Assessment of the impacts of bottom trawling on marine foundation species in northern Hecate Strait, British Columbia

by

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Abstract

I examine impacts of bottom-trawling on benthic foundation species (FS) in northern Hecate Strait, BC using photographic analysis of the benthos conducted over a gradient of trawling effort, substrate, and depth. Between 14-22 photos, from 31 remote-operated-vehicle transects, were analyzed to assess proportional coverage of FS. Using quasi-binomial regression I found that FS coverage is negatively associated with (in order of importance) the proportion of soft substrate (β_{Psm} = -1.09; *SE* = 0.15), depth (β_d = -0.31; *SE*: 0.29), trawled area (β_{S14} = -0.06; *SE* = 0.15), and surficial geology “sand/gravel” ($\beta_{sand/gravel}$ = -0.06; *SE*: 0.25). Surficial geology, inferred from substrate maps, is the least important variable associated with FS coverage, due to misclassification of substrate type at the scale of the survey. I found the true magnitude of trawling impact on FS to be uncertain due to inadequate power and contrast in my survey design.

Keywords: bottom trawling; foundation species; benthic habitat impacts; ecosystem based management; photographic analysis

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A_{FS}	Area covered by foundation species (cm^2)
A_{Tj}	Total area of a given photograph from a transect (cm^2)
d	Depth (m)
$Geology$	Substrate type inferred from geological substrate maps; Till or Sand/Gravel
h	Photograph from a transect
K	Substrate type
k	Number of parameters in a given model
n	Sample size
p_{FS}	Proportion of area covered by foundation species in a transect
p_K	Proportion of area covered by a given substrate type in a transect
p_{sm}	Proportion of area covered by the substrate type sand+mud in a transect
r^2	Coefficient of determination
$S_{i,y}$	Area swept by trawl gear per 1 km^2 grid cell in a given year
S_{14}	Area swept by trawl gear in a 1 km^2 grid cell averaged over all years from 1996-2009
Stp_{sm}	Proportion of area covered by the substrate type sand+mud in a transect standardized to one standard deviation
Std	Depth standardized to one standard deviation
t	Transect
w	Width of trawl gear used to determine area swept by trawl gear
X_n	Explanatory covariates in generalized linear model
β_n	Regression coefficients in generalized linear model
μ	Mean proportion of foundation species coverage
ϕ	Dispersion parameter for quasi-binomial variance estimator

List of Acronyms

ASVM	All Substrate Variables Model
BACI	Before-after-control-impact study design method
BC	British Columbia
DFO	Department of Fisheries and Oceans
EBM	Ecosystem based management
FAO	Food and Agriculture Organization of the United Nations
FS	Foundation species
GLM	Generalized Linear Model
ICES	International Council for the Exploration of the Sea
ISSM	In-situ Substrate Model
ME	Mean error
MSM	Mapped Substrate Model
NRC	National Research Council
QAICc	Akaike information criterion adjusted for quasi-binomial data with a small sample size
RMSE	Root mean square error
ROV	Remote operated vehicle
RVI	Relative variable importance
SFF	Sustainable Fisheries Framework
UN	United Nations

Introduction

Ecosystem based management (EBM) is often presented as an ideal means for addressing the effects of fishing on ocean ecosystems (Rice, 2005; Ruckelshaus et al., 2008). Although definitions of EBM vary, the common underlying concept is an integrated approach to natural resource management that aims to enhance or maintain ecosystem health and resilience while supporting sustainable human use of ecosystem goods and services (Bracken et al., 2007, Price et al., 2009). International conventions and agreements, such as the United Nations (UN) Fish Stock Agreement (UN, 1995), the Food and Agricultural Organization's (FAO) Code of Conduct for Responsible Fisheries (FAO, 1995), and the Reykjavik Declaration on Responsible Fisheries in the Marine Ecosystem (FAO, 2001), recognize that ecosystem based management is necessary for the sustainable management of fisheries. In response to these international commitments, Canadian legislation and policies, such as the Oceans Act, the Oceans Action Plan, and the Sustainable Fisheries Framework (SFF) Policy, require that Canadian fisheries now implement ecosystem based management.

A common element of EBM commitments is to "assess and minimize fishing impacts on non-target and associated or dependent species and their environment; protect biodiversity in marine environments; and protect habitats of special concern" (UN, 1995). Fishing activities that contact the sea floor, such as bottom trawling, dredging, long-lining, and trap fishing are increasingly scrutinized due to perceived negative impacts on benthic ecosystems and communities, as well as the seeming absence of ecosystem considerations in the management of these activities (Jones, 1992; Thrush et al., 1998; Watling and Norse, 1998; Collie et al., 2000a).

Sessile emergent epifauna are known to play an important role as habitat engineers in benthic ecosystems (Bruno and Bertness, 2001). The physical structure of these species, often known as benthic foundation species, creates biogenic habitat and increases habitat complexity and physical relief in benthic environments (Angelini et al., 2011). Habitat heterogeneity, increased rugosity, and an increase in available physical structure, all of which can be provided by foundation species, are positively correlated with species diversity (Coleman and Williams, 2002; Costello et al., 2005), juvenile survivorship of fish (Lindholm et al., 2001) and invertebrates (Stoner, 2009), as well as productivity of commercially important species (Bracken et al., 2007). For example, reef-forming corals are well known foundation species that increase topographic complexity of the benthic environment, thus increasing habitat features and species diversity (Idjadi and Edmunds, 2006). In the north Pacific, sponges also provide nursery habitat, shelter from predators, and habitat for a diversity of prey items for commercially important rockfish (*Sebastes sp*.) and flatfish (Richards, 1986; Jamieson et al., 2007; Marliave et al., 2009). Adult Pacific Ocean Perch (*Sebastes alutus*) are also known to shelter in forests of sea whips (*Halipteris willemoesi*), especially in the absence of high-relief rock substrates (Brodeur, 2001).

There is evidence that bottom trawling and dredging negatively impact some benthic ecosystems (Collie et al., 2000a; Kaiser et al., 2000a), particularly those involving biogenic habitat created by foundation species (Lambert et al., 2011). Bottom trawl gear directly removes, damages, and kills benthic organisms, and can modify substrate characteristics (Auster and Langton; 1999, Collie et al., 2000a). Removals or damage of vulnerable foundation species may limit the productivity of associated species due to the loss of habitat complexity and related ecological niches (Collie et al. 1997; Bradshaw et al. 2003).

Although the direct physical impacts of bottom fishing are clearly understood, the majority of research is conducted on spatial and temporal scales much smaller than the regional scales over which fisheries occur (Lokkeborg, 2005). For example, the majority of studies compare benthic biota before and after experimentally trawling an area of the sea floor, or compare areas with little or no trawling to areas that have been experimentally trawled (Collie et al., 2000a; Lokkeborg, 2005). Unfortunately, such *before-after-control-impact* (BACI) studies typically encompass spatial scales of less than 200 m, are often characterized by only one or two disturbance events, and infrequently look at impacts in more than one habitat type (Collie et al., 2000a). This disconnect between the scale of most fisheries and the scale of experimental bottom impact studies limits our ability to generalize results to ecosystem scales required for ecosystem-based management.

In the northeast Pacific Ocean, research on bottom fishing impacts has been even more limited. Canadian research on trawl and dredge impacts has only been undertaken by the Department of Fisheries and Oceans (DFO) in the north-western Atlantic (DFO 2006) and Collie et al. (2000a) found only two studies performed in the waters of “West North America” by Freese et al. (1999) and Engel and Kvetik (1998). The scales of these studies were 5 m and 3.7 km, respectively. In British Columbia (BC), Canada the annual footprint of the bottom trawl fishery between 1996 and 2005 was estimated to be approximately 19,000 km^2 (Sinclair, 2007). This equates to a required scale of statistical inference of more than 475,000 200 m x 200 m grid cells. Over this range of spatial area, bottom trawl fisheries in BC target a large variety of species that inhabit an equally wide variety of environmental characteristics such as substrate, depth, temperature and geo-chemical cycling zones (Sinclair et al., 2005).

Patterns and processes observed at small scales, in relatively homogenous environments and over short time-frames, may be vastly different from those observed at broader scales where environmental variability is increased (Wiens, 1989; Thrush et al., 1998). Scaling-up conclusions from small experimental studies that do not incorporate environmental variability may incorrectly inform management of bottom trawl fisheries at regional levels. Natural distributions of benthic invertebrates in BC, including foundation species, are highly dependent on environmental characteristics, such as those listed above (Brinkhurst, 1987; Leys et al., 2004; Burd et al., 2008). Thus, the potential response of benthic communities and foundation species to bottom trawling will not only depend on fishing effort, but also on environmental characteristics responsible for species distributions. To account for the large scale of typical fisheries in assessing bottom trawl impacts, the National Research Council (NRC, 2002) recommended examining areas repeatedly disturbed by fishing to determine the response of benthic ecosystems as a function of fishing effort and habitat type.

My research aims to quantify the impact of trawling on benthic habitat by measuring an index of benthic community response over a gradient of exposure to actual bottom trawling activity. Provided that the sampling frame includes all combinations of habitat type, fishing effort, and environmental covariates, this approach can be used to extrapolate assessments to unstudied areas (ICES, 2000; NRC, 2002). In contrast to experimental before-after-control-impact (BACI) studies, my approach uses observational data collected from existing bottom trawl fisheries to map fishing exposure. Using the observational approach allows for sampling over a range of bottom fishing exposures that represent actual fishery impacts, which is not achievable using experimental treatments applied on small spatial scales (Thrush et al., 1998; Kaiser et al., 2000a).

Materials and Methods

Study Area

Hecate Strait, BC (Figure 1) is an area of approximately 23,000 km^2 that forms a large portion of the northern BC continental shelf. Glaciations over the last million years have contributed to the diverse littoral sediments, landforms, and bathymetry of the strait (Thompson, 1981). Within Hecate Strait, depths range from approximately 20 to 420 m (Barrie and Bornhold, 1989). Four geological units (tertiary bedrock, glacial till, silts, and sands and gravels) make up the surficial sediment throughout the strait (Barrie and Bornhold, 1989). Near-substrate water velocities up to 0.65 m s^{-1} during summer months, and 0.99 m s^{-1} during winter storms, contribute to sediment erosion and transport and to the creation of substrate ripples, mega-ripples, and sand waves in areas of strong bottom current (Barrie and Bornhold, 1989; Crawford and Thomson, 1991).

Hecate Strait's dynamic environment and wide range of coastal features provide habitat for numerous marine organisms including culturally and economically important groundfish species, such as Pacific halibut (*Hippoglossus stenolepis*), rockfish (*Sebastes sp*.), lingcod (*Ophiodon elongatus*), and flatfishes (e.g. *Atheresthes stomias* and *Eopsetta jordani*) (James, 2003). Such species are directly targeted by First Nations, commercial hook and line, trap, and trawl fisheries, as well as by recreational harvesters (LGL 2004). The Groundfish trawl fishery has been operating in Hecate Strait since approximately 1940 (Beattie, 2002); however effort is not evenly distributed over the region, thus creating a gradient of trawling effort over the various substrate types.

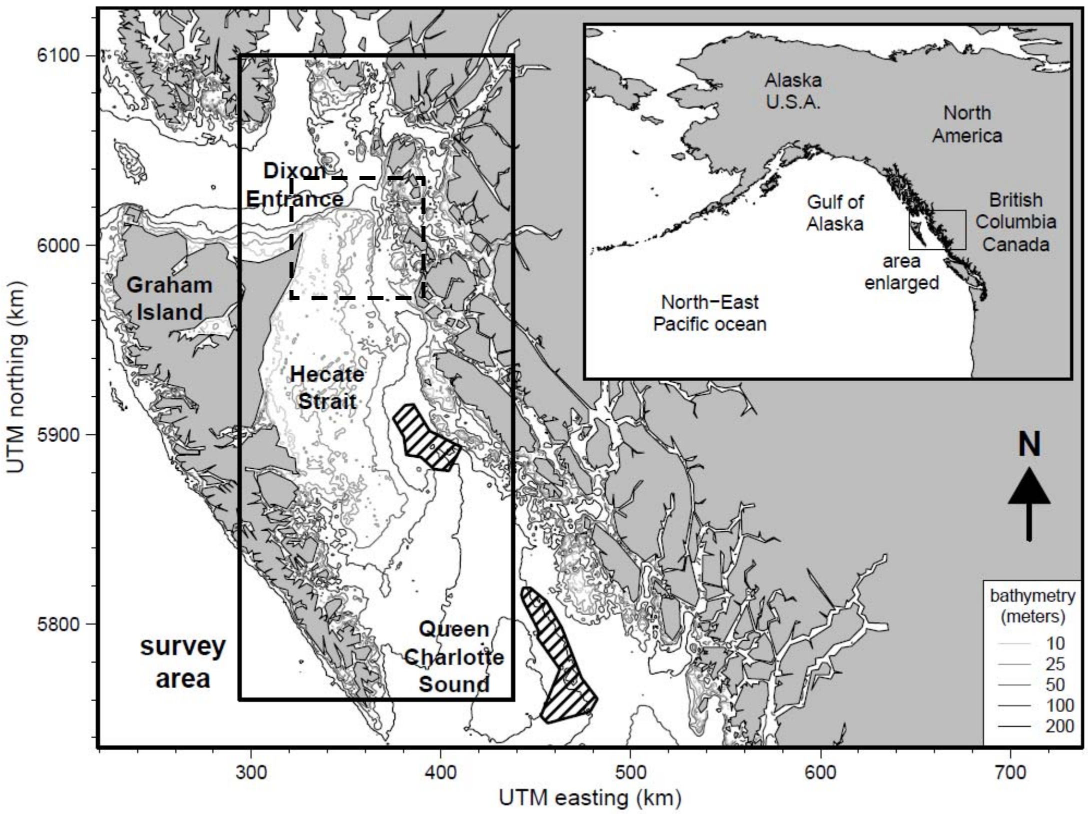

Figure 1: Hecate Strait, British Columbia Canada (black box) and northern Hecate Strait study area (dashed box). Bottom trawling is prohibited in Hexactinellid glass sponge reef protected areas (black hatched polygons). Coordinates are in Universal Transverse Mercator (UTM, zone 9) in kilometres (km).

Bottom Trawl Exposure

I used a bottom fishing exposure analysis developed by Cox et al. (in prep) to stratify my ROV survey. The trawling exposure analysis summarized the spatio-temporal pattern of fishing effort between 1996 and 2009 in each 1 km^2 grid cells of my study area. Geo-referenced location data of Groundfish bottom trawl fishing events, obtained from DFO, were used for the analysis. Trawling event start, mid-point, and end locations were used to calculate the total area swept (km^2) by trawl gear using the distance between start and end points along with an estimate of average door-to-door width of the trawl gear (w = 70 m). Area swept in a given cell and year ($S_{i,y}$) is the total area of that grid cell covered by the trawl gear and can exceed the total area of the cell when effort is high (i.e., > 1 km^2). Each grid cell was then grouped by effort exposure based on average swept area over the 14 year time frame (S_{14}) and the temporal trend of swept area (e.g., increasing or decreasing from 1996 to 2009). Grid cells were stratified by the five effort exposure groups, none, low, decreasing, high, and increasing (Figure 2) to randomly select locations for photographic ROV transects.

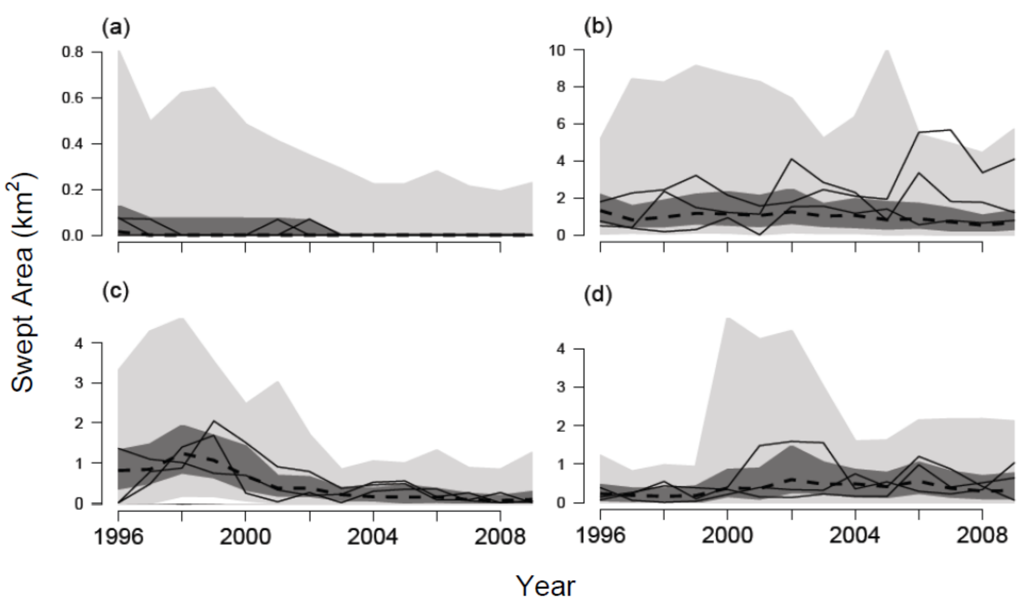

Figure 2: Swept area (km^2) profiles for bottom trawl exposure groups in the northern Hecate Strait survey area from 1996-2009. Thick dashed lines indicate medians, dark and light gray areas indicate 50th and 95th percentile ranges, and thin black lines are trajectories of swept area (km^2) for randomly selected grid cells within the trawl exposure group. Trawl exposure groups are a) low, b) high, c) decreasing, d) increasing, and none (not shown).

Substrate Classification

Substrate type in each 1 km^2 grid cell was determined via surficial geology maps provided by the Pacific division of the Geological Survey of Canada (Barrie and Bornhold, 1989; Barrie et al., 1990). These maps are interpretations of a combination of data sources including acoustic surveys, grab samples, seismic scanning, and other means of ground-truthing. Grid cells categorized as having relatively soft ("Sand/Gravel") or relatively hard (“Till”) bottom types were included in my ROV stratified survey design. Sand/Gravel grid cells were expected to include soft sediments or sediments with small grain size, whereas till sites were expected to have a greater proportion of hard substrates with larger grain size.

Benthic ROV Transects

Remotely operated underwater vehicle surveys were conducted in northern Hecate Strait from August 27 to September 3, 2010. Stratification of Hecate Strait into trawl exposure and substrate categories produced ten treatment groups (Table 1). A total of 31 cells were randomly selected from this design. A photographic survey of 500 m transects of the sea floor was conducted using a PHANTOM DHD2+2 remotely operated vehicle (ROV) equipped with an Olympus SP350 still camera and VEMCO Minilogger depth and temperature logger. Each transect began at a random starting position within the grid cell and was conducted as close as possible to 1 m above the substrate. Photographs were taken every 20 seconds, while temperature and depth were logged every 5 seconds. Photographs were colour-enhanced with *Corel Photo Album 6* software.

Table 1: ROV transects conducted in northern Hecate Strait within each treatment category and the depth (m) range of transects within each category.

Substrate Type (*Geology*)	Trawl Exposure Category	Depth Range (m)	Number of Transects
Sand/Gravel	None	N/A	0
Sand/Gravel	Low	132 – 193	5
Sand/Gravel	Decreasing	119	1
Sand/Gravel	High	80 – 144	6
Sand/Gravel	Increasing	73 – 156	4
Till	None	88 – 107	4
Till	Low	75 – 122	4
Till	Decreasing	106 – 112	3
Till	High	118 – 128	4
Till	Increasing	N/A	0
Total			**31**

I randomly selected between 14 and 22 photographs ($h_i = 1, 2 \ldots n_i$) from each transect for analysis. Transects with higher substrate and species variability received more analysis.

Organisms visible to the naked eye were identified to the lowest taxonomic level possible and the area covered by foundation species was measured. Organisms that could not be identified to the species or genus level were categorized via higher taxonomic groupings. Within each higher level taxonomic group several distinct species may have been observed despite species identification not being possible. The number of distinct species identified within the higher level groups of bryozoans and hydrozoans was not determined due to difficulty of differentiating these species in photographs. *Image-J* software was used, with 10 cm reference points provided by lasers mounted on the ROV, to measure area covered by foundation species and the total area of each photograph. I determined transect level proportional coverage of foundation species via the ratio-of-means estimator, which weights the contribution of each photograph by its area, i.e.

$$p_{FS,t} = \frac{\sum_{j=1}^{j=h_i} A_{FS,j}}{\sum_{j=1}^{j=h_i} A_{T,j}} \qquad \text{equation 1}$$

where $p_{FS,t}$ is the estimated total proportional area covered by foundation species in transect t, h_t is the number of photographs analysed from transect t, $A_{FS,j}$ and $A_{T,j}$ is the area covered by foundation species and total area, respectively in photograph j.

Substrate type was estimated using *Coral Point Count with Excel Extensions* along with DFO's substrate classification scheme for video analysis (Boutillier, personal communication, 2010) that defines substrate types as bedrock, boulders (> 75 cm diameter), cobble (7.5-75 cm), gravel (2-7.5 cm), pea-gravel (0.3-2 cm), sand (> 0.3 cm), and mud. Substrate type was determined at each of 70 randomly placed points on each photograph. The proportion of points associated with each substrate type was then multiplied by the area of the photograph to obtain an estimate of the area covered by each substrate type. Substrate types of sand and mud were indistinguishable in photographs, thus substrates observed to be either sand or mud were grouped into the category sand+mud. The same ratio-of-means estimator was used to determine proportional coverage by each substrate type $p_{K,t.}$, where K indicates the substrate type.

Finally, depths for each transect were averaged across photographs to estimate the mean depth for each transect.

Statistical Analysis

I modeled the relationships between proportional coverage by foundation species, environmental characteristics, and trawling effort exposure using generalized linear models (GLM) with a quasi-binomial error distribution and logit link function because my response variable is a proportion. Thus, the log-odds of proportional coverage is modeled as (subscripts on p are omitted here)

$$log\{p / (1 - p)\} = \beta_0 + \beta_1 X + \beta_2 X_2 + \beta_n X_n \qquad \text{equation 2}$$

where p is the proportional coverage by foundation species, $X_1, X_2, ...X_n$ are explanatory covariates, and $\beta_0, \beta_1, \beta_2, ... \beta_n$ are the regression coefficients. The odds-ratio $p/(1-p)$, which I refer to hereafter as "relative coverage", is then

$$p / (1 - p) = exp(\beta_0 + \beta_1 X + \beta_2 X_2 + \beta_n X_n) \qquad \text{equation 3}$$

In preliminary analyses, I found that proportional coverage was under-dispersed with respect to the assumed binomial error structure, i.e., the variance of proportional coverage was less than that expected from the mean-variance relationship of the binomial distribution. Therefore, I used a quasi-binomial error distribution that incorporates an additional dispersion parameter, so the variance of the quasi-binomial distribution takes the form $\mathrm{var}(y) = \phi\mu(1-\mu)$, where μ is the mean proportion of foundation species coverage observed and ϕ is the dispersion parameter (Warton and Hui, 2011).

Independent variables available for use in models included depth, substrate, and trawling effort. I included variables that commonly influence benthic epifauna abundance and distribution (Collie et al., 2000b; Burd et al., 2008). I used the continuous measure of trawl area swept in each 1 km^2 grid cell, temporally averaged across all fourteen years (S_{14}), as the trawling effort variable for foundation species models. The trawl effort categories used to stratify the survey design were not used because a complete survey was not achieved during the research cruise and not all effort category/substrate type combinations were sampled. As an in-situ variable for substrate type, I used the proportional coverage of sand+mud (p_{sm}). All other substrate types were excluded from further analyses because their measured ranges were narrow and not expected to have a differential effect on the coverage of foundation species within the survey area.

I developed two global models to compare the accuracy of model estimates based on direct in-situ observations rather than inferred substrate maps. The first, In-situ Substrate Model (ISSM), included depth (d), in-situ proportional coverage of sand+mud (p_{sm}), and average area swept by bottom trawl gear (S_{14}). The second model, Mapped Substrate Model (MSM), included depth, average area swept, and the inferred substrate type *Geology*. Due to the small sample size of 31 transects, interactions were not explored (Grueber et al., 2011). ISSM and MSM were checked for conformity to generalized linear model assumptions using diagnostic plots.

Independent regression variables p_{sm} and d were standardized in order to compare their coefficients on the same scale.

$$Stp_{sm,t} = \left(p_{sm,t} - \overline{p_{sm}}\right) / sdp_{sm} \qquad \text{equation 4a}$$

$$Std_t = \left(d_t - \overline{d}\right) / sd.d \qquad \text{equation 4b}$$

$Stp_{sm,t}$ is the standardized value of p_{sm} for a given transect, $\overline{p_{sm}}$ is the mean percent cover of sand+mud over all transects (96.2%), and sdp_{sm} is the standard deviation of p_{sm} (6.64%). Std_t is the standardized depth for transect t, $\overline{d}$ is the mean depth over all transects (117.5 m), and $sd.d$ is the standard deviation of depth (32.3 m). I chose to interpret the trawl effort coefficient without standardization, because my main objective was to assess the impacts of trawling.

All possible subsets of ISSM and MSM were examined to identify the set of models that best fit the data under each model scenario. For each model, a subset of the most plausible models was selected using the quasi-AICc model selection criteria corrected for small-sample bias (*QAICc*). In order to make inferences based on the weighted support from the subset of models, models with ≤ 95 percent of the cumulative *QAICc* weights were averaged. Model averaging produced coefficient estimates for independent variables found in the top subset of models (Burnham and Anderson, 2002).

Model subsets of the global models ISSM and MSM are not directly comparable using the information criterion QAICc because they are developed out of different global models with unique dispersion parameters (Burnham and Anderson, 2002). QAICc is calculated as:

$$QAICc = -2\log\left(L\left(\hat{\theta}\right)\right) / \hat{\phi} + \frac{2k(k+1)}{n-k-1} \qquad \text{equation 5}$$

where $L(\hat{\theta})$ is the likelihood of the model estimated parameters given the data, $\hat{\phi}$ is the estimated dispersion parameter of the global model, k is the number of parameters in the model, and n is the sample size. Model subsets are only comparable by QAICc if developed from the same global model because the dispersion parameter can significantly influence QAICc values (Burnham and Anderson, 2002). To compare the relative support for the in-situ substrate variable p_{sm} versus pre-stratified *Geology,* I developed a final global model, All Substrate Variables Model (ASVM), which included both substrate variables (Table 2). This allowed for direct comparison of the support for each substrate variable as a potential predictor variable of foundation species coverage via the relative variable importance of each variable (RVI, i.e., sum of the QAICc weights re-scaled relative to 1.0 for the top models that contained a given variable).

Table 2: GLMs used to model proportion of foundation species (p_{FS}). In-situ Substrate Model (ISSM) and Mapped Substrate Model (MSM) vary by substrate variables (Stp_{sm} or Geology, respectively); All Substrate Variables Model (ASVM) includes both p_{sm} and Geology.

Model	Structure
ISSM	$logit(p_{FS}) \sim Std + Stp_{sm} + S_{14}$
MSM	$logit(p_{FS}) \sim Std + Geology + S_{14}$
ASVM	$logit(p_{FS}) \sim Std + Stp_{sm} + Geology + S_{14}$

Other statistics were also used to compare model fits of ISSM and MSM. Squared measures of Pearson's correlation (r^2; coefficient of determination) between the observed and model estimated response were used to compare the amount of variability in the data that was explained by each model (Taylor, 2001). The mean error (ME; the mean difference between the measured and model estimated percent cover of foundation species across all transects) and the root mean squared error (RMSE; the square root of the mean squared difference between measured and model estimated percent cover of foundation species across transect sites) were also calculated for each final model. The mean error served as an estimate of model bias and the root mean squared error was used to assess model accuracy (Willmott 1982; Peterson et al. 2004).

Results

Summary Results from ROV Transects

ROV transect sites ranged from 74 to 193 m in average depth, and average trawl area swept (S_{14}) ranged from 0 to 6.3 km^2. The minimum observed cover of sand+mud substrate (p_{sm}) was 76% and the maximum was 100%. Transects in areas with higher proportions of hard substrate (< 90% p_{sm}; 19% of transects) were only conducted at the lower end of the depth range (75 to 130 m) and area swept range (S_{14} from 0-0.66 km^2). Whereas transects dominated by soft substrate (>90% p_{sm}; 81% of transects) occurred over the full range of surveyed depth and trawling effort except where both depth and trawling effort were highest (Table 3).

Table 3: Characteristics of 1 km^2 grid cells (Trawl Effort Class, Geology, and Mean Trawl Area Swept) and ROV transects (Mean depth, % Cover Sand+Mud, and % Cover Foundation Species, as well as number of photos analyzed). Trawl effort class was used for stratification of the ROV survey. S/G = Geology type Sand/Gravel.

Trawl Effort Class	*Geology*	Mean Trawl Area Swept (S_{14})	Mean Depth (d)	% Cover Sand+Mud (p_{sm})	% Cover Foundation Species (p_{FS})	No. photos analyzed
Low	S/G	0.02	188	100	0.000	20
Low	S/G	0.10	176	100	0.000	15
Declined	Till	0.24	115	100	0.000	20
Declined	Till	0.26	107	100	0.000	20
Increased	S/G	0.44	157	100	0.000	14
Steady	S/G	1.08	132	100	0.000	14
Steady	Till	2.29	128	100	0.000	14
Steady	S/G	4.51	105	100	0.000	14
Steady	S/G	1.51	130	100	0.006	20

Trawl Effort Class	*Geology*	Mean Trawl Area Swept (S_{14})	Mean Depth (d)	% Cover Sand+Mud (p_{sm})	% Cover Foundation Species (p_{FS})	No. photos analyzed
Increased	S/G	1.07	77	100	0.007	14
Increased	S/G	0.92	83	100	0.007	14
Low	S/G	0.02	132	100	0.024	14
Declined	S/G	0.24	119	99	0.037	14
Steady	S/G	1.51	144	100	0.043	22
Low	S/G	0.05	193	100	0.043	14
Steady	S/G	6.26	80	100	0.051	20
Steady	Till	0.20	118	96	0.054	14
None	Till	0.00	88	99	0.054	14
Low	S/G	0.38	163	100	0.085	19
Declined	Till	0.56	112	88	0.110	14
Low	Till	0.03	122	97	0.129	14
Steady	S/G	1.64	97	100	0.226	14
None	Till	0.00	87	93	0.280	14
Steady	Till	1.23	120	97	0.284	20
Increased	S/G	0.64	74	100	0.302	22
Low	Till	0.03	106	98	0.321	14
Steady	Till	0.66	128	90	0.351	14
None	Till	0.00	107	85	1.250	14
None	Till	0.00	91	85	1.255	22
Low	Till	0.03	88	80	2.185	20
Low	Till	0.01	76	76	4.413	22

I identified 32 unique foundation species in 31 ROV transects (Table 4). Dominant species included hydroids, scallop sponges (*Mycale adhaerens* or *Myxilla parasitica*), and other unidentified sponges. Overall, foundation species covered very small proportions of the surveyed area; the maximum percent cover of foundation species observed was 4.4%, but the majority of transects ranged between 0 and 1 percent coverage of foundation species in the analyzed photos (Table 3).

Table 4: Foundation species encountered in analyzed photographs from ROV transect surveys in northern Hecate Strait, BC. The number of occurrences, total area covered (cm²) by each species or taxonomic group, and the number of transects in which the species or group occurred are reported. UNID = unidentified; organisms of this class may be composed of several different species.

Group	Organism	Occurrences	Area (cm^2)	No. Transects
Anemones	Crimson anemone (*Cribrinopsis fernaldi*)	2	10.8	2
	Plumose anemone (*Metridium farcimen*)	4	126.7	2
	UNID Anemone (Phylum Cnidaria; Class Anthozoa); 1 species	3	39.8	3
Bryozoans	Rabbit-ear bryozoan (*Cellaria diffusa*)	19	87.0	4
	Spindly white tuft bryozoan (*Crisia sp.*)	136	201.46	6
	Staghorn bryozoan (*Heteropora sp.)*	120	473.5	5
	Thicker white tuft bryozoan (*Crisia sp.*)	15	51.8	3
	UNID Bryozoan (*Phylum Bryozoa*)	135	588.1	3
Corals	Orange cup coral (*Balanophyllia elegans*)	178	73.8	5
	UNID White soft coral (Phylum Cnidaria; Class Anthozoa); 1 species	1	8.0	1
Hydrocorals	Pink branching hydrocoral (*Stylaster sp.*)	5	13.1	1
Hydroids	Coarse sea fir hydroid (*Abietinaria sp.*)	4	159.0	2
	Embedded sea fir hydroid (*Thuiaria sp.*)	14	137.2	3
	Spindly embedded hydroid (*Grammaria sp.*)	15	96.7	2
	UNID Hydroids (Phylum Cnidaria; Class Hydrozoa)	153	1409.8	18
	Wine glass hydroid (*Obelia longissima*)	7	37.5	2
Sea Whip	Sea Whip (*Halipteris willemoesi*)	3	15.0	2
Sea Pen	Orange Sea Pen (*Ptilosarcus gurneyi*)	2	5.7	2
Sponges	Cloud sponge (*Aphrocallistes vastus*)	1	16.0	1
	Funnel shaped sponge (*Phakellia sp.*)	1	6.0	1
	Orange encrusting sponge (*Hamegera sp.*)	3	79.5	1
	Scallop Sponge (Mycale adhaerens or *Myxilla parasitica*)	247	2808.6	6
	Tough yellow branching sponge (*Syringella amphispicula*)	1	44.4	1
	UNID Sponge (Phylum Porifera); 14 distinct species	222	2050.4	10
	Yellow boring sponge (*Cliona californiana*)	74	130.9	3
	Yellow encrusting sponge (*Myxilla lacunosa*)	5	22.1	3

Group	Organism	Occurrences	Area (cm^2)	No. Transects
Tubeworms	Red trumpet calcareous tubeworm (*Serpula columbiana*)	15	1.2	3
	UNID Feather duster tubeworm (Phylum Annelida; Subclass Sedentaria); 1 species	32	54.5	5
	Twin eyed feather duster tubeworm (*Myxicola infundibulum*)	18	37.1	6
Tunicates	Gray encrusting compound tunicate (*Diplosoma listerianum*)	1	4.6	1
	UNID Tunicate (Phylum Chordata; Subphylum Tunicata); 3 distinct species	12	117.8	3
Zoanthids	Orange zoanthid (*Epizoanthus scotinus*)	1	96.0	1

Differences between survey sites were apparent through visual inspection of photographs for some, but not all sites. For instance, sites characterized by the highest percent cover of hard substrate, shallow depths, and low average trawling effort, showed the highest abundances of foundation species (Figure 3). In contrast, transects with no foundation species were found at various depths and trawling effort ranges, usually where substrate type was dominated by sand and mud (Figure 4).

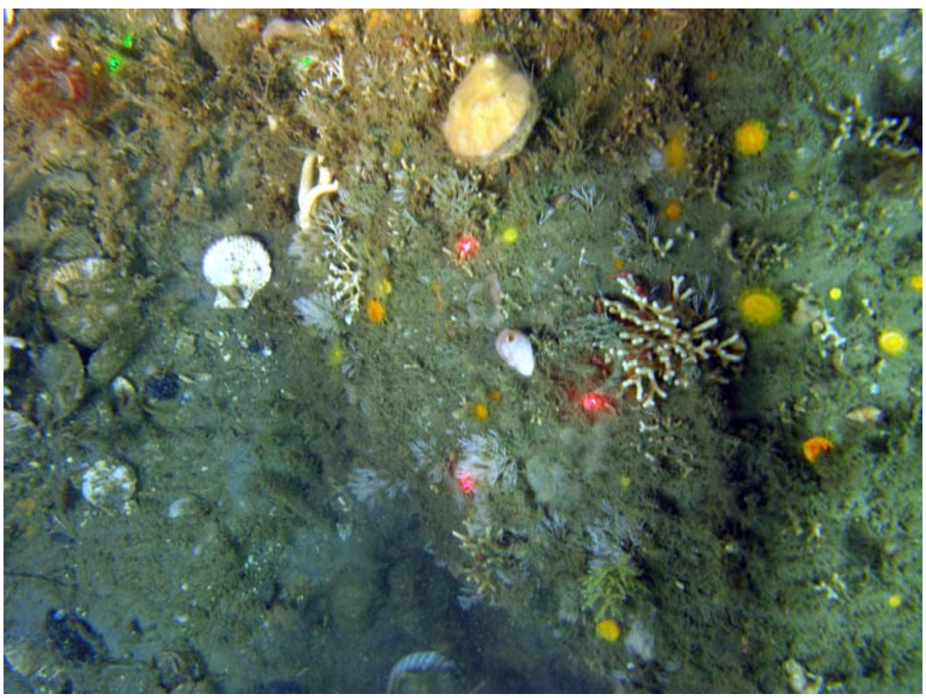

Figure 3: Example photograph from photographic ROV transect in a shallow, till site with little trawling effort.

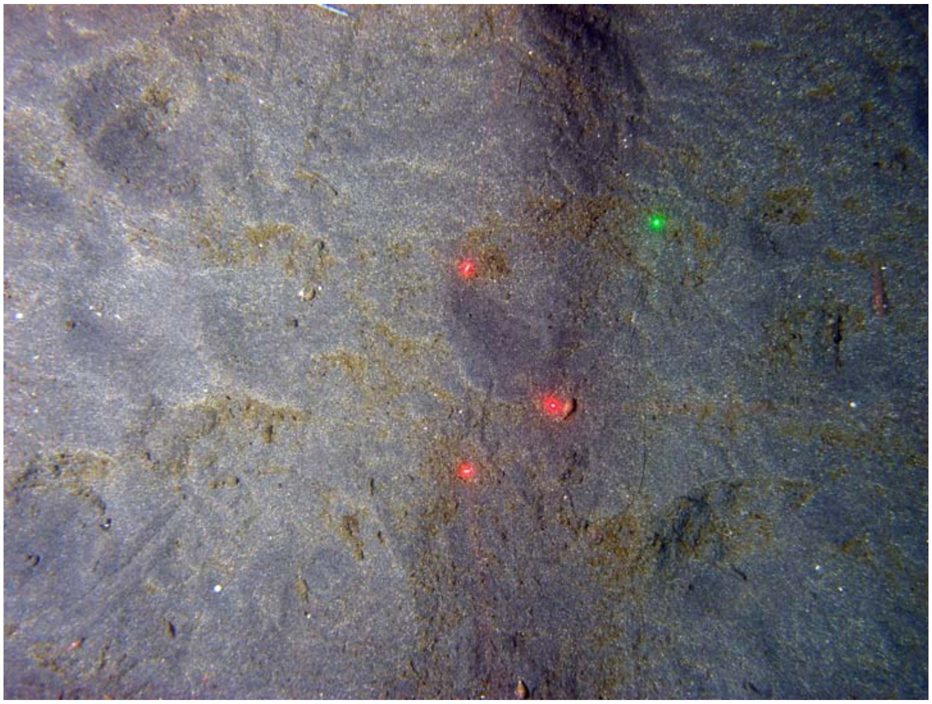

Figure 4: Example photograph from photographic ROV transect in a sand/gravel site with high trawling effort.

Modeling Percent Cover of Foundation Species

I used quasi-binomial regression to model the percent cover of foundation species using observed survey site characteristics. For both ISSM and MSM, the most plausible subset of models (cumulative QAICc weight of ≤ 95%) included all modeled main effects; a measure of substrate type (either p_{sm} or *Geology*), depth (d), and average area swept by trawl (S_{14}) (Table 5).

Relative variable for the in-situ substrate model (ISSM) showed that the proportional coverage by sand+mud and average depth had the highest importance (RVI = 1.00 and 0.75, respectively) followed by the average swept area (RVI = 0.26; Table 6). As expected, the proportional coverage by sand+mud (Stp_{sm}) was found to have a strong negative effect on the relative coverage (i.e., $p/(1-p)$) of foundation species. Depth (standardized for the model, *Std*) and area swept (S_{14}) were also negatively associates with relative coverage of foundation species; however, the confidence intervals of both coefficient estimates included 0 (Table 6).

Table 5: The most plausible subsets of candidate models (cumulative QAICc weight of ≤ 95%) from global models ISSM and MSM. Intercept, Stp_{sm}, Geology, Std, and S_{14} are parameters for the model intercept, the proportion of substrate composed of sand+mud (standardized), Geology ("Till" or "Sand/Gravel"), depth (standardized), and average area swept by trawl gear.

Model	Parameters	No. of parameters	QAICc	△QAICc	Weight
In-Situ Substrate Model (ISSM)					
1	*Intercept, Std,* Stp_{sm}	3	39.65	0.00	0.49
2	*Intercept,* Stp_{sm}, S_{14}, *Std*	4	40.95	1.29	0.26
3	*Intercept,* Stp_{sm}	2	40.98	1.33	0.25
Mapped Substrate Model (MSM)					
1	*Intercept, Std, Geology*	3	24.35	0.00	0.78
2	*Intercept, Std, Geology,* S_{14}	4	26.87	2.521	0.22

Table 6: In-Situ Substrate Model (ISSM) averaged results. Mean coefficient estimates and their unconditional standard errors (i.e., incorporates model selection uncertainty) and confidence intervals. Measures of relative variable importance (RVI) of independent variables present in the top subset of plausible models (cumulative QAICc weight of ≤ 95%). Model fit statistics include ME, mean error; RMSE, root mean square error; and r^2, coefficient of determination.

Parameter	Coef. Estimate	Unconditional Standard Error	Confidence Interval (95%)	RVI	ME	RMSE	r^2
Intercept	-6.716	0.212	(-7.132, -6.301)		0.18%	14%	0.98
Stp_{sm}	-1.085	0.141	(-1.361, -0.809)	1.00			
Std	-0.348	0.284	(-0.805, 0.208)	0.75			
S_{14}	-0.060	0.149	(-0.354, 0.233)	0.26			

Uncertainty in ISSM estimated percent cover of foundation species varies over the ranges of depth, sand+mud, and trawling effort over which ROV transects were conducted (Figure 5). Confidence intervals (95%) surrounding estimates of foundation species cover increase in areas of low sand+mud, especially when trawling effort and depth are high.

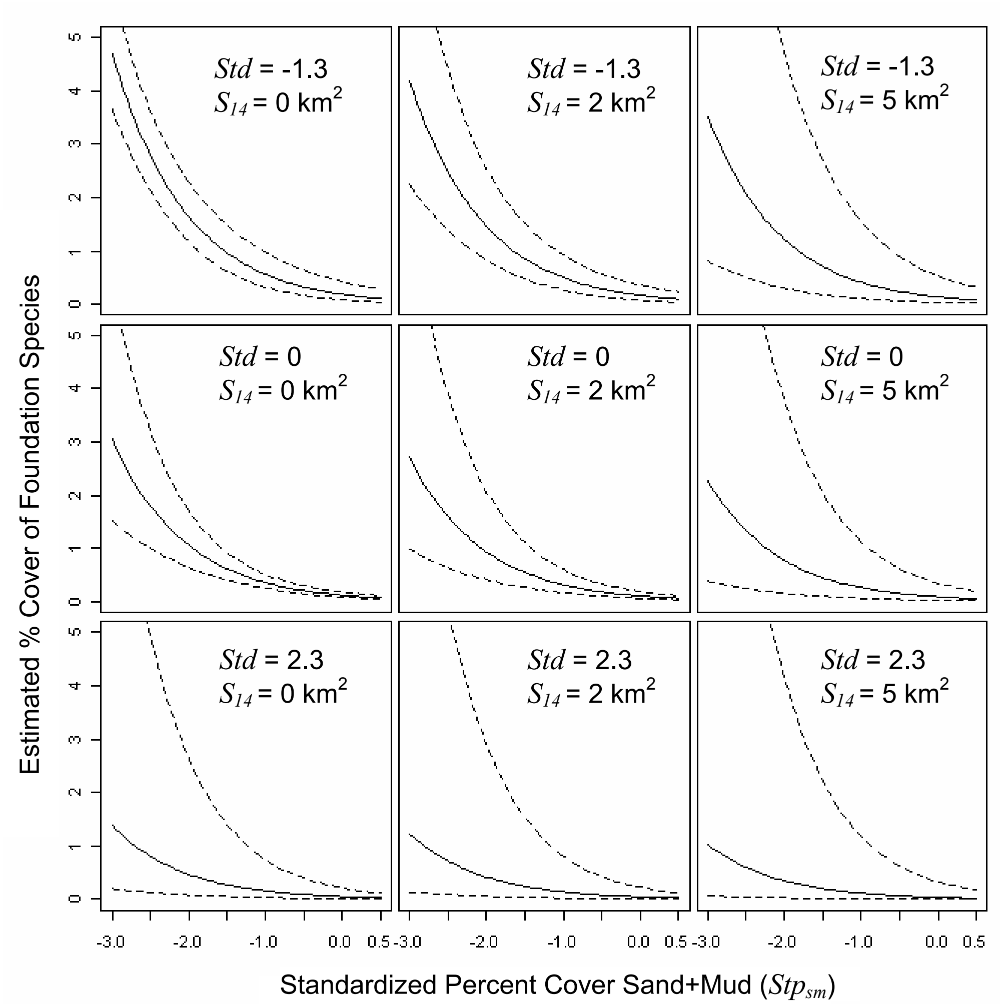

Figure 5: In-Situ Substrate Model (ISSM) estimates of percent cover of foundations species over a range of proportion coverage of sand+mud (Stp_{sm}). Solid lines represent the average response from the coefficient estimates ± 95% confidence intervals (dashed lines). From left to right plots increase in trawl area swept (S_{14}). From top to bottom plots increase in standardized depth (Std).

In the MSM model, the relative variable importance of depth and *Geology* were 1.00, indicating that they were present in all of the top model subsets and are supported as important predictors of foundation species coverage. Similar to ISSM, average swept area was found to have the lowest relative variable importance (RVI = 0.22; Table 7).

The *Geology* type sand/gravel was found to have the strongest negative association with the relative cover of foundation species followed by depth (*Std*). Confidence intervals for these coefficients do not include 0. Trawl area swept was also found to have a small negative association with relative cover of foundation species, however magnitude and direction of the effect were again uncertain, as shown by the confidence interval of the coefficient estimate encompassing 0 (Table 7). In both till and sand/gravel sites, greater uncertainty in model estimated foundation species coverage is observed in areas of high trawling effort and low depth (Figures 6).

Table 7: Mapped Substrate Model (MSM) averaged results. Mean coefficient estimates and their unconditional standard errors (i.e., incorporates model selection uncertainty) and confidence intervals. Measures of relative variable importance (RVI) of independent variables present in the top subset of plausible models (cumulative QAICc weight of ≤ 95%). Model fit statistics include ME, mean error; RMSE, root mean square error; and r^2, the coefficient of determination.

Parameter	Coef. Estimate	Unconditional Standard Error	Confidence Interval (95%)	RVI	ME	RMSE	r^2
Intercept	-6.132	0.684	(-7.473, -4.791)		0.09%	49%	0.70
Sand/Gravel[T]	-2.572	1.269	(-5.059, -0.085)	1.00			
Std	-2.030	0.732	(-3.456, -0.595)	1.00			
S_{14}	-0.071	0.341	(-0.739, 0.597)	0.22			

[T] *Till* was the reference category.

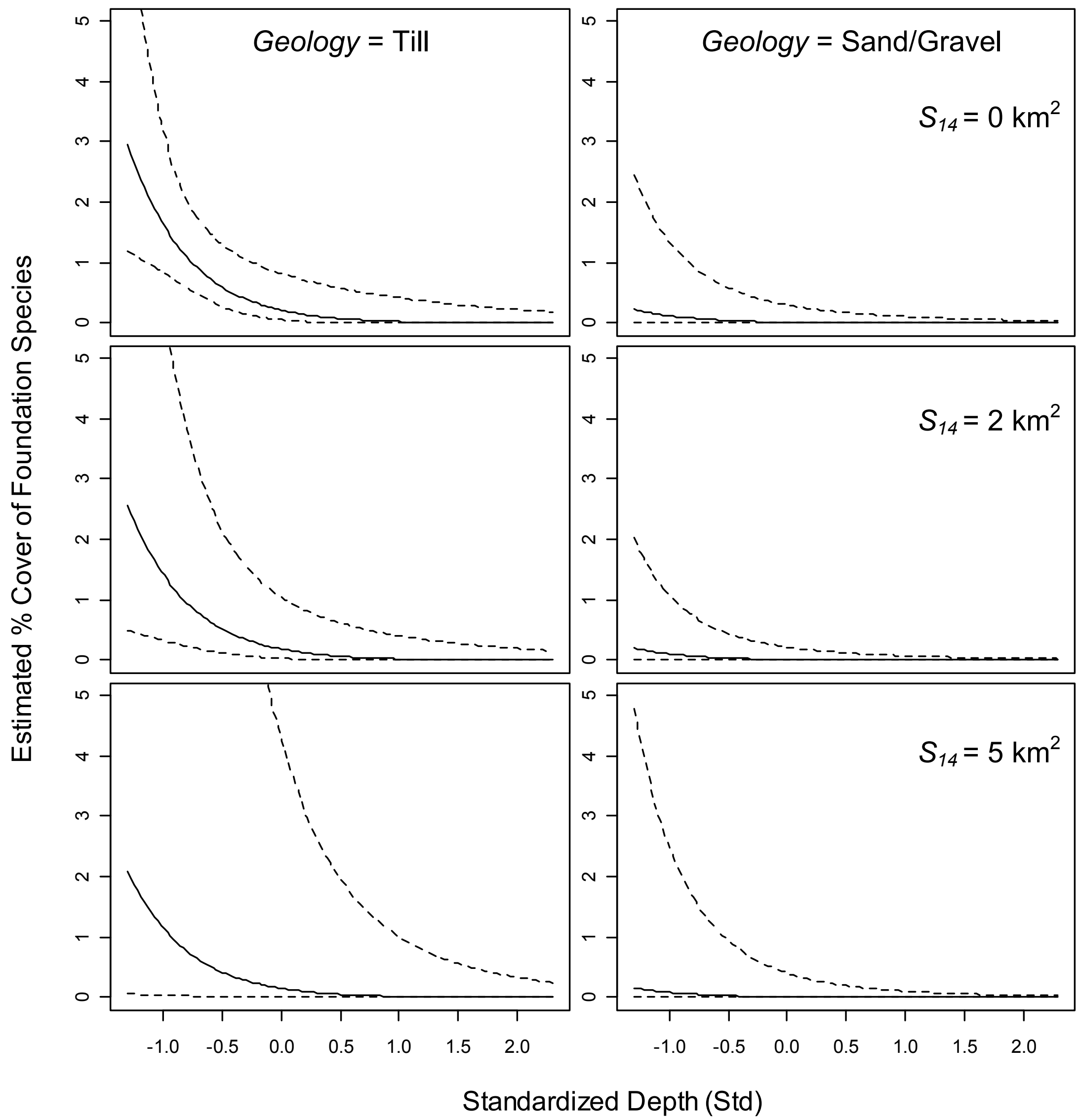

Figure 6: Mapped Substrate Model (MSM) estimated percent cover of foundations species over a range of standardized depth for Geology = Till (left panels) and Geology = Sand/Gravel (right panels). Solid lines represent the average response from the coefficient estimates ± 95% confidence intervals (dashed lines). From top to bottom plots increase in average area swept (S_{14}) as indicated in the right panels.

When both Geology and p_{sm} were included in the global model (ASVM), p_{sm} was selected in all model subsets (Table 8). Model subsets that included *Geology*, although selected in the top models (cumulative QAICc weight of ≤ 95%), had lower relative support (ΔQAICc > 2.20) and *Geology* was only selected as a variable of importance for estimating foundation species coverage in two model subsets (Table 8). The relative variable importance of *Geology* (RVI = 0.18) declined below that of both depth (d) and average area swept (S_{14}), whereas the relative variable importance of p_{sm} remained high (RVI = 1.00; Table 9). As with ISSM and MSM, depth and average area swept by trawling were also supported as important variables for estimating foundation species coverage (RVI of 0.66 and 0.26; Table 9).

Table 8: The most plausible subsets of candidate models (cumulative QAICc weight of ≤ 95%) from the All Substrate Variables Model (ASVM). Intercept, Stp_{sm}, Geology, Std, and S_{14} are parameters for the model intercept, the proportion of substrate composed of sand+mud (standardized), Geology ("Till" or "Sand/Gravel"), depth (standardized), and average area swept by trawl gear.

Model	Parameters	No. of parameters	QAICc	∆QAICc	Weight
1	*Intercept*, Stp_{sm}, *Std*	3	38.55	0.00	0.36
2	*Intercept*, Stp_{sm}	2	39.74	1.18	0.20
3	*Intercept*, Stp_{sm}, S_{14}, *Std*	4	39.91	1.35	0.19
4	*Intercept*, Stp_{sm}, *Geology* , *Std*	4	40.77	2.21	0.12
5	*Intercept*, Stp_{sm}, S_{14}	3	41.76	3.21	0.07
6	*Intercept*, Stp_{sm}, *Geology*	3	42.07	3.51	0.06

Effects of individual parameters of the ASVM on the relative cover of foundation species were similar to those of the ISSM. Proportion coverage of sand+mud, $p_{sm,}$ had the largest negative association, followed by depth (Table 9). In this model, the negative association of sand/gravel and of average area swept were similarly small in magnitude (Table 9). Confidence intervals of the parameter estimates for Geology, depth, and swept area all included 0 when both *Geology* and p_{sm} were included in the same model (Table 9).

Table 9: All Substrate Variables Model (ASVM) averaged results. Mean coefficient estimates and their unconditional standard errors (i.e., incorporates model selection uncertainty) and confidence intervals. Measures of relative variable importance (RVI) of independent variables present in the top subset of plausible models (cumulative QAICc weight of ≤ 95%). Model fit statistics include ME, mean error; RMSE, root mean square error; and r^2, the coefficient of determination.

Parameter	Coef. Estimate	Unconditional Standard Error	Confidence Interval (95%)	RVI	ME	RMSE	r^2
Intercept	-6.700	0.228	(-7.143, -6.251)		0.21%	13%	0.98
p_{sm}	-1.091	0.146	(-1.378, -0.805)	1.00			
Std	-0.313	0.293	(-0.886, 0.261)	0.66			
S_{14}	-0.055	0.150	(-0.350, 0.239)	0.26			
Sand/Gravel[T]	-0.061	0.250	(-0.551, 0.429)	0.18			

[T] *Till* was the reference category.

ISSM, MSM, and ASVM varied in their ability to estimate the percent cover of foundation species. Small values of mean error (ME < 1%) were observed for all three models, suggesting that the models were all relatively unbiased (Tables 6, 7, and 9). Estimates of the root mean squared error for ISSM and AVSM (RMSE = 14% and 13%, respectively) demonstrated a higher level of accuracy for these models than for MSM (RMSE = 49%). Pearson's correlations also show that ISSM and ASVM (r^2 = 0.98 for both) explain a greater proportion of the data's variance than MSM (r^2 = 0.70; Figure 7).

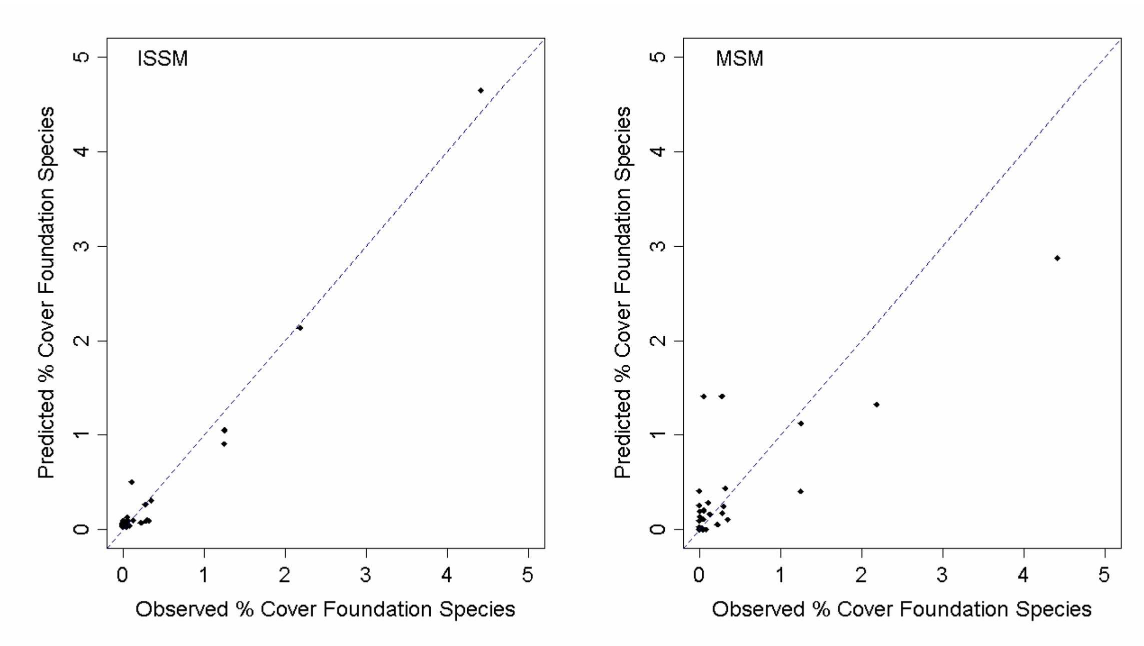

Figure 7: Observed percent cover of foundation species plotted against model estimated percent cover of foundations species from the In-Situ Substrate Model (ISSM; left) and the Mapped Substrate Model (MSM; right). The grey dashed line is the 1:1 line, where points would fall if the observed and estimated measures were perfectly correlated (i.e., if models were 100% accurate and unbiased).

Discussion

My research aimed to assess the impact of bottom trawl fishing on the coverage of foundation species in northern Hecate Strait. Using direct visual observations via ROV surveys, I demonstrated that proportional coverage of the seafloor by benthic foundation species in northern Hecate Strait is dependent (in order of importance) on bottom substrate type, depth, and the average area swept by bottom trawl gear over the past 14 years. However, despite consistent ranking as an important predictor of foundation species coverage, the effects of bottom trawl fishing remain highly uncertain, mainly because of the small sample size of my survey and high local environmental variability in Hecate Strait.

As expected, substrate type proved to be the most influential predictor of foundation species coverage in Hecate Strait. Regardless of whether substrate was inferred from substrate maps or measured from in-situ photographs, foundation species coverage was negatively associated with greater coverage of soft substrates such as sand and mud. These results are similar to other studies showing that the prevalence, coverage, and biomass of sessile, encrusting, and emergent biota is typically highest on stable, hard substrates such as gravel, cobble, boulders, and bedrock (Burd et al., 2008; Barrie et al., 2011; Lambert et al., 2011). The ecological reasons are somewhat obvious as many sessile, emergent fauna, including those present in BC waters, such as Hexactinellid (glass) sponges and the reef-building coral *Lophelia pertusa*, require hard substrate to attach and develop (Cimberg et al., 1981; Leys et al. 2007). Areas dominated by sand and mud would therefore be at lower risk of impact by bottom trawling for the primary reason that sensitive habitat-forming species are naturally less likely to occur in these areas. Thus, an important step in ecosystem based management planning is to develop reliable estimates of substrate on relatively fine spatial scales.

The use of substrate type as an indicator of potential foundation species presence or abundance is problematic for a few reasons. First, as my analyses indicate, all model estimates were more accurate when in-situ measures of substrate type were used compared to substrate inferred from maps. In-situ measures of substrate type are obviously challenging to obtain. Second, there are inconsistencies in model support for alternative substrate variables, which most likely arises from prediction error within substrate mapping. Surficial geology categories within each of my 1 km^2 grid cells is based on cluster analysis of several substrate classification techniques that integrate bottom type information over large spatial scales. This averaging process causes a loss of information at levels of 1 km^2 grid cells, and especially at finer scales of 1 m^2 photographs. For example, although 14 ROV transects were conducted in grid cells initially categorized as till based on inferred maps, no transect actually took place over large percentages of till, or hard substrate, and all but 6 transects had greater than 90 percent cover of sand+mud. Thus, sites pre-stratified as till were either incorrectly categorized due to limitations of substrate mapping, or are highly variable, with large patches of soft, sand and mud substrate interspersed among areas of hard, gravel, cobble, and boulder substrates.

Depth, which frequently plays a role in the distribution of marine species, also consistently ranked high in relative importance as a covariate of foundation species coverage. Again, foundation species coverage was found to be negatively associated with increased depth. These results are not surprising as depth is often correlated with other environmental variables, such as temperature and dissolved oxygen content, which can be limiting factors in marine species distributions (Zimmerman, 2006). In the South Pacific, shallow slope areas tend to hold the most diverse and greatest densities of invertebrate megafauna (Williams et al. 2011), which is consistent with the negative association I found between depth and coverage of foundation species. Other research, in various marine ecosystems, such as temperate latitude rocky reefs (Williams and Leach, 1999), submarine canyons (Vetter and Dayton, 1998), coral reefs (Cleary et al., 2005), and in the Strait of Georgia, BC, an area similar to Hecate Strait in depth profiles and proximity (Burd et al. 2008), also consistently show depth to be an important factor in determining the composition of benthic invertebrate assemblages.

The relative variable importance and certainty of the parameter estimate for depth varied across the models I examined. Uncertainty in the effect of depth may have been caused by the narrow depth range over which I conducted ROV transects (approximately 125 m from shallowest to deepest sites). Other studies showing effects of depth on species assemblages often occur over several hundred meters (Vetter and Dayton, 1998; Williams and Leach, 1999; Cleary et al., 2005). Greater contrast in species responses would be expected across very wide ranges of depth, but may not have been observed over 125 m. As well, uncertainty in the direction and magnitude of the effect of depth was more prevalent in models which used in-situ substrate measures. This may be an artefact of the lack of balance across all substrate, depth, and trawling effort combinations. For instance, sites categorized as the *Geology* type “till” were surveyed only in the shallow end of the survey depth range and were also the only sites observed to have high foundation species percent cover. Thus, as an artefact of the data, shallower depths may have become inherently associated with high percent cover of foundation species, causing the negative association between depth and foundation species to be more certain. When the proportion cover of sand+mud was used, uncertainty in the negative association between depth and foundation species coverage increased. Shallow depths were associated with highly variable foundation species cover, whereas foundation species cover was consistently low in transects at deeper sites. The variability of responses in the shallow range, uncoupled from the categorized substrate type, may have reduced the strength of the relationship between foundation species cover and depth when in-situ substrate was used.

Although the relative variable importance of trawl area swept consistently ranked lower than that of depth and in-situ substrate in all three models, the association between swept area and foundation species coverage is qualitatively similar to other bottom trawling impact studies. Point estimates of the swept area coefficient suggest that as trawling effort increases in a given grid cell, there is a corresponding decrease in foundation species coverage. Such a negative association is consistent with numerous studies of the direct and cumulative impacts of bottom trawling (Collie et al., 2000a; Pitcher et al., 2000; Hinz et al., 2009).

However, considerable uncertainty in the direction and magnitude of the trawling effect was observed in all models. Reasons for this uncertainty are similar to the reasons for uncertain effects of depth described above; that is, low sample size and lack of balanced representation of other factors across gradients of trawling effort. For example, in my ROV survey substrate was generally composed of high proportions of sand+mud in all transects (from 76-100% sand+mud cover). ROV transects that did encounter some hard substrate were only conducted in areas with low trawling effort (0-0.66 km^2). The magnitude of an effect of trawling over such a small gradient of trawling effort (in the hard substrate sites) would be smaller than over the entire trawling effort gradient, thus the probability of detecting a change in foundation species coverage is also small, especially given the small sample size and the variability in foundation species responses (Peterman, 1990).

The under-dispersed nature of the data may also have contributed to the lack of power in my study. For binomial models, in which the response variable is proportional (i.e., ranging from 0 to 1), under-dispersion is indicated by a residual variance that is lower than expected from a binomial distribution. Under-dispersion is rarely found in natural environments. One example can be found in offspring sex ratios of species that can select the sex of their offspring and who benefit from producing one sex over the other. The odds of producing the less beneficial sex are much lower than that expected by the binomial variance relationship (Aviles et al., 2000). In the case of foundation species, their patchily distributed, rare, or clumped populations are observed less than homogenously distributed populations (Ysebaert et al., 2002), leading to under-dispersion of the data. Here, the ratio of area covered by foundation species was very low in comparison to the area not covered, i.e., the probability of observing large relative coverage of foundation species is lower than that expected from the binomial distribution and thus only very small proportional coverage of foundation species was observed. Given the inherently small range of foundation species relative cover that may be observed, a larger sample size will be required to detect changes in foundation species cover caused by bottom trawling.

Variability in foundation species coverage is expected to increase when examining impacts of bottom fishing using an observational approach at the scale of the fishery, rather than in a controlled, experimental setting. The BC Groundfish trawl fishery is not uniform over space or time (Sinclair, 2007). Grid cells with high average area swept may experience intense fishing in only a portion of their area, but remain untrawled in others. Trawling effort also changes over time in any given grid cell. Technology that allows harvesters to hone in on precise fishing locations, and management tools that create incentives to reduce catch of non-target species, play a role in concentrating fishing effort to smaller areas (Kaiser et al, 2000b). Simultaneously, areas have also experienced increased fishing effort over time (Cox et al., in prep). These spatio-temporal patterns of the bottom trawl fleet may influence the response of foundation species. For example, Pitcher et al. (2000) found that areas where trawling effort was high, but also highly aggregated, were less impacted than areas where fishing is randomly or uniformly distributed. Pitcher et al. (2000) also suggested that unfished patches of the fishing ground, caused by deliberate or chance avoidance of trawl vessels, may provide refuge for foundation species, and be a source of recruits to disturbed areas, and areas that once were fished may experience recovery if fishing diminishes or is removed completely (Kaiser et al., 2006). Given the spatio-temporal dimension of the fishery, the responses of epibenthic fauna are likely to be less clear when measured at large scales than those gained from exploring the direct impact of trawling in experimental studies. Including the effort exposure classification developed by Cox et al. (in prep) as a model covariate to account for spatio-temporal fishing patterns is an important next step for benthic impacts research. Using such measures of fishing activity will allow researchers to explore questions such as i) is there potential for recovery in areas that have experienced decreased trawling over time? ii) If recovery is observed, what time frame is required to achieve partial or full recovery? and iii) if recovery is not observed, does bottom trawling pose a risk of irreversible harm to benthic ecosystems?

A fundamental assumption of my research is that reduced foundation species coverage leads to a reduction in habitat complexity, which may in turn, adversely affect species that rely on niche spaces provided by foundation species (Auster et al., 1996; Bradshaw et al. 2003; Scharf et al. 2006). However, functional differences in structure and life history traits between foundation species are known to play a large role in the sensitivity of benthic epifauna and resilience of benthic ecosystems to anthropogenic disturbance (de Juan et al., 2009). Some foundation species such as encrusting sponges, which are mound shaped and have low relief, are more resilient to bottom fishing and may show little response to trawling (Lambert et al., 2011). Foundation species that are flexible (e.g., sea whips, *Halipteris willemoesi*), or able to re-colonize disturbed areas quickly (e.g., some hydroids that experience seasonal senescence) will also have an advantage over fragile and slow growing species that cannot readily re-colonize trawled areas (Troffe et al., 2005; de Juan et al., 2009). Strong evidence of a fishing impact may not be observable on the entire group of foundation species, but rather, on distinct functional groups of benthic invertebrates (de Juan et al., 2009; Lambert et al., 2011). To address this additional complexity of the benthic environment, future research should consider functional traits and foundation species community composition, as well as overall abundance or coverage of indicator species.

As well, in some benthic environments foundation species may not be appropriate indicators for detecting the impact of bottom trawling. de Juan et al. (2009) suggest that epibenthic species are practical indicators of bottom fishing impacts; identification and sorting of epibenthic species is more efficient and thus, more cost effective than sampling infaunal species, and the ability to use non-destructive video or photographic analysis limits the requirements for laboratory space and specimen storage. However, on soft substrates, foundation species tend to be naturally less abundant and more patchily distributed (Schneider et al., 1987), and simply may not be observed via photographic sampling techniques. Impacts of bottom trawling and other bottom contact fisheries have been observed using infaunal species as indicators (Frid et al., 1999; Jennings et al., 2001a), which may be more appropriate in areas with little natural abundance of foundation species. Infaunal invertebrates contribute greatly to the diet and, therefore, the productivity of some commercially important fish (Jennings et al. 2001b), and may provide a different indicator of trawling impact on benthic ecosystems. As well, in BC, Sinclair et al. (2005) found that the effort of the groundfish trawl fleet was not randomly distributed across all substrate types, rather, bottom trawling effort is highly concentrated in areas of sand, mud, and gravel, and trawl effort tends to avoid areas of bedrock, rocky outcrops, and till. Where effort is concentrated in soft substrate areas, bottom trawling may not impact foundation species coverage as they are naturally less abundant in soft sediment habitats, however impacts to other components of the ecosystem from fishing activities may still occur. These will be overlooked if other indicators are not examined.

Our ability to identify sensitive benthic ecosystems, in order to mitigate negative impacts, is imperative if we are to move forward with ecosystem based management. Maps of sensitive benthic ecosystems, which use substrate type as one indicator of presence or abundance of foundation species, may provide a biological basis for area based management to reduce trawling effort, implement gear restrictions, or inform placement of marine protected areas. However, to meet the objectives of the management measures, substrate maps used to create area based restrictions need to be highly accurate. If inaccurate, misclassification of substrate types will occur and may result in unexpected responses of indicator species compared to those predicted based on assumed substrate features. Stevens and Connolly (2004) found that classification of benthic habitat types based on remotely measured abiotic features, such as depth and substrate characteristics, provided little ability to predict species distributions. As well, misclassification rates of up to 25 percent were observed even when remote substrate classification was enhanced using the relationship between acoustic multibeam and video captured substrate predictions (Rooper and Zimmerman, 2007). Misclassification rates for specific substrate types will be necessary inputs for decision analyses that assess viability of area based management measures. However, to fully account for potential misclassification of benthic substrate types, future research on bottom trawl impacts, and eventual use of such research for management planning, will need to coincide with ground-truthing of benthic substrate.

Although bottom trawl fisheries continue to draw criticism due to their perceived negative impacts on benthic environments, they also remain one of the largest contributors to the fishing industry in Canada (LGL, 2004; DFO, 2006). In order to pursue ecosystem based management, methods to assess the impact of bottom trawling on benthic ecosystems are necessary. My research shows that observational methods for quantifying and modeling the percent cover of foundation species across a gradient of bottom trawling effort is a viable option for measuring impacts to benthic habitat. However, this process is wrought with limitations similar to experimental studies. Although the observational approach allowed me to sample across a gradient of bottom trawling effort and to include natural variability in my survey design, my ability to achieve a large sample size, across the full range of each variable, was limited by logistic constraints of sampling over large survey areas. The tools available for data collection, the costs of research, and the desired efficiency of future research programs may not allow for the collection, and cost-effective monitoring, of appropriate indicators of trawling impact. Future use of predictive models to identify sensitive benthic ecosystems, which will inform management measures for bottom trawl fisheries, will require ground-truthing of substrate types to account for substrate misclassification in geological mapping.

Despite the limitations, my research provides evidence that bottom trawling plays an important role in the distribution of foundation species in benthic environments. The negative association between foundation species coverage and bottom trawling effort, was not consistent across other environmental characteristic. Substrate type, and to a lesser degree, depth, also play important roles in foundation species distribution and need to be considered carefully if area based management is to be effective in mitigating bottom trawling impacts. Given the importance of foundation species in creating habitat complexity in benthic environments, the conservation and management of these ecosystem features will be imperative in moving forward with ecosystem based management. The ability to predict where sensitive benthic ecosystems exist will be key in developing spatially explicit management tools to limit negative impacts of trawling on ecosystems. In BC, my research provides a first look at the impacts of bottom trawling on benthic habitat components, but continued research will be necessary to develop predictive models and to monitor bottom trawling impacts over a wider range of habitat types on the BC coast.

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