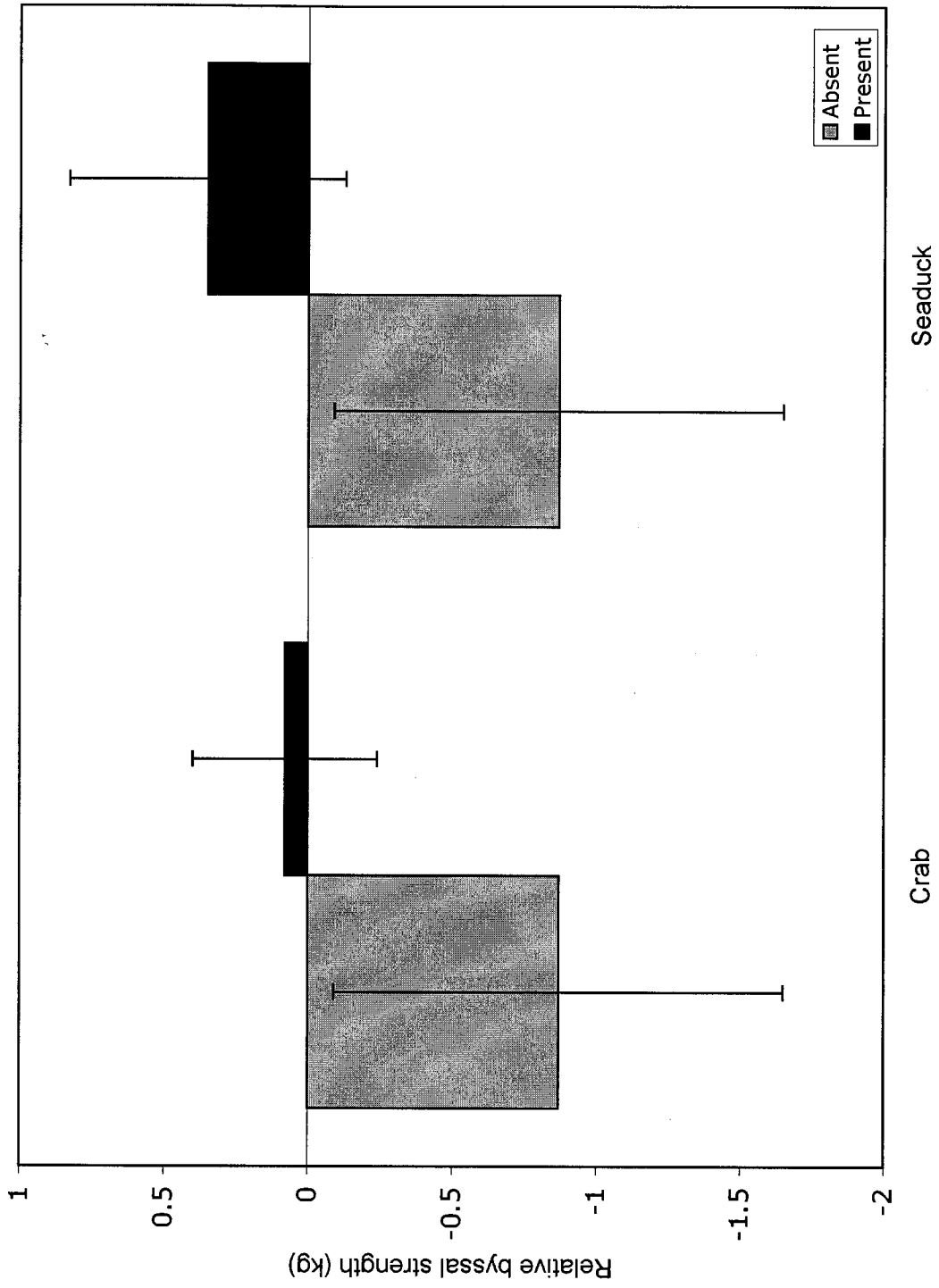
Table 2.3: Mean residual values of byssal strength, shell thickness, muscle tissue, adductor diameter, maintenance tissue, and gonad tissue, and shell shape ratios for each site x quadrat combination. Values with 95% CI that overlap zero, or the grand mean are grey, those which are less than the grand mean are in black, greater than the grand mean are in white. Habitat (co=cobble, br=bedrock, bo=boulder) and predator (0=absent, 1=present) characteristics are listed below.

	NB1	NB2	NB3	NB4	CC1	CC4	CC5	ML5	ML2	ML1	TB1	TB2	TB4	BB1	BB2	BB5	PI1	PI3	PI5
Byssal	0.4029	0.2450	-0.3308	0.6360	-0.4210	-0.1247	-0.0456	-0.4155	-0.4659	-0.4316	0.4228	0.3865	0.1158	-0.1265	-0.3574	-0.3777	0.3186	0.4545	0.0877
Shell	-0.2417	-0.0241	-0.0131	-0.1831	0.0893	-0.1784	-0.1077	0.3670	0.0372	-0.0139	0.2737	0.2311	-0.1648	-0.1497	-0.2009	0.0836	-0.0638	0.0703	0.1758
A. Diameter	0.1467	0.2868	-0.4874	-0.3233	-0.1514	-0.3385	-0.6363	0.6534	-0.5938	0.0285	-0.0747	0.1284	0.0670	0.4192	0.0401	-0.3986	0.0815	0.1992	0.3916
Muscle	0.0091	-0.0053	-0.0043	0.0023	0.0035	-0.0140	-0.0053	-0.0033	-0.0099	-0.0072	0.0115	0.0000	-0.0020	0.0057	-0.0124	0.0035	0.0014	0.0043	0.0110
Maintenance	0.0081	-0.0123	-0.0022	-0.0024	0.0064	-0.0107	-0.0096	-0.0052	0.0267	-0.0036	-0.0165	0.0032	0.0033	0.0082	-0.0040	0.0059	-0.0046	-0.0018	0.0238
Gonads	-0.0034	-0.0099	-0.0056	-0.0023	0.0004	-0.0114	-0.0118	-0.0055	0.0150	-0.0060	0.0140	-0.0011	-0.0091	0.0010	-0.0111	0.0003	0.0033	0.0128	-0.0020
D:L	0.40	0.41	0.41	0.42	0.41	0.40	0.40	0.41	0.42	0.47	0.45	0.40	0.41	0.41	0.42	0.44	0.40	0.42	0.42
H:L	0.49	0.48	0.45	0.49	0.50	0.49	0.47	0.46	0.47	0.55	0.49	0.47	0.51	0.52	0.47	0.52	0.49	0.51	0.48
D:H	0.80	0.87	0.90	0.86	0.81	0.83	0.84	0.91	0.89	0.85	0.91	0.86	0.81	0.80	0.89	0.84	0.81	0.82	0.88
Barnacles	1.2	2.6	0.0	0.8	0.0	2.2	1.2	0.2	0.4	1.2	0.2	0.2	0.0	5.6	12.0	0.2	0.1	0.1	0.0
Slope Angle	21	12	12	15	10	10	10	13	13	20	13	13	13	29	29	45	31	25	14
Littoral Height	3.17	3.37	3.56	4.07	3.59	3.79	4.07	4.66	4.33	5.49	4.09	4.04	5.54	4.93	4.99	5.06	4.47	5.32	4.85
Substrate	br	bo	bo	bo	co	co	co	co	co	br	co	bo	bo	br	br	br	br	br	br
duck	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
seastar	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
crab	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0

Table 2.4: Results of ANOVAs testing the importance of substrate, exposure, littoral height and the presence of predators in predicting morphological characteristics of mussels. Dashes indicate that the predictor was not included in the model because there was not a specific prediction with regards to the presence of the predator for the morphological trait. *P*-values larger than 0.05 are denoted as non-significant. Only byssal strength varies among predator regimes.

	Barnacles		Byssal strength		Shell thickness	D:H ratio	Adductor Diameter	Adductor mass	Maintenance tissue	Gonad tissue
	F	P	F	P						
Substrate	NS		12.1	<0.001	NS	NS	NS	NS	NS	NS
Exposure	6.79	0.01	7.3	0.008	NS	NS	NS	NS	NS	NS
Littoral Ht	NS		NS		NS	NS	NS	NS	NS	NS
Crab	NS		6.3	0.01	NS	NS	-	-	NS	NS
Seastar	-		-		NS	-	NS	NS	NS	NS
Seaduck	NS		6	0.02	NS	NS	-	-	NS	NS

Figure 2.2: Byssal attachment strength is stronger in areas of crab or seaduck predation relative to areas without.



## **CHAPTER THREE.**

# **PICKY EATERS: DO MORPHOLOGICAL TRAITS OF MUSSELS DEFEND THEM AGAINST THEIR PREDATORS?**

### ***Introduction***

Optimal foraging theory posits that prey items are incorporated into the diet such that net energy intake is maximized over time (Stephens and Krebs 1986). The profitability of a prey item will depend on several factors including its energy content, and search and handling times. Prey populations can respond to the selectivity of predators by altering behaviour and morphology, making them less profitable prey items by increasing time required for search or handling (ie West et al. 1991). The resulting arms race is likely to be unbalanced, because prey are under greater selection pressure to escape death than predators are to catch a meal (the life-dinner hypothesis, Abrams 2000).

Marine mussels and their predators have been the focus of classical studies of rocky intertidal community ecology (Paine 1966, Menge 1976), and variation and plasticity of morphology in response to environment (Blaylock 1981, Carrington 2002) and crab, whelk and seastar predators (Coté 1995, Reimer and Tedengren 1996, Reimer and Tedengren 1997, Leonard et al. 1999, Reimer 1999, Smith and Jennings 2000, Reimer and Harms-Ringdahl 2001, Cheung et al. 2004). Little research has attempted to measure how mussel trait variation affects foraging choices by their predators (but see Norberg and Tedengren 1995, Cheung et al. 2004).

Shore crabs (*Carcinus spp.*) show preference for certain characteristics, or species, of bivalves when presented with a choice (Mistri 2004, Palacios and Ferraro 2003, Enderlein et al. 2003, Mascaro and Seed 2001, Mascaro and Seed 2000, Richards et al. 1999, Nakaoka 1996). Crabs abandon excavation (Smith et al. 1999, *Cancer productus*) or crushing attempts (Mascaro and Seed 2000, *Carcinus maenus*) of difficult prey items resulting in survival of those prey individuals possessing “difficult” traits. *Asterias rubens* seastars kill more mussels with smaller adductors and are more likely to give up attack on mussels with larger adductors (Norberg and Tedengren 1995). Bird predators on molluscs also show preference for easy prey items (Oystercatchers: Meire and Ervynck 1986, Crows: Zach 1979).

Bivalves show a high degree of within species morphological diversity over relatively small geographic distances (Kautsky et al. 1990, Caceres-Martinez et al. 2003, Chapter 2). It is likely that mussel morphology is important to ease of handling by predators. Variation in profitability of individual prey items should result in differential predation within bivalve species and within prey patches.

In Howe Sound, British Columbia, four important predators on mussels (*Mytilus trossulus*) are the ochre seastar (*Pisaster ochraceous*), red rock crab (*Cancer productus*), whelk (*Nucella spp.*), and surf scoter (*Melanitta perspiculata*). Each has a different foraging mode for which a different suite of prey characteristics would make the prey individuals difficult to consume. In this chapter, I will focus on shell characteristics that I hypothesize make a mussel easy or difficult for crab and seastar predators to consume. Crabs pull prey from the substrate and then crush shells to expose the flesh (Elner 1978). Therefore, crabs should select prey items they can grasp and crack with their chelae, and

that are easy to remove from the substrate. *Pisaster* seastars forage by forcing mussel shells open and extruding their stomachs for external digestion (Mauzey 1966). They are likely to have an easier time opening mussels with smaller adductor muscles or with uneven shell margins because small gaps will allow them to begin digesting the mussel without fully opening the shell (Norberg and Tedengren 1995).

To test whether morphological traits defend mussels against predators with different foraging modes, I experimentally offered mussels of two distinct morphotypes to red rock crab and ochre seastar predators and measured relative survival of the two morphotypes. I predicted that crabs would preferentially feed on thin-shelled and smaller mussels relative to individual chelae size, and seastars would preferentially feed on shells with uneven shell margins.

## ***Methods***

Howe Sound, British Columbia, is a deep fjord estuary (49°20' N, 123°21' W) with rocky and mixed sand/rock shoreline that is nearly continuously lined with intertidal mussel beds (Harding 1992). Mussels were collected from source locations chosen for very distinct morphologies. One morphotype was from a fouling community created by hanging settlement tiles off of a dock at Popham Island (PI, 49°21.48' N, 123°29.07' W) for 5 months before the experiment, and another morphotype from an intertidal collection site at the north end of Batchelor Cove (NB, 49°22.17' N, 123°17.50' W) on the east side of the Sound one week prior to the experiment. PI has an exposed rocky shore characterized by dense mussel beds and many *Pisaster* seastars. NB is a relatively sheltered site with a mixture of bedrock and boulder/cobble/sand substrate. Crab

predation occurred in the intertidal zone but *Pisaster* densities at this site are extremely low. A small sample from each source location was bagged and frozen for later morphological measurement, and live mussels were housed in aerated tanks with seawater, and fed a diet of powdered *Spirulina pacifica* (approximately 2% of estimated dry mass per day) until the beginning of the experiment.

### **Mussel Morphology**

Frozen mussels (n=30 per morphotype) were thawed and the length, height and depth of the shell (described by Smith and Jennings 2000) and adductor diameter along the anterior-posterior axis were measured to the nearest 0.1 mm. Wet and dry mass were taken for shell, adductor, digestive and respiratory tissue, and gonads to the nearest 0.001 g. An index of shell thickness was calculated as dry mass (shell)/L×H×D; scores calculated this way were highly correlated to scores calculated as in Frandsen and Dolmer 2002 ( $R = 0.9$   $p < 0.0001$ ). Relative adductor size was calculated as adductor diameter/L (Frandsen and Dolmer 2002). I measured shell margin evenness by inking the edges of the valves (n=10 shells per morphotype) and stamping them onto paper on a flat surface. A discontinuity in the valve edge stamp indicated a spot where the shell didn't close firmly together. Five sections of the valve margin stamps, umbo, hinge, ventral, dorsal and posterior, were given a score of 1 for continuous or 0 for discontinuous. The score for each valve was added up, and the two valve scores were averaged; this number was considered an index of evenness of the shell margin, with lower scores being relatively uneven and higher scores being relatively even.



## Predation Experiment

I collected 6 male red rock crabs (*C. productus*) subtidally by SCUBA near the study area and purchased 6 others from a scientific supply (Seacology, West Vancouver BC). Crabs ranged in size from 90 to 160 mm carapace (mean = 123mm). Twelve ochre seastars were collected intertidally from Horseshoe Bay in Howe Sound (49°22.71' N, 123°16.39' W) during low tide. All animals were housed in aerated seawater tanks prior to the experiment. Crabs were fed mussels *ad libitum* for three days in the week prior to the experiment in order to estimate how many mussels they would likely eat over the course of the experiment. Each crab ate 6-12 mussels per day during this period. Therefore, I estimated that a crab ate 42- 84 mussels in a week, and that starting the experiment with 400 mussels would ensure some mussels remained to measure at the end of the experiment.

I randomly drew 200 PI fouling and 200 NB intertidal mussels from the holding tanks and assigned them to one of 36 ceramic tiles in compartmentalized tanks, such that each of the 36 tiles had 400 mussels on it. After two days for attachment by mussels, I randomly assigned tiles to control, crab, or seastar treatments. Each treatment was represented within each of 12 compartmentalized cages. The location of control, crab, and seastar treatments was randomized within each cage. Each crab was measured (carapace width in mm) at the start of the experiment and each crab and seastar was put in the appropriate treatment compartment in each of the cages. Cages (Figure 3.1a) were approximately 1m by 0.2m by 0.2m with three compartments, and were made of hardware cloth stapled to a wood frame.

Experimental cages were hung from a mid-water line, anchored at either end with cinder blocks and floated with five floats along the line (Figure 3.1b) in a bay sheltered

by a jetty at Popham Island. This procedure ensured that the cages would not be disturbed by other predators on the sea bottom, and allowed free flow of water and food to the mussels. After one week of treatment the cages were retrieved and the remaining mussels in each cage compartment were collected. In the lab the remaining mussels in each group were counted. The two groups were easily distinguishable because the PI fouling community mussels had no tidal rings, and thus were smooth shelled compared to the NB intertidal mussels. A sample ( $n=15$ , if less than 15 were left, all were measured) of each group and cage treatment replicate were measured (length only) to determine the size distribution of the surviving mussels.

### **Statistical Analysis**

All data were checked to ensure that the assumptions of parametric analysis were met. Morphology data, comparing morphological features of PI fouling mussels with NB intertidal mussels, were analysed using a student-t test. The alpha level considered significant was adjusted to 0.01 because I was making multiple comparisons. Counts of surviving mussels and mean mussel length were analysed using a split-plot ANOVA, because mussels from both morphotypes were in each treatment replicate, using predator treatment (control, crab or seastar), mussel morphotype (PI or NB), and their interaction (treatment $\times$ morphotype) as predictors, and cage and cage $\times$ treatment interaction as random effect factors. I lost one crab and one seastar treatment due to mortality and so used Satterthwaite degrees of freedom in the calculation of least square means to analyse the unbalanced design. Post-hoc Tukey-Kramer test was done on significant results. Log ratio PI:NB mussels remaining was regressed against crab carapace width to determine if

crab size influenced prey selection. All analyses were done in JMP IN 5.1 statistical package (SAS 2003).

## ***Results***

### **Mussel Morphology**

Several features of mussels from the different morphotypes were significantly different at the outset of the experiment (Table 3.1). NB intertidal mussels had significantly thicker shells than PI fouling mussels, whereas PI mussels had significantly higher shell margin evenness scores than NB mussels (Fig 3.2). Most measures of adductor size were not different, but NB intertidal mussels had larger diameter adductor attachments and marginally significant higher proportion adductor mass of flesh dry mass than PI fouling mussels (Fig 3.3).

### **Predation Experiment**

There was an interaction between treatment and morphotype for number of surviving mussels (Table 3.2). In the seastar treatment, the number of surviving PI fouling mussels was significantly higher than NB intertidal mussels (Tukey-Kramer,  $P=0.01$ , Fig 3.4) suggesting that seastars were preferentially feeding on NB mussels. However, there were more surviving NB intertidal mussels than PI fouling mussels in the crab treatment, though this difference is not significant.

I detected an interaction between treatment and morphotype in size distribution of surviving mussels (Table 3.2), however this difference was a result of different initial size distributions (about 3 mm difference in mean length), which disappeared after predator

treatment. This result was strongest in the seastar treatment, and suggests that predators may have been preferentially consuming large NB intertidal mussels. It is possible that larger predators were consuming larger, more profitable mussels if it was easier for them to do so. However, there was no difference in mean length of mussels from the same source location exposed to different predator treatments (Tukey-Kramer test, Fig 3.5) suggesting that the interaction detected has no biological significance; predators overall did not have a preferred size range of prey, nor did preferred size range depend on other morphological features.

Crab size is positively related to the relative proportion of NB intertidal mussels consumed ( $r^2=0.88$ , slope=0.05 ( $\pm 0.014$ ),  $P=0.0001$ , Fig 3.6). Smaller crabs consumed more PI fouling than NB intertidal mussels while larger crabs consumed more NB mussels. Because NB mussels were initially larger, this corroborates the result for the size distribution of surviving mussels. The crabs that were large enough to get into NB mussels might have picked the larger ones with higher payoff.

## ***Discussion***

I hypothesized that different trait values of morphological features would result in differential predation of individuals of the same species, within a patch. Shell morphology of *M. trossulus* varies greatly between sites in the same estuary. I found that small crabs preferentially feed on thin-shelled mussels, as predicted, and this preference appears to be dependent on the size of the crab, smaller crabs are more selective for shell morphology. Seastars preferentially feed on mussels with uneven shell margins. These

results support my hypothesis that crabs and seastars select prey individuals that are more profitable due to morphological characteristics.

### **Mussel Morphology**

The two morphotypes of mussels used in this experiment differed in several important features. PI fouling mussels could be crushed by hand whereas NB intertidal mussels had much harder shells. These differences could have resulted from mussels responding to predator chemical cues at NB (as there were no predators present on the PI fouling community), or from tidal differences. Thin shells are frequently observed in the aquaculture industry, where farmed shellfish have to have their shells “hardened” on the beach before shipping. My study concurs with several others that showed that shell thickness plasticity is likely an adaptation to environmental and predator exposure (Blaylock 1981, Reimer and Tedengren 1996, Smith and Jennings 2000). Lab studies of bivalves and molluscs have shown that many species lay thicker shells, as well as adjusting other behavioural or morphological characteristics, in the presence of chemical predator cues (Coté 1995, Reimer and Tedengren 1996, Reimer and Tedengren 1997, Leonard et al. 1999, Reimer 1999, Smith and Jennings 2000, Edelaar 2000, Reimer and Harms-Ringdahl 2001, Frandsen and Dolmer 2002, Cheung et al. 2004).

This is the first study to measure shell margin evenness. NB intertidal mussels, those with thicker shells, had uneven shell margins relative to PI fouling mussels. The unevenness of thicker shells may arise from uneven laying of calcareous matrix on the inside of the shell, suggesting a possible trade-off between evenness and thickness. Gaps

in the shell margin would make mussels vulnerable to seastar predation, as my data suggest, and also to desiccation.

Adductor diameter, relative to shell length, was larger in NB intertidal mussels than PI fouling mussels. The adductor proportion of flesh dry mass was also larger in NB intertidal mussels, but this may reflect that the larger diameter left less room inside the shell for reproductive tissue, rather than a real difference in adductor tissue (Table 3.1). All other measures of adductor size were not significant suggesting that this trait may not be very plastic, and might be constrained by internal shell volume, and internal space use trade-offs. Furthermore, seastar predation is prevalent on mussels in all habitats and so if plasticity is costly, selection may be for larger, less plastic adductor size, so mussels are always defended against seastars.

### **Predation Experiment**

Despite larger adductor muscle diameter, NB intertidal mussels were actually the preferred prey items of seastars. I suggest that this was due to unevenness of the NB intertidal shells, making them more vulnerable to seastar predation. Crabs did not appear overall to prefer any one prey morphotype. Prey preferences are likely to be obscured by the relationship between crab body size and prey preference. Large crabs preferentially fed on NB intertidal mussels, small crabs preferentially fed on PI fouling mussels. Prey preferences were probably related to individual strength, or risk of claw damage (Juanes and Hartwick 1990, Smallegange and Van der Meer 2003), as maximum chelae height was larger than the minimum mussel shell dimension for all crabs. Large crabs could be

preferentially preying on larger mussels because they are more profitable for crabs large enough to crush them without damaging claws (Seed and Hughes 1995).

If shell thickness is obtained at the expense of shell evenness, mussels must trade-off defense from crab and seastar predation. Mussels settle on all types of substrate in Howe Sound, but bedrock substrate, which makes good seastar habitat, makes very poor crab habitat. A combination of induced defenses and differential predation could contribute to the mosaic of morphological phenotypes observed in Howe Sound mussel populations (Chapter 2).

Prey species preferences of *Carcinus spp* have been well documented (Mascaro and Seed 2001, Palacios and Ferraro 2003, Mistri 2004), but little research has been done on prey preferences in *Cancer spp*, or differential predation with regard to within prey species morphological variation. While it has been documented that seastars may be limited by relative size when selecting bivalve prey (McClintock and Robnett 1986, Norberg and Tedengren 1995, Arsenault and Himmelman 1996, Sommer et al. 1999), little other research has revealed morphological features that deterred seastar predation. Shell thickness, which has been suggested as a possible defense against seastar predation (Norberg and Tedengren 1995), was not a strong deterrent in this study. If uneven shell margins provide an opportunity for seastars to begin digestion without fully opening the shells, and shell thickness is traded off against evenness, thick shells may actually be a disadvantage.

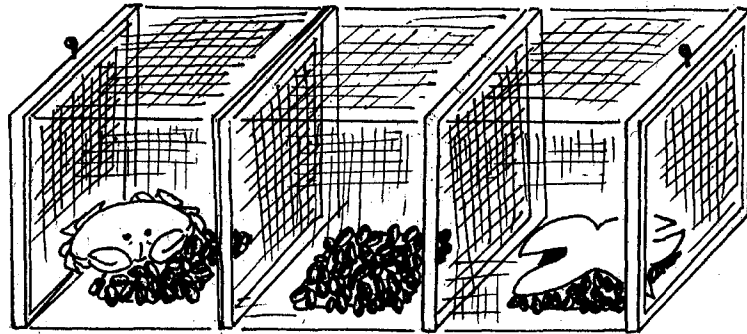
Variation in intra-specific shell characteristics appears to produce differential predation by predators. Shell characteristics have been shown to be highly heritable

(Toro et al. 2004), and this coupled with genetic structuring of populations produced by oceanographic features (Gilg and Hilbish 2003) generates the potential for local adaptation in some locations.

In this study the two morphotypes of mussels were presented to predators simultaneously so that predators had to test prey items before choosing whether to continue the attack and consumption. The mechanism by which crabs do this is known (Elner 1978) but for seastars it is not well understood (Norberg and Tedengren 1995). In field situations, this testing mechanism may not be as important since phenotypes of mussels tend to be clumped in space. Morphological variation between patches can be high, but within patches it is relatively low (Chapter 2), consequently, a predator would need to test only one or a few prey items to gain information about the entire patch, i.e. prey selection is done on the scale of patch selection (Micheli 1997, Gaymer et al. 2001). Patch choice of crab and seastar predators foraging on mussel patches of different phenotype mussels would be an appropriate future study that would allow us to scale up to trait-mediated community effects, allowing us to understand how morphological defenses of mussels have consequences for mussel population dynamics and other mussel predators.



a



b

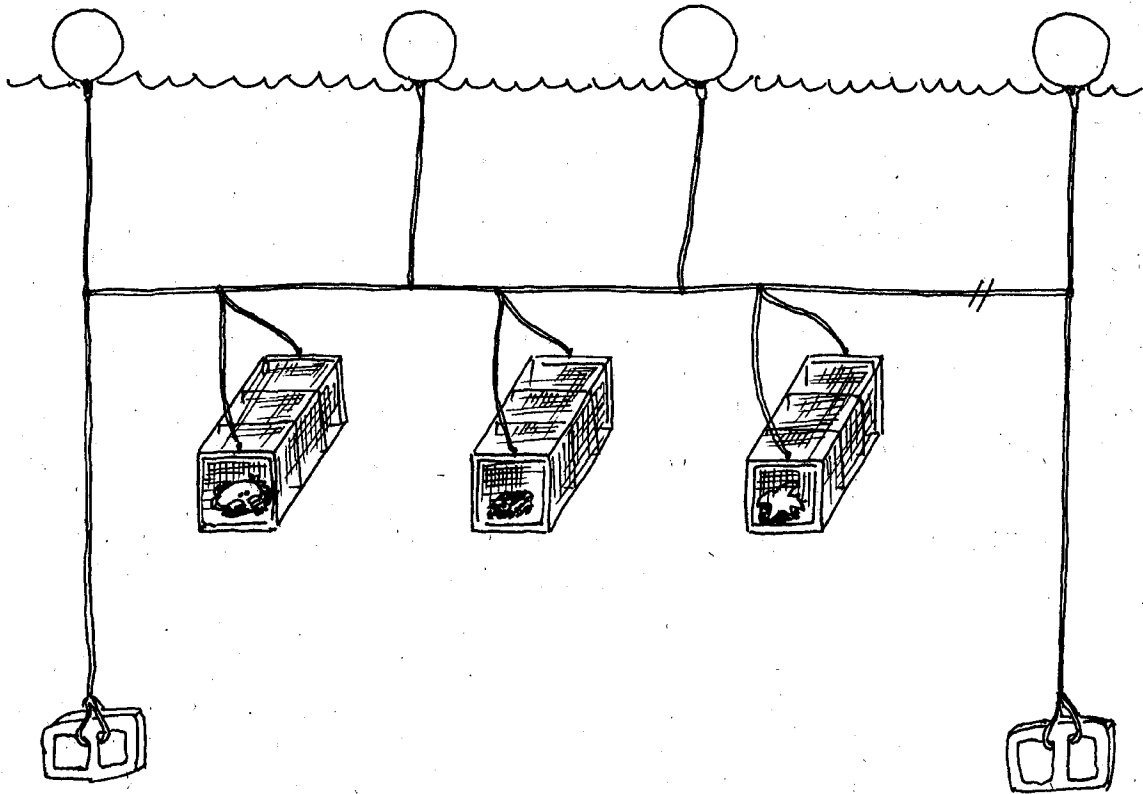


Figure 3.1: Cage setup (a) and field setup (b). Each of 12 cages had crab, seastar, and control predator treatments. The cages were hung from a midwater line to prevent disturbance by other predators and surf.

Table 3.1: Morphological features measured in mussels collected at Popham Island (fouling) and Batchelor Cove (intertidal), British Columbia in October 2003.

Measure	Units	Mean ( $\pm$ 95% CI)		P-value
		Batchelor Cove	Popham Island	
Shell thickness index	g/mm <sup>3</sup>	1.98 (0.07)	1.31 (0.07)	<0.0001
Shell evenness score		1.45 (0.38)	3.20 (0.38)	<0.0001
Adductor dry mass per shell volume	g/mm <sup>3</sup>	$3.5 \times 10^{-6}$ ( $4.4 \times 10^{-7}$ )	$3.6 \times 10^{-6}$ ( $4.4 \times 10^{-7}$ )	0.80
Adductor dry mass per shell length	g/mm	$4.23 \times 10^{-4}$ ( $6 \times 10^{-5}$ )	$3.71 \times 10^{-4}$ ( $6 \times 10^{-5}$ )	0.28
Adductor diameter per shell length		0.16 (0.004)	0.12 (0.004)	<0.0001
Proportion adductor of flesh dry mass		0.32 (0.02)	0.28 (0.02)	0.03
Proportion digestive/respiratory tissue of flesh dry mass		0.61 (0.03)	0.61 (0.03)	0.86
Proportion gonad tissue of flesh dry mass		0.07 (0.02)	0.10 (0.02)	0.06

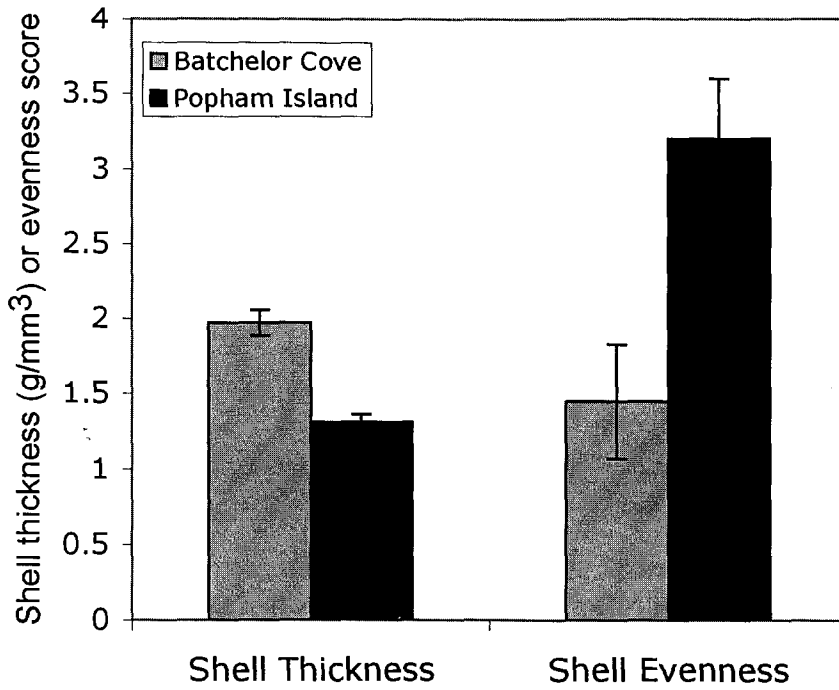


Figure 3.2: Shell thickness (n=30 per location) and shell evenness (n=10) indices of Batchelor Cove intertidal and Popham Island fouling community mussels. Batchelor Cove mussels were thicker and less tightly closing compared to Popham Island mussels.

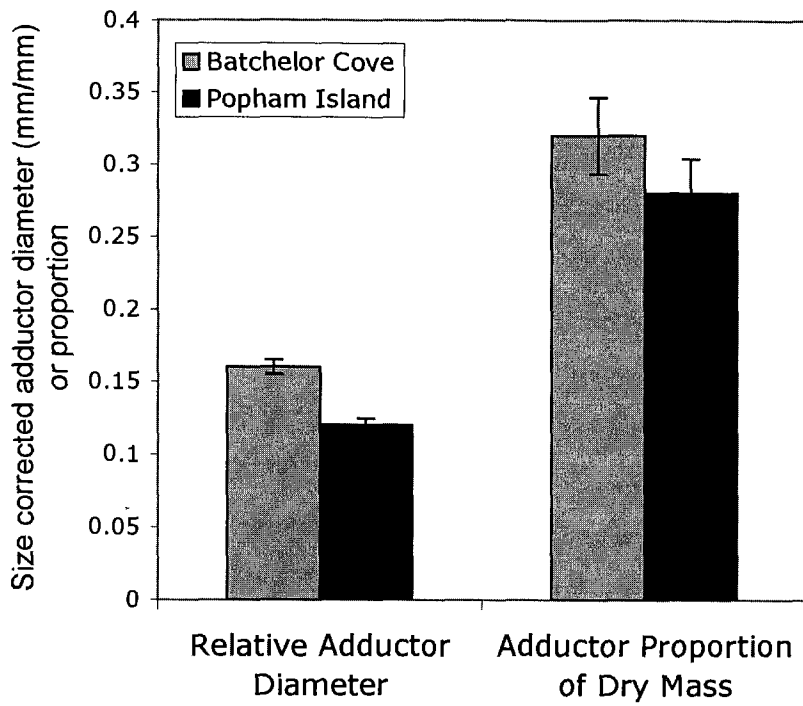


Figure 3.3: Adductor size measures of Batchelor Cove intertidal (n=30) and Popham Island fouling (n=30) community mussels. Batchelor Cove mussels; adductors were larger in diameter and proportional dry mass than Popham Island mussels'.

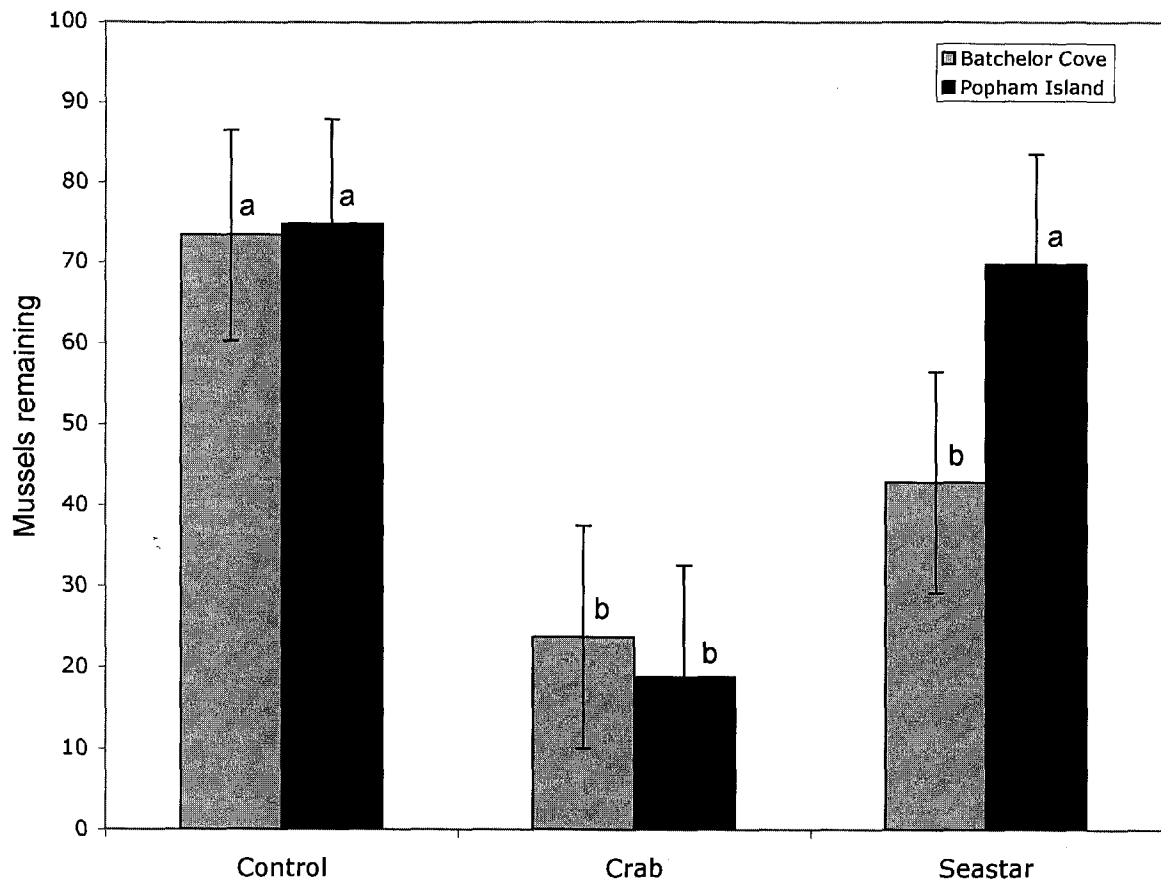


Figure 3.4: Mean (and 95% confidence intervals) count of the number of mussels remaining from each of the two morphotypes for each predator treatment. Letters connect means not significantly different (Tukey-Kramer,  $\alpha=0.05$ ).

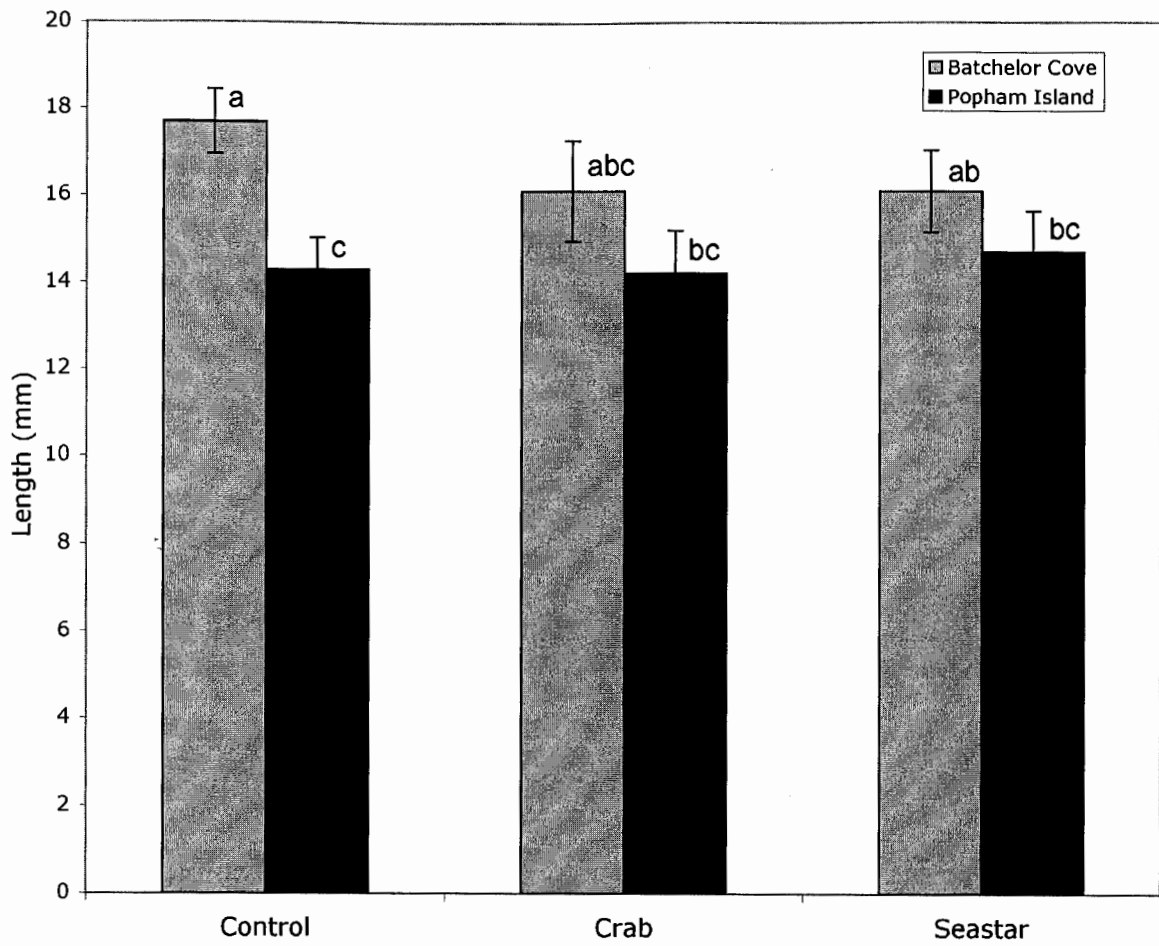


Figure 3.5: The mean (and 95% confidence intervals) size of mussels remaining for each morphotype after predator treatments. Letters connect means not significantly different (Tukey-Kramer  $\alpha=0.05$ ).

Table 3.2: F-table for fixed effects of split-plot ANOVA.

Test	Effect	Numerator Denominator		F-ratio	P-value
		DF	DF		
Mussels remaining	Predator Treatment	2	31	23.02	<0.0001
	Morphotype	1	31	3.34	0.08
	Treatment×Morphotype	2	31	5.07	0.01
Length (mm)	Predator Treatment	2	435	2.22	0.11
	Morphotype	1	1131	35.11	<0.0001
	Treatment×Morphotype	2	1131	3.41	0.03

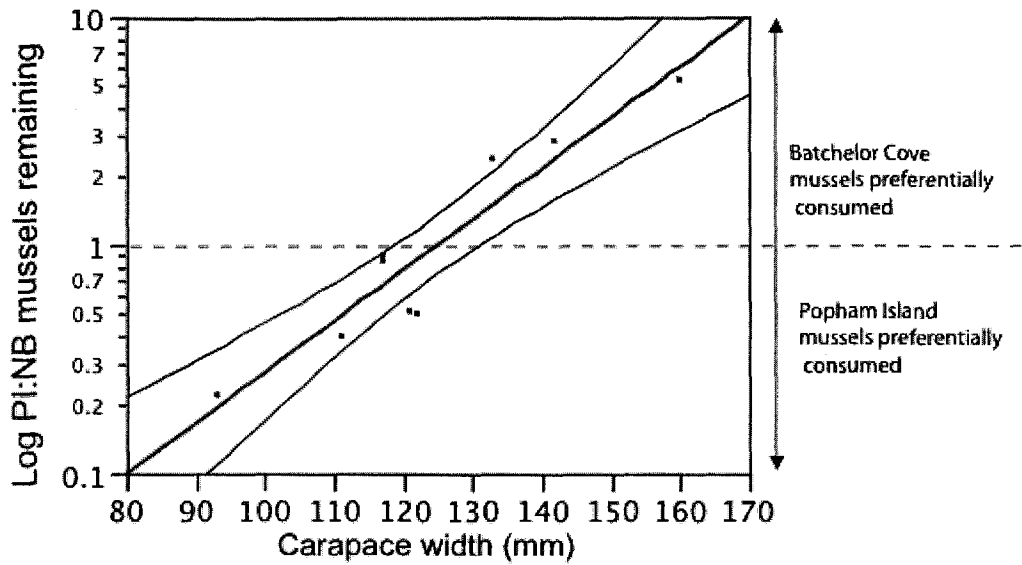


Figure 3.6: The relationship between crab carapace width and proportion Popham Island mussels remaining is described by the line  $\text{Log}(\text{PI}:\text{NB}) = -6.41 + 0.05 \text{ carapace width}$ . Larger crabs ate more Batchelor Cove mussels, leaving a greater proportion of Popham Island mussels.



## **CHAPTER FOUR. THE KEYSTONE CONCEPT AND TRAIT-MEDIATED INDIRECT INTERACTIONS: A NEW VIEW OF THE ROCKY INTERTIDAL COMMUNITY**

Ecology has been primarily concerned with describing the processes that control the numbers of individuals and species in an ecosystem. The dynamics of predator and prey species have been the focus of research that attempts to explain prey numbers with predator numbers and vice versa. Indirect interactions such as keystone predation (Paine 1966, 1969), diffuse predation (i.e. Menge and Lubchenco 1981) and exploitation competition (i.e. Navarrete et al. 2000) further explain numbers of individuals, as well as numbers of species, present in an ecosystem of interest. However, theory that describes density-mediation of prey and predator numbers has failed to accurately predict population numbers because it fails to account for other processes that alter interactions between species and individuals (Werner and Peacor 2003).

The rocky intertidal ecosystem has been a model community in the development of the keystone concept and other density-mediated indirect interactions (DMIIs, Paine 1966, 1969, Menge 1976, 1994, 1995), but relatively little research has addressed possible trait-mediated indirect interactions (TMIIs, Abrams 1995), though they could be important in structuring the rocky intertidal community (Trussell et al. 2002). In this chapter I will briefly review DMIIs and TMIIs, and then propose a new interaction web for the rocky intertidal community to illustrate how my thesis contributes to an understanding of this community, and suggest directions for future study.

### ***Density-mediated Indirect Interactions***

The direct effects of predators on prey are obvious: predators kill prey. This coupled with the dependence on consumption of prey for reproduction by predators generates classic predator-prey dynamics, as in the dynamics of lynx and hare populations of the boreal forest. Predator species can also have indirect effects on members of the community, as in the case of keystone predators. Paine (1966) documented indirect effects of the predatory ochre seastar *Pisaster ochraceus* on species that compete for space with the dominant *Mytilus californianus*. A keystone predator is “one of several predators in a community that alone determines most patterns of prey community structure, including distribution, abundance, composition, size and diversity” (Menge et al. 1994).

Keystone predation is the most famous type of DMII, but apparent competition, trophic cascades and exploitation competition among other defined and undefined indirect interactions (reviewed in Menge 1995) all are important processes in structuring and regulating communities. However, the usefulness of defined DMII in community ecology has been questioned (Mills et al. 1993). Just as trophic webs that only account for direct ecological interactions are an oversimplification of communities, so too are three and four species DMII webs (Abrams 1992, Strong 1992). It is difficult to model, or design full factorial experiments that account for the interactions of multiple species in an interaction web as in diffuse predation (Menge and Lubchenco 1981) and differentiated trophic cascades (Strong 1992). Furthermore, previous interaction web models have assumed that only populations were dynamic, when many species also have dynamic traits that can affect the outcome of interactions (Abrams 1995).

### ***Trait-mediated Indirect Interactions***

Trait plasticity has long been recognized, but little studied until recently. Reversible and irreversible traits develop in a given direction in response to environmental variables, such as freckles and sweat glands in humans, which increase in number expressed in response to sun and heat. The presence of other species can also cause plastic response of traits, such as the development of spines in cladocerans in response to predator presence (Tollrian and Dodson 1999). The alteration of morphology or behaviour of one species is the direct result of an interaction with another species, even if the interaction consisted only of the receiver species detecting the initiator species. The general outcome of these interactions is higher fitness, through increased survivorship or competitive ability, for the bearer of the modified trait; spiny cladocerans are less likely to be consumed by their predators. Trait-mediated interactions can influence the structure of the community, just as density-mediated trophic interactions cascade up the food web to other members of the community.

Trait-mediated indirect interactions occur when “a species reacts to the presence of a second species by altering their phenotype [and] the trait changes in the reacting species... alter[s] the per capita effect of the reacting species on other species, even in the absence of density effects of the second on the reacting species” (Werner and Peacor 2003). The alteration of phenotype of one species has cascading effects for other species that compete with, eat, or get eaten by, the receiving species. The theory and empirical research on trait-mediated indirect interactions thus far have focused on three-species interactions in which there is an initiator, a transmitter, and a receiver species (ie Werner

and Peacor 2003, Dill et al. 2003). The indirect interaction between the initiator and the receiver species can be positive or negative, depending on the nature of the trait change in the transmitter species and the ecology of the species involved. There are numerous possible configurations for the indirect interaction, and a useful criterion for description of TMIIs is outlined in Dill et al. 2003, and illustrated in Figure 4.1.

### ***A New View of the Rocky Intertidal***

The rocky intertidal community of Howe Sound is composed of benthic consumers and their predators (Figure 4.2). The mussel *M. trossulus* is the dominant space occupier in the intertidal zone, and barnacles (*Balanus* and *Semibalanus spp*) are generally restricted to the upper intertidal, or ephemeral holes in the mussel bed. While both consumers are preyed on, mussels are likely the preferred prey for ochre seastars, seaducks (*Melanitta perspiculata*, *Bucephala islandica*), red-rock crabs (*Cancer productus*), and whelks (*Nucella spp*). Gulls (*Larus spp*) also feed on mussels, as well as whelks, crabs and seastars. In addition to these ecological relationships, many of the members of this community respond plastically, through morphological and behavioural alterations, to other members of the community. Mussels alter shell thickness, adductor size and byssal attachment strength in response to crab and seastar presence (Nakaoka 2000, Leonard et al. 1999, Côté 1995, Cheung et al. 2004, Ishida and Iwasaki 2003). Marine and freshwater snails also alter shell growth and morphology, and behaviour in response to the presence of crab and other predators (Cotton et al. 2004, Palmer 1990, Keppel and Scrosati 2004). Barnacles also alter shell shape in response to snail predators (Lively 1986, Lively et al. 2000). Crabs respond behaviourally to the presence of

potential predators by reducing foraging activity (Christy et al. 1998) and hiding.

Behavioural and morphological plasticity in the context of complex food webs generates a large number of possible TMIIIs.

My observations indicate two possible TMIIIs that I did not directly test. First, in my selectivity of mussel predators experiment I found that small crabs preferred thin-shelled mussels, but seastars preferred mussels with uneven shell margins. And in my study, thinner shelled mussels had more even shell margins (Chapter 3). It is likely that the production of thick shells generates uneven shell margins, as the laying of extra calcareous matrix should exacerbate any margin imperfections already present. Therefore, mussels must trade-off protection from crab predators for defense against seastars. Since mussels respond to the presence of crabs by producing thicker shells (Leonard et al. 1999), crabs have a positive TMII with seastars. If mussels also respond to seastar presence, it is possible that this TMII is reciprocal; if seastars cause more even (thinner) shells, seastars have a positive TMII with crabs. To test this it would first be necessary to confirm that there is a trade-off between shell thickness and shell evenness. Second, it is necessary to determine if mussels respond to seastars by producing more even shells. Finally, the reciprocal TMII could be tested with a reciprocal transplant experiment. Mussels from a common stock would be raised in the presence of either crabs or seastars, and then transplanted to the opposite prey regime. Mussels raised in the presence of crabs should be subject to higher predation by seastars than a control group raised in the presence of seastars, and vice versa.

The second possible TMII that was indicated in my observations was a negative TMII between crabs and seaducks. I found no site where crab and seaduck foraging

activities overlapped. At North Batchelor Cove, there are adjacent bedrock and boulder/cobble substrates where seaducks and crabs foraged respectively. If the presence of crabs induces mussels to form stronger byssal attachments, it is possible that the mussels become so strongly attached that the seaducks cannot pull them from the substrate. In November 2004 I measured the byssal attachment strength of 10 mussels randomly selected from each of the crab and seaduck foraging areas. Byssal attachment strength on the crab foraging areas was 0.3 kg stronger than on seaduck foraging areas (Student t-test,  $F = 6.75$ ,  $P = 0.018$ ). This suggests that crabs may exclude seaducks from potential foraging sites by inducing mussels to produce strong byssal attachments, which increases seaduck's handling time, or makes it impossible for them to remove the mussels. Testing this negative TMII first requires information on how seaducks choose foraging patches in rocky mussel-prey areas. How does mussel attachment strength influence handling time for seaducks? How strongly do mussels have to be attached for a seaduck to leave a patch? It is important to understand more about the interactions between mussels and their seaduck predators before we can measure TMII's involving these links in the web. Introducing crabs to patches that seaducks normally forage on, and monitoring these and adjacent patches that crabs are excluded from, for seaduck predation, would test the TMII between crabs and ducks. Alternatively, crab predation can be simulated in patches within a scoter foraging area by introducing a caged crab, or tugging on the byssal attachments of mussels.

Additionally, I observed anecdotal evidence of a DMII between seaducks and seastars. Seaducks, especially surf scoters and Barrow's goldeneye, remove acres of mussel bed in Howe Sound each winter. Along the south shore of Bowen Island, long

stretches of the rocky intertidal were completely denuded of mussels by April after the 2003 winter. This complete removal of mussel bed might force seastars higher in the intertidal to forage on barnacles, or cause them to stay high to finish digestion despite receding tides. During spring in the Strait of Georgia region, when daytime tides are low, I frequently observed seastars getting caught out by the receding tides, exposing them to risk of desiccation and predation by gulls. This is a proposed four species indirect interaction where seaducks have a density-mediated interaction with seastars by removing their shared food resource (mussels), which causes a behavioural change in the seastars, which, combined with a change in the environment (daytime low tides), results in seastars becoming available to gulls as a prey item: a two-step TMII between seaducks and gulls. To test this experimentally I would monitor the up and down movements of seastars on control and experimental plots, where the experimental treatment is the removal of mussel bed in the low intertidal, simulating seaduck predation. If the seastars do spend more time in the high intertidal as a result of needing to climb higher before food is found, or needing to stay high to finish digestion where they found food, this would be evident by a higher mean intertidal height of seastars, and more seastars above the tide line after the tide has receded. The experimental test is necessary because seastars follow the tide and make their highest intertidal sprints during high slack plateau tides (J. Marliave pers. comm.), when the high low tide is very close to the low high tide, making it difficult to separate the effects of seaducks and seasonal tides.

### ***Conclusion***

Many of the direct ecological interactions of the rocky intertidal have been well established, and phenotypic responses of many intertidal organisms to the presence of

other species have been documented in the lab. There is now about 40 years of literature on DMIs in the rocky intertidal, but almost none on TMIs. Trussell (2002) found evidence of a TMII between green crabs (*Carcinus maenas*) and fucoid algae via predator-induced grazing suppression of littorinid snails. My observations have hinted at TMIs between seastars, seaducks and crabs, and there certainly may be many others. Research on rocky intertidal community ecology should focus on directly testing possible TMIs where phenotypic responses to predators and competitors have been documented. Of interest to evolutionary ecology is the evolution of reaction norms in intertidal species, and individual's solutions to trade-offs between conflicting needs of defense against a variety of predators (DeWitt et al. 2000), and growth and reproduction.



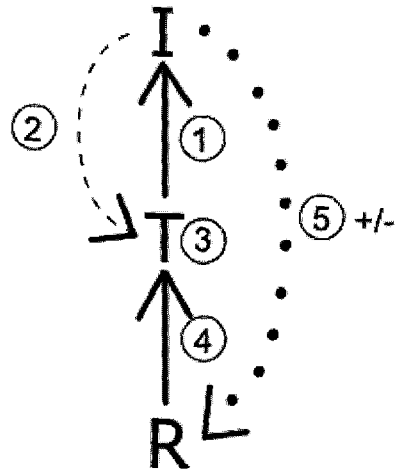


Figure 4.1: TMIs can be described as consisting of an initiator (I), a transmitter (T) and a receiver (R), and additionally 1) the initial ecological relationship between I and T 2) the action of I that affects T, 3) The trait of T that is altered 4) the initial ecological relationship between T and R and 5) the effect on R, which could be positive or negative.

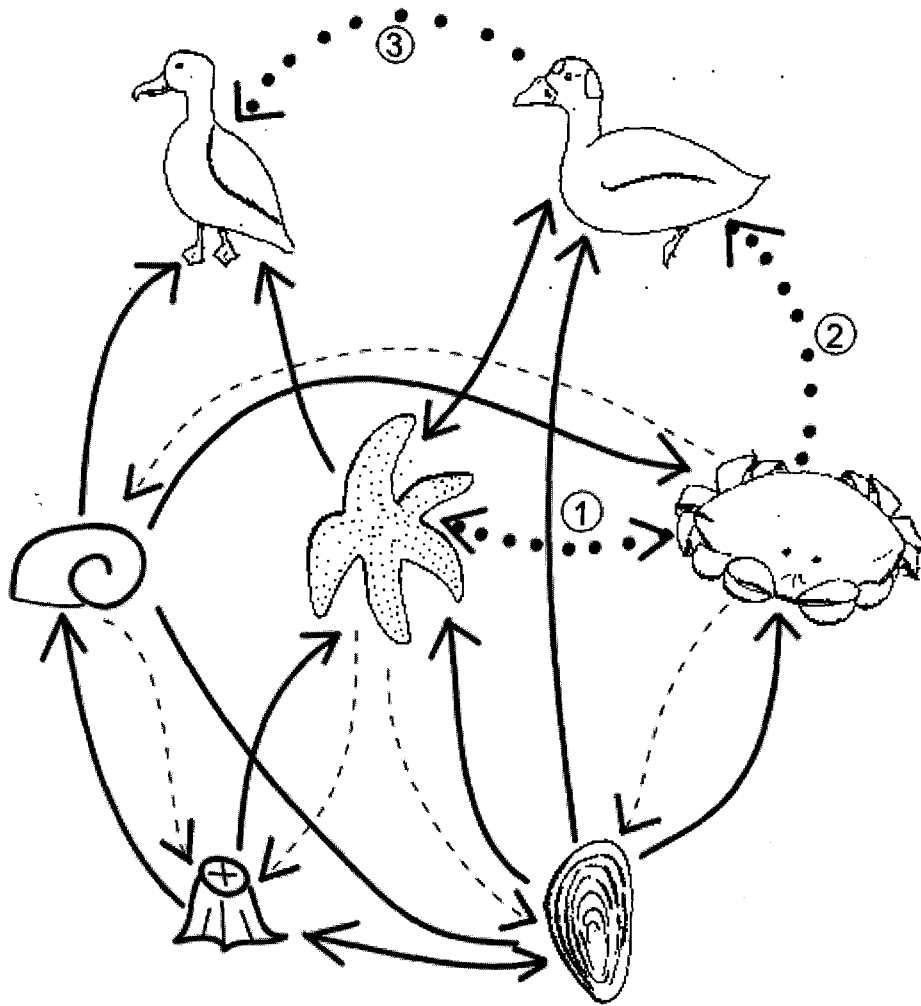


Figure 4.2: An interaction web for the Howe Sound rocky intertidal community. Solid arrows indicate direct ecological interactions with arrows pointing in the direction of energy flow. The double-headed solid arrow indicates a competitive interaction; mussels and barnacles compete for settlement substrate, and when very close, for phytoplankton food. Dashed lines indicate demonstrated or possible induction of trait modification. Numbered dotted lines indicate proposed indirect interactions. 1) Induction of mussel's defenses by crabs or seastars may facilitate predation by the other. 2) Induction of stronger byssal attachments by crabs may make mussels less profitable, or unexploitable by seaducks. 3) The removal of mussels by seaducks may induce riskier high intertidal foraging by seastars, making them more available to gulls.

## REFERENCE LIST

- Abrams PA. 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptations. *American Naturalist* 140: 573-600.
- Abrams PA. 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *American Naturalist* 146: 112-134.
- Abrams PA. 2000. The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics* 31: 79-105.
- Arsenault DJ and Himmelman JH 1996. Size related changes in vulnerability to predators and spatial refuge use by juvenile Iceland scallops *Chlamys islandica*. *Marine Ecology Progress Series* 140: 115-122.
- Bayne BL, Thompson RJ, and Widdows J. 1976. Physiology: I. In Bayne BL (ed), *Marine Mussels: their ecology and physiology*. Cambridge University Press, Cambridge, UK.
- Blaylock WM. 1981. Distribution, population overlap, and morphological shell variation in *Mytilus californianus* Conrad and *Mytilus edulis* Linnaeus on the west coast of Vancouver Island. MSc thesis, Simon Fraser University, Burnaby BC.
- Boulding EG and Labarbera M. 1986. Fatigue damage: repeated loading enables crabs to open larger bivalves. *Biological Bulletin* 171(3): 538-547.
- Boulding EG, Holst M, and Pilon V. 1999. Changes in selection on gastropod shell size and thickness with wave exposure on northeastern Pacific shores. *Journal of Experimental Marine Biology and Ecology* 232: 217-239.
- Buschbaum C. 2001. Selective settlement of the barnacle *Semibalanus balanoides* (L.) facilitates its growth and reproduction on mussel beds in the Wadden Sea. *Helgoland Marine Research* 55: 128-134.
- Butler RW, Ydenberg RC and Lank DB. 2003. Wader migration on the changing predator landscape. *Wader Study Group Bulletin* 100: 130-133.
- Caceres-Martinez J, Del Rio-Portilla MA, Gutierrez SC, and Humaran IMG. 2003. Phenotypes of the California mussel, *Mytilus californianus*, Conrad (1837). *Journal of Shellfish Research* 22: 135-140.
- Carrington E. 2002. Seasonal variation in attachment strength of blue mussels: causes and consequences. *Limnology and Oceanography* 47(6): 1723-1733.
- Cheung SG, Lam S, Gao QF, Mak KK, and Shin PKS. 2004. Induced anti-predator responses of the green mussel, *Perna viridis* (L.), on exposure to the predatory gastropod, *Thais clavigera* Kuster, and the swimming crab, *Thalamita danae* Stimpson. *Marine Biology* 144: 675-684.

- Coté IM. 1995. Effects of predatory crab effluent on byssus production in mussels. *Journal of Experimental Marine Biology and Ecology* 188: 233-241.
- Cotton PA, Rundle SD, and Smith KE. 2004. Trait compensation in marine gastropods: shell shape, avoidance behavior, and susceptibility to predation. *Ecology* 85(6): 1581-1584.
- Dayton PK. 1971. Competition, predation and community structure: the allocation and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41: 351-389.
- Dayton PK. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs* 45(2): 137-159.
- DeWitt TJ, Robinson BW, and Wilson DS. 2000. Functional diversity among predators of a freshwater snail imposes an adaptive trade-off for shell morphology. *Evolutionary Ecology Research* 2(2): 129-148.
- Dill LM, Heithaus MR and Walters CJ. 2003. Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology* 84: 1151-1157.
- Edelaar P. 2000. Phenotypic plasticity of burrowing depth in the bivalve *Macoma balthica*: experimental evidence and general implications. *Geological Society Special Publication* 177: 451-458.
- Elnor RW. 1978. Mechanics of predation by shore crab *Carcinus maenus* (L.), on edible mussel *Mytilus edulis* (L.). *Oecologia* 36: 333-344.
- Enderlein P, Moorthi S, Rohrsheidt H, and Wahl M. 2003. Optimal foraging versus shared doom effects: interactive influence of mussel size and epibiosis on predator preference. *Journal of Experimental Marine Biology and Ecology* 292: 231-242.
- Frandsen RP and Dolmer P. 2002. Effects of substrate type on growth and mortality of blue mussels (*Mytilus edulis*) exposed to the predator *Carcinus maenas*. *Marine Biology* 141: 253-262.
- Gaymer CF, Himmelman JH, and Johnson LE. 2001. Distribution and feeding ecology of seastars *Leptasterias polaris* and *Asterias vulgaris* in the northern Gulf of St Lawrence, Canada. *Journal of the Marine Biological Association of the United Kingdom* 81: 827-843.
- Geller JB. 1982. Chemically mediated avoidance response of a gastropod, *Tegula funebris* (A. Adams), to a predatory crab, *Cancer antennarius* (Stimpson). *Journal of Experimental Marine Biology and Ecology* 65: 19-27.
- Gilg MR and Hilbish TJ. 2003. The geography of marine larval dispersal: coupling genetics with fine-scale physical oceanography. *Ecology* 84: 2989-2998.
- Hancock DA. 1965. Adductor muscle size in Danish and British mussels and its relation to starfish predation. *Ophelia* 2: 253-267.

- Harding LE. 1992. Overview of the Marine Ecosystem of Howe Sound. *In* Levings CD, Turner RB, Ricketts B (eds), Proceedings of the Howe Sound Environmental Science Workshop. Canadian technical report of fisheries and aquatic sciences 1879.
- Hunt HL and Scheibling RE. 2001. Predicting wave dislodgement of mussels: variation in attachment strength with body size, habitat, and season. *Marine Ecology Progress Series* 213: 157-164.
- Innes DJ and Bates JA. 1999. morphological variation of *Mytilus edulis* and *Mytilus trossulus* in eastern Newfoundland. *Marine Biology* 133: 691-699.
- Ishida S and Iwasaki K. 2003. Reduced byssal thread production and movement by the intertidal mussel *Hormomya mutabilis* in response to effluent from predators. *Journal of Ethology* 21: 117-122.
- Juanes F and Hartwick EB. 1990. Prey size selection in Dungeness crabs: the effect of claw damage. *Ecology* 71(2): 744-758.
- Kautsky N, Johannesson K, and Tedengren M. 1990. Genotypic and phenotypic differences between Baltic and North Sea populations of *Mytilus edulis* evaluated through reciprocal transplants I Growth and morphology. *Marine Ecology Progress Series* 59: 203-210
- Keppel E and Scrosati R. 2004. Chemically mediated avoidance of *Hemigrapsus nudus* (Crustacea) by *Littorina scutulata* (Gastropoda): effects of species coexistence and variable cues. *Animal Behaviour* 68: 915-920.
- Lacroix DL. 2001. Foraging impacts and patterns of wintering surf scoters feeding on bay mussels in coastal Strait of Georgia, British Columbia. MSc thesis, Simon Fraser University, Burnaby BC.
- Lank DB and Ydenberg RC. 2003. Death and danger at migratory stopovers: problems with predation risk. *Journal of Avian Biology* 34: 225-228.
- Leonard GH, Bertness MD, and Yund PO. 1999. Crab predation, waterborne cues, and inducible defenses in the blue mussel, *Mytilus edulis*. *Ecology* 80: 1-14.
- Levings CD and McDaniel NG. 1976. Industrial disruption of invertebrate communities on beaches in Howe Sound, British Columbia. Fisheries and Marine Service Technical Report No. 663, 92 pp.
- Lively CM, Hazel WN, Schellenberger MJ, and Michelson KS. 2000. Predator-induced defense: variation for inducibility in an intertidal barnacle. *Ecology* 81(5): 1240-1247.
- Martel AL, Auffrey LM, Robles CD, and Honda BM. 2000. Identification of settling and early postlarval stages of mussels (*Mytilus spp.*) from the Pacific coast of North America, using prodissoconch morphology and genomic DNA. *Marine Biology* 137: 811-818.
- Mascaro M and Seed R. 2000. Foraging behavior of *Carcinus maenas* (L.): comparisons of size selective predation on four species of bivalve prey. *Journal of Shellfish Research* 19: 283-291.

- Mascaro M and Seed R. 2001. Foraging behavior of juvenile *Carcinus maenas* (L.) and *Cancer pagurus* L. *Marine Biology* 139: 1135-1145.
- Mauzey KP. 1966. Feeding behavior and reproductive cycles in *Pisaster ochraceus*. *Biological Bulletin* 127-144.
- McClintock JB and Robnett TJ. 1986. Size selective predation by the asteroid *Pisaster ochraceus* on the bivalve *Mytilus californianus*: a cost-benefit analysis. *Marine Ecology* 7(4): 321-332.
- McDonald JH, Seed R, and Koehn RK. 1991. Allozymes and morphometric characters of three species of *Mytilus* in the Northern and Southern hemispheres. *Marine Biology* 111: 323-335.
- Meire PM and Eryvynck A. 1986. Are oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*)? *Animal Behaviour* 34(5): 1427-1435.
- Menge BA and Lubchenco J. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecological Monographs* 51: 429-450.
- Menge BA, Berlow EL, Blanchette CA, Navarrete SA, and Yamada SB. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* 64: 249-286.
- Menge BA. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs* 46: 355-393.
- Menge BA. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance.
- Micheli F. 1997. Effects of experience on crab foraging in a mobile and sedentary species. *Animal Behaviour* 53(6): 1149-1159.
- Mills LS, Soule ME, and Doak DF. 1993. The keystone species concept in ecology and conservation. *BioScience* 43: 219-224.
- Mistri M. 2004. Prey preference of *Carcinus aestuarii*: possible implications with the control of an invasive mytilid and Manila clam culture in a northern Adriatic lagoon. *Aquaculture* 230: 261-272.
- Nakaoka M. 1996. Size-dependent survivorship of the bivalve *Yolida notabilis* (Yokoyama 1920): the effect of crab predation. *Journal of Shellfish Research* 15: 355-362.
- Norberg J and Tedengren M. 1995. Attack behavior and predatory success of *Asterias rubens* L. related to differences in size and morphology of the prey mussel *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology* 186: 207-220.
- Paine RT. 1966. Food web complexity and species diversity. *American Naturalist* 100: 65-75.

- Paine RT. 1969. A note on trophic complexity and community stability. *American Naturalist* 103: 91-93.
- Paine RT. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15: 93-120.
- Palacios KC and Ferraro SP. 2003. Green crab (*Carcinus maenus* Linnaeus) consumption rates on and prey preferences among four bivalve prey species. *Journal of Shellfish Research* 22: 865-871.
- Palmer AR. 1990. Effect of crab effluent and scent of damaged conspecifics on feeding, growth, and shell morphology of the Atlantic dogwhelk *Nucella lapillus* (L.). *Hydrobiologia* 193: 155-182.
- Phillips DW. 1977. Avoidance and escape responses of the gastropod mollusk *Olivella biplicata* (Sowerby) to predatory asteroids. *Journal of Experimental Marine Biology and Ecology* 28: 77-86.
- Reimer O and Harms-Ringdahl S. 2001. Predator-inducible changes in blue mussels from the predator-free Baltic Sea. *Marine Biology* 139: 959-965.
- Reimer O and Tedengren M. 1996. Phenotypical improvement of morphological defenses in the mussel *Mytilus edulis* induced by exposure to the predator *Asterias rubens*. *Oikos* 75: 383-390.
- Reimer O and Tedengren M. 1997. Predator-induced changes in byssal attachment, aggregation and migration in the blue mussel, *Mytilus edulis*. *Marine and Freshwater Behavior and Physiology* 30: 251-266.
- Reimer O. 1999. Increased gonad ratio in the blue mussel exposed to starfish predators. *Aquatic Ecology* 33:185-192.
- Richards MG, Huxham M, and Bryant A. 1999. Predation: a causal mechanism for variability in intertidal bivalve populations. *Journal of Experimental Marine Biology and Ecology* 241:159-177.
- Seed R and Hughes RN. 1995. Criteria for prey size-selection in molluscivorous crabs with contrasting claw morphologies. *Journal of Experimental Marine Biology and Ecology* 193: 177-195.
- Seed R and Suchanek TH. 1992. Population and community ecology of *Mytilus*. In Gosling E. (ed), *The Mussel Mytilus: ecology, physiology, genetics and culture*. Elsevier Science, Amsterdam.
- Seed R. 1968. Factors influencing shell shape in the mussel *Mytilus edulis*. *Journal of the Marine Biological Association of the United Kingdom*. 48: 561-584.
- Smallegange IM and Van der Meer J. 2003. Why do shore crabs not prefer the most profitable mussels? *Journal of Animal Ecology* 72: 599-607.
- Smith LD and Jennings JA. 2000. Induced defensive responses by the bivalve *Mytilus edulis* to predators with different attack modes. *Marine Biology* 136: 461-469.

- Smith TE, Ydenberg RC, and Elnor RW. 1999. Foraging behavior of an excavating predator, the red-rock crab (*Cancer productus* Randall) on soft-shell clam (*Mya arenaria* L.). *Journal of Experimental Marine Biology and Ecology* 238: 185-197.
- Sommer U, Meusel B, and Stielau C. 1999. An experimental analysis of the importance of body-size in the seastar-mussel predator-prey relationship. *Acta Oecologica* 20: 81-86.
- Springer SA. 2003. Rapid evolution of a gamete-recognition protein in a hybrid *Mytilus* population. MSc thesis, Simon Fraser University, Burnaby BC.
- Stephens DW and Krebs JR. 1986. *Foraging Theory*. Princeton University Press, Princeton, NJ, USA.
- Strathmann MF. 1987. *Reproduction and development of marine invertebrates of the northern Pacific coast*. University of Washington Press, Seattle, Washington, USA.
- Strong DR. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73: 747-754.
- Theisen BF. 1972. Shell cleaning and deposit feeding in *Mytilus edulis* L. (Bivalvia). *Ophelia* 10: 49-55.
- Tollrian R and Dodson SI. 1999. Inducible defenses in Cladocera: constraints, costs, and multipredator environments. *In* Tollrian R and Harvell CD (eds), *The ecology and evolution of inducible defenses*. Princeton University Press, Princeton, New Jersey, USA.
- Tollrian R and Harvell CD. 1999. *The ecology and evolution of inducible defenses*. Princeton University Press, Princeton, New Jersey, USA.
- Toro JE, Alcapan AC, Vergara AM and Ojeda JA. 2004. Heritability estimates of larval and spat shell height in the Chilean blue mussel (*Mytilus chilensis* Hupe 1854) produced under controlled laboratory conditions. *Aquaculture Research* 35: 56-61.
- Trussell GC, Ewanchuk PJ, and Bertness MD. 2002. Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. *Ecology Letters* 5: 241-245.
- Trussell GC. 2000. Phenotypic clines, plasticity, and morphological trade-offs in an intertidal snail. *Evolution* 54(1): 151-166.
- Walker JA and Bell MA. 2000. Net trajectories of body shape evolution within a microgeographic radiation of threespine sticklebacks (*Gasterosteus aculeatus*). *Journal of Zoology* 252: 293-302.
- Werner EE and Peacor SD. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84: 1083-1100.
- West K, Cohen A, and Baron M. 1991. Morphology and behavior of crabs and gastropods from Lake Tanganyika, Africa: Implications for Lacustrine predator-prey coevolution. *Evolution* 45(3): 589-607.



- Zach R. 1979. Shell dropping: decision-making and optimal foraging in northwestern crows. *Behaviour* 68: 106-117.
- Zaklan SD and Ydenberg R. 1997. The body size-burial depth relationship in the infaunal clam *Mya arenaria*. *Journal of Experimental Marine Biology and Ecology* 215: 1-17.

## APPENDIX I

Summary of surveys for mussel predators. I did several surveys which contributed to my classification of predation at each site. For diving surveys, the density (mean and 95% confidence interval) of predators was measured at Tunstall Bay (TB) but not at Miller's Landing (ML) or Batchelor Cove (NB). Density was measured as the number of seastars observed in a 2 m wide strip transect divided by the length of the transect. Three transects of 20.0 m, 23.6 m, and 10.5 m were done. The total number of surf scoters (SuSc) and Barrow's goldeneye (BaGo) observed at each site during 2003 bird surveys is listed in brackets. Bird surveys were completed once monthly between January and June. Low tide surveys were done at the time of collection and again in the spring. During low tide surveys I recorded predators observed, and mussel evidence of predation. Empty, splayed valves of mussel shells indicate seastar predation, crushed shells indicated crab predation, and extreme mussel bed depletion indicates seaduck predation. Presence (p) or absence (a) of these signs of predation are indicated.

Site	Predation	Diving Survey	Bird Survey	Low Tide Survey	Mussels			Bed Depletion
					Splayed Valves	Crushed Shells	Bed Depletion	
PI	Seaduck, Seastar	No survey	SuSc (900), BaGo (400)	Seastars	p	a	p	
BB	Seaduck, Seastar	No Survey	SuSc (188), BaGo (64)	Seastars	p	p (few)	p	
ML	Seastar, Crab	Seastars, crabs observed	No seaducks observed	Seastars	p	p	a	
TB	Seastar	Seastars (4.57 ± 3.14/m <sup>2</sup> )	No seaducks observed	Seastars	p	a	a	
NB	Seaduck, Crab	No predators observed	BaGo (541), SuSc (110)	Small crabs	a	p	p	
CC	Seastar, Crab	No survey	No seaducks observed	Seastars, dead crab	p	p	a	