BENTHIC HABITAT MAPPING OF AN ATLANTIC COD (GADUS MORHUA) REFUGE, SMITH SOUND, NEWFOUNDLAND, CANADA

by © Katherine Macpherson

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ABSTRACT

After the northern cod collapse, a surviving component of this stock took refuge in Smith Sound, a sub-arctic Newfoundland fjord. While benthic habitats used by recovering fish populations can provide important ecological services, habitats within this refuge have not been mapped. This study mapped Smith Sound's benthic habitats using Van Veen grab and videos samples of the seafloor. Habitats were mapped by combining ground truthing data with multibeam bathymetry terrain derivatives using a Maximum Likelihood Classifier. Eight habitats were observed and mapped with an overall map accuracy of 84.76% (Kappa 80.40%). Multiple habitats were observed that could be linked to cod ecology and services of an ecological refuge. Known spawning areas were characterised predominantly by Sandy Mud habitat, bordered by Small Boulders and Gravel habitats. Sub-optimal habitat consisted of Gravelly Muddy Sand with Small Boulders, bordered by Large Boulders. The habitats were linked to cod ecology providing shelter, sustenance and opportunities for reproduction, all services required by a refuge.

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iii

Table of Contents

ABSTRACT	۲	ii
ACKNOWI	LEDGEMENTS	iii
List of Table	es	vi
List of Figu	res	vii
List of Abbr	eviations	ix
List of Appe	endices	X
CHAPTER	1: INTRODUCTION	1
1.1.1 1.1.2 1.1.3 1.1.4 1.1.5 1.2 Res 1.3 Go 1.4 Me	ntext Benthic habitat mapping The fish-habitat relationship Habitat maps in Newfoundland, Canada Northern cod stock collapse Smith Sound search questions al and Objectives ethods	1
Co-authorsh	ip Statement	23
	2: BENTHIC HABITATS ASSOCIATED WITH AN ATLANTIC (MITH SOUND, NEWFOUNDLAND	
2.1 Ab	stract	24
2.2 Int	troduction	25
2.2.1	Refuges: roles and characteristics in marine benthic habitats	25
2.2.2	Atlantic cod-habitat relationships	26
2.2.3	Northern cod stock dynamics	29
2.2.4	Smith Sound as a refuge	
2.3 M	ethods	
2.3.1	Study area	
2.3.2	Multibeam acquisition and terrain derivatives	
2.3.3	Ground-truthing	
2.3.4	Substrate classification and biota identification	

2.3.5	Habitat characterisation	40		
2.3.6	Stomach content analysis	41		
2.3.7	Supervised classification			
2.3.8	-			
2.4 R	esults	45		
2.4.1	Multibeam acquisition	45		
2.4.2	Ground-truthing			
2.4.3	Substrate classification and biota identification			
2.4.4 Habitat characterisation		51		
2.4.5	Analysis of stomach content data (1995-2007)			
2.4.6	Supervised classification			
2.4.7	Habitat assessment			
2.5 D	iscussion			
2.5.1	Smith Sound habitat map	70		
2.5.2	Benthic habitats	72		
2.5.3	Refuge habitat for cod survival (1995-2007)	75		
2.5.4				
2.5.5				
Reference	es			
CHAPTER	3: CONCLUSION			
3.1 0	verview			
3.2 R	esearch questions	96		
3.2.1	Benthic habitats of Smith Sound			
3.2.2				
3.2.3	Cod stomach content and prey of Smith Sound			
3.3 Si	ummary of main results			
3.4 G				
3.5 A				
References				
APPENDI	CES			

List of Tables

Table 2. 1. Terrain derivatives investigated under ordinary least square regression45
Table 2. 2. Summary of exploratory SIMPER analysis for grab habitats, examiningorganisms as individual taxa records (IT) and with polychaetes described under functionalgroups (GS)
Table 2. 3. Sediment classes pertaining to the statistically significant results identified in ANOSIM_1 and ANOSIM_2 for reclassification under grouped habitat 'Gravelly Muddy Sand (n=17)'
Table 2. 4. Complete grab sample ANOSIM results using sediment class as a variable56
Table 2. 5. Complete grab sample ANOSIM results using habitat group as a variable57
Table 2. 6. SIMPER results for habitat 'Gravel (n=16)' samples
Table 2. 7. SIMPER results for habitat 'Sandy Gravel (n=20)' samples
Table 2. 8. SIMPER results for habitat 'Gravelly Muddy Sand (n=17)' samples60
Table 2. 9. SIMPER results for habitat 'Sandy Mud (n=28)' samples61
Table 2. 10. Summary of exploratory SIMPER analysis for video habitats, examining organisms as individual taxa records. 62

List of Figures

Figure 1. 1. Map of the Placentia Bay - Grand Banks Large Ocean Management Area and NAFO division 3L (DFO, 2012)
Figure 2. 1. Study area, Smith Sound with 100m contours and 200m contours showing the location of the fjord basins Inset: Trinity Bay and Bonavista Corridor
Figure 2. 2. Flowchart of research
Figure 2. 3. Smith Sound multibeam survey, collected using the Memorial Explorer, Autonomous Underwater Vehicle. Inset: Location of Smith Sound study area, Trinity Bay, Newfoundland, Canada (48°9'27"N, 53°41'47"W)
Figure 2. 4. Planned ground-truthing survey sites (n=143), over four classified depth zones across the multibeam extent
Figure 2. 5. Multibeam terrain derivative, 'Bathymetry'46
Figure 2. 6. Multibeam terrain derivative, 'Slope'46
Figure 2. 7. Multibeam terrain derivative, 'Distance to Ocean'
Figure 2. 8. Multibeam terrain derivative, 'Fine bathymetric positioning index'47
Figure 2. 9. Multibeam terrain derivative, 'Aspect'
Figure 2. 10. Collected grab and video samples, across the Smith Sound multibeam extent
Figure 2. 11. Trigon analysis, representing sediment groups visually (GRADISTAT v4.0) with expert knowledge guided by Dr. Evan Edinger
Figure 2. 12. Species accumulation curves of Van Veen grab and video samples (PRIMER V4)
Figure 2. 13. 'Non-parametric multidimensional scaling' plots, a) Van Veen grab habitats, b) Video habitats
Table 2. 2. Summary of exploratory SIMPER analysis for grab habitats, examining organisms as individual taxa records (IT) and with polychaetes described under functional groups (GS). 55
Table 2. 3. Sediment classes pertaining to the statistically significant results identified in ANOSIM_1 and ANOSIM_2 for reclassification under grouped habitat 'Gravelly Muddy

Sand (n=17)'
Table 2. 4. Complete grab sample ANOSIM results using sediment class as a variable56
Table 2. 5. Complete grab sample ANOSIM results using habitat group as a variable57
Table 2. 6. SIMPER results for habitat 'Gravel (n=16)' samples
Table 2. 7. SIMPER results for habitat 'Sandy Gravel (n=20)' samples
Table 2. 8. SIMPER results for habitat 'Gravelly Muddy Sand (n=17)' samples60
Table 2. 9. SIMPER results for habitat 'Sandy Mud (n=28)' samples.
Table 2. 10. Summary of exploratory SIMPER analysis for video habitats, examining organisms as individual taxa records. 62
Figure 2. 14. Stomach content of the Smith Sound aggregation (1995-2007)63
Figure 2. 15. Maximum likelihood classification of 'Sand with Small Boulders' using presence - absence (top), maximum likelihood classification with seven habitats (bottom).
Figure 2. 16. Final habitat map using a combination of the two maximum likelihood classifications. Inset (top): Habitat that overlapped with the cod spawning areas, Zone A and Zone B
Figure 2. 17. Habitat composition by study and sub-study area
Figure 2. 18. Misclassification matrix and accuracy assessment with Kappa equation for overall accuracy

List of Abbreviations

ANOSIM	_	Analysis of Similarity
Asp	_	Aspect
AUV	_	Autonomous Underwater Vehicle
Bath	_	Bathymetry
BBPI	_	Broad Bathymetric Positioning Index
CBaG	_	Coralline Boulders and Gravel
DtO	_	Distance to Ocean
East	_	Easterness
EBSA	_	Ecologically and Biologically Significant Area
FBPI	_	Fine Bathymetric Positioning Index
GMS	_	Gravelly Muddy Sand
GMSwSB	_	Gravelly Muddy Sand with Small Boulders
LOMA	_	Large Ocean Management Area
MLC	_	Maximum Likelihood Classification
nMDS	_	Non-Parametric Multidimensional Scaling Plot
NORT	_	Northerness
OLS	_	Ordinary Least Square
RDMV	_	Relative Deviation from Mean Variance
SD	_	Standard Deviation
SIMPER	_	Similarity Percentage
SLO	_	Slope
SwSB	_	Sand with Small Boulders
TASSE	_	Terrain Attributes Selection for Spatial Ecology
VIF	_	Variance Inflation Factor

List of Appendices

Appendix A: Summary of collected grab samples. Sample ID, longitude, latitude, GRADISTAT, and habitat categories (n=105).

Appendix B: Summary of Smith Sound grab biota. Organism taxonomic classification, sample presence and total abundance.

Appendix C: Summary of video transects, video ID, latitude and longitude of polyline track and habitat (n=65).

Appendix D: Summary of Smith Sound video biota. Organism taxonomic classification, sample presence and total abundance.

Appendix E: Grain size classification scheme of GRADISTAT. V4.

Appendix F: Polychaete functional groups with reference to feeding guild. Functional group, taxonomic family, feeding type, feeding stratum, motility pattern.

Appendix G: ANOSIM and SIMPER, summary and details of videos (Table 1-11).

Appendix H: Exploratory Regression I, Summary.

Appendix I: Exploratory Regression II, Summary.

Appendix J: Exploratory Regression II, Table.

Appendix K: Ordinary Least Square report for final model.

Appendix L: Results of 'Moran's I', spatial autocorrelation graph on sample sites.

Appendix M: Results of 'dendrogram', showing spatial co-occurrence between grab and video samples.

CHAPTER 1: INTRODUCTION

1.1 Context

1.1.1 Benthic habitat mapping

Habitats are areas that possess the required conditions for an organism to survive, and subsequently thrive (Hutchinson & MacArthur 1959; Morris, 2003). An organism's habitat requirements can be specific for highly specialised organisms, or be more general for organisms that can utilise broad environmental conditions (Hirzel & Le Lay, 2008). The occurrence of a benthic habitat is a determinant of the chemical, physical (e.g. substrate type), and biological (e.g. community composition) environments (Kostylev et al., 2001; Diaz et al., 2004; Brown et al., 2011). The type of seafloor substrate and topography determine many ecological conditions that organisms need to survive, such as providing attachment surfaces, managing desiccation rates and providing fine-scale water flow requirements (e.g. riffles vs shelter) (Aitken & Fournier, 1993; Morris, 2003; Hirzel & Le Lay, 2008).

As the distribution and abundance of benthic organisms within a community are influenced by the seafloor sediment type, it is possible to use the existing spatial relationships between topography, sediment, and biology to map discrete habitat data across both fine and broad spatial scales (Kostylev et al., 2001; Brown & Collier, 2008; Copeland et al., 2013). Kostylev et al. (2001, p.122) define habitat in a mapping context as "a spatially defined area where the physical, chemical, and biological environment is distinctly different from the surrounding environment." Although the combined chemical,

physical and biological environment characterizes habitats, the physical topography of the seafloor has been shown to account in some contexts for a large proportion of the variance in benthic habitat distribution (Bouchet et al., 2015). As such, seafloor topography derived from acoustic surveys can provide useful data when mapping seafloor habitats and is used in most habitat mapping exercises (Diaz et al., 2004; Brown et al., 2011). Oceanographic data (e.g. temperature) also has the ability to determine organism distributions, although it remains challenging to get appropriate oceanographic data for such analysis due to large spatial and temporal changes (Huang et al., 2011). Acoustic data was shown to capture more localized environmental features, at a scale that is more ecologically relevant to many organisms' fine-scale distributions (Huang et al., 2011). Terrain derivatives, such as slope, aspect, and bathymetric positioning index (BPI) (Weiss, 2001; Wilson et al., 2007), can be derived from bathymetric data, providing a selection of environmental characteristics that can explain spatial differences in the distribution of biological communities (Diaz et al., 2004; Brown et al., 2011). These terrain derivatives can be used in methods that map habitats across the broad geographic extent (Diaz et al., 2004; Brown et al., 2011). The final product is a visual thematic map of habitat distributions that presents the habitat data in a tangible, succinct format for use by experts and non-experts (Peterson, 2006; Cogan et al., 2009). These maps can be used for diverse applications, including conservation, marine spatial planning, resource exploration and development, and ecosystem-based management (Peterson, 2006; Cogan et al., 2009).

Ecosystem-based management is an environmental management approach increasingly promoted in fisheries management that acknowledges the broader ecology of an

ecosystem, registering interactions between species and services rather than single entities (Cogan et al., 2009). Seafloor habitat data were traditionally associated with research in benthic ecology, but the relevance of seafloor habitats to motile ecosystem components, such as demersal fishes, has been recognised in recent decades (Mangel, 2000; Levin & Stunz, 2005; Cogan et al., 2009).

1.1.2 The fish-habitat relationship

Many marine fish species use benthic habitats in diverse and sometimes subtle ways. Habitats can be used for spawning, prey-sourcing, protection, and as nursery areas for juveniles (Levin & Stunz, 2005). The mechanisms behind habitat selection by fish are complex and remain poorly understood (Grabowski et al., 2012). However, studies have suggested that gradients of environmental stimuli may aid some invertebrates and fish in navigating toward suitable habitats (Kingsford et al., 2002). Regardless of the complexities of these habitat interactions, seafloor habitats play an important role in fish ecology, and it is possible to study fish distributions using benthic habitat data (Langton, 1998; Levin & Stunz, 2005; Grabowski et al., 2012). Fine-scale marine features, such as pinnacles, rocks and artificial reefs are all seafloor structures that are characterised by high fish aggregation. Bathymetric maps created at a coarse spatial resolution cannot capture these fine details, but high-resolution mapping technologies are becoming increasingly available (Fernandes et al., 2002; Brown et al., 2011).

Atlantic cod (*Gadus morhua*), a formerly dominant species of the northwest Atlantic marine ecosystems, have been observed using seafloor habitats in diverse ways across multiple life stages. Although juvenile cod have been identified on different habitats,

survivability rates have shown decreased mortality on more complex substrate/habitat types (e.g. macroalgae, seagrass, and gravel) (Tupper & Boutilier, 1995; Gregory & Anderson, 1997; Grabowski et al., 2012; Sherwood & Grabowski, 2015). As juvenile cods mature into adults, their habitat use changes along with spawning, migrating, overwintering and feeding (Langton, 1998; Braithwaite & Salvanes, 2005). Due to the diverse use of seafloor environments by Atlantic cod, studies of cod-habitat interactions are complex. The variety of ecological strategies within and between populations further complicates this process (Robichaud & Rose, 2004; Knickle, 2009). Such complexity makes habitat maps an excellent tool to better understand and apply fish habitat interactions to research and management. Readability allows marine habitat maps to be assets in the difficult task of designing and implementing ecosystem-based management approaches (Cogan et al., 2009; Minns et al., 2011). Additionally, developments in acoustic telemetry, a method used to track organisms in space, now allow researchers to monitor fish movements at finer spatial scales (Dean et al., 2014). When combined with habitat maps, acoustic telemetry data help better understand the relationships that exist between fish and specific habitat types.

Even though technical developments support fish habitat mapping, other factors can slow this complex process. The essential fish habitat concept is intended to identify areas that are important in the life-history of fish (Levin & Stunz, 2005). As many fish are highly mobile species, often with diverse behaviours, records of essential fish habitat can quickly become exhaustive when all habitats visited by fish are recorded (Levin & Stunz, 2005). Consequently, this results in an over-estimation of essential habitat, slowing management and protection initiatives. As one solution, the relative importance of a habitat to the growth of a population can be investigated.

Levin & Stunz (2005) identified essential progeny stages that contribute to the recruitment of adult fish into populations, and subsequently identified the contribution of each habitat to the survival and growth of those essential progeny stages. That process systematically prioritized habitats and allowed creation of an indexed map of relative importance. Techniques such as this one can improve the identification of important fish habitat by management. Regardless of how the information is applied, benthic habitat maps form an initial stage in the aforementioned processes and are often a priority for many research and conservation schemes (McKenna Jr & Castiglione, 2010; Minns et al., 2011).

1.1.3 Habitat maps in Newfoundland, Canada

Some of the main applications of habitat maps to fish studies include conservation and ecosystem-based management. Complex and novel management systems, such as ecosystem-based management and marine protected area, require research and development on the use of habitats throughout fish life cycles. Implementation of ecosystem-based approaches is typically slow. Pitcher et al. (2009) reviewed the progress of 33 countries that had committed to implementing an ecosystem-based management approach. Overall, no country was found to perform well, although Canada was rated amongst the highest. Link et al. (2011) reviewed the progress of current initiatives to establish ecosystem-based management in the Northwest Atlantic. An important move toward ecosystem-based approaches in Canada is the commitment to conserve 10% of

coastal and marine areas by 2020, under the Convention of Biological Diversity (CBD), through equitably managed, ecologically representative and well-connected systems of protected areas (DFO, 2016).

Towards this spatial approach within Canada, the federal Department of Fisheries and Oceans worked on five Large Ocean Management Areas in 2005 (LOMA) (DFO, 2007). The primary aim of LOMA was to develop and implement an integrated management plan for each area as a collaborative coastal and ocean planning process under Canada's Oceans Act (DFO, 2007). The *Placentia Bay – Grand Banks* Integrated LOMA was established in 2012, encompassing 550,000 km² of the south and south-east coastal Newfoundland Ecoregion, including the Grand Banks (Figure 1.1) (DFO, 2012). The Northwest Atlantic Fisheries Organization (NAFO) zone 3L is included in this LOMA, and is part of Newfoundland's 'Northern' cod stock management zone (Figure 1.1) (DFO, 2012). The Newfoundland and Labrador Ecoregion aims to use both ecosystem-based management and habitat knowledge as a foundation, and to apply ecosystem-based fisheries management in accordance with the Food and Agriculture Organization (FAO). The 'FAO Code of Conduct for Responsible Fisheries' (1995, p.5) states under general principles 6.4., that "Conservation and management decisions for fisheries should be based on the best scientific evidence available, also taking into account traditional knowledge of a resource and their habitat,...". A framework was designed and implemented to identify conservation priorities under the title of Ecologically and Biologically Significant Areas (EBSA), areas that met specific criteria under this framework would be entitled to enhanced protection by the Department of Fisheries and Oceans under Canadas Ocean Act (DFO 2004). This framework was used to identify

EBSAs in the Newfoundland and Labrador Ecoregion in a 2007 assessment (Templeman 2007). An additional analysis was used to further clarify the attributes of each area and rank their priority for enhanced protection (Park et al., 2011). Ecosystem approaches to management are intended to take place across the Newfoundland and Labrador Ecoregion and within an EBSA; this shift in management regime requires habitat data (Park et al., 2011). One of the EBSA of the Newfoundland and Labrador Ecoregion is Smith Sound, a fjord that provided spawning and refuge habitat for a portion of the remaining northern cod stock after collapse of the Northwest Atlantic cod stocks.



Figure 1. 1. Map of the Placentia Bay - Grand Banks Large Ocean Management Area and NAFO division 3L (DFO, 2012).

1.1.4 Northern cod stock collapse

The Northwest Atlantic cod stock collapse has been primarily blamed on overfishing, mismanagement and changes in long term climate patterns (FRCC, 2011). Europeans began commercial exploitation of Newfoundland groundfish in the 1500 (FRCC, 2011). As the 1960s progressed, technological advancements in fisheries technologies led to an unsustainable commercial fishing effort by global fleets (FRCC, 2011). According to population modelling conducted, most Northwest Atlantic stocks declined to low levels during the 1970s, were thought to increase during the 1980s before declining even more severely during the late 1980s and early 1990s (Lilly et al., 2008). Several of the stocks have shown little or no recovery during the past decade despite severe reduction or even cessation of directed fishing (Shelton et al., 2006). A cooling event during the last three decades of the twentieth century is considered to have influenced the rapid decline of several Northwest Atlantic stocks (Lilly et al., 2008). This environmental cooling is also considered to have altered cod life-history traits (growth rate, age and size at maturity), the biotic environment (predators and prey), and may be contributing to slow recovery (Lilly et al., 2008; DFO, 2017).

The northern cod stock are considered to have been the largest of Newfoundland's five managed stocks, consisting of a network of metapopulations distributed over 300,000 km² (Walters & Maguire, 1996; Smedbol & Wroblewski, 2002). A metapopulation is a breeding group with opportunity for regular or episodic mixing, creating a population structure that is a function of fish behaviour and environmental dynamics (Hanski & Simberloff, 1997; Smedbol & Wroblewski, 2002). The northern cod stock complex was

estimated to have had a maximum biomass of 3.5 million tonnes (Walters & Maguire, 1996). These numbers dwindled to just tens of thousands of tonnes by the early 1990s (Walters & Maguire, 1996; Rose et al., 2010). Typical behaviour included the majority of the stock complex overwintering offshore and migrating along known routes in the summer and fall to spawn and feed across the inshore shelf area (Smedbol & Wroblewski, 1997; Rose et al., 2010). In the 1980 – early 1990, these migratory routes were sparsely used and the remaining stock complex was dispersed across inshore areas year round (Walters & Maguire, 1996; Smedbol & Wroblewski, 1997; Rose et al., 2010). Inshore distributions in the 1980 and early 1990 included the northern cod's most southerly migration routes of Trinity Bay and the Bonavista Corridor (Smedbol & Wroblewski, 1997; Rose & Kulka, 1999; Rose, 2003; Rose et al., 2010). However, fisheries acoustics uncovered an aggregation of northern cod overwintering and spawning in an inland fjord in 1995 (Rose, 2003). This aggregation was located in Smith Sound and became the largest overwintering and spawning group of northern cod known at the time (Rose, 2003).

The management of fish stocks has been highlighted as an indirect contributor to the cod collapse and to slow recovery. Despite the introduction of new excessive fishing pressures, fisheries management failed to act before 1973 (Hutchings et al., 1993). Population dynamics modelling was introduced in 1973 (Steele et al., 1992), but Atlantic cod fecundity and reproductive potential were overestimated (Marshall et al., 2006), giving a false picture of how quickly stocks would recover. More recently, the collapse has been attributed to models that failed to represent natural biomass fluctuations and non-human predation (Rose & Rowe, 2015), making it harder to accurately predict stock

levels. Stock assessments or restrictions of Total Allowable Catch (TAC), were not applied to early management which could have had a large impact on reversing the decline, or at least halting it (Hutchings et al., 1993). Once introduced, stock assessment numbers were based solely on commercial catch data and did not account for misreporting or fisheries discards, providing largely underestimated numbers of catches (Hutchings et al., 1993). Stock assessments were further criticised for inaccuracy and excessive optimism (Walters & Maguire, 1996). Despite knowledge of inshore cod spawning, fisheries spawning models used only offshore spawning locations into the 1990 (Smedbol & Wroblewski, 1997).

Currently, the northern cod stock is being assessed using a limit reference point (LRP) that was established in 2010 (DFO, 2011). This system defines the 1980 spawning stock biomass and the stock level below which recruitment is impaired and serious harm occurs (DFO, 2017). The 2016 assessment, using the catch-at-age, Northern Cod Assessment Model (Cadigan, 2016; DFO, 2016) determined that the spawning stock biomass has increased to 34% of the LRP since 2006 (DFO, 2017). Overall, the cod collapse resonated globally and is often considered as the key case study for fisheries mismanagement, and has a well-documented scientific chronology (Lilly et al., 2008; FRCC, 2011; Rose & Rowe, 2015).

1.1.5 Smith Sound

Smith Sound is a fjord that has been formally identified as an EBSA under the Newfoundland and Labrador Ecoregion with a 'medium' priority rating for the implementation of enhanced protect by the Department of Fisheries and Oceans (Park et

al., 2011). This recognition as an EBSA is in part due to the wealth of research that has been conducted in Smith Sound since the discovery of a large Atlantic cod aggregation in 1995 (Rose, 2003; Park et al., 2011). Smith Sound was considered to have historically held small numbers of inshore cod before the Newfoundland wide moratorium (cessation of fishing activity) on Atlantic cod in 1992. A moratorium is the cessation of an activity, in this case all fishing activity was prohibited in Newfoundland waters from 1992. However, the post-moratorium aggregation held the structure of a large offshore stock (similar to the pre-collapsed northern cod stock) (Wroblewski et al., 1994; Rose, 2000). In 1993, only two overwintering cod were sampled from Smith Sound (Brattey et al., 2008; Rose et al., 2010). Two years later, a cod aggregation was estimated at 10,000 tonnes (Rose, 2003). The fish were overwintering and spawning in the inner basins of the fjord, and their origin is the suspected consequence of immigration (Rose et al., 2010). The fjord has an open structure with regular mixing, the sill at the mouth sits around 150m. There are two main inner basins, the outer basin (closest to the mouth) is a long trench with a maximum depth of 240m. The inner basin reaches a depth of 205m, the two sills are separated by a 150m sill (Figure 2.3). The group was the largest known overwintering and spawning aggregation of the depleted northern cod stock at the time of discovery (Rose, 2003). Although cod were known to spawn and feed inshore across the shelf, bay activity of this scale was not previously reported or studied. This distribution is well known in other countries, however cod spawn annually in Norwegian fjords (Jakobsen, 1987). Additionally, a genetically isolated population of Atlantic cod maintains an annual distribution in the Labrador fjord of Gilbert Bay (Morris & Green, 2002). Unique from other stock aggregations at the time, fish from the Smith Sound

aggregation held a range of cohorts, and were larger, healthier, and more frequently fecund (Rose et al., 2010). This inspired hope for an eventual stock recovery, influencing > 20 years of local research and speculation on the origin of the Smith Sound cod (Rose et al., 2010).

Before discovering the Smith Sound aggregation, group spawning activity was considered common in the Bonavista Corridor, an incised passageway extending from Smith Sound to the continental shelf (Rose, 2000). Researchers hypothesized that some of the remaining fish from the northern cod stock migrated from their offshore location to the Bonavista Corridor and Trinity Bay, eventually moving into Smith Sound (Rose et al., 2010). As biomass of the northern cod stock declined, local density of Bonavista Corridor cod increased. This is thought to be a behavioural mechanism to increase protection and therefore survival (Rose & Kulka, 1999). When the density of a schooling fishes aggregation falls below a certain threshold needed for protection (varies according to species) it can be increased by a reduction in the occupied space (i.e. from open waters to a narrow fjord). During two decades of research, the Smith Sound aggregation witnessed retention and growth, to 26,000t in the early 2000s, until 2007 when the aggregation rapidly dispersed in conjunction with rising offshore numbers (Rose, 2010). Depleted offshore stocks entered Smith Sound, rebuilt their numbers to a more ecologically favourable threshold, and eventually readopted typical behaviours including migrations offshore (Rose et al., 2010; Rose & Rowe, 2015). Smith Sound is deemed a former refuge for the collapsed northern cod stock, and is referred to as the Smith Sound refuge in some assessments (Rose et al., 2010; Park et al., 2011; Rose & Rowe, 2015). Time spent there by cod is regarded by some authors to have been vital to the recovery of the northern cod

stock (Rose & Rowe, 2015). Although the origin of the Smith Sound aggregation has generated speculation (Rose et al., 2010), it is not yet known why the Smith Sound environment was selected by cod. This thesis maps benthic habitats in Smith Sound and considers cod-habitat ecology as a factor in cod retention and growth from 1995-2007.

1.2 Research questions

This thesis aims to answer three research questions concerned with the delineation and distribution of Smith Sound benthic habitats and their relationship to Atlantic cod.

- 1. What benthic habitats exist in Smith Sound, and what are their distributions?
- 2. What habitats coincide with the zones of cod aggregation and cod spawning in Smith Sound?
- 3. How does cod stomach content relate to benthic species found in Smith Sound?

1.3 Goal and Objectives

The goal of this research was to describe broad-scale benthic habitats found within the sampled area of Smith Sound.

The objectives of this study are to:

- Collect, process and use ground-truthing data such as video surveys and grab samples to help characterize benthic habitats in Smith Sound.
- Select terrain derivatives that are appropriate for mapping habitats determined from the dataset.
- Assess the ecological relationships between the benthic organisms collected in this study and Atlantic cod, using literature and past stomach content of the Smith Sound aggregation.
- Generate a thematic map of the benthic habitat distributions based on the topographic attributes of the sample dataset.
- Assess the accuracy of the Smith Sound benthic habitat map.

1.4 Methods

A ten day bathymetric survey was conducted between June 18th and July 18th 2014 using the Memorial Explorer autonomous underwater vehicle (AUV). Multibeam was collected using an R2 Sonic multibeam-echo sounder (200/400 kHz). The AUV was operated by the Marine Environmental Research Laboratory for Intelligent Vehicles (MERLIN). The author designed the survey, assisted in data collection and completed data processing of the multibeam using CARIS HIPS and SIPS 10.0. Ground-truthing was conducted over 12-days between August 20th and October 17th 2014 using a 24 litre Van Veen grab sampler and two drop camera systems. The author planned the survey and conducted collections with a team of research assistants from a fishing vessel. Data analysis was designed to address the specific research objectives of the thesis.

Univariate analysis was used for the determination of grain size profiles to describe seafloor sediments. Multivariate statistics analysed the relationship between the seafloor sediments and their faunal community composition, grouping samples into habitats. Exploratory regression determined an appropriate selection of digital terrain models for a correctly specified ordinary least square model for habitat classification. Maximum likelihood classification then classified the 5m² resolution bathymetric grid of the survey extent with the final habitat classes. An accuracy assessment was conducted on a subset of the data excluded from the modelling process. Data records of stomach content collected from the Smith Sound aggregation between 1995 and 2007 went under exploratory analysis to establish ecological links between the Smith Sound aggregation and benthic habitats during refuge occupation.

1.5 Thesis Layout

Chapter 2 is organised as a research paper, presenting the habitat mapping of Smith Sound. Benthic habitat is recognised as a crucial component in the life history of cod, for recovering benthic fish populations, and in the role of a refuge. The paper presents habitat maps of Smith Sound. The results provide additional information on the role Smith Sound played in cod refuge ecology. Chapter 3 outlines the research conclusions and provides suggestions for future work.

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Co-authorship Statement

This thesis is formatted in paper-based format. Chapter 2 has been prepared for a future submission to the peer-reviewed Journal of Coastal Conservation. The student's contributions to the thesis manuscript are as follows:

- Identified knowledge gap and research potential.
- Guided the finalization of research questions.
- Led the data collection (planning, field work), data processing and analysis.
- Lead author of all chapters, providing initial drafts for review.

Dr. Rodolphe Devillers (Memorial University of Newfoundland (MUN)) provided financial support and assisted in designing the study. Dr. Evan Edinger (MUN) assisted in designing the study and specifically laboratory protocols. Dr. Jonathan Fisher (Marine Institute) provided stomach content data and guidance on fisheries literature. All committee members assisted in the interpretation of results and the review of thesis' chapters.

CHAPTER 2: BENTHIC HABITATS ASSOCIATED WITH AN ATLANTIC COD REFUGE, SMITH SOUND, NEWFOUNDLAND

2.1 Abstract

This study maps benthic habitat maps in a coastal sub-arctic fjord that is considered a former refuge for Atlantic cod (*Gadus morhua*). The sediments and biology of benthic habitats were described and quantified to explore possible ecological connections to Atlantic cod. Video imagery and grab samples were used to ground-truth the acoustic data. Habitats were mapped across the multibeam bathymetry using a maximum likelihood classification. Eight habitats were identified in Smith Sound and a misclassification matrix determined that the habitats were mapped with an overall accuracy of 86.71% (Kappa = 80.40%). Habitats were consistent with current ecological knowledge of cod, providing sediments, features and associated organisms that offer shelter, sustenance and the opportunity for reproduction. Areas of high cod aggregation and spawning were predominantly fine-grained surrounded by elevated hard substrate and high slope features.

2.2 Introduction

2.2.1 Refuges: roles and characteristics in marine benthic habitats

A refuge is an area resilient to surrounding disturbances, providing organisms with spatial or temporal relief (Sedell et al., 1990; Keppel et al., 2012; Davis et al., 2013). Organisms can retreat to these locations and persist until the opportunity for re-emergence or recruitment is realised (Keppel et al., 2012). Identifying the characteristics of a former or current refuge is an important aspect of conservation and management, and is becoming more relevant as ecological stressors increase (e.g. climate change, overfishing) (Davis et al., 2013). Understanding refuge characteristics can aid in the identification of other suitable refuge areas, areas that could share the potential to contribute to survival and recruitment within depleted populations (Keppel et al., 2012). Habitat is considered to be an essential property of a refuge (Keppel et al., 2012). The benthic habitat used by fish has been identified as an important factor in the recovery of many stocks (Pauly & Maclean, 2003; Levin & Stunz, 2005) and plays a particularly important role in the reproduction and recruitment of cod (Grabowski et al., 2012). This paper presents a benthic habitat mapping exercise in Smith Sound, Newfoundland, a refuge used by the collapsed northern cod stock from 1995 to 2007.

It is essential to examine the contribution of ecological services provided by refuge habitats, services that support persistence and recovery of a refuging species (Keppel et al., 2012; Davis et al., 2013). A conceptual framework proposed by Keppel et al. (2012) uses knowledge and tools from multiple disciplines to support a habitat-based concept for refugia identification. One proposed approach is to identify the habitat parameters of a refuge, using biogeographic tools to identify local ecological patterns, and examine their contribution as components of a refuge (Keppel et al., 2012). Geographic tools are frequently utilised in this way to produce benthic habitat maps for a diverse array of applications (Diaz et al., 2004; Brown et al., 2011; Brown et al., 2012). The distributions of benthic species tend to have recognisable patterns related to the characteristics of the surrounding seafloor (Brown et al., 2011). Benthic habitat mapping combines seafloor topography with *in-situ* data to classify areas into zones with physical and biological characteristics that are distinct from adjacent areas (Kostylev et al., 2001). After identifying the habitat parameters from topographic patterns, ecological links to the refuge species need to be evaluated through data interpretation or reference to scientific literature. In terms of an ecosystem approach, identifying benthic habitats and therefore associated organisms is an important step in managing motile ecosystem entities (Cogan et al., 2009; Park et al., 2011). Benthic habitat features that influence survivability, and spawning within fish populations have been shown to contribute to research and conservation (Levin & Stunz, 2005; Grabowski et al., 2012). Benthic habitat type and quality (e.g. high biodiversity, health) have been identified as a key driver in cod activity and distribution remains a neglected aspect of biology and distribution studies (Sherwood & Grabowski, 2015).

2.2.2 Atlantic cod-habitat relationships

Cod are a demersal fish, distributed across the North Atlantic in temperate and Arctic waters, with diverse and complex habitat relationships that vary across life history stages. Studies of habitat use are complicated by the metapopulation structure of cod stocks and
the highly variable behaviours of populations and even individual fish (Beacham et al., 2002; Rose et al., 2010). A metapopulation consists of breeding groups that regularly or episodically interact, resulting in a population structure or stock complex dependent on fish behaviour and environmental dynamics (Hanski & Simberloff, 1997; Smedbol & Wroblewski, 2002). Cod both conduct lengthy seasonal spawning and feeding migrations or remain resident to a local area where they also spawn (Mullowney & Rose, 2014). Each behaviour occurs across variable temporal and spatial scales. In some cases, resident populations have become genetically isolated due to their small area of occupancy and highly localized spawning patterns (e.g. Gilbert Bay, Labrador) (Green & Wroblewski, 2000; Morris & Green, 2002).

Following a pelagic period as floating, dispersed eggs, hatched juvenile cods settle to benthic habitats and spend several years growing before recruitment into the adult population (Tupper & Boutilier, 1995). Shallow inshore habitats are recognised as important for the protection and sustenance of these juveniles (Tupper & Boutilier, 1995; Gregory & Anderson, 1997). Increased habitat complexity was found to be associated with increased survivability as it improves the opportunity for predator avoidance (Tupper & Boutilier, 1995; Gregory & Anderson, 1997). Known nursery grounds include seagrass and rhodolith beds that offer a complex horizontal and vertical structure (Tupper & Boutilier, 1995). This exposure to heterogeneous environments also benefits cod into adulthood, with fish demonstrating improved behavioural plasticity through rapid adaptation to new prey items, a behavioural characteristic that can improve survivability during periods of environmental change (Braithwaite & Salvanes, 2005). Heterogeneity

of bottom types was also shown to be linked to high biodiversity and can provide an abundance of forage species (Sherwood & Grabowski, 2015).

Studies have demonstrated that cod express widespread annual site fidelity, with records of populations regularly using a same site over 500 years (Bolster, 2012). Behavioural ecology of marine fishes states that reproductive strategies have evolved so that offspring hatch and develop at times and in areas favourable for growth and survival (Robichaud & Rose, 2001; Skjæraasen et al., 2011). Cod are considered to have substrate orientated mating systems and behaviours, choosing substrate that increases reproductive output (Grabowski et al., 2012). It has been hypothesised that the spawning locations are selected to increase reproductive fitness (Cushing, 1990). Recent fine-scale observations of spawning cod in the Gulf of Maine witnessed males aggregating on deep sandy bottoms with females at nearby boulder and gravel areas of higher relief (Dean et al., 2014). An additional observation witnessed cod maintaining a residency at an offshore deep boulder reef that occurs on an otherwise homogenous fine-grained seafloor in the Gulf of Maine, where they would also take part in temporal spawning activities (Lindholm et al., 2007). Variability in the life history within and between cod populations is common and adds to the complexity of researching spatial and temporal patterns of habitat use (Robichaud & Rose, 2004; Knickle, 2009).

Nutrition is an important aspect of the fish-habitat relationship. Biodiverse habitats such as reefs attract higher concentrations of foraging fish. Cod are generalist feeders (Mullowney & Rose, 2014; Sherwood & Grabowski, 2015), but small pelagic fish rich in essential fatty acids make up an important dietary component (Litzow et al., 2006; Mullowney & Rose, 2014). Northwest Atlantic stocks rely on capelin (*Mallotus villosus*), which suffered a decline and temporary range shift in concordance with the cod stock collapse (Mullowney & Rose, 2014). The reduction in lipid rich pelagic fish has been shown to influence regional lipid deficiencies in groundfish (Anderson & Piatt, 1999). When access to the essential fatty acids provided by capelin is restricted, cod experience effects such as decreased fecundity, impaired growth and decreased juvenile survival (Tocher, 2003).

2.2.3 Northern cod stock dynamics

The northern cod stock experienced an ecological extinction in the 1980's as numbers dwindled from 3.5 million tonnes to tens of thousands of tonnes (Walters & Maguire, 1996). An ecological extinction occurs when populations are reduced to such low numbers that they no longer interact significantly with other species in the community, enacting ecosystem changes (Cushing, 1988; Tittensor et al., 2009). In an attempt to protect the remaining fish a moratorium was implemented in 1992, whereby all fishing activity in Newfoundland waters was prohibited.

The remaining cod population hyperaggregated in the Bonavista Corridor, whereby local densities increased with decreasing biomass (Rose & Kulka, 1999). It is hypothesised that this occurred in response to the low fish abundance, additionally causing the population to deviate from their typical behaviours and distributions (Rose & Kulka, 1999). Typically the spawning sites used by the northern cod stock cover a large spatial range including inshore and offshore locations, supporting the meta-population structure (Beacham et al., 2002; Rose et al., 2010). Prior to collapse, usual cod behaviour involved the majority of

the stock migrating to overwinter offshore on the deep slope of the continental shelf (300-500m), then moving to shallow waters inshore for summer spawning (Templeman & Davis, 2006; Rose et al., 2010). They would use known migratory routes and spawn at locations on the continental shelf such as the Bonavista Corridor and Trinity Bay (Smedbol & Wroblewski, 1997; Rose et al., 2010).

Recovery of the northern cod stock has been slow, much of this being attributed to climatic variability and its effect on trophic structures. In the absence of capelin, the northern cod stock experienced poor health, low fecundity, and mass atresia and skipped spawning (Rideout et al., 2000). Subsequently a trophic shift toward benthic fauna (e.g. shrimp, crabs) were recorded from stomach content (Mullowney & Rose, 2014). The importance of benthic prey items were overlooked pre-moratorium, as was feeding activity during spawning and overwintering, which is now known to occur but at a reduced rate (Krumsick & Rose, 2012). The northern cod stock demonstrated strong recruitment to the fishery in 2015 demonstrating an increase in the spawning stock biomass, but the stock still remained in a vulnerable state (DFO, 2017). The 2017 stock assessment uses a conservation limit reference point (LRP) to define the minimum spawning stock biomass below which serious harm is occurring and recruitment is incapacitated (300,000 tonnes) (DFO, 2011; DFO, 2017). In 2017, spawning stock biomass was estimated to be 34% of the LRP, meaning the stock was still suffering serious harm, and recruitment remains compromised (DFO, 2017).

2.2.4 Smith Sound as a refuge

A hyperaggregation of the northern cod stock entered Smith Sound after their population collapsed (Rose et al., 2010). The group of fish overwintered and spawned in this deep inland fjord and became known as the Smith Sound aggregation (Rose et al., 2010). This hyperaggregation of cod was the largest and healthiest spawning aggregation of northern cod stock in Newfoundland waters in 1995 (Rose, 2000; Rose et al., 2010). The hyperaggregation was hypothesized to increase survivability and boost chances of reproduction (Lima, 1998; Rose & Kulka 1999). Comparisons of stomach content and measures of fecundity of the Smith Sound aggregation during the Smith Sound occupation indicated that the fish had access to adequate nutrition despite their spatial confinement and without consistent access to capelin, compared to other fish within the northern cod stock range (Mullowney & Rose, 2014). Compared to other groups of cod throughout Newfoundland, the Smith Sound aggregation experienced lowered mortality and higher fecundity, which gradually led to retention and growth of the population (Mullowney & Rose, 2014). Smith Sound was considered a refuge for the collapsed stock until dispersal in 2007 and appears to have been pivotal to the recovery process of the northern cod stock.

Coastal cod spawning habitats, such as those identified in the Smith Sound refuge, remain largely unknown in Newfoundland (Smedbol & Wroblewski, 1997). Fjords have been identified as spawning areas in other countries, and are also utilised in Labrador (Smedbol & Wroblewski, 1997; Morris & Green, 2002). The Smith Sound aggregation was the first spawning aggregation recorded in the coastal bays of Newfoundland. The only evidence of pre-moratorium spawning of the northern cod stock in Smith Sound is from anecdotal accounts from fishermen, with claims that 'mothers' or 'breeders' were present in the Sound during years of northwest winds (Neis et al., 1999). Near-shore spawning events are now known to occur in Placentia Bay, Trinity Bay and Gilbert Bay (Smedbol & Wroblewski, 1997). Though not well researched it is assumed that bay-scale spawning groups are more common than previously thought and could be crucial components in stock rebuilding (Smedbol & Wroblewski, 1997). Subsequent investigations could reveal that SS has a unique set of habitat variables not found in any other embayment.

2.3 Methods

This research uses habitat mapping techniques to identify the habitat characteristics of this former refuge and discusses their ecological contribution to the persistence and growth of the northern cod stock (Figure 2.2). Seafloor sediments and benthic community compositions were collected using grab and video imagery to characterize benthic habitats within the refuge. Terrain derivatives are derived from multibeam bathymetry and an appropriate selection of terrain derivatives are selected for mapping using ordinary least square regression (OLS). A thematic map of Smith Sound benthic habitats is created using a Maximum Likelihood Classification and tested for accuracy. The results are used to infer the role of the Smith Sound benthic habitats in cod refuge use and recovery, through the examination of cod-habitat relationships with reference to past stomach content of the Smith Sound aggregation.

2.3.1 Study area

Smith Sound is a sub-arctic fjord located in Trinity Bay, on the northeast coast of Newfoundland, Canada (Figure 2.1). Smith Sound acted as a major dispersal zone during the glacial retreat from the Bonavista Peninsula (Batterson & Taylor, 2001). The carved waterway is eroded through the diverse geological strata of the Bonavista Peninsula, creating Random Island to the south (Batterson & Taylor, 2001). The ~2km wide waterway extends ~20km from the community of Clarenville to the mouth. The incised passage of the open fjord continues to the shelf edge as a substantial benthic depression known as the Bonavista Corridor, this channel is incised through Trinity Bay (Figure 2.1). The Bonavista Corridor was traditionally an area of northern cod stock spawning activity prior to the 1990's stock collapse (Brattey, 1996) (Figure 2.1). The central basins of Smith Sound reach depths between 200-240m with an inner sill depth of 40m and 150m towards the fjord mouth. Fjords generally have circulation patterns of outward fluxing surface waters and inward movements of sub-surface layers although wind forcing can reverse this pattern (Svendsen & Thompson, 1978).

Due to abundant records of cod activity from 1995, Smith Sound was identified as an 'Ecologically and Biologically Significant Area' (EBSA) in 2007 and was ranked of medium priority for enhanced protection by the Department of Fisheries and Oceans in 2010 (Park et al., 2011). EBSAs were identified within the Large Ocean Management Area (LOMA) of the Newfoundland and Labrador Ecoregion for conservation and management purposes. This occurred as part of Canadas' agreement with the United Nations Convention of Biological Diversity and commitment to protecting 10% of coastal areas by 2020. Seagrass is known to be in abundance at the head of Smith Sound. Snow crab (*Chionoecetes opilio*) were present in high abundance and dwindled shortly after the arrival of the cod in 1995 (Rose et al., 2010). Concurrently, offshore biomass of snow crab increased in the absence of cod (Rose et al., 2010).



Figure 2. 1. Study area, Smith Sound with 100m contours and 200m contours showing the location of the fjord basins. Inset: Trinity Bay and Bonavista Corridor.



Figure 2. 2. Flowchart of research.

2.3.2 Multibeam acquisition and terrain derivatives

Multibeam bathymetry was collected using an R2Sonic multibeam echo sounder (200/400 kHz) mounted on the Memorial Explorer autonomous underwater vehicle (AUV) (Figure 2.3). Bathymetric data were post-processed using the hydrographic software CARIS HIPS and SIPS (v. 10.2) to correct for vessel motion, sound velocity and tides. The AUV was equipped with an iXBlue PHINS inertial navigation system, paroscientific depth sensor, and gyroscope for the collection of motion data. An SBE 19plus V2 SeaCAT profiler conductivity-temperature-depth sensor was used to collect regular sound velocity profiles. Tidal corrections were performed using the Canadian Hydrographic Services tide station 975 at Clarenville, NL. Twelve terrain variables were derived from the bathymetry using three tools. First, the 'Terrain Attributes Selection for Spatial Ecology' (TASSE) ArcMap extension was used to generate seven terrain derivatives (Lecours et al., 2017a). Second, the 'Benthic Terrain Modeller' ArcGIS extension (Wright et al., 2005) was used to produce four terrain variables not derived by TASSE. Finally, a variable was created using ArcGIS 10.3 'Trend' tool to measure 'distance to the ocean' that could indicate changes in environmental conditions from the mouth to the end of the fjord.



Figure 2. 3. Smith Sound multibeam survey, collected using the Memorial Explorer, Autonomous Underwater Vehicle. Inset: Location of Smith Sound study area, Trinity Bay, Newfoundland, Canada (48%) 27"N, 53% 1'47"W).

2.3.3 Ground-truthing

Seafloor surficial sediments and benthic species were characterised using grab samples and video imagery. ArcMap 10.2 was used to plan sampling stations. The reclassified bathymetric raster was used to randomly generate sampling points across four depth zones (n=92), the number of samples in each zone being representative of their spatial extents (km²). Additionally, denser points were generated within two zones that were historically important for cod (n=51), these were named Zone A and Zone B, but have also been called the '205 Hole' and 'Petley Trench' respectively (Rose, 2003). Zone A was considered to be optimal and Zone B sub-optimal areas of aggregation and spawning with expert knowledge from Dr. George Rose. In total 143 stations were identified in Smith Sound (Figure 2.4).



Figure 2.4. Planned ground-truthing survey sites (n=143), over four classified depth zones across the multibeam extent.

A 241 Van Veen grab sampler was used to collect quantifiable seafloor sediment and biota. The GPS position was recorded on contact with the seafloor. Two 90ml substrate samples were randomly collected from each grab and the remainder of the sediment and rinsed with seawater through a 1mm mesh sieve. Infauna and epifauna were collected from the grab samples, fixed in formalin for 48 hours, and then stored in 70% ethanol.

Larger specimens such as urchins and large quantities of tube worms were photographed for identification, counted and discarded. Video was collected with Shark Marine (<70 m) and Deep Blue Pro Splash (>70 m) camera systems. Where possible the drop cameras were deployed from a stationary vessel and were allowed to drift for ~4 minutes over the seafloor. Otherwise the camera was deployed in shallow waters and the vessel and camera were allowed to drift toward deeper sites. Recording was ended when contact with the seafloor was lost, due to the depth limits of the camera cable. The GPS position was recorded continuously and was used to georeference video transects.

2.3.4 Substrate classification and biota identification

Grab sample surficial sediments were used to classify substrates (n=81). Sediment grain size analyses were calculated through a combined method of Wentworth sieve analysis (>63µm) and LA-960 HORIBA laser diffraction analysis (<63 µm). Grain size profiles of sediment samples were processed in GRADISTAT 4.0 software, with a substrate classification assigned according to the Folk & Ward method (1957) (Appendix E) (Blott & Pye, 2001). The broad substrate classifications identified from GRADISTAT were incorporated into more general groups using the GRADISTAT trigon diagram (Figure 2.5). The Folk and Ward method of substrate classification was applied to the qualitative assessment of video substrate classification. Videos were reviewed in 10 second intervals, and a dominant bottom type assigned.

Biota sampled within the Van Veen grabs were identified using a Nikon SMZ 1000 stereomicroscope. Abundance was recorded for most taxa but presence was recorded where organisms were not discrete individuals (e.g. coralline algae). Organisms were

identified at the lowest possible taxonomic level, although polychaetes were identified to family level and then categorised into functional groups (Appendix F) (Fauchald & Jumars, 1979; Gagnon & Haedrich, 1991). Due to their abundance, one polychaete (*Northria conchylega*) was identified to the species level. Biota visible in video were identified to the lowest taxonomic level and recorded in ten second increments.

2.3.5 Habitat characterisation

Non-parametric multivariate analyses of biological community similarity was used to characterise habitats in PRIMER-E V6 (Clarke, 1993; Clarke & Gorley, 2006). To account for differences in grab and video sampling resolution (e.g. endo vs epi-benthos), datasets were analysed separately (Copeland et al., 2013). Species accumulation curves were generated to demonstrate the rate of new species discovery as a proxy for sampling adequacy (Clarke & Gorley, 2006). Species abundance data were 4th root transformed with a Bray-Curtis triangular similarity matrix across substrate types (Clarke & Gorley, 2006). The Bray-Curtis is a widely used and reliable coefficient for data standardization and prevents abundant species from dominating the similarity analysis (Clarke, 1993). Non-parametric multidimensional scaling ordination plots (nMDS) were generated for the graphical representations of the community in two-dimensional space (Clarke, 1993). A statistical test in the form of a one-way analysis of similarities (ANOSIM) was then conducted on the rank similarities of the triangular similarity matrix to determine relationships between the species compositions of substrate groups (Clarke & Warwick, 2001). ANOSIM tests results were considered reliable when $p=\leq 0.1$ (Clarke, 1993). The tested pairs yield an R statistic to test the null hypothesis that 'no differences exist

between sites', 0 < R < 1 if there is some discrimination between sites; whereas sites with $R = \le 0$ indicates that similarities across different groups are higher than those within sites (Clarke, 1993). Pairs of tested data groups that yielded ANOSIM results with $R = \le 0$ were considered to have statistically similar community compositions and were combined into a habitat type. A second ANOSIM test was conducted on the new data categories to ensure 0 < R < 1 so that the null hypothesis can be rejected and the habitat categories are reliable. Similarity percentages (SIMPER) analyses were conducted, as an exploratory analysis that compares sample groups to provide similarity within a between habitat categories, additionally identifying a group's influential species through a ranking of their contribution to the faunal community (Clarke & Warwick, 2001).

2.3.6 Stomach content analysis

Cod stomach content data were collected in Smith Sound and analysed by the Fisheries Conservation Chair group, Marine Institute, between 1995 and 2007 as part of an ongoing fisheries monitoring programme. Part of the dataset underwent exploratory analysis to identify benthic organisms utilised by Smith Sound cod for nutrition during the time of refuge occupancy. Counts of organism occurrence (n=5020) in cod stomachs were used to build a profile of primary benthic contributors to Smith Sound aggregation refuge nutrition. A table was generated that displayed the contribution of each cod stomach organisms to the faunal communities sampled at each habitat delineated in this study. The resolution of species recovered from stomach content was highly variable due to the large number of research participants involved in the fisheries monitoring programme. Despite high variability, some IDs held consistency and taxonomic descriptions were combined

into high order groups to consolidate and standardize result resolution. The subset of data selected for this study does not discriminate samples by cod metrics (e.g. sex, maturity, length) or environmental variables (e.g. collection season) as such analysis was beyond the scope of the study.

2.3.7 Supervised classification

The thematic map showing the benthic habitat distributions of Smith Sound was produced using a supervised classification process. Supervised classification used multibeam terrain derivatives and discrete habitat samples to classify a 5m² bathymetric grid of the study extent. The habitat mapping process was conducted using ArcGIS 10.2, and a maximum likelihood classification (MLC) was computed using five terrain variables. Mapping was completed using 90% of the habitat samples, and 10% were retained to test map accuracy using a misclassification matrix.

The 'Exploratory Regression' Arcmap tool was used to identify an appropriate set of terrain derivatives for habitat mapping the local area under an OLS regression analysis. Exploratory Regression models were run using pre-set threshold criteria (Appendix H, Note 1). Spatial auto-correlation is an accepted artefact of transects. The dataset was independently tested for auto-correlation using Global Moran's I (Euclidean distance), with the grab sample sites and only the start locations for each video transect. Where initial Exploratory Regression highlighted redundancies between terrain derivatives using a measure of Variance Inflation Factor (VIF), these terrain derivatives were removed. Terrain derivatives that had a low significance to the habitat samples (<70%) were also highlighted for removal. Subsequent Exploratory Regression analysis operated OLS using

the remaining terrain derivatives. Preliminary mapping was used to assess the validity of the terrain variables using expert knowledge. In cases where the preliminary maps yielded distributions with low accuracy, terrain derivatives were excluded according to the Exploratory Regression. A dendrogram was used to identify where grab and video habitats experienced terrain variable co-occurrence. If the dendrogram identified cooccurrence between grab and video habitats, these were combined into a single habitat group. The dendrogram identified topographic co-occurrence for habitats 'Sand with Small Boulders' (SwSB) and 'Gravelly Muddy Sand' (GMS). Observations determined that this co-occurrence only existed below the sloped boulder walls. To account for this, an overlay of where the two habitats co-occurred was integrated into the final habitat map using two MLCs that were later combined using a raster calculator tool in ArcGIS. The first MLC modelled presence-absence of 'SwSB' and the output was reclassified as 0=absence, 10=presence. The second MLC excluded 'SwSB', mapping the other seven habitats. Raster calculator was used to combine the values of the two maps, highlighting areas where 'SwSB' intersected with 'GMS'. Any areas where 'SwSB' and 'GMS' overlapped were combined under a new habitat designation, Gravelly Muddy Sand with Small Boulders' (GMSwSB). Areas where 'SwSB' overlapped with other habitats were reverted to their previous classification.

2.3.8 Habitat assessment

An accuracy assessment was performed in the form of an error matrix, using 10% of the dataset. A sample was considered correctly classified if it was within 5m of the correct habitat, the same resolution used by the terrain variables raster data. In the case of 'GMS', the habitat was considered accurate if the test samples were located on habitat 'GMS' or 'GMSwSB'. The error matrix was used to assess four types of accuracy as described by Congalton (1991): "overall", "user's", "producer's", and "Kappa accuracy". Additionally the coverage of each habitat type was identified for the entire thematic map and within Zone A and Zone B, the two subsections of cod activity.

2.4 Results

2.4.1 Multibeam acquisition

Multibeam bathymetry was outputted to a 5m² resolution grid, covering a total of 14.33km² (Figure 2.3 & 2.5). Bathymetric depth ranged from -50m to -237m. To ensure ground truthing would be representative of the bathymetric zones the raster was separated into four depth zones: 50-100m, 100m-160m, 160m-200m and >200m, covering 0.48, 2.99, 7.00 and 3.81 km² respectively. A total of ten bathymetric terrain derivatives were created (Table 2.1). TASSE generated seven terrain derivatives surfaces; Aspect (Figure 2.9), Mean Bathymetry, Slope (Figure 2.6), Relative Deviation from the Mean (RDMV), Standard Deviation, Eastness and Northness. The 'Benthic Terrain Modeller' ArcMap extension generated four terrain derivatives; Finescale Bathymetric Positioning Index (FBPI) (Figure 2.8) at three spatial scales (annulus dimensions of 3m x 5m; 3m x 9m; 9 x 21m) and Broadscale Bathymetric Positioning Index (BBPI) (25m x 75m). Finally, a proxy terrain derivative "Distance to Ocean" was produced (Figure 2.9).

Source	Terrain Derivative	Abbreviation
TASSE, ArcGIS (Lecours et al.,	Aspect	ASP
2017)	Mean Bathymetry	MEAN
	Slope	SLO
	Relative Deviation from the Mean Variance	RDMV
	Standard Deviation	SD
	Eastness	EAST
	Northness	NORT
Benthic Terrain Modeller, ArcGIS	Finescale Bathymetric Positioning Index	FBPI
(Wright et al., 2005)	(FBPI)	BBPI
	Broadscale Bathymetric Positioning Index	
	(BBPI)	
Trend, ArcGIS	Distance to Ocean	DtO

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Figure 2. 5. Multibeam terrain derivative, 'Bathymetry'.



Figure 2. 6. Multibeam terrain derivative, 'Slope'.



Figure 2. 5. Multibeam terrain derivative, 'Distance to Ocean'.



Figure 2. 6. Multibeam terrain derivative, 'Fine bathymetric positioning index'.



Figure 2. 7. Multibeam terrain derivative, 'Aspect'.

2.4.2 Ground-truthing

Grab samples were successfully triggered at 95 sites: 81 sites returned quantifiable sediment and infauna with 61 occurring where multibeam data was available (Figure 2.10). The remaining samples (n=14) were determined to be hardground habitat and were omitted from analysis, as hardground could be more accurately assessed and categorized from video analysis. Underwater video imagery was collected along 24 transects and covered about 5.89km (Figure 2.10). Video transects were subdivided into 65 sub-transects to increase sample size for ANOSIM and SIMPER led habitat classification. Samples were georeferenced in 10 second increments with sediment type and organisms recorded, resulting in 1275 data points.



Figure 2. 8. Collected grab and video samples, across the Smith Sound multibeam extent. Polygons with a black outline identify the extent of the Zone A (left) and Zone B (right).

2.4.3 Substrate classification and biota identification

Quantitative classification of grab sediments (n=81) in GRADISTAT 4.0 suggested 20 substrate classes (Figure 2.11; Appendix A). More general groupings from the trigon diagram resulted into five sediment classes (n=81): Gravel (n=16), Sandy Gravel (n=20), Gravelly Sand (n=10), Muddy Sand (n=7), and Sandy Mud (n=28) (Figure 2.11). Qualitative classification of video substrates revealed 19 substrates (n=97).



Figure 2. 9. Trigon analysis, representing sediment groups visually (GRADISTAT v4.0) with expert knowledge guided by Dr. Evan Edinger.

Grab biota (n= 2320) were identified as belonging to 78 taxa (Appendix B). Polychaetes were identified to family level (n=30); these were condensed into nine functional groups (Appendix F). Tube building Annelida, *Nothria conchylega* was retained as a lower level of taxonomic classification due to high abundance and potential importance as a habitat engineer (Freeland, 2012). Video biota (n=13044) were identified to a lower taxonomic resolution and were categorised under 54 taxa (Appendix D).

2.4.4 Habitat characterisation

Species accumulation curves suggest that the grabs have been adequately sampled with the Jacknife 2 curve reaching a plateau after around 80 samples (Figure 2.12). Analyses suggests that the video dataset is subject to oversampling, with a plateau being reached at around 20-30 samples. The video dataset does not include all habitats present in Smith Sound, and is only representative of the dataset sampled. Interpretation of nMDS plots using Kruskal's stress formula, indicates a 'useable' picture with a two-dimensional stress value of 0.19 and moderate clustering of grab sediment types (Figure 2.13a) (Kruskal & Wish, 1978; Clarke, 1993). Video nMDS plots showed more distinct clustering of sediment types. The ordination plot had a, two-dimensional stress value of 0.12 indicating good ordination with little risk of drawing false assumptions (Figure 2.13b).



Figure 2. 10. Species accumulation curves of Van Veen grab and video samples (PRIMER V4).

Grab ANOSIM found three sediment groups to have statistically distinct faunal assemblages: 'Gravel' (n=16), 'Sandy Gravel' (n=20) and 'Sandy Mud' (n=28). These groups were classed as discrete habitats. Sediment classes 'Muddy Sand' (n=7) and 'Gravelly Sand' (n=10) were determined to have statistically similar biological communities (Table 2.2, 2.3, & 2.4). The smaller sample sizes of the two classes offer less power to a permutation based ANOSIM analysis to identify difference between the classes. The classes were combined into the habitat type 'Gravelly Muddy Sand' (n=17) and SIMPER results were examined to support the connection with a high 45.53% group similarity (Table 2.5).

An nMDS plot displaying habitats visually clarifies the relationship between the 'Muddy Sand' and 'Gravelly Sand' habitats, further supporting their combination into 'Gravelly Muddy Sand' (Figure 2.13a). ANOSIM conducted for videos found two sediment groups to have statistically distinct faunal assemblages, 'Sand with Small Boulders' (SwSB) (n= 15) and 'Sand' (n=17) (Appendix G, Table 1). These groups were classed as discrete habitats. Statistically significant relationships were found between various combinations of the 19 sediments (Appendix G, Tables 1-6). These combined to form habitats: 'Large Boulders' (n=20), 'Small Boulders' (n=22) and 'Coralline Boulders and Gravel' (CBaG) (n=19) (Appendix G, Table 2-5). An nMDS plot displaying habitats visually clarifies the relationships identified through ANOSIM analysis (Figure 2.13b).

Grab SIMPER analysis on faunal assemblages within habitats showed samples to have moderate within-group similarity: 'Gravel' (18.59%), 'Sandy Gravel' (37.38%), 'Gravelly Muddy Sand' (45.53%) and 'Sandy Mud' (57.83%) (Table 2.6-2.9). Results from the video SIMPER 'within group similarity' yielded varying results, as grain-size decreased similarity between samples increased (Table 2.2) (Appendix G, Table 7-11). SIMPER analysis showed samples to have moderate within group similarity, 'Large Boulders' (57.96%), 'Small Boulders' (56.41%), 'CBaG' (47.75%), 'SwSB' (60.63%) and 'Sand' (43.30%) (Table 2.3) (Appendix G, Tables 7-11).





Figure 2. 11. 'Non-parametric multidimensional scaling' plots, a) Van Veen grab habitats, b) Video habitats.

Habitat	IabitatWithin group similarityDominant contributing organisms (n=3)		Percent contribution (%)
Gravel	IT 17.91%	Nothria conchylega (family: Onuphidae)	18.54%
		Chaetopteridae	14.52%
		Lumbrineridae	14.46%
	GS 18.59%	Polychaete FG1	27.22%
		Polychaete FG3	18.84%
		Nothria conchylega	16.40%
Sandy Gravel	IT 23.34%	Nothria conchylega (family: Onuphidae)	23.11%
		Chaetopteridae	13.79%
		Nuculana pernula	11.29%
	GS 37.38%	Polychaete FG1	22.27%
		Nothria conchylega	20.41%
		Polychaete FG3	12.97%
Gravelly Muddy Sand	IT 33.65%	Lumbrineridae	15.37%
		Spionidae	11.39%
		Pectinariidae	9.90%
	GS 45.53%	Polychaete FG1	24.87%
		Amphipoda	10.89%
		Polychaete FG8	10.18%
Sandy Mud	IT 46.69%	Gammarus oceanicus	24.67%
5		Lumbrineridae	12.75%
		Spionidae	11.50%
	GS 57.83%	Amphipoda	26.30%
		Polychaete FG1	18.60%
		Polychaete FG8	11.69%

Table 2. 2. Summary of exploratory SIMPER analysis for grab habitats, examining organisms as individual taxa records (IT) and with polychaetes described under functional groups (GS).

Table 2. 3. Sediment classes pertaining to the statistically significant results identified in ANOSIM_1 and ANOSIM_2 for reclassification under grouped habitat 'Gravelly Muddy Sand (n=17)'.

Sub Group	Statistically Significant Group Connections	R- Value	Sig %	R- Value	Sig %
Gravelly Sand (n=10)	Muddy Sand (n=7)	-0.04	62.7	-0.01	44
Muddy Sand (n=7)	Gravelly Sand (n=10)	-0.04	62.7	-0.01	44

Pairwise test		(R Statist	ual Taxa tic = 0.331) nce =0.1%)	Grouped Taxa (R Statistic = 0.331) (Significance = 0.1%)	
Sediment Class 1	Sediment Class 2	R-Stat.	Signif. %	R-Stat.	Signif. %
Gravel (n=16)	Sandy Gravel (n=20)	0.009	40.2	0.013	39.3
Gravel (n=16)	Gravelly Sand (n=10)	0.568	0.1	0.581	0.1
Gravel (n=16)	Muddy Sand (n=7)	0.009	39.4	0.032	27.6
Gravel (n=16)	Sandy Mud (n=28)	0.031	16.5	0.042	11.8
Muddy Sand (n=7)	Sandy Gravel (n=20)	0.234	5.3	0.208	6.8
Muddy Sand (n=7)	Gravelly Sand (n=10)	-0.04	62.7	-0.01	44
Muddy Sand (n=7)	Sandy Mud (n=28)	0.061	29.3	0.026	38.6
Sandy Mud (n=28)	Sandy Gravel (n=20)	0.395	0.2	0.405	0.1
Sandy Mud (n=28)	Gravelly Sand (n=10)	0.573	0.1	0.575	0.1
Gravelly Sand (n=10)	Sandy Gravel (n=20)	0.039	30.9	0.013	40.8

Table 2. 4. Complete grab sample ANOSIM results using sediment class as a variable.

Pairwise test		Individual Taxa (R Statistic = 0.375) (Significance =0.1%)		Grouped Taxa (R Statistic = 0.381) (Significance = 0.1%)	
Habitat Group 1	Habitat Group 2	R-Stat	Signif. %	R-Stat.	Signif. %
Gravel (n=16)	Gravelly Muddy Sand (n=17)	0.192	0.3	0.227	0.3
Gravel (n=16)	Sandy Mud (n=28)	0.587	0.1	0.602	0.1
Gravel (n=16)	Sandy Gravel (n=20)	0.058	6.5	0.07	5.6
Gravelly Muddy Sand (n=17)	Sandy Mud (n=28)	0.249	0.2	0.245	0.2
Gravelly Muddy Sand (n=17)	Sandy Gravel (n=20)	0.192	0.5	0.187	0.1
Sandy Mud (n=28)	Sandy Mud (n=28)	0.637	0.1	0.639	0.1

Table 2. 5. Complete grab sample ANOSIM results using habitat group as a variable.

Individual Taxa Group Similarity 17.91%			-	oed Taxa ilarity 18.59	%
Organism	%	Av. Abun.	Organism	%	Av. Abun.
Nothria conchylega	18.54	0.84	Polychaete FG 1 (n=11)	27.22	1.05
Chaetopteridae	14.52	0.67	Polychaete FG 3 (n=3)	18.84	0.84
Lumbrineridae	14.46	0.66	Nothria conchylega (spp)	16.40	0.90
Nuculana pernula	7.93	0.46	Nuculanoida (order) (n=3)	9.53	0.55
Spionidae	7.42	0.36	<i>Ophiuroidea</i> (class) (n=3)	8.09	0.56
Ophiopholis aculeata	6.19	0.38	Polychaete FG 8 (n=2)	6.36	0.38
Serpulidae	4.73	0.32	Polychaete FG 5 (n=1)	3.91	0.35
Polynoidae	3.97	0.32			
Periploma papyratium	2.67	0.25			
Ophiura robusta	2.44	0.33			
Nephtyidae	2.16	0.29			
Aphroditidae	2.05	0.27			
Glyceridae	1.94	0.27			
Phyllodocidae	1.26	0.19			

Table 2. 6. SIMPER results for habitat 'Gravel (n=16)' samples

Individual Taxa Group Similarity 23.34%			Grouped Taxa Group Similarity 37.38%			
Organism	0⁄0	Av. Abun.	Organism	%	Av. Abun.	
Nothria conchylega	23.11	1.16	Polychaete FG 1 (n=11)	22.27	1.06	
Chaetopteridae	13.79	0.78	Nothria conchylega (spp)	20.41	1.29	
Nuculana pernula	11.29	0.70	Polychaete FG 3 (n=3)	12.97	0.90	
Odostomia trifida	9.87	0.62	Nuculanoida (order) (n=3)	12.28	0.84	
Lumbrineridae	8.55	0.55	<i>Odostomia trifida</i> (spp)	8.82	0.69	
Astarte spp	5.32	0.49	Astarte (spp)	4.64	0.55	
Pectinariidae	4.42	0.38	Pectinariidae (family)	3.88	0.42	
Maldanidae	3.75	0.34	Polychaete FG 6 (n=2)	3.31	0.38	
Glyceridae	3.10	0.34	Polychaete FG 5 (n=2)	2.89	0.39	
Aphroditidae	2.67	0.36				
Polynoidae	1.78	0.26				
Flabelligeridae	1.76	0.27				
Mya arenaria	1.42	0.26				

Table 2. 7. SIMPER results for habitat 'Sandy Gravel (n=20)' samples.

	vidual Taxa milarity 33.65	5%	Grouped Taxa Group Similarity 45.53%		
Contributing Fauna	%	Av. Abun.	Contributing Fauna	%	Av. Abun.
Lumbrineridae	15.37	1.06	Polychaete FG 1 (n=11)	24.87	1.48
Spionidae	11.39	0.90	Amphipoda (order) (n=5)	10.89	0.97
Pectinariidae	9.90	0.88	Polychaete FG 8 (n=2)	10.18	0.90
Glyceridae	9.81	0.82	<i>Nuculanoida</i> (order) (n=3)	8.92	0.86
Maldanidae	7.54	0.83	Pectinariidae (family)	8.77	0.88
Gammarus oceanicus	6.71	0.74	Polychaete FG 5 (n=2)	8.77	0.82
Nuculana pernula	6.66	0.70	Polychaete FG 6 (n=2)	8.14	0.90
Nephtyidae	5.79	0.55	Polychaete FG 7 (n=2)	4.78	0.64
Nothria conchylega	3.92	0.65	Polychaete FG 3 (n=3)	4.20	0.72
Opheliidae	3.12	0.50	Nothria conchylega	3.31	0.65
Phyllodocidae	2.20	0.36			
Astarte spp	1.85	0.44			
Yoldia hyperborea	1.64	0.33			
Ampeliscidae	1.57	0.32			
Odostomia trifida	1.50	0.33			
Cirratulidae	1.35	0.31			

Table 2. 8. SIMPER results for habitat 'Gravelly Muddy Sand (n=17)' samples.

Indiv	Individual Taxa			Grouped Taxa			
Group Sin	nilarity 46.6	9%	ANOSIM_2: Group Similarity 57.83%				
Contributing Fauna	%	Av. Abun.	Contributing Fauna	%	Av. Abun.		
Gammarus oceanicus	24.67	1.80	Amphipoda (order) (n=5)	26.30	1.86		
Lumbrineridae	12.75	1.07	Polychaete FG 1 (n=11)	18.60	1.38		
Spionidae	11.50	1.05	Polychaete FG 8 (n=2)	11.69	1.05		
Maldanidae	11.27	1.15	Polychaete FG 6 (n=2)	11.46	1.17		
Pectinariidae	7.98	0.85	Polychaete FG 7 (n=2)	8.47	0.84		
Opheliidae	5.88	0.70	Pectinariidae (family)	8.10	0.85		
Nephtyidae	5.81	0.67	Polychaete FG 3 (n=3)	6.74	0.75		
Polynoidae	3.50	0.53					
Terebellidae	3.34	0.51					
Periploma papyratium	2.60	0.48					
Chaetopteridae	1.89	0.38					

Table 2. 9. SIMPER results for habitat 'Sandy Mud (n=28)' samples.

Table 2. 10. Summary of exploratory SIMPER analysis for video habitats, examining organisms as individual taxa records.

Habitat	Within group similarity	Dominant contributing organisms (n=3)	Percent contribution (%)
Large Boulders	57.96%	Polaris	25.33%
		Hydroid, Nemertesia antennina	14.28%
		Ophiuroidea	11.99%
Small Boulders	57.96%	Polaris	31.84%
		Pandalus spp	15.85%
		Hydroid, Nemertesia antennina	12.80%
Coralline Boulders and	47.75%	Corallinaceae	73.36%
Gravel		Strongylocentrotus droebachiensis	18.56%
Sand with Small	60.63%	Hormathia nodosa	26.45%
Boulders		Pandalus spp.	21.31%
		Polaris	19.67%
Sand	43.30%	Euphausiid	49.51%
		Polaris	20.22%
		Pandalus spp.	17.87%
2.4.5 Analysis of stomach content data (1995-2007)

The stomach content data provided 5020 organism records between 1995 and 2007. These were described under 63 varying levels of taxonomic resolution and were consolidated to 28 benthic organism categories. Any organism that contributed >1% to the stomach content record of the Smith Sound aggregation was visually represented in a bar chart. Organism counts were represented under 16 taxa (n=4909) (Figure 2.14). The taxa that co-occurred in the stomach content and Smith Sound habitat community compositions included: Mysidacea, Crustacea, Hyperiidae, Polychaete (Unidentified), Euphausiacea, Gammaridae, Ophiuroidea, Amphipoda and Actiniaria.



Figure 2. 12. Stomach content of the Smith Sound aggregation (1995-2007).

2.4.6 Supervised classification

Global Moran's I analysis suggest no spatial autocorrelation of video sample sites with a Moran's Index of 0.093, z-value of 0.48 and a p-value of 0.63. The results do not allow rejecting the null hypothesis that the data experiences spatial autocorrelation. It is therefore accepted that the pattern does not appear to be significantly different than random (Appendix L).

Exploratory Regression initially identified six terrain derivatives that could be removed from subsequent analysis (Arcgis, 2018a). Three presented high multicollinearity (VIF >7.5) with other explanatory variables; MEAN (8.72), SD (14.78), and BPI (12.65). Three displayed low relevance to the dependant variables with low significance value (<70%); RDMV (63.02%), FBPI_3_5 (50.91%) and FBPI_3_9 (52.05%) (Appendix H). Exploratory Regression identified a model using terrain derivatives; Bathymetry, Slope, Aspect, Distance to Ocean and FBPI 9_21 (Appendix J, Note 1). The passing model criteria established by the Exploratory Regression analysis was validated using a more detailed OLS (Appendix K) (Arcgis, 2018b). The Adjusted R-Squared showed the model to explain 54.04% of the variation in the dependent variables. The Joint Wald Statistic was used to determine overall model significance, at a measure of 2608.66 ($p = \le 0.001$) the model is statistically significant. The Koenker (BP) statistic demonstrates a stationary model, and therefore the Coefficients and Robust Probability for each terrain derivative were examined (Arcgis, 2018b). These measures showed that each variable was significant to the overall model (p=<0.005). Measures of redundancy were <1.88, demonstrating that there is no redundancy amongst the variables (Appendix K).

These examinations found models including Eastness and Northness to be good predictors of the dependent variable. Preliminary mapping with Eastness and Northness produced habitat maps with poor accuracy compared to using the explanatory variable Aspect. This can possibly be explained by the presence of data artefacts in the multibeam data. Therefore, the first model that excluded Northness and Eastness was tested for the OLS and was used for modelling (Appendix J, Note 1). The dendrogram showed topographic co-occurrence between quantitative grab habitat 'Sandy Mud' (n=7) and qualitative video habitat 'Sand' (n=17) (Appendix M). These habitats were consolidated into the group 'Sandy Mud' (n=24). The dendrogram also showed topographic cooccurrence between quantitative grab habitat 'GMS' (n=17) and 'SwSB' (n=15) (Appendix M). Habitat 'SwSB' was mapped over 'GMS' and intersecting areas became habitat 'GMSwSB', whilst only 'GMS' locations remained their own habitat (Figure 2.15 & 2.16).





Figure 2. 13. Maximum likelihood classification of 'Sand with Small Boulders' using presence - absence (top), maximum likelihood classification with seven habitats (bottom).



Figure 2. 14. Final habitat map using a combination of the two maximum likelihood classifications. Inset (top): Habitat that overlapped with the cod spawning areas, Zone A and Zone B.

2.4.7 Habitat assessment

The final habitat map includes eight statistically distinct habitats (Figure 2.16). Fine grained habitats were spatially dominant; habitat 'Sandy Mud' represented 5.29km² of the 14.33km² extent. 'Coralline Boulders and Gravel' had the smallest extent with 0.02km² in one discrete location. The observed Smith Sound spawning areas, located within the fjord's inner basins, differed in dominant habitat parameters (Figure 2.16 - 2.17). Each basin was dominated by soft-bottomed sediments with gravelly transition zones at the margins, which met steep boulder walls between 50-100m. Optimal spawning habitat (Zone A) was dominated by the finest grained substrate, 'Sandy Mud' (89.76%), at the bottom of the deep basin with some elevated patches of other habitat types ('Large Boulders', 'Small Boulders', 'Gravel' and 'Sandy Gravel'; Figure 2.16). The sub-optimal habitat (Zone B) consisted predominantly of 'GMS' (69.19%) (GMS = 18.93%;



Figure 2. 15. Habitat composition by study and sub-study area.

GMSwSB = 50.26%) The transition zones of 'Sandy Gravel' occurred to the east, with 'Sandy Mud' and a raised 'Gravel' area to the west (Figure 2.16).

The habitat map had an 84.76% overall classification accuracy, with 128 of 151 correct classifications (Figure 2.17). The Kappa coefficient of the misclassification matrix resulted in an accuracy of 80.40%. Producer's Accuracy ranged between 25% and 100%, averaging 77.84%. Average Producer's Accuracy was higher for predominantly video sampled habitats ('Large Boulders', 'Small Boulders', 'CBaG', 'GMSwSB', 'Sandy Mud') (89.55%) than it was for grab sampled habitats ('Gravel', 'Sandy Gravel', 'GMS') (58.33%). User's Accuracy ranged between 66.67% and 100% with an average of 8.02%. Average User's Accuracy was higher for predominantly video sampled habitats (84.83%) than it was for grab sampled habitats (66.67%).

Habitat			Reference Data								Total	User's
			LB	SB	CBaG	G	SG	GMS	GMSwSB	SM	Total	Accuracy (%)
Classified Map	Large Boulders (LB)		40	2							42	95.24
	Small Boulders (SB)		4	12		1					17	70.59
	Coralline Boulders and Gravel (CBaG)				8						8	100
	Gravel (G)		1			2					3	66.67
	Sandy Gravel (SG)			1			2				3	66.67
	Gravelly Muddy Sand (GMS)						1	2			3	66.67
	GMS with Small Boulders (GMSwSB)		3			4	1		18	1	27	66.67
	Sandy Mud (SM)			3		1				44	48	91.67
	Total		48	18	8	8	3	2	18	45	∑128	
Producer's Accuracy (%)			83.33	66.67	100	25.00	50.00	100	100	97.78		∑151
<i>K</i> =	$= \frac{N \sum_{i=i}^{k} x_{ii} - \sum_{i=i}^{k} x_{ii}}{N^2 - \sum_{i=i}^{k} (x_i)}$	$K = \frac{151(128) - 5074}{151^2 - 5074}$					K = 0.8040					
Correctly Classified Values 128												
Available Reference Data 151												
Overall Accuracy 84.76%												
Kappa Coefficient (K) 80.40%												

Figure 2. 16. Misclassification matrix and accuracy assessment with Kappa equation for overall accuracy.

2.5 Discussion

This research aimed to identify and map benthic habitats found within part of Smith Sound, Newfoundland. The study has identified eight distinct habitats from the collected dataset and created a map of their distributions. Specific habitats coincided with the zones of cod aggregation during the time the Smith Sound aggregation utilised Smith Sound as a refuge. These habitats have been linked to the ecology of the Smith Sound aggregation using records of benthic species recovered from stomach content during refuge occupation.

2.5.1 Smith Sound habitat map

The high accuracy of the habitat classifications suggests that the map is a reliable representation of benthic habitats in the studied area. The accuracy results are comparable with nearby areas mapped using similar techniques (Copeland et al., 2006; Novaczek et al., 2017) and habitat maps produced using MLC (Brown et al., 2005). Fjords are not often the focus of habitat mapping work, and their distinct coastal characteristics may present unique challenges to accurately capture habitat distributions (i.e. steep sloping sides, shallow margins and sills, difficult sampling conditions) (Copeland et al., 2013). Increased current action toward the mouth of some fjords causes winnowing, whereby fine sediments are retained at the inner reaches and coarser grains are increasingly present with proximity to the mouth (Dale et al., 1989). To account for this phenomena, a variable 'Distance to Ocean' was introduced that was found to have a significant influence on habitat distributions with high relevance to the dataset (p<0.001) (Appendix K). This technique has previously been applied to rivers and estuaries and could be a

useful proxy for variables from the mouth to the end of a fjord (Stevens & Connolly, 2004; Capinha & Anastácio, 2011). The implementation of OLS regression to guide the MLC was successful overall, providing a stream-lined decision making tool for terrain selection. However, the OLS initially suggested the variables 'Easterness' and 'Northerness' for mapping, which despite their high statistical significance, were in practice found to decrease the map accuracy. This was potentially related to multibeam artefacts that have been shown to significantly impact the accuracy of habitat maps (Lecours et al., 2017b). The final selection of topographic variables explained 54% of the dataset variance, indicating that additional information may improve the model. The unexplained variance may be interpreted as missing topographic derivatives or other environmental variables such as, bottom temperature, light attenuation, etc. Alternatively, this explained low variance could result from low to medium 'within habitat' similarity (Appendix G).

Species accumulation curves suggest that enough of the survey area was sampled to conduct statistical analysis. However, there was disparity between sample quantities for video and grabs, a typical occurrence in this type of survey (Copeland et al., 2013; Novaczek et al., 2017). Equal weighting was allocated to the MLC to account for differences in sample sizes for each habitat type, assigning the cells to a category based upon the highest probability of habitat occurrence (Strahler, 1980). A dendrogram was used to link topographically similar grab and video habitats to prevent a habitat from being given two separate classifications. These new combined habitats were predicted with high accuracy (Appendix M), suggesting that the dendrogram was effective in mitigating this type of error.

2.5.2 Benthic habitats

I compared the main features and fauna of the Smith Sound habitats with other fjords in Atlantic Canada. Smith Sound habitats are similar to those previously recorded in Canadian arctic and sub-arctic fjords that share similar characteristics (i.e. single input, open sill) (Dale et al., 1989; Syvitski, 1989; Copeland et al., 2013) and others worldwide (Ekdale, 1984). The sediment grain size increases down-fjord and also changes within basins (Ekdale, 1984; Dale et al., 1989). The series of basins are separated by small sills composed of bedrock or moraines, with the deepest part of each basin harbouring muddy substrates.

Three distinct boulder habitats were revealed ('Large Boulders' (LB), 'Small Boulders' (SB) and 'Coralline Boulders and Gravel' (CBaG)), characterised by the presence of green urchin (*S. droebachiensis*). Abundance of urchins was highest in the depth limited, photogenic habitat 'CBaG', where the characterising coralline algae photosynthesise and urchins feed on kelp and other algae (Frey & Gagnon, 2016). Although 'Large Boulders' and 'Small Boulders' had similar communities, 'Large Boulders' had more vertical surfaces and the community was characterised by the presence of sponges (Porifera). These filter-feeders have been positively associated to depth, high velocity currents, high slopes, and hard-bottom topography (Bell & Barnes, 2000; Buzeta & Singh, 2008). Sponges act as baffles on water currents, increasing food supply to filter feeders such as Ophiuroidea (Konnecker, 2002). Clumps of *Nemertesia* hydroids and Echinodermata also demonstrate strong associations with sponge characterised boulder habitats (Lancaster et al., 2014). The structural complexity of 'Small Boulders' disrupts flow and offers more horizontal surfaces (Grabowski et al., 2012), which provide better attachment

opportunities for rugose anemones (H. nodosa) (Riemann-Zürneck, 1994). H. nodosa have been described as most abundant in patches of warmer water and fisheries regions, where they serve as prey for cod and dogfish (Calgren, 1933; Brown & Cheng, 1946). The habitat 'CBaG' remain an understudied high latitude habitat (Nelson 2009; Adey et al., 2013; Jørgensbye & Halfar, 2017). Photosynthetic coralline algae (Foster, 2001), require stable areas of moderate wave action, and an abundance of grazers (S. droebachiensis) to remove algal growth and epiphytes (Kamenos et al., 2004; Teichert et al., 2012). Studies have identified encrusting coralline algae habitats to have high biodiversity and species richness (Gagnon et al., 2012; Teichert et al., 2012). However, our study identified few organisms on 'CBaG', it is possible that the full community was not captured by the sampling method. 'CBaG' was only sampled using video, the quality of the video affects the sampling resolution, typically macrofauna can be identified and only to a low taxonomic resolution (Sameoto et al., 2008). The mottled, camouflaged surface of the 'CBaG' habitat is a feature that increases biodiversity and abundance but concurrently lowers identification success from video data (Sameoto et al., 2008). 'CBaG' habitat is indicative of rhodolith beds that are important to cod, providing nursery habitats for gadoids across the North Atlantic (Kamenos et al., 2004). These Corallinaceae habitats are widely distributed along the Newfoundland and Labrador coast (Gagnon et al., 2012), including in fjords such as Newman Sound (Copeland, 2006) and Gilbert Bay (Copeland et al., 2013). In Gilbert Bay, Corallinaceae habitats provide primary spawning habitat for Golden cod, a fjord dwelling, phenotypically distinct and reproductively isolated population of G. morhua (Copeland et al., 2013). More generally, the habitat provides complex nursery substrate for juvenile cod (Wroblewski et al., 2009).

'CBAG' habitat was not sampled during the fisheries acoustic surveys studies that were used to assess cod distribution in Smith Sound and indicate optimal and sub-optimal sites; therefore its cannot be ruled out as an influential habitat in Smith Sound.

Three gravel related habitats were identified in Smith Sound ('Gravel', 'Sandy Gravel' and 'Gravelly Muddy Sand' (GMS)). Gravel has been frequently identified as a structurally complex, highly biodiverse habitat that increases the survival of juvenile cod (Lough & Trites, 1989; Lough, 2010). The community composition reflected benthic macrofauna (the 'Onuphid association') described from the Baffin Island fjords, Cambridge, McBeth, and Itirbilung (Syvitski, 1989; Aitken & Fournier, 1993). Typically, the 'Onuphid association' occurs on gravel over soft-ground substrates, and the primary characteristic is an abundance of Nothria conchylega (Aitken & Fournier, 1993). Other 'Onuphid association' organisms found in Smith Sounds 'Gravel' habitat include; Lumbrineridae, Nuculanidae, Ophiuroidea (Ophiura robusta), and Nephtyidae (Aitken & Fournier, 1993). The 'Sandy Gravel' and 'GMS' habitats better reflect the 'Onuphid association', also characterised by Maldanidae polychaetes and Yoldia bivalves (Aitken & Fournier, 1993; Syvitski, 1989). The 'Sandy Gravel' community harboured an abundance of Chaetopteridae (Polychaete), a family that was not included in the 'Onuphid association'. The four predominantly fine-grained (or soft-ground) habitats identified in Smith Sound are 'Gravelly Muddy Sand' (GMS), 'Sand with Small Boulders' (SwSB), 'Sand' and 'Sandy Mud'. 'GMS' reflected the 'Onuphid association' with an abundance of characterising polychaetes (Lumbrineridae, Spionidae, Maldanidae, Nephtyidae, and Onuphidae), and Bivalves (Nuculana, Astarte, and Yoldia) (Syvitski, 1989; Aitken & Fournier, 1993).

'SwSB' was identified from video on a fine-grained bottom type, indicated by the dendrogram analysis to be 'GMS'. The habitat consists of independent boulders at the bottom of the sloped boulder wall. This habitat was only observed in the outer basin. 'SwSB', and therefore 'GMSwSB' are characterised by H. nodosa, Pandalus spp., and Euphausiids. Previous studies have found *H. nodosa* to be associated with Ophiuroidea, findings that are consistent with the results of this study (Riemann-Zürneck, 1994). H. nodosa, are typically observed attached to hard substrates, even when located on seafloor that appears to be a sandy bottom (Riemann-Zürneck, 1994). The presence of H. nodosa on 'Sandy Mud' indicates to a hard attachment surface, most likely a boulder buried in soft-ground. This phenomenon occurred at the transition zones between 'Sandy Mud' and 'GMSwSB' habitat. Subsequently, this indicates a more stable habitat where the effects of flowing water could be lessened, possibly contributing to the preference of the inner basin for cod overwintering and spawning (Rose et al., 2010). The communities in 'Sandy Mud' resemble the 'Onuphid association' but the community composition indicates that the habitat is spatially transitioning into a 'Maldanid association': whereby Nuculana disappear, Maldanidae abundance increases and Periploma papyratium is introduced in low abundance (Syvitski, 1989; Aitken & Fournier, 1993).

2.5.3 Refuge habitat for cod survival (1995-2007)

Habitat is considered to play a pivotal role in ecological life histories of fish populations and therefore recovery (Levin & Stunz, 2005). Refuge habitats must be ecologically relevant to the refuge species, supplying shelter and sustenance that ensure survival, until the potential for reproduction, recruitment and growth is realised (Keppel et al., 2012).

The hyperaggregation of northern cod in the Bonavista Corridor occurred when stock biomass was very low. It has been hypothesised that hyperaggregation decreases the need for individual anti-predation vigilance, reducing stress and allowing more time for foraging (Lima, 1998). Decreasing occupied space and increasing biomass allows stressed populations to reduce vigilance, and increase time spent foraging (Lima, 1998); increased foraging time could have been imperative to the survival of the northern cod stock during this time of reduced availability of their primary food source, capelin (Mullowney & Rose, 2014).

The topographic characteristics of the Smith Sound fjord may have contributed to overall shelter from predation, potentially a behavioural alternative to hyperaggregation (Lima, 1998). Smith Sound offered deep, high slope habitats that mimic those observed being used for offshore overwintering by components of the northern cod stock (Rose et al., 2010). The structures provided by some of the habitats have been identified as being significant to cod at multiple life stages. Juvenile survival is a function of camouflage and predator avoidance on mottled or complex surfaces (Lough & Trites, 1989; Tupper & Boutilier, 1995; Lough, 2010). Habitats that have been linked to juvenile survival and have mottled complex surfaces include boulders, macroalgae, rhodolith beds, seagrass, and gravel (Lough & Trites, 1989; Tupper & Boutilier, 1995; Lough, 2010). Associated organisms can further decrease mortality, this was demonstrated in a study where cod survival rates increased in conjunction with increased sponge density on cobbles (Lindholm et al., 1999); this community composition shares attributes of the 'Large Boulder' habitat identified in Smith Sound. Additionally, boulder habitats have demonstrated their importance to resident and transient cod in offshore environments,

providing complex structures for spawning and foraging on an otherwise homogenous seafloor (Lindholm et al., 2007). Multiple studies have demonstrated the importance of structurally complex habitats for sub-adult cod (2-3 years) that actively select boulders, with or without macroalgae and establish residencies less than 10ha (Tupper & Boutilier, 1995; Côte et al., 2003; Lindholm et al., 2007). It has also been demonstrated that the transitional zones between habitats attract higher fish biomass and biodiversity than surrounding habitats (Wiens, 1976; Ries et al., 2004). In other studies, the transition area between boulder and sand habitat were characterised by higher fish density (Grabowski et al., 2012). These habitats in Smith Sound would include habitats 'Gravel' and 'GMSwSB'.

2.5.4 Cod – benthos associations

Benthic habitats must provide sustenance adequate for survival, growth and eventually fecundity to make it a successful refuge. Habitat used for foraging is not always synonymous with that used for shelter, and even resident fish conduct short transient foraging trips Nutritional deficiencies are considered the main source of reproductive stress and the key limiting factor in cod growth, additionally inhibiting stock recovery (Levin & Stunz, 2005; Mello & Rose, 2005; Mullowney & Rose, 2014). Due to the lack of primary food source capelin benthic organisms contributed a larger proportion of the post-collapse diet of cod (Mullowney & Rose, 2014). Heterogeneity of bottom types is linked to high biodiversity and can provide an abundance of forage species (Sherwood & Grabowski, 2015). This response has been exemplified by increased biodiversity in areas

closed to fisheries, and subsequently increased cod abundance and health (Sherwood & Grabowski, 2015).

Examining past stomach content records of the Smith Sound aggregation between 1995 and 2007 reinforces the ecological relevance of the benthic species and habitats delineated in this study (Figure 2.11). Smith Sound cod have been shown to have a higher proportion of benthic fauna in their stomach contents than fish from the Bonavista Corridor (Krumsick & Rose, 2012). Crustacea contributed a high proportion to Smith Sound aggregation diets, including (in order of contribution; Amphipoda (incl. Gammaroidea and Hyperiidea), Mysida, Euphausia, Pandalus spp. and snow crab (*Chionoecetes opilio*) (Figure 2.11). Amphipoda can have a range of feeding strategies. Gammaroidea (Amphipoda) were sampled from Smith Sounds 'GMS' and 'Sandy Mud' communities, reflecting findings (mud/silt) in fjords like Conception Bay of southeast Newfoundland (Parrish et al., 2009) Such habitat associations suggest that these Amphipoda have a scavenger or detritivore feeding strategy (Parrish et al., 2009). Hyperiidea have parasitic adult stages, commonly associated with temporary occupation of gelatinous zooplankton (Fleming et al., 2014). Jellyfish, Cyanea capillata and Scyphozoans, are abundant in Newfoundland waters and Smith Sound during the summer months. As a predominently closed embayment, Smith Sound has high retention potential and can capture high proportions of these planktonic organisms, subsequently providing a large supply of *Hyperriidae* to the Smith Sound aggregation. Euphausiids (Meganyctiphanes norvegica) are a dietary component for juvenile cod despite their low lipid content, particularly in fjords (Dalpadado & Bogstad, 2004; Jónsdóttir et al., 2012).

These epibenthic organisms conduct diurnal migrations to avoid predation, occurring -

100m in fjords during the day and moving through the water column to the surface at night (Onsrud & Kaartvedt, 1998). The sloped fjord walls of Smith Sound could provide an excellent foraging surface for cod during Euphausiid night migrations, whilst the 'Sandy Mud' habitat could provide daytime protection from predators. Snow crab (*Chionoecetes opilio*) and *Pandalus spp.* were identified as the top benthic replacers for capelin across the northern cod stock range (Mullowney & Rose, 2014). Pandalus spp. are dominant in the diet of inshore cod and have been recorded making seasonal migrations into fjords replenishing the local populations (Jónsdóttir et al., 2012). Preferred habitat is considered to be in deep basins with temperatures ranging from 1-6°C, occurring regularly on the Newfoundland Shelf, reducing the need for migrations that commonly occur in nordic fjords (Koeller, 2000). Pandalus spp. is present on 'Sand with Small Boulders', 'Sand', 'Small Boulders', and 'Large Boulders'. They were commonly associated with Actiniaria and Porifera, found on structurally complex features. Snow crab, the largest of the Crustacea sampled from Smith Sound, traditionally supported a strong fishery in Smith Sound that rapidly declined after arrival of the Smith Sound aggregation (Rose et al., 2010). Distributions are related to temperature and depth, with optimal habitat occurring in deepwater >60m on gravelly mud, sand and most preferably mud bottoms (Klemetsen, 1982; Robichaud et al., 1989; Lovrich et al., 1995). Seasonal migrations occur from depth to shallow waters, up and down boulder slopes (Lovrich et al., 1995).

The second largest dietary contributor were Polychaete marine worms categorised under the Phylum Annelida. Polychaetes become a dietary component for cod at >7cm length (Lough, 2010) and are identified as a significant contributor across the Atlantic and in fjords (Klemetsen, 1982; Enoksen, 2015). Most frequently found within Smith Sound were families: Onuphidae (*N. conchylega*), Chaetopteridae, Lumbrineridae, Spionidae, Serpulidae, Pectinariidae, Glyceridae, Maldanidae, Nephtyidae, and Opheliidae. Enoksen (2015) examined the stomach content of cod in two Norwegian fjords, where polychaetes contributed a large proportion, including Glyceridae, Onuphidae, Opheliidae, Serpulidae. Klemetsen (1982) found that Polynoidae, Nephtyidae, Lumbrineridae, Maldanidae and Pectinariidae contribute to the diet of fjord cod. Quijón & Snelgrove (2005) completed a comprehensive review of polychaete distributions and habitat associations for the east Canadian coastline. The habitat associations of Smith Sound polychaetes were consistent with the Quijón & Snelgrove (2005) study, Lumbrineridae, Glyceridae, Pectinariidae were sampled from sandy habitats, whilst, Maldanidae and Opheliidae increased on muddier substrates (Quijón & Snelgrove, 2005). However, patterns were less clear for Spionidae, Pectinariidae and Nephtyidae due to their distribution across sand and mud substrates (Quijón & Snelgrove, 2005).

Other important benthic contributors include Ophiuroidea (Klemetsen, 1982). Ophiuroidea are commonly associated with other organisms and occur across a range of habitat types, but are most abundant in rhodolith beds and 'CBaG', 'Gravel', 'Large Boulders' and 'Small Boulders'. Actiniaria were present as *H. nodosa* on 'Large Boulders', 'Small Boulders' and transition zones such as 'GMSwSB', which supply more horizontal attachment surfaces (Riemann-Zürneck, 1994). Actiniaria are known to be prey for cod (Calgren, 1933; Brown & Cheng, 1946) and though considered an unconventional dietary component have been shown to be an organism with high nutritional value (Lippert & Iken, 2003). Bivalve Myidae (*Mya arenaria*) occurs across a range of habitats

on the eastern Canada coastline but are predominantly associated with sand and mud habitats (St-Onge & Miron, 2007). However, in Smith Sound, they were sampled in low abundance from 'Sandy Gravel' habitat (St-Onge & Miron, 2007). This atypical habitat association could be explained by more effective, rapid sampling avoidance of Mya in sand and mud habitats.

2.5.5 Habitat influence on spawning

Habitat and substrate are considered to be a primary considerations in the reproductive activities of fish, contributing to reproductive output and success (Robichaud & Rose, 2001; Skjæraasen et al., 2011). There is indication of this spawning behaviour occurring in Gilbert Bay and Smith Sound, whereby optimal and sub-optimal spawning areas exist, consisting of different substrates (Rose et al., 2010; Copeland et al., 2013; Personal communications with George Rose, 2014). Optimal habitats exist in the inner basins where water movement is reduced. In Gilbert Bay, Labrador, the optimal substrate was complex rhodolith beds with high egg capture, supporting the endemic ecology of the population (Morris & Green, 2002; Copeland et al., 2013). In Smith Sound, spawning habitats (personal communications with George Rose, 2014), were predominantly finegrained: the optimal habitat was mostly 'Sandy Mud', and sub-optimal mostly 'GMS' and 'GMSwSB'. The optimal habitat was flanked by elevated 'Small Boulder' and 'Gravel', whereas sub-optimal was flanked by less structurally complex 'Large Boulders'. These topographies reflect other spawning habitats identified at finer scales (Dean et al., 2014). Offshore spawning areas and other inshore have been described as boulder reefs and sloped features (Morgan & Trippel, 1996; Brattey & Healey, 2003; Lindholm et al.,

2007). Inshore Newfoundland spawning locations include Bar Haven, among several shoals and islets, the topography and sediments have not been identified (Lawson & Rose, 2000). The sexually segregated spawning behaviours of cod include an identified difference in habitat use across a spawning area. Fine-scale habitat use through multi-year acoustic tracking of spawning individuals found males to aggregate in soft-ground seafloor impressions, while females utilise elevated coarse habitats including boulders and gravel (Dean et al., 2014). These findings were consistent with laboratory behaviours where females remained on separate peripheral habitats to the male spawning territories until courting began (Brawn, 1961; Hutchings et al., 1999).

The initial motivation for refuge in Smith Sound whilst other similar, nearby water ways remained uninhabited remains unclear. It is possible that the reason to refuge in Smith Sound related to the bathymetry or temperature of the environment, rather than the biology or substrate of benthic habitats that were focussed upon in this study. Despite this ambiguity, the Smith Sound aggregation were able to persist in the fjord experiencing retention and growth, a reduction in Smith Sound numbers was con-current with offshore increases, suggesting that fish had returned to more historical behavioural patterns. All of these attributes point to the use of a refuge and successful re-establishment suggests that Smith Sound performed refuge services. The Smith Sound Atlantic cod refuge offers a heterogeneous environment with a range of habitat types that resembles the benthic habitat associations typically found in sub-arctic and arctic Canadian fjords. The habitats offer shelter and dietary requirements that were consistent with previous studies of cod habitat preferences throughout different stages of life history, supporting juveniles to spawning adults. Habitats supported a wealth of dietary organisms that cod have been

shown to utilise when their primary dietary component, capelin, is reduced. The fjord structure in terms of topography, sediment distribution and biology of Smith Sound suggests that fjords that share similar topographic features could offer suitable locations for cod activity. The methods used in this study may aid the expansion of habitat mapping applications into these atypical coastal environments to further develop marine coastal management and the continued application of ecosystem-based management.

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CHAPTER 3: CONCLUSION

3.1 Overview

This research identified and mapped benthic habitats in Smith Sound, a fjord that has proved ecologically important as a refuge for Atlantic cod. Research on the Smith Sound aggregation sampled locations of aggregation and spawning. Due to the good health, fecundity, retention, and growth recorded for the Smith Sound aggregation, Smith Sound has been considered a key rebuilding point for the northern cod stock (Rose et al., 2010). Habitats used for key life processes, particularly spawning, are considered the most critical for the recovery of many stocks (Mangel, 2000; Levin & Stunz, 2005). Although the reason for cod occupation in Smith Sound over other similar waterways remains unclear, the mechanisms of persistence provide an important aspect of refuge ecology (Keppel et al., 2012; Davis et al., 2013). Although the reason for initial cod occupation in Smith Sound may have been independent from benthic habitat choice (e.g. temperature), the ability to persist in Smith Sound until the opportunity for recruitment is realised indicated that the benthic habitat may have provided the essential ecosystem services of a successful refuge (Keppel et al., 2012; Davis et al., 2013). The research presented in this thesis was undertaken to explore the benthic habitats that could have contributed to the refuge role of Smith Sound and therefore toward the recovery of the northern cod stock, as these spawning and refuge grounds provided suitable conditions for retention and growth during 1995 to 2007 (Rose et al., 2010).

The goal of this research was to identify Smith Sound benthic habitats, map their distributions, and discuss their potential role in cod ecology. Multivariate statistics were

used to categorise discrete seafloor samples (grab and video) into habitat types. Ordinary least square (OLS) regressions, in the form of Exploratory Regressions (ER), were used to identify a selection of mapping variables for the local area. A maximum likelihood classification (MLC) was used to assess the spatial distribution of the habitats in the study area.

3.2 Research questions

The thesis answered three research questions:

- 1. What benthic habitats exist in Smith Sound and what are their distributions?
- 2. What habitats coincide with the zones of cod aggregation and spawning?

3. How does cod stomach content relate to benthic species found in Smith Sound? These research questions were examined at five different levels of observation; 1) habitat classifications, 2) MLC distributions, 3) accuracy assessment as a misclassification matrix, 4) review of cod stomach content (1995-2007), and 5) examination of literature.

3.2.1 Benthic habitats of Smith Sound

The first question, "What benthic habitats exist in Smith Sound, and what are their distributions?" was answered using field data collection, analysis of samples and a multivariate analysis approach. Habitats were described from video and grab, ANOSIM and SIMPER were then used to group samples into habitat types based on sediments and community composition. A dendrogram of topographic occurrence was used to link any video and grabs. The habitat distributions were then determined using a MLC, a method chosen for its ease of use and for being widely regarded as a satisfactory approach for habitat mapping (Brown et al., 2005). The resulting map was assessed for reliability using an accuracy assessment in the form of a misclassification matrix (Congalton, 1991; Congalton & Green, 2003).

At least eight statistically distinct benthic habitats exist in Smith Sound: 'Large Boulders', 'Small Boulders', 'Coralline Boulders and Gravel', 'Gravel', 'Sandy Gravel', 'Gravelly Muddy Sand', 'Gravelly Muddy Sand with Small Boulders' and 'Sandy Mud'. The description and distribution of these habitats can be found in Section 2.4.6 and in Figure 2.10. The misclassification matrix used to assess the accuracy of the habitat map, gave an overall accuracy of 84.76% and Kappa accuracy of 80.40%, determining that the distributions are reliable. Additionally the measurable area of occupied space can be observed in Figure 2.11.

The habitat data provided excellent coverage of the research extent and speciesaccumulation-curves determined the dataset to be complete enough to reliably represent the local habitats. The ER and OLS examined a wide range of terrain derivatives that

could have been applied to the dataset and chose a selection that was most relevant preventing the use of collinear terrain derivatives. The OLS determined the final model to be appropriate for the habitat data and to meet relevant criteria of a passing regression model. The accuracy assessment determines that the mapped distributions have a high accuracy and therefore that the map can be trusted as a realistic representation of the habitat distributions. The interpretation should be straightforward, but considerations of overall map use apply.

3.2.2 Cod aggregation and spawning habitat

The second question "What habitats coincide with the zones of cod aggregation and spawning?" was answered using two subsections of the classified MLC and descriptive statistics. Two zones were identified as the areas of the fjord that were most typically occupied by cod through the 1995 to 2007 period of occupation and used for spawning (personal communication: George Rose, 2014). Zone A was described as the primary area of spawning activity and Zone B the secondary one, thus Zone A was considered optimal habitat and Zone B sub-optimal for discussion purposes. The habitat coverages in each subsection were quantified (m²) and their contribution compared to each other and the overall allotted habitat areas (km²) of the MLC (Figure 2.11).

The main conclusions were that the two zones overlapped with predominantly softbottomed benthic habitats, 'Sandy Mud' for Zone A (89.76%) and 'GMS' for Zone B (69.19%) (GMS = 18.93%; GMSwSB = 50.26%). Collection of additional data on cod activity within Smith Sound being beyond the scope of this study, using expert knowledge from Dr. George Rose helped providing useful information. Descriptive
statistics was used to measure the extent of contributing habitats, this method was appropriate for the information available. The map presented is at a scale ecologically relevant to cod, as the 5 m² mapping resolution is within the reported horizontal range of male Atlantic cod spawning territories (Hutchings, 1999) and annual spawning returns of female cod (Dean et al., 2014).

Habitat maps use discrete samples to identify patterns and make broader environmental inferences. It is therefore an accepted practice that maps should be interpreted with caution and would always benefit from additional testing and adaptive management (Day, 2008; Lecours et al., 2017a). There are differences in the habitats at both locations but as stated above they should be treated as optimal and sub-optimal sites. The sites were selected based on the expert knowledge of Dr. George Rose in reference to two decades of research on fisheries acoustics and population dynamics of the Smith Sound aggregation. Site A was considered optimal as it constituted the bulk of cod activity in early surveys of aggregation activity. Site B was considered optimal as it became the secondary area of concentrated activity as the fish biomass grew.

3.2.3 Cod stomach content and prey of Smith Sound

The third question "How does cod stomach content relate to benthic species found in Smith Sound?" was answered through the cross-examination of past stomach content data with the organisms sampled from Smith Sound, to identify the benthic organisms that contributed to nutrition during occupation. The main conclusions relate to the stomach content analysis of the Smith Sound aggregation between 1995 and 2007. The results demonstrated that the cod preyed upon a large proportion of the benthic fauna identified in Smith Sound during this research. Organisms found in the stomach contents could be sampled across all the habitat types. This attribute of Smith Sound may have contributed to the locations ability to support the large and growing biomass of cod for such an extensive time.

Using past stomach content of the Smith Sound aggregation was appropriate for examining ecological links between the habitats and cod. The review did not discriminate between cod, age, size, sex, or year. Each organism recorded during the stomach content study was also recorded at varying levels of taxonomic resolution. This can in part be attributed to the large participatory base of researchers of the Chair in Fisheries Conservation, fisheries monitoring programme. The validity of the links highlighted through this study must be interpreted with caution, but can also be used to shape more temporally relevant further research.

3.3 Summary of main results

Smith Sound provides diverse habitats, all with community compositions, topography and substrates that can be linked to cod in a way that is ecologically important. Results identify habitats of Smith Sound that may have contributed to a favourable environment for shelter, sustenance and spawning, activities that support recruitment and growth from a successful refuge environment. More specific results include:

- At least eight benthic habitats exist in Smith Sound, Newfoundland: 'Large Boulders', 'Small Boulders', 'Coralline Boulders and Gravel', 'Gravel', 'Sandy Gravel', 'Gravelly Muddy Sand' (GMS), 'GMS with Small Boulders' and 'Sandy Mud'.
- 2. The habitat map produced has a high accuracy (overall accuracy of 86.74% and Kappa accuracy of 80.40%).
- 3. The deep areas that harboured the largest aggregations of cod and were used for spawning (1995-2007) were dominated by soft-bottom habitat and were bordered by areas of coarser substrate. Zone A was characterised by 'Sandy Mud', 'Small Boulders' and 'Gravel' habitats. Zone B was characterised by 'Gravelly Muddy Sand with Small Boulders', 'Gravelly Muddy Sand' and 'Sandy Gravel' habitats.
- 4. All habitats in Smith Sound had contributing organisms that were linked to cod diet of the Smith Sound aggregation between 1995 and 2007.

3.4 General considerations

It must be acknowledged that interpretation of remotely sensed distribution maps contain errors introduced from a number of sources (GPS inaccuracies, cumulative calculation offsets, human error etc.) (Congalton & Green, 1993). Habitat mapping can yield vastly dissimilar results depending on the algorithms, variables and collected datasets involved (Lecours et al., 2017). In this study an OLS guided MLC allowed a large set of variables to be swiftly and fully examined in every combination. Several benefits of the process were observed. The method efficiently identified relationship metrics between topographic variables and the habitat data. This enabled the selection of topographic variables that contributed to a correctly specified OLS model. The process is repeatable yet flexible enough to be applied in other study areas, or to other datasets that may require different topographic variables; allowing researchers to identify relevant changes whilst maintaining a consistent methodology. Another advantage is the ability to complete every stage of classifying the multibeam in a single programme (ArcGIS v10.3). This becomes increasingly relevant with maps being produced by non-mapping experts (e.g. ecologists, biologists) (Lecours et al., 2017), who could benefit from a simplified and more linear approach. The selection of variables for mapping Smith Sound were also moderately streamlined for non-expert use. The Terrain Attributes Selection for Spatial Ecology extension (TASSE) is a user friendly tool, designed for non-experts to generate the most applicable topographic surfaces for marine habitat mapping (Lecours et al., 2017). It is always possible for habitats to be over- or under-represented, particularly if subject to differences in sampling resolution and effort. During MLC modelling, equal weighting

was given to all habitat samples to mitigate the correlation between data abundance and overall mapped representation. It is likely that 'Gravel' has been over-represented as the available sample data for mapping was low, the predicted area of occurrence across the thematic map was extensive with a diverse distribution and the accuracy assessment yielded a low result. This demonstrates that additional sampling would strengthen the topographic associations of the habitat and clarify distribution. 'CBaG' has been underrepresented across the fjord area, it was only found in one discrete location. Multibeam sampling excluded shallower locations that would include this habitat restricted to the photic zone. Additionally, Corallinaceae habitats of CBaG and rhodolith beds have been extensively observed within the study area by the author outside of sampling. The method used in this research, of combining video and grab samples into a single habitat type, is unconventional due to the difficulties in combining data of different sampling resolutions. This innovative method was successfully implemented to ensure the best use of both datasets. However, the misclassification matrix of the MLC yielded high accuracies under these categories, suggesting that the method of joining them was suitable. The misclassification matrix revealed a lower accuracy for the "grab only" habitats, and was greater for habitats using video data. This can be explained by the lower sampling resolution for video, as taxa identification is limited to macrofauna the delineated community compositions are less diverse and complex, strengthening 'within habitat similarity' and resulting in higher accuracy during classification. Additionally the increased sampling effort for video described habitats (continuous transects) strengthens the topographic profiles for the habitat type, again improving predictive power during the classification process. Incorrectly plotted test samples may be victim of an edge effect, a

phenomenon associated with the classification of a continuous raster and fuzzy borders between habitat transition zones. This means that the accuracy of the map can in reality be higher or lower than is observed by the accuracy assessment. Interpretation of modelled systems should always be conducted with these considerations in mind. Many challenges were encountered during this study, explicitly sampling challenges and methodological adaptation. Though the area had relatively small tides (average 1-2m), active undercurrents were observed in the waterway during AUV surveying and ground truthing. These effects were particularly noticeable and disruptive during daily ebbing and flooding, particularly in the outer basin and central channels. The use of an AUV to collect multibeam data has many benefits, including the ability to collect data at a constant resolution on slopes. The dynamic water conditions coupled with the high sloped features induced the AUVs fail-safe mechanisms. This is a possible indication that dynamic waters within open fjords can be challenging when using AUVs, compared to environments with more stable waters. The water movements also had an effect on ground-truthing. Grabs deployed in the Petley Trench (Zone B) and the eastern end of the fjord, closer to open ocean, had a higher fail rate. Undercurrents would either displace the grab, or surface currents would quickly displace the boat, sometimes triggering the release mechanism before bottom contact. These effects caused sampling inefficiencies, gaps, and introduced larger positional errors. Positional error would most likely effect video samples in this instance due to the increased angle between the surface recorded GPS and the seafloor recorded camera system as the two were not linked through position correcting hardware such as an ultra-short baseline receiver. Grabs are less of a concern as sampling would likely fail in the case that the cable angle extended beyond the 5m

resolution of the bathymetric grid. This can be mitigated through strategic sampling plans, ensuring that the more dynamic parts of the fjord are sampled close to monthly neap tides and around daily slack tides.

Video sampling was an additional challenge. It is desirable to use video and grab at each sample site, but for this research that goal was unobtainable. Tool availability impacted the sampling strategies. Deploying the camera in deep waters was unsuccessful as the undercurrents prevented the camera from reaching the seafloor, even with additional weights. The solution was to deploy the camera in shallow areas, and allow it to drift out to deeper waters, maintaining contact with the seafloor. To make this an efficient method, considerably longer transects were completed. This made it difficult to coordinate a crossover with grabbed sites and increased the spatial auto-correlation of samples. It also meant that a single habitat could be represented through both grab and video sampling. This would negatively affect the predictive capability of the MLC and produce lower accuracy thematic habitat maps. To mitigate the possibility of representing a single habitat twice (through grab and video), a dendrogram was used to combine habitats sampled under both tools. This method was an innovative novel approach at using all the community composition samples without reducing predictive accuracy from confounding variables. Sediment transport in the fjord resulted in substrate of a finer particulate within the inner reaches of the fjord while outer reaches harbour coarser sediment types (Dale et al., 1989). The sediment distribution is due to increased oceanographic activity at the mouth of the fjord, and is a phenomenon common in rivers, fjords and estuaries (Stevens & Connolly, 2004; Capinha & Anastácio, 2011). This phenomenon was not captured by the other variables used for mapping, this negatively affected the accuracy of preliminary

habitat maps being produced. In response the variable Distance to Ocean (DTO) was created that acted as a proxy for the changing oceanography and thus the change in sediment coarseness. The implementation of this variable greatly improved the accuracy throughout habitat mapping and according to OLS regression, constituted a useful terrain derivative in the production of a final habitat map.

3.5 Applications and further research

The results presented in this thesis should present useful data for researchers. Habitat maps can be used across diverse applications, ranging from scientific to commercial (Diaz et al., 2004; Brown et al., 2011). In particular, habitat maps play an important role in ecosystem-based management and ecosystem-based fisheries management (Cogan et al., 2009). Both of these management strategies place habitat maps as a key foundational piece for the building of policy and strategies (Cogan et al., 2009). These management strategies are being established for the Newfoundland and Labrador Ecoregion, as part of a wider scheme in Canada to implement Large Ocean Management Areas (LOMA) (DFO, 2012). Under the Newfoundland and Labrador Ecoregion, Smith Sound has the status of a 'moderate' priority 'Ecologically and Biologically Significant Area' (Park et al., 2011), requiring a habitat map as a first stage of implementation (DFO, 2012). The habitat map produced in this thesis could set a preliminary guide for this process. This map could be used to revisit previous observations within Smith Sound, from the already established diverse bibliography.

Despite the overall high accuracy of the map presented in the thesis standard interpretation practices should be considered. Any thematic map being applied to support

decisions should undergo adaptive management based on continued testing and monitoring (Day, 2008). This includes additional testing of the final habitat map, particularly for any habitat categories that had small sample sizes or low accuracy. The results of the misclassification matrix highlights points of weakness in the map that could be investigated and enhanced through further data collection. Care should also be taken when interpreting fuzzy borders between habitat categories. If future research were to address the limitations of this study, it would first be advisable to increase the multibeam extent used for mapping. The areas indicated as important to cod in this study were subject to bias as they are based on fisheries acoustic observations that maintained a relatively consistent search pattern in deep waters (Rose, 2000). This pattern excluded the shallower areas of Smith Sound, areas more likely to be important to juvenile cod (Tupper & Boutilier, 1995), a key demographic in stock rebuilding of marine fish (Levin & Stunz, 2005). Gaining knowledge of these habitats and their influence on progeny survival can further indicate the role of Smith Sound in cod recruitment and recovery. Alternatively, as the maps have been produced to an ecological scale relevant to cod, it could be beneficial to conduct tagging investigations on fine-scale habitat use. In addition, subsequent ground-truthing could be used to complete *in situ* application of the produced maps, particularly in habitat zones that tested for low accuracy, and across habitat transition zones.

The reason for initial cod entry into Smith Sound instead of other similar nearby waterways remains unclear. However, the well documented ability of Smith Sound to contain large quantities of healthy spawning biomass that experienced local retention and growth supplies the evidence that the fjord could have performed refuge services (Rose et

al., 2010). A refuge environment ensures the persistence, growth and reproductive potential for a refuge species (Keppel et al 2012; Davis et al., 2013). These qualities of a refuge are consistently recognised as linked to habitat, specifically benthic habitats in the marine environment and for demersal fish such as cod. However habitats may not be the only factor that contribute to the required environmental parameters of a cod refuge. The research presented in this study identified benthic habitats of Smith Sound, an area where cod followed patterns of refuging behaviour. The results were used to confer ecological links between the findings and the refuge species, furthering the ecological knowledge of this refuge location.

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APPENDICES

Appendix A: Summary of collected grab samples. Sample ID, longitude, latitude, GRADISTAT and habitat categories (n=105).

Sample ID	Longitude	Latitude	GRADISTAT category	Habitat category
1	48.15162	-53.69044	Gravel	Gravel
2	48.15192	-53.69151	Gravel	Gravel
3	48.15106	-53.69553	N/A (Hard bottom)	N/A
4a	48.15205	-53.69744	N/A (Hard bottom)	N/A
4b	48.15213	-53.69736	N/A (Hard bottom)	N/A
5	48.15464	-53.69379	Muddy Sand	Gravelly Muddy Sand
6	48.15203	-53.70301	Sandy Mud	Sandy Mud
7	48.15380	-53.72284	Gravel	Gravel
8	48.15619	-53.72190	Sandy Mud	Sandy Mud
9	48.15780	-53.71940	Sandy Mud	Sandy Mud
10	48.15728	-53.71721	Sandy Mud	Sandy Mud
11a	48.15757	-53.73526	N/A (Hard bottom)	N/A
11b	48.15728	-53.73407	Gravel	Gravel
12a	48.15929	-53.73686	N/A (Hard bottom)	N/A
12b	48.15911	-53.73724	Gravel	Gravel
13	48.15433	-53.70866	Sandy Mud	Sandy Mud
14	48.15428	-53.71444	Sandy Mud	Sandy Mud
15	48.15913	-53.71218	Gravel	Gravel
16	48.16062	-53.71019	Gravel	Gravel
18	48.16262	-53.70714	Sandy Mud	Sandy Mud
19	48.15985	-53.70459	Gravel	Gravel
20	48.15660	-53.70234	Sandy Mud	Sandy Mud
21c	48.15627	-53.70155	Sandy Mud	Sandy Mud
22	48.16058	-53.69806	Sandy Mud	Sandy Mud

24	48.16251	-53.69173	Gravel	Gravel
25	48.16355	-53.68938	Gravel	Gravel
26	48.15955	-53.68656	Muddy Sand	Gravelly Muddy Sand
27	48.15842	-53.68973	Sandy Mud	Sandy Mud
28	48.15620	-53.69184	Sandy Mud	Sandy Mud
29	48.15621	-53.69527	Gravelly Sand	Gravelly Muddy Sand
30	48.16757	-53.67533	Gravelly Sand	Gravelly Muddy Sand
33	48.16431	-53.66165	Gravelly Sand	Gravelly Muddy Sand
34	48.16434	-53.65836	Sandy Gravel	Sandy Gravel
35	48.16156	-53.67304	Muddy Sand	Gravelly Muddy Sand
36a	48.15903	-53.67216	N/A (Hard bottom)	N/A
36b	48.15926	-53.67252	N/A (Hard bottom)	N/A
40	48.16150	-53.73158	Sandy Mud	Sandy Mud
41	48.17008	-53.65614	Gravel	Gravel
42	48.16168	-53.72152	Sandy Mud	Sandy Mud
43	48.18171	-53.62492	N/A (Hard bottom)	N/A
44	48.18004	-53.62300	Sandy Gravel	Sandy Gravel
45	48.16399	-53.69343	Sandy Gravel	Sandy Gravel
46	48.18055	-53.60906	Gravelly Sand	Gravelly Muddy Sand
48	48.16390	-53.69891	Sandy Mud	Sandy Mud
49	48.16941	-53.64385	Gravel	Gravel
50a	48.17249	-53.64130	Sandy Gravel	Sandy Gravel
51	48.15837	-53.68975	Sandy Mud	Sandy Mud
59	48.17202	-53.63778	Sandy Gravel	Sandy Gravel
61	48.17321	-53.63407	Sandy Gravel	Sandy Gravel
62	48.17571	-53.63366	Muddy Sand	Gravelly Muddy Sand
63	48.17630	-53.63042	Gravelly Sand	Gravelly Muddy Sand
64	48.18055	-53.62678	N/A (Hard bottom)	N/A
65	48.17901	-53.62637	Sandy Gravel	Sandy Gravel

67	48.17950	-53.61876	Sandy Gravel	Sandy Gravel
68	48.18349	-53.61447	Sandy Gravel	Sandy Gravel
69	48.18599	-53.61104	N/A (Hard bottom)	N/A
70	48.18908	-53.60497	Sandy Gravel	Sandy Gravel
71	48.18357	-53.60818	Sandy Gravel	Sandy Gravel
80	48.19212	-53.59729	Sandy Gravel	Sandy Gravel
81	48.19510	-53.58669	N/A (Hard bottom)	N/A
82	48.19632	-53.58443	N/A (Hard bottom)	N/A
85	48.16108	-53.72974	Sandy Mud	Sandy Mud
86	48.16316	-53.73066	Sandy Mud	Sandy Mud
87a	48.16606	-53.73150	Gravelly Sand	Gravelly Muddy Sand
87b	48.16605	-53.73146	N/A (Hard bottom)	N/A
88	48.16558	-53.73669	Gravelly Sand	Gravelly Muddy Sand
89	48.17078	-53.73899	Gravelly Sand	Gravelly Muddy Sand
90	48.17100	-53.74644	Gravel	Gravel
91	48.17424	-53.74135	Gravel	Gravel
92	48.17678	-53.74001	Muddy Sand	Gravelly Muddy Sand
93	48.17656	-53.74241	Gravel	Gravel
94	48.17969	-53.75225	Sandy Mud	Sandy Mud
95	48.18261	-53.76657	Sandy Mud	Sandy Mud
96	48.18451	-53.76815	Sandy Mud	Sandy Mud
97	48.18424	-53.77735	Sandy Mud	Sandy Mud
98	48.18312	-53.79209	Sandy Mud	Sandy Mud
99	48.18519	-53.79015	Muddy Sand	Gravelly Muddy Sand
100	48.18782	-53.78597	Sandy Mud	Sandy Mud
101	48.19076	-53.77930	Gravelly Sand	Gravelly Muddy Sand
102	48.19212	-53.77562	Sandy Gravel	Sandy Gravel
103	48.19021	-53.77399	Sandy Gravel	Sandy Gravel
105	48.18098	-53.74585	Sandy Mud	Sandy Mud

106	48.17987	-53.73823	Sandy Gravel	Sandy Gravel
107	48.17610	-53.73474	Sandy Gravel	Sandy Gravel
i03	48.16592	-53.71737	Sandy Gravel	Sandy Gravel
i05	48.16006	-53.67339	Gravelly Sand	Gravelly Muddy Sand
i10	48.15947	-53.68137	N/A (Hard bottom)	N/A
i21	48.15910	-53.68137	Sandy Gravel	Sandy Gravel
i33	48.16640	-53.73323	Sandy Mud	Sandy Mud
i35	48.16929	-53.73945	Sandy Gravel	Sandy Gravel
i41	48.16260	-53.72920	Sandy Mud	Sandy Mud
i44	48.17209	-53.73535	Gravel	Gravel
i58	48.16408	-53.73510	Sandy Mud	Sandy Mud
Auxiliary	48.16272	-53.68414	Sandy Gravel	Sandy Gravel
Aux 2	48.19819	-53.57876	Muddy Sand	Gravelly Muddy Sand

	Taxonomic Classification	Sample presence	Total abundance
	Kingdom Animalia		
	Phylum Annelida		
1	Acoetidae	1	1
2	Aphroditidae	16	27
3	Cirratulidae	5	4
4	Echiura	1	1
5	Flabelligeridae	9	13
6	Glyceridae	31	53
7	Goniadidae	2	2
8	Hesionidae	5	6
9	Lacydoniidae	4	7
10	Lumbrineridae	56	170
11	Maldanidae	32	69
12	Nephtyidae	35	54
13	Onuphidae (Nothria conchylega)	1	2
14	Opheliidae	30	60
15	Oweniidae	8	13
16	Pectinariidae	39	120
17	Phyllodocidae	16	26
18	Poecilochaetidae	1	1
19	Polynoidae	28	35

Appendix B: Summary of Smith Sound grab biota. Organism taxonomic classification, sample presence and total abundance.

20	Scalibregmidae	10	16
21	Chaetopteridae	34	122
	Spiochaetopterus		
22	Spionidae	42	134
23	Spirorbidae	3	3
24	Syllidae	15	24
25	Terebellidae	24	37
	Annelida Total		1304
	Phylum Anthozoa		
26	Actinauge cristata	5	6
27	Bunodactis stella	1	1
	Anthozoa Total		7
	Phylum Arthropoda		
28	Ampeliscidae	467	45
29	Crangon septemspinosa	75	23
30	Gammarus oceanicus	42	516
31	Meganyctiphanes norvegica	4	4
32	Microdeutopus gryllotalpa	6	8
33	Nebalia bipes	1	2
34	Oxyurostylis smithi	8	11
35	Pagurus arcutus	1	1
36	Stenothoidae	2	2
37	Hyperiidae	1	1
	Arthropoda Total		565

	Phylum Bivalvia		
38	Astarte	17	67
39	Chlamys islandicus	1	1
40	Geukensia demissa	1	1
41	Mulinia lateralis	2	2
42	Mya arenaria	12	25
43	Nuculana pernula	32	79
44	Periploma papyratium	24	37
45	Tellina agilis	1	2
46	Yoldia hyperborea	17	25
47	Yoldia thraciaeformis	1	2
	Bivalvia Total		67
	Phylum Branchipoda		
48	Terebratulina septentrionalis	6	6
	Branchipoda Total		6
	Phylum Bryozoa		
49	Cheilostomatida	1	1
	Bryozoa Total		1
	Phylum Cephalorhyncha		
50	Pripulus caudatus	3	3
	Cephalorhyncha Total		3
	Phylum Cnidaria		
51	Medusa	1	1
	Cnidaria Total		1

	Phylum Echinodermata		
52	Ctenodiscus crispatus	2	2
53	Echinarachnius parma	2	3
54	Echinoidea	2	3
55	Ophiopholis aculeata	11	22
56	Ophiura robusta	9	45
57	Ophiura spp.	2	2
	Echinodermata Total		77
	Phylum Gastropoda		
58	Acmaea testudinalis	8	12
59	Buccinum undatum	10	13
60	Crucubulum striatum	1	1
61	Cylichna alba	2	2
62	Eupleura caudate	5	5
63	Euspira heros	1	1
64	Littorina saxatilis	1	1
65	Margarites groenlandicus	5	5
66	Odostomia trifida	20	35
55	Skeneopsidae	1	1
	Gastropoda Total		76
	Phylum Hemichordata		
56	Harrimaniidae	8	8
57	Stereobalanus	1	1
	Hemichordata Total		9

	Phylum Mollusca		
58	Ischnochiton ruber	8	8
59	Onchidoris	2	2
	Mollusca Total		
	Phylum Nemertea		
60	Nemertea	11	13
	Nemertea Total		
	Phylum Porifera		
61	Hamacantha carteri	1	1
	Porifera Total		
	Phylum Rhodophyta		
62	Corallinaceae	1	1
	Rhodophyta Total		
	Phylum Rhynchocoela		
63	Lineidae	2	2
	Rhynchocoela Total		
	Phyla Unidentified		
64	Unidentified spp.	2	2
	Unidentified Total		2
	Total Individuals		2320

	Video ID	Start Longitude	Start Latitude	End Longitude	End Latitude	Habitat
1	Transect_2	-53.68789087	48.164247	-53.68830829	48.1640893	Coralline Boulders and Gravel
2	Transect_5	-53.68377808	48.16518967	-53.68488632	48.16458296	Coralline Boulders and Gravel
3	Transect_6	-53.6846296	48.16430616	-53.68505196	48.16413722	Coralline Boulders and Gravel
4	Ti37	-53.74397167	48.170515	-53.742955	48.170985	Large Boulders
5	T24_P1	-53.69133588	48.16312228	-53.69095254	48.16297894	Large Boulders
6	T24_2_P1	-53.6868063	48.16172697	-53.6865613	48.16177697	Large Boulders
7	T24_4_P1	-53.68435333	48.16206667	-53.68424333	48.16198667	Large Boulders
8	T24_4_P2	-53.68417167	48.16194333	-53.68380833	48.16184833	Large Boulders
9	T24_4_P3	-53.68381167	48.16184833	-53.6838	48.16189	Large Boulders
10	T24_5_P1	-53.68354333	48.1616	-53.68335333	48.161575	Large Boulders
11	T24_5_P2	-53.682785	48.1613	-53.682845	48.16130333	Large Boulders
12	T24_9_P1	-53.66521044	48.16860788	-53.6651971	48.16837788	Large Boulders
13	T24_9_P2	-53.66522044	48.16838122	-53.66546877	48.16812122	Large Boulders
14	T24_9_P3	-53.66552377	48.16806455	-53.6656471	48.16805955	Large Boulders
15	T24_11_P2	-53.64850167	48.16391667	-53.64849167	48.16390667	Large Boulders
16	T24_11_P3	-53.64848833	48.163905	-53.64808	48.16374833	Large Boulders
17	T24_11_P4	-53.64808	48.16374833	-53.64806833	48.16372833	Large Boulders
18	Tarbitary_P3	-53.69347	48.15305333	-53.69328333	48.15247	Large Boulders
19	Tarbitary_P4	-53.693325	48.15247667	-53.69321833	48.1523	Large Boulders
20	TD3_P1	-53.69344833	48.15227167	-53.69343167	48.15254333	Large Boulders
21	T94	-53.75118167	48.179705	-53.75096833	48.179885	Sand
22	T105	-53.74607894	48.18053081	-53.74559061	48.18092915	Sand
23	Ti36	-53.73818167	48.16578333	-53.73786833	48.166225	Sand
24	Ti22_P1	-53.68348	48.15567	-53.68345	48.15544167	Sand
25	Ti30	-53.68112667	48.15729167	-53.68157	48.15673167	Sand
26	T11_P1	-53.73652333	48.15843667	-53.73701667	48.15873333	Sand
27	T205_2_P1	-53.73468833	48.165195	-53.73478833	48.16534333	Sand

Appendix C: Summary of video transects, video ID, latitudes and longitudes of polyline track, and habitat (n=65).

28	T205_2_P2	-53.73479167	48.165365	-53.73476333	48.165625	Sand
29		-53.73376667	48.17145833	-53.733325	48.17206667	Sand
30	T95	-53.76544667	48.18263917	-53.76490426	48.1829541	Sand
31	T97	-53.77594372	48.18474494	-53.77560372	48.18549828	Sand
32	T104	-53.76185833	48.18473833	-53.76156833	48.18493667	Sand
33	Ti34	-53.73314246	48.16608617	-53.73364167	48.16635333	Sand
34	Ti34_2	-53.73443833	48.16660167	-53.734625	48.16681	Sand
35	TX	-53.78755667	48.18262667	-53.78685167	48.18305333	Sand
36	Ti55	-53.79132017	48.18185762	-53.72925333	48.163585	Sand
37	Ti55_2_P1	-53.729125	48.16378833	-53.729275	48.16405167	Sand
38	Ti55_2_P2	-53.72929	48.16406167	-53.72934333	48.16423	Sand
39	Ti55_2_P3	-53.729345	48.16422833	-53.72919667	48.16465333	Sand
40	T24_6_P1	-53.68213333	48.16076667	-53.68208	48.16065	Sand with Small Boulders
41	T24_6_P2	-53.68208	48.16065	-53.68212167	48.16056833	Sand with Small Boulders
42	T24_9_P4	-53.665655	48.16689167	-53.66575	48.166595	Sand with Small Boulders
43	T24_10_P1	-53.66575	48.16658333	-53.66579667	48.16644833	Sand with Small Boulders
44	T24_11_P1	-53.64909667	48.16482333	-53.64851167	48.16391333	Sand with Small Boulders
45	T24_12_P1	-53.672965	48.15980333	-53.67330667	48.16027833	Sand with Small Boulders
46	T24_12_P2	-53.67296649	48.15993255	-53.67331833	48.16045833	Sand with Small Boulders
47	T24_12_P3	-53.67332	48.16048167	-53.673465	48.16039	Sand with Small Boulders
48	T24_12_P4	-53.67346833	48.160385	-53.67289333	48.15992833	Sand with Small Boulders
49	Ti22_P2	-53.68344833	48.15541667	-53.68346833	48.15507333	Sand with Small Boulders
50	Ti22_P3	-53.683475	48.155065	-53.683405	48.15489833	Sand with Small Boulders
51	T11_3_P1	-53.73868833	48.16157833	-53.73893833	48.16169	Sand with Small Boulders
52	T11_3_P2	-53.73894333	48.16169333	-53.73857	48.16293333	Sand with Small Boulders
53	T11_4_P1	-53.73857667	48.16295	-53.73864	48.16309333	Sand with Small Boulders
54	Ti56	-53.74121333	48.17000833	-53.74064167	48.1702	Small Boulders
55	T24_P2	-53.69087421	48.16295894	-53.69013921	48.16282228	Small Boulders
56	T24_P3	-53.6887163	48.16220475	-53.68794797	48.16181141	Small Boulders
57	T24_P4	-53.6879463	48.16180808	-53.6870213	48.16162141	Small Boulders
58	T24_7	-53.66495667	48.16972	-53.66517833	48.16960167	Small Boulders
59	T24_11_P1	-53.64851167	48.16391333	-53.64851	48.16391333	Small Boulders

60	T24_11_P2	-53.64851	48.16391333	-53.64850167	48.16391667	Small Boulders
61	Tarbitary_P1	-53.69358167	48.15342667	-53.69345167	48.15312333	Small Boulders
62	Tarbitary_P2	-53.69344333	48.153115	-53.69347333	48.15306	Small Boulders
63	T11_2_P3	-53.73843667	48.16078333	-53.73874	48.16083333	Small Boulders
64	T106	-53.73840763	48.17989759	-53.7384043	48.1804876	Small Boulders
65	TY	-53.79157099	48.18128989	-53.79133946	48.18181395	Small Boulders

	Taxonomic classification	Sample presence	Total abundance
	Kingdom Animalia		
	Phylum Annelida		
1	Nothria conchylega	11	13
2	Pectinariidae	7	18
3	Pyramidellidae		
4	Sabellidae	4	4
	Myxicola		
5	Sabellidae Unidentified	3	3
	Annelida Total		
	Phylum Arthropoda		
6	Brachyura	37	75
7	Cancer irroratus	1	1
8	Crangon septemspinosa	61	730
9	Meganyctiphanes norvegica	43	402
10	Paguroidea	20	26
	Arthropoda Total		
	Phylum Chordata		
11	Elasmobranchii egg case	1	1
12	Gadidae spp.	3	3
13	Gadus spp.	4	6
14	Macrouridae	2	2

Appendix D: Summary of Smith Sound video biota. Organism taxonomic classification, sample presence and total abundance.

15	Myoxocephalus	3	3
16	Pleuronectiformes	5	5
17	Rajiformes	1	1
18	Unidentified Pisces spp. 1	2	2
19	Unidentified Pisces spp. 2	1	1
	Chordata Total		
	Phylum Cnidaria		
20	Athenaria	16	35
21	Hormathia nodosa	43	2054
22	Stomphia coccinea	1	15
23	Unidentified Actiniaria	11	26
24	Urticina felina	4	9
25	Nemertesia spp 1.	45	467
26	Nemertesia spp 2.	23	75
27	Alcyonium digitatum	9	10
28	Gersemia rubiformis	2	3
29	Alcyonacea	9	20
30	Ptychogastria polaris (Stübing & Piepenburg, 1998)	7747	63
31	Aurelia aurita	2	3
	Cnidaria Total		2780
	Phylum Echinodermata		
32	Henricia sanguinolenta	1	1
33	Leptasterias polaris	11	20
34	Solasteridae	13	15

35	Asteriidae Unidentified	28	75
36	Echinarachnius parma	1	1
37	Strongylocentrotus droebachiensis	54	368
38	Holothuroidea	2	2
39	Gorgonocephalidae	3	4
40	Ophiuroidea spp.	34	472
	Echinodermata Total		958
	Phylum Mollusca		
41	Astartidae	25	64
42	Chlamys islandicus	1	1
43	Pectinidae	4	5
44	Buccinidae	28	61
45	Euspira heros	1	1
46	Patellogastropoda	3	4
47	Tegulidae	3	4
48	Boreochiton ruber	3	5
	Mollusca Total		145
	Phylum Porifera		
49	Porifera spp.	26	175
	Porifera Total		175
	Unidentified		
50	Unidentified spp. 1 (suspected soft coral)	1	1
51	Unidentified spp. 2 (resembles a sea-pen)	1	1
52	Unidentified spp. 3 (Branching stag horn form)	1	1

	Unidentified Total		3
	Kingdom Plantae		
	Phylum Ochrophyta		
53	Agarum spp.	1	11
	Total Ochrophyta		11
	Phylum Rhodophyta		
54	Bonnemaisoniaceae	р	р
55	Lithothamnium ³	Р	Р
	Total Rhodophyta		р

Grain size GRADISTAT Descriptive			escriptive Te	rminology
ohi	mm/µm			
11	≥ 2048mm	-		
10	≥ 1024mm	Very Large		
9	≥ 512mm	Large		
8	≥ 256mm	Medium	<u> </u>	Boulders
7	≥ 128mm	Small		
6	≥ 64mm	Very Small		
5	≥ 32mm	Very Coarse	-	
4	≥16mm	Coarse		
3	≥8mm	Medium	-	Gravel
2	≥4mm	Fine		
1	≥ 2mm	Very Fine		
)	≥1mm	Very Coarse		
-	≥ 500µm	Coarse		
2	≥ 250µm	Medium	-	Sand
5	≥ 125µm	Fine		
ŀ	≥ 63µm	Very Fine		
5	≥ 31µm	Very Coarse		
5	≥ 16µm	Coarse		
7	≥ 8µm	Medium	>	Silt
3	≥ 4µm	Fine		
)	≥ 2µm	Very Fine		
	< 2µm	Clay		

Appendix E: Grain size classification scheme of GRADISTAT. V4 (Blott and Pye, 2001).

Functional Group	Family	Feeding type	Feeding stratum	Motility pattern
Group 1	Acoetidae			
	Aphroditidae			
	Eunicida	Macrophage	Surface	Discretely motile
	Hesionidae			
	Lacydonidae			
	Lumbrineridae	Macro or	Surface	Motile
	Nephtyidae	Microphage	Surface	Motile
	Onuphidae	Macrophage	Surface	Motile
	(Nothria	Macrophage	Surface	Motile
	conchylega)	Macrophage	Surface	Motile
	Phyllodocidae	Macrophage	Surface	Motile
	Polynoidae	Macrophage		
	Syllidae			
Group 2	Cirratulidae	Microphage	Subsurface or	Motile
			surface	
Group 3	Echiuridae			
	Chaetopteridae	Microphage	Surface	Sessile
		Microphage	Surface	Discretely motile or
	Terebellidae			sessile

Appendix F: Polychaete functional groups with reference to feeding guild (Gagnon and Haedrich, 1991). Functional group, taxonomic family, feeding type, feeding stratum, motility pattern.

Group 4	Flabelligeridae	Microphage	Surface	Discretely motile
Group 5	Glyceridae	Macrophage	Surface	Discretely motile
	Goniadidae	Macrophage	Surface	Discretely motile
Group 6	Maldanidae	Microphage	Subsurface	Sessile
	Oweniidae	Microphage	Subsurface	Sessile
Group 7	Opheliidae	Microphage	Subsurface	Motile
	Pectinariidae	Microphage	Subsurface	Motile
	Scalibregmidae	Microphage	Subsurface	Motile
Group 8	Poecilochaetidae			
	Spionidae	Microphage	Water-surface	Discretely motile-
				sessile
Group 9	Serpulidae	Microphage	Water	Sessile

Table 1. Complete ANOSIM record for video data.			
Pairwise test, substrate groups R-Value 0.579			
			nificance vel 0.1 %
Substrate 1	Substrate 2	R-Stat	Level %
Gravelly Small Boulders (n=7)	Sandy Small Boulders (n=4)	0.316	3.3
Gravelly Small Boulders (n=7)	Bouldery Gravel (n=5)	0.006	40.7
Gravelly Small Boulders (n=7)	Gravel (n=4)	0.384	2.1
Gravelly Small Boulders (n=7)	Bouldery Sand (n=1)	0.551	12.5
Gravelly Small Boulders (n=7)	Small Boulders (n=1)	-0.224	62.5
Gravelly Small Boulders (n=7)	Gravelly Sand (n=1)	0.374	12.5
Gravelly Small Boulders (n=7)	Sand (n=17)	0.954	0.1
Gravelly Small Boulders (n=7)	Large Boulders on Gravelly Sand (n=8)	0.993	0.1
Gravelly Small Boulders (n=7)	Small Boulders on Gravelly Sand (n=11)	0.978	0.1
Gravelly Small Boulders (n=7)	Large Boulders on Sandy Gravel (n=7)	0.992	0.1
Gravelly Small Boulders (n=7)	Small Boulders on Sandy Gravel (n=5)	0.993	0.1
Gravelly Small Boulders (n=7)	Large Boulders on Sandy Gravel (n=3)	0.976	0.8
Gravelly Small Boulders (n=7)	Sand with Small Boulders (n=15)	1	0.1
Gravelly Small Boulders (n=7)	Sandy Gravel (n=1)	1	12.5
Gravelly Small Boulders (n=7)	Small Boulders on Sand (n=3)	1	0.8
Gravelly Small Boulders (n=7)	Sandy Large Boulders (n=2)	1	2.8
Gravelly Small Boulders (n=7)	Gravelly Sandy Small Boulders (n=1)	0.293	37.5

Appendix G: ANOSIM and SIMPER, summary and details of videos (Table 1-11).

	Sandy Gravelly Small Boulders		
Gravelly Small Boulders (n=7)	(n=1)	-0.156	75
Sandy Small Boulders (n=4)	Bouldery Gravel (n=5)	0.116	23
Sandy Small Boulders (n=4)	Gravel (n=4)	0.146	8.6
Sandy Small Boulders (n=4)	Bouldery Sand (n=1)	-0.375	100
Sandy Small Boulders (n=4)	Small Boulders (n=1)	-0.083	40
Sandy Small Boulders (n=4)	Gravelly Sand (n=1)	-0.292	60
Sandy Small Boulders (n=4)	Sand (n=17)	0.819	0.1
Sandy Small Boulders (n=4)	Large Boulders on Gravelly Sand (n=8)	0.891	0.2
Sandy Small Boulders (n=4)	Small Boulders on Gravelly Sand (n=11)	0.916	0.2
Sandy Small Boulders (n=4)	Large Boulders on Sandy Gravel (n=7)	0.845	0.3
Sandy Small Boulders (n=4)	Small Boulders on Sandy Gravel (n=5)	0.797	0.8
Sandy Small Boulders (n=4)	Large Boulders on Sandy Gravel (n=3)	0.639	8.6
Sandy Small Boulders (n=4)	Sand with Small Boulders (n=15)	0.976	0.1
Sandy Small Boulders (n=4)	Sandy Gravel (n=1)	0.458	20
Sandy Small Boulders (n=4)	Small Boulders on Sand (n=3)	0.731	5.7
Sandy Small Boulders (n=4)	Sandy Large Boulders (n=2)	0.5	13.3
Sandy Small Boulders (n=4)	Gravelly Sandy Small Boulders (n=1)	0.083	40
Sandy Small Boulders (n=4)	Sandy Gravelly Small Boulders (n=1)	-0.333	100
Bouldery Gravel (n=5)	Gravel (n=4)	0.125	21.4
Bouldery Gravel (n=5)	Bouldery Sand (n=1)	0.36	16.7
Bouldery Gravel (n=5)	Small Boulders (n=1)	0.32	33.3
Bouldery Gravel (n=5)	Gravelly Sand (n=1)	0.08	50
Bouldery Gravel (n=5)	Sand (n=17)	0.96	0.1

Bouldery Gravel (n=5)	Large Boulders on Gravelly Sand (n=8)	0.996	0.1
Bouldery Gravel (n=5)	Small Boulders on Gravelly Sand (n=11)	0.977	0.1
Bouldery Gravel (n=5)	Large Boulders on Sandy Gravel (n=7)	0.996	0.1
Bouldery Gravel (n=5)	Small Boulders on Sandy Gravel (n=5)	1	0.8
Bouldery Gravel (n=5)	Large Boulders on Sandy Gravel (n=3)	1	1.8
Bouldery Gravel (n=5)	Sand with Small Boulders (n=15)	1	0.1
Bouldery Gravel (n=5)	Sandy Gravel (n=1)	1	16.7
Bouldery Gravel (n=5)	Small Boulders on Sand (n=3)	1	1.8
Bouldery Gravel (n=5)	Sandy Large Boulders (n=2)	1	4.8
Bouldery Gravel (n=5)	Gravelly Sandy Small Boulders (n=1)	0.8	16.7
Bouldery Gravel (n=5)	Sandy Gravelly Small Boulders (n=1)	0.6	16.7
Gravel (n=4)	Bouldery Sand (n=1)	0.75	20
Gravel (n=4)	Small Boulders (n=1)	0.75	20
Gravel (n=4)	Gravelly Sand (n=1)	-0.417	100
Gravel (n=4)	Sand (n=17)	0.975	0.1
Gravel (n=4)	Large Boulders on Gravelly Sand (n=8)	1	0.2
Gravel (n=4)	Small Boulders on Gravelly Sand (n=11)	0.998	0.3
Gravel (n=4)	Large Boulders on Sandy Gravel (n=7)	1	0.3
Gravel (n=4)	Small Boulders on Sandy Gravel (n=5)	1	0.8
Gravel (n=4)	Large Boulders on Sandy Gravel (n=3)	1	2.9

Gravel (n=4)	Sand with Small Boulders (n=15)	1	0.2
Gravel (n=4)	Sandy Gravel (n=1)	1	20
Gravel (n=4)	Small Boulders on Sand (n=3)	1	2.9
Gravel (n=4)	Sandy Large Boulders (n=2)	1	6.7
Gravel (n=4)	Gravelly Sandy Small Boulders (n=1)	0.917	20
Gravel (n=4)	Sandy Gravelly Small Boulders (n=1)	0.917	20
Bouldery Sand (n=1)	Sand (n=17)	0.93	5.6
Bouldery Sand (n=1)	Large Boulders on Gravelly Sand (n=8)	1	11.1
Bouldery Sand (n=1)	Small Boulders on Gravelly Sand (n=11)	1	8.3
Bouldery Sand (n=1)	Large Boulders on Sandy Gravel (n=7)	1	12.5
Bouldery Sand (n=1)	Small Boulders on Sandy Gravel (n=5)	1	16.7
Bouldery Sand (n=1)	Large Boulders on Sandy Gravel (n=3)	1	25
Bouldery Sand (n=1)	Sand with Small Boulders (n=15)	1	6.3
Bouldery Sand (n=1)	Small Boulders on Sand (n=3)	1	25
Bouldery Sand (n=1)	Sandy Large Boulders (n=2)	1	33.3
Small Boulders (n=1)	Sand (n=17)	0.931	5.6
Small Boulders (n=1)	Large Boulders on Gravelly Sand (n=8)	1	11.1
Small Boulders (n=1)	Small Boulders on Gravelly Sand (n=11)	0.993	8.3
Small Boulders (n=1)	Large Boulders on Sandy Gravel (n=7)	0.986	12.5
Small Boulders (n=1)	Small Boulders on Sandy Gravel (n=5)	1	16.7
Small Boulders (n=1)	Large Boulders on Sandy Gravel (n=3)	1	25
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Small Boulders (n=1)	Sand with Small Boulders (n=15)	1	6.3
Small Boulders (n=1)	Small Boulders on Sand (n=3)	1	25
Small Boulders (n=1)	Sandy Large Boulders (n=2)	1	33.3
Gravelly Sand (n=1)	Sand (n=17)	0.978	5.6
Gravelly Sand (n=1)	Large Boulders on Gravelly Sand (n=8)	1	11.1
Gravelly Sand (n=1)	Small Boulders on Gravelly Sand (n=11)	1	8.3
Gravelly Sand (n=1)	Large Boulders on Sandy Gravel (n=7)	1	12.5
Gravelly Sand (n=1)	Small Boulders on Sandy Gravel (n=5)	1	16.7
Gravelly Sand (n=1)	Large Boulders on Sandy Gravel (n=3)	1	25
Gravelly Sand (n=1)	Sand with Small Boulders (n=15)	1	6.3
Gravelly Sand (n=1)	Small Boulders on Sand (n=3)	1	25
Gravelly Sand (n=1)	Sandy Large Boulders (n=2)	1	33.3
Sand (n=17)	Large Boulders on Gravelly Sand (n=8)	0.479	0.1
Sand (n=17)	Small Boulders on Gravelly Sand (n=11)	0.43	0.1
Sand (n=17)	Large Boulders on Sandy Gravel (n=7)	0.547	0.1
Sand (n=17)	Small Boulders on Sandy Gravel (n=5)	0.422	0.1
Sand (n=17)	Large Boulders on Sandy Gravel (n=3)	0.525	0.5
Sand (n=17)	Sand with Small Boulders (n=15)	0.256	0.1
Sand (n=17)	Sandy Gravel (n=1)	0.61	11.1
Sand (n=17)	Small Boulders on Sand (n=3)	0.27	7.1

Sand (n=17)	Sandy Large Boulders (n=2)	0.5	1.8
Sand (n=17)	Gravelly Sandy Small Boulders (n=1)	0.948	5.6
Sand (n=17)	Sandy Gravelly Small Boulders (n=1)	0.943	5.6
Large Boulders on Gravelly Sand (n=8)	Small Boulders on Gravelly Sand (n=11)	0.04	24.8
Large Boulders on Gravelly Sand (n=8)	Large Boulders on Sandy Gravel (n=7)	0.084	12.8
Large Boulders on Gravelly Sand (n=8)	Small Boulders on Sandy Gravel (n=5)	0.086	23.4
Large Boulders on Gravelly Sand (n=8)	Large Boulders on Sandy Gravel (n=3)	0.067	33.3
Large Boulders on Gravelly Sand (n=8)	Sand with Small Boulders (n=15)	0.691	0.1
Large Boulders on Gravelly Sand (n=8)	Sandy Gravel (n=1)	0.446	22.2
Large Boulders on Gravelly Sand (n=8)	Small Boulders on Sand (n=3)	0.204	19.4
Large Boulders on Gravelly Sand (n=8)	Sandy Large Boulders (n=2)	-0.056	53.3
Large Boulders on Gravelly Sand (n=8)	Gravelly Sandy Small Boulders (n=1)	1	11.1
Large Boulders on Gravelly Sand (n=8)	Sandy Gravelly Small Boulders (n=1)	0.991	11.1
Small Boulders on Gravelly Sand (n=11)	Large Boulders on Sandy Gravel (n=7)	-0.003	45.6
Small Boulders on Gravelly Sand (n=11)	Small Boulders on Sandy Gravel (n=5)	-0.109	77.9
Small Boulders on Gravelly Sand (n=11)	Large Boulders on Sandy Gravel (n=3)	0.085	34.1
Small Boulders on Gravelly Sand (n=11)	Sand with Small Boulders (n=15)	0.438	0.1

Small Boulders on Gravelly Sand (n=11)	Sandy Gravel (n=1)	0.213	25
Small Boulders on Gravelly Sand (n=11)	Small Boulders on Sand (n=3)	-0.125	68.1
Small Boulders on Gravelly Sand (n=11)	Sandy Large Boulders (n=2)	0.065	37.2
Small Boulders on Gravelly Sand (n=11)	Gravelly Sandy Small Boulders (n=1)	0.993	8.3
Small Boulders on Gravelly Sand (n=11)	Sandy Gravelly Small Boulders (n=1)	0.964	8.3
Large Boulders on Sandy Gravel (n=7)	Small Boulders on Sandy Gravel (n=5)	0.054	29
Large Boulders on Sandy Gravel (n=7)	Large Boulders on Sandy Gravel (n=3)	-0.107	68.3
Large Boulders on Sandy Gravel (n=7)	Sand with Small Boulders (n=15)	0.663	0.1
Large Boulders on Sandy Gravel (n=7)	Sandy Gravel (n=1)	0.401	37.5
Large Boulders on Sandy Gravel (n=7)	Small Boulders on Sand (n=3)	0.099	31.7
Large Boulders on Sandy Gravel (n=7)	Sandy Large Boulders (n=2)	-0.019	55.6
Large Boulders on Sandy Gravel (n=7)	Gravelly Sandy Small Boulders (n=1)	1	12.5
Large Boulders on Sandy Gravel (n=7)	Sandy Gravelly Small Boulders (n=1)	1	12.5
Small Boulders on Sandy Gravel (n=5)	Large Boulders on Sandy Gravel (n=3)	0.108	30.4
Small Boulders on Sandy Gravel (n=5)	Sand with Small Boulders (n=15)	0.791	0.1
Small Boulders on Sandy Gravel (n=5)	Sandy Gravel (n=1)	0	33.3
Small Boulders on Sandy Gravel (n=5)	Small Boulders on Sand (n=3)	0.395	7.1

Small Boulders on Sandy Gravel (n=5)	Sandy Large Boulders (n=2)	0.236	28.6
Small Boulders on Sandy Gravel (n=5)	Gravelly Sandy Small Boulders (n=1)	1	16.7
Small Boulders on Sandy Gravel (n=5)	Sandy Gravelly Small Boulders (n=1)	1	16.7
Large Boulders on Sandy Gravel (n=3)	Sand with Small Boulders (n=15)	0.786	0.2
Large Boulders on Sandy Gravel (n=3)	Sandy Gravel (n=1)	0.556	50
Large Boulders on Sandy Gravel (n=3)	Small Boulders on Sand (n=3)	0.074	40
Large Boulders on Sandy Gravel (n=3)	Sandy Large Boulders (n=2)	-0.25	90
Large Boulders on Sandy Gravel (n=3)	Gravelly Sandy Small Boulders (n=1)	1	25
Large Boulders on Sandy Gravel (n=3)	Sandy Gravelly Small Boulders (n=1)	1	25
Sand with Small Boulders (n=15)	Sandy Gravel (n=1)	0.95	6.3
Sand with Small Boulders (n=15)	Small Boulders on Sand (n=3)	0.285	8.1
Sand with Small Boulders (n=15)	Sandy Large Boulders (n=2)	0.698	1.5
Sand with Small Boulders (n=15)	Gravelly Sandy Small Boulders (n=1)	1	6.3
Sand with Small Boulders (n=15)	Sandy Gravelly Small Boulders (n=1)	1	6.3
Sandy Gravel (n=1)	Small Boulders on Sand (n=3)	1	25
Sandy Gravel (n=1)	Sandy Large Boulders (n=2)	1	33.3
Small Boulders on Sand (n=3)	Sandy Large Boulders (n=2)	0.167	30
Small Boulders on Sand (n=3)	Gravelly Sandy Small Boulders (n=1)	1	25
Small Boulders on Sand (n=3)	Sandy Gravelly Small Boulders (n=1)	1	25

Sandy Large Boulders (n=2)	Gravelly Sandy Small Boulders (n=1)	1	33.3
Sandy Large Boulders (n=2)	Sandy Gravelly Small Boulders (n=1)	1	33.3

Table 2. Sediment classes pertaining to the statistically significant results identified in ANOSIM for reclassification under grouped habitat 'Large Boulders (n=20)'

Sediment Class	Statistically Significant Connections	R-Stat	Sig %
Large Boulders on Gravelly Sand (n=8)	Sandy Large Boulders (n=2)	-0.25	90
Large Boulders on Sandy	Large Boulders on Sandy Shell Hash (n=3)	-0.107	68.3
Gravel (n=7)	Sandy Large Boulders (n=2)	-0.019	55.6
Large Boulders on Sandy	Large Boulders on Sandy Gravel (n=7)	-0.107	68.3
Shell Hash (n=3)	Sandy Large Boulders (n=2)	-0.25	90
	Large Boulders on Gravelly Sand (n=8)	-0.25	90
Sandy Large Boulders (n=2)	Large Boulders on Sandy Gravel (n=7)	-0.019	55.6
(11-2)	Large Boulders on Sandy Shell Hash (n=3)	-0.25	90

Table 3. Sediment classes pertaining to the statistically significant results identified in ANOSIM for reclassification under grouped habitat '*Large Boulders* (n=20)'

Sediment Class	Statistically Significant Connections	R-Stat	Sig %
Large Boulders on Gravelly Sand (n=8)	Sandy Large Boulders (n=2)	-0.25	90
Large Boulders on Sandy	Large Boulders on Sandy Shell Hash (n=3)	-0.107	68.3
Gravel (n=7)	Sandy Large Boulders (n=2)	-0.019	55.6
Large Boulders on Sandy Shell Hash (n=3)	Large Boulders on Sandy Gravel (n=7)	-0.107	68.3
	Sandy Large Boulders (n=2)	-0.25	90
Sandy Large Boulders (n=2)	Large Boulders on Gravelly Sand (n=8)	-0.25	90
	Large Boulders on Sandy Gravel (n=7)	-0.019	55.6
	Large Boulders on Sandy Shell Hash (n=3)	-0.25	90

Table 4. Sediment classes pertaining to the statistically significant results identified in ANOSIM for reclassification under grouped habitat '*Small Boulders* (n=22)'

Sediment Class	Statistically Significant Connections	Dissimila rity	R-Stat	Sig %
Small Boulders on	Small Boulders on Sandy Gravel (n=7)		-0.109	77.9
Gravelly Sand (n=11)	Small Boulders on Sand (n=3)		-0.125	68.1
Small Boulders on Sandy Gravel (n=7)	Small Boulders on Gravelly Sand (n=11)		-0.109	77.9
Small Boulders on Sand (n=3)	Small Boulders in Gravelly Sand (n=11)		-0.125	68.1
Sandy Gravel (n=1)	Small Boulders on Gravelly Sand (n=11)	48.15 %		
(Connections based on SIMPER dissimilarity values)	Small Boulders on Sandy Gravel (n=7)	42.66 %		
varues)	Small Boulders on Sand (n=3)	47.00 %		

Table 5. Sediment classes pertaining to the statistically significant results identified in ANOSIM for reclassification under grouped habitat '*Coralline Boulders and Gravel* (n=19)'

Sediment Class	Statistically Significant Connections	R-Stat	Sig %
	Bouldery Gravel (n=5) (Presence/Absence Transform)	-0.004	44.2
Gravelly Small Boulders (n=7)	Small Boulders (n=1)	-0.224	62.5
	Sandy Gravelly Small Boulders (n=1)	-0.156	75
Bouldery Gravel (n=5)	Gravelly Small Boulders (n=7) (Presence/Absence Transform)	-0.004	44.2
Sandy Small Boulders	Small Boulders (n=1)	-0.083	40
(n=4)	Sandy Gravelly Small Boulders (n=1)	-0.333	100
Gravel (n=4)	Gravelly Sand (n=1)	-0.417	100
	Gravelly Small Boulders (n=7)	-0.224	62.5
Small Davidson (n. 1)	Sandy Small Boulders (n=4)	-0.083	40
Small Boulders (n=1)	Bouldery Sand (n=1) (-0.375, 100)	-0.375	100
	Gravelly Sand (n=1)	-0.292	60
	Gravel (n=4)	-0.417	100
Gravelly Sand (n=1)	Small Boulders (n=1)	-0.292	60
Sandy Gravelly Small	Gravelly Small Boulders (n=7)	-0.156	75
Boulders (n=1)	Sandy Small Boulders (n=4)	-0.333	100
Bouldery Sand (n=1)	Small Boulders (n=1)	-0.375	100

Table 6: Complete Video Sample ANOSIM results using Habitat Group as a variable			
Pairwise test		R- Statistic 0.641 Significance 0.1 %	
Sediment Class 1	Sediment Class 2	R-Stat.	Signif %
Coralline Boulders and Gravel (n=19)	Sand (n=17)	0.928	0.1
Coralline Boulders and Gravel (n=19)	Large Boulders (n=20)	0.915	0.1
Coralline Boulders and Gravel (n=19)	Small Boulders (n=22)	0.913	0.1
Coralline Boulders and Gravel (n=19)	Sand with Small Boulders (n=15)	0.945	0.1
Sand (n=17)	Large Boulders (n=20)	0.696	0.1
Sand (n=17)	Small Boulders (n=22)	0.591	0.1
Sand (n=17)	Sand with Small Boulders (n=15)	0.256	0.1
Large Boulders (n=20)	Small Boulders (n=22)	0.075	1
Large Boulders (n=20)	Sand with Small Boulders (n=15)	0.654	0.1
Small Boulders (n=22)	Sand with Small Boulders (n=15)	0.472	0.1

Table 7: SIMPER results for habitat ' <i>Large Boulders (n=20)</i> ' samples				
With	Within Group Similarity 57.96%			
Contributing Fauna	Contribution %	Av. Abundance		
Polaris	25.33	3.26		
Hydroid, Nemertesia antennina	14.28	1.64		
Ophiuroidea	11.99	1.53		
Strongylocentrotus droebachiensis	10.6	1.4		
Pandalus spp.	9.96	1.44		
Porifera	6.6	1.04		
Astarte	6.38	0.93		
Brachyura	3.87	0.67		
Asteriidae	3.03	0.68		

Table 8: SIMPER results for habitat 'Small Boulders (n=22)' samples			
Within Group Similarity 57.96%			
Contributing Fauna	Contribution %	Av. Abundance	
Polaris spp.	31.84	3.09	
Pandalus spp.	15.85	1.56	
Hydroid, Nemertesia antennina	12.80	1.45	
Strongylocentrotus droebachiensis	12.78	1.27	
Ophiuroidea	8.74	1.2	
Hormathia nodosa	6.15	1.06	
Asteriidae	2.52	0.52	

Table 9: SIMPER results for habitat 'Coralline Boulders and Gravel (n=19)' samples							
Within Group Similarity 47.75%							
Contributing Fauna	Contribution %	Av. Abundance					
Corallinaceae	73.36	1.59					
Strongylocentrotus							
droebachiensis	18.56	0.96					

Table 10: SIMPER results for habitat 'Sand with Small Boulders (n=15)' samples									
Within Group Similarity 60.63%									
Contributing Fauna Contribution % Av. Abundance									
Hormathia nodosa	26.45	2.7							
Pandalus spp.	21.31	1.92							
Polaris spp.	19.67	2							
Euphausiid	14.45	1.43							
Brachyura	3.94	0.7							
Hydroid, Nemertesia antennina	3.39	0.78							
Buccinum undatum	3.28	0.62							

Table 11: SIMPER results for habitat 'Sand (n=17)' samples									
Within Group Similarity 43.30%									
Contributing Fauna	Contribution %	Av. Abundance							
Euphausiid	49.51	1.69							
Polaris spp.	20.22	1.25							
Pandalus spp.	17.87	0.94							
Hormathia nodosa	3.48	0.75							

Choose 1 of 13 Summary		
Highest Adjusted R-Squared Results		
AdjR2 AICc JB K(BP)	VIF Model	
0.41 5424.67 0	0.02 1 -BPI***	
0.36 5530.13 0	0 1-SLO***	
0.33 5573.4 0	1.04 1 -MEAN***	
· · · · · ·		
Choose 2 of 13 Summary		
Highest Adjusted R-Squared Results		
AdjR2 AICc JB K(BP)	VIF Model	
0.55 5111.99 0.01	0 1.02 -SLO*** +NORT***	
0.52 5172.62 0	0 1-BPI*** +NORT***	
0.47 5295.2 0	0 1 -EAST*** -BPI***	
Choose 3 of 13 Summary		
Highest Adjusted R-Squared Results		
AdjR2 AICc JB K(BP)	VIF Model	
0.62 4912.98 0.04	0 1.83 -SLO*** -BPI*** +NORT***	
0.6 4974.31 0	0 1.41 -SLO*** -BATH*** +NORT***	
0.6 4975.33 0	0 1.41 -SLO*** -MEAN*** +NORT***	
Choose 4 of 13 Summary		
Highest Adjusted R-Squared Results		
AdjR2 AICc JB K(BP)	VIF Model	
0.65 4790.61 0.23	0 1.84 -SLO*** -EAST*** -BPI*** +NORT***	
0.64 4846.99 0	0 1.41 -SLO*** -EAST*** -BATH*** +NORT***	
0.64 4848.2 0	0 1.42 -SLO*** -MEAN*** -EAST*** +NORT***	
Passing Models		
AdjR2 AICc JB K(BP)	VIF Model	
0.65365 4790.613 0.225	0 1.84 -SLO*** -EAST*** -BPI*** +NORT***	
0.62924 4872.203 0.13	0 2.37 -SLO*** +F9_21*** -BPI*** +NORT***	
0.56829 5054.524 0.409	0 1.63 -SLO*** -EAST*** -BATH*** +DtO***	
0.56802 5055.281 0.415	0 1.64 -SLO*** -MEAN*** -EAST*** +DtO***	
0.56791 5055.582 0.394	0 1.43 -SLO*** +DtO*** +ASP*** +NORT***	
0.564 5066.394 0.516	0 1.05 -MEAN*** -EAST*** +DtO*** +NORT***	
0.5628 5069.67 0.556	0 1.05 -EAST*** -BATH*** +DtO*** +NORT***	
0.54707 5112.017 0.224	0 1.96 -SLO*** -EAST*** +DtO*** -BPI***	
0.51731 5188.266 0.111	0 1.22 -SD*** -EAST*** +DtO*** +NORT***	

Appendix H: Exploratory Regression I, Summary.

Choose 5 d	of 13 Summa	arv								
	justed R-Squ		Results							
		JB	K(BP)	VIF					Ν	Model
0.66	4758.48	0.19	0	13.2	-SLO***	+SD***	-EAST***	-BPI***	+NORT***	
0.66	4760.2	0.06	0	2.38	-SLO***	-EAST***	+F9_21***	-BPI***	+NORT***	
0.66	4767.08	0.11	0	2.56	-SLO***	-EAST***	-ASP***	-BPI***	+NORT***	
			Passing Mode				layos con			
AdjR2	AICc	JB		VIF	Model					
0.66068	4767.08	0.112	0	2.56	-SLO***	-EAST***	-ASP***	-BPI***	+NORT***	
0.66023	4768.636	0.736	0	2.12	-SLO***	-EAST***	+DtO***	-BPI***	+NORT***	
0.65564	4784.736	0.332	0	2.06	-SLO***	-EAST***	+F3_9***	-BPI***	+NORT***	
0.65475	4787.83	0.234	0		-SLO***	-RDMV**	-EAST***	-BPI***	+NORT***	
0.65341	4792.45	0.39	0	1.84	-SLO***	-EAST***	-BATH***	+DtO***	+NORT***	
0.65321	4793.165	0.389	0	1.85	-SLO***	-MEAN***	-EAST***	+DtO***	+NORT***	
0.63812	4844.18	0.179	0	1.71	-SD***	-EAST***	+DtO***	-BPI***	+NORT***	
0.62476	4887.621	0.132	0		-SLO***	+F3_9***	-BPI***	+NORT***	-F3_5***	
0.62125	4898.764	0.127	0	1.84	-SLO***	-BATH***	+DtO***	+ASP***	+NORT***	
0.62096	4899.677	0.426	0	1.57	'-SD***	-EAST***	-BATH***	+DtO***	+NORT***	
0.62094	4899.758	0.117	0		-SLO***	-MEAN***	+DtO***	+ASP***	+NORT***	
0.62066	4900.626	0.393	0	1.58	-MEAN***	-SD***	-EAST***	+DtO***	+NORT***	
0.57169	5046.094	0.672	0	1.9	-SLO***	-EAST***	-BATH***	+DtO***	+F9_21***	
0.57134	5047.053	0.76	0	1.68	-SLO***	-EAST***	-BATH***	+DtO***	+F3_9***	
0.57132	5047.108	0.621	0			-MEAN***	-EAST***	+DtO***	+F9_21***	
0.57095	5048.152	0.722	0		-SLO***	-MEAN***	-EAST***	+DtO***	+F3_9***	
0.57041	5049.667	0.219	0	1.34	-MEAN***	-EAST***	+DtO***	-F9_21***	+NORT***	
0.57023	5050.156	0.493	0		111-11-11-10-10	+DtO***	+ASP***	+NORT***	-F3_5**	
0.57017	5050.327	0.637	0		-SLO***	-EAST***	-BATH***	+DtO***	+F3_5**	
0.56985	5051.205	0.44	0	204061024074	-SLO***	+DtO***	-F3_9**	+ASP***	+NORT***	
0.56973	5051.541	0.564	0	100 100 100 100 100 100 100 100 100 100	-SLO***	+DtO***	-F9_21**	+ASP***	+NORT***	
0.56965	5051.77	0.611	0		-SLO***	-MEAN***	-EAST***	+DtO***	+F3_5**	
0.56933	5052.672	0.213	0		-EAST***	-BATH***	+DtO***	-F9_21***	+NORT***	
0.5691	5053.312	0.405	0		-SLO***	-RDMV**	-EAST***	-BATH***	+DtO***	
0.56858	5054.737	0.406	0		-SLO***	-MEAN***	-RDMV**	-EAST***	+DtO***	
0.56684	5059.58	0.224	0	1.06	-MEAN***	-RDMV***	-EAST***	+DtO***	+NORT***	
0.5662	5061.348	0.239				-EAST***	-BATH***	+DtO***	+NORT***	
0.55651	5087.797	0.696	0		-SLO***	-EAST***	+DtO***	+F3_9***	-BPI***	
0.55242	5098.815	0.107	0		-SLO***	-RDMV**	+DtO***	-F9_21**	+NORT***	
0.55241	5098.831	0.498	0		-SLO***	-EAST***	+DtO***	-BPI***	+F3_5***	
0.54794	5110.722	0.158	0		-SLO***	-RDMV**	-EAST***	+DtO***	-BPI***	
0.50031	5230.753	0.791	0	1.58	-SD***	+DtO***	-F9_21***	+ASP***	+NORT***	

	divisional D. Cau		loculto.								
	justed R-Squ										
,		JB	K(BP)	VIF						Model	
0.67	4725.33	0.09	0		2 -SLO***	+SD***	-EAST***	+F9_21***	-BPI***	+NORT***	
0.67	4736.36	0.06	0		5 -SLO***	-EAST***	+F9_21***	-ASP***	-BPI***	+NORT***	
0.67	4743.93	0.94	0	2.38	3 -SLO***	-EAST***	+DtO***	+F9_21***	-BPI***	+NORT***	
Passing M	odels										
AdjR2	AICc	JB	K(BP)	VIF						Model	
0.66745	4743.932	0.944	0	2.38	3 -SLO***	-EAST***	+DtO***	+F9_21***	-BPI***	+NORT***	
0.66311	4759.469	0.305	0	3.09	-SLO***	-EAST***	+DtO**	-ASP***	-BPI***	+NORT***	
0.66291	4760.178	0.139	0	2.6	-SLO***	-RDMV***	-EAST***	-ASP***	-BPI***	+NORT***	
0.66201	4763.381	0.502	0	2.12	2 -SLO***	-EAST***	+DtO***	+F3 9***	-BPI***	+NORT***	
0.66197	4763.511	0.672	0	2.13	3 -SLO***	-RDMV***	-EAST***	+DtO***	-BPI***	+NORT***	
0.65912	4773.587	0.422	0	7.24	I-SLO***	-EAST***	+F3 9***	-BPI***	+NORT***	-F3_5***	
0.65482	4788.587	0.448	0		-SLO***	-RDMV***	-EAST***	-BATH***	+DtO***	+NORT***	
0.65439	4790.075	0.434	0		5-SLO***	-MEAN***	-RDMV**	-EAST***	+DtO***	+NORT***	
0.64463	4823.462	0.386	0		9 -SD***	-EAST***	+DtO***	-ASP***	-BPI***	+NORT***	
0.63984	4839.498	0.143	0		3-SD***	-EAST***	+DtO***	+F3 9***	-BPI***	+NORT***	
0.63297	4862.14		0		7 -SLO***	+F3 9***	+ASP***	-BPI***	+NORT***	-F3 5***	
0.62185		0.259	-		-RDMV**	-SD***	-EAST***	-BATH***	+DtO***	+NORT***	
0.61044	4933.491	0.158	0	7.12		-MEAN***	+DtO***	+F3 9***	+NORT***	-F3 5***	
0.61034	4933.805	0.166				-BATH***	+DtO***	+F3 9***	+NORT***	-F3 5***	
0.57478	5038.436	0.613	0			-EAST***	+DtO***	-F9 21***	-ASP***	+NORT***	
0.57461	5038.917	0.719	125	2,020.02		-EAST***	+DtO***	-F9 21***	+F3 9**	+NORT***	
0.57424	5039.935	0.296	0			-RDMV***	-EAST***	+DtO***	-F9 21***	+NORT***	
0.57375	5041.332	0.311	0			-EAST***	-BATH***	+DtO***	-F9 21***	+NORT***	
0.57373	5041.381	0.751	0	3.55	and the second	-BATH***	+DtO***	-F9 21***	+F3 9***	+NORT***	
0.57343	5042.226	0.676	0			-BATH***	+DtO***	-F9 21***	-ASP***	+NORT***	
0.57141	5047.883	0.584	0	1.44		-RDMV**	+DtO +DtO***	+ASP***	+NORT***	-F3 5***	
0.57141	5047.885	0.504	0	1.4	F_3L0		1010	'AJI	inom	-15_5	
	(1 2 2										
	of 13 Summa										
	justed R-Squ										
		JB	K(BP)	VIF	Model						
0.68	4716.95	0.15	0		7 -SLO***	+SD***	-EAST***	+DtO***	+F9_21***	-BPI***	+NORT***
0.67	4718.93	0.13	0			+SD***	-EAST***	+F9_21***	-BPI***	+NORT***	-F3_5***
0.67	4719.07	0.12	0	13.3	3 -SLO***	+SD***	-EAST***	+F9_21***	-F3_9**	-BPI***	+NORT***
Passing M											
		JB	K(BP)	VIF	Model						
0.66885	4739.918	0.734	0		8 -SLO***	-EAST***	+DtO***	+F9_21***	-BPI***	+NORT***	-F3_5**
0.66842	4741.467	0.869	0		3 -SLO***	-RDMV**	-EAST***	+DtO***	+F9_21***	-BPI***	+NORT***
0.66554	4751.837	0.356	0	3.13	3 -SLO***	-RDMV***	-EAST***	+DtO**	-ASP***	-BPI***	+NORT***
0.66487	4754.221	0.165	0	3.09	9 -SLO***	-EAST***	+DtO**	+F3_9***	-ASP***	-BPI***	+NORT***
0.66415	4756.807	0.1	0	2.62	-SLO***	-RDMV***	-EAST***	+F3_9**	-ASP***	-BPI***	+NORT***
							Contraction of the second second				

Choose 6 of 13 Summary

		2016	2									
0.66319 4760.207	0.477		3 -SLO***	-RDMV**	-EAST***	+DtO***	+F3_9**	-BPI***	+NORT***			
0.64673 4817.388	0.413	0 3.3	2 -RDMV***	-SD***	-EAST***	+DtO***	-ASP***	-BPI***	+NORT***			
0.64632 4818.77	0.615	0 3.2	9 -SD***	-EAST***	+DtO***	+F3_9***	-ASP***	-BPI***	+NORT***			
0.62216 4897.921	0.255	0 7.1	8 -SLO***	-BATH***	+DtO***	+F3_9**	+ASP***	+NORT***	-F3_5**			
0.62208 4898.191	0.245	0 7.	2 -SLO***	-MEAN***	+DtO***	+F3_9**	+ASP***	+NORT***	-F3_5**			
0.61359 4924.808	0.147	0 7.4	3 -SLO***	-RDMV***	-BATH***	+DtO***	+F3_9***	+NORT***	-F3_5***			
0.61348 4925.138	0.139	0 7.4	6 -SLO***	-MEAN***	-RDMV***	+DtO***	+F3_9***	+NORT***	-F3_5***			
0.57987 5025.038	0.173	0 3.2	5 -MEAN***	-RDMV***	-EAST***	+DtO***	-F9_21***	-ASP***	+NORT***			
0.57918 5026.989	0.19	0 3.2	4 -RDMV***	-EAST***	-BATH***	+DtO***	-F9_21***	-ASP***	+NORT***			
0.57867 5028.431	0.268	0 3.5	6 -MEAN***	-EAST***	+DtO***	-F9_21***	+F3_9**	-ASP***	+NORT***			
0.57754 5031.642	0.299	0 3.5	6 -EAST***	-BATH***	+DtO***	-F9_21***	+F3_9**	-ASP***	+NORT***			,
0.57743 5031.964	0.517	0 3.5	6 -MEAN***	-RDMV***	-EAST***	+DtO***	-F9_21***	+F3_9**	+NORT***			,
0.57704 5033.077	0.547	0 3.5	5 -RDMV***	-EAST***	-BATH***	+DtO***	-F9_21***	+F3_9**	+NORT***			
			•									
Choose 8 of 13 Summar	Γ γ											
Highest Adjusted R-Squ	ared Results											
AdjR2 AICc J	B K(BP)	VIF						Model				
0.68 4709	0.23	0 13.	4 -SLO***	-RDMV***	+SD***	-EAST***	+F9_21***	-BPI***	+NORT***	-F3_5***		
0.68 4710.91	0.15	0 14.	8 -SLO***	-RDMV***	+SD***	-EAST***	+DtO***	+F9_21***	-BPI***	+NORT***		
0.68 4712.32	0.18	0 13.	5 -SLO***	-RDMV***	+SD***	-EAST***	+F9_21***	-F3_9***	-BPI***	+NORT***		
Passing Models												
AdjR2 AICc J	B K(BP)	VIF						Model				
0.6708 4733.853	0.58	0 3.0	5 -SLO***	-RDMV***	-EAST***	+DtO***	+F9_21***	-BPI***	+NORT***	-F3_5***		
0.66665 4748.866	0.203	0 3.1	3 -SLO***	-RDMV***	-EAST***	+DtO**	+F3_9**	-ASP***	-BPI***	+NORT***		
0.64782 4814.707	0.616	0 3.3	2 -RDMV***	-SD***	-EAST***	+DtO***	+F3_9**	-ASP***	-BPI***	+NORT***		
0.58261 5018.223	0.102	0 3.5	7 -MEAN***	-RDMV***	-EAST***	+DtO***	-F9_21***	+F3_9**	-ASP***	+NORT***		
0.58203 5019.868	0.11	0 3.5	7 -RDMV***	-EAST***	-BATH***	+DtO***	-F9_21***	+F3_9**	-ASP***	+NORT***		
Choose 9 of 13 Summar	Υ.											,
Highest Adjusted R-Squ	ared Results											
AdjR2 AlCc J	B K(BP)	VIF						Model				
0.68 4702.32	0.06	0 16.	6 -SLO***	-RDMV***	+SD***	-EAST***	+F9_21***	-ASP***	-BPI***	+NORT***	-F3_5***	
0.68 4702.54	0.41	0 14.	8 -SLO***	-RDMV***	+SD***	-EAST***	+DtO**	+F9_21***	-BPI***	+NORT***	-F3_5***	
0.68 4704.58	0.46	0 1	5 -SLO***	-RDMV***	+SD***	-EAST***	+DtO**	+F9_21***	-F3_9**	-BPI***	+NORT***	
												,
Choose 10 of 13 Summa	ary											
			Hig	nest Adjusted	R-Squared Re	sults						
AdjR2 AlCc J	B K(BP)	VIF		•	•			Model				
	0.10		0.0***	DDAU/***		FACTES		. 50 21 ***	100*	001***	NODINE FO FINE	

-EAST***

-EAST***

+DtO

+DtO

-EAST***

+F9_21*** -ASP*

+F9_21*** -F3_9** +F9_21*** -ASP*** -BPI***

-BPI***

-ASP*

+NORT*** -F3_5***

+NORT*** -F3_5***

+NORT***

-BPI***

4700.59 0.18

0.19

0.05

4703.04

4704.27

0.68

0.68

0.68

0 16.9 -SLO***

0 17.1 -SLO***

0 16.6 -SLO***

-RDMV***

-RDMV***

-MEAN

+SD***

+SD***

-RDMV*** +SD***

Choose 11	of 13 Sumr	nary													
Highest Ac	justed R-Sq	uared R	esults												
AdjR2	AICc	JB	K(BP)	VIF						Model					
0.68	4701.56	0.14	0	16.9	-SLO***	-MEAN	-RDMV***	+SD***	-EAST***	+DtO*	+F9_21***	-ASP**	-BPI***	+NORT***	-F3_5***
0.68	4701.58	0.14	0	16.9	-SLO***	-RDMV***	+SD***	-EAST***	-BATH	+DtO*	+F9_21***	-ASP**	-BPI***	+NORT***	-F3_5***
0.68	4702.62	0.18	0	17.3	-SLO***	-RDMV***	+SD***	-EAST***	+DtO	+F9_21***	-F3_9	-ASP*	-BPI***	+NORT***	-F3_5*

Choose 12	of 13 Summ	nary													
Highest Ac	ljusted R-Squ	uared R	esults												
AdjR2	AICc	JB	K(BP)	VIF						Model					
0.68	4703.59	0.14	0	17.	4 -SLO***	-MEAN	-RDMV***	+SD***	-EAST***	+DtO*	+F9_21***	+F3_9	-ASP**	-BPI***	+NORT***
0.68	4703.62	0.14	0	17.	4 -SLO***	-RDMV***	+SD***	-EAST***	-BATH	+DtO*	+F9_21***	+F3_9	-ASP**	-BPI***	+NORT***

Appendix I, Note 1.

Percent	tage of Search Criteria Passed			
	Search Criterion Cutoff	# Passed	% Passed	Trials
Min Adjusted R-Squared	>0.5	4500	73.25	614
Max Coefficient p-value	<0.05	2014	32.79	614
Max VIF Value	<7.5	3015	49.08	614
Min Jarque-Bera p-value	>0.1	1298	21.13	614
Min Spatial Auticorrelation p-value	>0	120	100	12

	Summ	ary of Variable Signific	ance
Var	% Sig.	% Negative	% Positive
SLO	100	100	0
SD	100	50	50
NORT	100	0	100
EAST	99.48	100	0
BPI	98.5	100	0
DtO	96.88	0	100
ASP	83.95	39.32	60.68
BATH	79.59	82.08	17.92
MEAN	79.15	81.98	18.02
F9_21	71.71	25	75
RDMV	63.02	95.9	4.1
F3_9	52.05	31.51	68.49
F3_5	50.91	76.5	23.5

			Summary of Multicollinearity*
Var	VIF	Vio	Covariates
SLO	17.37	1536	SD (75.00), BPI (23.83), F3_9 (13.43), F3_5 (11.23), MEAN (1.86), BATH (1.86)
MEAN	8.72	142	BPI (6.93), F3_5 (2.54), F3_9 (2.54), SD (1.86), SLO (1.86)
RDMV	1.18	0	
SD	14.78	1536	SLO (75.00), BPI (23.83), F3_9 (13.43), F3_5 (11.23), MEAN (1.86), BATH (1.86)
EAST	3.63	0	
BATH	8.68	141	BPI (6.88), F3_5 (2.49), F3_9 (2.49), SD (1.86), SLO (1.86)
DtO	1.87		
F9_21	6.64	0	
F3_9	14.78	1081	F3_5 (42.24), BPI (19.92), SLO (13.43), SD (13.43), MEAN (2.54), BATH (2.49)
ASP	4.21	0	
BPI	12.65	1567	SD (23.83), SLO (23.83), F3_9 (19.92), F3_5 (15.33), MEAN (6.93), BATH (6.88)
NORT	1.38		
F3_5	8.86	870	F3_9 (42.24), BPI (15.33), SLO (11.23), SD (11.23), MEAN (2.54), BATH (2.49)

* At least one model failed to solve due to perfect multicollinearity.

Please review the warning messages for further information.

	Summary of Residual Normality (JB)											
JB												
0.99982	0.325841	5590	0	2.77	EAST*** +DtO*** -F9_21*** +ASP*** +F3_5***							
0.99932	0.557211	5088	0	16	-SLO*** -MEAN*** +SD*** -EAST*** +ASP -BPI*** +F3_5***							
0.9989	0.55758	5086	0	13.7	-SLO*** -MEAN*** +SD*** -EAST*** -BPI*** +F3_5***							

Summary of Residual Spatial Autocorrelation (SA) (Not Applicable)

Table Abbreviations AdjR2 Adjusted R-Squared AlCc Akaike's Information Criterion JB Jarque-Bera p-value K(BP) Koenker (BP) Statistic p-value VIF Max Variance Inflation Factor SA Global Moran's I p-value Model Variable sign (+/-) Model Variable significance (* = 0.10, ** = 0.05, *** = 0.01)

	6-									
		Summary	1.							
		ted R-Squared Re		(22)	h					
AdjR2	1.00		JB	K(BP)	19970120	SA	Model			
0.3		5525.46	0	0		NA	-SLO***			
0.3		5569.71 5848.56	0	0.05		NA NA	-BATH*** +DtO***			
0	10	5848.50	0	0	1	NA	+DIO			
Choose 2	of 7	Summary								
		ted R-Squared Su	mmary							
AdjR2		AICc	JB	K(BP)	VIF	SA	Model			
0.5	55	5109.51	0.01	0	1.02	NA	-SLO***	+NORT***		
0.4	46	5312.19	0	0	1.32	NA	-SLO***	-BATH***		
0.4	44	5353.21	0	0	1.01	NA	-BATH***	+DtO***		
Choose 3	of 7	Summary								
		ted R-Squared Re	sults							
AdjR2			JB	K(BP)	VIF	SA	Model			
).6	4969.21	0	0	1.4	NA	-SLO***	-BATH***	+NORT***	
0.5	58	5009.79	0	0	1.03	NA	-SLO***	-EAST***	+NORT***	
0.5	56	5083	0	0	1.06	NA	-SLO***	+ASP***	+NORT***	
Passing M	lode	els								
AdjR2	4		JB	K(BP)		SA	Model			
0.51913	37	5179.374336	0.106612	0	1.014079	NA	-BATH***	+DtO***	-EAST***	
		Summary								
	-	ted R-Squared Re			S-merup	701101				
AdjR2	-	AICc	JB	K(BP)		SA	Model			
0.0	_	4842.7	0	0			-SLO***	-BATH***	-EAST***	+NORT***
0.0	-	4937.4	0.05	0		5,0576	-SLO***	-BATH***	+DtO***	+NORT***
	0.6	4954.65	0	0	1.43	NA	-SLO***	-BATH***	+ASP***	+NORT***
Passing M			10	(22)	h.u.=					
AdjR2			JB	K(BP)		SA	Model		D · D + + + +	
0.56679	_	5055.450389	0.475511	0		_	-SLO***	-BATH***	+DtO***	-EAST***
0.56612		5057.299468	0.243701	0			-SLO***	+DtO***	+ASP***	+NORT***
0.5601	19	5073.763405	0.498632	0	1.054318	NA	-BATH***	+DtO***	-EAST***	+NORT***

Appendix I: Exploratory Regression II, Summary.

Choose 5 of	7 Summary										
	usted R-Squared Re	sults				_					
AdjR2	AICc	JB	K(BP)	VIF	SA	Model					
	0.66	4783.35	0	0	2.73	NA	-SLO***	-BATH***	-ASP***	-EAST***	+NORT***
	0.65	4793.44	0.25	0	1.83	NA	-SLO***	-BATH***	+DtO***	-EAST***	+NORT***
	0.64	4843.21	0	0	1.58	NA	-SLO***	-BATH***	#NAME?	-EAST***	+NORT***
Passing Mod	dels										
AdjR2	AICc	JB	K(BP)	VIF	SA	Model					
0.652257	4793.43984	0.249452	0	1.825103	NA	-SLO***	-BATH***	+DtO***	-EAST***	+NORT***	
0.570579	5045.975338	0.41671	0	1.892878	NA	-SLO***	-BATH***	+DtO***	+F9_21***	-EAST***	
0.567852	5053.552631	0.361647	0	1.745256	NA	-SLO***	+DtO***	-F9_21**	+ASP***	+NORT***	
0.566421	5057.508631	0.566126	0	1.344691	NA	-BATH***	+DtO***	-F9_21***	-EAST***	+NORT***	
Choose 6 of	7 Summary										
Highest Adju	usted R-Squared Re	sults									
AdjR2	AICc	JB	K(BP)	VIF	SA	Model					
0.66	4764.19	0	0	3.2	NA	-SLO***	-BATH***	+DtO***	-ASP***	-EAST***	+NORT***
0.66	4782.88	0	0	2.74	NA	-SLO***	-BATH***	+F9_21	-ASP***	-EAST***	+NORT***
0.65	4794.69	0.19	0	2.03	NA	-SLO***	-BATH***	+DtO***	+F9_21	-EAST***	+NORT***
Passing Mod	dels										

Choose 7 of	Choose 7 of 7 Summary											
Highest Adju	sted R-Squared Re	sults										
AdjR2	AICc	JB	K(BP)	VIF	SA	Model						
0.66	4764.62	0	0	3.21	NA	-SLO***	-BATH***	+DtO***	+F9_21	-ASP***	-EAST***	+NORT***

Model

-BATH*** +DtO***

-F9_21*** -ASP***

-EAST*** +NORT***

************* Exploratory Regression Global Summary **************

K(BP)

0.37355

AdjR2

0.571094

AICc

5045.559701

JB

Percentage of Search Criteria Passed											
	Search Criterion Trials # Passed % Pa										
Min Adjusted R-Squared	>0.5	127	57	44.88							
Max Coefficient p-value	<0.05	127	96	75.59							
Max VIF Value	<7.5	127	127	100							
Min Jarque-Bera p-value	>0.1	127	20	15.75							
Min Spatial Autocorrelation p-value	>0	29	29	100							

VIF

0 3.192341 NA

SA

	Summary of Variable Significance										
Variable	% Sig	% Neg	% Pos								
SLO	100	100	0								
BATH	100	100	0								
DtO	100	0	100								
EAST	100	100	0								
NORT	100	0	100								
ASP	85.94	37.5	62.5								
F9_21	62.5	67.19	32.81								

	Summary of Multicollinearity											
Variable	VIF	Violations	Covariates									
SLO	2.04	0										
BATH	1.65	0										
DtO	1.58	0										
F9_21	1.5	0										
ASP	3.21	0										
EAST	2.81	0										
NORT	1.28	0										

	Summary of Residual Normality (JB)												
JB	AdjR2 AICc K(BP) VIF SA Model												
0.56724	0.25186	5707.443057	0	1.048838	NA	+DtO***	+ASP***						
0.566126	0.566421	5057.508631	0	1.344691	NA	-BATH***	+DtO***	-F9_21***	-EAST***	+NORT***			
0.519474	0.567121	5055.57569	0	3.038635	NA	-SLO***	-BATH***	+DtO***	-ASP	-EAST***			

	Table Abbreviations
AdjR2	Adjusted R-Squared
AICc	Akaike's Information Criterion
JB	Jarque-Bera p-value
K(BP)	Koenker (BP) Statistic p-value
VIF	Max Variance Inflation Factor
SA	Global Moran's I p-value
Model	Variable sign (+/-)
Model	Variable significance (*=0.1, **=0.05, ***=0.01)

Appendix J: Exploratory Regression II, Table.

DuralD	A	AIC-	ID		Maul/IE	CA.	Ni una Via na	V1	¥2	V2	V4	VE	VC
RunID 1	AdjR2	AICc 5525.455	JB 0.000	K_BP 0.000	MaxVIF 1.000	SA 0	NumVars	X1 SLO	X2	X3	X4	X5	X6
2	0.357	5569.709			/		1						
	0.333		0.000	0.049	1.000	0	1	BATH					
3	0.158	5848.563	0.000	0.000	1.000	0	1	DtO					
4	0.075	5960.936	0.000	0.000	1.000	0	1	F9_21					
5	0.045	5998.157	0.000	0.000	1.000	0	1	ASP					
6	0.081	5953.028	0.000	0.000	1.000	0	1	EAST					
7	0.128	5890.273	0.000	0.002	1.000	0	1	NORT					
8	0.462	5312.186	0.000	0.000	1.319	0	2	SLO	BATH			-	
9	0.381	5479.732	0.000	0.000	1.221	0	2	SLO	DtO				
10	0.392	5458.722	0.000	0.000	1.002	0	2	SLO	ASP				
11	0.415	5413.169	0.000	0.000	1.005	0	2	SLO	EAST				
12	0.546	5109.512	0.005	0.000	1.015	0	2	SLO	NORT				
13	0.444	5353.207	0.000	0.000	1.013	0	2	BATH	DtO				
14	0.346	5546.888	0.000	0.000	1.031	0	2	BATH	ASP				
15	0.406	5431.385	0.000	0.000	1.001	0	2	BATH	EAST				
16	0.407	5428.619	0.000	0.000	1.023	0	2	BATH	NORT				
17	0.209	5773.378	0.000	0.000	1.014	0	2	DtO	F9_21				
18	0.252	5707.443	0.567	0.000	1.049	1	2	DtO	ASP				
19	0.240	5725.540	0.000	0.000	1.000	0	2	DtO	EAST				
20	0.248	5712.955	0.000	0.000	1.023	0	2	DtO	NORT				
21	0.125	5894.329	0.000	0.000	1.002	0	2	F9_21	ASP				
22	0.165	5838.743	0.000	0.000	1.003	0	2	F9_21	EAST				
23	0.243	5721.145	0.000	0.000	1.030	0	2	F9_21	NORT				
24	0.149	5861.965	0.000	0.000	1.040	0	2	ASP	NORT				
25	0.189	5804.315	0.000	0.000	1.012	0	2	EAST	NORT				
26	0.501	5222.677	0.000	0.000	1.612	0	3	SLO	BATH	DtO			
27	0.474	5286.131	0.000	0.000	1.521	0	3	SLO	BATH	F9 21			
28	0.480	5272.985	0.000	0.000	1.360	0	3	SLO	BATH	ASP			
29	0.523	5170.384	0.000	0.000	1.326	0	3	SLO	BATH	EAST			
30	0.597	4969.213	0.001	0.000	1.404	0	3	SLO	BATH	NORT			
31	0.438	5366.012	0.005	0.000	1.309	0	3	SLO	DtO	ASP			
32	0.443	5354.842	0.000	0.000	1.230	0	3	SLO	DtO	EAST			
33	0.550	5101.190	0.029	0.000	1.286	0	3	SLO	DtO	NORT			
34	0.556	5082.997	0.002	0.000	1.059	0	3	SLO	ASP	NORT			
35	0.583	5009.787	0.000	0.000	1.030	0	3	SLO	EAST	NORT			
36	0.484	5262.647	0.000	0.000	1.094	0	3	BATH	DtO	ASP			-
37	0.519	5179.374	0.107	0.000	1.014	0	3	BATH	DtO	EAST			
38	0.497	5233.854	0.000	0.000	1.042	0	3	BATH	DtO	NORT			
39	0.347	5545.442	0.000	0.000	1.288	0	3	BATH	F9 21	ASP			
40	0.347	5428.686	0.000	0.000	1.288	0	3	BATH	F9_21	EAST			
40	0.408	5408.591	0.000	0.000	1.323	0	3	BATH	F9_21	NORT			
41 42	0.418	5386.533	0.000	0.000	2.623	0	3	BATH	ASP	EAST			
42	0.428	5420.580	0.000	0.000	1.063	0	3	BATH	ASP	NORT			
43	0.412	5303.401	0.000	0.000	1.063	0	3	BATH	EAST	NORT			
44						0	3		F9 21				
	0.307	5617.548	0.025	0.000	1.062	-		DtO	-	ASP		-	
46	0.301	5627.766	0.078	0.000	1.017	0	3	DtO	F9_21	EAST			
47	0.334	5569.824	0.000	0.000	1.062	0	3	DtO	F9_21	NORT			
48	0.257	5700.391	0.160	0.000	2.768	0	3	DtO	ASP	EAST			
49	0.307	5616.411	0.286	0.000	1.111	0	3	DtO	ASP	NORT			
50	0.314	5604.347	0.005	0.000	1.035	0	3	DtO	EAST	NORT			
51	0.265	5686.435	0.000	0.000	1.069	0	3	F9_21	ASP	NORT			
52	0.312	5608.635	0.000	0.000	1.040	0	3	F9_21	EAST	NORT			
53	0.193	5799.417	0.000	0.000	2.551	0	3	ASP	EAST	NORT			
54	0.510	5203.601	0.001	0.000	1.865	0	4	SLO	BATH	DtO	F9_21		
55	0.537	5135.576	0.007	0.000	1.618	0	4	SLO	BATH	DtO	ASP		
56	0.567	5055.450	0.476	0.000	1.624	0	4	SLO	BATH	DtO	EAST		
57	0.607	4937.404	0.048	0.000	1.796	0	4	SLO	BATH	DtO	NORT		
58	0.489	5253.711	0.000	0.000	1.521	0	4	SLO	BATH	F9_21	ASP		

Appendix J, Note 1.

59	0.530	5154.095	0.000	0.000	1.539	0	4	SLO	BATH	F9_21	EAST		
60	0.598	4966.716	0.000	0.000	1.555	0	4	SLO	BATH	F9_21	NORT		
61	0.531	5149.439	0.001	0.000	2.698	0	4	SLO	BATH	ASP	EAST		
62	0.602	4954.649	0.000	0.000	1.428	0	4	SLO	BATH	ASP	NORT		
63	0.637	4842.702	0.000	0.000	1.406	0	4	SLO	BATH	EAST 4	NORT		
64	0.447	5346.638	0.001	0.000	2.822	0	4	SLO	DtO	ASP	EAST		
65	0.566	5057.299	0.244	0.000	1.431	0	4	SLO	DtO	ASP	NORT		
66	0.588	4994.761	0.002	0.000	1.293	0	4	SLO	DtO	EAST	NORT		
67	0.585	5005.447	0.000	0.000	1.366	0	4	SLO	F9_21	EAST	NORT		
68	0.587	4997.927	0.000	0.000	2.551	0	4	SLO	ASP	EAST	NORT		
69	0.501	5224.326	0.000	0.000	1.342	0	4	BATH	DtO	F9_21	NORT		
70	0.521	5175.348	0.000	0.000	1.147	0	4	BATH	DtO	ASP	NORT		
71	0.560	5073.763	0.499	0.000	1.054	0	4	BATH	DtO	EAST	NORT		
72	0.424	5397.296	0.000	0.000	1.355	0	4	BATH	F9 21	ASP	NORT		
73	0.480	5274.577	0.000	0.000	1.327	0	4	BATH	F9 21	EAST	NORT		
74	0.502	5221.578	0.000	0.000	2.682	0	4	BATH	ASP	EAST	NORT		
75	0.314	5604.922	0.326	0.000	2.773	0	4	DtO	F9_21	ASP	EAST		
76	0.389	5467.701	0.061	0.000	1.125	0	4	DtO	F9 21	ASP	NORT		
77	0.405	5434.457	0.121	0.000	1.073	0	4	DtO	F9_21	EAST	NORT		
78	0.318	5598.758	0.241	0.000	2.944	0	4	DtO	ASP	EAST	NORT		
79	0.318	5599.448	0.000	0.000	2.553	0	4	F9_21	ASP	EAST	NORT		
80	0.541	5126.490	0.042	0.000	1.890	0	5	SLO	BATH	DtO	F9_21	ASP	
81	0.571	5045.975	0.417	0.000	1.893	0	5	SLO	BATH	DtO	F9 21	EAST	
82	0.620	4900.643	0.089	0.000	1.832	0	5	SLO	BATH	DtO	ASP	NORT	
83	0.652	4793.440	0.249	0.000	1.825	0	5	SLO	BATH	DtO	EAST	NORT	
84	0.539	5130.071	0.001	0.000	2.708	0	5	SLO	BATH	F9 21	ASP	EAST	
85	0.655	4783.355	0.001	0.000	2.733	0	5	SLO	BATH	ASP	EAST	NORT	<u> </u>
86	0.568	5053.553	0.362	0.000	1.745	0	5	SLO	DtO	F9 21	ASP	NORT	
87	0.591	4987.880	0.004	0.000	1.693	0	5	SLO	DtO	F9 21	EAST	NORT	
88	0.590	4991.783	0.000	0.000	3.071	0	5	SLO	DtO	ASP	EAST	NORT	
89	0.589	4992.778	0.000	0.000	2.554	0	5	SLO	F9 21	ASP	EAST	NORT	
90	0.527	5161.465	0.000	0.000	1.363	0	5	BATH	DtO	F9 21	ASP	NORT	<u> </u>
91	0.566	5057.509	0.566	0.000	1.345	1	5	BATH	DtO	F9 21	EAST	NORT	<u> </u>
92	0.565	5060.729	0.011	0.000	3.187	0	5	BATH	DtO	ASP	EAST	NORT	<u> </u>
93	0.512	5198.745	0.000	0.000	2.701	0	5	BATH	F9 21	ASP	EAST	NORT	<u> </u>
94	0.661	4764.187	0.004	0.000	3.201	0	6	SLO	BATH	DtO	ASP	EAST	NO
95	0.592	4984.943	0.000	0.000	3.071	0	6	SLO	DtO	F9 21	ASP	EAST	NO
96	0.571	5045.560	0.374	0.000	3.192	0	6	BATH	DtO	F9 21	ASP	EAST	NO

Appendix K: Ordinary Least Square report for final model.

Summary of OLS Results - Model Variables

Variable	Coefficient [a]	StdError	t-Statistic	Probability [b]	Robust_SE	Robust_t	Robust_Pr [b]	VIF [c]
Intercept	-1.171198	0.465234	-2.517440	0.011941*	0.666278	-1.757821	0.079041	
SLO_5M_SUR	-0.078688	0.006565	-11.986031	0.000000*	0.008537	-9.216991	0.000000*	1.889608
5M_SURFACE	-0.025521	0.001560	-16.364691	0.000000*	0.001255	-20.338109	0.000000*	1.466517
DISTANCE	0.304552	0.026020	11.704449	0.000000*	0.043565	6.990795	0.000000*	1.339212
FBPI_9_21	0.023863	0.007309	3.264982	0.001141*	0.008271	2.885288	0.003987*	1.465298
ASP_5M_SUR	0.005176	0.000558	9.267994	0.000000*	0.000674	7.675178	0.000000*	1.124209

OLS Diagnostics

Input Features:	classification_rules3	Dependent Variable:	DENDRO
Number of Observations:	1197	Akaike's Information Criterion (AICc) [d]:	5109.985203
Multiple R-Squared [d]:	0.542884	Adjusted R-Squared [d]:	0.540965
Joint F-Statistic [e]:	282.893162	Prob(>F), (5,1191) degrees of freedom:	0.000000*
Joint Wald Statistic [e]:	2608.666682	Prob(>chi-squared), (5) degrees of freedom:	0.000000*
Koenker (BP) Statistic [f]:	170.258582	Prob(>chi-squared), (5) degrees of freedom:	0.000000*
Jarque-Bera Statistic [g]:	6.670952	Prob(>chi-squared), (2) degrees of freedom:	0.035598*

Histogram of Standardized Residuals







Appendix L: Results of 'Moran's I' spatial autocorrelation graph on sample sites.



Given the z-score of 0.476681366063, the pattern does not appear to be significantly different than random.

Appendix M: Results of 'dendrogram' showing spatial co-occurrence between grab and video samples.

		s of Combined Classes e of merging)		
	Merged Class	Between-Class Distance		
7 9 2 6 2 6 2 2 2	8 10 3 7 5 9 6 4	0.737434 1.108896 1.209622 1.232213 1.398417 2.062354 2.576308 7.132979		
C DISTANCE A S 0 0.7926 1.5851 2.3777 3.1702 3.9628 4.7553 5.5479 6.3404 7.1330 S 8 7 6				
10				