

**POPULATION VIABILITY AND BIODIVERSITY: IMPLICATIONS FOR  
MARINE PROTECTED AREA SITE SELECTION**

by

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B.Sc. (Hons.), Queen's University, 1996

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

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

(Department of Botany)

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August 2000

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Date September 6th 2000

## Abstract

Marine protected areas have been identified as an essential tool in marine conservation strategies, however, to date there has been very little scientific basis for their design or location. Areas of high species richness are often emphasized for protection because of the possibility of protecting multiple species simultaneously. This study examined the relationship between intertidal biodiversity and the population viability of an ecologically important intertidal chiton, *Katharina tunicata*, in Barkley Sound, British Columbia. *Katharina*'s potential reproductive output, the metric used to quantify population viability, and Randomized Species Richness were found to be significantly different between the 10 sites under investigation. Potential reproductive output and both Species Richness and Randomized Species Richness, two indices used to describe biodiversity, were significantly negatively correlated, as a result, areas of high algal and invertebrate species richness encompassed chiton populations with relatively low potential reproductive output. Consequently, viable, self-replenishing, source populations that contribute disproportionate numbers of offspring may not be protected if reserve selection focuses on species richness as a site selection criterion. This thesis identifies and discusses significant deviations from the anticipated ecological outcomes of various marine protected area site selection criteria, design policies, and monitoring strategies stemming from the potential ecological interactions that may take place within a marine reserve.

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## List of Abbreviations

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MPA = Marine Protected Area  
PRO = Potential Reproductive Output  
MRO = Mean Reproductive Output  
PRO<sub>R</sub> = Randomized Potential Reproductive Output (derived from re-sampling procedure)  
MRO<sub>R</sub> = Randomized Mean Reproductive Output (derived from re-sampling procedure)  
MLRO = Mean Log Reproductive Output  
GDW = Gonad Dry Weight  
S = Species Richness  
H' = Shannon-Wiener Diversity  
S<sub>R</sub> = Randomized Species Richness (derived from re-sampling procedure)  
H'<sub>R</sub> = Randomized Shannon-Wiener Diversity (derived from re-sampling procedure)

### Abbreviated Site Names:

EK E = Edward King Exposed  
EK S = Edward King Sheltered  
Sep E = Seppings Exposed  
Sep S = Seppings Sheltered  
San S = Sanford Sheltered  
San E = Sanford Exposed

## Acknowledgements

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This thesis is the product of many people's ideas and energy. First, I would like to thank my supervisor Dr. Rob DeWreede for his intellectual support, patience and humor. Always willing to share his time and welcome new ideas, Rob is among a rare breed of supervisors that encourages students to ask their own questions and pursue their own research ideas. Special thanks to Dr. Jennifer Ruesink for her creative insight, statistical prowess and enthusiasm. Jennifer has been an inspiring mentor both scientifically and personally. I would also like to thank my committee members Dr. Tomas Tomascik, Dr. Tony Sinclair, and Dr. Mike Hawkes, all of whom provided encouragement and support throughout this research.

Thanks to my wonderful field assistant and friend Diane Orhiel with whom I spent many hours on the surf swept shores of Barkley Sound. Her bravery while kayaking in big swell and fierce winds and while on our reconnaissance missions was instrumental to this research. Thanks also to Su Ning Strube, Nigel Waller, Sabina Iseli-Otto, Mark Zegler, Jason Thompson and Steve Martel for their help in the field. I would also like to acknowledge the staff at Bamfield Marine Station; Nathan Web, Shirley Spakula and particularly Shane Servant for his maverick boat handling skills in the October storms. Many thanks to Dana Hagarty, Kella Sadler, Adrian Marchetti, and Dr. Jordan Rosenfeld for sharing their knowledge and acting as sounding boards for ideas.

Tim Storr, Katrina Pacey, Jackie O'Connell, and Hilary Pada provided the distractions, friendship, and personal support required to complete this thesis.

Thanks to my big brother Peter Salomon for introducing me to the concept of maximum wave force in Maui, and to my "parental unit", Shirley and Martin Salomon for their continual encouragement, support, and interest.

Finally, I am grateful for the financial assistance of both Parks Canada and NSERC.

### 1.1 INTRODUCTION

Humans are currently imposing unprecedented pressure on marine systems worldwide (Norse 1993, Lubchenco et al. 1995, Vitousek et al. 1997, National Research Council 1999). As a result, marine resources and the ecosystems in which they are embedded have become severely threatened (Botsford 1997, Pauly 1998). Accompanying this global crisis is the growing support for a radical departure from conventional marine management. The establishment of marine protected areas (MPAs) has become a strongly advocated approach to marine conservation strategies (Bohnsack 1996, Agardy 1997, Roberts 1998, Walters 1998, Hastings and Botsford 1999). However, to date, there has been little scientific basis for their design or location (Allison et al. 1998).

Marine protected areas, otherwise known as fishing refugia, marine reserves or marine sanctuaries, are spatially explicit areas where the exploitation of marine resources is restricted<sup>1</sup>. Though the concept of spatial restriction<sup>2</sup> as a management tool is not new (Beverton and Holt 1957), the implementation of MPAs is relatively recent and the theoretical and empirical framework for their design is in its infancy. Consequently, marine conservation theory must be expanded to assure the ecological effectiveness of MPAs (Allison et al. 1998). Rational methods for selecting the location of MPAs will undoubtedly improve our ability to design effective conservation strategies for marine ecosystems (McNeill 1994). The primary goal of this thesis is to explore the theoretical basis for MPA site selection by investigating the relationship between population viability and biodiversity using the temperate rocky intertidal ecosystem as a model system, and *Katharina tunicata* as a model broadcast spawning species.

### 1.2 THE ROLE OF MARINE PROTECTED AREAS

#### 1.2.1 Biodiversity Conservation and Fisheries Management

The exploitation of living marine resources exerts a profound effect on marine species, populations, communities and ecosystems. Spatial protection in the form of marine protected areas has been gaining credibility as an effective ecosystem-based management tool to control this threat. MPAs may be established to meet a variety of conservation objectives that can be

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<sup>1</sup> In this thesis, the terms marine protected area (MPA) and marine reserve are used interchangeably to describe “no-take” zones in the ocean, whereas, the terms national marine conservation areas, harvest refugia, marine sanctuaries, and marine parks describe marine areas subject to only a limited degree of protection.

<sup>2</sup> Here, spatial restriction implies restricting the exploitation of a resource in a defined space (i.e. a marine protected area) rather than simply setting a limit to the degree of exploitation (i.e. fisheries quotas).



broadly divided into two categories; the conservation of biodiversity (biodiversity reserves) and the enhancement of fisheries yields (fishing refugia) (Allison et al. 1998). Ultimately, fishing refugia are created to increase the biomass of a commercially important target species through the emigration of adults and juveniles from the refuge and/or the export of larvae to surrounding exploited areas (Allison et al. 1998). They are also established to provide undisturbed habitat for an intensively fished species (Dugan and Davis 1993) and to serve as an "insurance policy" by acting as a buffer against recruitment failure and unanticipated yet potentially disastrous fisheries management mistakes (Walters 1998). Because catch limits are based on predictions of highly variable environmental parameters and inaccurate stock assessments, uncertainty in fisheries management is prevalent and the probability of error is high. Therefore, a protected population could promote recovery elsewhere if that population was self-replenishing and a source of individuals (Carr and Reed 1993).

Biodiversity reserves may be established to protect critical areas, a vulnerable species or population, or a sensitive habitat. They may also be created with the intent to conserve ecological processes and trophic structure while establishing baseline information against which future change can be judged (Norse 1993, Arcese and Sinclair 1997). All of these specific objectives are important and while some may overlap, others are conflicting. Nonetheless, the ecological rationale is equivalent for both types of reserves. Both harvest refugia and biodiversity reserves are established to decrease the chances of organisms and habitats interfacing with anthropogenic threats (Wallace 1999a).

Table 1.1 Marine protected areas can be designated for biodiversity conservation and fisheries management. Some objectives may be complementary while others may be conflicting.

<b>Conservation of Biodiversity</b>	<b>Improvement of Fishery Yields</b>
Protect ecosystem structure and function	Protect spawning stock and increase biomass
Protect food webs and ecological processes	Enhance reproductive output
Maintain trophic structure	Export larvae to adjacent waters
Retain keystone species	Supply spill-over of adults and juveniles
Prevent the loss of vulnerable / threatened species	Improve spawning sites by minimizing disturbance
Preserve "natural" community composition	Reduce chances of recruitment overfishing
Maintain physical structure of habitat	Prevent over-fishing of vulnerable species
Maintain high quality feeding or rearing grounds	Mitigate adverse genetic impacts of fishing
Preclude fishing gear impacts	Reduce bycatch mortality
Retain "natural" trophic interactions	Provide insurance against stock collapse
Provide controlled areas for assessing human impacts	Provide baseline information on unexploited ecosystems

### 1.2.2 Ecological Conflicts and Limitations

MPA objectives can be conflicting due to the complex ecological interactions that may play out within a reserve. For example, Ecospace, a spatially-explicit, ecosystem model (Walters et al. 1998), predicts that top predators that build up within a reserve can deplete local prey species within reserve boundaries (Walters 1998, Salomon et al. 1999). This may be followed by a subsequent increase in the biomass of even lower trophic groups. This indirect effect of spatial protection has in fact been documented in a marine reserve in New Zealand (Cole and Keuskamp 1998). In such cases, although large predator biomass may accumulate in a reserve, Ecospace suggests that certain prey species may become extirpated from the area resulting in a local decrease in biodiversity (Salomon et al. 1999). Conversely, protecting a species with high per capita interaction strength, for example a keystone species, may cause a local increase in biodiversity if a competitive dominant species is prevented from monopolizing a resource (Castilla and Duran 1985). As a result, methods for evaluating the biological effectiveness of a reserve will undoubtedly depend on the reserve's goal.

Ecospace further suggests that as fish densities increase within a reserve, the distribution of fishing effort intensity will build up on a reserve's periphery. This concentration of human "predators" at reserve boundaries may result in a spatially organized density gradient across reserve boundaries with high predator biomass at the center of the reserve and low predator biomass at the edges of the reserve. This biomass gradient should begin to decrease as top predators disperse outside of the protected area in response to declining food availability within the reserve.

Trophic cascades and biomass gradients are nontrivial departures from the simple expectations of how MPAs protect species. These predictions have important conservation implications. They warn that in reality, the ecological interactions that transpire within MPAs may give rise to unforeseen outcomes, such as a decrease in biodiversity or the extirpation of a certain prey species. Furthermore, MPAs should not be immediately judged as ineffective if high densities of a particular species are not documented within the reserve boundaries. Instead, reserve assessment should include an evaluation of the ability of a MPA to act as a source of larval propagules or individuals to adjacent waters which can occur if a population consists of large but sparse individuals (Salomon 2000a).

MPAs have several other important limitations. Firstly, spatial protection effectively reduces the total area available to be fished and so tends to increase fishing pressure elsewhere (Fogarty 1999). Therefore, MPAs must be coupled with restrictions on exploitation (i.e. quotas)

outside of their boundaries. Furthermore, although spatial protection may confer a high degree of protection for organisms with limited dispersal, MPAs will likely provide very little protection to widely dispersing and migrating species such as salmon, herring and whales (Walters et al. 1998, Walters 1998, Salomon et al. 1999). This again illustrates that MPAs are inadequate protection alone and must be accompanied by regulations in adjacent unprotected waters. Furthermore, marine reserves offer no protection from threats originating from outside the protected area such as oil spills and contamination by other pollutants. Finally, episodic climatic events such as El Nino-Southern Oscillations (ENSOs) can span thousands of kilometers and can have a dramatic impact on both protected and nonprotected populations. In conclusion, marine reserves are but one tool in a suite of tools to be used in an effective marine conservation strategies.

### **1.2.3 Status of Marine Protected Areas in British Columbia**

Depending on the definition used, the number of MPAs in British Columbia varies radically. Based on the International Union for the Conservation of Nature's 1988 definition<sup>3</sup>, 121 marine protected areas exist in B.C.'s marine waters: 85 provincial marine parks, 15 provincial ecological reserves, 4 wildlife management areas, 16 wildlife reserves and 1 protected area (Tomascik 2000, personal comment). Of these, only 2, Porteau Cove and Whytecliff Park, are closed to all resource exploitation. As a result, less than 0.1% of British Columbia's marine waters are in fact totally protected. Clearly, the present system confers little protection to British Columbia's marine biological diversity.

## **1.3 PROTECTED AREA DESIGN AND SITE SELECTION THEORY**

### **1.3.1 Comparison between Marine and Terrestrial Ecosystems and Reserve Design**

Although the marine environment encompasses two-thirds of the earth's surface, marine conservation strategies have lagged behind terrestrial conservation efforts (Norse 1993). Presently, the burgeoning body of scientific work on protected area design and site selection theory has been formulated almost exclusively on terrestrial concepts such as equilibrium island biogeography, patch dynamics, the effectiveness of corridors and minimum viable populations (Soule and Simberloff 1986). However, because marine and terrestrial systems differ

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<sup>3</sup> Marine protected area: "any area of intertidal or subtidal terrain, together with its overlying waters and associated flora and fauna, and historical and cultural features, which has been reserved by legislation to manage and protect part or all of the enclosed environment." (IUCN 1998).

fundamentally in both the scale and variability of processes (Steele 1985), the applicability of these terrestrially based concepts to marine systems remains unclear.

In the marine environment, oceanographic features (currents, gyres and upwellings) have a profound effect on primary production, the dispersal and survival of organisms, and the expansion of anthropogenic threats such as pollution and introduced species. These factors are all greatly influenced by oceanographic events over much larger spatial scales as compared to terrestrial systems. Furthermore, the life histories of many marine species are generally more complex than terrestrial organisms due to distinct life stages that require specific habitat types. Patterns of trophic linkages have also been described as more intricate in marine systems (Werner and Gilliam 1984). For example, top trophic level predators in their early life stages are often prey to species which they later consume as adults. On land, primary production is mostly derived from long-lived, sessile trees, whereas the basis of marine food webs is short-lived, mobile phytoplankton. Lastly, the major sources of primary production in marine systems, apart from kelp beds, typically do not provide habitat for marine organisms. In contrast, trees provide the structural habitat for most terrestrial animals. Consequently, terrestrial reserves, which often are based on forested areas, protect both the physical structure providing habitat (i.e. trees) and the fundamental energy source of the food web.

Human exploitation of terrestrial environments is principally through the consumption or destruction of primary production by forestry, agriculture and development. Herbivores are also commonly exploited. Conversely, in marine systems, anthropogenic impact is directed towards higher trophic levels such as top predators (i.e. piscivorous fish). Although a number of reserve design concepts are equally applicable to land or water, the differences between marine and terrestrial systems outlined above indicate how reserve design issues may radically differ in the two ecosystems. Marine conservation biologists may gain some insight by examining terrestrial protected area site selection and design theory, however, marine conservation theory itself needs to be further developed.

### **1.3.2 Reserve Site Selection Criteria**

Though socio-economic considerations and feasibility will ultimately influence where exactly protected areas are sited (Ballantine 1997, Ballantine 1999), ecological site selection criteria play a paramount role in determining the location of a reserve if conservation goals are to be attained (Fogarty 1999). Biological diversity, representativeness, species vulnerability to threats, species rarity, critical habitat, and connectedness between reserves are several ecological

site selection criteria. All of these criteria are important considerations, however, to date, modern site selection theory, formed almost exclusively for terrestrial ecosystems, has done little to incorporate population viability. Furthermore, site selection algorithms have mainly been studied in terrestrial environments on indicator groups such as birds, mammals, and plants. Although it is not clear if these terrestrial reserve selection methods hold for marine systems, an investigation into such methods is warranted.

### **1.3.3 Terrestrial Reserve Site Selection Methods**

Effective conservation of biological diversity requires efficient methods for selecting the location of protected area networks (Pressey et al. 1996, Williams et al. 1996, Reid 1998). Deciding what geographical regions should be protected to maximise conservation efforts is central to the design of effective conservation strategies because poor design and location may compromise conservation goals. Several quantitative approaches for selecting areas of high value for terrestrial biodiversity conservation have been developed including GAP analysis (Kiestler 1996), richness hotspot analysis (Myers 1990, Curnutt et al. 1994), rarity hotspot analysis (Csuti et al. 1997), and complementarity theory (Kirkpatrick 1983). GAP analysis involves mapping hotspots of species richness and using various selection algorithms to select the minimum set of grid cells that encompasses unprotected species. Though the goal of GAP analysis is to maximise representatives of as many types of species as possible, species rarity (low abundance, limited range and uneven distribution) is not integrated into this algorithm. Site selection algorithms based on identifying hotspots of species richness fail to capture rare species, therefore they are less efficient at maximising the protection of species diversity (Williams et al. 1996). Furthermore, poor correspondence between hotspots for various taxa implies that priorities based on hotspot analysis for one taxon may not benefit other taxa. Identifying rarity hotspots, sites richest in those species with the most restricted range, may be more efficient than the previous as they boost the representation of more restricted species. However, this method tends to reduce the total sites identified for conservation (Reid 1998).

Presently, the most efficient mechanism for maximising the number of species protected in a given area is the complementarity algorithm (Williams et al. 1996, Reid 1998). This site selection mechanism takes into account the species complement of existing reserves considering both richness and rarity. Sites are then selected in a stepwise fashion to add areas that contribute the greatest number of new species (Williams et al. 1996). However, this method, like the methods described above, does not address the critical issue of population viability.

## **1.4 FACTORS GOVERNING MARINE PROTECTED AREA DESIGN AND SITE SELECTION**

### **1.4.1 Larval Dispersal and Open Populations**

Dispersal governs the dynamics and persistence of populations, the distribution and abundance of species and therefore community structure. In marine systems, habitats are functionally linked over wide distances due to the way many marine species reproduce, i.e. through broadcast spawning. Broadcast spawners have a dispersal phase during their early life history (Roughgarden et al. 1985, Agardy 1997). Eggs and sperm are released into the water column, fertilization occurs and larvae are transported to surrounding areas via ocean currents. Therefore, larvae may settle in areas far away from where they were originally conceived. Organisms with this type of life history have "open" populations, where recruitment is decoupled from local parent fecundity (Roughgarden et al. 1985).

Larval dispersal is affected by both intrinsic and extrinsic factors. The distance a species will disperse is predicted to correlate to its planktonic duration. For example the planktonic phase of *Pisaster ochraceus* has been estimated to be between 75-230 days (Strathmann 1987), thus, it may spend that amount of time in the water column before settling. External factors such as upwellings, eddies, jets, gyres, tidal currents and coastal topography, affect the speed and distance to which larvae disperse.

### **1.4.2 Source/Sink Dynamics and Marine Protected Area Site Selection**

It is possible that some populations provide a greater contribution to population replenishment than others. Pulliam (1988) described source populations as those that contribute disproportionately large quantities of recruits and thus produce a net export of larvae. Conversely, sink populations produce few recruits and receive a net import from source populations. As a result, some populations, though apparently thriving, may be reliant on larval recruits produced elsewhere. Therefore, focusing conservation efforts on an area where a species is especially abundant may be an inappropriate guide to a habitat's overall importance to species maintenance (Paine 1994). Populations subject to source/sink dynamics have also been described as marine metapopulations, highly fragmented populations connected and replenished by larval dispersal (Quinn et al. 1993).

Patterns of larval replenishment may play a significant role in determining the location of a MPA within a reserve network (Carr and Reed 1993). It has been proposed that reserves that encompass source populations are likely to be more effective than those that protect sink

populations (Guénette et al. 1998, Roberts 1998, Fogarty 1999) (Figure 1.1). Source populations within a reserve are likely to contribute to population maintenance within a reserve while supplying recruits to surrounding exploited waters. In contrast, a protected sink population may collapse if the associated unprotected source population is overexploited. Therefore, MPA design that incorporates source/sink dynamics will both increase the possibility of fisheries enhancement and have higher biodiversity conservation value. This conceptual model also illustrates the importance of considering oceanographic patterns as well as biological ones. For instance, the predominant currents of a region should be incorporated into site selection criteria. Admittedly, accounting for source/sink dynamics becomes complex because every community has a mix of species, presumably with various patterns of dispersal. Therefore, a given site will probably not encompass the source populations of all species.

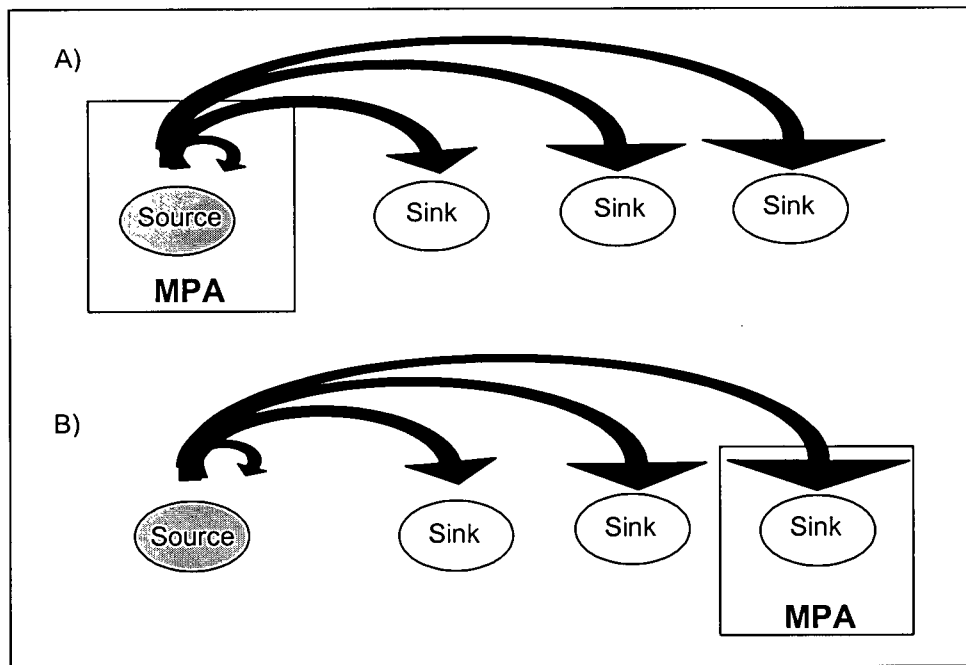


Figure 1.1 Marine protected areas that encompass source populations are more effective than marine protected areas that encompass sink populations. A) Protected source populations contribute to population maintenance within a reserve while supplying recruits to adjacent exploited waters. B) If the unprotected source population is overexploited, the sink population though protected, will eventually dwindle. This illustrates the importance of MPA site selection to a reserve's ecological effectiveness (modified from Allison et al. 1998).

### 1.4.3 Identifying Sources and Sinks

Locating and delineating the actual parental source of recruits has been identified as one of the greatest challenges to ecologists working in the field of conservation biology (Allison et al. 1998). Molecular techniques and radioisotope labeling have been attempted (Allison et al. 1998), however, it would be financially impractical and time consuming to apply these techniques to populations of several species along the entire West Coast of BC. Therefore, it is critical that practical ways to identify source populations are explored. One possible solution is to estimate the reproductive output of a population based on its size structure and density.

In general, larger benthic invertebrates are more likely to be reproductively mature and fecund than smaller individuals (Strathmann 1987). Therefore, populations with a higher density of larger size class individuals are likely to have a higher reproductive potential and thus be more of a source than those populations with a higher proportion of smaller size classes. Because source populations produce a net export of recruits one would expect the population size structure of a source to have a disproportionately high percentage of large size classes. Sink populations, those populations that receive a net import of recruits would have a disproportionately high percentage of small size classes.

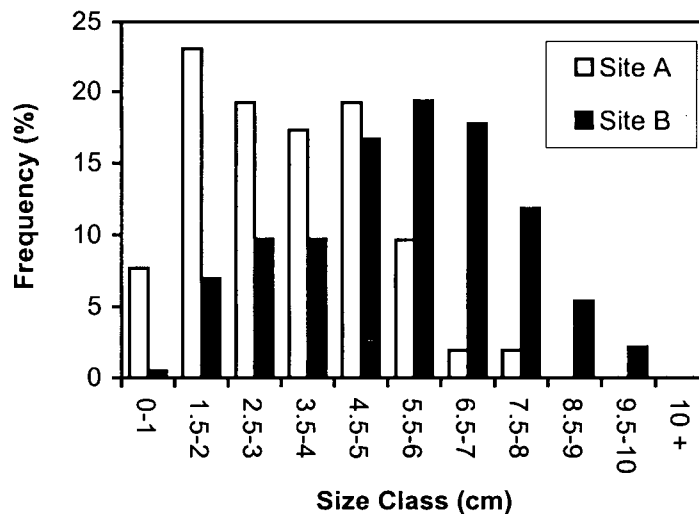


Figure 1.2 Site B is a source population relative to site A. Site B contains higher densities of larger individuals. Because fecundity is positively related to size, reproductive output will be higher at site B than site A. Populations with disproportionately many larger individuals are sources because individuals must have higher growth and survival rates.



#### **1.4.4 The Allee Effect**

With consideration to design and site selection, MPA networks may decrease the chance of Allee effects; the depressed per capita survivorship or fecundity as populations become small (Lande 1987). Experimental evidence and hydrodynamic considerations indicate that benthic marine invertebrates with planktonic larvae may suffer greatly reduced fertilization efficiencies as densities decline (Quinn et al. 1993). Further evidence suggests that for species whose adults provide refuge to their offspring from predators and other sources of mortality, (i.e. the red sea urchin), post-dispersal recruitment success declines at low adult densities (Quinn et al. 1993). Harvesting may have a drastic impact on species displaying strong Allee effects, therefore, harvest refugia may be a necessary conservation strategy to prevent population collapses for some heavily exploited benthic marine invertebrates such as abalone, sea urchins, and scallops.

The populations of many marine species that broadcast spawn can be described as metapopulations; highly fragmented populations connected by low levels of dispersal (Quinn et al. 1993). As described earlier, source populations can allow for the persistence of sink populations, hence, disrupting a source area can lead to population collapse on a much wider scale. Source areas have been described as areas with particularly favorable habitats or high resource levels (Quinn et al. 1993). Conservation strategies should focus on insuring that high-density source areas are protected to maintain regional population viability.

### **1.5 MOTIVATION FOR RESEARCH**

Effective methods for selecting the site of a MPA within a protected area network will undoubtedly improve the design of conservation strategies for marine ecosystems (McNeill 1994). Scientifically based methods of reserve selection that attempt to maximize the representation of species and/or habitats within a protected area network have been developed for terrestrial (Kirkpatrick 1983, Myers 1990, Prendergast et al. 1993, Pressey et al. 1996, Reid 1998) and marine systems (Dethier 1992, Vanderklift et al. 1998, Zacharias and Howes 1998). However, the conservation of biodiversity cannot be accomplished by simply setting aside areas that encompass each species or habitat we wish to protect. While this strategy might fulfill a criterion of representation, it does not assure population viability. In fact, to date, site selection theory has poorly assured that the species encompassed within a protected area will persist into the future.

Areas of high species diversity, also known as biodiversity "hotspots" are often identified as top priorities for conservation because the protection of "hotspots" should prevent the

extinction of a larger number of species than would the protection of areas of a similar size elsewhere (Reid 1998). In fact section 35 of Canada's *Oceans Act*, one legislative tool used to implement MPAs in Canada, explicitly states that MPAs should protect "marine areas of high biodiversity". From the literature reviewed in this chapter, it is clear that population viability is a critical site selection criterion for marine reserves, particularly for open marine populations that are subject to source/sink dynamics. However, it remains unclear if areas of high species diversity actually encompass viable, self-replenishing, source populations and thus truly represent optimal areas for protection.

### 1.5.1 Research Objectives

The objective of this thesis was to examine the relationship between biological diversity and population viability, two marine protected area site selection criteria, using the intertidal as a model system and the black chiton, *Katharina tunicata*, as a model species. Specifically, this study investigated if areas of high faunistic and floristic species diversity contained *Katharina* populations with high reproductive output relative to areas of lower biodiversity. This was achieved by comparing the population viability of *Katharina tunicata*, as measured by its potential reproductive output, in areas of high and low species diversity. A gradient of wave-exposure, the primary disturbance thought to structure rocky intertidal communities (Denny 1995), was used to ensure varying levels of biodiversity at each site. The overall goal of this investigation was to contribute to the theoretical basis for selecting the location of both rocky intertidal and subtidal MPAs that encompass both representative and viable populations.

### 1.5.2 Rationale

The rocky intertidal ecosystem is an ideal model system in which to test MPA site selection theory for several reasons. Firstly, intertidal benthic organisms have life histories similar to subtidal marine species, however, the intertidal is more easily accessible and thus more financially practical to study. Furthermore, many intertidal species are functionally important to coastal ecosystems as they form the basis of food webs for more charismatic marine mammals, birds and fish whose declines have prompted public concern. The intertidal is an important system to consider for protection in its own right because intertidal invertebrates and algae, accessible to both harvesters and tourists, represent a threatened and poorly known resource (Hawkes 1994, West 1997). Moreover, the effects of intertidal shellfish and algal harvesting have been shown to radically alter coastal ecosystems (Castilla and Duran 1985, Castilla and

Bustamante 1989). In North America, shoreline-harvesting intensity has increased dramatically over the past decade and remains largely unregulated and unmonitored (West 1997).

The Black Chiton, *Katharina tunicata*, phylum Mollusca, class Polyplacophora, was the model species investigated because it is a broadcast spawner and thus subject to source/sink dynamics, is ubiquitous in Barkley Sound and is easily found. Furthermore, it is common across a range of wave-exposures, and its population size structure and reproductive output are easily quantifiable. Lastly, *Katharina tunicata* has been well studied in the Pacific Northwest (Duggins and Dethier 1985, Dethier and Duggins 1988, Markel and DeWreede 1998), therefore, much is known about its ecological interactions in the rocky intertidal.

### 1.5.3 Hypotheses

Two ecological hypotheses make opposing predictions about the relationship between population viability and biological diversity. The Intermediate Disturbance Hypothesis (Paine 1969, Connell 1978, Kilar and McLachlan 1989, Aronson and Precht 1995, Dial and Roughgarden 1998), predicts that species diversity will be greatest at intermediate levels of disturbance<sup>4</sup> (Figure 1.3). When disturbance is low or infrequent, a community is dominated by a few competitively dominant species. When disturbance is high or frequent, quick growing, opportunistic, early colonizers dominate a community. Therefore, multiple species can co-exist only when a competitive dominant is prevented from monopolizing a resource (Paine 1969, Connell 1978, Castilla and Duran 1985), such as space in the rocky intertidal. At intermediate levels of disturbance, both competitive dominants and early opportunistic species may persist but no single species does particularly well. Under such circumstances, species are living at the limit of their ecological range and competing for resources, rather than thriving at their ecological optimum (Figure 1.4 A). Consequently, the Intermediate Disturbance Hypothesis suggests that diverse sites encompass populations of species with relatively low population viability. Following this conjecture, biodiversity hotspots may not prove to be sources of larvae, at least for dominant species.

In contrast, the Productivity-Diversity Hypothesis proposes that over a range of resource levels, the presence of more resources will allow more species to co-exist (Huston 1979) (Figure 1.4 B). This relationship may arise because higher productivity allows species to reach higher population densities (Srivastava and Lawton 1998) and rare species become sufficiently common

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<sup>4</sup> Disturbance can be due to predation, herbivory or physical impacts such as fire, floods or wave-exposure (Krebs 1994).

to observe. Therefore, the Productivity-Diversity Hypothesis suggests that high species richness should occur where species are most productive (i.e. source populations). Nevertheless, at enhanced resource levels (i.e. eutrophication), competitive dominants may eliminate other species or conditions may become anoxic and livable for most species.

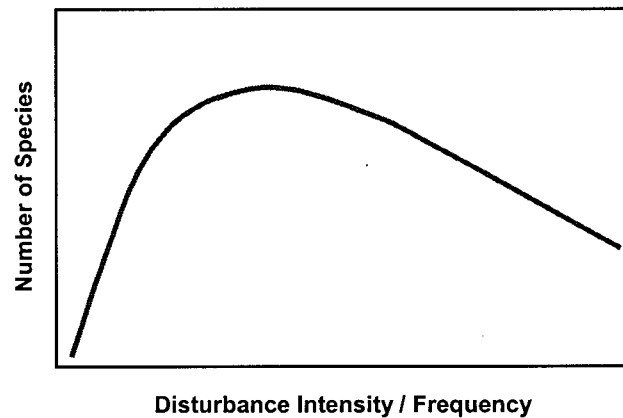


Figure 1.3 The relationship between species richness and disturbance as predicted by the Intermediate Disturbance Hypothesis. High diversity occurs at intermediate levels of disturbance (modified from Connell, 1978).

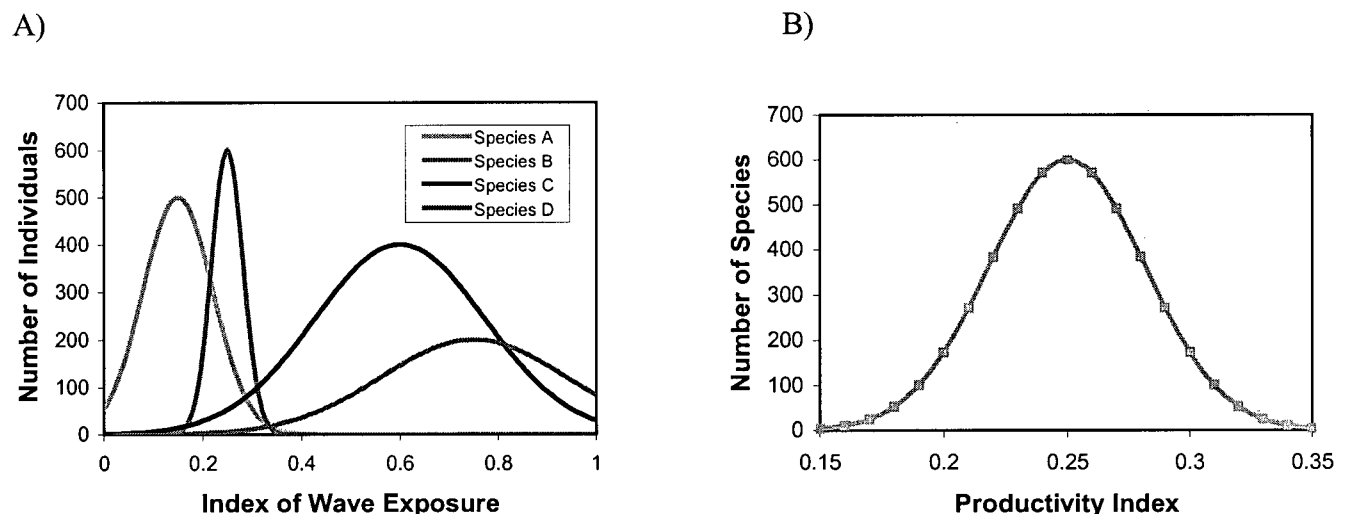


Figure 1.4 A&B (A) Distributions of species across an environmental gradient, where diversity is highest where the edges of species ranges overlap. Therefore, the potential reproductive output of populations may be low in areas of high species diversity. (B) A distribution of species richness across an environmental gradient where diversity is highest where all species are productive. Thus, the potential reproductive output of a population may be high in areas of intermediate productivity and high species diversity.

In this thesis, the main null and alternative hypotheses were tested:

- H<sub>0</sub> No relationship exists between biological diversity and population viability as measured by potential reproductive output.
- H<sub>A1</sub> Areas of high biological diversity encompass populations of relatively high potential reproductive output.
- H<sub>A2</sub> Areas of high biological diversity encompass populations of relatively low potential reproductive output.

In marine systems, both the Intermediate Disturbance Hypothesis and the Productivity-Diversity Hypothesis play out within a context established by larval dispersal. Because wave force was speculated to be the predominant factor structuring rocky intertidal biodiversity, it was postulated that the Intermediate Disturbance Hypothesis was likely the mechanism responsible for variation in site biodiversity and thus areas of high biodiversity were likely to encompass sink populations with relatively low population viability.

Biological diversity can be defined at a number of hierarchical levels, e.g. genetic, species, and ecosystem. In this thesis, biological diversity is described in terms of species diversity, which in itself can be quantified by a plethora of indices (Magurran 1988). Here, I use species richness and the Shannon-Wiener Diversity index to measure species richness.

## 1.6 OUTLINE OF CHAPTERS

The literature review provided in Chapter 1 of this thesis was designed to introduce the reader to the concept of marine protected areas and some of the ecological issues relevant to marine protected area design and site selection. This chapter provides the rationale for using the rocky intertidal as a model system and why the Black chiton, *Katharina tunicata*, was used as a model broadcast spawning species. Chapter 2 describes how the potential reproductive output of the 10 *Katharina* subpopulations under investigation was estimated and discusses the association between reproductive output and wave-exposure. Chapter 3 uses this information to explore the relationship between *Katharina*'s population viability and intertidal biodiversity. It is in this chapter that the role of biodiversity as a protected area site selection criterion is ultimately questioned. A side project, which coincidentally led to the funding of this thesis, is presented in Chapter 4. Here, published empirical evidence demonstrating the ecological impacts of temperate MPAs is analyzed and critiqued. Finally, Chapter 5 provides a synthesis and summary of the work presented and discusses some of the socio-economic issues pertinent to MPA site

selection and design. This thesis was written with the intent that Chapter 2,3 and 4 be used as a foundation on which to write 3 unique manuscripts for publication. Because of this some repetition occurs.

## **2.1 INTRODUCTION**

The spatial protection of viable, self replenishing, source populations in the form of marine protected areas has been suggested as an essential conservation strategy for marine metapopulations subject to source/sink dynamics (Carr and Reed 1993, Quinn et al. 1993, Roberts 1997a, Allison et al. 1998, Roberts 1998). This has prompted the need for new methods to identify source populations and estimate their population viability in terms of potential reproductive output.

Both gamete production and fertilization efficiency influence zygote production and therefore the potential reproductive output of a population. While various studies have demonstrated that gamete production and body size of marine invertebrates are directly proportional (Himmelman 1978, Suchanek 1981), estimating reproductive success from gamete production alone can be inappropriate (Levitan 1991). This is because the abundance, density and behavior of conspecifics may significantly affect individual fertilization success and therefore zygote production. In marine systems, the fertilization efficiency of free-spawning invertebrates that broadcast their gametes is likely a function of population density (Denny and Shibata 1989, Quinn et al. 1993). Higher densities increase the chance of fertilization. However, this relationship is complicated by the likelihood that organisms may exhibit an inverse relationship between body size and population density due to resource limitation or variation in recruitment and survivorship. As a result a tradeoff exists between a) a large individual size and high individual gamete production at low population density and b) a smaller individual size and lower gamete production at higher population density (Levitan 1991). In this study, the black chiton, *Katharina tunicata*, was used as a model species to explore this trade-off, determine if it is associated to wave-exposure and further investigate the implications of population viability to marine protected area site selection.

*Katharina tunicata*, found from Alaska southward to Point Conception, California (Himmelman 1978), is a free-spawning mollusc present in the mid to low temperate rocky intertidal (Kozloff 1973). This invertebrate is a herbivore that exerts high grazing pressure on articulated coralline algae, bladed macroalgae and epiphytic diatoms. Past studies suggest that *Katharina* plays a critical role in structuring lower intertidal communities through herbivory (Dethier and Duggins 1984, Dethier and Duggins 1988, Markel and DeWreede 1998).

### 2.1.1 Reproduction and Development of *Katharina tunicata*

The annual reproductive cycle of *Katharina tunicata* involves the periodic growth and development of gonads, followed by a seasonally moderated release of gametes (Strathmann 1987). Adults become sexually mature when they reach a length of 33-36 mm, usually 2 years after settlement. Spawning occurs from April to July and peaks in June, coinciding with spring phytoplankton blooms (Himmelman 1978). Gametes from both males and females are released from a single dorsal gonad contained by a germinal epithelium. Typically, males begin spawning first which has been suggested to stimulate female spawning events (Strathmann 1987). Ovaries are not emptied in a single spawning event, rather, individuals may release gametes repeatedly for several days. Each female egg is approximately 230  $\mu\text{m}$  in diameter and is surrounded by a vitelline membrane known as a hull, which measures 425  $\mu\text{m}$  in diameter. Fertilization is external. It has been demonstrated that spermatozoa become active in sea water and show species specific chemotaxis to eggs (Miller 1977). Once fertilized, young hatch from the egg hull as actively swimming trochophores. Larvae are pelagic for approximately 6 days, during which their trajectory is governed by local current patterns. Research suggests that settlement and metamorphosis of *Katharina tunicata* are induced by the encrusting coralline algae *Lithothamnion* sp. (Rumrill and Cameron 1983). Clearly, the recruitment and development of *Katharina* is greatly influenced by water currents and wave-exposure.

### 2.1.2 Wave-exposure and Reproductive Output

The intertidal communities of surf-swept rocky shores are profoundly affected by wave-exposure, the degree to which a site is exposed to the force of wave-impact. In the intertidal, wave-exposure varies with tidal height, the proximity to open ocean swell and topographic features which modify wave breaking patterns (Milligan 1998). A compression force capable of damaging and dislodging intertidal organisms is created when waves impact the shore. However, the greatest hydrodynamic force is created by the subsequent turbulent flow moving parallel to the substratum generated from wave surge (Denny 1988). It was this component of wave-exposure that was quantified in the following study by maximum wave force recorders.

Wave-exposure has been hypothesized to affect fertilization efficiency (Denny and Shibata 1989), the demographic rates of a population such as recruitment<sup>5</sup> and mortality, and population densities (Magalhaes 1998). Furthermore, wave-exposure has been postulated to alter

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<sup>5</sup> Recruitment is the addition of new individuals to a population (Doherty and Williams 1988). In this thesis, recruitment is specifically defined as the appearance of macroscopic sized individuals.



the reproductive output of both intertidal invertebrates (Denny et al. 1985) and algae (Gaylord et al. 1994).

### 2.1.3 Research Objectives

The goal of this chapter was to assess variation in potential reproductive output among subpopulations of *Katharina*. Those subpopulations with high reproductive output are most likely to be sources of larvae and disproportionately valuable for conservation via marine protected areas. The specific questions addressed in this chapter are: How do the size structure, density and potential reproductive output of *Katharina tunicata* subpopulations vary among sites? Is this variation related to physical factors such as wave-exposure or tide height? Answering these questions required establishing the relationship between *Katharina* length and gonad weight and testing whether this relationship was valid across sites of varying wave-exposure. Potential reproductive output (PRO) was then calculated from size-specific gonad weight estimates and densities at 10 sites.

This research was conducted within the larger context of this thesis: the critical role of population viability as a site selection criterion for marine protected areas. Chapter 3 will then make use of this chapter's information and determine if a significant relationship exists between a population's potential reproductive output and biodiversity.

## 2.2 METHODS

### 2.2.1 Study Site

This research was conducted at 10 sites on 6 islands within the Deer Group Archipelago located in Barkley Sound, British Columbia, Canada ( $49^{\circ} 50' \text{ N } 125^{\circ} 12' \text{ W}$ ) (Figure 2.1). Five exposed (E) and 5 semi-sheltered (S) sites were chosen (Table 2.1). When sites were being identified for study, highly articulated coastline was avoided to reduce within site variability. In order to restrict between site variability to wave-exposure, care was taken to maintain slope consistency among sites. Each site was approximately 40 m in length.

In the Sound, the predominant wind and swell direction runs southwest to northeast creating a gradient of wave-exposure. Outer islands, particularly Edward King and Seppings, were subject to greater wave-exposure than the inner semi-protected islands of Helby and Sandford, yet local site variability in aspect and topography plus adjacent seafloor topography dampened or magnified the degree of wave-exposure at each site.

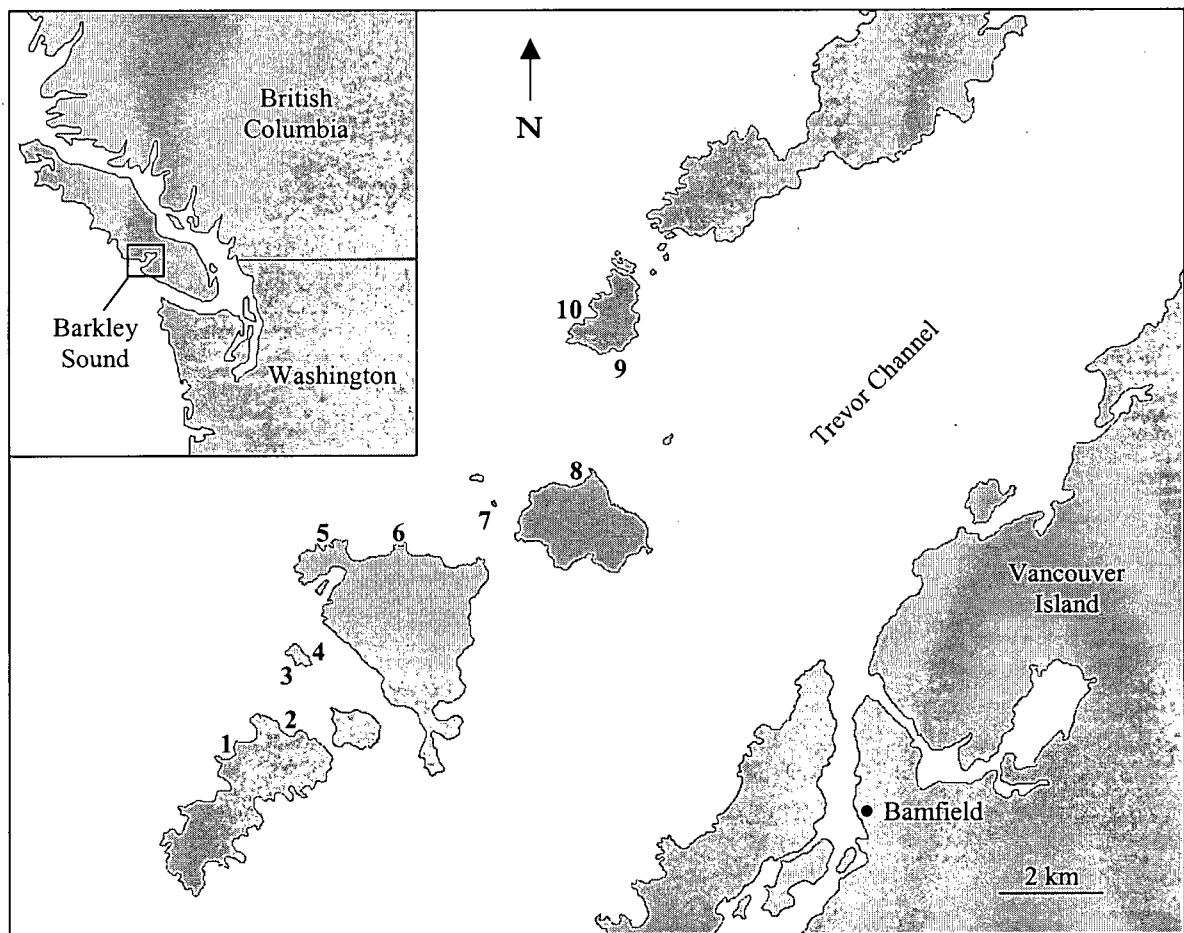


Figure 2.1 Deer Group archipelago, Barkley Sound, British Columbia, Canada ( $49^{\circ} 50' N$   $125^{\circ} 12' W$ ). The potential reproductive output of *Katharina* populations was estimated at 10 sites, 5 exposed and 5 semi-sheltered. 1 = Edward King Exposed, 2 = Edward King Sheltered, 3 = Seppings Exposed, 4 = Seppings Sheltered, 5 = Kirby, 6 = Diana, 7 = Wee, 8 = Helby, 9 = Sanford Exposed, 10 = Sanford Sheltered.

Table 2.1 The population size structure and potential reproductive output of *Katharina* was determined at 10 sites, 5 exposed and 5 semi-sheltered. \* indicates those sites where *Katharina* individuals were collected for dissection to establish the length-fecundity relationship.

Exposed Sites	Semi-sheltered Sites
1 Edward King Exposed	2 Edward King Sheltered
3 Seppings Exposed*	4 Seppings Sheltered*
6 Diana*	5 Kirby
8 Helby*	7 Wee*
9 Sanford Exposed	10 Sanford Sheltered

### 2.2.2 Length-Fecundity Model

To estimate the potential reproductive output (PRO) of *Katharina tunicata* populations at each site, a length-fecundity model was generated. A total of 75 *Katharina* were randomly collected from 5 sites of varying exposure (Seppings E, Seppings S, Wee, Helby, and Diana) just prior to spawning season. The maximum body length of each individual was measured with a pair of calipers to the nearest 0.5 cm. Five individuals were randomly collected from 3 pre-established size classes (3.5-5 cm, 5.5-7 cm, 7.5+ cm). Individuals smaller than 3.5 cm were not collected because below this length *Katharina* are not yet reproductive (Strathmann 1987). The gonads of each animal were excised and a wet and dry weight to the nearest 0.01g was recorded (Appendix I).

Variance in the gonad wet and dry weight data increased with increasing body length resulting in heterogeneity of variance, therefore, gonad weight was log transformed to normalize the data. A correlation analysis was used to compare the relationship between log gonad wet weight and dry weight. Dry weight values were chosen for the length-fecundity model as they generally afford a better comparison among biological material (Brower et al. 1989) because wet weight values are subject to more extreme variance stemming from fluctuations in water content and evaporation rates. The relationship between body length and gonad dry weight was determined by linear regression. The resulting length-fecundity model was based on 70 individuals (no gonad could be recovered from 4 individuals and 1 individual was an extreme outlier whose Studentized Residual value provided rationale for its elimination from the data set).

An analysis of co-variance (ANCOVA), using length as the covariate, was used to determine if the length-fecundity relationship varied between sites of varying wave-exposure and population density. By using an ANCOVA, the main effect and interactions of the independent

variable (length) is assessed after the dependent variable scores (gonad dry weight) are adjusted for differences associated with one or more covariate(s) (length). By accounting for the relationship between the dependent variable and the covariate, an ANCOVA effectively reduces the error term resulting in increased test sensitivity (Tabachnick and Fidell 1996). In other words, an ANCOVA increases the power of an F-test by removing the predictable variance associated with the covariate from the error term. In conclusion, the main goal of using an ANCOVA was to test the null hypothesis that all 5 sites from which *Katharina* had been collected and dissected had the same mean gonad dry weight after adjusting for differences in maximum body length.

### 2.2.3 Population Size Structure and Density

A 40 m long transect line, with 10 randomly stratified points along it, was placed parallel to the shore in the middle of the *Hedophyllum* zone. It had been observed that larger *Katharina* tended to be located in the lower intertidal, and smaller individuals tended to be found in the higher reaches of the *Hedophyllum* zone (DeWreede 1998, personal comment). As a result, a vertical band sampling procedure was developed to account for the variation in the potential spatial distribution of size classes. Five randomly placed 0.5 m wide sampling bands, running perpendicular to the shore, were used to quantify the population size structure and density of *Katharina* at 8 of the 10 sites sampled (Appendix II). (Ten perpendicular 0.5 m wide bands were used at the first 2 sites sampled, Wee and Seppings S, but due to tidal time constraints, the procedure was modified to 5 0.5 m wide bands for the remaining 8 sites.) This procedure was accomplished by placing a 0.25 cm<sup>2</sup> quadrat above one of the 5 randomly selected stratified points in the upper reaches of *Katharina* habitat. Within the quadrat, the maximum body length of all *Katharina* was measured with calipers to the nearest 0.5 cm. The quadrat was then lowered sequentially and the procedure continued to the extent of the low water line. In addition, the distance between each individual *Katharina* and the upper reaches of the *Hedophyllum* zone (*Katharina* habitat) was measured to test the observation that led to this sampling procedure.

Two-sample, Bonferroni adjusted, Kolmogorov-Smirnov paired comparisons were used to determine if size-frequency distributions of *Katharina* differed significantly between sites. This nonparametric test is sensitive to the location, dispersion, skewness and kurtosis of frequency distributions (Sokal and Rohlf 1969). Because pairwise comparisons were conducted between each of the 10 sites, a total of 45 comparisons were made. Probability values from each paired comparison were compared to alpha values which were sequentially Bonferroni adjusted

for multiple comparisons (Appendix III) in such a manner that the most significantly different paired comparison had to be  $p < 0.05 / 45$  (0.00111) to be significant. The next most significantly different paired comparison had to be  $p < 0.05 / 44$ , (0.00114) to be significant and so forth.

Significant differences between the body length of *Katharina* at each site were determined with an analysis of variance (ANOVA), followed by a Bonferroni Post Hoc test. *Katharina* densities at each site were also compared with an ANOVA and a Bonferroni Post Hoc test.

#### 2.2.4 Estimating Potential Reproductive Output

The potential reproductive output (PRO) of *Katharina* populations at each site was estimated in two distinct ways. The first method entailed substituting the mean length of *Katharina*, calculated for each of the 10 sites, into the length-fecundity model described above, to determine each population's mean log reproductive output. This was then converted into mean reproductive output (MRO) by taking its antilogarithm. To account for the Allee effect and density dependence, a population's PRO was then determined by multiplying its MRO by its mean density of *Katharina* (number of individual *Katharina* per 0.25m<sup>2</sup> quadrat):

$$\text{PRO} = \text{MRO (g/individual)} \times \text{mean density of } \textit{Katharina} \text{ (n/Quadrat)} \quad (1)$$

Because establishing a population's PRO resulted in one final datum per site, no error structure could be associated with the PRO metric thereby preventing statistical analysis between sites. As a result, a second re-sampling method was designed to develop an error structure and allow for statistical analysis.

The second method used to calculate *Katharina*'s potential reproductive output at each site involved the creation of a Visual Basic Randomized Re-sampling Program (Appendix IV). Thirteen size classes were established (3 cm or less, 4, 4.5, 5, 5.5, 6, 6.5, 7, 7.5, 8, 8.5, 9, 9.5+ cm). In this method, the known frequency of individuals in a size class was multiplied by a randomly chosen gonad dry weight (GDW) value established for that size class (Appendix I)<sup>6</sup>. This product was calculated for each size class, summed over all the size classes and then multiplied by site density. To generate an error structure, this scenario was reiterated 100 times

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<sup>6</sup> The size class 3 cm or less was always assigned a value of 0g GDW because *Katharina* below this size are not reproductive (Strathmann 1987).

for each site (Appendix V). As a result a mean  $PRO_R$  and associated error could be established.

\*Note: To distinguish between these two methods used to quantify potential reproductive output, the values derived from the Visual Basic Randomized Re-sampling method have been designated as randomized potential reproductive output ( $PRO_R$ ).

### 2.2.5 Measuring Maximum Wave Force

A stainless steel rock-climbing anchor was drilled into the rock in the middle of the *Hedophyllum sessile* zone, in the center of each site. Overhanging algae surrounding the bolts were removed to prevent recorder entanglement. During the August, September, and October low tide cycle, a wave force recorder was attached to the climbing anchor with zip ties at each field site. Recorders were deployed and were revisited 3 times during the tidal cycle at low tide. Each day, spring extensions were measured to the nearest 0.5 mm and were then reset. Spring extension data collected in the field were then converted to maximum wave force (N) with the calibration curves established earlier in the lab (Appendix VI).

Maximum wave force recorders (Figure 2.2) were calibrated in the lab by hanging known masses from each recorder and measuring their spring extension. The force required to extend the spring within each recorder was calculated by:

$$F = M \cdot a_g \quad (2)$$

where  $F$  is the force measured in Newtons (N),  $M$  is the known mass measured in kilograms (kg), and  $a_g$  is the gravitational acceleration constant ( $9.81 \text{ m} \cdot \text{s}^{-2}$ ). For each recorder, force was plotted against the resulting spring extension (m). Linear regressions were calculated and plotted so that forces could be estimated in the field from the observed spring extensions (Appendix VI). Equation (2) can be written more specifically to describe spring extension:

$$F = (k \cdot x_{\text{spring}}) + c \quad (3)$$

where  $k$  is the spring extension constant ( $\text{N} \cdot \text{m}^{-1}$ ),  $x_{\text{spring}}$  is the spring extension (m), and  $c$  is the force required to overcome the initial spring compression. Two different spring tensions were used in the wave force recorders. “Heavy” springs (spring extension constant  $\cong 1999 \text{ N} \cdot \text{m}^{-1}$ ) were used at exposed sites and “light” springs (spring extension constant  $\cong 199 \text{ N} \cdot \text{m}^{-1}$ ) were used at semi-protected sites.

Maximum wave force data were normally distributed. Because October maximum wave force data were missing from Edward King Exposed, Diana, and Sanford Exposed due to hazardous conditions, a repeated measures ANOVA was not possible due to missing data. Rather, an ANOVA and a Bonferroni Post Hoc Test were run on each month's data individually to determine whether sites were subject to significantly different maximum wave forces within each month.

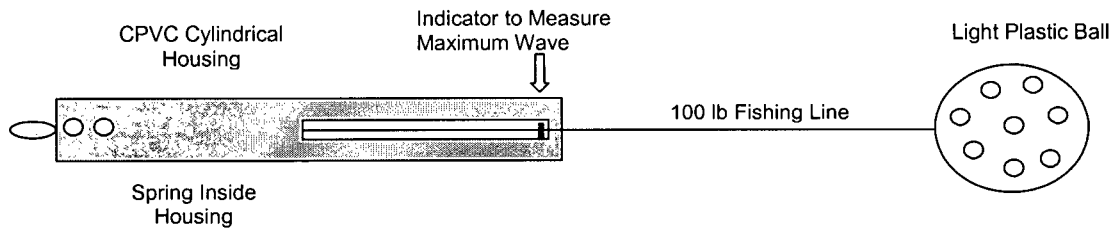
Sites were then lumped into 2 wave-exposure categories; exposed and semi-sheltered, based on September and October maximum wave force data. Unpaired t-tests were run to determine if there was a significant difference between sites categorized as exposed and semi-sheltered and if this distinction held monthly.

*Katharina* body length data were not normally distributed (skewness/SE skewness = 2.493, kurtosis/SE kurtosis = 3.284)<sup>7</sup>, consequently, a Mann-Whitney U test was used to investigate whether there was a significant difference in *Katharina* body length between exposed and sheltered sites. A Spearman's rank correlation test, a nonparametric rank order test, was then used to determine if a significant correlation existed between September maximum wave force data and *Katharina* body length. The relationship between *Katharina* density and maximum wave force was also examined with the use of the Spearman's Rank correlation test. This nonparametric rank order test was appropriate in both cases given that September maximum wave force data had a high skewness value. September data were used because exposure categories were shown to be significant and data were available from all 10 sites, unlike the October sampling period. A correlation was determined to be significant when the correlation coefficient  $r > r_{\text{critical}}$ . When  $n = 10$  and d.f. = 8,  $r_{\text{critical}[0.05]} = 0.632$ , and  $r_{\text{critical}[0.01]} = 0.765$  (Sokal and Rohlf 1969).

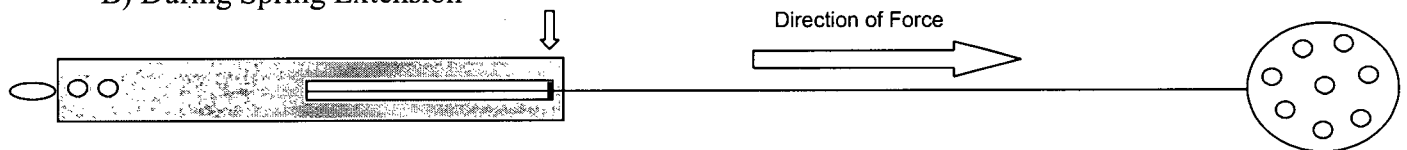
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<sup>7</sup> Skewness is a measure of the symmetry of a distribution about its mean. If skewness is significantly nonzero, the distribution is asymmetric. The skewness coefficient is significant if the absolute value of skewness/SE skewness is  $> 2$ . Kurtosis is a measure of the "pointyness" of the distribution. A kurtosis coefficient is considered significant if the absolute value of kurtosis/SE kurtosis is  $> 2$  (Tabachnick and Fidell 1996).

A) Before Spring Extension



B) During Spring Extension



C) After Spring Extension

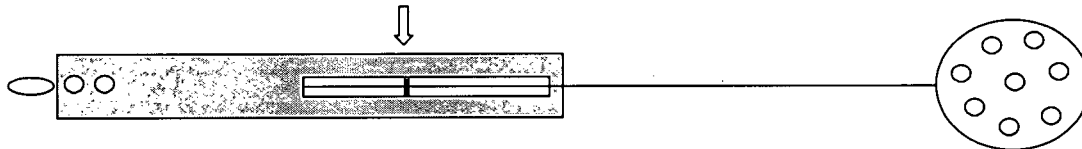


Figure 2.2 A schematic diagram of a maximum wave force recorder, the device used to quantify maximum wave force at each site. (A) A recorder was attached to a stainless steel rock-climbing anchor that had been drilled into the rock at each site. (B) As the plastic ball is pulled away from the PVC housing, the spring inside the housing is stretched and the indicator shifts in position. (C) When the spring relaxes, the indicator remains in the new position, which is related to maximum wave force based on a prior calibration.



## 2.3 RESULTS

### 2.3.1 Length-Fecundity Model

Gonad wet and dry weights (log transformed) were significantly positively correlated ( $n = 70$ , d.f. = 68, Pearson  $r = 0.942$ ,  $p < 0.01$ ) (Figure 2.3). When length was accounted for, an ANCOVA revealed that there was no significant difference in gonad dry weight between sites of varying wave-exposure ( $n = 5$ , d.f. = 4,  $F = 1.677$ ,  $p = 0.167$ ). Furthermore, no significant difference in gonad dry weight was found between male and female *Katharina* ( $n = 70$ , d.f. = 1,  $F = 0.2$ ,  $p = 0.656$ ). However, gonad dry weight was found to vary significantly with body length ( $n = 70$ , d.f. = 1,  $F = 107.32$ ,  $p = 2.139 \times 10^{-11}$ ).

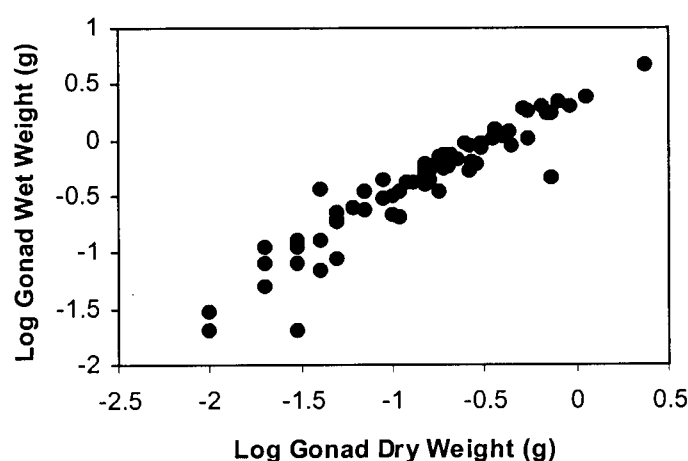


Figure 2.3 The relationship between gonad wet and dry weights. Measurements were log-transformed to improve normality ( $n = 70$ , d.f. = 68, Pearson  $r = 0.942$ ,  $p < 0.01$ ).

A linear regression described the significant relationship between body length and gonad dry weight (log transformed) ( $n = 70$ , d.f. = 1,  $R^2 = 0.5616$ ,  $p = 8.506 \times 10^{-14}$ ) and was used as the basis for the length-fecundity model (4) (Figure 2.4):

$$y = 0.2359x - 2.3859 \quad (4)$$

where:

$y$  = gonad dry weight log transformed (g)

$x$  = body length (cm)

The relationship between body length and gonad wet weight (log transformed) had a slightly lower  $R^2$  value ( $R^2 = 0.5313$ ) than that of the length relationship based on dry weight ( $R^2 = 0.5616$ ) (Figures 2.4 & 2.5).

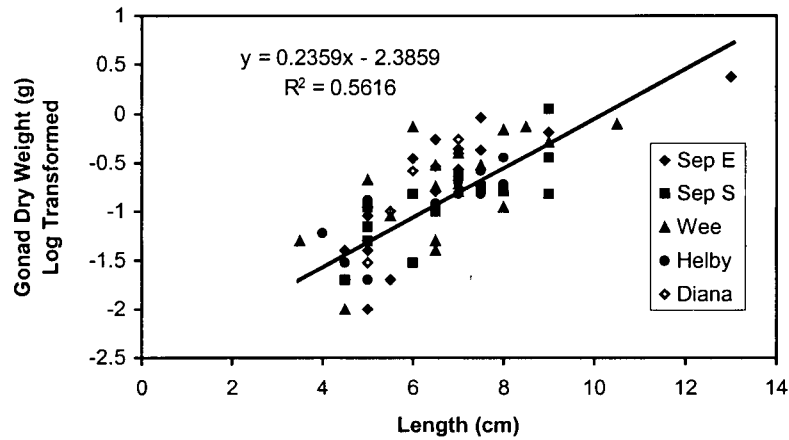


Figure 2.4 The relationship between length and gonad dry weight of *Katharina tunicata* ( $n = 70$ , d.f. = 1,  $R^2 = 0.5616$ ,  $p = 8.506 \times 10^{-14}$ ). Individuals were collected from 5 sites of varying wave-exposure in the Deer Group Archipelago. Measurements were log-transformed to improve normality. This relationship was used to calculate the potential reproductive output (PRO) of all 10 *Katharina* subpopulations.

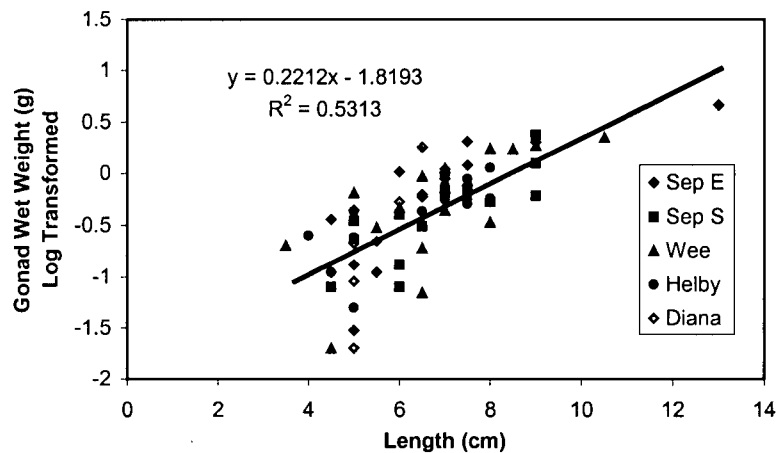


Figure 2.5 The relationship between length and gonad wet weight of *Katharina tunicata* ( $n = 70$ , d.f. = 1,  $R^2 = 0.5313$ ,  $F = 77.085$ ,  $p = 8.437 \times 10^{-13}$ ). Individuals were collected from 5 sites of varying wave-exposure in the Deer Group Archipelago. Measurements were log-transformed to improve normality. Because the  $R^2$  value was lower for the relationship between length and gonad wet weight than for dry weight, the length-fecundity model was based on gonad dry weight.

### 2.3.2 Location of *Katharina* in the *Hedophyllum* Zone

At each of the 10 sites, *Katharina* body length did not vary significantly with respect to its location in the *Hedophyllum* zone. Edward King Exposed ( $n = 52$ ,  $R^2 = 5 \times 10^{-7}$ ), Edward King Sheltered ( $n = 186$ ,  $R^2 = 0.026$ ), Seppings Exposed ( $n = 148$ ,  $R^2 = 0.028$ ), Seppings Sheltered ( $n = 184$ ,  $R^2 = 0.008$ ), Kirby ( $n = 72$ ,  $R^2 = 0.028$ ), Diana ( $n = 249$ ,  $R^2 = 0.039$ ), Wee ( $n = 287$ ,  $R^2 = 0.003$ ), Helby ( $n = 267$ ,  $R^2 = 0.143$ ), Sanford Exposed ( $n = 136$ ,  $R^2 = 0.003$ ), Sanford Sheltered ( $n = 31$ ,  $R^2 = 0.022$ ) (Appendix VII).

### 2.3.3 Population Size Structure and Density

Table 2.2 reveals which *Katharina* size-frequency distributions, shown in Figure 2.6, were significantly different from one another. Wave-exposed populations had a higher proportion of smaller individuals whereas sheltered populations tended to have a greater proportion of larger individuals. A significant difference in body length existed between sites ( $n = 1612$ , d.f. = 1602,  $F = 22.74$ ,  $p = 1.067 \times 10^{-11}$ ) (Figure 2.7 & Table 2.3).

*Katharina* densities varied significantly among sites ( $n = 369$ , d.f. = 359,  $F = 10.278$ ,  $p = 1.431 \times 10^{-11}$ ) (Figure 2.8 & Table 2.4). A slight negative trend existed between body length and density yet this relationship was not significant within the Deer Group Archipelago ( $n = 10$ , d.f. = 8,  $R^2 = 0.022$ ,  $p = 0.685$ ) (Figure 2.9).

Table 2.2 Adjusted Kolmogorov-Smirnov paired comparison, two-sided probabilities. Bold values indicate those size-frequency distribution pairs that are significantly different (see Appendix III for adjusted alpha values).

	Diana	EK E	EK S	Helby	Kirby	San E	San S	Sep E	Sep S
<b>Diana</b>									
<b>EK E</b>	0.252								
<b>EK S</b>	<b><math>1.192 \times 10^{-7}</math></b>	<b><math>1.789 \times 10^{-7}</math></b>							
<b>Helby</b>	0.104	0.009	<b><math>1.192 \times 10^{-7}</math></b>						
<b>Kirby</b>	0.539	0.106	<b><math>1.490 \times 10^{-6}</math></b>	0.791					
<b>San E</b>	0.421	0.090	<b><math>1.192 \times 10^{-7}</math></b>	0.021	0.136				
<b>San S</b>	0.202	0.149	0.013	0.394	0.427	0.041			
<b>Sep E</b>	0.013	1.000	<b><math>1.192 \times 10^{-7}</math></b>	<b><math>4.113 \times 10^{-5}</math></b>	0.017	0.003	0.028		
<b>Sep S</b>	0.077	0.577	<b><math>1.192 \times 10^{-7}</math></b>	0.002	0.562	0.018	0.213	0.066	
<b>Wee</b>	0.018	0.002	<b><math>1.192 \times 10^{-7}</math></b>	0.016	0.790	<b><math>1.519 \times 10^{-4}</math></b>	0.059	<b><math>5.305 \times 10^{-6}</math></b>	0.009

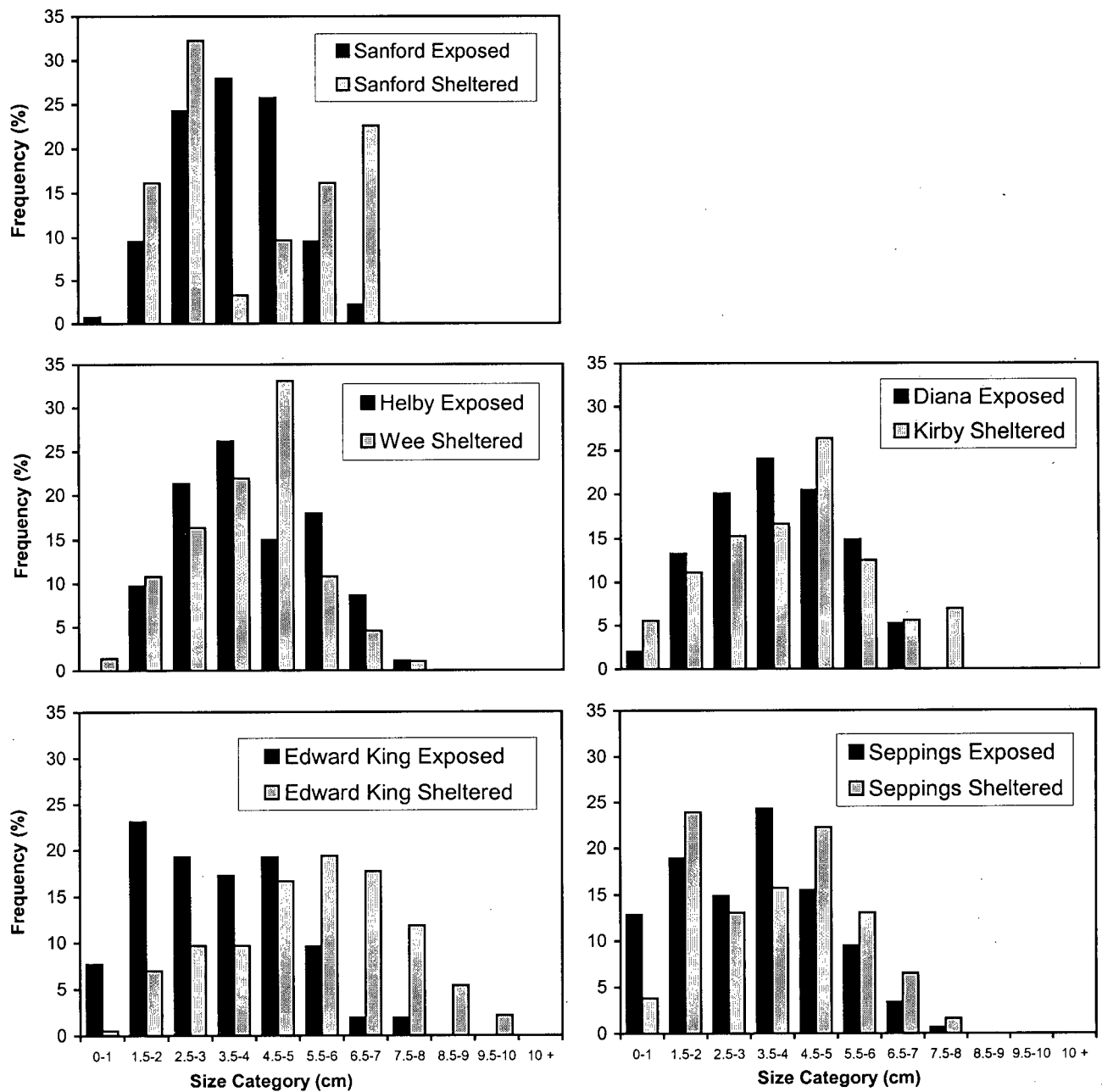


Figure 2.6 Population size structure of *Katharina* at all 10 sites. Bonferroni-adjusted two-sided probabilities of Kolmogorov-Smirnov paired comparisons indicate those frequency distributions that are significantly different from one another (Table 2.2).

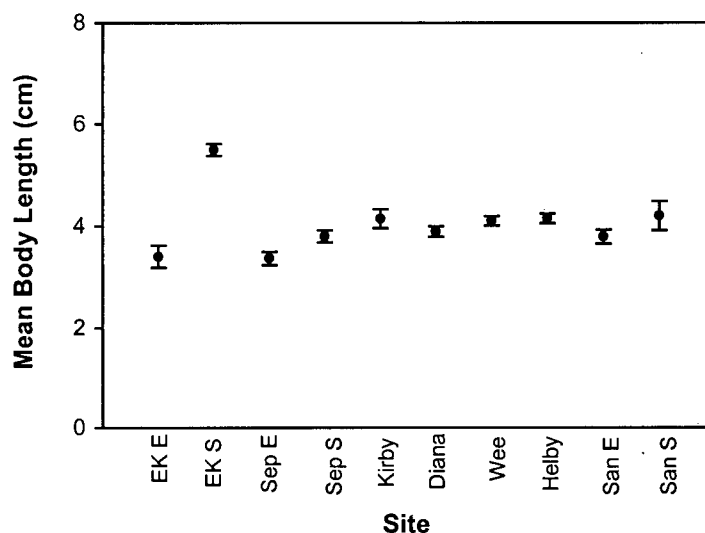


Figure 2.7 Least square means and associated standard error of *Katharina* body length at each site. An ANOVA revealed that a significant difference in body length existed among sites ( $n = 1612$ , d.f. = 1602,  $F = 22.74$ ,  $p = 1.067 \times 10^{-11}$ ). A Bonferroni Post Hoc test indicated where those significant differences occurred.<sup>8</sup>

Table 2.3 Bonferroni pairwise comparison probabilities of *Katharina* body length at each site.

	Diana	EK E	EK S	Helby	Kirby	San E	San S	Sep E	Sep S
<b>Diana</b>									
<b>EK E</b>	1.000								
<b>EK S</b>	1.000	$4.496 \times 10^{-14}$							
<b>Helby</b>	$4.496 \times 10^{-14}$	0.090	$4.496 \times 10^{-14}$						
<b>Kirby</b>	1.000	0.467	$3.354 \times 10^{-8}$	1.000					
<b>San E</b>	1.000	1.000	$4.496 \times 10^{-14}$	1.000	1.000				
<b>San S</b>	1.000	1.000	0.001	1.000	1.000	1.000			
<b>Sep E</b>	0.068	1.000	$4.496 \times 10^{-14}$	$7.834 \times 10^{-5}$	0.030	1.000	0.361		
<b>Sep S</b>	1.000	1.000	$4.496 \times 10^{-14}$	0.983	1.000	1.000	1.000	0.625	
<b>Wee</b>	1.000	0.161	$4.496 \times 10^{-14}$	1.000	1.000	1.000	1.000	$2.385 \times 10^{-4}$	1.000

<sup>8</sup> Unless otherwise noted, when all 10 sites appear on a graph, they will be arranged in their geographic location from West to East.

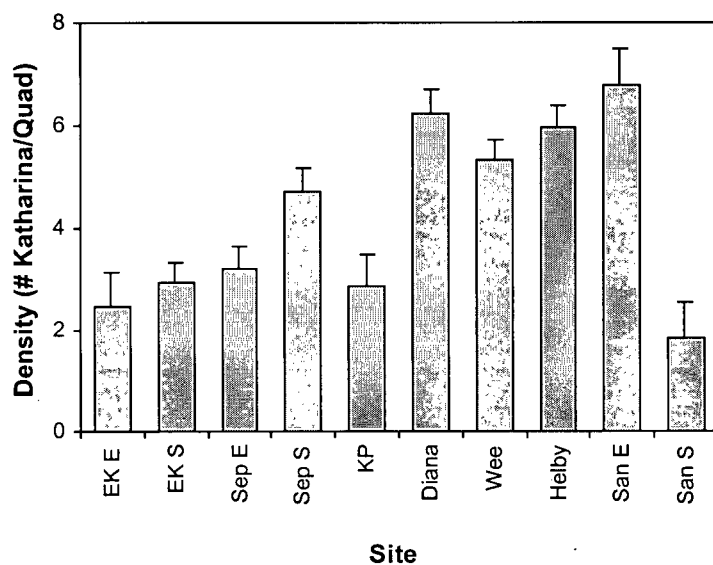


Figure 2.8 Mean *Katharina* density and associated standard error. *Katharina* density was significantly different among sites ( $n = 369$ , d.f. = 359,  $F = 10.278$ ,  $p = 1.431 \times 10^{-11}$ ).

Table 2.4 Bonferroni pairwise comparison probabilities of *Katharina* densities at each site.

	Diana	EKE	EKS	Helby	Kirby	Sep S	San E	San S	Sep E
<b>Diana</b>									
<b>EKE</b>	$2.756 \times 10^{-4}$								
<b>EKS</b>	$7.379 \times 10^{-6}$	1.000							
<b>Helby</b>	1.000	0.001	$2.772 \times 10^{-5}$						
<b>Kirby</b>	0.001	1.000	1.000	0.003					
<b>Sep S</b>	1.000	0.325	0.230	1.000	0.906				
<b>San E</b>	1.000	$3.070 \times 10^{-4}$	$5.225 \times 10^{-5}$	1.000	0.001	0.534			
<b>San S</b>	$3.731 \times 10^{-5}$	1.000	1.000	$1.103 \times 10^{-4}$	1.000	0.055	$4.498 \times 10^{-5}$		
<b>Sep E</b>	$2.754 \times 10^{-4}$	1.000	1.000	0.001	1.000	1.000	0.001	1	
<b>Wee</b>	1.000	0.014	0.002	1.000	0.045	1.000	1.000	0.002	0.029

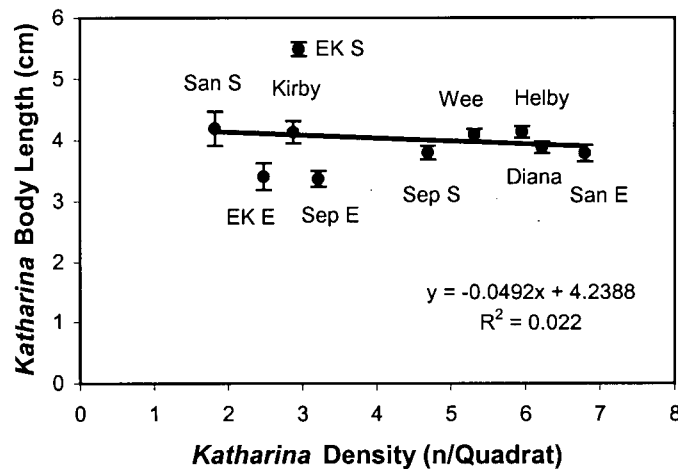


Figure 2.9 *Katharina* density and body length ( $n = 10$ , d.f. = 8,  $R^2 = 0.022$ ,  $p = 0.685$ ).

### 2.3.4 Maximum Wave Force and Site Exposure

No significant differences in maximum wave force were found among sites in August ( $n = 28$ , d.f. = 27,  $F = 0.962$ ,  $p = 0.500$ ) (Figure 2.10). However, in September, wave forces did differ among the 10 sites ( $n = 29$ , d.f. = 28,  $F = 12.316$ ,  $p = 3.383 \times 10^{-6}$ ) (Figure 2.10 & Table 2.5). In October, sites receiving highest September wave force were inaccessible and there were no differences in wave force among other sites ( $n = 11$ , d.f. = 10,  $F = 4.750$ ,  $p = 0.077$ ) (Figure 2.10). Even without the most exposed sites, maximum wave force was higher in October than in previous months.

When the 10 sites were divided equally into 5 exposed and 5 semi-sheltered sites, a t-test indicated that a significant difference in maximum wave force occurred in September ( $n = 10$ , d.f. = 8,  $t = 2.802$ ,  $p = 0.023$ ) yet not in August ( $n = 10$ , d.f. = 8,  $t = 1.120$ ,  $p = 0.295$ ), or October ( $n = 7$ , d.f. = 5,  $t = 1.549$ ,  $p = 0.082$ ) (Figure 2.11).

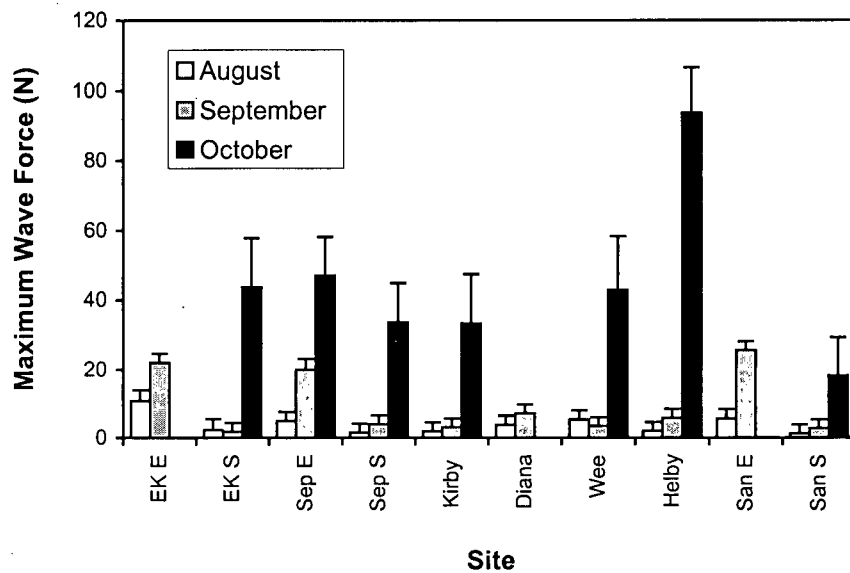


Figure 2.10 No significant differences in maximum wave force among sites were found in August ( $n = 28$ , d.f. = 27,  $F = 0.962$ ,  $p = 0.500$ ) or October ( $n = 11$ , d.f. = 10,  $F = 4.750$ ,  $p = 0.077$ ). However, note that October is lacking data from Edward King Exposed, Diana, and Sanford Exposed due to hazardous sea states and high wave-exposure. In September, a significant difference in maximum wave force was found among the 10 sites ( $n = 29$ , d.f. = 28,  $F = 12.316$ ,  $p = 3.383 \times 10^{-6}$ ).

Table 2.5 Bonferroni pairwise comparison probabilities of September's maximum wave force at each site.

	Diana	EK E	EK S	Helby	Kirby	San E	San S	Sep E	Sep S
<b>Diana</b>									
<b>EK E</b>	0.025								
<b>EK S</b>	1.000	0.001							
<b>Helby</b>	1.000	0.011	1.000						
<b>Kirby</b>	1.000	0.002	1.000	1.000					
<b>San E</b>	0.003	1.000	$1.170 \times 10^{-4}$	0.001	$2.411 \times 10^{-4}$				
<b>San S</b>	1.000	0.002	1.000	1.000	1.000	$2.066 \times 10^{-4}$			
<b>Sep E</b>	0.214	1.000	0.011	0.103	0.022	1.000	0.019		
<b>Sep S</b>	1.000	0.003	1.000	1.000	1.000	$4.031 \times 10^{-4}$	1.000	0.037	
<b>Wee</b>	1.000	0.003	1.000	1.000	1.000	$2.967 \times 10^{-4}$	1.000	0.027	1.000



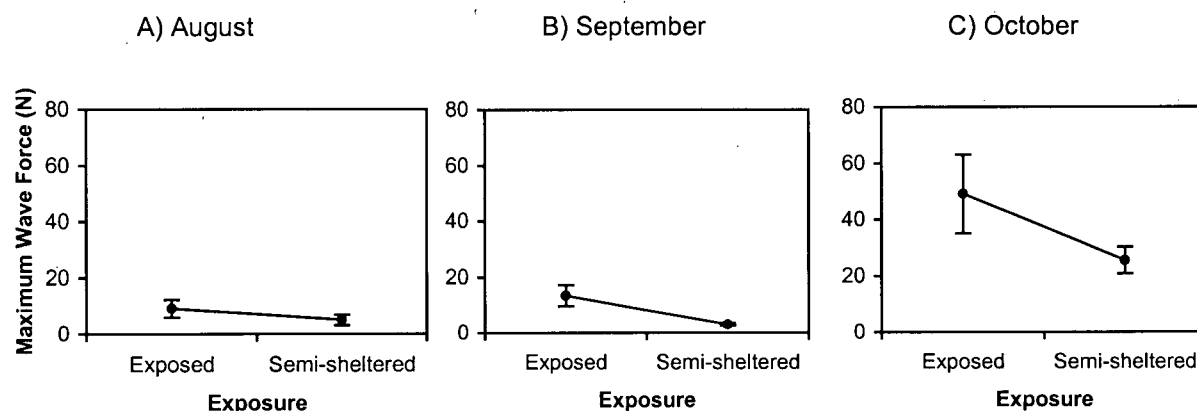


Figure 2.11 Mean monthly maximum wave force ( $\pm$  standard error) at 5 exposed and 5 sheltered sites. T-tests indicated that a significant difference in maximum wave force between exposed and semi-sheltered sites occurred in September ( $n = 10$ , d.f. = 8,  $t = 2.802$ ,  $p = 0.023$ ). However, no significant difference existed in August ( $n = 10$ , d.f. = 8,  $t = 1.120$ ,  $p = 0.295$ ) or in October ( $n = 7$ , d.f. = 5,  $t = 1.549$ ,  $p = 0.082$ ). The high variance associated with the exposed sites data in October was due to extremely hazardous wave force impacting 3 out of the 5 sites. As a result only two of the five sites could be reached and sampled in October.

### 2.3.5 Wave-exposure and *Katharina*'s Body Length and Density

No significant difference was found in *Katharina* body length between exposed and semi-sheltered sites ( $n = 10$ , d.f. = 8, Mann-Whitney U test statistic = 4.000,  $p = 0.076$ ). However, September maximum wave force was significantly negatively correlated to *Katharina* body length ( $n = 10$ , d.f. = 8, Spearman  $r = -0.794$ ,  $p < 0.01$ ). No significant correlation existed between maximum wave force and *Katharina* density ( $n = 10$ , d.f. = 8, Spearman  $r = 0.467$ ,  $p > 0.05$ ).

### 2.3.6 Estimating Potential Reproductive Output

When derived from the length-fecundity model, the *Katharina* subpopulations at Edward King Sheltered and Helby had the greatest potential reproductive output (PRO) values; **0.240** and **0.232** ( $n/\text{Quad} \cdot g \text{ GDW/ind}$ ) respectively. Sanford Exposed, Diana, and Wee also had similarly high PROs; **0.219**, **0.212**, and **0.202** ( $n/\text{Quad} \cdot g \text{ GDW/ind}$ ) respectively (Table 2.6 & Figure 2.12). No significant correlation existed between PRO and September's maximum wave force data ( $n = 10$ , d.f. = 8, Spearman  $r = -0.091$ ,  $p > 0.05$ ). Furthermore, no significant difference in PRO exists between wave exposed and semi-sheltered sites ( $n = 10$ , d.f. = 8,  $t = 0.131$ ,  $p = 0.899$ ).

Table 2.6 The mean reproductive output (MRO) and potential reproductive output (PRO) of *Katharina* populations as calculated from the length-fecundity model (see Equation 4).

Location	Mean Density (n/Quadrat)	SE Mean Density	Mean Length (mm)	SE Mean Length	Mean Log Reproductive Output ( $\log g = 0.2359 \times L - 2.3859$ )	Mean Reproductive Output ( $10^{\log g = 0.2359 \times L - 2.3859}$ )	Potential Reproductive Output (Mean Density x MRO)
EK E	2.476	0.661	3.404	2.775	-1.583	0.026	<b>0.065</b>
EK S	2.952	0.382	5.492	4.004	-1.090	0.081	<b>0.240</b>
Sep E	3.217	0.447	3.368	2.716	-1.591	0.026	<b>0.082</b>
Sep S	4.692	0.485	3.796	2.82	-1.490	0.032	<b>0.152</b>
KP	2.88	0.606	4.139	3.093	-1.410	0.039	<b>0.112</b>
Diana	6.225	0.479	3.888	2.13	-1.469	0.034	<b>0.212</b>
Wee	5.321	0.416	4.096	1.941	-1.420	0.038	<b>0.202</b>
Helby	5.956	0.452	4.142	2.13	-1.409	0.039	<b>0.232</b>
San E	6.8	0.678	3.787	1.447	-1.493	0.032	<b>0.219</b>
San S	1.824	0.735	4.194	3.538	-1.397	0.040	<b>0.073</b>

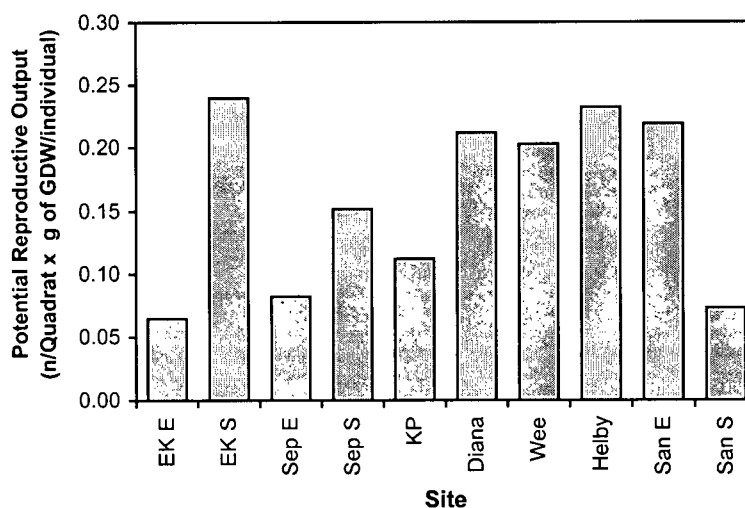


Figure 2.12 The potential reproductive output (PRO = MRO (g/individual) x mean density of *Katharina* (n/Quadrat)) of *Katharina* populations at all 10 sites as derived from the length-fecundity model.

A significant difference in randomized potential reproductive output ( $PRO_R$ ) was found between sites ( $n = 1000$ , d.f. = 9,  $F = 285.155$ ,  $p = 5.897 \times 10^{-12}$ ) (Figure 2.13). A Bonferroni Post Hoc test indicated that significant differences exist between all sites except Edward King Exposed, Kirby, Sanford Sheltered and Seppings Exposed.  $PRO_R$  did not vary significantly between exposed and semi-sheltered sites ( $n = 10$ , d.f. = 8,  $t = -0.304$ ,  $p = 0.177$ ), and no significant correlation was found between  $PRO_R$  and September's maximum wave force ( $n = 10$ , d.f. = 8, Spearman  $r = -0.200$ ,  $p > 0.05$ ) (Figure 2.14).

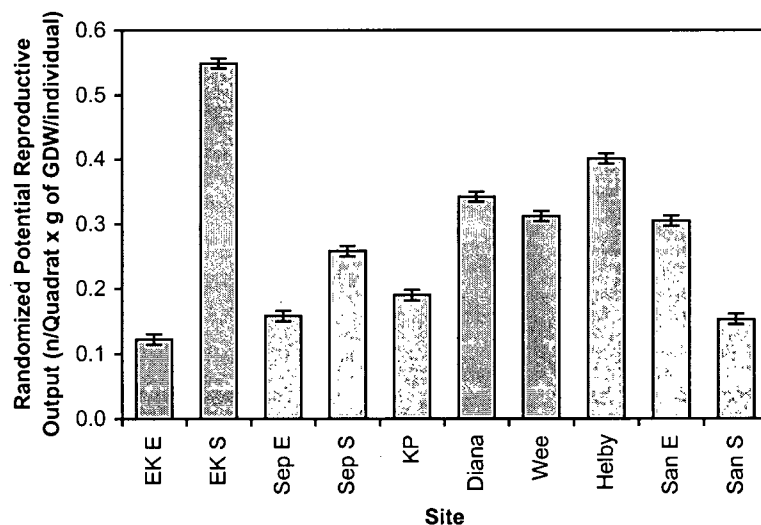


Figure 2.13 Randomized potential reproductive output ( $PRO_R = MRO_R$  (g/individual)  $\times$  mean density of *Katharina* (n/Quadrat)) of *Katharina* populations at all 10 sites as determined by a visual basic randomized re-sampling program.  $PRO_R$  differed significantly between sites ( $n = 1000$ , d.f. = 9,  $F = 285.155$ ,  $p = 5.897 \times 10^{-12}$ ). Error bars represent the standard deviation of the re-sampled data which is equivalent to the standard error of the bootstrap mean.

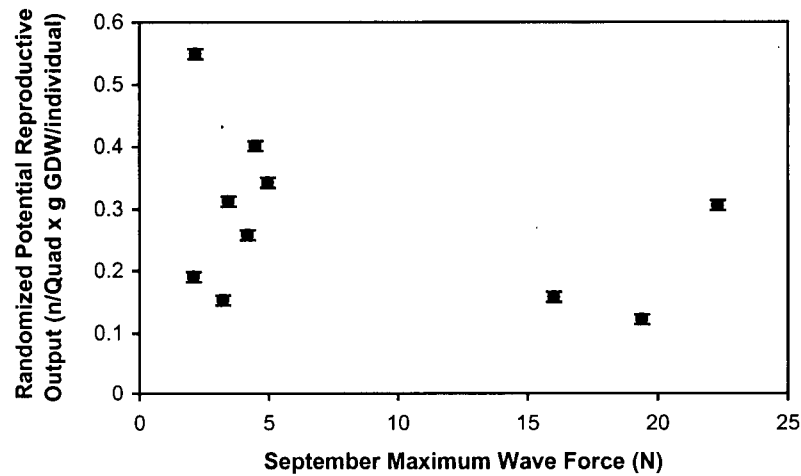


Figure 2.14 The relationship between randomized potential reproductive output ( $PRO_R$ ) and September's maximum wave force ( $n = 10$ , d.f. = 8, Spearman  $r = -0.200$ ,  $p > 0.05$ ).

## 2.4 DISCUSSION

### 2.4.1 Wave-Exposure

Along surf-swept rocky shores, larval recruitment, post settlement growth and adult survival all play out within a context of disturbance in the form of wave-exposure. Wave-exposure, along with biological factors, has been shown to structure intertidal communities by freeing space (Dayton 1971, Paine 1979, Menge and Farrell 1989), influencing reproductive strategies, the course of succession (Sousa 1979), and by enforcing a mechanical limit on an organism's maximum size (Denny et al. 1985).

Although the 10 sites investigated could be grouped into two consistent wave-exposure categories: exposed and semi-sheltered, based on September and October maximum-wave force data, their relative rank in those categories altered daily and monthly. Wave-exposure rankings may change seasonally depending on fluctuations in current patterns, and predominant wind and swell direction and strength. In reality, the 10 sites investigated in this study fell out within a gradient of wave-exposure, therefore, the delineation between exposed or semi-sheltered categories was arbitrarily set in the middle of the maximum wave force values recorded for September and October. As a result, a correlation analysis between maximum wave force and a dependent variable more strongly reflects ecological reality than a t-test comparing a dependent variable at 5 exposed and 5 semi-sheltered sites.

#### 2.4.2 *Katharina's* Position in the Intertidal

I expected larger *Katharina* to be found within the lower intertidal and smaller individuals to be found within the upper reaches of the *Hedophyllum* zone, however, the results did not support this expectation (Appendix VII). No significant relationship was found between *Katharina's* body length and location in and below the *Hedophyllum* zone. This was primarily because young recruits were found in the high *Hedophyllum* zone down to the lowest low water line. However, at Helby, Wee, Kirby, Seppings Sheltered and Diana, *Katharina* larger than 7.5 cm were consistently found towards the lower intertidal resulting in a nonsignificant positive trend between body length and proximity to the lowest low water line.

It has been suggested that wave-exposure may set a mechanical limit on the maximum body size of organisms located in wave-swept environments; large organisms are more likely to be dislodged than smaller ones (Denny et al. 1985, Paine and Levin 1981). This is because, in an accelerating fluid, the stress experienced by an organism is a function of the organism's length: the larger the organism the greater the stress (Denny et al. 1985). Therefore, for any given accelerational flow, if an organism's length exceeds a certain value, the force per unit area exceeds the stress that the organism can sustain. The result is dislodgment or breakage.

Organisms may employ different strategies to avoid being exposed to wave-action. Except during extreme spring tides, the lower an organism is found in the intertidal, the less frequently it is exposed to wave action. Consequently, in the lower intertidal, larger *Katharina* spend most of their time submerged and reduce the threat of wave-action. This is possibly why the gum boot chiton, *Cryptochiton stelleri*, a chiton species which can grow to 25 cm, is generally found in the lower intertidal and subtidal (Kozloff 1973). Microhabitat also seems to play a critical role in the location of larger sized *Katharina*. For instance, large *Katharina* could be found inhabiting large cracks in the lower intertidal. Such refugia likely allow larger size classes to escape from extreme wave force and predators. Nonetheless, future studies that require data on *Katharina's* population size structure need not employ such extensive vertical sampling procedures as outlined in this research.

#### 2.4.3 The Relationship Between *Katharina's* Length and Fecundity

An organism's size and gonad weight in the intertidal may be constrained by both biological (Levitan 1989, Menge 1972, Paine 1976b) and physical factors (Denny et al. 1985, Paine and Levin 1981). The relationship between gonad dry weight and length of *Katharina* did not vary among 5 sites representing different wave exposures and *Katharina* densities yet

September's maximum wave force data was significantly negatively correlated to *Katharina*'s mean body length at each site. As mentioned earlier, in highly wave-exposed sites with strong wave-driven, oscillatory flow regimes, the main physical limitation in the intertidal is from high flow-induced forces that impose a mechanical limit to size enforced through dislodgment. Denny et al. (1985) proposed that observed limits to size in wave-swept organisms are due primarily to mechanical rather than biological factors. If this is indeed the case, rather than altering the amount of energy allocated to gonad development relative to growth, it may be that smaller *Katharina* simply prosper under high wave-exposure due to a mechanical advantage whereas larger individuals get ripped off the rock (Denny et al. 1985). Following this logic, *Katharina*'s relationship between gonad weight and length would then stay the same under varying wave-exposures, as was documented. The mechanically imposed size limit concept upon which this hypothesis is based is further substantiated by the size-frequency graphs of *Katharina* subpopulations (Figure 2.6). The distributions of *Katharina* at Edward King Exposed and Seppings Exposed are truncated to the right illustrating greater adult mortality. Several other intraspecific studies have also demonstrated that larger benthic marine organisms tend to live in more protected habitats (Ebert 1982, Harger 1970, Paine 1976a).

Many biological factors may be responsible for size constraints such as food limitation and size-specific predation. However, biological interactions must operate within the mechanical confines set by the physical environment. The results described above provide evidence of this. For example, if a density-driven limitation in food due to competition was the principal biological factor imposing a size constraint on *Katharina*, one might anticipate a significant difference in the length-fecundity relationship between sites of varying densities. The higher the density, the greater the competition for food, and the less energy to allocate towards gonad development. Although this was not found to be the case with *Katharina*, it has been demonstrated with the sea urchin *Diadema antillarum*. When body size is limited by available resources contingent on population density, somatic and gonadal tissue are produced and reabsorbed as a function of body size (Levitan 1989).

Experimental manipulation of *Katharina* densities at exposed and sheltered sites would be required to untangle the effects of density and wave-exposure on the relationship between *Katharina*'s length and fecundity. Nonetheless, the data presented here suggests that wave-induced mechanical factors define the upper boundary of *Katharina*'s size at each site and that individual gonad weight is simply a function of size that is governed by wave-force. However, because *Katharina* densities were not statistically significantly different between 3 of the 5 sites

(Figure 2.8), it is possible that the effects of density were not extreme enough to cause a significant difference in the length-fecundity relationship between sites. Because *Katharina* are so patchily distributed, there may always be a large degree of variance associated with their density. As a result, experimental manipulation is required to provide conclusive evidence on this issue.

#### 2.4.4 Estimating Potential Reproductive Output

The potential reproductive output of the 10 *Katharina* subpopulations investigated was estimated using both a visual basic randomized re-sampling procedure and a length-fecundity model. Each method was based on the same 70 dissected individual *Katharina* and each method had its benefits and hindrances. A subpopulation's PRO obtained from the length-fecundity model was based on that subpopulation's mean length. Therefore, unlike the re-sampling procedure, the final PRO value derived from the length-fecundity model did not account for the size-frequency data later collected for each subpopulation in the field. Furthermore, this method required a series of calculations to derive one PRO value for each site, consequently, statistical comparison between sites was not possible due to the lack of an associated error structure for each site's PRO value. The randomized re-sampling method did however allow for the 10 *Katharina* subpopulations  $PRO_R$  to be statistically compared as multiple iterations of the procedure for each site resulted in an associated error structure for each site's  $PRO_R$ . However, some size classes (ex: 3.5, 4 and 8.5 cm) had only two or less pre-established gonad weights to be randomly selected from. This was because, individual *Katharina* were originally collected for dissection based on 3 wide size classes (3.5-5, 5.5-7, 7.5+), rather than the 12 more distinct size classes used for the re-sampling procedure (3 or less, 3.5, 4, 4.5, 5, 5.5, 6, 6.5, 7, 7.5, 8, 8.5, 9, 9+). While sampling for 3 wide ranging size classes was appropriate for the length-fecundity model, the collection and dissection of more individuals for each of the narrow ranging size classes established for the randomized re-sampling procedure, albeit destructive, would have increased the confidence in the  $PRO_R$  values derived from this method. Interestingly, the  $PRO_R$  data derived from the randomized re-sampling procedure were consistently twice as great than the PRO data obtained from the length-fecundity model. As a result, both methods revealed similar between site differences (Figure 2.12 & 2.13).

#### 2.4.5 Reproductive Output, Density and Disturbance

Smaller individuals at high population densities may have similar per capita zygote production as large individuals at low population densities. Consequently, the potential reproductive output of *Katharina* subpopulations in the Deer Group Archipelago is a function of body length and density, both of which may be influenced by wave-exposure. *Katharina*'s population size structure, body length, and density were significantly different among certain sites (Figures 2.6, 2.7 & 2.8). As previously mentioned, *Katharina*'s body length was significantly negatively correlated to September's maximum wave force. However, no significant correlation existed between September's maximum wave force and *Katharina* density, nor was there a correlation between *Katharina* mean body length and density among sites in the Deer Group (Figure 2.9). This was surprising as one would expect a significant negative relationship through indirect effects; larger individuals at a less exposed site would likely be found at lower densities due to resource limitation while smaller individuals at more exposed sites would likely be found at higher densities. While some sites did illustrate this conjecture, others did not. For example, *Katharina* at Edward King Sheltered and Sanford Sheltered had the 2 greatest mean body lengths (Figure 2.7) and were found at low densities (Figure 2.8). This makes ecological sense as larger *Katharina* require more space to graze and may out compete smaller individuals for space and food. Furthermore, as predicted, Diana, Helby and Sanford Exposed, three relatively exposed sites had small *Katharina* at high densities (Figure 2.7 & 2.8 & 2.9). However, while *Katharina* at 2 of the most exposed sites, Edward King Exposed and Seppings Exposed, had the lowest mean body lengths as one would anticipate, they also had low overall *Katharina* densities. Upon close inspection of the size-frequency graphs, Edward King Exposed and Seppings Exposed have a considerably higher proportion of 0-1 cm and 1.5-2 cm recruits than the other 8 sites (Figure 2.6). So in fact, the density of young recruits is relatively quite high yet the low survival of larger conspicuous size classes results in lower overall *Katharina* densities. Size-frequency distributions of these two populations shed insight into their demographic trends; high recruitment and high mortality at larger size classes. This may lead one to conclude that these two subpopulations are sink populations receiving recruits yet producing few. This is further substantiated by the fact that Edward King Exposed and Seppings Exposed have the 2 lowest potential reproductive output values ( $PRO$  &  $PRO_R$ ) of all 10 *Katharina* subpopulations (Figure 2.12 & 2.13).



Like a history book, size-frequency distributions are static pictures of dynamic processes. They can suggest information about the relative recruitment, growth, and mortality rates of a population. For example, high recruitment rates will tend to shift distributions to the left. Sanford Sheltered is particularly interesting because one can speculate about 2 widely separated recruitment events causing peaks in the size-frequency distribution. Higher growth rates will tend to shift size-frequency distributions to the right. Figure 2.6 suggests that growth rates of *Katharina tunicata* may be proportionally highest at semi-sheltered sites and that recruitment rates may be proportionally highest at wave-exposed sites. If mortality is not size-specific, size-frequency distributions will shift to the left yet if mortality is selective for large individuals, i.e. through dislodgment by waves, distributions will be truncated on the right side. Both Seppings Exposed and Edward King Exposed (Figure 2.6) exemplify the latter scenario. When mortality is highest for young individuals distributions will have a paucity of data for small size classes. Most of the distributions in Figure 2.6 illustrate this, although this pattern could also be due to fast early growth or crypsis of small individuals. In terms of application, a time series of size-frequency distributions can help conservation biologists identify source populations that should be protected. In this study, source populations are those where the *Katharina* that arrive as new recruits have high growth and survival rates. This may be the case for the subpopulation at Edward King Sheltered (Figure 2.6).

When small individuals are existing at high densities a gain in fertilization success balances the cost of reduced gamete production (Levitan 1991). *Katharina*'s PRO and PRO<sub>R</sub> differed among sites (Figures 2.12 & 2.13) yet there was no relationship between September's maximum wave force and *Katharina*'s PRO or PRO<sub>R</sub> (Figure 2.14). This may be because a subpopulation of smaller individuals living at high densities in a wave-exposed environment may have a similar PRO value as a subpopulation of larger individuals living at lower densities in a sheltered environment. However, source populations can not be identified by PRO or PRO<sub>R</sub> values alone because information on the relative larval delivery to these sites is also critical.

As mentioned earlier, Seppings Exposed, a proposed sink population, had the highest proportion of 0-1 cm recruits of any site (Figure 2.6). It is possible that it may be receiving recruits from the *Katharina* subpopulation at Edward King Sheltered. This subpopulation had the greatest calculated PRO and PRO<sub>R</sub> values out of the ten sites and is located directly "upstream/upcurrent" from Seppings Exposed. As the prevailing swell direction runs northwest to southeast, it is possible that the *Katharina* subpopulation at Edward King Sheltered is acting as a source of larvae that are being locally retained in the bay between Edward King Island and

Seppings. Once the planktonic larvae are physiologically able to settle, they could possibly settle at Seppings Exposed. To provide support for this hypothesis extensive larval tagging experiments, a high-resolution circulation model, and DNA analysis would be required. Nonetheless, a subpopulation's potential reproductive output and its size-frequency distribution, provide information on its role as a source of larvae.

#### **2.4.6 Placing Population Viability into a Context of Conservation**

Selecting the location of a protected area within a network of protected areas is critical to the success of a conservation strategy based on spatial protection. Population viability is a paramount site selection criterion. Because source populations, those that produce an excess of larvae, allow the persistence of sink populations, disrupting a relatively limited source population can result in a population collapse at a wider regional scale (Quinn et al. 1993). For those populations subject to source/sink dynamics, marine protected area network planning must insure that source areas are protected to maintain regional population stability.

In the following study, the *Katharina* subpopulation at Edward King Sheltered had the greatest potential reproductive output ( $PRO$  &  $PRO_R$ ) of the 10 subpopulations investigated (Figures 2.13 & 2.15). Its size-frequency distribution indicates that it may also have high growth and survival rates (Figure 2.6). Hypothetically, if *Katharina* was a rare species, threatened in some way, or a commercially important resource, and if a network of marine reserves were to be created in Barkley Sound to conserve this species and the ecosystem in which it is embedded, this subpopulation would be important to protect.

### 3.1 INTRODUCTION

Areas of high biological diversity are often touted as critical areas to protect (Prendergast et al. 1993, Pressey et al. 1996, Reid 1998, Howard et al. 1998, Balmford 2000, Howard et al. 2000). However, it remains unclear if such areas encompass viable, self-replenishing, source populations and thus truly represent optimal areas for protection. In this chapter, the relationship between biological diversity and population viability is examined using the rocky intertidal as a model system and the black chiton, *Katharina tunicata*, as a model broadcast spawning species. Based on the Intermediate Disturbance Hypothesis, it was suggested in Chapter 1 that areas of high biodiversity may prove to encompass sink populations (populations of relatively low population viability), in contrast, areas of low biodiversity may encompass source populations (populations of relatively high population viability). If this prediction is true, biodiversity and population viability may be conflicting site selection criteria for marine protected areas.

#### 3.1.1 Objectives

In Chapter 2, the potential reproductive output of 10 *Katharina* subpopulations was quantified as a measure of their population viability. In this chapter, the information furnished by Chapter 2 has been applied to investigate if areas of high faunistic and floristic species diversity contained viable *Katharina* subpopulations relative to areas of lower biodiversity. This was achieved by comparing the population viability of *Katharina*, as measured by its potential reproductive output, in areas of high and low species diversity. To determine if disturbance in the form of wave-exposure was responsible for the predictions outlined in Chapter 1, the relationship between wave-exposure and rocky intertidal biodiversity and the extent to which wave-exposure influences community composition was also investigated.

### 3.2 METHODS

#### 3.2.1 Study Site

The potential reproductive output of *Katharina tunicata*, wave-exposure (please refer to Chapter 2) and sessile species diversity was quantified at 10 sites, 5 wave-exposed (E) and 5 semi-sheltered (S), within the Deer Group Archipelago (Table 3.1). This string of islands is located in Barkley Sound, British Columbia, Canada (49° 50' N 125° 12' W) (Figure 3.1). When sites were being identified for study, highly articulated coastline was avoided to reduce within

site variability. To restrict between site variability to wave-exposure, care was taken to maintain slope consistency among sites. Each site was approximately 40 m in length.

In the Sound, the predominant wind and swell direction runs southwest to northeast creating a gradient of wave-exposure. Outer islands, Edward King and Seppings, were subject to greater wave-exposure than the inner semi-protected islands of Helby and Sandford, yet local site variability in aspect and topography plus adjacent seafloor topography dampened or magnified the degree of wave-exposure at each site.

Table 3.1 The diversity of sessile species, wave-exposure and potential reproductive output of *Katharina tunicata* was determined at 10 sites, 5 exposed and 5 semi-sheltered. \* indicates where *Katharina* individuals were collected for dissection to establish the length-fecundity relationship upon which the potential reproductive output of each *Katharina* subpopulation was estimated.

Exposed Sites	Semi-sheltered Sites
Edward King Exposed	Edward King Sheltered
*Seppings Exposed	*Seppings Sheltered
*Diana	Kirby
*Helby	*Wee
Sanford Exposed	Sanford Sheltered

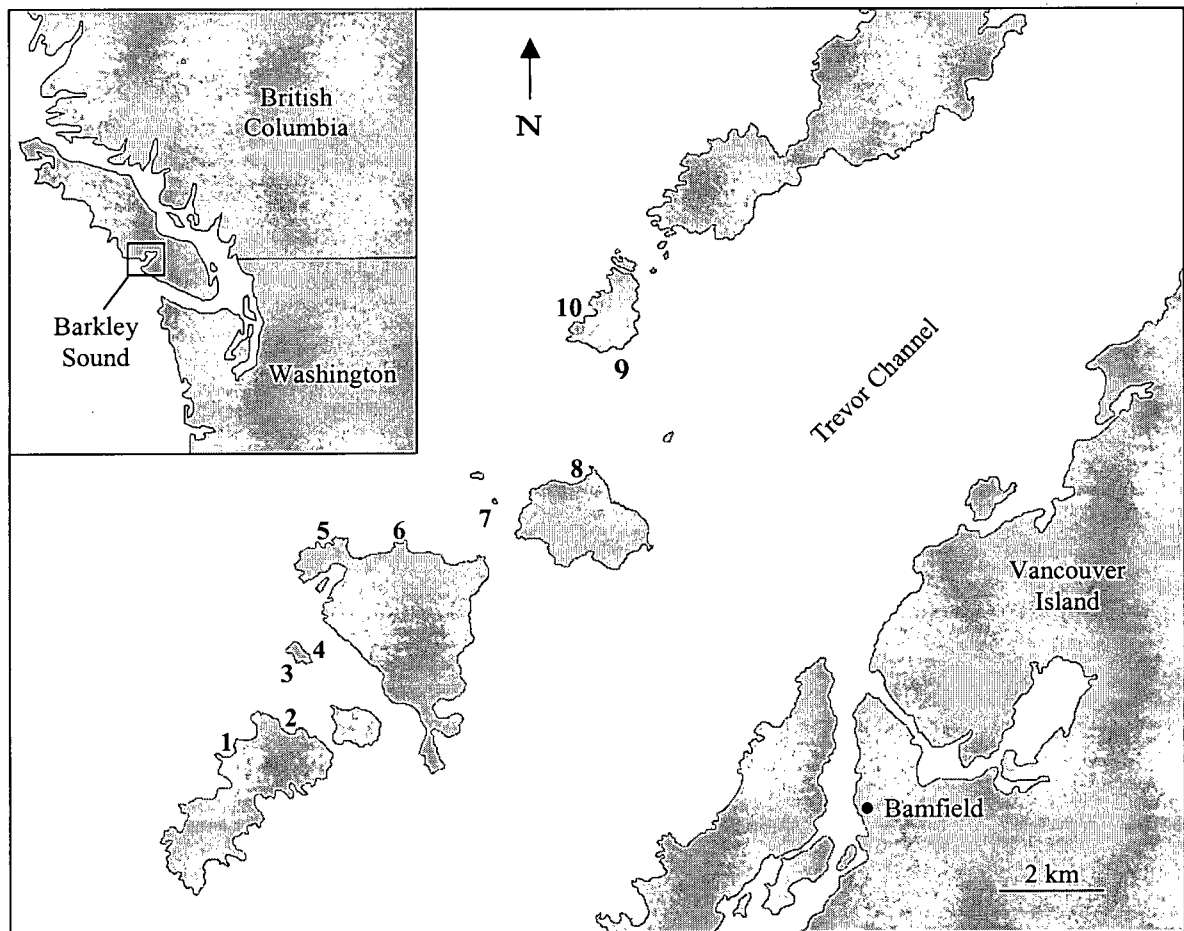


Figure 3.1 The diversity of sessile macroscopic species, maximum wave force, and potential reproductive output of *Katharina* subpopulations was estimated at 10 sites, 5 exposed and 5 semi-sheltered, within the Deer Group archipelago, Barkley Sound, British Columbia, Canada ( $49^{\circ} 50' \text{ N } 125^{\circ} 12' \text{ W}$ ). The outer islands located to the southeast are more exposed than the inner islands located to the northwest due to the predominant swell direction that runs from the southwest to the northeast. 1 = Edward King Exposed, 2 = Edward King Sheltered, 3 = Seppings Exposed, 4 = Seppings Sheltered, 5 = Kirby, 6 = Diana, 7 = Wee, 8 = Helby, 9 = Sanford Exposed, 10 = Sanford Sheltered.

### 3.2.2 Quantifying Site Biodiversity

To quantify intertidal species diversity, a 40 m long transect line, with 10 randomly stratified markers positioned along it, was placed horizontally to the shore in the middle of the *Hedophyllum* zone<sup>9</sup>. The percent cover of all macroscopic invertebrates and algae was quantified using ten 0.0625 m<sup>2</sup> (25 cm x 25 cm) each having 50 points randomly positioned on a grid. Organisms appearing under each point were recorded. To account for extensive species overlap and the three-dimensional nature of the community, 3 distinct layers were surveyed per quadrat: the canopy, understory and substrate. The percent cover for each species was expressed as a percentage of the number of points occupied over the total number of points. With 50 points per layer, each random point occupied was equivalent to 2% cover. In 3 layers, the total number of points was 150, consequently, the total percent cover possible in one quadrat was 300%. To account for species rarity, any organism within the quadrat that was not found directly below a random point was accounted for as <1%. Non-living substrata (e.g. bed rock) was also recorded.

Organisms were identified to the lowest taxonomic level possible with the use of several field guides and keys (Kozloff 1973, Kozloff 1987, Gabrielson et al. 2000) (Appendix IX). Species without positive taxonomic classifications were given pseudonyms based on field observation and kept constant throughout the data analysis. These species were later identified with the help of specialists at the University of British Columbia and Bamfield Marine Station.

Species accumulation curves describing the number of new species encountered in successive quadrats along the transect line were used to determine if the sampling methodology was adequate in describing the species richness of these assemblages. Percent cover data were used to compute Shannon-Wiener Diversity values.

### 3.2.3 Statistical Analysis of Site Biodiversity

Species Richness and the Shannon-Wiener Diversity Index were used to quantify the species diversity of intertidal algae and sessile invertebrates. The variance associated with these two measures of biodiversity were calculated in two distinct ways resulting in 4 measures of biodiversity: Species Richness (S), Shannon-Wiener Diversity (H'), Randomized Species Richness (S<sub>R</sub>), and Randomized Shannon-Wiener Diversity (H'<sub>R</sub>).

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<sup>9</sup> The *Hedophyllum* zone is an intertidal zone biologically characterized by several dominant species; *Katharina tunicata*, *Hedophyllum sessile*, *Lithothamnion* spp., *Hildenbrandia* spp., *Corallina* spp., and *Bossiella* spp.

Species Richness (S) was calculated simply as the number of species observed at a site, while the Shannon-Wiener Diversity index (H') accounted for the number of species as well as their relative abundance:

$$H' = - \sum_{i=1}^s p_i \ln p_i \quad (5)$$

Where s = total number of species at a site

$p_i$  = the average percent cover of a species at a site / total percent cover of all species at a site

$\ln$  = natural logarithm

Because H' values were normally distributed (skewness/SEskewness = 0.080, kurtosis/SEkurtosis = 1.176), parametric statistics were appropriate. Paired comparisons of H' between sites were made by calculating the variation in H' (Var H'), a t-statistic (t), and degrees of freedom (d.f) based on the following equations (Hutcheson 1970, Magurran 1988):

$$\text{Var } H' = \frac{\sum p_i (\ln p_i)^2 - (\sum p_i \ln p_i)^2}{N} + \frac{S-1}{2N^2} \quad (6)$$

$$t = \frac{H_1' - H_2'}{(\text{Var } H_1' + \text{Var } H_2')^{1/2}} \quad (7)$$

$$\text{d.f.} = \frac{(\text{Var } H_1' + \text{Var } H_2')^2}{[(\text{Var } H_1')^2 / N_1] + [(\text{Var } H_2')^2 / N_2]} \quad (8)$$

Where  $p_i$  = the average percent cover of a species at a site / total percent cover of all species at a site

$\ln$  = natural logarithm

S = total number of species at a site

N = total average percent cover of a species at a site

$H_1'$  = Shannon-Wiener Diversity Index at site 1

$H_2'$  = Shannon-Wiener Diversity Index at site 2

Var  $H_1'$  = Variation in  $H_1'$  at site 1

Var  $H_2'$  = Variation in  $H_2'$  at site 2

$N_1$  = total average percent cover of species at site 1

$N_2$  = total average percent cover of species at site 2

Because pair wise comparisons were conducted on each of the 10 sites, a total of 45 comparisons were made. Probabilities were compared to sequentially Bonferroni adjusted alpha values (Appendix III) in such a manner that the most significant p-value had to be  $p < 0.05 / 45$  (0.00111) to be significant. The next most significant p-value had to be  $p < 0.05 / 44$ , (0.00114) to be significant and so forth. Although effective, this parametric method which assumes

homogeneity of variance, revealed very few significantly different comparisons due to the small alpha values resulting from the 45 sequential comparisons. Moreover, as only one species richness value was generated per site, no error structure could be associated with the species richness value thereby preventing statistical analysis between sites. As a result, a second randomized re-sampling method with re-placement was designed to generate an error structure for a Randomized Species Richness value ( $S_R$ ) and a Randomized Shannon-Wiener Diversity value ( $H'_R$ ).

This bootstrapping procedure (randomized re-sampling with replacement) involved quantifying a site's Randomized Species Richness ( $S_R$ ) and its Randomized Shannon-Wiener Diversity ( $H'_R$ ) after the random removal of 2 out of the 10 quadrats surveyed per site. This process was then reiterated 20 times with replacement generating 20 replicates per site (Appendix X). The removal of 2 quadrats was justified because the asymptotes on the species accumulation curves occurred at approximately 8 quadrats (Figure 3.2 A&B). The standard deviation of the 20 bootstrap replicates was used to estimate the standard error of the Randomized Species Richness ( $S_R$ ) and Randomized Shannon-Wiener Diversity value ( $H'_R$ ) calculated for each site.

Both the  $S_R$  bootstrap data (skewness/SE skewness = 1.605, kurtosis/SE kurtosis = 2.246) and the  $H'_R$  bootstrap data (skewness/SE skewness = 4.99, kurtosis/SE kurtosis = 1.254) were not normally distributed. Data transformations did not rectify the extreme heterogeneity of variance. Therefore, Kruskal-Wallis tests, the non-parametric analog of the one-way analysis of variance (ANOVA), were performed to determine if Randomized Species Richness ( $S_R$ ) and Randomized Shannon-Wiener Diversity values ( $H'_R$ ) differed significantly between sites.<sup>10</sup> Wilcoxon signed rank paired comparisons were then used to indicate which sites were significantly different. Probabilities were Bonferroni adjusted for multiple comparisons (Appendix III) in the same manner described above.

### 3.2.4 Measuring Maximum Wave Force

As described in detail in Chapter 2, section 2.2.5, maximum wave force was quantified using maximum wave force recorders. Once calibrated, recorders were deployed at each site and revisited 3 times per tidal cycle.

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<sup>10</sup> Although robust, an analysis of variance, the parametric equivalent to the Kruskal-Wallis, would not have been appropriate under these circumstances because the bootstrap data violated the assumption of homoscedasticity to a relatively extreme degree (Sokal and Rohlf 1969).



Extreme wave action in October prevented wave-exposure measurements to be made at 3 extremely exposed sites. Therefore, a linear model was designed to estimate the maximum wave force impacting those sites based on a comparison made between maximum wave force data collected in September and October. The equation of the line that resulted in the lowest residuals was used to approximate the October maximum wave force for Sanford Exposed, Edward King Exposed and Diana (Appendix XI).

### **3.2.5 Biodiversity and Maximum Wave Force**

Linear Regression analyses were performed to determine if Species Richness (S) and Shannon-Wiener Diversity ( $H'$ ) varied as a function of maximum wave force. Because a distinct trend between biodiversity and wave-exposure became apparent at low wave forces, sites subject to extreme wave-exposure were removed from the data set prior to the regression analyses. Although these sites represent biologically significant and valid data, their removal prior to the regression analyses allowed me to determine the relationship between biodiversity and maximum wave force at low wave-exposure. In the September maximum wave force data set, Sanford Exposed, Seppings Exposed and Edward King Exposed were removed. Edward King Exposed and Sanford Exposed were removed before the analysis of the October data set. Regression coefficients were calculated and an analysis of variance (ANOVA) was then used to test the significance of each relationship's regression coefficient.

### **3.2.6 Community Structure and Maximum Wave Force**

To investigate if maximum wave force influenced the community composition at each site, the degree of similarity or dissimilarity in the species assemblages between sites was described. A multivariate approach was used to summarize patterns of species abundance and co-occurrence among the 10 communities investigated. Multivariate techniques are viewed as an objective method to describe community structure and facilitate a greater understanding of the relationships between community composition and environmental conditions (Jackson 1993). Multivariate methods can thereby provide insight into the underlying causes of community structure. Principal Component Analysis (PCA) and correlation coefficients were selected because they have been shown to provide the most consistent results among the multitude of multivariate techniques (Jackson 1993). When used in an exploratory fashion, PCA does not involve some of the strict parametric assumptions of other tests. Furthermore, PCA does not make assumptions about the distributions of variables, although the analysis is degraded with

decreasing normality. PCA does however assume that the relationships among pairs of variables are linear (Tabachnick and Fidell 1996).

PCA was used to summarize the patterns of correlations among observed variables, the percent cover values of various species at each site. Because each component/factor empirically summarizes these correlations, factors are thought to reflect the underlying processes that have created these correlations (Tabachnick and Fidell 1996). To investigate the influence of maximum wave-exposure on community structure, a PCA was performed on the percent cover of invertebrate and algal species, which were grouped by site using 68.3% confidence ellipses. These confidence ellipses represent the variation in the data at each site, specifically, one standard deviation around the mean. Species that were recorded in fewer than 5 % of the quadrats were deleted from the data set to clarify relationships. The size and distinction of the confidence ellipses on the PCA axes were used to interpret the amount of variation between quadrats at each site. In essence the more overlap between the ellipses, the more similar the communities between sites. Relationships between species percent cover data and wave-exposure (maximum wave force and geographic relationship to predominant swell direction, i.e. outer versus inner islands) were then determined by Pearson correlation coefficients.

### **3.2.7 Estimating the Potential Reproductive Output of *Katharina* Subpopulations**

As specified in Chapter 2, section 2.2.4, the potential reproductive output of *Katharina* subpopulations was estimated using both a length-fecundity model and a Visual Basic Randomized Re-sampling procedure. In the former method the mean length of *Katharina* quantified for each site's subpopulation was substituted in to the length-fecundity model [ $PRO = 0.2359 \times \text{mean body length} - 2.3859$ ] established in section 2.3.1. This resulted in one PRO value per site. The latter re-sampling method involved multiplying the known frequency of individuals in a size class by a randomly chosen observed gonad dry weight value already established for that site class. Values were then summed over all size classes. This procedure was reiterated 100 times per site, consequently, mean  $PRO_R$  values and their associated error could be compared between sites (Appendix V).

### **3.2.8 Biodiversity and Potential Reproductive Output**

Correlation analyses were performed to investigate the association between biodiversity and potential reproductive output, a metric for population viability. Species Richness (S), Shannon-Wiener Diversity ( $H'$ ), Randomized Species Richness ( $S_R$ ), and Randomized Shannon-

Wiener Diversity ( $H'_R$ ) were correlated to the potential reproductive output of *Katharina* calculated for each site's subpopulation by A) the length-fecundity model (PRO) and B) the visual basic randomized re-sampling procedure (PRO<sub>R</sub>) (summary of raw data in Appendix XII). All the variables examined in the correlation analyses; S,  $H'$ ,  $S_R$ ,  $H'_R$ , PRO, PRO<sub>R</sub>, were normally distributed (skewness/SE skewness = 0.732, 0.084, 0.493, 1.697, 0.377, 1.179, kurtosis/SE kurtosis = 0.667, 1.178, 0.532, 1.436, 1.461, 0.342 receptively). Therefore, the parametric Pearson Product correlation coefficient was calculated for each correlation. A correlation was determined to be significant when the correlation coefficient  $r > r_{critical}$ . When  $n = 10$  and d.f. = 8,  $r_{critical}[0.05] = 0.632$ , and  $r_{critical}[0.01] = 0.765$  (Sokal and Rohlf 1969). Because two methods were used to determine a subpopulation's population viability and two methods were used to quantify biodiversity in terms of both Species Richness and Shannon-Wiener Diversity, a total of 8 final correlations were conducted.

### 3.3 RESULTS

#### 3.3.1 Species Accumulation Curves

The asymptotes on the species accumulation curves occurred between 6-10 quadrats contingent on the site surveyed (Figure 3.2 A&B).

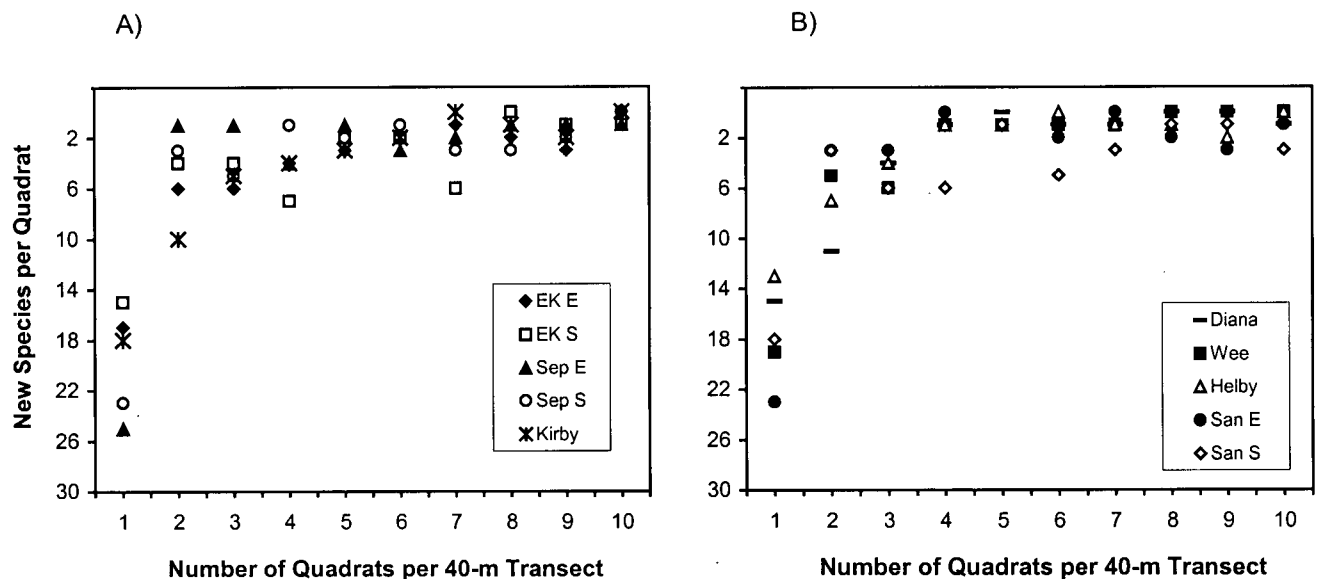


Figure 3.2 A&B: Species accumulation curves show the number of new species recorded in successive random 25 x 25 cm quadrats at the 10 sites investigated in the Deer Group Archipelago. The asymptotes occurred between 7 and 10 quadrats, depending on the site sampled, indicating that using 10 quadrats was adequate for sampling the species diversity at each site. This is illustrated for (A) the 5 southwesterly sites and (B) the 5 northeasterly sites.

### 3.3.2 Site Biodiversity

Sanford Sheltered had the highest Species Richness and Shannon-Wiener Diversity values ( $H'$ ) whereas Helby had the lowest (Figures 3.3 & 3.4). Sheltered sites had greater Species Richness and Shannon-Wiener Diversity values than did exposed sites (Figures 3.3 & 3.4). The only significant differences in  $H'$  were found between Helby and Sanford Sheltered ( $d.f. > 120$ ,  $t = 4.657$ ,  $p < 0.001$ ) and Diana and Sanford Sheltered ( $d.f. > 120$ ,  $t = 3.725$ ,  $p < 0.001$ ) (Table 3.2, 3.3 & Figure 3.4).

When randomly re-sampled with replacement, Sanford Sheltered still had the highest Randomized Species Richness and Randomized Shannon-Wiener Diversity value whereas Helby had the lowest (Figure 3.5, 3.6). Randomized Species Richness ( $S_R$ ) and Randomized Shannon-Wiener Diversity values ( $H'_R$ ) varied significantly between sites ( $n = 10$ ,  $d.f. = 9$ , Kruskal-Wallis test statistic = 180.722,  $p = 9.992 \times 10^{-16}$ ) and ( $n = 10$ ,  $d.f. = 9$ , Kruskal-Wallis test statistic = 177.177,  $p = 9.992 \times 10^{-16}$ ) (Figures 3.5 & 3.6). Significant difference in  $S_R$  existed between all paired comparisons except Edward King Exposed and Seppings Sheltered and Edward King Sheltered and Seppings Exposed (Table 3.4) whereas significant differences in  $H'_R$  existed between only 41 paired comparisons. Those sites that did not differ in their  $H'_R$  were: Seppings Exposed and Diana, Seppings Sheltered and Kirby, Seppings Sheltered and Diana, and Wee and Sanford Exposed (Table 3.5). Both  $S$  and  $S_R$ , and  $H'$  and  $H'_R$  were highly correlated ( $n = 10$ ,  $d.f. = 8$ ,  $r = 0.995$ ,  $p < 0.001$ ) ( $n = 10$ ,  $d.f. = 8$ ,  $r = 0.941$ ,  $p < 0.001$ ) respectively.

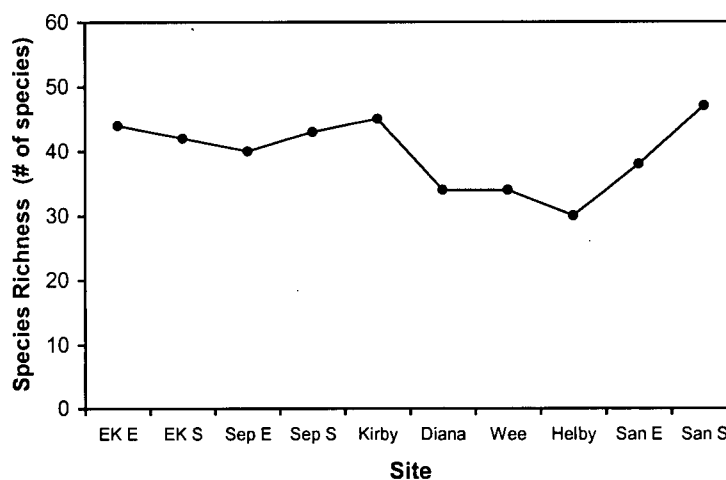


Figure 3.3 Species Richness ( $S$ ) of the 10 sites investigated within the Deer Group Archipelago, Barkley Sound, British Columbia, Canada. ( $S$  = total number of species found in the 10 quadrats surveyed per site).

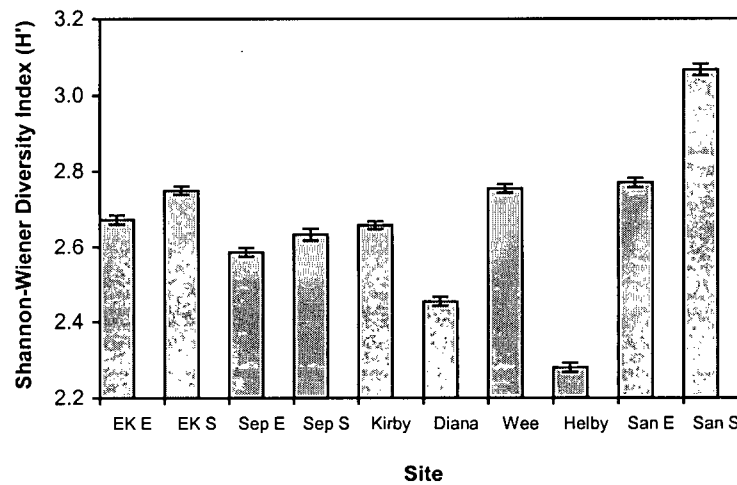


Figure 3.4 Shannon-Wiener Diversity Index ( $H'$ ) of the 10 sites investigated within the Deer Group Archipelago, Barkley Sound, British Columbia, Canada.

Table 3.2 Comparison of Shannon-Wiener Diversity ( $H'$ ) between pairs of sites in Barkley Sound. Values are t-statistics calculated for each paired comparison. Bold values indicate significant paired comparisons once alpha values had been Bonferroni adjusted (See Appendix III).

Site	EK E	EK S	Sep E	Sep S	KP	Diana	Wee	Helby	San E	San S
EK E	0.000									
EK S	-0.511	0.000								
Sep E	0.569	1.099	0.000							
Sep S	0.237	0.716	-0.291	0.000						
KP	0.098	0.631	-0.492	-0.154	0.000					
Diana	1.426	1.973	0.866	1.090	1.380	0.000				
Wee	-0.538	-0.037	-1.115	-0.738	-0.657	-1.973	0.000			
Helby	2.473	3.030	1.934	2.079	2.463	1.082	3.014	0.000		
San E	-0.630	-0.138	-1.199	-0.821	-0.749	-2.045	-0.099	-3.072	0.000	
San S	-2.400	-1.979	-2.943	-2.473	-2.567	<b>-3.725</b>	-1.914	<b>-4.657</b>	-1.800	0.000

Table 3.3 Degrees of freedom (d.f.) calculated for each Shannon-Wiener ( $H'$ ) paired comparison. In each case d.f. >120.

Site	EK E	EK S	Sep E	Sep S	KP	Diana	Wee	Helby	San E	San S
EK E	0.000									
EK S	246.608	0.000								
Sep E	268.493	266.279	0.000							
Sep S	239.759	233.177	250.854	0.000						
KP	261.803	260.592	285.596	241.408	0.000					
Diana	243.538	238.884	259.893	235.437	252.459	0.000				
Wee	227.386	222.061	242.114	222.471	233.990	221.641	0.000			
Helby	236.124	230.248	249.339	233.426	240.587	230.951	216.948	0.000		
San E	238.737	233.730	254.238	232.189	246.421	232.650	217.592	227.216	0.000	
San S	199.727	192.178	206.925	207.769	196.797	197.077	186.491	198.375	194.846	0.000

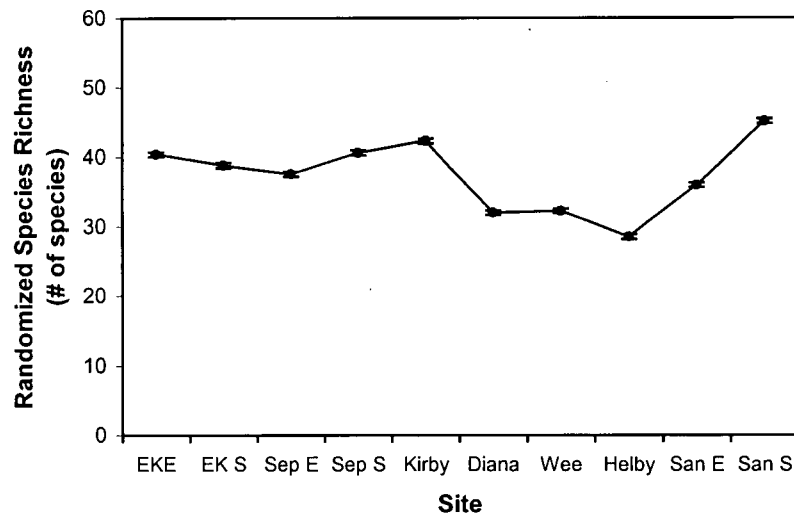


Figure 3.5 Mean Randomized Species Richness ( $S_R$ ) and standard deviation at each of the 10 sites within the Deer Group Archipelago.  $S_R$  = number of species found in 8 out of the possible 10 quadrats surveyed per site.  $S_R$  was generated from 20 bootstrapped replicates, each of which was calculated from randomly selecting, with replacement, 8 out of the 10 quadrats surveyed per site.

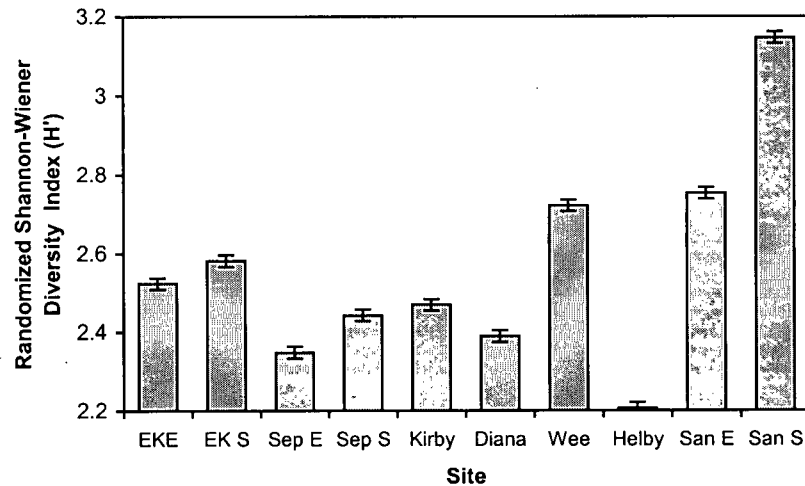


Figure 3.6 Mean Randomized Shannon-Wiener Diversity Index ( $H'_R$ ) and standard deviation at each of the 10 sites investigated within the Deer Group Archipelago.  $H'_R$  = Shannon-Wiener Diversity Index generated from 20 bootstrapped replicates. Each replicate  $H'_R$  was calculated by randomly selecting, with replacement, 8 out of the 10 quadrats surveyed per site.

Table 3.4 Two-sided probabilities for Randomized Species Richness ( $S_R$ ) derived from 45 Wilcoxon Signed Rank paired comparison tests using normal approximation. Bold values indicate significant differences between pairs once alpha values had been Bonferroni adjusted (see Appendix III).

Site	EKE	EK S	Sep E	Sep S	KP	Diana	Wee	Helby	San E	San S
EKE	1.000									
EK S	<b>0.005</b>	1.000								
Sep E	<b><math>8.09 \times 10^{-5}</math></b>	0.041	1.000							
Sep S	0.683	<b>0.005</b>	<b><math>3.903 \times 10^{-4}</math></b>	1.000						
KP	<b>0.001</b>	<b><math>8.282 \times 10^{-5}</math></b>	<b><math>1.140 \times 10^{-4}</math></b>	0.02	1.000					
Diana	<b><math>8.247 \times 10^{-5}</math></b>	<b><math>8.082 \times 10^{-5}</math></b>	<b><math>1.216 \times 10^{-5}</math></b>	<b><math>8.390 \times 10^{-5}</math></b>	<b><math>8.342 \times 10^{-5}</math></b>	1.000				
Wee	<b><math>7.977 \times 10^{-5}</math></b>	<b><math>8.451 \times 10^{-5}</math></b>	<b><math>8.438 \times 10^{-5}</math></b>	<b><math>8.523 \times 10^{-5}</math></b>	<b><math>8.258 \times 10^{-5}</math></b>	0.813	1.000			
Helby	<b><math>7.771 \times 10^{-5}</math></b>	<b><math>8.306 \times 10^{-5}</math></b>	<b><math>8.023 \times 10^{-5}</math></b>	<b><math>8.402 \times 10^{-5}</math></b>	<b><math>8.199 \times 10^{-5}</math></b>	<b><math>3.560 \times 10^{-4}</math></b>	<b><math>1.700 \times 10^{-4}</math></b>	1.000		
San E	<b><math>8.187 \times 10^{-5}</math></b>	<b><math>3.872 \times 10^{-4}</math></b>	0.006	<b><math>1.265 \times 10^{-4}</math></b>	<b><math>8.342 \times 10^{-5}</math></b>	<b><math>1.210 \times 10^{-4}</math></b>	<b><math>1.253 \times 10^{-4}</math></b>	<b><math>8.402 \times 10^{-7}</math></b>	1.000	
San S	<b><math>1.228 \times 10^{-4}</math></b>	<b><math>8.487 \times 10^{-5}</math></b>	<b><math>8.621 \times 10^{-5}</math></b>	<b><math>8.487 \times 10^{-5}</math></b>	0.001	<b><math>8.402 \times 10^{-5}</math></b>	<b><math>7.884 \times 10^{-5}</math></b>	<b><math>8.402 \times 10^{-7}</math></b>	<b><math>8.438 \times 10^{-5}</math></b>	1.000

Table 3.5 Two-sided probabilities for Randomized Shannon-Wiener diversity values ( $H'_R$ ) derived from 45 Wilcoxon Signed Rank paired comparison tests. Bold values indicate significant differences between pairs once alpha values had been Bonferroni adjusted.

Site	EK E	EK S	Sep E	Sep S	KP	Diana	Wee	Helby	San E	San S
EK E	1.000									
EK S	<b>0.012</b>	1.000								
Sep E	$8.845 \times 10^{-5}$	$8.857 \times 10^{-5}$	1.000							
Sep S	0.001	<b>0.001</b>	<b>0.003</b>	1.000						
KP	0.005	$1.401 \times 10^{-4}$	$8.845 \times 10^{-5}$	0.191	1.000					
Diana	$1.033 \times 10^{-4}$	$8.857 \times 10^{-5}$	0.108	0.093	<b>0.002</b>	1.000				
Wee	$1.401 \times 10^{-4}$	0.001	$8.857 \times 10^{-5}$	$8.857 \times 10^{-5}$	$8.857 \times 10^{-5}$	$8.845 \times 10^{-5}$	1.000			
Helby	$8.857 \times 10^{-5}$	$8.845 \times 10^{-5}$	$1.033 \times 10^{-4}$	$8.857 \times 10^{-5}$	$8.857 \times 10^{-5}$	$1.204 \times 10^{-4}$	$8.857 \times 10^{-5}$	1.000		
San E	$8.857 \times 10^{-5}$	$8.857 \times 10^{-5}$	$8.845 \times 10^{-5}$	$8.857 \times 10^{-5}$	$8.857 \times 10^{-5}$	$8.857 \times 10^{-5}$	0.263	$8.857 \times 10^{-5}$	1.000	
San S	$8.857 \times 10^{-5}$	$8.857 \times 10^{-5}$	$8.845 \times 10^{-5}$	$8.857 \times 10^{-5}$	$8.857 \times 10^{-5}$	$8.845 \times 10^{-5}$	$8.857 \times 10^{-5}$	$8.857 \times 10^{-5}$	$8.857 \times 10^{-5}$	1.000

### 3.3.3 Maximum Wave Force and Site Exposure

In summary, no significant differences in maximum wave force were found between sites in August ( $n = 28$ , d.f. = 27,  $F = 0.962$ ,  $p = 0.500$ ) or October ( $n = 11$ , d.f. = 10,  $F = 4.750$ ,  $p = 0.077$ ) (Figure 2.10). However, in September, a significant difference in maximum wave force was found between the 10 sites ( $n = 29$ , d.f. = 28,  $F = 12.316$ ,  $p = 3.383 \times 10^{-6}$ ) (Figure 2.10). For details, please refer to Chapter 2 section 2.3.5.

Although the relationship between wave force in September and October across 7 sites where data were available was not significant ( $n = 6$ , d.f. = 5,  $F = 1.332$ ,  $p = 0.313$ ), it was used as a crude estimate for approximating the maximum wave force at Sanford Exposed, Edward King Exposed and Diana (Appendix XI). Field observations, from a safe vantage point, led to estimations that maximum wave forces at Sanford Exposed and Edward King Exposed were approximately 3 times greater than those at Helby. The linear model confirmed this estimation.

### 3.3.4 Biodiversity and Maximum Wave Force

Figures 3.7 A,B,C&D suggested a negative trend between maximum wave force and both Species Richness (S) and Shannon-Wiener Diversity ( $H'$ ) with the exception of 3 exposed sites during the September data set and 2 exposed sites during the October data set where diversity was high. Prior to the regression analyses used to investigate the relationship between September's maximum wave force and biodiversity, Sanford Exposed, Seppings Exposed and Edward King Exposed were removed (Figure 3.7 A&B). When the remaining 7 sites were considered in the regression analyses, no significant relationship was found between A)



September maximum wave force and Species Richness (S) ( $n = 7$ , d.f. = 6,  $F = 3.427$ ,  $p = 0.123$ ) or B) September maximum wave force and Shannon-Wiener Diversity ( $n = 7$ , d.f. = 6,  $F = 2.265$ ,  $p = 1.93$ ) (Figure 3.8 A&B).

Edward King Exposed and Sanford Exposed were removed prior to the analysis of the October data set (Figure 3.7 C & D). When the remaining 8 sites were considered Species Richness (S) and Shannon-Wiener Diversity ( $H'$ ) varied significantly as a function of October maximum wave force; ( $n = 8$ , d.f. = 7,  $F = 23.710$ ,  $p = 0.003$ ), ( $n = 8$ , d.f. = 7,  $F = 39.928$ ,  $p = 0.0007$ ) respectively (Figure 3.9).

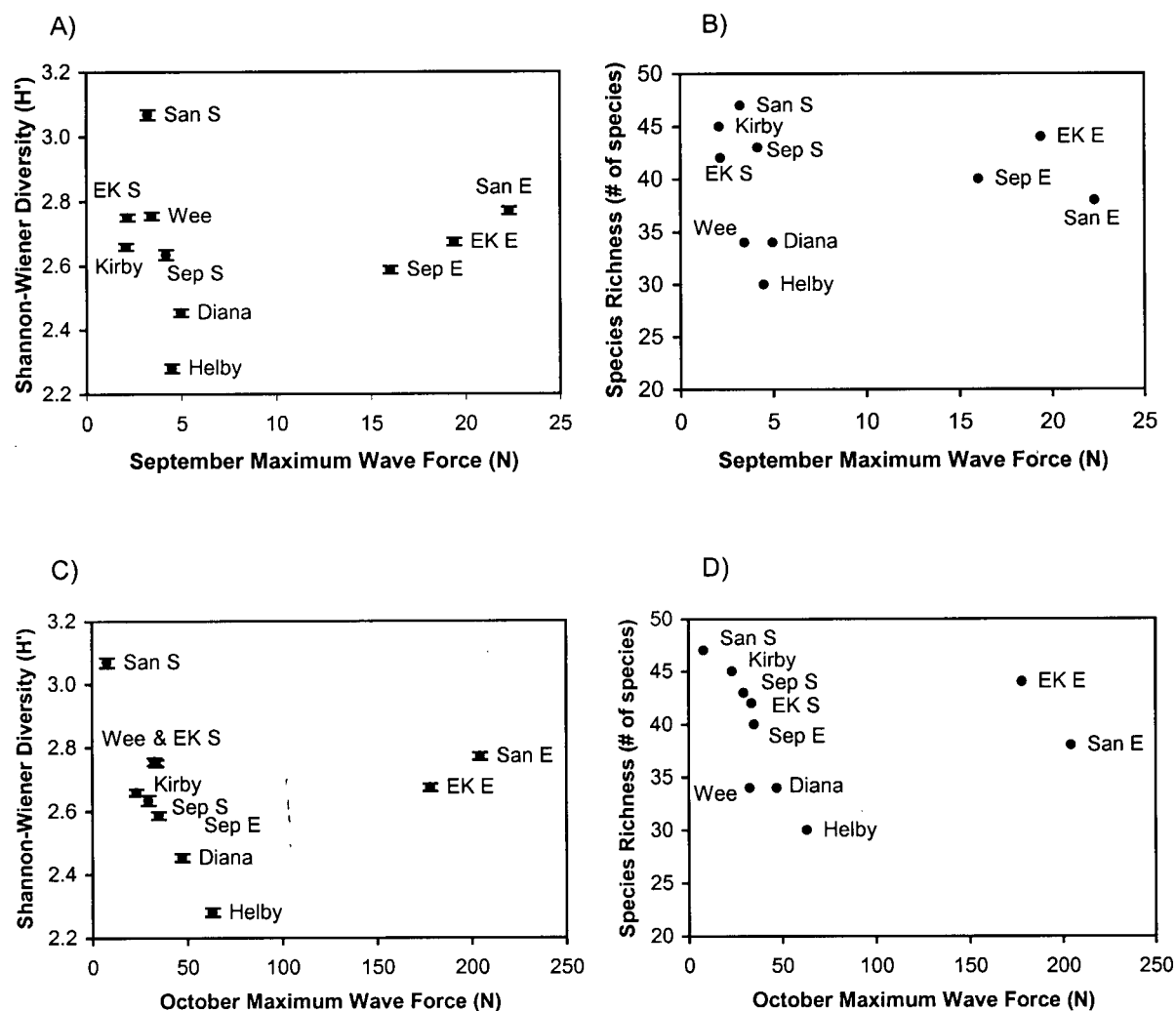
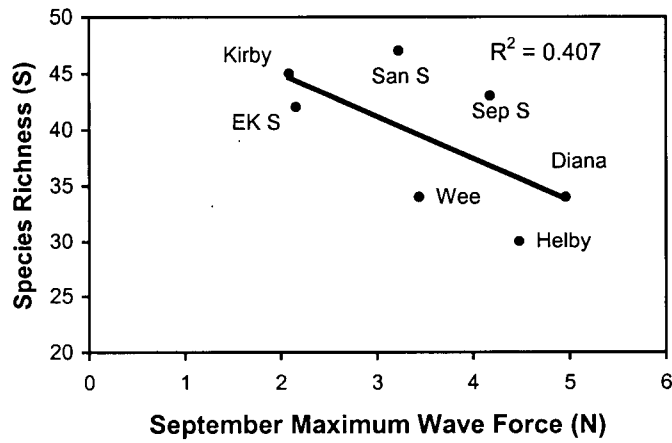


Figure 3.7 Shannon-Wiener Diversity ( $H'$ ) and Species Richness (S) as a function of A) & B) September maximum wave force and C) & D) October maximum wave force including all 10 sites. \* Note: October maximum wave force data for Edward King Exposed, Sanford Exposed and Diana was estimated based on a linear relationship established between observed September and October maximum wave force (Appendix XI).

A)



B)

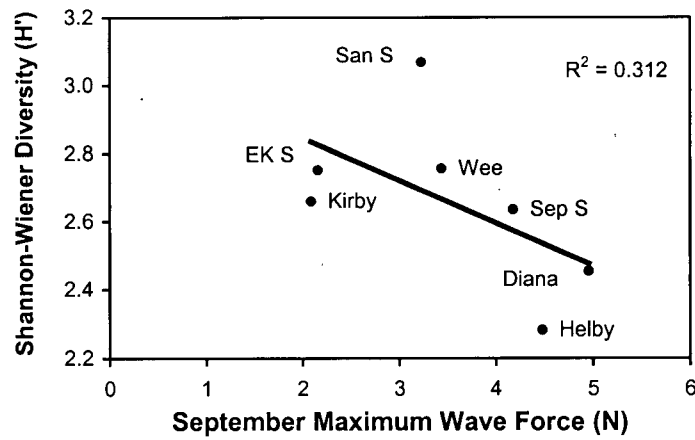
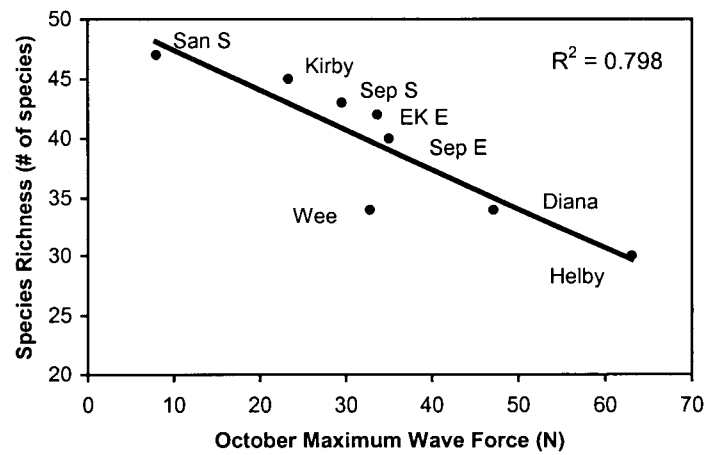


Figure 3.8 When Sanford Exposed, Edward King Exposed and Seppings Exposed were removed from the September data set, no significant relationship was found between September maximum wave force and A) Species Richness (S) ( $n = 7$ , d.f. = 6,  $F = 3.427$ ,  $p = 0.123$ ) or B) Shannon-Wiener Diversity ( $n = 7$ , d.f. = 6,  $F = 2.265$ ,  $p = 1.93$ ).



B)

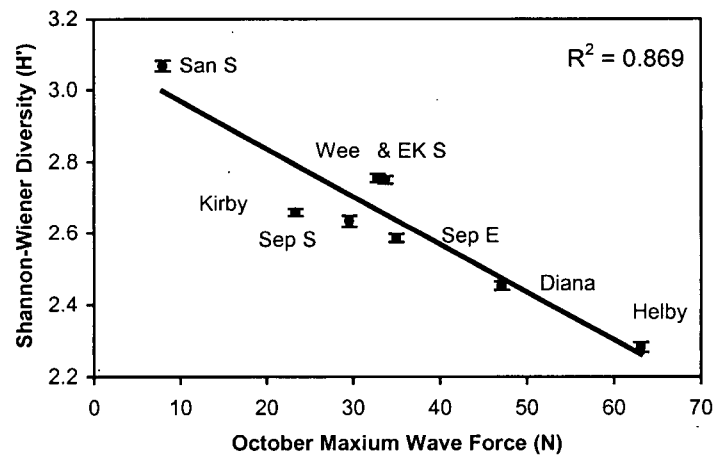


Figure 3.9 Species Richness (S) varied and Shannon-Wiener diversity ( $H'$ ) varied significantly as a function of October maximum wave force; ( $n = 8$ , d.f. = 7,  $F = 23.710$ ,  $p = 0.003$ ) ( $n = 8$ , d.f. = 7,  $F = 39.928$ ,  $p = 0.0007$ ) respectively, when Edward King exposed and Sanford exposed were removed from the October data set.

### 3.3.5 Community Structure and Wave-exposure

Figure 3.10 illustrates the position of 100 quadrats (10 per site) in relation to PCA axis I and axis II, using site as a grouping variable. Axis I and axis II account for 16% of the variation in the data. Axis I (Factor 1), the axis that explains the most variation in the data, is positively correlated with the relative geographic location of the 10 sites, i.e. outer versus inner islands (Pearson Correlation  $r = 0.673$ ). Axis II (Factor 2) is negatively correlated to the October maximum wave force data (Pearson correlation  $r = -0.617$ ) and moderately negatively correlated to the September maximum wave force data (Pearson correlation  $r = -0.461$ ).

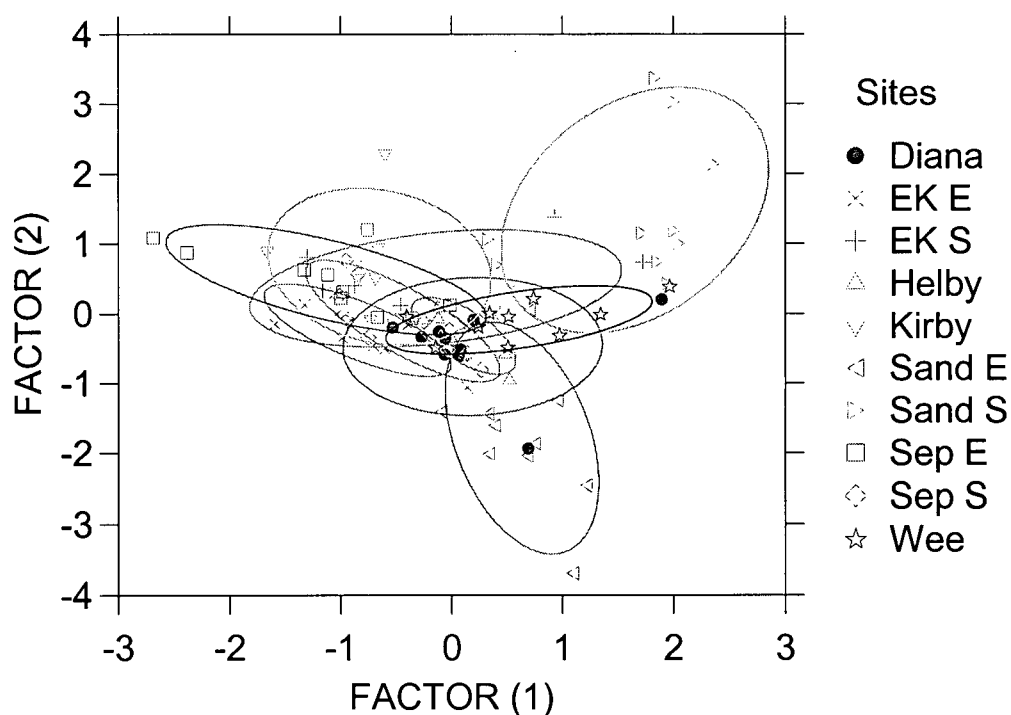


Figure 3.10 The degree of similarity in the species composition at each site. Each data point represents one quadrat. Quadrats are grouped by site using 68% confidence ellipses. Positions of quadrats on PCA axes are produced from algal and invertebrate percent cover data collected from each of the 10 sites investigated. To clarify patterns of correlations, species that were recorded in less than 5 % of quadrats were deleted from the data set.

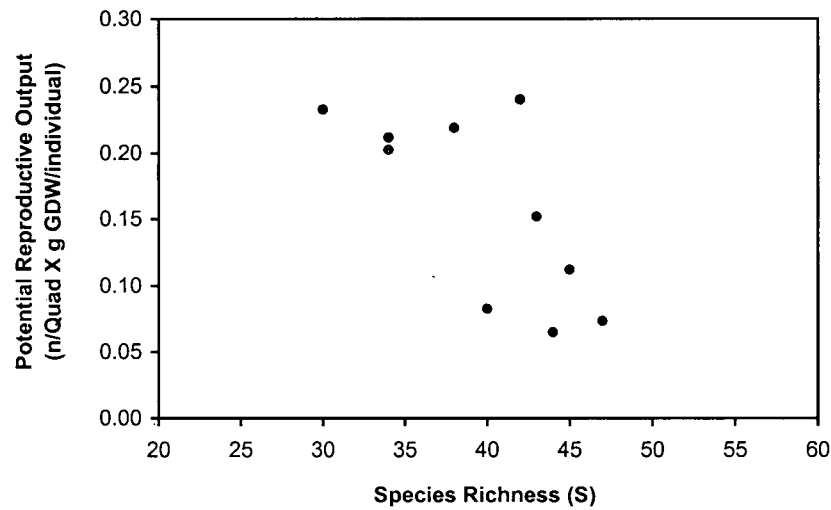
### 3.3.6 Reproductive Output of *Katharina* Subpopulations

In summary, the potential reproductive output of the 10 *Katharina* subpopulations investigated was estimated using a visual basic randomized re-sampling procedure and a length-fecundity model detailed in Chapter 2. The former allowed for statistical analysis between sites while the latter did not as only one value was obtained for each site. When derived from the length-fecundity model, the *Katharina* subpopulations at Edward King Sheltered and Helby had the highest PROs; **0.240** (n/Quad • g GDW/ind) and **0.232** (n/Quad • g GDW/ind) respectively. While Sanford Exposed, Diana, and Wee also had similarly high PROs; **0.219** (n/Quad • g GDW/ind), **0.212** (n/Quad • g GDW/ind), and **0.202** (n/Quad • g GDW/ind) respectively, Edward King Exposed, Sanford Sheltered and Seppings Exposed had the smallest; **0.065** (n/Quad • g GDW/ind), **0.073** (n/Quad • g GDW/ind), and **0.082** (n/Quad • g GDW/ind) respectively, (Table 2.2 & Figure 2.14). When derived from the visual basic re-sampling procedure, a significant difference in PRO<sub>R</sub> was found between sites ( $n = 1000$ , d.f. = 9,  $F = 285.155$ ,  $p = 5.897 \times 10^{-12}$ ) (Figure 2.16). Again, Edward King Sheltered had the greatest PRO<sub>R</sub> while Edward Kind Exposed, Sanford Sheltered and Seppings Exposed had the lowest. Both methods used to quantify potential reproductive output revealed similar between site differences (Figure 2.14 & 2.16). For details, please refer to Chapter 2 section 2.3.7

### 3.3.7 Biodiversity and Potential Reproductive Output

Species Richness (S) and Potential Reproductive Output (PRO) were significantly negatively correlated ( $n = 10$ , d.f. = 8,  $r = -0.711$ ,  $p < 0.05$ ), whereas no significant association was found between Shannon-Wiener Diversity (H') and Potential Reproductive Output (PRO) ( $n = 10$ , d.f. = 8,  $r = -0.388$ ,  $p > 0.05$ ) (Figure 3.11 A&B). Randomized Species Richness (S<sub>R</sub>) and Potential Reproductive Output (PRO) were significantly negatively correlated ( $n = 10$ , d.f. = 8,  $r = -0.714$ ,  $p < 0.05$ ), however the association between Randomized Shannon-Wiener Diversity (H'<sub>R</sub>) and Potential Reproductive Output (PRO) was not significantly different from zero ( $n = 10$ , d.f. = 8,  $r = -0.241$ ,  $p > 0.05$ ) (Figure 3.12 A&B). No significant association was found between Species Richness (S) and Randomized Potential Reproductive Output (PRO<sub>R</sub>) ( $n = 10$ , d.f. = 8,  $r = -0.503$ ,  $p > 0.05$ ), or between Shannon-Wiener Diversity (H') and Randomized Potential Reproductive Output (PRO<sub>R</sub>) B) ( $n = 10$ , d.f. = 8,  $r = -0.295$ ,  $p > 0.05$ ) (Figure 3.13 A&B). No significant correlation was found between Randomized Species Richness (S<sub>R</sub>) and Randomized Potential Reproductive Output (PRO<sub>R</sub>) ( $n = 10$ , d.f. = 8,  $r = -0.520$ ,  $p > 0.05$ ), or between Randomized Shannon-Wiener Diversity (H'<sub>R</sub>) and Randomized Potential Reproductive Output (PRO<sub>R</sub>) B) ( $n = 10$ , d.f. = 8,  $r = -0.222$ ,  $p > 0.05$ ) (Figure 3.14 A&B).

A)



B)

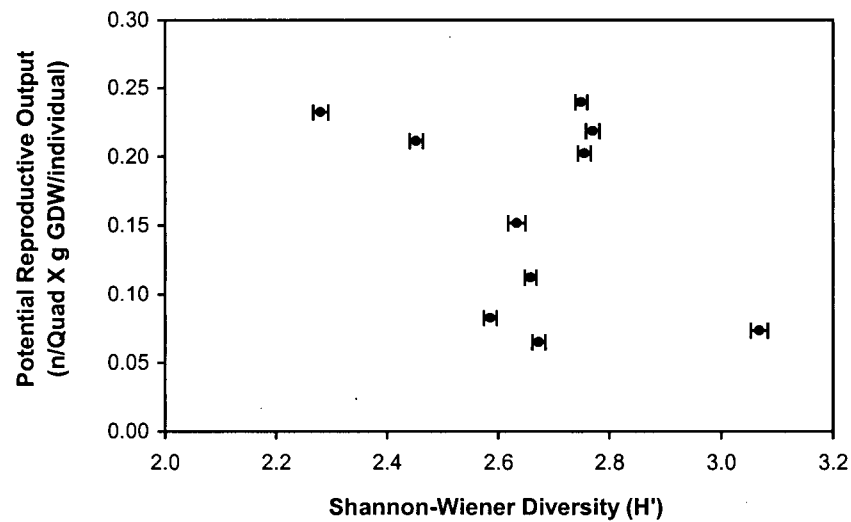
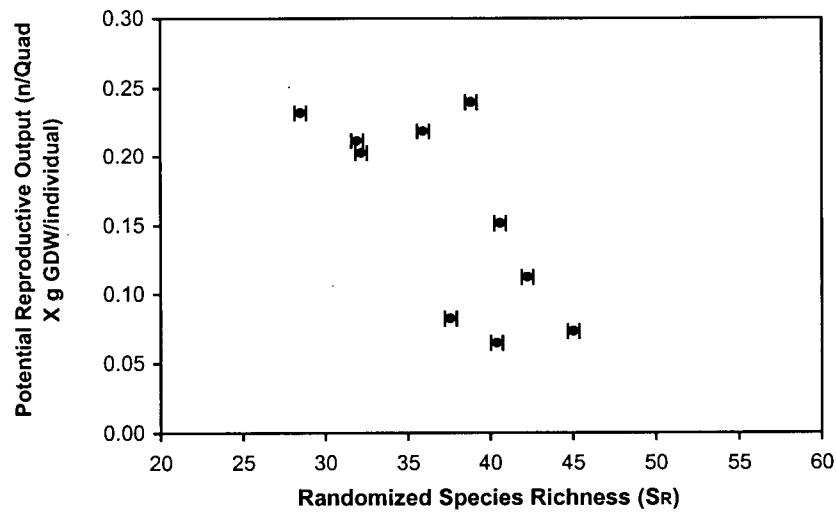


Figure 3.11 (A) Species Richness (S) and Potential Reproductive Output (PRO) were significantly negatively correlated ( $n = 10$ , d.f. = 8,  $r = -0.711$ ,  $p < 0.05$ ), whereas no significant association was found between (B) Shannon-Wiener Diversity ( $H'$ ) and Potential Reproductive Output (PRO) ( $n = 10$ , d.f. = 8,  $r = -0.388$ ,  $p > 0.05$ ).

A)



B)

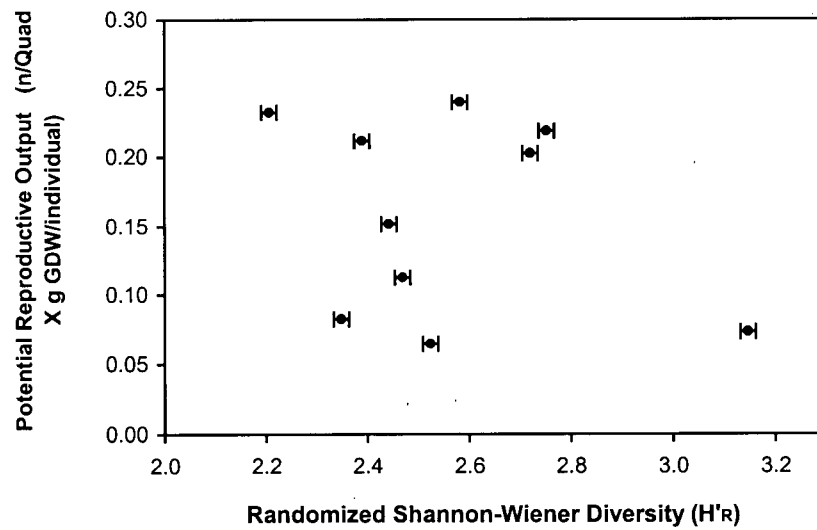
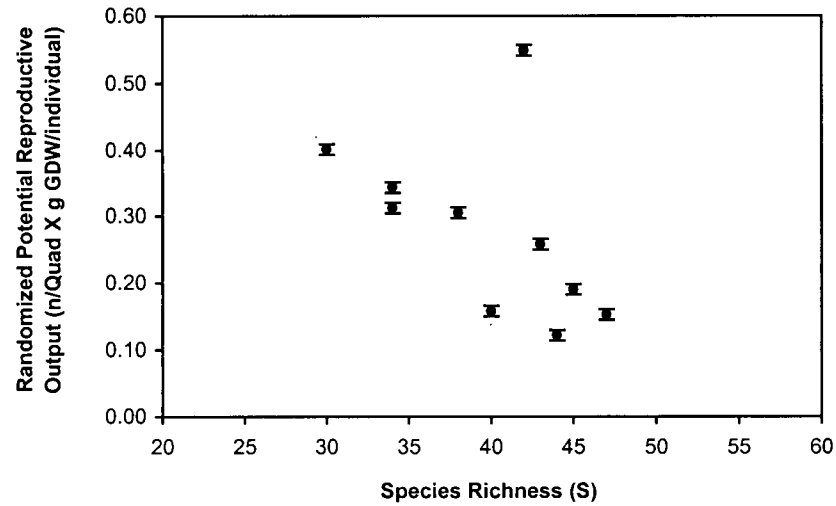


Figure 3.12 (A) Randomized Species Richness ( $S_R$ ) and Potential Reproductive Output (PRO) were significantly negatively correlated ( $n = 10$ , d.f. = 8,  $r = -0.714$ ,  $p < 0.05$ ). However the association between (B) Randomized Shannon-Wiener Diversity ( $H'_R$ ) and Potential Reproductive Output (PRO) was not significantly different from zero B) ( $n = 10$ , d.f. = 8,  $r = -0.241$ ,  $p > 0.05$ ).

A)



B)

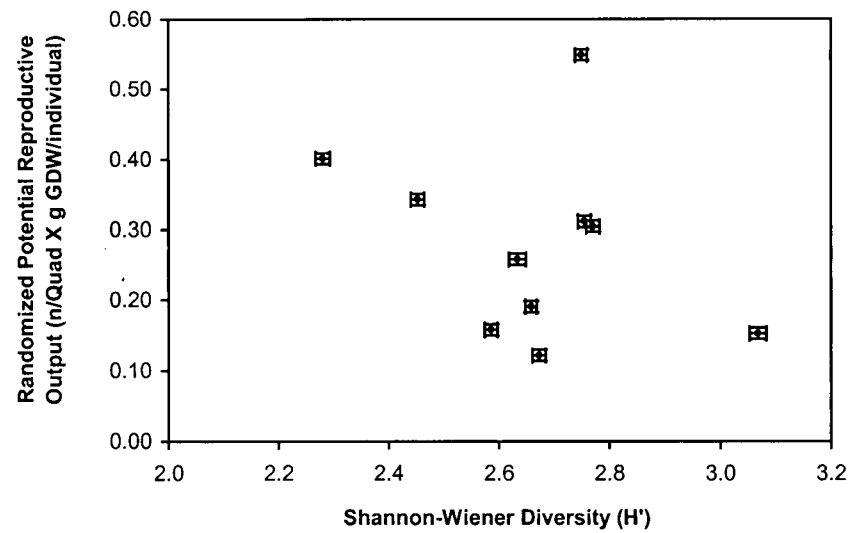
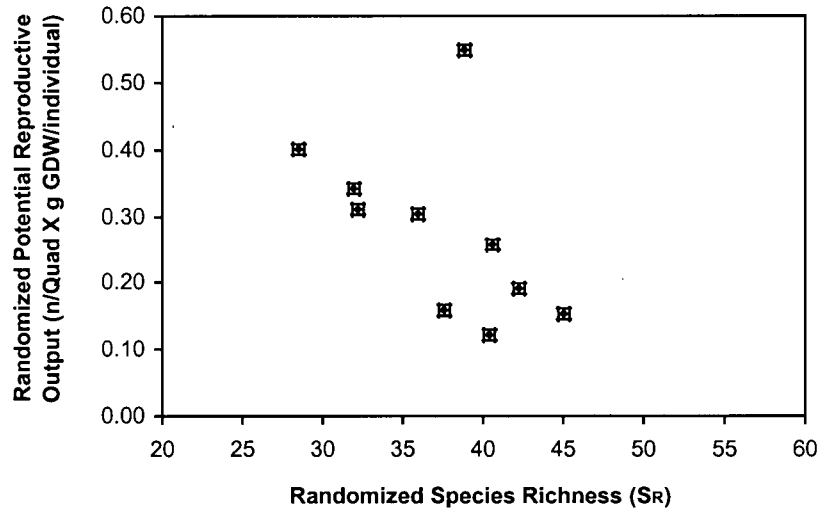


Figure 3.13 No significant correlation was found between (A) Species Richness (S) and Randomized Potential Reproductive Output (PRO<sub>R</sub>) ( $n = 10$ , d.f. = 8,  $r = -0.503$ ,  $p > 0.05$ ), or between (B) Shannon-Wiener Diversity (H') and Randomized Potential Reproductive Output (PRO<sub>R</sub>) ( $n = 10$ , d.f. = 8,  $r = -0.295$ ,  $p > 0.05$ ).



A)



B)

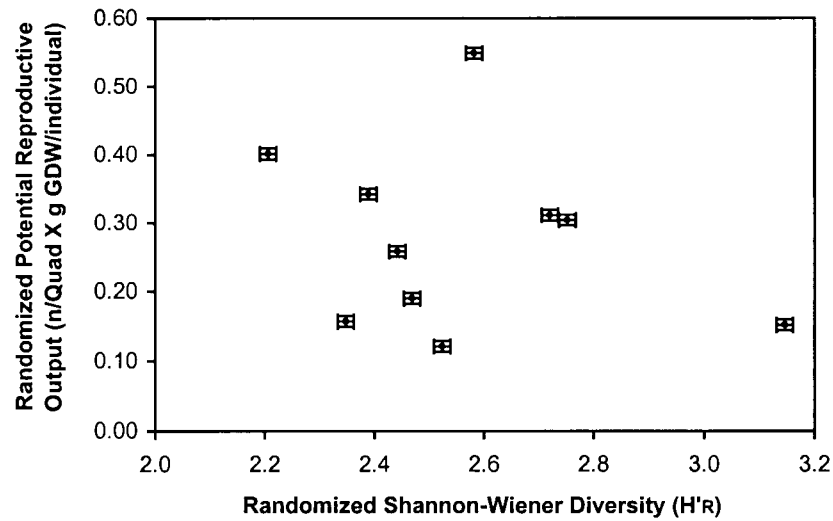


Figure 3.14 No significant correlation was found between (A) Randomized Species Richness ( $S_R$ ) and Randomized Potential Reproductive Output ( $PRO_R$ ) ( $n = 10$ , d.f. = 8,  $r = -0.520$ ,  $p > 0.05$ ), or between (B) Randomized Shannon-Wiener Diversity ( $H'_R$ ) and Randomized Potential Reproductive Output ( $PRO_R$ ) ( $n = 10$ , d.f. = 8,  $r = -0.222$ ,  $p > 0.05$ ).

### 3.4 DISCUSSION

#### 3.4.1 Estimating Site Biodiversity

Although 10 replicate quadrats were surveyed per site, calculating the Species Richness (S) at each site only resulted in one value per site. A lack of error structure associated to Species Richness (S) values prevented between site comparisons. Therefore, a bootstrapping method was designed to rectify this problem by creating Randomized Species Richness ( $S_R$ ) values. This procedure was also employed to derive a set of Randomized Shannon-Wiener Diversity values ( $H'_R$ ) from which a new error structure could be derived. Because  $S_R$  values were derived from 8 quadrats rather than 10,  $S_R$  values were consistently lower than S values. Although these two indices were significantly correlated and could both be used to describe the biodiversity at each site, the former, despite lacking an error structure, more accurately estimated the true number of macroscopic invertebrate and algal species at each site.

While various biodiversity indices have been developed to account for relative abundance, Shannon-Wiener Diversity was the only index calculated because it is the most widely used diversity index. Furthermore, many of the differences between diversity indices lie in the relative weighting that they give to evenness and species richness, as a result, they are all strongly correlated (Magurran 1988). With the exception of Sanford Sheltered,  $H'$  values were generally greater than  $H'_R$  values because  $H'_R$  values were obtained from 8 rather than 10 quadrats.  $H'$  and  $H'_R$  were also significantly correlated, however, out of the two indices,  $H'$  likely best approximated true species numbers and relative abundance. Nonetheless, in practice, when used for a site selection criterion, biodiversity is often quantified in terms of as species richness or species endemism (Balmford 2000, Howard et al. 2000, Howard et al. 1998, Prendergast et al. 1993, Pressey et al. 1996, Reid 1998). Furthermore, the use of  $H'$  and  $H'_R$  values to describe an intertidal site's biodiversity is questionable.

In the rocky intertidal organisms are notoriously patchily distributed. Although the asymptotes on the species accumulation curves indicated that the area sampled at each site was sufficiently large to describe a site's biodiversity in terms of Species Richness (Figure 3.1 A&B), this may not be the case for Shannon-Wiener Diversity values. The Shannon-Wiener Diversity index is dependent upon the number of species present and their relative proportions. Marked dominance of one species gives low diversity, while codominance of several species gives high diversity. If an  $H'$  value would have been calculated for each of the 10 quadrats surveyed per site, the variance surrounding the mean  $H'$  at each site would have been extremely large due to

the patchiness of most species. Instead,  $H'$  was derived from the average percent cover of species from the 10 quadrats. Therefore, depending on the quadrat size used and the size and distribution of the patches,  $H'$  may under or overestimate codominance and/or rarity. Although diversity indices are more informative than species counts alone, in the intertidal, the patchiness of many organisms demand that sampling protocols capture this patchiness in order to derive accurate diversity measurements. As a result, Species Richness may be a more transferable index to compare biodiversity between sites.

### **3.4.2 Biodiversity, Community Structure and Wave-Exposure**

Wave-exposure has been shown to be the predominant source of disturbance structuring rocky intertidal communities (Dayton 1971, Denny 1985). The 10 sites investigated in this research were located along a gradient of wave-exposure and it was revealed that biodiversity, as measured by  $H'$ ,  $S_R$ , and  $H'_R$ , was significantly different between sites (Figure 3.4, 3.5, 3.6). One would expect that site biodiversity may be most strongly correlated to wave-exposure values when communities are most impacted by wave force; i.e. when wave-induced forces are the greatest and the most significantly different between sites (October, November, and December). During these months, winter storms rip out patches of algae and invertebrates thereby creating space, a scarce resource in the intertidal. This new available of space allows for the settlement of new individuals and for succession to occur (Sousa 1979). This may explain why the trend between biodiversity and wave-exposure at sites subject to lower maximum wave force is more pronounced when diversity indices were graphed against October wave force data rather than September wave force data (Figure 3.7 A,B,C&D).

The Intermediate Disturbance Hypothesis, discussed in Chapter 1, predicts that biodiversity is greatest at sites with intermediate levels of disturbance. Figures 3.7 C& D depict only half of this hypothesis. This may be because the range of disturbance over which biodiversity was investigated in this study was too narrow to illustrate Connell's complete biodiversity/disturbance relationship (Figure 1.3). For instance, if ten extremely sheltered sites had been additionally surveyed, one might have observed Connell's prediction that at some inflection point, biodiversity begins to decrease with decreasing disturbance.

The Intermediate Disturbance Hypothesis further suggests that low levels of biodiversity should be observed at sites where disturbance is greatest. The unexpectedly high levels of biodiversity at Edward King Exposed and Sanford Exposed in Figure 3.7 C&D may be explained by the possibility that the  $S$  and  $H'$  values of the other 8 sites were underestimated. If mobile

species such as crabs, worms and gunnels had been accounted for in the biodiversity estimates, such organisms would be present at semi-sheltered sites, thus increasing Species Richness, but would likely be dislodged at exposed sites. In which case, S and H' values at Edward King Exposed and Sanford Sheltered would remain the same where as S and H' values at the other 8 sites would be greater. Biodiversity may also be unexpectedly high at the very exposed sites due to intertidal zonation mixing. The intertidal has biologically defined zones characterized by distinct species assemblages (Kozloff 1973). The shoreward surge of water in the surf zone acts as a major contributing factor in setting the species specific vertical limits to habitation on the shore. The more violent the flow, the higher on the shore plants and animals are tossed (Gaylord et al. 1994) and the greater the possibility of zonation mixing. At Edward King Exposed and Sanford Exposed, species such as *Nucella canaliculata*, *Pollicipes polymerus*, *Balanus glandula*, and *Mytilus californianus*, species characteristic of higher intertidal zones, and species such as *Balanus nubulis* and *Aplidium* spp., characteristic of lower intertidal zones, were all present in the *Hedophyllum* zone. Although the maximum wave force values for Edward King Exposed, Diana, and Sanford Exposed were estimated for the October data set, and thus their position along the x-axis not precise, their wave force values were observed to be considerably greater than the other 7 sites.

The unexpectedly high biodiversity documented at Edward King Exposed, Sanford Exposed and Seppings Exposed was biologically significant, therefore these sites should not be deemed as outliers *per se*. However, exposed sites were removed from the September and October data set to statistically examine the relationship between biodiversity and wave-exposure at the remaining sites subject to lower maximum wave forces. Although no significant relationship was found between biodiversity (S and H') and September's maximum wave force values (Figure 3.8), a highly significant relationship was found between biodiversity and October's maximum wave force data (Figure 3.9). As described above, if maximum wave force is the main factor structuring communities and the greatest wave-induced forces occur during the winter months, this result may be anticipated. Nonetheless, because measures of biodiversity do not reflect differences in species assemblages, a multivariate approach was taken to determine whether wave force structured the community composition at each site.

A principal component analysis (PCA) was used to summarize the patterns of correlations among observed variables. In this case, the observed variables were the percent cover values of species at each site. In Figure 3.10, the confidence ellipses surrounding the quadrats surveyed at each site overlap extensively, indicating that the same dominant species

were present at each site. These species; *Katharina tunicata*, *Hedophyllum sessile*, *Corallina* spp., and *Bossiella* spp are all characteristic of the rocky intertidal *Hedophyllum* zone of the Deer Group Archipelago. Axis I (Factor 1) was correlated with the relative geographic location of the 10 sites investigated (Figure 3.10). In fact, the center of each confidence ellipse line up along axis I as they do along a southwest/northeast axis on a nautical chart of the area. This indicates that sites located in close proximity had similar species compositions. This may be due to wave-exposure as outer islands are subjected to more frequent and intense wave-induced disturbance than inner islands located further down Barkley Sound. Furthermore, axis II (Factor 2) was correlated to the October maximum wave force data. Because each component, or factor, empirically summarizes these correlations, factors are thought to reflect the underlying processes that have created these correlations. Therefore, because both axes are correlated to an aspect of wave-exposure, one can conclude that wave-exposure is likely one of the factors responsible for structuring intertidal community composition in the Deer Group Archipelago.

Species assemblages are predictable along wave-exposure gradients (Dayton 1971, Paine 1979). This may be attributed to the selective forces acting on populations at various levels of disturbance. At highly wave-exposed sites, wave-impact and resultant wave surges may dislodge organisms (Denny et al. 1985), therefore, species more resistant to high flow-induced forces may be selected for at such sites. In contrast, at low-wave exposed sites, biological interactions may become the more predominant selective agents (Menge 1972). Nonetheless, it has been demonstrated that the demographic rates of a population, such as recruitment and mortality, are correlated to the wave-exposure gradient within which a species is found (Milligan 1998). Therefore, changes in species assemblages along wave-exposure gradients suggest that there is a limited range of wave-exposure in which species can successfully persist.

### **3.4.3 Biodiversity and Potential Reproductive Output**

The potential reproductive output (PRO) of *Katharina tunicata*, quantified by the length-fecundity model, was significantly negatively correlated to biodiversity as measured by Species Richness (S) and Randomized Species Richness ( $S_R$ ) (Figures 3.11A & 3.12A). However, due to the high Randomized Potential Reproductive Output value ( $PRO_R$ ) calculated for Edward King Sheltered, no significant correlation was found to exist between Randomized Potential Reproductive Output ( $PRO_R$ ) and biodiversity as measured by Species Richness (S) and Randomized Species Richness ( $S_R$ ) (Figure 3.13A & 3.14A). Edward King Sheltered was the only site that had individual *Katharina* measuring between 8.5 to 10 cm in length (Figure 2.7).

The visual basic randomized re-sampling method used to calculate  $PRO_R$  (Chapter 2, section 2.2.4) substituted only one high dry gonad weight (0.74 g) for individuals in the 8.5 cm category because out of all the individuals dissected, only one measured 8.5 cm (Appendix I). Therefore, the Randomized Potential Reproductive Output value for Edward King Sheltered may have been overestimated.

No significant association was found between reproductive output, in terms of both  $PRO$  and  $PRO_R$ , and biodiversity as measured by Shannon-Wiener Diversity ( $H'$ ) and Randomized Shannon-Wiener Diversity ( $H'_R$ ) (Figures: 3.11B, 3.12B, 3.13B, & 3.14B). As discussed previously, the quadrat size dependent sampling procedure used to derive  $H'$  and  $H'_R$  values may misrepresent codominance and rarity in the patchy environment of the intertidal. Furthermore, the Intermediate Disturbance Hypothesis predicts the relationship between disturbance and the number of species present at a particular disturbance intensity or frequency. Because this hypothesis is suggested as the ecological rationale for why areas of high biodiversity are likely to encompass sink populations, Species Richness ( $S$ ) seems to be the appropriate measure of biodiversity when investigating the relationship between biodiversity and population viability. Interestingly, when protected areas are established in terrestrial systems to represent a country's biodiversity, site selection is often based on maximizing biodiversity in terms of species richness and / or species rarity (Balmford 2000, Howard et al. 2000) not Shannon-Wiener Diversity. A similar mindset may evolve in marine system site selection.

Figures 3.11A & 3.12A illustrate that sites with high algal and invertebrate species richness contain chiton populations of low potential reproductive output ( $PRO$ ). Conversely, areas of low species richness encompass chiton populations of relatively high potential reproductive output ( $PRO$ ). This inverse relationship between species richness and *Katharina*'s population viability as measured by a subpopulation's  $PRO$ , makes sense in an ecological context. Past studies suggest that *Katharina tunicata* plays a critical role in structuring lower intertidal communities (Dethier and Duggins 1984, Dethier and Duggins 1988, Markel and DeWreede 1998) primarily by exerting intense grazing pressure on bladed and coralline algae. *Katharina* also consumes sponges, juvenile limpets, and bryozoans (Dethier and Duggins 1984). At sites of high species richness, it is conceivable that multiple species can coexist because competitive dominant species are prevented from monopolizing space. Therefore, in areas of high biodiversity, multiple species persist yet no single species thrives, including *Katharina*. Areas of high biodiversity may consist of *Katharina* subpopulations existing at the limit of their ecological range rather than at their ecological optima (Figure 1.4A). Hence, *Katharina*

subpopulations living under such conditions have relatively low PROs and thus relatively low population viability. Consequently, high diversity sites are not sources of *Katharina* larvae relative to low diversity sites. Conversely, sites of relatively low diversity such as Helby encompassed subpopulations of *Katharina* with relatively high PRO. In such cases, *Katharina* dominates the community and may prevent new species from proliferating.

However, *Katharina* doesn't exclude all species. Interestingly, some limpet species, such as *Lottia pelta* and *Tectura scutum*, are dependent upon the grazing pressure of *Katharina* to keep the intertidal substrate clear of macroalgae (Dethier and Duggins 1984). *Lottia pelta* and *Tectura scutum* rarely eat macroalgae and are not sufficiently large to clear macroalgal sporelings, instead they feed on microalgal diatoms. It has been demonstrated that increased densities of adult *Katharina* can result in the increased reproductive output of both *Katharina* and the two limpets through an indirect commensalism relationship (Dethier and Duggins 1984). In the absence of *Katharina*, macroalgae thrive, outcompeting microalgae and removing both the food and habitat of the limpets. Therefore, in this particular case, if both *Katharina* and the two limpets species have high growth and survival rates, a site that is a source of *Katharina* larvae may also be a source for *Lottia pelta* and *Tectura scutum* larvae.

Source sites for *Katharina* are areas that provide good conditions for growth, survival and reproduction. However, the only way to definitively determine if a population is a source is to trace the fate of reproduction from that site. This was not done in this study. Such a task would have been formidably complex due to the nature of physical transport processes in Barkley Sound but would make a fascinating modelling project for a Ph.D. Finally, though these data indicate how much one population is a source relative to another, it does not indicate how much gonad per dry weight matters in terms of being a viable, self-replenishing source population. Decision makers may want to know what this prediction means in terms of a sustained functioning ecosystem or the long term conservation of biological diversity. While the answers to these questions are not provided, one can however conclude that out of the 10 possible subpopulations sampled, the Edward King Sheltered subpopulation has the greatest potential to be a source population (Figures 2.6, 2.11 & 2.12).

### **3.4.4 Conservation Implications**

Patterns of larval replenishment will play a significant role in determining the location of a MPA within a reserve network (Carr and Reed 1993). This study illustrated that the population viability of *Katharina* and biodiversity, quantified as species richness, were significantly

negatively correlated. It is possible that this relationship may be true for other competitively dominant species. These conclusions suggest that although protecting areas of high biodiversity makes intuitive sense, biodiversity hotspots, though apparently thriving, may encompass populations that are strongly reliant on replenishment by larval recruits produced elsewhere. As a result, protecting sites of high biodiversity may not always be the optimum way to conserve marine biodiversity. Alternatively, conserving viable source populations may be a more effective conservation strategy for marine systems. This is because source populations within a reserve are likely to contribute to population maintenance within that reserve while supplying recruits to adjacent exploited waters. In contrast, a protected sink population may collapse if the associated unprotected source population is overexploited (Figure 1.1). Therefore, MPA design that incorporates source/sink dynamics will both increase the possibility of fisheries enhancement and have higher biodiversity conservation value.

Since currents are the main agents of larval transport, these results also illustrate the importance of considering predominant oceanographic current patterns in marine protected area site selection criteria and network design. Admittedly, accounting for source / sink dynamics becomes complex because a community is composed of many species each with their own unique dispersal pattern. Therefore, a given site will clearly not encompass the source populations of all species. However, it is possible that source populations of several species overlap, as is potentially the case with *Katharina tunicata*, *Lottia pelta* and *Tectura scutum*. However, despite the fact that we may have confidence in identifying source populations, concluding which areas they supply presents an enormous challenge to the design of marine reserve networks.

#### **3.4.5 The Issue of Scale and Spatial and Temporal Variability**

Hopefully, marine protected areas will be established on a scale larger than that examined in this thesis. However, it is possible that small “no-take”<sup>11</sup> zones equivalent in size to the sites examined herein will be created within larger marine conservation areas. If so, the scale of this research is indeed relevant. The 8 voluntary Rockfish reserves in the San Juan Islands and BC’s 3 marine reserves are equivalent in scale to the sites presented here. However, if marine protected areas are to avoid edge-induced trophic cascades and biomass gradients as described in Chapter 1, they need to be larger (Walters 1998, Salomon et al. 1999). It remains unclear if the

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<sup>11</sup> “No-take” zones are areas where the exploitation of all living organisms and non-living resources is completely prohibited.



negative relationship between species richness and reproductive output reported in this chapter exists at greater scales.

Source populations may be ephemeral or be subject to temporal variability (Roberts 1998). For example, sites may vary from year to year in their supply and receipt of larvae. Nonetheless, populations presumably thrive at their ecological optimum, in which case such populations are likely sources of larvae. Following this logic, potential source sites should be predictable to a degree based on oceanographic parameters and habitat type. Consequently, source/sink dynamics should not be dismissed simply due to spatial or temporal variability.

#### **3.4.6 Biodiversity; a "Non Concept"**

Four measures of biodiversity were quantified in this chapter each having a different association with reproductive output. Which one should be used and deemed better than the others? Although diversity is a central theme in ecology, the term itself often eludes definition due to the extensive range of indices and models that measure it in disparate ways. In fact, Hurlbert (1971) went so far as to decry species diversity as a "non-concept". Magurran (1988) stated that "for a number of years, it was standard practice for an author to review existing indices, denounce them as useless and promptly invent a new index." Nonetheless, measures of diversity are often used as indicators of the wellbeing of ecological systems (Magurran 1988) and are used as a basis in protected areas site selection (Canada 1998a, Canada 1998b). In light of the quandary surrounding the concept of biodiversity, it is reasonable to caution managers to reconsider what makes a site biologically diverse, how biodiversity should be quantified, and what the diversity value given to a site indicates about its ecology. This thesis suggests that conservation biologists and protected area managers should rethink and question the concept of biodiversity and how it is used as a protected area site selection criterion.

### **3.5 CONCLUSION**

In conclusion, highly species rich sites were found to encompass relative sinks (*Katharina* subpopulations of relatively low reproductive output) whereas sites of low species richness were found to encompass sources (*Katharina* subpopulations of relatively high potential reproductive output). This thesis illustrates the possibility that conserving marine biological diversity may not always involve the protection of highly diverse areas.

### **Opening Note**

This chapter is based on a report written for the Department of Canadian Heritage (Parks Canada), Western Canada Service Center entitled "The Role of Marine Protected Areas in Temperate Marine Ecosystems; an Analysis of Empirical Evidence, Site Selection Methodology and Design Principles" (Salomon 2000b). The material in this report was later presented as a conference contribution at the Science and Management of Protected Areas Association (SAMPAA V) conference held in Waterloo, Ontario and was entitled "The Ecological Benefits of Temperate Marine Protected Areas; In Search for Empirical Evidence" (Tomascik et al. 2000).

## **4.1 INTRODUCTION**

The exploitation of living marine resources is considered to be the single greatest threat to marine biodiversity (National Research Council 1995). The spatial restriction of human activities in the marine environment in the form of marine protected areas (MPAs) is becoming recognized worldwide as a tool to control this threat. The use of MPAs in BC and Canada as a method for conserving marine biodiversity and enhancing fishery yields is slowly gaining credibility among scientists, fisheries managers, fishers and the general public. Although acceptance is increasing, uncertainty and opposition exists in part due to the lack of empirical evidence demonstrating the function of marine reserves in temperate regions.

The ecological impacts of marine reserves in tropical ecosystems have been studied extensively (Alcala 1988, Alcala and Russ 1990, Attwood and Bennett 1994, Bennett and Attwood 1991, Polunin and Roberts 1993), however, until recently, very few empirical studies in temperate marine ecosystems have been conducted (Estes and Carr 1999, Palsson and Pacunski 1995, Babcock et al. 1999). Although current mathematical and ecosystem-based models of temperate marine systems (Guénette and Pitcher 1999, Salomon et al. 1999) indicate that spatial protection from exploitation should serve as an effective fisheries management tool in temperate marine ecosystems, little empirical evidence exists. This lack of research is in part due to the reality that there are few marine reserves located in temperate waters which can be used to test their ecological impact. This chapter reviews the research that has been conducted in temperate systems, most of which demonstrate or suggest reserve effects, including increased density and size of exploited species and several of which report indirect ecosystem effects.

#### **4.1.1 Objectives**

The specific objective of this chapter is to analyze and critique current empirical evidence demonstrating the ecological impacts of MPAs located in temperate and subtropical ecosystems. It is also intended to promote active discussion on the theoretical underpinnings that should form the basis of MPA evaluation, and prompt management agencies to take action based on our current knowledge.

### **4.2 CASE STUDIES**

#### **4.2.1 Abalone on BC's West Coast**

In a study comparing 3 forms of marine reserves on British Columbia's West Coast, Wallace (1999b) found that 5 of the 6 sites subject to a coast-wide abalone closure since 1990 had insufficient abalone to provide the necessary sample size for statistical comparisons; this was presumably due to poaching. Abalone sizes differed significantly among the 4 enforced reserve areas surveyed (an ecological reserve, a military site and a prison reserve) and were significantly larger at the *de facto* prison reserve which had, by default, provided 39 years of protection from exploitation (Wallace 1999b). When relative abundance was accounted for, abalone at the military site had the highest potential reproductive output. Assuming adequate enforcement, these results provide evidence supporting the role of reserves in re-establishing populations of marine species with a low dispersing adult stage. However, it is difficult to determine if these results can be attributed causally to the enforced marine reserves primarily because patterns of abalone recruitment are influenced by a number of factors such as regional hydrodynamics, benthic topography and composition, as well as settlement and survival rates. The conclusion that reserves are more productive than exploited areas is weakened by the lack of replicate reserves of similar habitat.

The research summarized above does however provide an example of the importance of considering population viability when it comes to selecting the location of a "no-take" reserve within a MPA network. If a MPA is to be self-replenishing and export larvae (Roberts 1997a), marine reserves must incorporate a viable population of the target species. Abalone are broadcast aggregate spawners that require high densities to ensure fertilization. Therefore, biogeographic representation of the species is obviously insufficient criteria on which to select reserve location. Furthermore, providing evidence for the ecological effectiveness of MPAs on a species-by species basis may justify marine reserves whose goal is to protect a single species from overexploitation. However, ecosystem impacts, such as the change in biomass of other

trophic levels, should not be neglected in the evaluation process. Cumulative spatial effects, such as the ability of MPAs to provide seed sources for surrounding areas, should be taken into account in assessments of ecological effectiveness.

#### **4.2.2 Lingcod in the Strait of Georgia**

Lingcod populations in the Strait of Georgia and Puget Sound have become severely depleted (West 1997). In fact, due to recreational and commercial over-harvesting in the Strait of Georgia, lingcod biomass has decreased to an estimated 3% of its historical level (Martell and Wallace 1998). The doctoral research of Wallace (1999a) compared lingcod populations in two coastal marine reserves, Porteau Cove and Whytecliff Park, with populations in the adjacent non-protected areas of Howe Sound, British Columbia. Three studies were conducted from 1996-1998; a demographic study, an egg mass survey and a tagging study to determine the resident behavior of lingcod. The 1998 tagging data discussed in Wallace (1999a) was further analyzed by Martell et al. (1998) in terms of lingcod density.

Previous research conducted in tropical marine reserves (Alcala 1988, Alcala and Russ 1990, Polunin and Roberts 1993, Russ and Alcala 1996, Edgar 1999) and spatially explicit ecosystem-based models (Walters et al. 1998) suggest that the abundance of top predators within a reserve will increase once fishing pressure is removed. In Wallace (1999a), the relative abundance of lingcod between sites was determined as a function of the number of lingcod encounters per unit of search effort. Whytecliff Park showed a significantly higher rate of encounter compared to all exploited locations and Porteau Cove in 1997. However, because 63% of the fish encountered were under 50 cm, the high rate of encounter at Whytecliff is likely a factor of habitat suitability for juveniles rather than a reduction in fishing pressure (Wallace 1999a). These results suggest that there have been strong recruitment events since the establishment of the park in 1993 and the potential for a greater frequency of larger size classes in the future.

Martell et al. (1998) used a Bayesian statistical approach to estimate lingcod densities in Porteau Cove, Whytecliff and 10 non-reserve sites. Unlike Wallace's 1998 abundance analysis, Martell et al. (1998) found no significant difference in lingcod density between reserve and non reserve sites (exception: Kelvin Grove, a site open to fishing, had a significantly lower density of lingcod relative to Lookout Point, a transect within the Whytecliff reserve). However, similar to Wallace's 1998 data, the Lookout Point transect in Whytecliff Park had the greatest mean lingcod density of all 11 sites. Note that Martell et al. (1998) used mark-recapture data

plus a Bayesian statistical method and estimated lingcod density by dividing the mean population size (obtained from each location's posterior distribution) by the total reef area in the survey location as determined by bathymetry charts. Wallace (1999a), on the other hand, determined the relative abundance of lingcod between sites as a function of the number of lingcod encounters per unit of search effort. The data were then analyzed with an analysis of variance (ANOVA). This illustrates how survey methods and analysis techniques can result in conflicting conclusions.

Martell et al. (1998) found no significant difference in lingcod density among the 3 nonexploited sites sampled, however, the lowest mean density out of all 3 sites was observed in Porteau Cove, the oldest reserve surveyed. The authors suggest that this may be attributed to either poaching or to the territorial and nest guarding behavior of males which may limit immature lingcod from recruiting to this area i.e. larger lingcod require larger territories thereby reducing available habitat. If the latter is true, the relationship between home range size and age of fish is a critical factor that should be considered when judging the effectiveness of MPAs based on the relative density of a particular target species (Kramer and Chapman 1999). For instance, if older/larger individuals increase under spatial protection, their territories may increase with age, therefore, their densities may not always be greater within protected areas.

Martell et al. (1998) and Wallace (1999a) documented that lingcod in Porteau Cove were significantly larger than lingcod in all of the other locations sampled. Furthermore, both studies reported that reserve sites had a greater proportion of larger fish (>65 cm) compared to fished sites. The older age structure at Porteau Cove may be related to the fact that it has been part of B.C.'s Provincial Park system for 20 years, whereas Whytecliff Park was established in 1993. Notwithstanding, the size of lingcod in Porteau Cove can not be causally attributed to the restriction on fishing because this site's habitat differs markedly from all other sites sampled. Unlike the bedrock substrate that dominates all of the exploited reference sites, Porteau Cove has a sandy bottom and an artificial reef. Palsson and Pacunski (1995) also documented older size classes of lingcod in Edmunds Underwater Park in Puget Sound, a reserve which consists of a sandy bottom and an isolated artificial reef structure. A greater number of replicate reserves of similar habitat would help alleviate the confounding issue of habitat differences when comparing the abundance of species in reserves and adjacent waters.

Wallace (1999a) and Martell et al. (1998) found no significant difference between the average length of lingcod in protected areas and fished areas. This was due to the observation

that the Whytecliff Park reserve contained high densities of relatively small fish compared to the Porteau Cove reserve and the exploited sites.

The degree of adult and/or juvenile emigration from a reserve (i.e. spillover effect) and the export of larvae or eggs to exploited areas will determine the ability of a reserve to contribute to a fishery and surrounding biodiversity (Dugan and Davis 1993). Wallace (1999a) used the encounter rate of egg masses as an indicator of spawning potential. Porteau Cove showed significantly higher encounter rates of egg masses per hour diving compared to harvested locations whereas Whytecliff did not. In his tagging study, the resident behavior of lingcod at each site was measured by Wallace (1999a) based on the ratio between the encounter rate with tagged lingcod and the original tagging rate, where a higher value represents increased resident behavior. Out of the 13 sites sampled, lingcod at Porteau Cove had the greatest rate of resighting and thus the greatest resident behavior. Observational accounts indicate that larger fish exhibit greater resident behavior than do small fish, therefore, this result may be explained by Porteau Cove's greater proportion of larger fish.

Using the same visual census data as Wallace (1999a), Martell et al. 1998 analyzed it monthly to examine if seasonal movement of lingcod exists. Changes in the length frequency data and encounter rates over time suggest that small immature fish are displaced from the study sites during the spawning season and that large mature fish disappear from the study sites immediately after spawning season (Martell et al. 1998). These seasonal changes imply that a significant proportion of fish is moving outside reserve boundaries. This finding has several important implications. Firstly, small-scale movements need to be taken into account when selecting the size of reserves. Therefore, MPAs need to be big to decrease edge to area ratios to account for organism dispersal and fishing effort that is likely to concentrate at MPA boundaries. This further suggests that effective MPA design will include buffer zones in which harvest intensity is decreased. Secondly, because marine reserves displace fishing effort and cause it to concentrate in a resulting smaller area, MPAs are insufficient protection alone and must be coupled with protection outside reserve boundaries i.e. strict quotas (Allison et al. 1998).

#### **4.2.3 Lingcod and Rockfish in Puget Sound**

Palsson and Pacunski (1995) compared the size, density, and reproductive output of lingcod, copper and quillback rockfish in 5 exploited and 2 reserve sites located in central and northern Puget Sound. The Edmonds Underwater Park (EUP), a reserve established in 1970, had a greater density, biomass, egg production and mean size of both lingcod and copper rockfish

compared to the 4 exploited sites sampled in central Puget Sound. Lingcod density was twice as great in the EUP reserve than harvested sites while copper rockfish density was six times greater in the reserve than the average density at fished sites. Conversely, while EUP had a greater proportion of larger size class quillbacks (>40 cm), quillback densities were found to be the greatest at Boeing Creek (BC), one of the fished sites surveyed. These results could be due to habitat differences favoring juvenile fish at BC, and this would suggest that we require replicate MPAs in similar habitats to empirically test the effect of spatial protection on quillbacks. On the other hand, these results may be due to the possibility that the larger size class quillbacks at EUP are cannibalistic and impose natural predation pressure on the juveniles. This natural predation pressure is absent at BC which lacks larger size class quillbacks presumably due to human predation on legally sized quillbacks. This is an excellent example of how the ecological interactions that play out within a reserve can often produce some unexpected and opposing results that challenge the goals we set out for reserves and how we deem them biologically effective. These results do not suggest that the EUP is "not working" for quillbacks but rather that under some situations an increase in apex predator density may cause a decrease in the density of lower trophic level species or juveniles of the same species. Undoubtedly, field research and experimentation is required to corroborate these predictions. Similar comparative studies also show that not all species increase in abundance with spatial protection (Buxton and Smale 1989, Bennett and Attwood 1991). Size and density differences were not as pronounced at Shady Cove (SC), a reserve located in Northern Puget Sound, as they were at EUP. Given that rockfish grow slowly and mature late in life, these results may be attributed to the fact that SC had been established for a mere 4 years prior to the survey.

Egg production for lingcod and copper rockfish, based on documented length-fecundity relationships (DeLacy et al. 1964, Hart 1967), was estimated to be greater in the reserves than the fished sites. Based on the observations that lingcod and rockfish in both EUP and SC had a significantly greater reproductive output than the exploited sites, Palsson and Pacunski (1995) conclude that lingcod and rockfish populations in Puget Sound are likely stressed. These results are further substantiated by Wallace's (1999a) research in Howe Sound, British Columbia. It should be noted that increased densities of large fish and an ensuing competition for limited food and space resources may lead to a decrease in fecundity or frequency of spawning, therefore, egg production in this study may have been overestimated. Such effects require further investigation.

A comparison of the population size structure of each site revealed that the two harvest refugia, EUP and SC, had dramatically higher proportions of larger sized fish which were either not observed in the exploited sites or were extremely rare. These size related increases associated with reserves have been well documented in the tropics (Dugan and Davis 1993).

The results from this study suggest that reserves promote greater densities of large, high trophic level fish. Although there is a striking contrast between EUP and the exploited sites, due to a lack of replicate reserves, one can not causally attribute the greater density, population size structure, and reproductive output to spatial protection. For example, the EUP reserve could be more productive due to local abiotic factors such as current, exposure or upwelling. Furthermore, because EUP contains a sunken dry dock and thus an artificial reef, variation could be ascribed to habitat differences. In order to provide a strong empirical case for temperate MPAs, more reserves need to be designated. Once established, a long-term, comprehensive monitoring program should be implemented to document ecological changes.

#### **4.2.4 Marine Reserves in New Zealand**

The history and experience in researching and establishing marine reserves in New Zealand has provided valuable insight into the ecological impacts and socioeconomic implications of temperate marine reserves (Ballantine 1999). Cole et al.'s 1990 investigation into the effects of marine reserve protection in northern New Zealand illustrates the difficulty of rigorously assessing the ecological impacts of marine reserves. Their objective was to determine the effects of spatial protection on the densities of several reef fish and large invertebrates yet they were confronted with the complicating factors of patchy distribution and dispersal behavior. Temporal changes in fish abundance within the Cape Rodney to Okakari Point "Leigh" Marine reserve were monitored for 6 years (1976-1982). They demonstrated that red moki density significantly increased whereas the 5 other fish surveyed showed no significant increase in abundance. In fact snapper, goatfish and blue cod all had lower mean densities in 1982 than in 1980. Furthermore, no consistent differences in fish densities at sites within the reserve were detected between 1978 and 1988.

A detailed survey conducted in 1988 compared sites inside and outside the marine reserve. It revealed no clear pattern for sea urchins, increased abundances of snapper, blue cod and red moki, and a trend towards increased snapper size within the reserve. It was suggested that most trends were not statistically significant due to the low power of the tests used (Cole et al. 1990). It is possible that the visual census method used was not adequate. A striking



difference in the densities of rock lobster between exploited and protected sites was found as no lobsters were observed outside the reserve. In terms of species diversity, significantly more fish species were observed within the reserve than outside.

In this study, replication of exploited sites was minimal. Furthermore, when interpreting the results from this research it is important to recognize that the 5 protected sites were sampled within one marine reserve therefore, the "within" reserve data were pseudoreplicated. The design of this study thus prevents an accurate assessment of the effects of spatial protection on marine fish and invertebrates in the New Zealand marine ecosystem. This research illustrates that marine reserves may affect the local abundance of certain species, particularly sedentary marine organisms, but may not benefit others, especially widely dispersing species. It further highlights the need for baseline monitoring, long term data, and replication.

Work by McCormick and Choat (1987) revealed that 62% of the reef fish within the Leigh Marine reserve were larger than 300 mm whereas only 38% were greater than 300 mm in harvested areas. Furthermore, the total abundance of temperate reef fish was 2.3 times greater than in adjacent exploited areas (McCormick and Choat 1987).

More current research by Babcock et al. (1999) in the Leigh and Tawharanui marine reserves recorded a significantly greater abundance of snapper and spiny lobster within the reserves than outside. Furthermore, Babcock et al. (1999) demonstrated that pronounced indirect causes of changes in community structure occurred within these reserves. This innovative study illustrated how an increase in predators (snapper and rock lobster) caused a decline in the density of grazers (sea urchins), consequently allowing an increase in the kelp population. This in turn resulted in an increase in primary and secondary productivity within the reserve as a consequence of protection (Babcock et al. 1999). The statistical power of this research was high due to the number of exploited and reserve replicate sites surveyed.

This study provides empirical evidence for the spatial modelling predictions made by Walters et al. (1998) and Salomon et al. (1999) who suggested that trophic cascades would occur within marine reserves. This has direct implications on how we judge marine reserve effectiveness in the future. The ecological interactions that transpire within a reserve may produce some unexpected results. For example, trophic interactions may lead to the local extirpation of a particular prey species or a decrease in species diversity. In contrast, harvest protection of a key predator may allow for an increase in diversity (Castilla and Duran 1985). Babcock et al.'s (1999) work suggests that a large-scale reduction of benthic primary production in temperate marine ecosystems may be an indirect result of fishing activity. Most importantly,

these results indicate that fishing activities have indirect ecological impacts far beyond the exploitation of a target species.

#### 4.2.5 Chilean Rocky Intertidal MPAs

Several research projects conducted in central and southern Chile have provided considerable information into the ecological interactions that play out within a reserve once exploitation pressure is removed and apex predator density increases. Two years after the establishment of a 100m long rocky intertidal human exclusion zone at Punta El Lacho, central Chile, there was a significant density increase in the large, previously exploited, predatory gastropod *Concholepas concholepas* relative to surrounding exploited sites (Castilla and Duran 1985). A trophic cascade was then documented as the predatory snail began feeding on the dense intertidal mussel bed that had developed in the absence of *C. concholepas*. Castilla and Duran (1985) suggest that the dramatic decline in the density of the competitively dominant mussel could lead to a pattern of increasing species diversity by permitting the use of space by other sessile invertebrates and algal species. The authors conclude that in the absence of human exploitation, the economically important carnivorous *C. concholepas* plays a key role in structuring intertidal communities in central Chile.

The results described above were corroborated by the work of Moreno et al. (1986) which was conducted in Southern Chile. They too found that *C. concholepas* populations increased significantly 6 years after the establishment of a marine reserve. Furthermore, the mean size of the predators was markedly larger within the protected area compared to harvested areas. It had been previously proposed that adults of this species lived only in subtidal habitats yet these data provide evidence that the absence of adult size classes in harvested areas is due to fishing mortality rather than suboptimal habitat. The exploitation of intertidal invertebrate and algal populations has occurred on the coast of Chile for the last 1300 years (Dillehay 1984).

Moreno et al. (1986) cleverly examined the effects of experimentally excluding *C. concholepas* from within the marine reserve. By doing so, the confounding issue of "habitat differences" between reserve and non-reserve density data was solved and a mechanism substantiated. Like the work of Castilla and Duran (1985), this research revealed that *C. concholepas* had a significant impact on mussel beds and community structure (Moreno 1986). In terms of providing empirical evidence for the ecological impact of temperate marine reserves, the weakness of these two studies was the lack of reserve replication. However, they clearly

illustrate how human exploitation of a target species can alter trophic interactions and thus drastically affect an entire ecosystem (also see Babcock et al. 1999).

Our lack of knowledge about ecological processes governing ecosystem functioning presents a major constraint in understanding the effects of fishing on population dynamics and ecosystem function (Hilborn and Walters 1992). Castilla and Fernandez (1998) discuss how understanding relevant ecological processes is critical to the management and sustainable use of the Chilean inshore benthic small-scale fishery. They further describe the benefits of co-managing community-owned shellfish grounds by the government and fishers and suggest that these areas be considered replicates when evaluating the effects of human perturbations on marine ecosystems (Castilla and Fernandez 1998).

#### **4.2.6 Benthic Community Structure in Southern California**

Bottom trawling has been identified as one of the most disruptive anthropogenic disturbances to coastal benthic communities, however, a cause and effect relationship has yet to be established due to the lack of replicate non-impacted, control sites required for statistical comparison. Engel and Kvitek (1998) examined the impact of bottom trawling on benthic community structure by comparing two sites within the Monterey Bay National Marine Sanctuary; one site had been exposed to restricted levels of trawling intensity while the other had been affected by intense trawling pressure. The latter site had significantly more trawl tracks, exposed sediment and shell fragments and significantly fewer rocks, mounds and flocculent matter (i.e. detritus) than the lightly trawled site. Four out of the seven invertebrate epifauna counted were significantly more abundant in the lightly trawled site, yet, the heavily trawled site had a greater abundance of opportunistic species such as oligochaetes, ophiuroids, and nematodes (Engel and Kvitek 1998). This work suggests that intensive trawling can decrease benthic community complexity and biodiversity and cause an increase in opportunistic species.

The role of habitat complexity in structuring ecosystems has been well documented (Auster and Malatesta 1995, Ferrell and Bell 1991, Orth et al. 1984). However, because Engel and Kvitek's (1998) research had small sample sizes and no site replication, one can not exclude the possibility that the differences observed may have been due to physical differences between the sites surveyed. Furthermore, the lightly trawled site was not a "true control" because the area had been harvested in the 70's. Nonetheless, Engel and Kvitek (1998) based their comparison on a fishing pressure gradient; high versus low rather than exploited versus not exploited. This absence of true unfished control sites is near universal and severely hinders our ability to

determine appropriate levels of harvest for maintaining sustainable fisheries and marine biodiversity. The authors suggest that there is a critical need for large-scale, long-term, manipulative experiments within marine reserves in order to identify optimal levels of trawling for conserving fisheries and biodiversity. Otherwise, such experiments will continue to be unreplicated and poorly controlled.

#### **4.2.7 Estuarine No-Take Sanctuary in Florida**

Johnson et al. (1999) sampled subtropical estuarine fish species located in exploited and reserve sites found in and around the Merritt Island National Refuge, Florida, an area which has been closed to fishing and public access for 38 years. This extensive study was unique and informative because along with abundance, density, diversity and size class data, covariate data such as salinity, depth, temperature, season and month of sampling were recorded to account for factors, besides fishing effort, that affected fish abundance between sites.

Fishing was the primary factor affecting catch per unit effort (CPUE) at each site while salinity and depth had important secondary effects followed by temperature, season and month. Catch rates were higher in reserve sites in part due to environmental variables at these sites that favored high fish abundance i.e. shallower depths and lower salinities. By accounting for environmental factors with the Lo method, which involves calculating a relative abundance index using a delta-lognormal approach (Lo et al. 1992), standardized CPUE data represented differences directly attributable to fishing. Johnston et al. (1999) found that standardized CPUE demonstrated significantly higher densities of all game fish and several nongame species in reserve sites compared to exploited sites. Data clearly document greater abundances and larger size classes in two replicate reserve sites than in adjacent exploited areas.

Rarefaction curves suggested that species diversity was significantly greater in reserve sites compared to exploited sites (Johnson 1999). However, both Mosquito Lagoon, a fished site, and West Banana Creek, a reserve site, had the highest number of cumulative species. It is also important to note that Mosquito Lagoon was the largest site sampled therefore, the greater number of potential habitats may have contributed to such high species diversity. Low salinity sites had lower species diversity indicating that salinity may be a limiting factor, therefore, the distance between a site and the ocean may influence species composition.

Tagging studies demonstrated that fish dispersed from reserve sites to exploited sites. Although circumstantial, increased recreational fishing effort just outside reserve boundaries further substantiates the likely export of large size class fish from reserve areas to fished areas.

By sampling replicate unfished areas and by accounting for environmental differences between sites, this paper provided strong evidence for the ecological benefits of estuarine reserves.

#### **4.3 RECOMMENDATIONS**

The research presented and critiqued above provides initial evidence for the ecological benefits of temperate marine reserves. However, to undertake reliable comparative studies needed to accurately assess the potential benefits of reserves, field studies need to be expanded both spatially and temporally. Replicate reserves are urgently required to provide a greater number of controlled areas for assessing anthropogenic impacts on marine systems. Having replicate reserves will increase the statistical power of such research and decrease our chances of making type II errors i.e. failing to reject the null hypothesis when in fact an impact does exist (Dayton 1998a).

The detection of trends in an ecosystem requires baseline information against which changes can be quantitatively measured and a distinction between natural and anthropogenic influences (Dayton 1998b). Long-term data sets collected in marine reserves will allow confounding factors such as climatic responses and natural cycles to be discerned from anthropogenic impacts. Ideally, Before - After - Control (inside) - Impact (outside) studies, (BACI) design (Underwood 1996), should be conducted to effectively test the ecological impacts of marine reserves. Without replicate marine reserves, our ability to separate human impacts from the natural variability of a system will become severely compromised.

We can learn from previous empirical case studies about factors that may be crucial in future experimental design. For example, many studies of coastal no-take areas that document the differences in population densities between reserve and non-reserve sites may not always indicate the magnitude of the reserve effect, especially if non-reserve data are taken from sites located in close proximity to reserves. This is primarily due to spillover that tends to homogenize fish populations at reserve boundaries (Walters 1998). However, while the flux of adults out of reserves may decrease the perceived effect of protection, it is one of the two ways by which marine reserves can sustain or enhance fisheries. The other way being the production of larvae which disperse out of reserves and increase the production of exploitable populations outside reserves (Carr and Reed 1993, Allison et al. 1998, Roberts 1998, Estes and Carr 1999). Empirical studies and the monitoring of marine reserves are essential. Continued research of this type will help the scientists, management agencies and the public make informed decisions about MPA establishment.

### 5.1 SUMMARY

We are in the throes of revolutionising fisheries and marine ecosystem conservation. Tropical and a smattering of temperate empirical studies plus various mathematical models provide evidence that marine protected areas, coupled with additional management tools, are an effective way of conserving marine biodiversity. This is an exciting time as scientists, government agencies, and conservation organisations are all advocating spatial protection. However, as on any bandwagon, the danger lies in the realities that fall short of our expectations.

Areas of high species richness are often identified as priority areas to protect (Reid 1998, Balmford 2000, Howard et al. 2000). The research presented in this thesis suggests that protecting marine areas of high species richness does not guarantee the future viability of these species. This is because areas of high species richness may not always encompass viable self-replenishing, source populations. Alternatively, viable populations that can contribute to population maintenance within a reserve and provide recruits to adjacent waters should be considered as top priorities for protection. In essence, the open population nature of many marine organisms must be taken into account in any marine protected area design plan.

Establishing priorities in conservation is unavoidable. When contemplating site selection criteria in marine ecosystems, the behaviour, habitat preferences and larval dispersal of the organisms a reserve is intending to protect must be considered. However, while marine protected area site selection and design should be governed by biological, ecological and oceanographic information, socio-economics and management strategies must also be carefully considered.

#### 5.1.1 Adaptive Management and MPA Design

To assure effective marine conservation strategies, science should inform MPA policy and help direct management decisions through an adaptive, ecosystem-based management approach where management policies are deliberately used as experiments (Walters 1986). This would entail setting up replicate MPAs of various designs, monitoring biotic changes over time and quantifying the ecological impact of each policy/experimental treatment both inside and outside the reserves. The framework for marine reserve management must be sufficiently responsive and flexible to allow for change as better scientific information is gathered and as socio-economic conditions shift. Ultimately, marine conservation policies should be based on

ecological factors and consider social and economic needs. Unfortunately, in reality, short-term social and economic costs often act as barriers to MPA establishment and limit MPA design. Therefore, it is important to demonstrate that the long-term gains of preserving ecosystem integrity outweigh short-term job losses and the ensuing economic costs.

### **5.1.2 Community Involvement; Hindrance versus Compliance**

A conflicting social paradox underlies the establishment of any marine protected area. Compliance to marine zoning restrictions hinges upon the local collaboration of coastal communities, yet waiting for stakeholder agreement and community involvement can be an enormous hindrance to an already slow process. Past case studies and present management strategies suggest that local community involvement from the onset of a marine protected area design plan is essential to achieve adherence to exploitation restrictions and allowances (Fenton et al. 2000, Vincent 1998). This can be accomplished through participatory planning, co-management and partnerships between government and coastal community interest groups such as commercial fishermen, First Nations, non-governmental organizations, sports fishermen, tourist outfitters, and dive operators.

Participatory planning entails collaborative and transparent decision making involving communities at various levels of the establishment process, from MPA site identification, to day to day management activities associated with individual MPAs. Community involvement can be achieved through workshops on marine reserve system planning, discussion papers, and educational seminars with the goal to build support for MPA establishment. Such concepts seem obvious, as fishers for example often know where spawning aggregations and juvenile nursery grounds tend to be located. However, in light of the differences among interest groups, stakeholder agreement can take an exceedingly long time and slow the establishment process considerably. For evidence of this predicament, one needs only to look as far as British Columbia's West Coast. Although a federal-provincial agreement was signed for the proposed Gwaii Haanas National Marine Conservation Area in 1988, it remains to be legally established. Furthermore, the Gulf Islands National Marine Conservation area feasibility study and public consultation process has been underway for the past 3 years yet, unfortunately, the establishment of the proposed marine park is far from imminent. Local buy-in is critical, but to what cost?

When the Great Barrier Reef Marine Park was declared in 1975, the Australian government did not wait for all stakeholders to reach an agreement nor did they wait for a plethora of ecological and oceanographic data before they established the multi-use management

zones, of which the park is composed. However, public support for the park is presently high perhaps due to the alternative economic benefits derived from the park such as ecotourism (Day 2000a personal comment). Furthermore, park managers are currently using the principles of adaptive management and are re-zoning the park based on biogeography and source/sink dynamics (Day 2000b). So the question remains; Should the government set up a network of reserves in British Columbia based on existing biological knowledge and hope for compliance or should they wait for public consensus? Undoubtedly, if marine protected areas are to be established, economic alternatives and diversification must be encouraged and endorsed in order to promote stewardship of the reserve among local communities.

### **5.1.3 The Future of MPAs in British Columbia**

Declaring protected areas in British Columbia's marine ecosystems has lagged far behind the establishment of protected areas in the province's terrestrial environment. This is not for a shortage of legislative tools as the *Oceans Act*, passed in 1997, allows the Department of Fisheries and Oceans to designate marine protected areas under Section 35 (Canada 1998b). Furthermore, there are many municipal and provincial legislative tools, such as the Park Act and the Ecological Reserves Act, which can also be used to restrict exploitation in British Columbia's coastal waters. Lastly, if passed, pending legislation cited as the *Marine Conservation Act* (Bill-C48), will assist Parks Canada to designate National Marine Conservation Areas. Clearly, the major barriers to the establishment of marine protected areas in British Columbia are not legal in origin, rather, social and political obstacles present the greatest hurdle.

These sociopolitical obstacles are rooted in cultural and economic principles. During the recent Atlantic Canada lobster dispute between Natives and non-natives, both parties proclaimed that they had an intrinsic "right to fish". The former claimed a constitutional right (Constitution Act 1982, *Delgamuukw vs. British Columbia* 1997), while the latter often asserted a cultural / historical right<sup>12</sup>. Similar cases in B.C. over salmon attest that a paradigm shift must take place where fishing is no longer viewed as a right but as a privilege and with that privilege comes responsibility; the sustainable use of that resource. Furthermore, Fishers understandably fear the threat of job loss resulting from marine protected areas. Therefore, it is important to demonstrate that the long-term ecological and economic gains of a marine protected area out-weigh the short-

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<sup>12</sup> [www.mastiffassociation.org/news/canada/rc11.htm](http://www.mastiffassociation.org/news/canada/rc11.htm) & [www.fosters.com/news99d/october/11/bu1011a.htm](http://www.fosters.com/news99d/october/11/bu1011a.htm) visited July 8, 2000



term economic costs. As previously mentioned economic diversification must be encouraged and supported by the government.

Many British Columbians may be oblivious to the threats facing our marine ecosystems because, unlike a glaring clear-cut, these threats take place underwater and out of sight. Science and monitoring coupled with public education is needed to gain public support for MPAs. British Columbia is making small strides towards the establishment of marine protected areas as the Department of Fisheries and Oceans announced 4 pilot marine protected areas in 1998; the Endeavour Hydrothermal Sea Vent, Race Rocks Ecological Reserve, Gabriola Passage and the Bowie Sea Mount (Canada 1998a). However, the current *ad hoc* approach to establishing reserves as small isolated entities falls short of what is needed to assure the long term sustainability of marine biodiversity and fisheries conservation in British Columbia.

#### **5.1.4 Monitoring Marine Protected Areas**

When judging the ecological effectiveness of British Columbia's future network of marine protected areas, two critical issues should be kept in mind. First, systems are dynamic, therefore, population densities will fluctuate over time. Monitoring programs that assess the ecological impact of spatial protection will have to take this into account. Second, trophic cascades may occur within reserves (Castilla and Duran 1985, Babcock et al. 1999, Walters et al. 1998, Salomon et al. 1999). Therefore, the ecological interactions that play out within a reserve may deal us some unexpected results, such as a decrease in biodiversity or a severe decline in a certain prey species. These predictions do not imply reserve ineffectiveness, instead they force us to rethink our marine conservation goals and question how we judge MPA design effectiveness.

#### **5.1.5 The "Art" of Science?**

Chapter 2 and Chapter 3, may prompt one to contemplate the distinction between science and art. In these two chapters, various methods were used to derive the uncertainty surrounding both known and calculated values. The methods presented revealed slightly different stories in terms of statistical significance. Despite the rigorous objectivity of stratified random sampling, hypothesis testing and quantitative techniques commanded by the scientific method, in reality, scientists have creative license to analyze and present their work how they wish. Experimental tests of logically constructed hypotheses have undoubtedly advanced ecology (Underwood 1996), however, many scientists, policy makers, and the general public have been indoctrinated

to “believe” that science is always objective. Even the best ecological detectives may describe an ecological case and supporting evidence to substantiate their allegations. It is for this reason that the two randomized re-sampling methods were described and their slightly different results discussed. Then again, with the “belief” of objectivity, the “hope” for statistical significance, and demonic intrusion all too prevalent in ecological fieldwork, it could be argued that science should be likened to a faith rather than an art form.

## **5.2 CONCLUSION; AN ISSUE OF URGENCY**

Humans now dominate the majority of the world’s marine and terrestrial ecosystems (Vitousek et al. 1997). The disturbing reality of sliding baselines (Dayton 1998b, Pauly 1995) trophic level changes due to serial depletion, otherwise known as “fishing down the food chain” (Pauly 1998) and the reduction of keystone species (Castilla and Duran 1985) all illustrate the urgency and importance of establishing marine reserves. In order to reliably evaluate the extent of anthropogenic impacts some areas need to be kept free of human disturbance and monitored over a long-term basis.

Though scientific knowledge about marine and coastal ecosystems is far from complete, this paucity of information should not stop conservation strategies. At the very least, marine protected areas can provide valuable baseline information that will allow for the comparison of exploited and nonexploited populations, upon which exploitation regimes can be based. Scientific uncertainties regarding the effectiveness of marine reserves still remain, however, without the creation and monitoring of reserves, these uncertainties can not be investigated. Presently, we have adequate ecological, biological, oceanographic, geological, and fisheries information to begin experimenting with marine reserves (Ballantine 1999, Wallace 1999a). It is only through the establishment of marine reserves in a replicated and representative manner, coupled with long-term monitoring, that we will gain insight into their design uncertainties.

The scientific community is rightfully responsible for informing marine conservation policy on such issues as MPA site selection criteria, design and assessment. Scientists and managers need to be accountable for providing realistic predictions regarding the ecological effects of MPAs. Advocating MPAs under false pretence could cause public support to evaporate. To avoid this worrisome possibility we need to recognize that simple expectations should be questioned and that departures from such expectations exist. By acknowledging the weaknesses of some site selection criteria and providing evidence for the strengths of others, we

can prevent misperceptions from undermining further MPA establishment and improve the ability of marine protected areas to conserve marine biodiversity.

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# Appendix I Length-Fecundity Model Raw Data

	Site	Sex	Length (cm)	Body Weight (g)	Gonad Wet Weight (g)	Gonad Wet Weight Log Transformed (g)	Gonad Dry Weight (g)	Gonad Dry Weight Log Transformed (g)
1	Sepp E	f	7	20.68	1.1	0.04	0.40	-0.40
2	Sepp E	f	7.5	21.07	1.2	0.08	0.43	-0.37
3	Sepp E	f	6	13.43	1.03	0.01	0.35	-0.46
4	Sepp E	f	5	6.55	0.44	-0.36	0.09	-1.05
5	Sepp E	m	7.5	28.13	2.04	0.31	0.92	-0.04
6	Sepp E	m	6.5	27.05	1.8	0.26	0.55	-0.26
7	Sepp E	m	9	40.85	2.01	0.30	0.65	-0.19
8	Sepp E	m	6.5	12.24	0.59	-0.23	0.16	-0.80
9	Sepp E	m	4.5	6.91	0.36	-0.44	0.04	-1.40
10	Sepp E	m	5	5.62	0.03	-1.52	0.01	-2.00
11	Sepp E	m	5	6.91	0.13	-0.89	0.04	-1.40
12	Sepp E	m	5.5	10.6	0.11	-0.96	0.02	-1.70
13	Sepp E	m	4.5	6.89	0.11	-0.96	0.02	-1.70
14	Sepp E	m	13	73.24	4.61	0.66	2.36	0.37
15	Sepp S	f	6.5	14.82	0.31	-0.51	0.10	-1.00
16	Sepp S	f	7	22.76	0.67	-0.17	0.23	-0.64
17	Sepp S	f	6	10.62	0.4	-0.40	0.15	-0.82
18	Sepp S	f	8	23.02	0.53	-0.28	0.16	-0.80
19	Sepp S	m	6	6.94	0.08	-1.10	0.03	-1.52
20	Sepp S	m	9	34.65	1.25	0.10	0.36	-0.44
21	Sepp S	m	6	6.54	0.13	-0.89	0.03	-1.52
22	Sepp S	m	9	25.48	2.38	0.38	1.12	0.05
23	Sepp S	m	5	9.63	0.35	-0.46	0.07	-1.15
24	Sepp S	m	9	39.51	0.61	-0.21	0.15	-0.82
25	Sepp S	m	4.5	4.92	0.08	-1.10	0.02	-1.70
26	Sepp S	m	7.5	19.41	0.7	-0.15	0.18	-0.74
27	Sepp S	m	5	7.66	0.23	-0.64	0.05	-1.30
28	Sepp S	m	5	9.54	0.35	-0.46	0.11	-0.96
29	Wee	f	3.5	6.32	0.2	-0.70	0.05	-1.30
30	Wee	f	10.5	45.79	2.24	0.35	0.79	-0.10
31	Wee	f	6.5	16.04	0.19	-0.72	0.05	-1.30
32	Wee	f	7	24.14	1.12	0.05	0.40	-0.40
33	Wee	f	8	26.61	0.34	-0.47	0.11	-0.96
34	Wee	f	4.5	5.98	0.02	-1.70	0.01	-2.00
35	Wee	f	7.5	21.29	0.85	-0.07	0.30	-0.52
36	Wee	f	6.5	14.1	0.07	-1.15	0.04	-1.40
37	Wee	f	7	26.24	0.44	-0.36	0.16	-0.80
38	Wee	m	9	42.08	1.87	0.27	0.52	-0.28
39	Wee	m	5.5	8.47	0.3	-0.52	0.09	-1.05
40	Wee	m	8	27.87	1.75	0.24	0.69	-0.16
41	Wee	m	5	10.79	0.65	-0.19	0.21	-0.68
42	Wee	m	7	17.37	0.73	-0.14	0.19	-0.72
43	Wee	m	6.5	19.32	0.94	-0.03	0.30	-0.52

	Site	Sex	Length (cm)	Body Weight (g)	Gonad Wet Weight (g)	Gonad Wet Weight Log Transformed (g)	Gonad Dry Weight (g)	Gonad Dry Weight Log Transformed (g)
44	Wee	m	8.5	28.45	1.72	0.24	0.74	-0.13
45	Wee	m	6	13.3	0.47	-0.33	0.74	-0.13
46	Wee	m	6.5	13.64	0.34	-0.47	0.18	-0.74
47	Helby	f	8	35.48	0.57	-0.24	0.19	-0.72
48	Helby	f	7	24.03	0.59	-0.23	0.20	-0.70
49	Helby	f	4.5	6.41	0.11	-0.96	0.03	-1.52
50	Helby	m	4	7.14	0.25	-0.60	0.06	-1.22
51	Helby	m	7	24.17	0.75	-0.12	0.21	-0.68
52	Helby	m	5	18.91	0.43	-0.37	0.13	-0.89
53	Helby	m	7.5	27.17	0.88	-0.06	0.26	-0.59
54	Helby	m	7	14.77	0.56	-0.25	0.15	-0.82
55	Helby	m	8	28.05	1.13	0.05	0.36	-0.44
56	Helby	m	7.5	18.54	0.56	-0.25	0.16	-0.80
57	Helby	m	5	8.33	0.24	-0.62	0.07	-1.15
58	Helby	m	7	18.38	0.95	-0.02	0.25	-0.60
59	Helby	m	5	6.21	0.05	-1.30	0.02	-1.70
60	Helby	m	6.5	17.32	0.43	-0.37	0.12	-0.92
61	Helby	m	7.5	30.77	0.51	-0.29	0.15	-0.82
62	Diana	f	6.5	22.56	0.62	-0.21	0.29	-0.54
63	Diana	f	5	7.18	0.02	-1.70	0.03	-1.52
64	Diana	f	7	29.82	1.02	0.01	0.55	-0.26
65	Diana	f	5	7.92	0.09	-1.05	0.05	-1.30
66	Diana	f	7	25.88	0.64	-0.19	0.27	-0.57
67	Diana	m	7	24.95	0.88	-0.06	0.44	-0.36
68	Diana	m	5.5	10.72	0.22	-0.66	0.10	-1.00
69	Diana	m	5	7.81	0.21	-0.68	0.11	-0.96
70	Diana	m	6	15.5	0.53	-0.28	0.26	-0.59



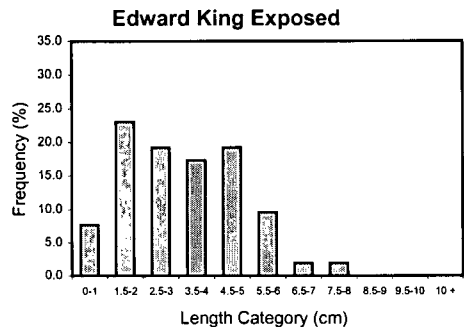
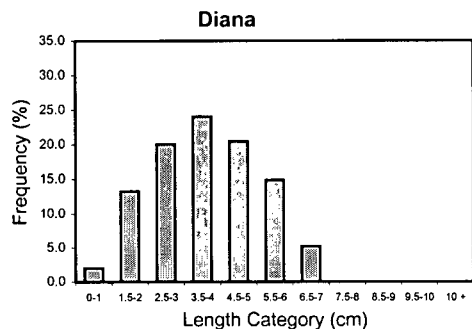
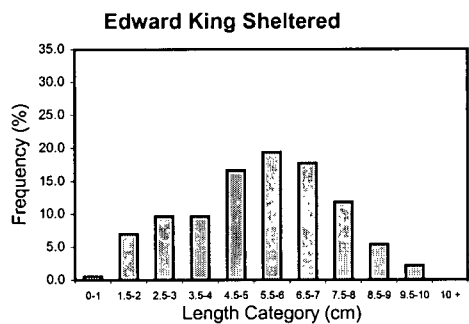
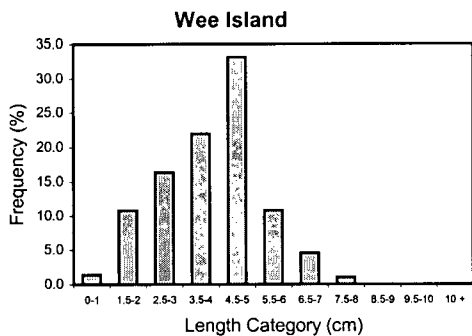
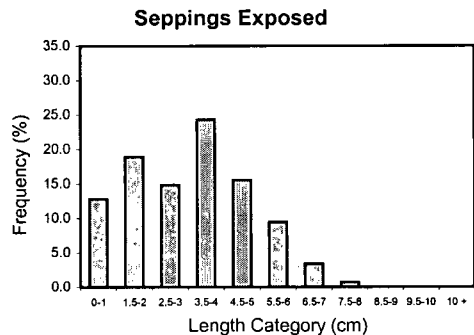
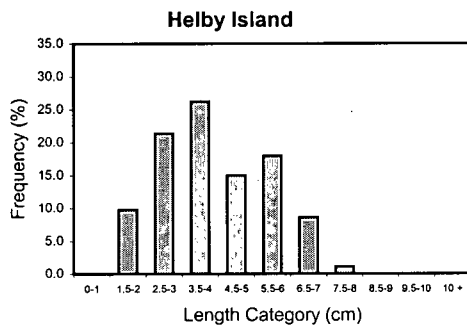
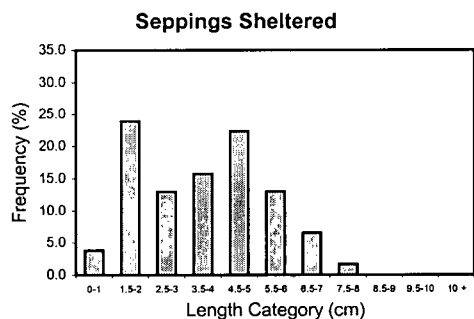
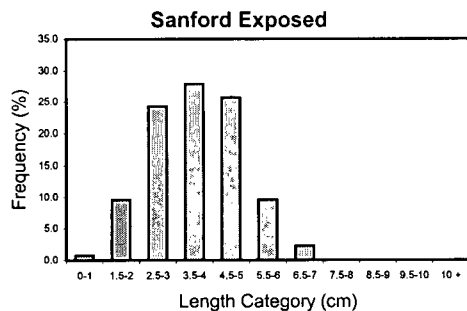
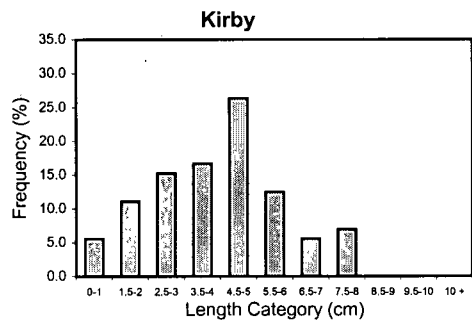
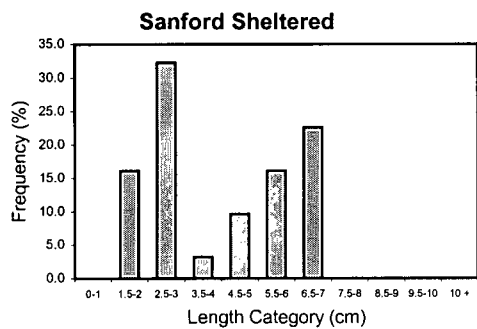
## Appendix II Population Size Structure Raw Data

Absolute Size-frequency Data (#)

Range (cm)	Sanf S	Sanf E	Helby	Wee	Diana	Kirby P	Sep S	Sep E	EK S	EK E
0-1	0	1	0	4	5	4	7	19	1	4
1.5-2	5	13	26	31	33	8	44	28	13	12
2.5-3	10	33	57	47	50	11	24	22	18	10
3.5-4	1	38	70	63	60	12	29	36	18	9
4.5-5	3	35	40	95	51	19	41	23	31	10
5.5-6	5	13	48	31	37	9	24	14	36	5
6.5-7	7	3	23	13	13	4	12	5	33	1
7.5-8	0	0	3	3	0	5	3	1	22	1
8.5-9	0	0	0	0	0	0	0	0	10	0
9.5-10	0	0	0	0	0	0	0	0	4	0
10 +	0	0	0	0	0	0	0	0	0	0
n =	31	136	267	287	249	72	184	148	186	52

Relative Size-frequency Data (%)

Range (cm)	Sanf S	Sanf E	Helby	Wee	Diana	Kirby P	Sep S	Sep E	EK S	EK E
0-1	0.0	0.7	0.0	1.4	2.0	5.6	3.8	12.8	0.5	7.7
1.5-2	16.1	9.6	9.7	10.8	13.3	11.1	23.9	18.9	7.0	23.1
2.5-3	32.3	24.3	21.3	16.4	20.1	15.3	13.0	14.9	9.7	19.2
3.5-4	3.2	27.9	26.2	22.0	24.1	16.7	15.8	24.3	9.7	17.3
4.5-5	9.7	25.7	15.0	33.1	20.5	26.4	22.3	15.5	16.7	19.2
5.5-6	16.1	9.6	18.0	10.8	14.9	12.5	13.0	9.5	19.4	9.6
6.5-7	22.6	2.2	8.6	4.5	5.2	5.6	6.5	3.4	17.7	1.9
7.5-8	0.0	0.0	1.1	1.0	0.0	6.9	1.6	0.7	11.8	1.9
8.5-9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.4	0.0
9.5-10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.0
10 +	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0



### Appendix III Bonferroni Adjusted Alpha Values

Alpha Value (a)	Comparison Number (z)	Adjusted Alpha ( $a^* = a/z$ )
0.05	45	0.00111111
0.05	44	0.00113636
0.05	43	0.00116279
0.05	42	0.00119048
0.05	41	0.00121951
0.05	40	0.00125
0.05	39	0.00128205
0.05	38	0.00131579
0.05	37	0.00135135
0.05	36	0.00138889
0.05	35	0.00142857
0.05	34	0.00147059
0.05	33	0.00151515
0.05	32	0.0015625
0.05	31	0.0016129
0.05	30	0.00166667
0.05	29	0.00172414
0.05	28	0.00178571
0.05	27	0.00185185
0.05	26	0.00192308
0.05	25	0.002
0.05	24	0.00208333
0.05	23	0.00217391
0.05	22	0.00227273
0.05	21	0.00238095
0.05	20	0.0025
0.05	19	0.00263158
0.05	18	0.00277778
0.05	17	0.00294118
0.05	16	0.003125
0.05	15	0.00333333
0.05	14	0.00357143
0.05	13	0.00384615
0.05	12	0.00416667
0.05	11	0.00454545
0.05	10	0.005
0.05	9	0.00555556
0.05	8	0.00625
0.05	7	0.00714286
0.05	6	0.00833333
0.05	5	0.01
0.05	4	0.0125
0.05	3	0.01666667
0.05	2	0.025
0.05	1	0.05
0.05	0	n/a

## Appendix IV Visual Basic Randomized Re-Sampling Program

```
Sub GonadVar()  
,  
' GonadVar Macro  
' Macro recorded 3/18/00 by Anne Salomon  
For i = 1 To 100  
    Range("TotGonad").Select  
    Selection.Copy  
    Range("Results").Columns(1).Rows(i).Select  
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _  
        False, Transpose:=False  
Next i  
  
End Sub
```

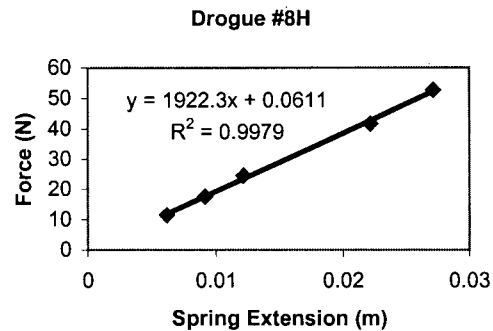
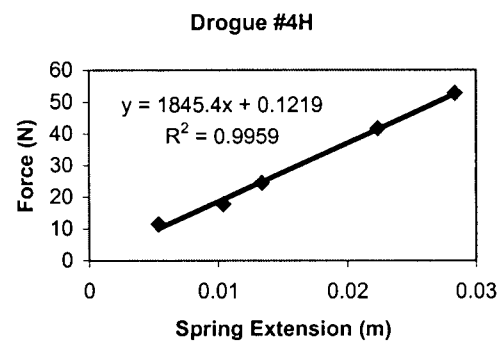
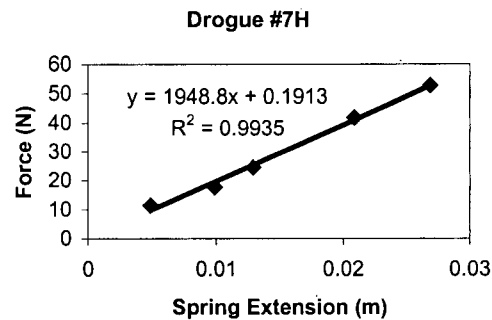
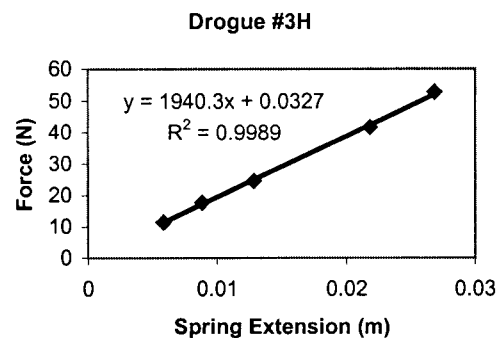
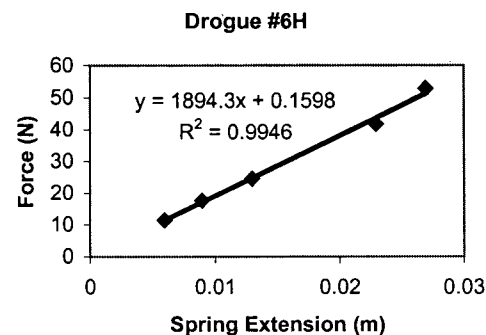
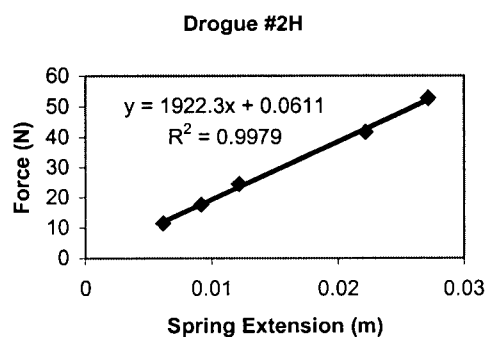
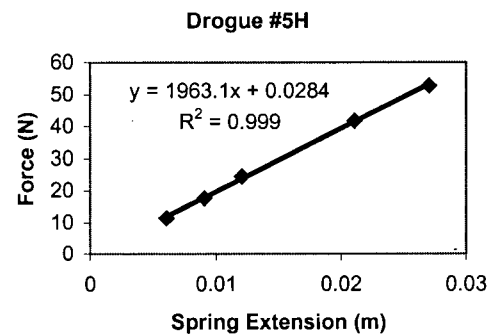
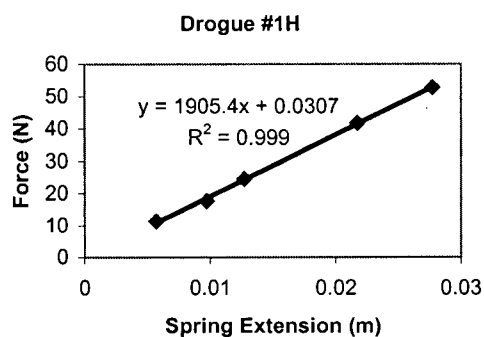
# Appendix V Visual Basic Randomized Re-sampling Program Results

Iteration	EKE	EKS	Sep E	Sep S	KP	Diana	Wee	Helby	San E	San S
1	0.0325	0.296827957	0.046891892	0.071195652	0.052222222	0.037831325	0.055783972	0.060037453	0.031691176	0.065483871
2	0.033461538	0.245268817	0.059054054	0.072336956	0.069027778	0.059277108	0.047804878	0.042546816	0.052058824	0.047419355
3	0.0642230769	0.247204301	0.073918919	0.0475	0.04875	0.085220883	0.049303136	0.056367041	0.041470588	0.041612903
4	0.080384615	0.197473118	0.061418919	0.0525	0.044722222	0.065582329	0.043379791	0.075955056	0.050147059	0.118709678
5	0.030192308	0.170483871	0.060878379	0.058478261	0.109444445	0.086024096	0.065017422	0.054419476	0.044705882	0.06
6	0.066346154	0.263118279	0.051891892	0.061847826	0.058472222	0.052128514	0.06174216	0.053333333	0.058308824	0.036129032
7	0.031923077	0.155268817	0.036891892	0.039130435	0.067777778	0.047871486	0.042891986	0.069550562	0.041397059	0.029032258
8	0.066538462	0.181021506	0.056756757	0.059456522	0.049583334	0.046224899	0.051254356	0.064831461	0.047132353	0.032580645
9	0.038653846	0.192903226	0.054594595	0.040434783	0.055277778	0.088192771	0.066445993	0.103220974	0.061764706	0.07967742
10	0.054807692	0.127473119	0.045810811	0.062444562	0.069583334	0.059076305	0.063344948	0.061235955	0.031029412	0.043548387
11	0.078269231	0.219247312	0.060608108	0.060434783	0.06	0.056385542	0.058954704	0.068014981	0.056691176	0.051935484
12	0.040192307	0.148602151	0.044594595	0.060163043	0.072083334	0.088192771	0.063414634	0.058089888	0.044485294	0.126451613
13	0.039038461	0.176827957	0.066621622	0.044130435	0.103472223	0.032449799	0.062229965	0.043745318	0.038455882	0.054193549
14	0.056346154	0.194784946	0.061283784	0.071630435	0.055833334	0.052008032	0.059790941	0.075280899	0.059926471	0.129032258
15	0.087692308	0.17016129	0.052027027	0.02701087	0.104027778	0.08317269	0.061567944	0.094044944	0.04125	0.081935484
16	0.085192308	0.197419355	0.081824324	0.057554348	0.045833334	0.03373494	0.037456446	0.064981273	0.043161765	0.102258065
17	0.0325	0.168548387	0.041824324	0.085271739	0.075555556	0.046506024	0.074773519	0.049138577	0.041691176	0.14
18	0.059615384	0.15483871	0.042567568	0.057608696	0.070277778	0.083413654	0.064181185	0.099850187	0.039632353	0.075806452
19	0.039423077	0.228064516	0.081756757	0.045434783	0.054027778	0.075983936	0.051951219	0.06494382	0.029411765	0.033225807
20	0.057884615	0.147204301	0.043648649	0.036195652	0.075277778	0.052971887	0.053972125	0.062659176	0.049632353	0.100322581
21	0.05	0.296344086	0.066283784	0.044347826	0.066666667	0.067429719	0.038989547	0.056217228	0.072573529	0.12967742
22	0.096538461	0.17172043	0.034054054	0.054945652	0.045416667	0.047550201	0.05358885	0.043220974	0.053382353	0.081290323
23	0.058269231	0.142473118	0.037905406	0.054347826	0.066527778	0.036305221	0.066864111	0.058988764	0.03875	0.047741936
24	0.035576923	0.205322581	0.071081081	0.031576087	0.057638889	0.028594377	0.057874564	0.061048689	0.034191176	0.077096774
25	0.093461538	0.198172043	0.061621622	0.07423913	0.05625	0.093935743	0.0571777	0.085692884	0.036617647	0.056451613
26	0.04	0.228602151	0.040540541	0.041956522	0.0675	0.046305221	0.070452962	0.051460674	0.041617647	0.075806452
27	0.058653846	0.196827957	0.064121622	0.042391304	0.078472223	0.045341365	0.060209059	0.087340824	0.057058824	0.082258065
28	0.045	0.119946237	0.044324324	0.033913043	0.062083334	0.036626506	0.069686411	0.061985019	0.03625	0.05483871
29	0.044807692	0.175	0.036554054	0.055108696	0.057361111	0.053855421	0.058118467	0.07411985	0.053088235	0.070967742
30	0.031346154	0.157365591	0.032297297	0.028804348	0.099305556	0.074016064	0.062020906	0.082734082	0.034485294	0.084193549
31	0.0725	0.157473118	0.075878378	0.049184783	0.069444445	0.035421687	0.054878049	0.059363296	0.049191176	0.051612903
32	0.025961538	0.271935484	0.068783784	0.043369565	0.070277778	0.028955823	0.055574913	0.07153558	0.036029412	0.166451613
33	0.067692308	0.133817205	0.054189189	0.05173913	0.056944445	0.059598393	0.067386759	0.092808989	0.029852941	0.068709678
34	0.046346154	0.191344086	0.028445946	0.050434783	0.0675	0.053413655	0.04261324	0.044756554	0.076617647	0.066129032

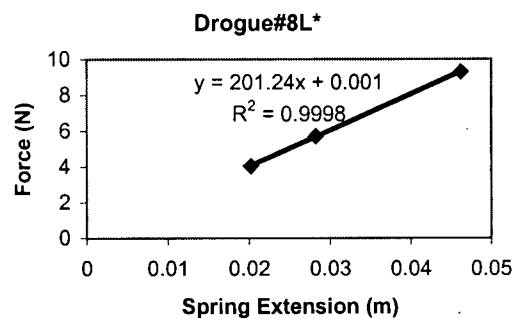
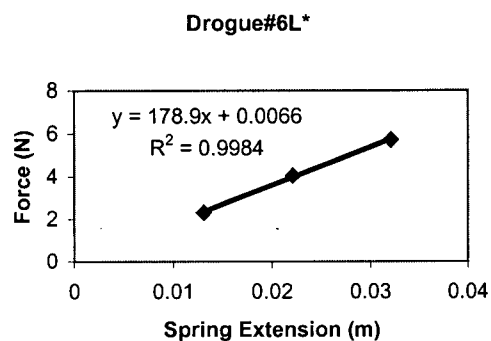
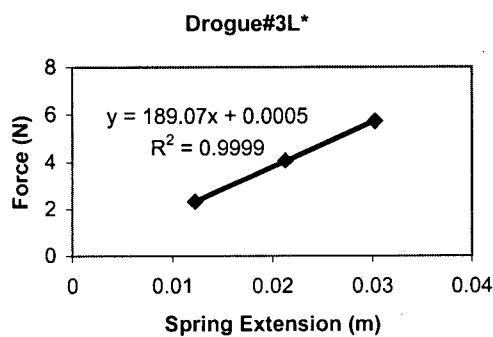
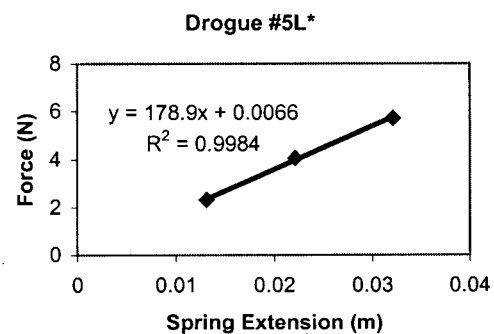
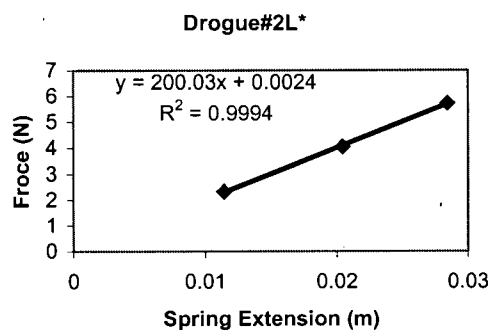
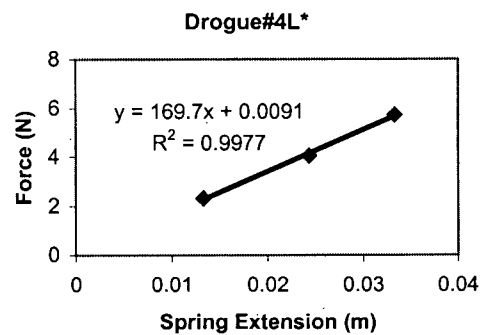
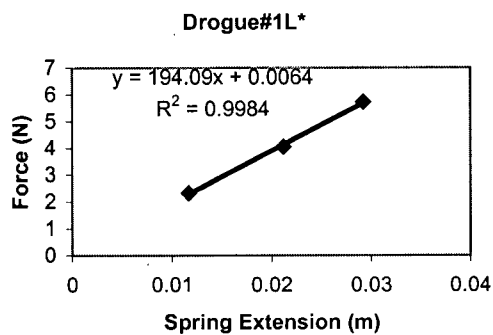
35	0.033653846	0.205860215	0.082297297	0.077065217	0.049027778	0.050321285	0.050243902	0.073820225	0.043455882	0.071612904
36	0.0325	0.163064516	0.067635135	0.04423913	0.110555556	0.045261044	0.044808362	0.051235955	0.046029412	0.09967742
37	0.073461539	0.135913979	0.029054054	0.052717391	0.075416667	0.053855422	0.069477352	0.080224719	0.031764706	0.058064516
38	0.040384615	0.186827957	0.044189189	0.040434783	0.062638889	0.0543337349	0.064285714	0.073108614	0.038529412	0.077419355
39	0.058076923	0.191989247	0.047364865	0.05326087	0.090972223	0.048072289	0.059860627	0.051273408	0.036838235	0.03483871
40	0.031538461	0.146344086	0.054054054	0.070597826	0.051527778	0.04373494	0.072369338	0.064419476	0.044852941	0.117096774
41	0.0475	0.212903226	0.031486487	0.058097826	0.050833334	0.082048193	0.077770034	0.097153558	0.05257353	0.090645162
42	0.043076923	0.189032258	0.040337838	0.054891304	0.078333334	0.029959839	0.059094076	0.059288389	0.044044118	0.058387097
43	0.061153846	0.178064516	0.034594595	0.057826087	0.062083334	0.061365462	0.054250871	0.051348315	0.069191177	0.1
44	0.038269231	0.185537634	0.080337838	0.039891304	0.07	0.054216867	0.072961673	0.062771536	0.036838235	0.032580645
45	0.056538461	0.152419355	0.052837838	0.058152174	0.085277778	0.060281124	0.050139373	0.085205992	0.047352941	0.04516129
46	0.03076923	0.169354839	0.040405405	0.053967391	0.083194445	0.045140562	0.063205575	0.076179775	0.045514706	0.073225807
47	0.043269231	0.250483871	0.043783784	0.050380435	0.082500001	0.077469879	0.043484321	0.070524345	0.055882353	0.119032259
48	0.055576923	0.135	0.04777027	0.052391304	0.045972222	0.080441767	0.106864111	0.064606742	0.043970588	0.070645161
49	0.030384615	0.113010753	0.066148649	0.065543478	0.052361111	0.042771084	0.071916376	0.046029963	0.037647059	0.072580645
50	0.031538461	0.134032258	0.05195946	0.04048913	0.073055556	0.064216867	0.049756098	0.046479401	0.038161765	0.160322581
51	0.066153846	0.204086021	0.044054054	0.079347826	0.070555556	0.04939759	0.06989547	0.056516854	0.040220588	0.08967742
52	0.05	0.154677419	0.047027027	0.080163044	0.052777778	0.045943775	0.064320557	0.082022472	0.060514706	0.065483871
53	0.028269231	0.146290323	0.029256757	0.06576087	0.049305556	0.070441767	0.092090592	0.049288389	0.055367647	0.051290323
54	0.078653846	0.173763441	0.036554054	0.066413043	0.048611111	0.067028112	0.061881533	0.051947566	0.059485294	0.117419355
55	0.065384615	0.134193549	0.028108108	0.067119565	0.079444445	0.040562249	0.079337979	0.068426966	0.031176471	0.104516129
56	0.029038461	0.183225807	0.029256757	0.073804348	0.063888889	0.065100402	0.051602787	0.059101123	0.046691176	0.062258065
57	0.054038461	0.147096775	0.03945946	0.04201087	0.04875	0.052008032	0.052473867	0.029026217	0.056323529	0.063548387
58	0.05	0.232903226	0.044594595	0.045434782	0.064861111	0.055823293	0.061463414	0.054419476	0.033676471	0.126451613
59	0.041153846	0.246129032	0.054594595	0.095271739	0.062083334	0.027469879	0.063031359	0.061460674	0.052867647	0.074193549
60	0.042692308	0.225268817	0.035945946	0.065163044	0.062083334	0.03811245	0.05174216	0.090074906	0.042058824	0.072903226
61	0.023076923	0.137634409	0.052635135	0.077336957	0.062916667	0.050923695	0.051045296	0.06565543	0.034191176	0.059032258
62	0.088269231	0.15483871	0.048716217	0.044184783	0.110277778	0.062891566	0.045121951	0.077827715	0.039632353	0.141612904
63	0.071153846	0.19467742	0.026351351	0.039782609	0.113611112	0.063975904	0.039268293	0.065543071	0.038676471	0.059354839
64	0.040576923	0.152043011	0.083716216	0.06201087	0.047361111	0.029598393	0.047630662	0.061310861	0.046838235	0.065161291
65	0.049038461	0.206935484	0.023851352	0.062934783	0.060138889	0.062449799	0.046864111	0.043183521	0.052058824	0.06
66	0.035961538	0.120645161	0.051283784	0.088097826	0.058888889	0.047590361	0.049372823	0.05752809	0.040073529	0.077419355
67	0.046346154	0.241344086	0.046148649	0.039076087	0.046388889	0.030120482	0.06728223	0.079250936	0.044117647	0.147096775
68	0.043653846	0.166505377	0.048648649	0.07951087	0.100972223	0.045943775	0.05087108	0.094794007	0.042205882	0.107096775
69	0.043076923	0.122204301	0.034662162	0.079239131	0.073888889	0.079678715	0.056062718	0.050636704	0.064705882	0.143548388
70	0.051538461	0.196935484	0.048310811	0.049293478	0.065277778	0.096465863	0.050627178	0.062322097	0.038014706	0.091290323
71	0.032307692	0.105430108	0.037702703	0.072391304	0.05625	0.050722891	0.045818815	0.066516854	0.043823529	0.054516129

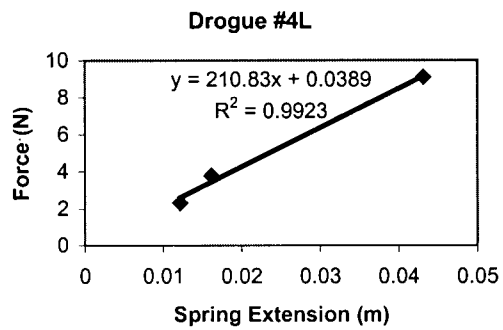
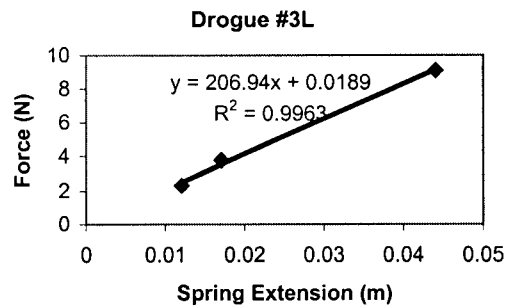
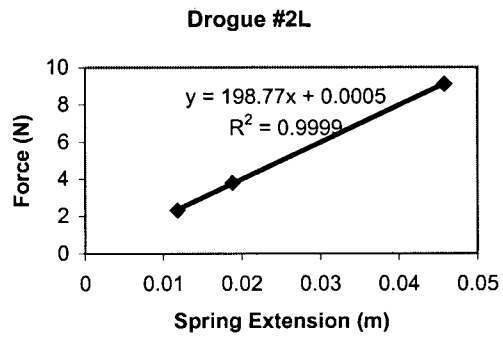
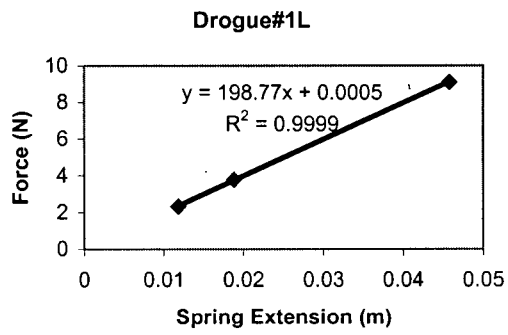
72	0.041346154	0.14451613	0.03695946	0.052934783	0.038194445	0.054216867	0.052508711	0.072397004	0.030220588	0.07967742
73	0.04826923	0.134247312	0.046216216	0.046521739	0.066111111	0.051927711	0.079477351	0.08752809	0.044779412	0.067419355
74	0.061346154	0.173870968	0.028513514	0.056630435	0.044583334	0.04690763	0.057909408	0.093857678	0.052205882	0.101612904
75	0.058076923	0.14467742	0.030878379	0.038206522	0.062083334	0.048995984	0.082264808	0.096329588	0.052426471	0.092903226
76	0.038269231	0.172258065	0.036554054	0.029347826	0.059583334	0.034016064	0.050627178	0.069400749	0.039044118	0.13483871
77	0.038461538	0.23672043	0.046486487	0.042282609	0.0425	0.037469879	0.05804878	0.075805243	0.042279412	0.198387097
78	0.050961538	0.128548388	0.0425	0.043641304	0.071805556	0.079156626	0.050069686	0.081573033	0.037647059	0.135806452
79	0.050192307	0.271612903	0.054527027	0.037065218	0.044444445	0.040040161	0.062857143	0.055543071	0.054338235	0.14483871
80	0.058269231	0.186021505	0.037635135	0.044293478	0.049166667	0.04875502	0.044390244	0.055430712	0.046323529	0.055483871
81	0.0325	0.170645161	0.036486487	0.04451087	0.075138889	0.069839357	0.055679443	0.080711611	0.029338235	0.115483871
82	0.038269231	0.145645161	0.048243243	0.069673913	0.068194445	0.051726907	0.049547038	0.083071161	0.037205882	0.180645162
83	0.035961538	0.154354839	0.052162162	0.070380435	0.055416667	0.06128514	0.049756097	0.097228464	0.035955882	0.040967742
84	0.040576923	0.22655914	0.053378378	0.058804348	0.064305556	0.039317269	0.061045296	0.046928839	0.042132353	0.088387097
85	0.055384615	0.158763441	0.044864865	0.033097826	0.056527778	0.056425703	0.0571777	0.061498127	0.038529412	0.076129032
86	0.047307692	0.16483871	0.046418919	0.075271739	0.0725	0.065421687	0.069303135	0.061011236	0.025808824	0.062903226
87	0.038269231	0.145376344	0.044256757	0.059184783	0.088750001	0.081566265	0.049512195	0.066779026	0.0382335294	0.048064516
88	0.082692308	0.107741936	0.04722973	0.044619565	0.112500001	0.056987952	0.061358885	0.074082397	0.059191177	0.069354839
89	0.023846154	0.122956989	0.03445946	0.049402174	0.054305556	0.044738956	0.07348432	0.081835206	0.053161765	0.032580645
90	0.051346154	0.164892473	0.036418919	0.039728261	0.060972223	0.085823293	0.069407665	0.07164794	0.039411765	0.125161291
91	0.0325	0.113602151	0.052162162	0.065597826	0.068611111	0.055502008	0.047979094	0.076029963	0.043602941	0.028709677
92	0.032884615	0.189946237	0.064391892	0.064945652	0.050277778	0.044698795	0.056864111	0.077265917	0.033382353	0.147741936
93	0.046538461	0.121290323	0.031554054	0.0675	0.047222222	0.041686747	0.065609756	0.053595506	0.062720588	0.101612904
94	0.057884615	0.162580645	0.07	0.053206522	0.041944445	0.057670683	0.046933798	0.050674157	0.040588235	0.073548387
95	0.045576923	0.192849462	0.057094595	0.038967391	0.102083334	0.039718875	0.07456446	0.078127341	0.058602941	0.13483871
96	0.046153846	0.204623656	0.075878379	0.059510869	0.063611111	0.044618474	0.04707317	0.085280899	0.057205882	0.112903226
97	0.038269231	0.140752689	0.033175676	0.067173913	0.084861111	0.05064257	0.043449477	0.060524345	0.049558824	0.043225807
98	0.033846154	0.188709678	0.073783784	0.069402174	0.055972222	0.062088353	0.053658537	0.060112359	0.024926471	0.064516129
99	0.038653846	0.170537635	0.042635135	0.035815217	0.053888889	0.035140562	0.082926829	0.057490637	0.038161765	0.086129032
100	0.065769231	0.138655914	0.05445946	0.03125	0.068611111	0.047670683	0.044808362	0.091048689	0.044558824	0.041612903
Average:	0.049112	0.177035	0.049054	0.055004	0.066089	0.054994	0.058573	0.067369	0.044807	0.083632

## Appendix VI Maximum Wave Force Recorder Calibration Graphs

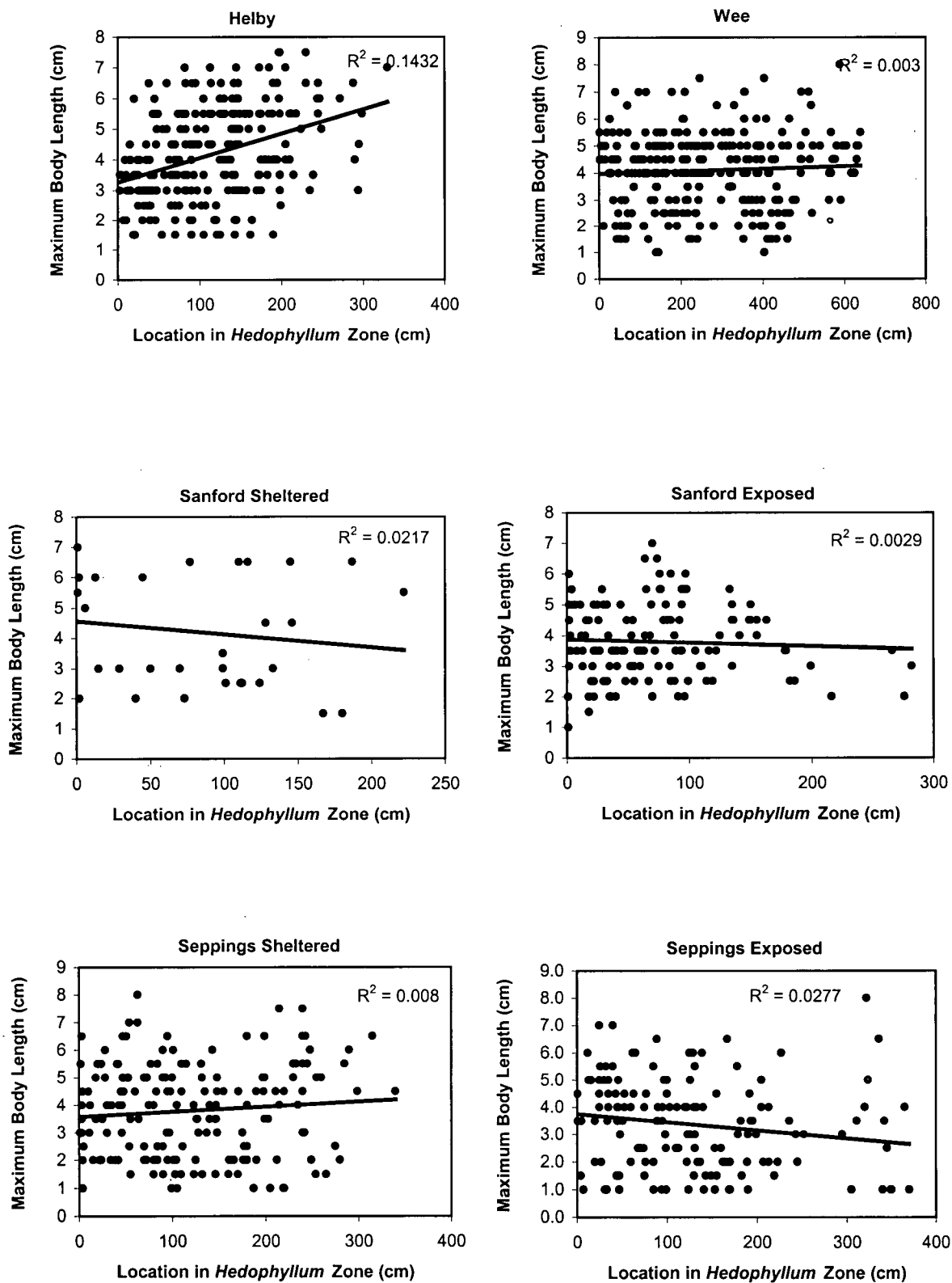


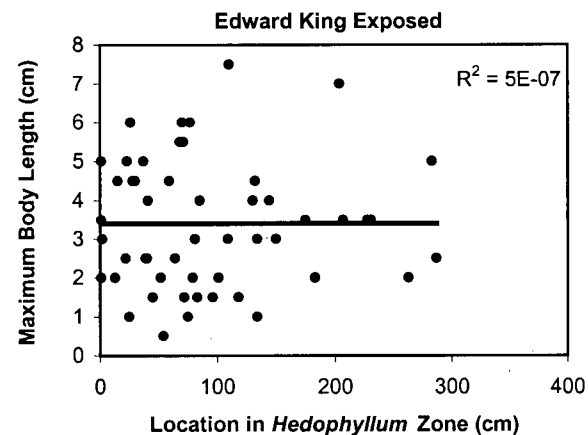
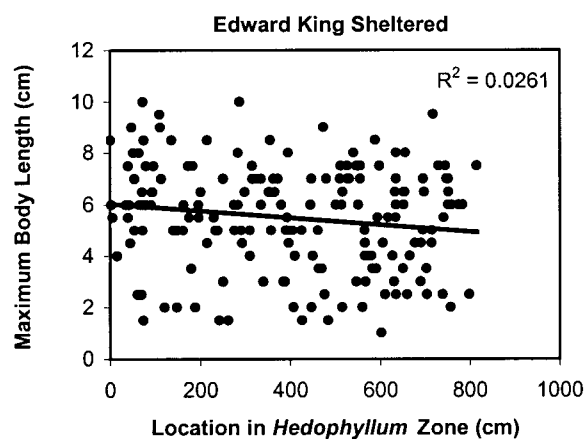
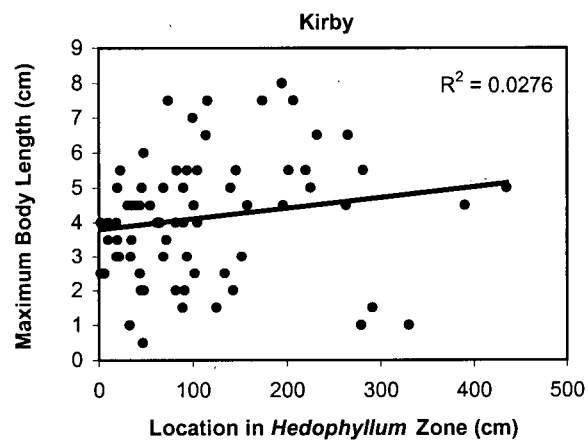
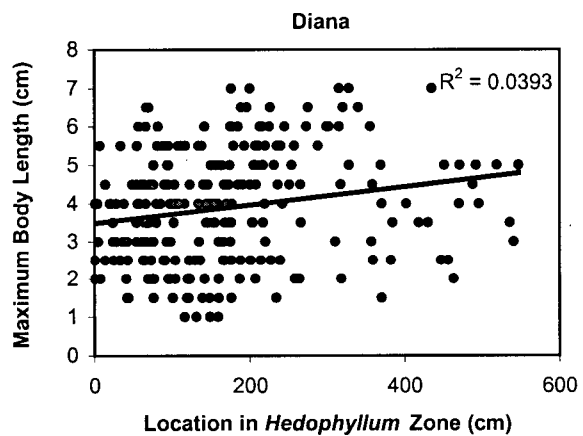






## Appendix VII Location of *Katharina* in *Hedophyllum* Zone





# Appendix VIII Variance Data for Site Shannon-Wiener Diversity Index

Site	H'	Species Richness (S)	Sum Pi(ln Pi) <sup>2</sup>	H' <sup>2</sup>	N	2*(N <sup>2</sup> )	Evenness H' / ln S	Var H'
EK E	2.6731	44	8.4570	7.1456	125.30	31400.18	0.7064	0.0118
EK S	2.7497	42	8.6843	7.5610	121.70	29621.78	0.7357	0.0106
Sep E	2.5860	40	8.2336	6.6874	145.10	42108.02	0.7010	0.0116
Sep S	2.6340	43	8.6341	6.9378	120.30	28944.18	0.7003	0.0156
KP	2.6586	45	8.3533	7.0683	141.20	39874.88	0.6984	0.0102
Diana	2.4529	34	7.3036	6.0167	118.55	28108.21	0.6956	0.0120
Wee	2.7552	34	8.6164	7.5913	103.50	21424.50	0.7813	0.0114
Helby	2.2805	30	6.5916	5.2008	113.65	25832.65	0.6705	0.0134
Sand E	2.7705	38	8.8928	7.6755	114.20	26083.28	0.7616	0.0121
Sand S	3.0679	47	10.5432	9.4118	90.95	16543.81	0.7968	0.0152

## Appendix IX Species Diversity Recorded in the *Hedophyllum* Zone

	EK E	EK S	Sep E	Sep S	Kirby	Diana	Wee	Helby	San E	San S
<b>Sponges (Porifera, Demospongiae)</b>										
<i>Haliclona permollis</i>		0.1	1.2	1		0.1	0.1	0.4	0.8	0.6
<i>Halichondria panicea</i>	0.4		0.5	0.8	0.4				2.3	1
<i>Ophlitaspongia pennata</i>	0.5		1.5	1.7	1.1		0.2	0.2		
<b>Chitons (Mollusca, Polyplacophora)</b>										
<i>Kathrina tunicata</i>	1.8	2.3	1.3	2.3	2.8	4.8	3.3	5.3	3.5	1.3
<i>Tonicella lineata</i>	0.6	0.2	0.5	0.9	0.5	0.4		0.3	0.2	
<i>Lepidochitona dentiensi</i>	0.2	1.8	0.7	2	0.7	1.1	0.8	1.2	0.3	0.8
<i>Cryptochiton stelleri</i>		1.6								
<i>Mopalia lignosa</i>				0.2						
<i>Unidentified Chiton</i>	0.4	0.3	0.5	1	0.1	0.4	0.4	0.6		0.1
<b>Limpets (Mollusca, Gastropoda)</b>										
<i>Acmea mitra</i>	0.1		0.2		0.1		0.2		0.1	
<i>Lottia digitalis</i>				0.1						
<i>Lottia pelta</i>	0.4	0.6	0.9	1.2	0.5	0.7	1.8	1.5	1.5	0.9
<i>Tectura scutum</i>							0.1	0.2		0.1
<i>Juvenile limpet spp.</i>				0.2		0.6		0.1	0.9	0.5
<i>Unidentified Limpet</i>						0.1				
<b>Snails (Mollusca, Gastropoda)</b>										
<i>Nucella canaliculata</i>	0.2					0.2				
<i>Calliostoma ligatum</i>	0.2		0.4		0.1					0.1
<i>Amphissa versicolor</i>					0.1					
<i>Tegula funebris</i>										
<b>Sea Stars (Echinodermata, Asteroidea)</b>										
<i>Pisaster ochraceus</i>	* 1.3	0.9	3.5	7.5	6.7	0.6	0.4	2.6	1.5	1.2
<i>Leptasterias hexactis</i>					0.1			0.2		
<i>Henicia spp.</i>	0.2	0.1	0.4		0.1					
<i>Solaster stimpsoni</i>		0.2								
<i>Evasterias troschellii</i>				0.1						
<b>Sea Cucumber (Echinodermata, Holothuroidea)</b>										
<i>Cucumaria miniata</i>				0.3						
<b>Sea anemones (Cnidaria, Anthozoa)</b>										
<i>Anthopleura elegantissima</i>	0.9	4.9	1.9	3	1.8	7.7	1.3	9.4	6.2	12.9
<i>Anthopleura. xanthogrammica</i>	0.1				0.6				0.6	
<b>Compound Ascidians (Urochordata, Ascidiacea)</b>										
<i>Aplidium spp. #1</i>	0.8	0.2	3.9	0.4	0.8					
<i>Aplidium spp. #2</i>	0.8	5.2	7.5	0.4	5.6					
<b>Solitary Ascidian (Urochordata, Ascidiacea)</b>										
<i>Cnemidocarpa finmarkiensis</i>	0.1		0.1	0.1						0.1
<b>Encrusting Bryozoans (Bryozoa)</b>										
<i>Eurystomella bilabiata</i>	0.8				0.2					
<i>Membranipora tuberculata</i>	2.5	2.8	1.7	0.6	4.4	0.1				0.8
<i>Hippodiplosia insculpta</i>										0.2

	EK E	EK S	Sep E	Sep S	Kirby	Diana	Wee	Helby	San E	San S
<b>Bushy Bryozoan (Bryozoa)</b>										
<i>Flustrellidra corniculata</i>			0.6							
<b>Hydroids (Cnidaria, Hydrozoa)</b>										
<i>Sertularella spp.</i>	0.3		0.1							
<i>Aglophenia spp.</i>					0.8					
<b>Tube worms (Annelida, Polychaeta)</b>										
<i>Dodecaceria fewkesi</i>	6.4	2.9	1.7	2.4	2.7	3.4	1.8	0.2	0.2	0.2
<i>Sepula vermicularis</i>		0.2	0.7	0.6	0.3	0.4	0.6	0.3	0.2	0.3
<b>Sea urchin (Echinodermata, Echinoidea)</b>										
<i>S. purpuratus</i>	0.2		0.9	0.1	0.8				0.1	
<b>Sea slugs (Mollusca, Gastropoda)</b>										
<i>Anisodoris nobilis</i>										0.1
<i>Rostanga pulchra</i>			0.1							
<i>Phidiana crassicornis</i>					0.1					
<b>Barnacles (Crustacea, Cirripedia)</b>										
<i>Pollicipes polymerus</i>	0.8					0.2			1.6	
<i>Balanus glandula</i>	0.6		1.5	0.2	0.3	0.6	3		0.6	2.7
<i>Cthamalus</i>		3.8	0.5	1.7	0.2	0.6	2.1	0.6	2	9
<i>Balanus nubulis</i>	1.1	0.1	0.1	0.2		1		0.2	2.4	
<i>Semibalanus</i>	0.5	0.1		2.1			1.1		3.1	0.3
<b>Mussels (Mollusca, Bivalvia)</b>										
<i>Mytilus californianus</i>	4.2				0.2					
<i>Mytilus trossulus (edulis)</i>								0.1		
<b>Brown algae (Phaeophyta)</b>										
<i>Hedophyllum sessile</i>	19.3	22.4	38.3	29	22.5	8.65	14.8	22.7	6.6	
<i>Egregia menziesii</i>	9.9	13.3	8	0.5	2.25	16.3	6	1.95	9.9	1.6
<i>Laminaria setchellii</i>	0.4	0.5							0.2	
<i>Lessoniopsis littoralis</i>	0.7									
<i>Leathesia difformis</i>		0.15				0.25	2.6	0.25		0.55
<i>Fucus gardneri</i>										0.5
<i>Laminaria saccharina</i>										0.1
<i>Scytosiphon simplicissimus</i>									0.5	
<i>Nemalion helminthoides</i>		0.4				0.1			0.1	1.2
<b>Green algae (Chlorophyta)</b>										
<i>Codium fragile</i>	0.5	0.3	0.3	0.15						0.1
<i>Ulva fenestrata</i>	0.2	3.85		0.4		0.3	1.9	0.25	0.75	1.6
<i>Enteromorpha intestinalis</i>							0.1			
<i>Acrosiphonia spp.</i>							0.65			1.15
<i>Cladophora columbiana</i>		0.1		0.5	0.1					

	EK E	EK S	Sep E	Sep S	Kirby	Diana	Wee	Helby	San E	San S
<b>Red algae (Rhodophyta)</b>										
<i>Mazzaella splendens</i>		1.5		1.1	2.8					1
<i>Mazzaella linearis</i>	3.1		4.75	1.5		0.5	0.1		1.2	
<i>Mazzaella cornucopiae</i>										0.1
<i>Chondracanthus exasperatus</i>	0.2	0.1	0.2	0.1						
<i>Schizymenia pacifica</i>									0.65	
<i>Prionitis lanceolata</i>	0.5		0.5		0.5		0.4			0.1
<i>Mastocarpus papillatus</i>					0.8					1.2
<i>Mastocarpus jordinii</i>		0.1	0.4		0.25					2.8
<i>Cryptopleura ruprechtiana</i>	11.65	2.1	4.65	2.75	2.4	1.15	0.65	2		0.9
<i>Porphyra perforata</i>		0.15			0.5					0.6
<i>Halosaccion glandiforme</i>	0.5	0.15		0.3	0.5	0.2	0.45			0.5
<i>Ceranium californicum</i>						4.9	0.7			6.8
<i>Microcladia coulteri</i>			0.2	0.4						
<i>Microcladia borealis</i>	0.5	0.4			0.25	1	1.5	1.3	2	1.4
<i>Callithamnion pikeanum</i>		0.5	0.5	0.15	0.2			0.2	0.3	0.45
<i>Neorhodomela larix</i>										
<i>Endocladia muricata</i>		1.1				0.1			0.2	3.4
<i>Plocamium cartilagineum</i>									0.5	
<i>unidentified filamentous red</i>									7.9	
<b>Crustose algae</b>										
<i>Lithothamnion spp.</i>	17.6	16.6	14	25.4	14	23	8.7	17.2	8	1
<i>Ralfsia spp.</i>		1.8		3.2	0.4	1.2	11.6	1.6	0.7	3.7
<i>Petrocelis / Mastocarpus</i>	0.2	0.1			1.2		1.8	0.6	1.9	4.2
<i>Hildenbrandia spp.</i>	1.8	6.7	6.3	5.2	14.2	1.7	7	4.2	4	3
<b>Coraline algae (Rhodophyta)</b>										
<i>Bossiella/Calliathron spp.</i>	18.2	1.8	9.4	8.2	6.4	1.4	15.8	6.4	18.2	8
<i>Corallina spp.</i>	15	11.2	25.6	1.8	23.2	25.8	11.6	31.6	23.4	11.2
<b>Sea grass (Zosteraceae)</b>										
<i>Phyllospadix</i>							0.4			1.5

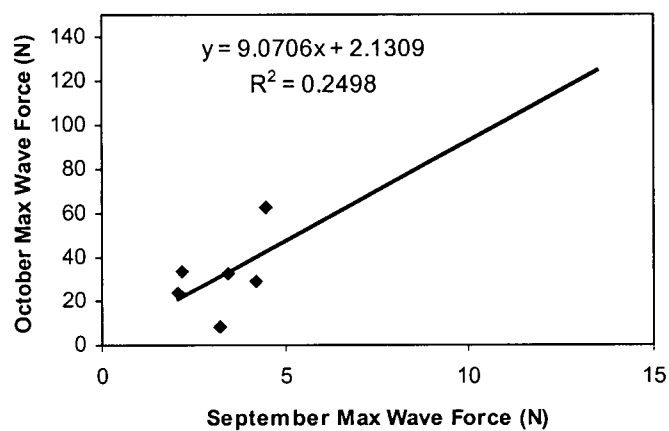


## Appendix X Biodiversity Bootstrapping Results

EK E H <sub>R</sub>	EK E S <sub>R</sub>	EK S H <sub>R</sub>	EK S S <sub>R</sub>	Sep E H <sub>R</sub>	Sep E S <sub>R</sub>	Sep S H <sub>R</sub>	Sep S S <sub>R</sub>	Kirby H <sub>R</sub>	Kirby S <sub>R</sub>
2.4316	39	2.5962	41	2.2987	34	2.5726	40	2.4702	44
2.6055	42	2.5311	38	2.409	38	2.2529	39	2.4702	44
2.4846	41	2.5057	40	2.3451	37	2.464	43	2.4518	42
2.4413	39	2.4973	39	2.3927	38	2.4065	39	2.5369	41
2.5121	40	2.7005	40	2.2661	36	2.3393	40	2.4551	43
2.4413	39	2.6359	41	2.3927	38	2.3842	41	2.4591	43
2.5501	40	2.5311	38	2.3459	36	2.5551	43	2.4336	41
2.5354	40	2.5356	35	2.25	39	2.5142	43	2.442	39
2.5373	41	2.5709	38	2.3175	36	2.3635	38	2.5302	43
2.531	40	2.5385	36	2.3892	38	2.5458	41	2.5103	40
2.4611	40	2.5929	37	2.3971	39	2.4065	39	2.4796	44
2.4636	39	2.6607	40	2.3451	37	2.2906	41	2.4551	43
2.6068	41	2.6963	40	2.3077	38	2.5164	41	2.4518	42
2.548	42	2.4973	39	2.3416	40	2.531	38	2.4749	42
2.5373	41	2.5486	40	2.3682	39	2.5282	40	2.4702	44
2.5532	41	2.5311	38	2.3971	39	2.4334	43	2.4796	44
2.5342	40	2.6359	41	2.3241	37	2.2906	41	2.4161	42
2.5532	41	2.5311	38	2.3751	36	2.5078	41	2.442	39
2.5354	40	2.6344	38	2.3077	38	2.4274	38	2.5047	43
2.6097	42	2.6658	40	2.3828	39	2.5142	43	2.4518	42

Diana H <sub>R</sub>	Diana S <sub>R</sub>	Wee H <sub>R</sub>	Wee S <sub>R</sub>	Helby H <sub>R</sub>	Helby S <sub>R</sub>	San E H <sub>R</sub>	San E S <sub>R</sub>	San S H <sub>R</sub>	San S S <sub>R</sub>
2.4427	34	2.8425	33	2.2469	28	2.7721	36	3.1941	46
2.4488	33	2.802	33	2.2349	29	2.7778	38	3.0293	42
2.2343	27	2.7697	33	2.0737	29	2.8079	36	3.1164	45
2.3604	32	2.7096	32	2.123	29	2.7168	37	3.1329	46
2.4796	33	2.7279	33	2.1077	28	2.7594	33	3.1097	45
2.3517	33	2.6243	32	2.2691	28	2.7803	34	3.175	42
2.5061	34	2.7033	32	2.2349	29	2.725	35	3.227	46
2.3517	33	2.7697	33	2.2724	29	2.6985	37	3.1889	47
2.5061	34	2.6613	33	2.16	28	2.6976	36	3.1868	47
2.4118	33	2.7697	33	2.224	28	2.7123	34	3.156	46
2.3938	33	2.8315	33	2.26	30	2.7123	34	3.1941	46
2.3517	33	2.6613	33	2.2183	27	2.7168	37	3.1531	47
2.3434	33	2.64	30	2.1988	30	2.7844	38	3.1433	45
2.2343	27	2.7812	32	2.294	30	2.7719	37	3.1547	43
2.48	33	2.5544	30	2.294	30	2.7803	34	3.1433	45
2.4796	33	2.736	32	2.2691	28	2.7376	34	3.1106	44
2.2343	27	2.7812	32	2.1851	27	2.7554	37	3.1321	44
2.3517	33	2.7958	33	2.1499	28	2.7797	37	3.1889	47
2.2991	28	2.6921	32	2.0884	27	2.7844	38	3.0651	44
2.5209	33	2.5544	30	2.2239	28	2.7719	37	3.1106	44

## Appendix XI Predicting October Maximum Wave Force



Site	October MWF (N)	September MWF (N)	Linear Predicted October MWF (N)
EK E	n/a	19.39	178.01
EK S	33.67	2.16	21.09
Sep E	34.99	16.01	147.35
Sep S	29.54	4.18	40.05
Kirby	23.32	2.09	21.09
Diana	n/a	4.96	47.12
Wee	32.79	3.44	33.33
Helby	63.1	4.48	42.77
San E	n/a	22.3	204.41
San S	7.97	3.23	31.43

## Appendix XII Biodiversity and Potential Reproductive Output Summary

Location	Species Richness (S)	Shannon- Wiener Diversity (H')	(H') SE	Randomized Species Richness (SR)	(SR) SE	Randomized Shannon- Wiener Diversity (H'R)	(H'R) SE	Potential Reproductive Output (PRO)	Randomized Potential Reproductive Output (PROR)	(PROR) SE
EK E	44	2.673	0.012	40.4	0.352	2.524	0.015	0.0647	0.122	0.008
EK S	42	2.750	0.011	38.85	0.352	2.582	0.015	0.2398	0.549	0.008
Sep E	40	2.586	0.012	37.6	0.352	2.348	0.015	0.0824	0.158	0.008
Sep S	43	2.634	0.016	40.6	0.352	2.442	0.015	0.1517	0.258	0.008
KP	45	2.659	0.010	42.25	0.352	2.469	0.015	0.1122	0.190	0.008
Diana	34	2.453	0.012	31.95	0.352	2.389	0.015	0.2116	0.342	0.008
Wee	34	2.755	0.011	32.2	0.352	2.72	0.015	0.2025	0.312	0.008
Helby	30	2.281	0.013	28.5	0.352	2.206	0.015	0.2324	0.401	0.008
San E	38	2.770	0.012	35.95	0.352	2.752	0.015	0.2188	0.305	0.008
San S	47	3.068	0.015	45.05	0.352	3.146	0.015	0.0732	0.153	0.008