BOTTOM TRAWLING IMPACTS ON DIVERSITY AND COMPOSITION OF HABITAT-FORMING BENTHIC COMMUNITIES IN HECATE STRAIT, BRITISH COLUMBIA

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ABSTRACT

Quantitative estimates of fishing gear impacts on vulnerable seafloor habitats are an important component of an ecosystem approach to fisheries management. Currently, procedures do not exist for assessing the regional-scale impact of bottom trawling on benthic ecosystems on Canada's west coast. In this study, I used metrics of diversity and composition to evaluate the response of habitat-forming benthic communities in Hecate Strait, B.C. to varying intensities of bottom trawling. Results demonstrated that trawling effort and substrate are important factors associated with the diversity and composition of habitat-forming species in Hecate Strait. Rockier habitats with less sand/mud substrate and minimal trawling effort displayed the highest abundance and diversity of habitat-forming species. Results will help managers to identify habitats most sensitive to bottom trawling in Hecate Strait and subsequently inform management decisions regarding conservation and protection of these areas.

Keywords: bottom trawl fishing; benthic communities; photographic survey; fishing impact; model averaging; Hecate Strait

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1: INTRODUCTION

With global concern over the health of marine ecosystems, and the growing commitment of governments and international bodies to develop an ecosystem approach to fisheries, managers need to understand the effects of their management actions on not only the target stocks, but on the benthos as well (FAO 2003, Tillin et al. 2006). Unlike traditional fisheries management, which focuses on optimizing the catch of a single species, an ecosystem approach requires managers to take into account the environmental impacts of fishing practices, specifically the effects on non-target species and marine habitats (Pikitch et al. 2004, Hiddink et al. 2006). The impacts of bottom trawling on seabed habitats is a concern for managers because such activities alter the structure and function of benthic marine ecosystems (e.g., Kaiser et al. 2000, Duplisea et al. 2002, Tillin et al. 2006).

Emergent sessile epifauna such as corals (e.g., *Paragorgia pacific*, *Primnoa* spp.), sponges (*Aphrocallistes* spp.), and sea whips (*Halipteris* spp.) provide important habitat complexity in benthic marine ecosystems (Coleman & Williams 2002, Bracken et al. 2007). Such “foundation species” contribute to and maintain the diversity and abundance of many commercially and recreationally important fish species (Turner et al. 1999, Thrush & Dayton 2002, Bracken et al. 2007). The three-dimensional structure supplied by these organisms provides food resources, refuge from predators, critical nursing or spawning habitat, and protection from physical stresses such as tidal currents (Tupper & Boutilier 1995, Turner et al. 1999, Henkel & Pawlik 2005). Chronic disturbance by bottom trawling represents a significant threat to the diversity and composition of this three-dimensional structure (Hiddink et al. 2006, Quieros et al 2006, Hinz et al. 2009). Removal of foundation species affects benthic community structure by facilitating the dominance and abundance of short-lived scavenging species (Auster & Langton 1999, Thrush & Dayton 2002, Blanchard et al. 2004) and can indirectly disrupt functioning of benthic marine ecosystems by reducing levels of epifaunal productivity (Hermsen et al. 2003) and lowering the structural complexity of the benthic environment (Asch & Collie 2008).

Quantifying fishing impacts on benthic communities is often challenging because of the complexity and natural variability of benthic ecosystems (NRC 2002), difficulty of sampling at the scale of the commercial fishery, and lack of precise estimates of fishing effort (Kaiser et al. 2000). Natural variation in physical processes including tidal currents, temperature, nutrient supply, substratum stability, and hydrodynamical conditions affect the distribution and resilience of benthic communities, thus making it difficult to separate the impacts of trawling disturbance from the impacts of natural disturbance (NRC 2002, Lambert et al. 2011). Furthermore, many trawl impact studies explore the small-scale and short-term experimental effects of trawling disturbance, yet impacts of bottom trawling on fishing grounds occur chronically over large spatial scales and are expected to lead to more serious effects than those assumed from experimental studies (Collie et al. 2000b, Kaiser et al. 2000, Hinz et al. 2009). Assessment of chronic trawling disturbance at the scale of a fishery is especially difficult because precise estimates of the spatial and temporal distribution of fishing effort are often not collected or not available at appropriate scales (Kaiser et al. 2000, Jennings et al. 2002).

Although catch and effort statistics for offshore bottom trawling in British Columbia (BC) date back to the mid-1940s (Rutherford 1999), information on the possible impacts of this activity on the associated seafloor habitat is limited. For example, attempts to study the effects of shrimp beam trawling on sea whips in BC were inconclusive because of small sample sizes and positioning error of the survey trawl (Troffe et al. 2005). Studies using acoustic surveys and video transects show trawl damage to hexactinellid (*Aphrocallistes* spp.) sponge reefs in BC (Conway 1999, Conway et al. 2001, Krautter et al. 2001), and other research maps the distribution of coral and sponge bycatch by groundfish trawl fisheries in BC (Ardron & Jamieson 2006), yet no studies consider the regional spatial scale impact of bottom trawl fishing gear on the benthic ecosystems of Canada's west coast.

In this study, I assess how habitat-forming benthic communities in Hecate Strait, B.C. are potentially influenced by both local environmental conditions and bottom trawling intensity. Specifically, my objectives are to determine how bottom trawling affects foundation species (1) diversity, as measured by Shannon diversity, density, and percent cover, and (2) community composition, as measured by multivariate analysis, including ordination. I use an observational study design to address these objectives at the regional scale of the Hecate Strait fishery. Key features of the design that allow for differentiation of the natural effects of habitat type from the effects of trawling intensity included stratification of the area based on depth, bottom type, and trawl exposure history. I used high-resolution, geo-referenced bottom trawl data, based on 100% at-sea observer monitoring of BC's groundfish trawl fishery, to reliably estimate trawled area at scales of 1 km^2. Impacts of this activity on diversity and community composition of habitat-forming species across gradients in depth and substrate were measured via remotely operated underwater vehicle (ROV) surveys at 34 sites. Measures of species diversity can supply information on changes in community structure as well as effects of anthropogenic disturbance (Olsweski 2004, Magurran & McGill 2011). Thus, I used univariate metrics of Shannon diversity, density, and total percent cover to quantify foundation species diversity. Shannon diversity combines measures of species richness and evenness; density provides a measure of species richness; and total percent cover provides a measure of abundance of foundation species. However, these response metrics summarize species information into a single value, and do not consider the potential differential responses of individual species to disturbance, thereby limiting their ability to detect compositional changes in communities (Clarke 1993, Hewitt et al. 2005). Therefore, I also employed multivariate techniques to test the effects of bottom trawling disturbance on benthic community composition. Multivariate metrics such as ordination use the abundance and identity of each species to arrange samples in terms of species composition or environmental characteristics and are found to be more sensitive at detecting changes in community composition than univariate measures (Quinn & Keough 2002, Magurran & McGill 2011, Atkinson et al. 2011). Multivariate techniques may have higher statistical power to detect impacts of trawling disturbance, and as such sometimes reveal effects of disturbance on community composition where univariate indices of diversity detect no effects (Kaiser & Spencer 1996, Kaiser et al. 2000). Results of this study will help managers to implement an ecosystem approach to fisheries management by providing a better understanding of the impacts of past and current bottom fishing practices on benthic marine ecosystems off the coast of British Columbia.

2: MATERIALS AND METHODS

2.1 Data Collection

2.1.1 Survey Design and Field Sampling

My study area was located at the northern end of Hecate Strait off the north coast of British Columbia (BC), Canada between 53.93°N and -131.74°W and 54.67° N and -130.55° W (Figure 1). This area is part of section 5D of Fisheries and Oceans Canada's (DFO's) integrated groundfish species management areas (DFO 2008) and was chosen because of the long history of bottom trawl activity in the region as well as the availability of at sea observer and substrate composition data.

Prior to the ROV surveys, the study area was discretized into 14 337 1-km^2 grid cells and stratified according to historical effort exposure, bottom type, and depth. I defined trawling effort as a combination of the total area of the bottom contacted by the gear (i.e., swept area) and how that contact is spread over the bottom (i.e., uniformity). I derived annual statistics specific to each of these metrics for each grid cell by year from 1996-2010. Geo-referenced bottom trawl data for all of these years were obtained from DFO's PacHarvTrawl (DFO 2006) and GFFOS (DFO 2012) databases based on a 100% at-sea observer monitoring program (DFO 2007). The tow-by-tow trawl segments included the start, end, and sometimes midpoint locations, which facilitates mapping of the spatial distribution of trawling effort on relatively fine spatial scales ~ 1 km^2. The area, $a_{j,i,t}$, of each trawl segment *j* that contacts cell *i* in year *t* is:

$$a_{j,i,t}=w \times l_{j,i} \quad (1)$$

where, *w* is the door-to-door width of impact of the bottom trawl gear deployed in these fisheries (*w*=0.07km, G. Workman, pers. comm., 2009), and $l_{j,i}$ is the length of trawl segment *j* that contacts cell *i*. Swept area ($S_{i,t}$) of cell *i* in year *t* is defined as the total area of the 1 km^2 grid cell covered by trawl gear in year *t*. I calculated these values as the sum of the area of all trawl segments in year *t* that contact cell *i*:

$$S_{i,t}=\sum_{\forall j} a_{j,i,t} \cap c_i \quad (2)$$

where the intersection operator ∩ selects only segments that intersected the cell, c_i. Cells with high fishing effort in a particular year can have swept area values that are greater than one because the areas of trawl segments overlap.

Effort uniformity (U_{it}), which measures the concentration of trawling effort within each 1 km^2 grid cell per year, is based on the union of the swept area by all segments that intersect the cell. It is computed as the ratio of swept area within a cell ($S_{i,t}$) to the area of the cell that is contacted by bottom trawl gear at least once in a given year, E_{it}. Uniformity of a grid cell *i*, year *t* is thus:

$$U_{i,t}=\frac{E_{i,t}}{S_{i,t}} \quad (3)$$

Areas that have a high degree of overlap of fishing events within a cell will have low uniformity compared to areas where effort is more evenly spread over the cell. If no fishing effort is present within a grid cell, uniformity will have a value of one. I calculated both swept area and uniformity statistics using the *joinPolys* function in the *PBS Mapping* (Schnute et al. 2004) package in R (version 2.13.0) (R Development Core Team, 2011).

Annual swept area and uniformity statistics for the collection (N=14 337) of grid cells were categorized via non-metric Multidimensional Scaling (nMDS) in the following temporal patterns: Low, Decreasing, Steady, and Increasing. These exposure histories, along with an additional category (None) for areas with no historical trawling effort, constitute the five effort categories used in the survey design.

I classified substrate types in each grid cell into "Till" (i.e., hard bottom) and "Sand/Gravel" (i.e., soft sand, mud, gravel) because hard bottom and soft bottom environments can support fundamentally different benthic communities (Asch & Collie 2008). I used surficial geology maps provided by the Pacific division of the Geological Survey of Canada (Barrie & Bornhold 1989; Barrie et al. 1991) to classify each substrate type. These maps combine data sources including acoustic surveys, grab samples, seismic scanning, and other means of ground-truthing. Bottom substrate classes were obtained as polygons, which were then rasterized to 1 km^2 grid cells using ArcGIS software. Grid cells categorized as Till were expected to contain hard substrates with large grain size, whereas cells categorized as Sand/Gravel were expected to contain softer sediments with smaller grain size.

Depth data obtained from the nepacLL dataset from the *PBS Mapping* package (Schnute et al. 2004) in R (version 2.13.0) (R Development Core Team,

2011) were averaged by 1 km^2 grid cell and split into Shallow (<100m) and Deep (≥100m) categories.

Survey sites were selected at random by sampling grid cells in proportion to stratum occurrence. A minimum of four survey sites were required for each stratum. Sites that could not be sampled due to adverse weather conditions were replaced with the next appropriate survey site.

Two research surveys of the study area were carried out in late August of 2010 and mid-September of 2011 aboard the Canadian Coast Guard Service (CCGS) vessel "Vector" (Figure 2). During the surveys, an ROV ('Phantom') provided by DFO was deployed to take still photographs of the seafloor. The ROV system included an 8-megapixel Olympus SP350 digital camera, SD video camera (Sony EVI 330), HD video camera (Mini Zeus, Insite Pacific), temperature datalogger (Vemco Minilog) and continuous CTD (conductivity, temperature, and depth) (Falmouth Scientific Instruments). Two parallel lasers placed 10 cm apart were used to scale the size of objects on the seafloor. Still photographs were taken every 20 s during 30-minute ROV transects (approximately 500 m in length). Each photograph covered an area of approximately 0.02 m^2 to 0.81 m^2 of the seafloor. Transects were randomly located within a selected sampling site and varied in depth between 73 m and 193 m. Thirty-one transects were completed with the ROV in 2010 and only three transects were completed in 2011 due to severe weather conditions restricting the deployment of the ROV.

2.1.2 Data Analysis

I quantified substrate type and percent cover of habitat-forming species present in each transect based on a random subsample of 14-22 still photographs per transect. The number of photographs analysed varied based on the amount of variability (i.e., standard deviation) in the observed percent cover of foundation species among photographs; I assessed a larger number of photographs for transects with higher variability and fewer photographs where variability was low. Where suspended sediments and other particulate matter potentially affected the resolution of the still photographs (Busby et al. 2005), I chose the next appropriate randomly selected photograph for analysis. Overall, 574 still photographs were analysed from the 34 transects sampled, covering a total area of 161.0 m^2 of the seafloor.

Fish and invertebrates in each photograph were identified to the lowest taxomonic level possible; however, due to the limited resolution of the still photographs, some organisms could not be identified below the level of Phylum. Any "Undetermined hydroid" species was not included in the remainder of the analysis because it was difficult to distinguish whether the specimens were alive or dead. In addition, it is likely that some organisms were missed because small organisms can remain hidden in bushy epifauna (Collie et al. 2000a).

I used the area measurement function in the program ImageJ v.1.45 (Rasband 2011) to calculate the area covered by each species in each photograph. I then summed these individual species areas across photographs and divided by the sum total area of all photographs within a transect to determine the percent cover of each species in each transect. This calculation weights each percent cover observation proportional to its area, thereby accounting for variation in total area covered by each individual photograph.

I used the percent cover of each species per transect and the total number of species observed per transect to calculate the Shannon diversity index, species density, and total percent cover of foundation species per transect. The Shannon diversity index (*H'*), measures uncertainty in correctly predicting the species of the next individual to be collected in a sample via (Krebs 1999),

$$H'_p = -\sum_{\forall g} \frac{n_{g,p}}{N_p} \log \frac{n_{g,p}}{N_p} \qquad (4)$$

where $n_{g,p}$ is the percent cover of the *g*th species in transect *p,* and N_p is the total percent cover of all foundation species in transect *p*. I used the ratio-of-means estimator in which total percent cover in transect *p* (N_p) is calculated by summing all species areas across all photographs in transect *p* and then dividing by the total area over all photographs. I measured Shannon diversity using the *diversity* function in the *vegan* package (version 1.17-11) (Oksanen et al. 2011) in R (version 2.13.0) (R Development Core Team 2011). I calculated species density by dividing the observed number of species per transect by the total area of each transect. I measured the total percent cover of foundation species per transect using the same calculation as N_p for the Shannon diversity index mentioned above.

My statistical analyses included three alternate forms of substrate definition: (1) "percent SandMud" is an *in situ* continuous variable defined by the average percentage of combined sand and mud present in each transect; (2) "*In situ* categorical substrate" is a categorical variable for which transects with an average of 90% sand/mud or greater were categorized as “sand/mud” and transects with an average less than 90% sand/mud were categorized as “till”; and (3) “Surficial geology-based categorical substrate" is the categorical variable used in the ROV survey design and defined as “Sand/Gravel” or “Till”. I developed statistical models based on all three of the above forms to determine the sensitivity of my results to the definition of substrate.

I used the Visual Basic program Coral Point Count estimate (CPCe) with excel extensions (Kohler & Gill 2006) to determine the *in situ* continuous and categorical substrate for the statistical analysis. CPCe is commonly used to increase image analysis efficiency when identifying coral reef habitats and determining substrate type from underwater photographs (Kohler & Gill 2006). I visually identified the substrate at 90 randomly selected points on each photograph as sand, mud, boulder, cobble, gravel, or pea gravel based on DFO’s substrate classification system for all Pacific dive surveys (see Table A1.1 in Appendix 1 for DFO substrate classification scheme). Where organisms masked the substrate, I used the surrounding substrate as an indicator of the substrate composition beneath the species. I determined the total percent cover of each substrate type per transect by calculating a weighted average of the percent cover of each substrate type over all photographs analysed per transect, with weights corresponding to the area of each photograph. Because it was difficult to differentiate sand and mud in the still photographs and the substrate was likely a combination of both sand and mud (J.Pegg, pers.comm, 2011), I combined the average percent cover of sand and mud per transect into one value; percent SandMud.

The small sample size (n=34) of my study, and need to categorize the historical fishing effort data into five treatment types, led to overparameterized models in the statistical analyses described below. Thus, I defined fishing effort using continuous swept area measures in the statistical analysis rather than the categorical measures from the survey design. To help preserve the different temporal trends of fishing exposure defined by the five categorical effort variables, I averaged the continuous swept area data over two five year increments and one four year increment (1996-2000, 2001-2005, 2006-2009 for the 2010 survey and 1997-2001, 2002-2006, 2007-2010 for the 2011 survey). Effort variables representing these year blocks were then labelled as follows: "Early" corresponded to years 1996-2000 for the 2010 survey, and 1997-2001 for the 2011 survey; "Middle" corresponded to years 2001-2005 for the 2010 survey, and 2002-2006 for the 2011 survey; "Recent" corresponded to years 2006-2009 for the 2010 survey, and 2007-2010 for the 2011 survey; and "All Years" corresponded to continuous swept area data averaged over all 14 years (1996-2009 for the 2010 survey and 1997-2010 for the 2011 survey). Similar to substrate, I compared these alternative effort metrics to test the sensitivity of my results to the definition of effort.

2.2 Statistical Analysis

2.2.1 Univariate Analysis of Foundation Species Response

I used an *a priori* list of generalized linear models (GLMs) to explore associations between physical and anthropogenic factors (depth, substrate, and trawling effort) and foundation species diversity, density, and total percent cover. I natural-log transformed Shannon diversity to account for skewness (Sokal and Rohlf 1995). Because zeros were present in the data, I added half of the minimum non-zero value to all observations of Shannon diversity prior to transforming them. Total percent cover of foundation species was arcsine square root transformed to meet the assumptions of normality (Legendre & Legendre 1998, Krebs 1999). Models were used to measure the associations of three independent variables and their interactions with the dependent variable, and were subsets of the full model,

$$Y = a + b_1S + b_2E + b_3D + b_4SE + b_5SD + b_6ED + v \quad (5)$$

where Y is the response (i.e., log-transformed Shannon diversity, density, or transformed total percent cover), a is the intercept, b_i are effect sizes, S is substrate, D is depth, E is trawl effort (i.e., swept area), and v is the error term whose distribution is described below. I limited the models to only one effort variable (i.e., swept area with only one time increment of Early, Middle, Recent, or All Years) to minimize specifying overparameterized models. I employed a Gaussian distribution with an identity link function in GLMs for adjusted and transformed Shannon diversity and for transformed total percent cover of foundation species. For Gaussian regression using adjusted and transformed

Shannon diversity, I used weighted regression, with weights equal to the area analyzed per transect, to account for the fact that the proportions underlying the Shannon diversity estimates were derived from unequal areas. For models involving species density, I used GLMs with a Poisson error distribution and a logarithmic link function. However, in preliminary analyses, I found that the count data were overdispersed with respect to the Poisson distribution; therefore, I employed negative binomial regression, which is a commonly used alternative to the Poisson distribution (Ver Hoef & Boveng 2007). For both the Poisson and negative binomial regressions, I applied the logarithm of the total area analysed per transect as an offset to properly reflect differences in the total size of photographs analysed per transect. Depth and *in situ* continuous substrate data were standardised by subtracting their means and dividing by their standard deviations to allow for comparison of main effects when interactions are present (Greuber et al. 2011).

I calculated Akaike's Information Criterion (Akaike 1973) corrected for small sample size (AIC_c:) to select the most parsimonious models for each response variable,

$$AIC_c = -2\log L + 2k + \frac{2k(k+1)}{n-k-1} \quad (6)$$

where k is the number of parameters in the model, L is the likelihood of the model, and n is the sample size (Burnham & Anderson 2002). The model with the lowest the AIC_c value was considered the most parsimonious, optimizing the trade-off between model fit and complexity (Burnham & Anderson 2002). To measure the amount of relative support for each model given the data, the AIC_c

difference (ΔAIC_c) was calculated by rescaling the AIC_c value for each model q relative to that of the most parsimonious model:

$$\Delta AIC_{c,q} = AIC_{c,q} - \min(AIC_c) \quad (7)$$

where $\min(AIC_c)$ is the minimum AIC_c value across all a priori models (Burnham & Anderson 2002). The model estimated to have the most relative support given the data, has a ΔAIC_c value of zero (Burnham & Anderson 2002). A generally accepted rule of model selection is that models having a ΔAIC_c value of ≤2 have substantial support, those in which $4 \leq \Delta AIC_c \leq 7$ have considerably less support than the best model, and models having ΔAIC_c >10 have essentially no support (Burnham & Anderson 2002).

To directly account for model selection uncertainty and obtain robust parameter estimates, I employed a model averaging approach (Greuber et al. 2011). Model averaging uses the Akaike weights, i.e.,

$$w_i = \frac{\exp(-0.5\Delta AIC_{c,q})}{\sum_{\forall q} \exp(-0.5\Delta AIC_c)} \quad (8)$$

to calculate a weighted average of parameter estimates and variances (i.e., standard errors) from each model in the top model set (Greuber et al. 2011). As a result, model selection uncertainty is incorporated directly into parameter estimates, and models that do not contribute much information about the variance in the response variable are given little weight (Greuber et al. 2011). I generated a top model set consisting of models that fell within 4 ΔAIC_c units of the top model.

I obtained parameter estimates and unconditional standard errors (i.e., not conditional on a particular model) for each explanatory variable according to the zero method (Burnham & Anderson 2002). This method is used to substitute a parameter estimate and an error both equal to zero into the models where a given parameter is absent, and parameter estimates are obtained by averaging over all models in the top model set (Burnham & Anderson 2002). Thus, the zero method is used to decrease the effect sizes and errors of explanatory variables that only appear in models with small model weights, thereby diluting the parameter estimates of these variables (Grueber et al., 2011). I assessed the relative variable importance by summing the Akaike weights of all models that included the corresponding parameter of interest. Model averaging was calculated using the *model.avg* function in the *MuMIn* package in the statistical program R (version 2.13.0) (R Development Core Team, 2011).

2.2.2 Multivariate Analysis of Foundation Species Response

I applied nonmetric multidimensional scaling (nMDS) ordination (Kruskal 1964) to untransformed foundation species percent cover data and used vector fitting to correlate explanatory variables of effort, depth, and substrate to the nMDS ordination with significance tests based on 1000 permutations. I also plotted the positions of all foundation species in ordination space using the weighted average of the transect scores with weights representing the abundance of a particular taxon at each transect. Ordination is a multivariate technique for arranging species and samples that reduces a large number of observations (i.e. species abundances) taken from a set of objects (i.e. transects), to a smaller number of dimensions (axes) (Krebs 1999). nMDS is an ordination technique that is used to map samples in two or more dimensions in which relative distance between samples on the map reflects the relative differences in species composition of biological communities (Clarke 1993, Asch & Collie 2008). Vector fitting is used for overlaying environmental information onto ordination plots to facilitate interpretation of the ordination, and follows methods outlined in Oksanen (2011). I used a Bray Curtis dissimilarity matrix (Bray & Curtis 1957) for the species composition data because it is robust to non-linearities in species' response and zero-inflated ecological data (Faith et al. 1987, Clarke 1993, Oksanen 2011). Because dissimilarity indices are based on percent cover of foundation species, I removed transects that contained zero foundation species (i.e., 12 transects out of 34). Additionally, I removed all species that occurred only once across the entire data set to reduce noise (McCune & Grace 2002). Generally accepted guidelines of interpreting nMDS configurations are that goodness-of-fit or "stress" values greater than 30 indicate the configuration is a random representation of the dissimilarities between samples, and configurations with stress values of greater than 20 should not be interpreted (Clarke 1993, Quinn & Keough 2002). The three dimensional nMDS configuration had a stress value of 12.84 indicating that the nMDS ordination provided a reasonable representation of the actual dissimilarities between samples (Clarke 1993). I used permutation-based multivariate analysis of variance (PerMANOVA) with species dissimilarities as the input matrix, to test whether trawling effort, substrate type, and depth and their interactions were significantly associated with foundation species community composition (Anderson 2001). Analyses were performed via *metaMDS*, *envfit* and *adonis* functions from the *Vegan* package (Oksanen et al. 2011) in R (version 2.13.0) (R Development Core Team 2011).

3: RESULTS

3.1 Site Characteristics

A total of 62 foundation species, 40 non-foundation species, and 13 fish species were identified across all transects (see Table A2.1 in Appendix 2 for a list of all species). The number of foundation species per transect ranged from 0 to 33. The average observed percent SandMud in each transect ranged from 77% to 100% (Table 1). Sites containing less than 100% SandMud were often characterized by the presence of boulders, cobble, gravel and pea gravel. Surficial geology-based categorical substrate was not an accurate predictor of continuous and observed categorical substrate and was misclassified in 11 of the 34 transects when compared to *in situ* categorical substrate (Table 1). The average transect depth ranged from 73.6 m to 192.6 m.

3.2 Univariate Analysis of Foundation Species Response

Trawl effort and substrate were associated with Shannon diversity; and because analyses using multiple definitions of effort provided similar results (Table A3.1 in Appendix 3), I only considered results using one definition of effort, swept area averaged over fourteen years. The presence of interactions between percent SandMud and effort in the top models and model-averaged results demonstrated that the effect of effort on Shannon diversity was dependent on substrate (Table 2). Shannon diversity was negatively associated with soft bottom substrate at average depth (117.8 m) and average effort (0.76

km^2/year) (Table 3). Diversity at average depth and average percent SandMud (95.7%) was also lower where swept area was high. However, this observed negative effect of swept area on diversity decreased as the bottom type became softer (i.e., percent SandMud increased). For example, in a 1 km^2 grid cell at average depth (117.8 m), increasing swept area from 0 km^2 per year to 0.7 km^2 per year decreased the diversity of foundation species in hard bottom (i.e. ~80% SandMud) substrates by 59%, whereas diversity only decreased by 3.3% in soft bottom substrates (i.e.~100% SandMud) (Figure 3). The unconditional standard errors of the effect sizes were large (i.e., larger than that of the effect size itself) for all of the main effects of swept area, substrate, depth and their interactions (Table 3). The relative variable importance (RVI) of effort was 0.51 indicating that effort was approximately half as important as substrate (RVI=1.00).

Goodness of fit criteria (i.e., R^2 and ΔAIC_c) demonstrate that a lot of explanatory power is lost when considering models with *in situ* categorical and surficial geology-based substrate (Table A3.2 in Appendix 3). However, the presence of effort in the top models with *in situ* continuous, *in situ* categorical, and surficial geology-based substrate suggests that the influence of effort on foundation species diversity is robust to the definition of substrate type (Table A3.2). Thus, my results are based on *in situ* continuous substrate models because these provide much better fit to the data than models based on surficial geology and *in situ* categorical substrate (Figure 4).

Shannon diversity was correlated with total percent cover and species density; however, plots of the indices showed strong non-linearities and were analysed further (Figure A3.1 in Appendix 3). I obtained similar model results for each response variable and thus, I only present results for Shannon diversity; results for total percent cover and species density are found in Appendices 4 and 5 respectively.

3.3 Multivariate Analysis of Foundation Species Response

Similar to the response of foundation species diversity, foundation species composition varied with both substrate and effort (Figure 5). Substrate and effort were strongly correlated (R^2 = 0.54, p = 0.002 for percent SandMud; R^2 = 0.39, p = 0.001 for Swept $Area_{All\ Years}$) with the nMDS configuration, indicating that these variables are associated with differences in foundation species composition between transects. Depth was not strongly correlated with the nMDS configuration (R^2 = 0.05, p = 0.615).

The individual response of foundation species to trawling effort and substrate was generally uniform across all foundation species as the majority of foundation species were in highest abundance at transects in the lower right quadrant of the nMDS plot characterized by hard bottom substrates (i.e. lower percent SandMud) and low or no swept area. Only a few foundation species, including the sea whip (*Halipteris* spp.), were associated with the transects in the upper left hand quadrant of the nMDS plot, which was characterized by increasing trawling effort and soft bottom (i.e. high percent SandMud) substrate.

Results of PerMANOVAs were congruent with patterns visualized in the nMDS plot (Table 4). Foundation species composition varied significantly (i.e., $p<0.05$) with the interactions between percent SandMud and effort (PerMANOVA;

F = 1.85, p = 0.019) indicating that the effect of effort on foundation species composition was dependent upon substrate.

4: DISCUSSION

Fisheries are increasingly scrutinized for their potential impacts on seabed habitat. Although there is strong experimental evidence that contact between bottom trawl fishing gear and epibenthic invertebrates results in high mortality to the latter, the regional scale effects on seabed habitat requires fishery-scale impact studies over a representative range of habitats. I examined associations between population and community indicators of habitat-forming species in 34 sites spread over northern Hecate Strait, B.C. where trawl fisheries have operated since at least the mid-1940s. My research represents the first attempt to quantify the regional spatial scale impact of bottom trawl fishing gear on the diversity and composition of habitat-forming foundation species on Canada's west coast. Even with limited data, I demonstrated that trawling effort is associated with the diversity and composition of foundation species in Hecate Strait, BC. Areas with higher percentages of hard substrate and little or no trawling activity showed the highest abundance and diversity of foundation species. Results can guide future scientific research on areas that are more vulnerable to trawling activity and subsequently inform management decisions regarding conservation and protection of these areas.

This research demonstrated that trawling effort and substrate type potentially influence the diversity and composition of habitat-forming species and the effect of effort changes depending on substrate type. However, the small sample size (n=34) of my study, as well as the patchy distribution of foundation species in Hecate Strait likely contributed to increased variation in the data and high uncertainty around the effect size estimates for substrate, effort, and their interactions. Nevertheless, my results are consistent with existing studies showing that trawling effort and its interaction with substrate are important factors associated with foundation species diversity and composition (i.e.,Kaiser et al. 2000, Queirós et al. 2006, Hinz et al. 2009, Shepard et al. 2010, Lambert et al. 2011). Foundation species were found in highest abundance in hard bottom substrates rather than soft bottom substrates which could be due to lower trawling intensity in those areas as well as the availability of hard substratum (i.e., gravel, cobble, boulder), upon which habitat-forming species have a tendency to settle and develop (Collie et al. 2000a, Lambert et al. 2011). Furthermore, the negative association between effort and diversity was lower in sandy substrates, which could be because benthic communities in sandy sediments may have little emergent structure and tend to be less sensitive to trawling disturbance (i.e., Collie et al. 2000a, Collie et al. 2000b, Queirós et al. 2006, Shepard et al. 2010). Thus, I may see reduced diversity and abundance of foundation species at transects with a higher percentage of SandMud because foundation species do not generally inhabit the sandy sediments.

Similar to Hinz et al. (2009), I found that trawling effort consistently influences both univariate indices of foundation species diversity, density, and total percent cover, and multivariate indices of community composition. This contrasts with results from other studies that identified an effect of trawl treatments on community composition, but no overall effects of trawling on abundance, biomass, and diversity (Kaiser et al. 1998, Sanchez et al. 2000). However, the previous studies use experimental methods to examine short-term effects of trawl disturbance on benthic communities, which may not reflect the large-scale, long-term trawling disturbances experienced at the scale of a commercial fishery. Thus, it may be more difficult to detect effects of trawling disturbance from small-scale experimental studies, especially when using univariate metrics such as diversity, which are less sensitive to the detection of trawling effects than multivariate metrics (Kaiser et al. 2006).

I found that the individual response of sea whips to trawling effort and substrate type was different from the response of the majority of other foundation species. Sea whips were found in highest abundance at a transect with low trawling effort, but were also associated with areas of increasing trawling effort and soft bottom substrates, whereas the majority of foundation species were associated with hard bottom substrates with low or no trawling effort. This difference in response could occur because sea whips generally inhabit sandy, soft bottom substrates (Troffe et al. 2005) and may be resistant to trawling disturbance. For example, Stone et al. (2005) found the density of sea whips was not significantly different between areas open and closed to bottom trawling, indicating that sea whips may be resistant to trawling. However, individuals in untrawled sites were larger (i.e., >80 cm), than individuals in trawled sites (i.e., 20-80 cm), which could suggest a shift in the size-frequency distribution of sea whips due to long-term effects of trawling (Stone et al. 2005). Furthermore, Malecha and Stone (2009) found that sea whips are impacted by bottom trawling events through abrasion, fracture, and dislodgement, which negatively affects their survival. Thus, there is some discrepancy regarding the possible impacts to sea whips from bottom trawling. Further research is needed to determine if the difference in response between sea whips and other foundation species to trawling effort and substrate type is due to a possible tolerance of sea whips to higher trawling effort or to a preference for soft bottom habitats.

Although I found the effect of trawling on foundation species diversity to be lower in sandy substrates than hard bottom substrates, my study only considered the impacts of fishing disturbance on the habitat-forming epifauna that tend to settle on hard bottom types, and did not consider the effects on infaunal species living within the sediments. Infaunal species play a key role in bioturbation and benthic community production, which in turn supports the production of commercially important fish species (Duplisea et al. 2001, Jennings et al. 2002). Furthermore, my study did not consider the different physical characteristics and life history traits that contribute to the functioning of benthic communities and influence the distribution of benthic species as well as their vulnerability to bottom trawling (Lambert et al. 2011). Biological trait analysis can be used to assess how ecosystem functioning varies between communities by examining a range of biological taxon characteristics including: life history variables such as body size, longevity, and reproductive techniques (i.e., asexual vs. sexual); and ecological function variables such as species mobility (i.e., sedentary vs. swimmer), habitat (i.e., epifaunal vs. infaunal), and feeding type (deposit feeder vs. filter feeder)

(Tillin et al. 2006). Thus, a useful extension to this study would be to examine the impact of bottom trawling on benthic community function through biological trait analysis, grouping foundation species based on their life history and ecological function characteristics. By taking into consideration the responses of each major functional group, this research could provide information on the vulnerability of benthic communities to fishing impacts (Lambert et al. 2011).

Bottom substrate mapping is clearly a critical requirement for managing impacts of bottom fishing on benthic communities. Because *in situ* sampling of biological communities can be time consuming and expensive, estimated bottom substrate is often used as a proxy for local biological diversity (Dunn & Halpin 2009). However, my ground-truthing of bottom substrate maps showed that proxies remain highly uncertain because 11 of the 34 transects were mis-classified. This misclassification is likely because substrate data collected at large scales lack the resolution necessary for meaningful comparative studies conducted at smaller sampling scales (Kaiser et al. 2000). These uncertainties propagate into bottom fishing impact assessments. For example, my statistical analyses involving the surficial geology-based substrate based on substrate maps from the survey design had substantially less explanatory power than the models based on *in situ* continuous and categorical substrate. These results could have serious implications for the spatial management of the fishery and potential design of marine protected areas (e.g., National Marine Conservation Areas, NMCAs) as substrate maps need to be very precise if management decisions are to be based on them. For instance, if managers used the existing substrate maps to determine areas of suitable habitat to set aside for conservation purposes, there is a possibility that they could classify areas as suitable habitat that are extremely unsuitable, and vise versa. Future research could look at ways to update and improve the precision of existing habitat maps or create new habitat maps with substrate information provided at a smaller scale.

Due to the short amount of available ship time and the unforseen hurricane warnings during our 2011 field sampling, I was unable to sample as many sites as I had planned. As a result, I was not able to use the five categorical trends of effort from the survey design in my statistical analysis. Thus, further research could involve the collection of more samples which could provide the statistical power necessary to incorporate the five trends of effort into my analysis. By including the five effort trends, I may also be able to explore the possible recovery of foundation species at certain sites where the effort pattern shows decreasing effort over time.

Like many bottom impacts studies (e.g, Engel & Kvitek 1998, Collie et al. 2000a, McConnaughey et al. 2000, Kaiser et al. 2002), mine also lacked unfished control sites that encompass the range of physical and biological conditions present in fished sites. Bottom trawlers have operated in Hecate Strait since at least the mid-1940s (Rutherford 1999), yet we are only able to obtain reliable on-board observer data regarding trawl effort and location from 1996 to the present. Since historical data collection methods have changed over time, and fishing restrictions and gear types have changed over time, information on areas that had been fished prior to 1996 cannot be incorporated into the trawl effort estimates. Thus, our estimates of trawl effort may be lower than the actual levels of trawl effort experienced at each site. In addition, when determining the impact of fishing activities on benthic communities, we are often unable to determine the original composition of the fauna because data gathered prior to historical bottom trawl fishing is usually non-existent (Collie et al. 2000a, Kaiser et al. 2002). Furthermore, in large-scale studies replication is challenging due to many factors such as costs, weather conditions, research priorities, and available ship time (Asch & Collie 2008, Atkinson et al. 2011). As a result, conclusions derived from unreplicated treatments with sites that have no “true” controls, are difficult to extrapolate for broader application (Engel & Kvetik 1998, Atkinson et al. 2011).

5: CONCLUSIONS

This study demonstrates that higher bottom trawling effort and softer substrate types are associated with areas of lower diversity and abundance of habitat-forming species in Hecate Strait, British Columbia. Areas with harder bottom types and low or no trawling effort are of conservation importance because they displayed the highest abundance and diversity of foundation species and likely provide a source of food and shelter for many marine organisms (Asch & Collie 2008). Furthermore, these areas are likely the most sensitive to trawling activity because they contain sessile habitat-forming species with emergent growth forms that are vulnerable to damage by trawl gear (Auster & Langton 1999, Thrush & Dayton 2002, Asch & Collie 2008). Managers need to recognize areas of high habitat complexity because studies show that the removal of epifaunal organisms by trawling may render habitats unsuitable for associated species (Kaiser et al. 2000, Brodeur 2001). For example, Brodeur (2001) found that complex habitats in the Bering Sea were less frequented by Pacific Ocean perch after disruption by otter trawling. Since only ~68% of substrate types in my study were classified correctly using the surficial geology maps from the survey design, it may be difficult for managers to determine the precise locations of sensitive hard bottom habitats within Hecate Strait. Therefore, further research regarding improvements to the precision of existing habitat maps of Hecate Strait should be conducted. Furthermore, I found effort and substrate type were associated with foundation species diversity in Hecate Strait consistent with numerous previous studies (Kaiser 2000, Collie et al. 2000a, Shepard et al. 2010); however, the small sample size of my study resulted in high uncertainty in the estimates of the effect sizes of these variables. Thus, managers interested in determining the overall impact of bottom trawling in the Hecate Strait fishery need to consider these uncertainties and should be careful not to extrapolate impacts of bottom trawling beyond the observed range of trawling effort associated with each substrate type.

As an ecosystem approach becomes more prevalent in fisheries management, an understanding of the impacts of bottom fishing on habitat-forming benthic communities in Hecate Strait will be highly valuable to fisheries managers. With further research to refine the location of areas most sensitive to bottom trawling in Hecate Strait, managers will be able to use the information from this study to apply management tools that are best suited for maintaining healthy, sustainable bottom fisheries while taking into account the habitats most sensitive to bottom fishing in Hecate Strait.

TABLES

Table 1. Environmental characteristics for ROV transects in Hecate Strait, BC including starting position (latitude and longitude), *in situ* continuous substrate (i.e., mean percentage of sand/mud), *in situ* categorical substrate, surficial geology-based categorical substrate, average depth, and all four definitions of swept area (i.e., "Early", "Middle", "Recent" and "All Years").

Transect ID*	Longitude (degrees)	Latitude (degrees)	Mean %Sand/Mud	*In Situ* Categorical Substrate	Surficial Geology-Based Categorical Substrate	Mean Depth (m)	Swept Area Early[1]	Swept Area Middle[2]	Swept Area Recent[3]	Swept Area All Years[4]
7	-131.03	54.24	96.96	Sand/Mud	Till	116.15	0.389	0.120	0.241	0.251
8	-130.94	54.24	82.13	Till	Sand/Gravel	96.33	0.000	0.000	0.000	0.000
9	-130.93	54.31	91.49	Sand/Mud	Sand/Gravel	151.33	0.000	0.000	0.000	0.000
27	-131.04	54.47	100.00	Sand/Mud	Sand/Gravel	131.86	0.098	0.039	0.000	0.049
28	-131.11	54.48	100.00	Sand/Mud	Sand/Gravel	143.70	1.311	2.036	1.101	1.510
29	-131.17	54.47	100.00	Sand/Mud	Sand/Gravel	131.98	1.553	0.901	0.931	1.143
30	-131.20	54.47	100.00	Sand/Mud	Sand/Gravel	129.50	1.993	1.579	1.179	1.613
31	-131.23	54.39	100.00	Sand/Mud	Sand/Gravel	96.77	1.405	2.512	0.647	1.584
32	-131.21	54.38	100.00	Sand/Mud	Sand/Gravel	83.00	0.789	1.126	0.600	0.855
33	-131.56	54.33	100.00	Sand/Mud	Sand/Gravel	192.60	0.033	0.012	0.121	0.050
34	-131.48	54.32	100.00	Sand/Mud	Sand/Gravel	175.77	0.155	0.082	0.122	0.119
35	-131.41	54.35	100.00	Sand/Mud	Sand/Gravel	187.88	0.036	0.016	0.003	0.019
36	-131.41	54.33	100.00	Sand/Mud	Sand/Gravel	162.70	0.444	0.323	0.349	0.373
37	-131.38	54.33	100.00	Sand/Mud	Sand/Gravel	156.85	0.527	0.504	0.449	0.496
38	-131.28	54.30	100.00	Sand/Mud	Sand/Gravel	80.20	5.339	4.682	8.586	6.032
39	-131.25	54.35	100.00	Sand/Mud	Sand/Gravel	104.55	1.613	8.049	2.748	4.236
40	-131.21	54.37	100.00	Sand/Mud	Sand/Gravel	77.34	0.408	1.584	1.085	1.021
41	-131.19	54.37	100.00	Sand/Mud	Sand/Gravel	73.62	0.169	0.713	1.006	0.603
42	-131.04	54.33	76.35	Till	Till	75.94	0.007	0.012	0.000	0.007
43	-131.05	54.32	81.00	Till	Till	88.45	0.044	0.049	0.000	0.033
44	-131.08	54.32	87.57	Till	Till	112.43	0.972	0.483	0.110	0.551
45	-131.00	54.28	97.12	Sand/Mud	Till	122.13	0.039	0.064	0.001	0.037
46	-131.05	54.28	89.53	Till	Till	128.04	1.239	0.441	0.232	0.666
47	-131.05	54.27	100.00	Sand/Mud	Till	128.09	3.774	1.644	1.264	2.296
49	-131.53	54.26	98.59	Sand/Mud	Sand/Gravel	118.57	0.522	0.106	0.179	0.275
50	-131.03	54.23	95.65	Sand/Mud	Till	118.32	0.417	0.098	0.194	0.240
51	-131.01	54.14	83.79	Till	Till	91.15	0.000	0.000	0.000	0.000
52	-131.04	54.10	100.00	Sand/Mud	Till	114.55	0.698	0.157	0.070	0.326
53	-131.04	54.09	100.00	Sand/Mud	Till	106.93	0.727	0.196	0.070	0.350
54	-131.01	54.08	98.37	Sand/Mud	Till	106.20	0.106	0.008	0.000	0.041
55	-130.95	54.09	84.51	Till	Till	107.43	0.000	0.000	0.000	0.000
56	-130.93	54.02	93.34	Sand/Mud	Till	87.48	0.000	0.000	0.000	0.000
58	-131.06	54.30	97.22	Sand/Mud	Till	119.55	2.022	1.071	0.317	1.195
59	-130.94	54.01	99.44	Sand/Mud	Till	87.50	0.000	0.000	0.000	0.000

*Transects 7, 8, 9 sampled in September 2011, transects 27-59 sampled in late August and September 2010

[1] Early effort grouping represents years 1996-2000 for 2010 survey, 1997-2001 for 2011 survey

[2] Middle effort grouping represents years 2001-2005 for 2010 survey, 2002-2006 for 2011 survey

[3] Recent effort grouping represents years 2006-2009 for 2010 survey, 2007-2010 for 2011 survey

[4] All Years effort grouping represents years 1996-2009 for 2010 survey, 1997-2010 for 2011 survey

Table 2. Model selection statistics for log Shannon diversity. Models shown are within 4 ΔAIC_c units of the top model and ordered by ΔAIC_c. Parameters in the models include average depth per transect (Depth), *in situ* continuous substrate (i.e., average percent SandMud per transect), and swept area averaged over 14 years ($SweptArea_{All\ Years}$). Also shown are the Akaike Information Criteria differences from the best model (ΔAIC_c), Akaike model weights (w_i) and R^2 values. The "x" represents the main effects and interactions in the linear model.

Model (Log Shannon diversity)	ΔAICc	w_i	R^2
% Sand/Mud	0.00	0.23	0.62
% Sand/Mud x Depth + % Sand/Mud x $SweptArea_{All\ Years}$	0.09	0.22	0.73
% Sand/Mud x Depth	0.43	0.19	0.67
% Sand/Mud x Depth + % Sand/Mud x $SweptArea_{All\ Years}$ + Depth x $SweptArea_{All\ Years}$	1.84	0.09	0.74
% Sand/Mud + Depth	2.39	0.07	0.62
% Sand/Mud + $MeanSweptArea_{All\ Years}$	2.43	0.07	0.62
% Sand/Mud + Depth + $SweptArea_{All\ Years}$ + % Sand/Mud x Depth	3.35	0.04	0.67
% Sand/Mud x $SweptArea_{All\ Years}$	3.46	0.04	0.64
% Sand/Mud x Depth + Depth x $SweptArea_{All\ Years}$	3.75	0.04	0.70

Table 3. Multi-model averaged parameter estimates, unconditional standard errors (SE), and relative variable importance (RVI) of parameters appearing in the top set of models within 4 ΔAICc units of the top model for log Shannon diversity. All parameters were estimated from a dataset with depth and *in situ* continuous substrate (i.e., percent SandMud) measured in standard deviation units (SDUs). The colon (:) represents an interaction between two variables.

Parameter	Estimate	SE	RVI
Intercept	-8.16E-01	1.88E-01	-
Depth	7.29E-02	1.46E-01	0.66
Swept $Area_{All\ Years}$	-2.83E-01	4.12E-01	0.51
%SandMud	-1.03E+00	2.62E-01	1.00
%SandMud : Depth	-2.61E-01	2.62E-01	0.58
%SandMud : Swept $Area_{All\ Years}$	4.50E-01	6.46E-01	0.36
Depth : Swept $Area_{All\ Years}$	-2.86E-02	5.84E-02	0.13

Table 4. Tests of mean swept area averaged over 14 years (All Years), *in situ* continuous substrate (i.e. percent SandMud), and depth on foundation species composition at each transect using permutational multivariate analysis of variance (PerMANOVA), with p-values based on 1000 permutations.

Variable	Pseudo-F	P-value
%Sand/Mud	3.33	<0.001
Depth	0.80	0.736
Swept Area$_{\text{All Years}}$	1.50	0.017
%Sand/Mud x Depth	0.92	0.555
%Sand/Mud x Swept Area$_{\text{All Years}}$	1.85	0.019
Depth x Swept Area$_{\text{All Years}}$	1.17	0.222
%Sand/Mud x Depth x Swept Area$_{\text{All Years}}$	1.22	0.155

FIGURES

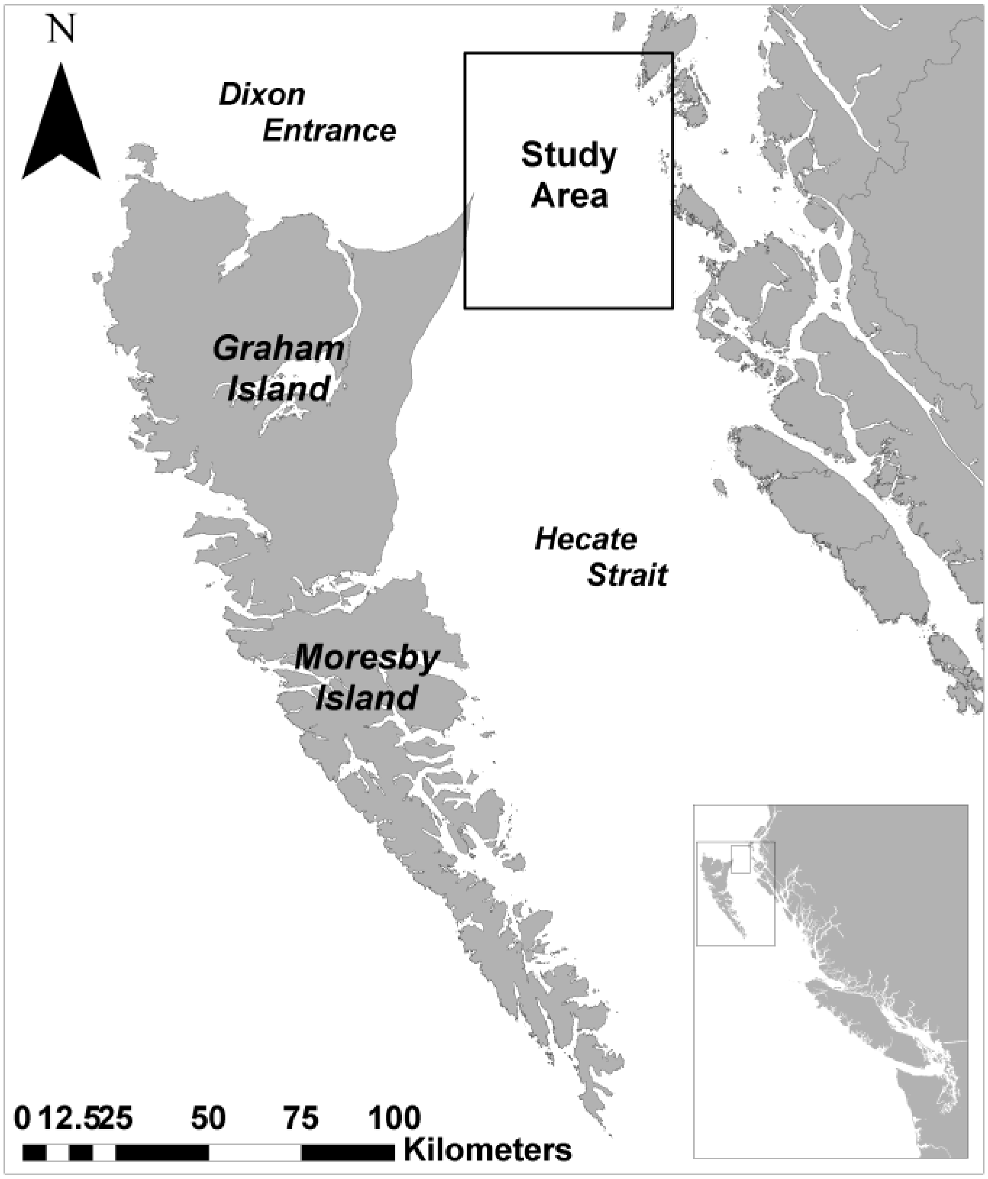

Figure 1. Location of study area in northern Hecate Strait, British Columbia, Canada.

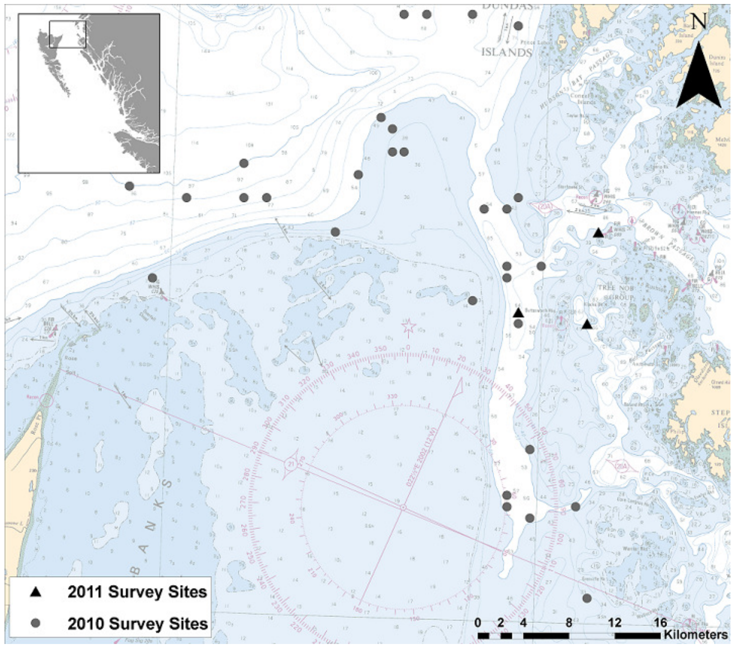

Figure 2. Locations of transects sampled during the 2010 (grey circles) and 2011 (black triangles) research surveys in Hecate Strait.

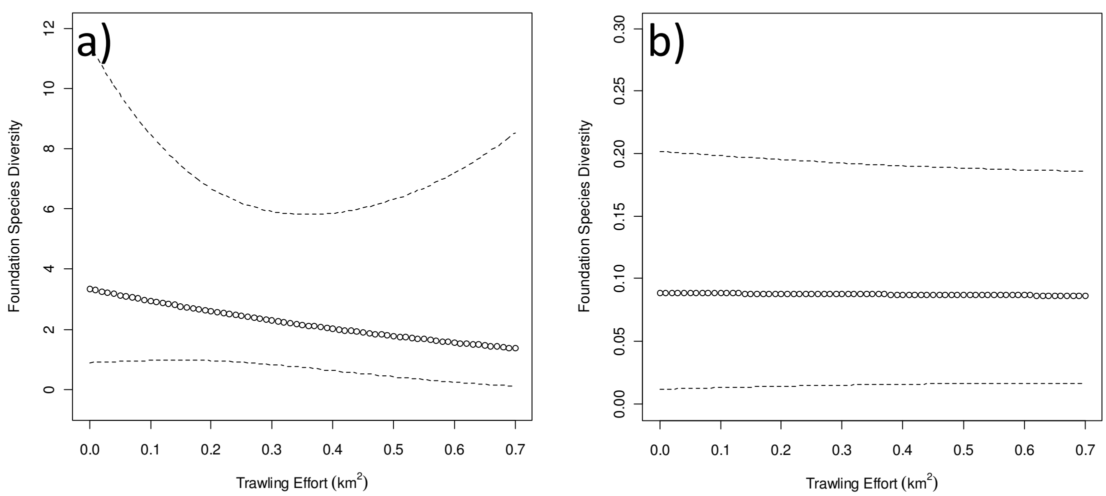

Figure 3. Predicted and 95% confidence interval relationships between foundation species diversity and trawling effort (km^2) in a) Till substrate with ~80% SandMud, and b) SandMud substrate with ~100% SandMud.

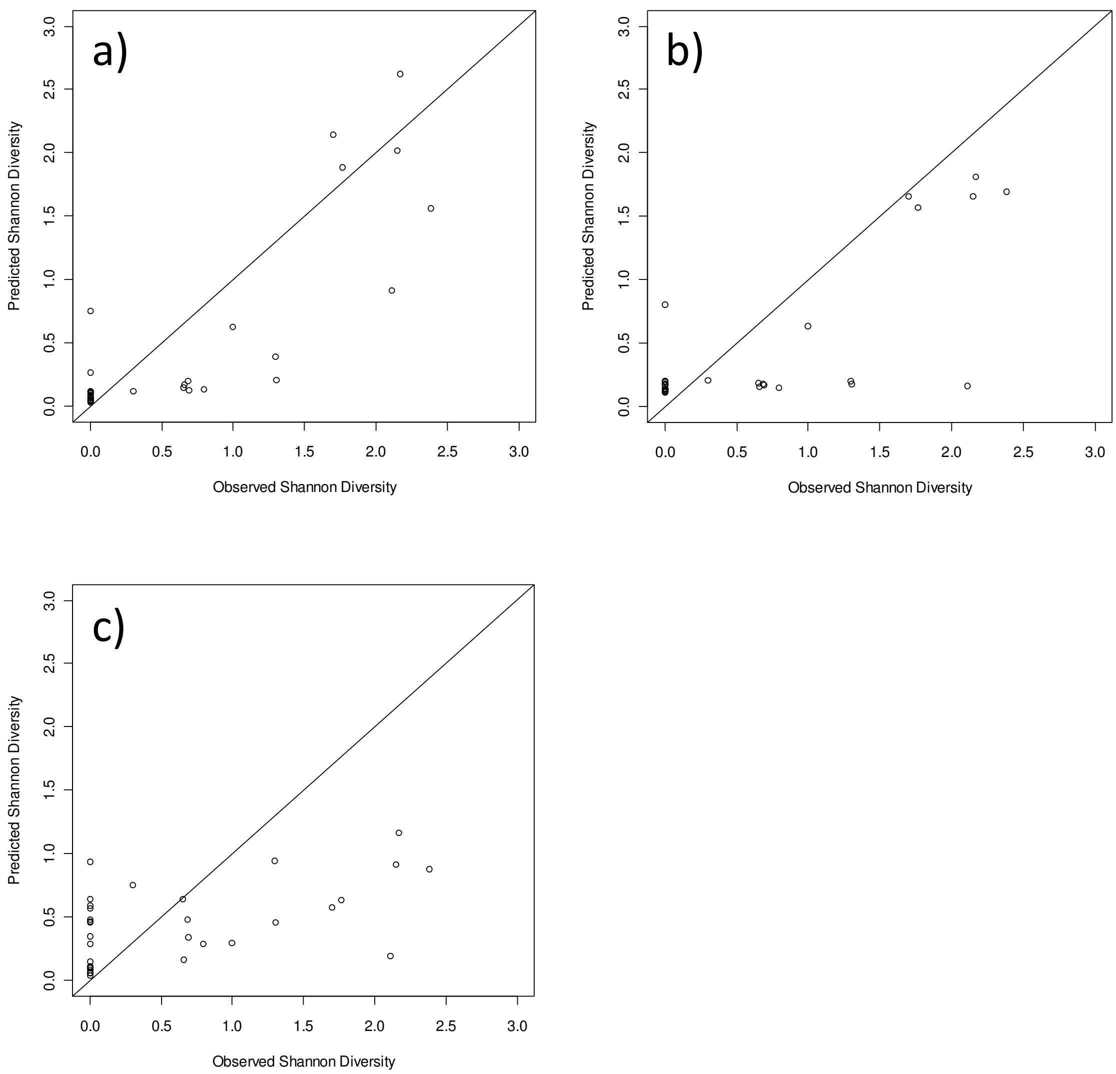

Figure 4. Predicted vs. observed Shannon diversity using the model-averaged regression equation with a) *in situ* continuous substrate (i.e., percent SandMud), b) *in situ* categorical substrate, and c) surficial geology-based categorical substrate.

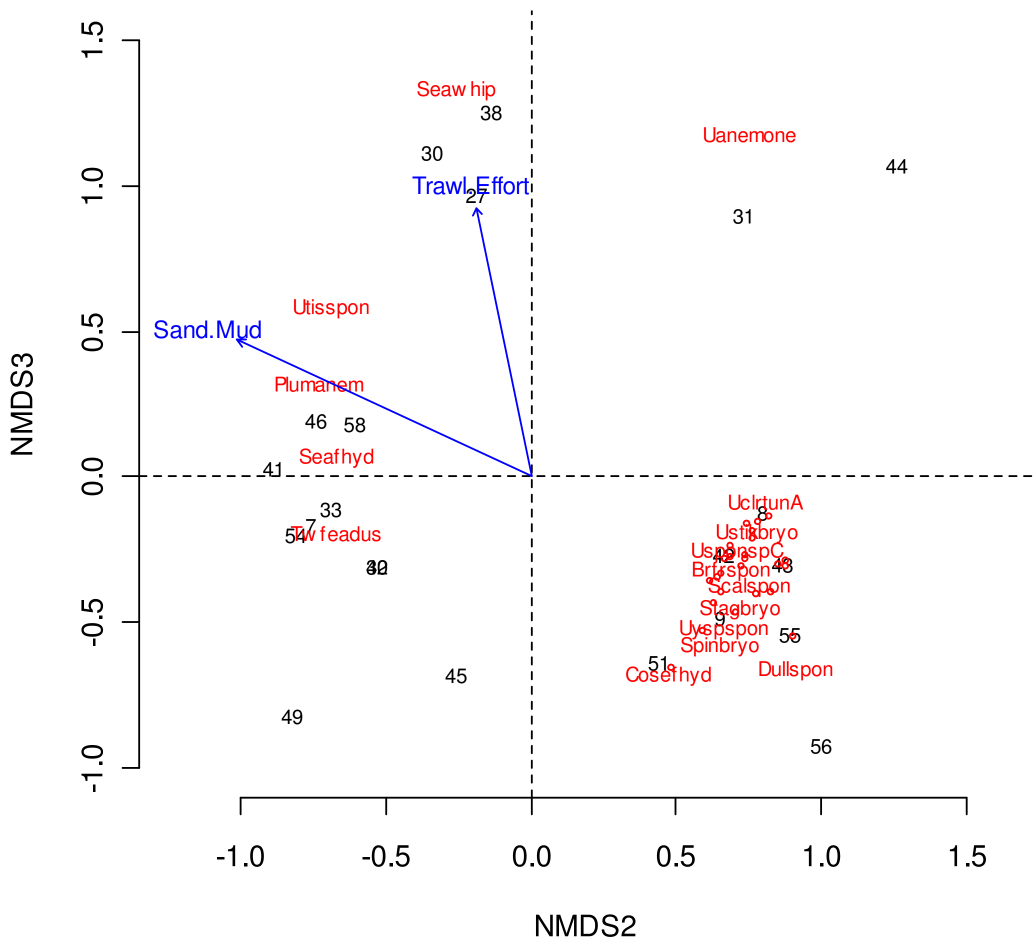

Figure 5. Non-metric multidimensional scaling (nMDS) ordination of transects based on percent cover of foundation species with vectors indicating direction of increasing percent SandMud (Sand.Mud), and mean swept area (Trawl.Effort) averaged over 14 years. Only explanatory variables (i.e., percent SandMud, swept area, and depth) with p-values less than 0.05 are plotted as vectors. Display priority of non-overlapping species scores was given to the most abundant species, with dots given to the remaining species. Species labels are an eight-letter abbreviation of the species name; corresponding species and common names are in Table A2.1.

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APPENDICES

Appendix 1

Table A1.1. Fisheries and Oceans Canada bottom substrate classification system used in all Pacific dive surveys (J.Pegg, pers.comm, 2010).

Classification Number	Substrate Type	Size Description
1	Bedrock, smooth without crevices	-
2	Bedrock with crevices	-
3	Boulders	Larger than a basketball (24cm and above)
4	Cobble	Between 3 inches and basketball size (7.6 to 23.9cm)
5	Gravel	Between 3/4 inch and 3 inch (1.9 to 7.6cm)
6	Pea Gravel	Between 1/8 inch and 3/4 inch (0.3 to 1.9cm)
7	Sand	-
8	Shell	-
9	Mud	-

Appendix 2

Table A2.1. All taxa collected over the duration of the study, grouped into foundation species, non-foundation species, and fish. Scientific names were provided where possible. All indeterminate species were labelled as "Undetermined." Abbreviated names were given to foundation species only for use in multivariate analysis.

Common Name	Scientific Name	Phylum	Abbreviated Name*
Foundation Species			
Brown tissue sponge		Porifera	Brtispon
Brown frond sponge		Porifera	Brfrspon
Calcareous tubeworm	*Serpula vermicularis*	Annelida	Calctube
Cloud sponge	*Aphrocallistes vastus*	Porifera	Clouspon
Coarse sea fir hydroid	*Abietinaria* spp.	Cnidaria	Cosefhyd
Crimson anemone	*Cribrinopsis fernaldi*	Cnidaria	Crimanem
Dull branching sponge		Porifera	Dullspon
Embedded sea fir hydroid	*Thuiaria* spp.	Cnidaria	Emsefhyd
Feather duster	*Sabellidae* spp.	Annelida	Feathdus
Fibre optic sponge		Porifera	Fiopspon
Finger sponge	*Neoesperiopsis* spp.	Porifera	Fingspon
Frilly bryozoan		Bryozoa	Frilbryo
Funnel sponge	*Phakellia* spp.	Porifera	Funnspon
Gray encrusting compound tunicate	*Diplosoma listerianum*	Chordata	Grenctun
Large yellow sponge		Porifera	Lrgyspon
Orange cup coral	*Balanophyllia elegans*	Cnidaria	Orenspon
Orange encrusted sponge		Porifera	Orcupcor
Orange feather duster		Annelida	Orfeadus
Orange sea Pen	*Ptilosarcus gurneyi*	Cnidaria	Orseapen
Orange zoanthid	*Epizoanthus scotinus*	Cnidaria	Orzoanth
Pink encrusting sponge		Porifera	Pencspon
Plumose anemone	*Metridium farcimen*	Cnidaria	Plumanem
Rabbit-ear bryozoan	*Cellaria diffusa*	Bryozoa	Rabebryo
Scallop sponge	*Mycale adhaerens*, *Myxilla parasitica*	Porifera	Scalspon
Sea fir hydroid	*Abietinaria* spp.	Cnidaria	Seafhyd
Sea whip	*Halipteris* spp.	Cnidaria	Seawhip
Spindly embedded hydroid	*Grammaria* spp.	Cnidaria	Spindhyd
Spindly white tuft bryozoan	*Crisia* spp.	Bryozoa	Spinbryo
Staghorn bryozoan	*Heteropora* spp.	Bryozoa	Stagbryo
Pink branching hydrocorals	*Stylaster* spp.	Cnidaria	Stylastr
Thicker white tuft bryozoan	*Crisia* spp.	Bryozoa	Thicbryo
Tough yellow branching sponge	*Syringella amphispicula*	Porifera	Tougspon
Twin eyed feather duster	*Myxicola infundibulum*	Annelida	Twfeadus
Undetermined anemone		Cnidaria	Uanemone
Undetermined compound tunicate		Chordata	Ucomptun
Undetermined clear tunicate A		Chordata	UclrtunA
Undetermined clear tunicate B		Chordata	UclrtunB
Undetermined fan bryozoan		Bryozoa	Ufanbryo
Undetermined flaccid sponge		Porifera	Uflaspon
Undetermined hole tunicate		Chordata	Uholetun
Undetermined red tunicate		Chordata	Uredtuni
Undetermined stick bryozoan		Bryozoa	Ustikbryo
Undetermined solitary tunicate		Chordata	Usolitun

*Only foundation species were given abbreviated names for multivariate analysis.

Table A2.1 (continued)

Common Name	Scientific Name	Phylum	Abbreviated Name*
Foundation Species (continued)			
Undetermined sponge species A		Porifera	UsponspA
Undetermined sponge species B		Porifera	UsponspB
Undetermined sponge species C		Porifera	UsponspC
Undetermined sponge species D		Porifera	UsponspD
Undetermined sponge species E		Porifera	UsponspE
Undetermined sponge species F		Porifera	UsponspF
Undetermined tissue sponge		Porifera	Utisspon
Undetermined tunicate		Chordata	Utunicat
Undetermined white soft coral		Cnidaria	Uwsoftcor
Undetermined white spherical sponge		Porifera	Uwhispon
Undetermined white tunicate		Chordata	Uwhitun
Undetermined yellow spherical sponge		Porifera	Uyspspon
Undetermined yellow sponge species A		Porifera	UylsponA
Undetermined yellow sponge species B		Porifera	UylsponB
Undetermined yellow tunicate		Chordata	Uyeltun
White encrusting sponge		Porifera	Whenspon
Wine glass hydroid	*Obelia* spp.	Cnidaria	Wineghyd
Yellow boring sponge	*Cliona californiana*	Porifera	Ylbospon
Yellow encrusting sponge		Porifera	Ylenspon
Non-Foundation Species			
Baetic olive snail	*Olivella baetica*	Mollusca	
Basket star	*Gorgonocephalus* sp., *Astrophyton eucnemis*	Echinodermata	
Bering hermit crab	*Pagurus beringanus*	Arthropoda	
Blood star	*Henricia* sp.	Echinodermata	
Brittle star	*Ophiura* sp.	Echinodermata	
Burrowing brittle star	*Amphiodia periercta*	Echinodermata	
Burrowing worm		Annelida	
Crangon shrimp	*Crangon* sp.	Arthropoda	
Eualid shrimp	*Eualus* sp.	Arthropoda	
Giant pink star	*Pisaster brevispinus*	Echinodermata	
Giant sea cucumber	*Parastichopus californicus*	Echinodermata	
Halls whelk	*Colus halli*	Mollusca	
Hermit crab	*Pagurus* sp.	Arthropoda	
Isopod		Arthropoda	
Moonsnail	*Euspira* sp.	Mollusca	
Octopus		Mollusca	
Orange peel nudibranch	*Tochuina tetraquetra*	Mollusca	
Oregon triton	*Fusitriton oregonensis*	Mollusca	
Pandalus prawn	*Pandalus* sp.	Arthropoda	
Pink scallop	*Chlamys* sp.	Mollusca	
Purple ringed topsnail	*Calliostoma annulatum*	Mollusca	
Slime star	*Pteraster tesselatus*	Echinodermata	
Spot prawn	*Pandalus platyceros*	Arthropoda	
Squat lobster		Arthropoda	
Sun star	*Crossaster papposus*	Echinodermata	
Ten tentacled burrowing anenome	*Halcampa decemtentaculata*	Cnidaria	
Tile brittle star	*Ophiosphalma jolliense*	Echinodermata	
Topsnail	*Calliostoma* sp.	Mollusca	

*Only foundation species were given abbreviated names for multivariate analysis.

Table A2.1 (continued)

Common Name	Scientific Name	Phylum	Abbreviated Name*
Non-Foundation Species (continued)			
Undetermined bubblesnail		Mollusca	
Undetermined clam		Mollusca	
Undetermined purple snail		Mollusca	
Undetermined prawn		Arthropoda	
Undetermined shrimp		Arthropoda	
Undetermined sea star		Echinodermata	
Undetermined snail		Mollusca	
Undetermined whelk		Mollusca	
Undetermined white nudibranch		Mollusca	
Velcro star	*Stylasterias forreri*	Echinodermata	
Vermillion star	*Mediaster aequalis*	Echinodermata	
Wrinkled star	*Pteraster militaris*	Echinodermata	
Fish			
Arrowtooth flounder	*Atherestes stomias*	Chordata	
Blackfin sculpin	*Malacocottus kincaidi*	Chordata	
Dover sole	*Microstomus pacificus*	Chordata	
Pacific halibut	*Hippoglossus stenolepis*	Chordata	
Juvenile flatfish		Chordata	
Pacific snake prickleback	*Lumpenus Sagitta*	Chordata	
Poacher sp.		Chordata	
Ratfish	*Hydrolagus colliei*	Chordata	
Rex sole	*Glyptocephalus zachirus*	Chordata	
Rock sole	*Lepidopsetta bilineata*	Chordata	
Sculpin sp.		Chordata	
Undetermined fish		Chordata	
Walleye pollock	*Theragra chalcogramma*	Chordata	

*Only foundation species were given abbreviated names for multivariate analysis.

Appendix 3

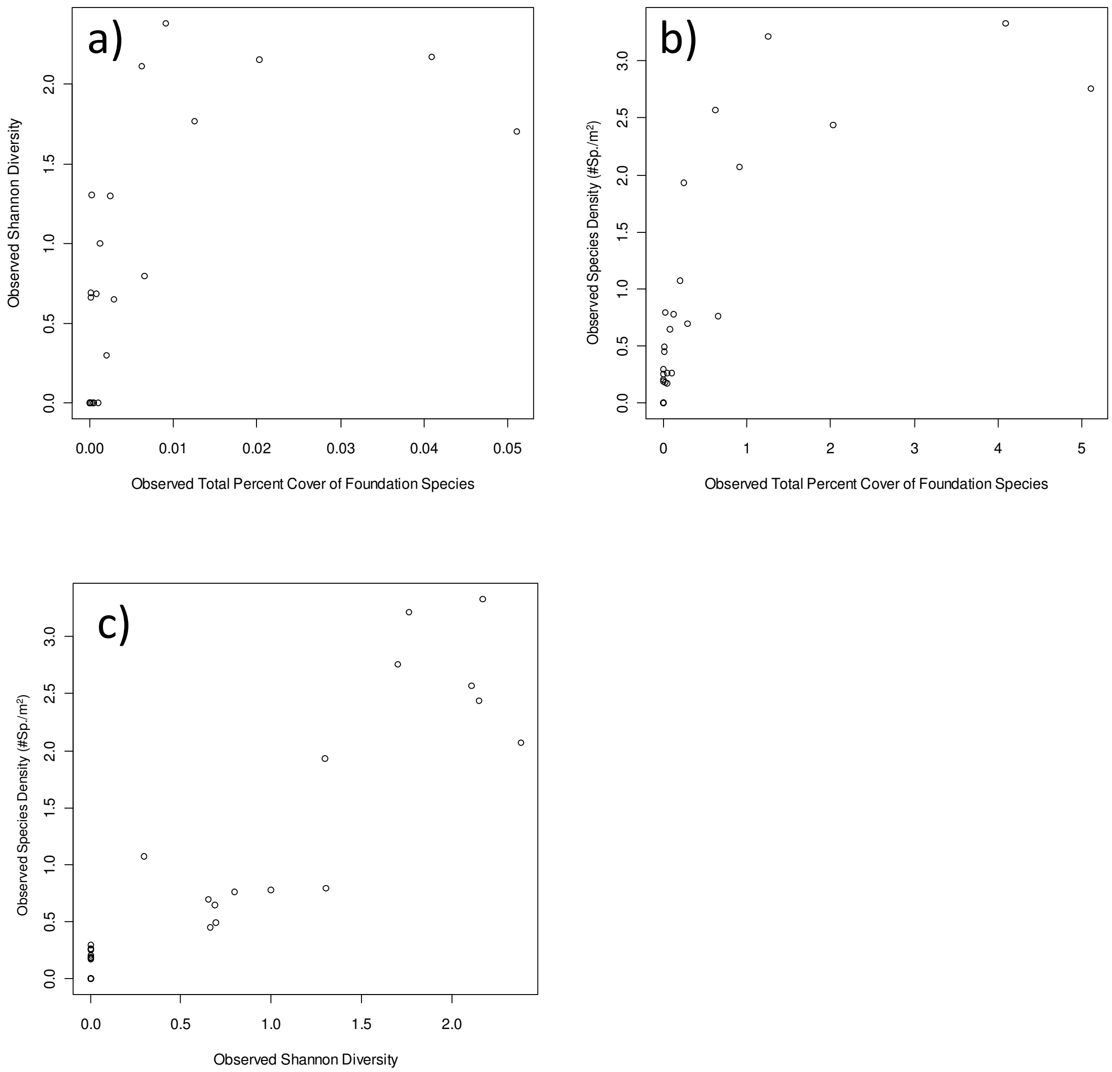

Figure A3.1. Correlation plots of a) observed Shannon diversity vs. observed total percent cover of foundation species (r = 0.66), b) observed species density vs. observed total percent cover of foundation species (r = 0.77), and c) observed species density vs. observed Shannon diversity (r = 0.93).

Table A3.1. Model selection statistics for log Shannon diversity. Models shown are within 4 ∆AICc units of the top model and ordered by ΔAIC_c. Parameters in the models include average depth per transect (Depth), *in situ* continuous substrate (i.e., average percent SandMud per transect), and all four definitions of swept area (i.e. $\text{Swept Area}_{Early}$, $\text{Swept Area}_{Middle}$, $\text{Swept Area}_{Recent}$ and $\text{Swept Area}_{AllYears}$). Also shown are the Akaike Information Criteria differences from the best model (ΔAIC_c), Akaike model weights (w_i) and R^2 values. The "x" represents the main effects and interactions in the linear model.

Model (Log Shannon diversity)	AICc	∆AICc	w_i	R^2
% Sand/Mud x Depth + % Sand/Mud x $\text{Swept Area}_{Early}$	87.30	0.00	0.11	0.73
% Sand/Mud x Depth + % Sand/Mud x $\text{Swept Area}_{Middle}$	87.35	0.05	0.11	0.73
% Sand/Mud	87.61	0.31	0.10	0.62
% Sand/Mud x Depth + % Sand/Mud x $\text{Swept Area}_{All Years}$	87.71	0.40	0.09	0.73
% Sand/Mud x Depth	88.04	0.74	0.08	0.67
% Sand/Mud + $\text{Swept Area}_{Recent}$	89.02	1.71	0.05	0.63
% Sand/Mud x Depth + Depth x $\text{Swept Area}_{All Years}$ + % Sand/Mud x $\text{Swept Area}_{All Years}$	89.46	2.15	0.04	0.74
% Sand/Mud x Depth + Depth x $\text{Swept Area}_{Middle}$ + % Sand/Mud x $\text{Swept Area}_{Middle}$	89.47	2.16	0.04	0.74
% Sand/Mud x Depth + Depth + $\text{Swept Area}_{Early}$ + % Sand/Mud x $\text{Swept Area}_{Early}$	89.63	2.33	0.04	0.74
% Sand/Mud + Depth + $\text{Swept Area}_{Recent}$ + % Sand/Mud x Depth	89.90	2.60	0.03	0.68
% Sand/Mud x Depth + % Sand/Mud x $\text{Swept Area}_{Recent}$	89.98	2.68	0.03	0.71
% Sand/Mud + Depth	90.01	2.71	0.03	0.62
% Sand/Mud + $\text{Swept Area}_{All Years}$	90.05	2.74	0.03	0.62
% Sand/Mud + $\text{Swept Area}_{Early}$	90.11	2.80	0.03	0.62
% Sand/Mud + $\text{Swept Area}_{Middle}$	90.14	2.84	0.03	0.62
% Sand/Mud x Depth + Depth x $\text{Swept Area}_{Recent}$	90.68	3.38	0.02	0.70
% Sand/Mud x $\text{Swept Area}_{Middle}$	90.70	3.40	0.02	0.64
% Sand/Mud + Depth + $\text{Swept Area}_{Middle}$ + % Sand/Mud x Depth	90.81	3.50	0.02	0.67
% Sand/Mud + Depth + $\text{Swept Area}_{All Years}$ + % Sand/Mud x Depth	90.96	3.66	0.02	0.67
% Sand/Mud + Depth + $\text{Swept Area}_{Early}$ + % Sand/Mud x Depth	91.00	3.69	0.02	0.67
% Sand/Mud x $\text{Swept Area}_{Early}$	91.02	3.71	0.02	0.64
% Sand/Mud x $\text{Swept Area}_{All Years}$	91.07	3.77	0.02	0.64
% Sand/Mud + Depth + $\text{Swept Area}_{Recent}$ + Depth x $\text{Swept Area}_{Recent}$	91.08	3.78	0.02	0.67
% Sand/Mud x Depth + Depth x $\text{Swept Area}_{Recent}$ + % Sand/Mud x $\text{Swept Area}_{Recent}$	91.24	3.93	0.02	0.73

Table A3.2. Model selection statistics for log Shannon diversity using *in situ* continuous substrate (i.e., percent SandMud), *in situ* categorical sand/mud and surficial geology-based sand/gravel. The model set with percent SandMud as substrate shows models within 10 ΔAIC_c units of the top model, ordered by ΔAIC_c. Model sets with *in situ* categorical substrate and surficial geology-based categorical substrate show models within 4 ΔAIC_c units of the top model, ordered by ΔAIC_c. The dashed line indicates the cutoff of models within 4 ΔAIC_c units of the top model for model averaging using percent SandMud as substrate. Also shown are the Akaike Information Criteria corrected for small sample sizes (AIC_c), the Akaike Information Criteria differences from the best model (ΔAIC_c), Akaike model weights (w_i) and R^2 values for model fit. The "x" represents the main effects and interactions in the linear model.

Model (Log Shannon diversity)	AICc	ΔAICc	w_i	R^2
Models with substrate as % Sand/Mud				
% Sand/Mud	87.61	0.00	0.22	0.62
% Sand/Mud x Depth + % Sand/Mud x $SweptArea_{All\ Years}$	87.71	0.09	0.21	0.73
% Sand/Mud x Depth	88.04	0.43	0.18	0.67
% Sand/Mud x Depth + % Sand/Mud x $SweptArea_{All\ Years}$ + Depth x $SweptArea_{All\ Years}$	89.46	1.84	0.09	0.74
% Sand/Mud + Depth	90.01	2.39	0.07	0.62
% Sand/Mud + $SweptArea_{All\ Years}$	90.05	2.43	0.07	0.62
% Sand/Mud + Depth + $SweptArea_{All\ Years}$ + % Sand/Mud x Depth	90.96	3.35	0.04	0.67
% Sand/Mud x $SweptArea_{All\ Years}$	91.07	3.46	0.04	0.64
% Sand/Mud x Depth + Depth x $SweptArea_{All\ Years}$	91.36	3.75	0.03	0.70
% Sand/Mud + Depth + $SweptArea_{All\ Years}$ + Depth x $SweptArea_{All\ Years}$	92.28	4.67	0.02	0.66
% Sand/Mud + Depth + $SweptArea_{All\ Years}$	92.72	5.10	0.02	0.62
% Sand/Mud + Depth + $SweptArea_{All\ Years}$ + % Sand/Mud x $SweptArea_{All\ Years}$	94.02	6.40	0.01	0.64
Depth x $SweptArea_{All\ Years}$ + % Sand/Mud x $SweptArea_{All\ Years}$	94.24	6.63	0.01	0.67
Models with substrate as In Situ Categorical Sand/Mud				
In Situ Categorical Sand/Mud	102.66	0.00	0.25	0.40
In Situ Categorical Sand/Mud x $SweptArea_{All\ Years}$	102.82	0.17	0.23	0.49
Depth + In Situ Categorical Sand/Mud	104.19	1.53	0.12	0.42
Depth x In Situ Categorical Sand/Mud	104.86	2.20	0.08	0.46
In Situ Categorical Sand/Mud + $SweptArea_{All\ Years}$	104.95	2.30	0.08	0.41
Depth + In Situ Categorical Sand/Mud+ $SweptArea_{All\ Years}$ + In Situ Categorical Sand/Mud x $SweptArea_{All\ Years}$	105.22	2.56	0.07	0.50
$SweptArea_{All\ Years}$ x Depth + $SweptArea_{All\ Years}$ x In Situ Categorical Sand/Mud	105.37	2.72	0.06	0.54
Depth + In Situ Categorical Sand/Mud + $SweptArea_{All\ Years}$ + Depth x $SweptArea_{All\ Years}$	105.78	3.13	0.05	0.49
Depth + In Situ Categorical Sand/Mud + $SweptArea_{All\ Years}$	106.06	3.41	0.05	0.44
Models with substrate as Surficial Geology-Based Categorical Sand/Gravel				
Depth + $SweptArea_{All\ Years}$	112.21	0.00	0.26	0.27
Depth x $SweptArea_{All\ Years}$	112.68	0.47	0.21	0.32
Depth	114.13	1.92	0.10	0.16
Depth + Surficial Geology-Based Categorical Sand/Gravel + $SweptArea_{All\ Years}$ + Depth x $SweptArea_{All\ Years}$	114.28	2.07	0.09	0.34
Depth + Surficial Geology-Based Categorical Sand/Gravel + $SweptArea_{All\ Years}$	114.29	2.07	0.09	0.28
Depth + Surficial Geology-Based Categorical Sand/Gravel	114.57	2.36	0.08	0.22
Depth x Surficial Geology-Based Categorical Sand/Gravel	114.63	2.42	0.08	0.28
Surficial Geology-Based Categorical Sand/Gravel	115.40	3.19	0.05	0.13
Depth + Surficial Geology-Based Categorical Sand/Gravel + $SweptArea_{All\ Years}$ + Depth x Surficial Geology-Based Categorical Sand/Gravel	115.94	3.73	0.04	0.31

Appendix 4

Table A4.1. Model selection statistics for the total percent cover of foundation species using *in situ* continuous substrate (i.e., percent SandMud), *in situ* categorical sand/mud and surficial geology-based sand/gravel. The model set with percent SandMud as substrate shows models within 10 ΔAIC_c units of the top model, ordered by ΔAIC_c. Model sets with *in situ* categorical sand/mud and surficial geology-based categorical sand/gravel show models within 4 ΔAIC_c units of the top model, ordered by ΔAIC_c. The dashed line indicates the cutoff of models within 4 ΔAIC_c units of the top model for model averaging using percent SandMud as substrate. Also shown are the Akaike Information Criteria corrected for small sample sizes (AIC_c), the Akaike Information Criteria differences from the best model (ΔAIC_c), Akaike model weights (w_i) and R^2 values for model fit. The "x" represents the main effects and interactions in the linear model.

Model (Total Percent Cover)	AICc	ΔAICc	w_i	R^2
Models with substrate as % Sand/Mud				
% Sand/Mud x Swept Area$_{\text{All Years}}$	-141.35	0.00	0.62	0.80
% Sand/Mud + Depth + Swept Area$_{\text{All Years}}$ + % Sand/Mud x Swept Area$_{\text{All Years}}$	-138.62	2.73	0.16	0.80
% Sand/Mud	-137.05	4.30	0.07	0.74
% Sand/Mud x Swept Area$_{\text{All Years}}$ + Depth x Swept Area$_{\text{All Years}}$	-135.46	5.89	0.03	0.80
% Sand/Mud x Depth + % Sand/Mud x Swept Area$_{\text{All Years}}$	-135.46	5.89	0.03	0.80
% Sand/Mud + Depth	-135.07	6.29	0.03	0.74
% Sand/Mud x Depth	-134.79	6.56	0.02	0.76
% Sand/Mud + Swept Area$_{\text{All Years}}$	-134.47	6.88	0.02	0.74
% Sand/Mud + Depth + Swept Area$_{\text{All Years}}$	-132.38	8.97	0.01	0.74
% Sand/Mud x Depth + % Sand/Mud x Swept Area$_{\text{All Years}}$ + Depth x Swept Area$_{\text{All Years}}$	-132.06	9.29	0.01	0.80
% Sand/Mud + Depth + Swept Area$_{\text{All Years}}$ + % Sand/Mud x Depth	-131.89	9.46	0.01	0.76
Models with substrate as In Situ Categorical Sand/Mud				
In Situ Categorical Sand/Mud x Swept Area$_{\text{All Years}}$	-131.52	0.00	0.65	0.73
Depth + In Situ Categorical Sand/Mud + Swept Area$_{\text{All Years}}$ + In Situ Categorical Sand/Mud x Swept Area$_{\text{All Years}}$	-129.49	2.03	0.24	0.74
Depth x In Situ Categorical Sand/Mud	-128.09	3.42	0.12	0.71
Models with substrate as Surficial Geology-Based Categorical Sand/Gravel				
Depth + Swept Area$_{\text{All Years}}$	-99.01	0.00	0.42	0.25
Depth x Surficial Geology-Based Sand/Gravel	-96.72	2.29	0.13	0.26
Depth x Swept Area$_{\text{All Years}}$	-96.40	2.62	0.11	0.25
Depth	-96.35	2.66	0.11	0.13
Depth + Surficial Geology-Based Sand/Gravel + Swept Area$_{\text{All Years}}$	-96.32	2.70	0.11	0.25
Depth + Surficial Geology-Based Sand/Gravel + Swept Area$_{\text{All Years}}$ + Depth x Surficial Geology-Based Sand/Gravel	-96.20	2.81	0.10	0.31

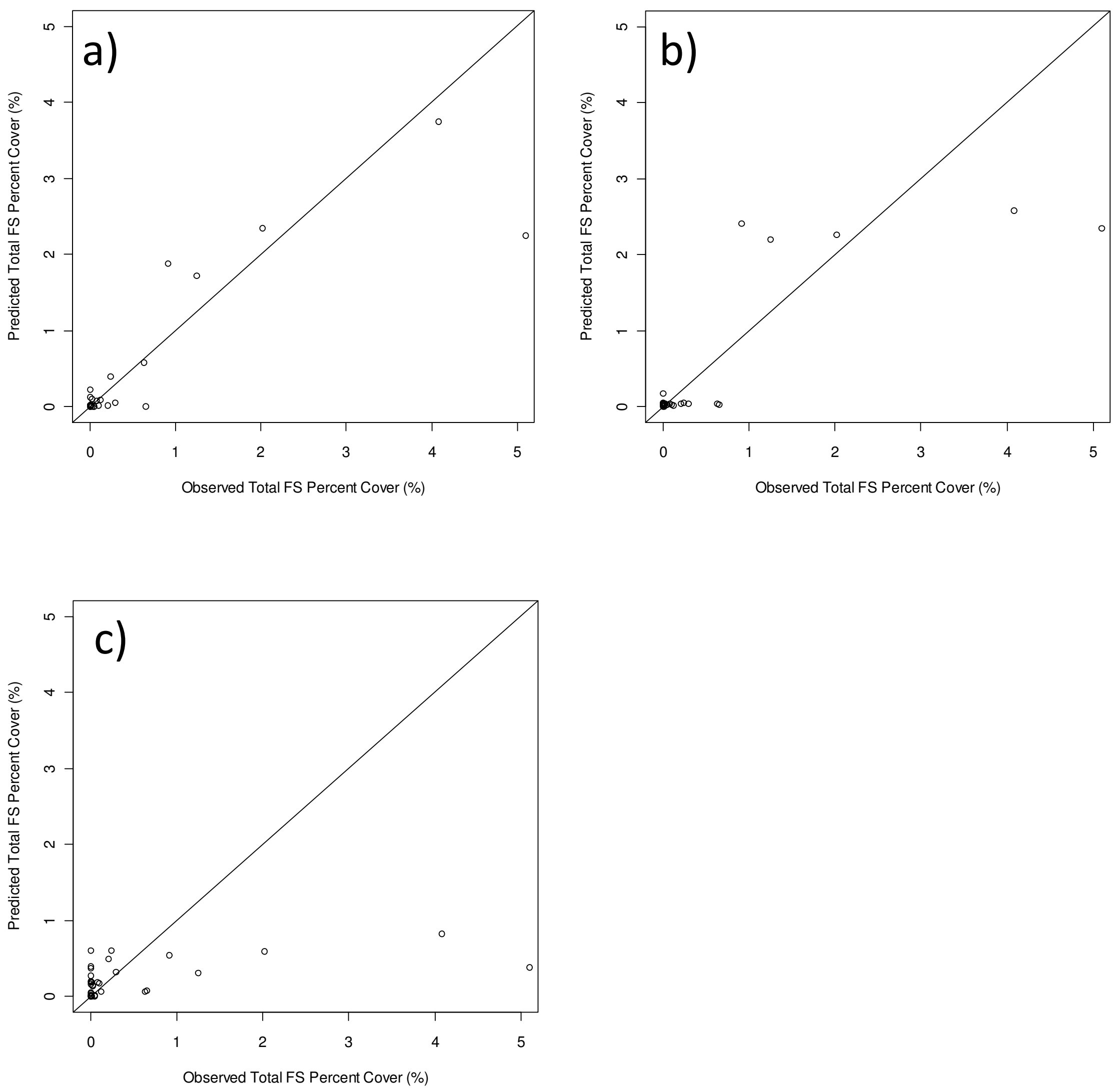

Figure A4.1. Predicted vs. observed total percent cover of foundation species (FS) using the model-averaged regression equation with a) *in situ* continuous substrate (i.e., percent SandMud), b) *in situ* categorical substrate, and c) surficial geology-based categorical substrate.

Table A4.2. Multi-model averaged parameter estimates, unconditional standard errors (SE), and relative variable importance (RVI) of parameters appearing in the top set of models within 4 ΔAIC_c units of the top model for the total percent cover of foundation species using *in situ* continuous substrate (i.e., percent SandMud) (Table A4.1). Multi-model parameter estimates are presented for both raw data (Raw) and for depth and *in situ* continuous substrate data in standard deviation units (Standardized). The colon (:) represents an interaction between two variables.

	Standardized			*Raw*		
Parameter	**Estimate (SDUs)**	**SE**	**RVI**	**Estimate (Raw)**	**SE**	**RVI**
Intercept	4.37E-02	5.74E-03	-	7.97E-01	7.24E-02	-
Depth	-4.97E-04	1.57E-03	0.20	-1.58E-05	4.98E-05	0.20
Swept Area$_{\text{All Years}}$	-3.79E-02	1.27E-02	1.00	-8.89E-01	2.86E-01	1.00
%SandMud	-5.36E-02	5.31E-03	1.00	-7.85E-03	7.78E-04	1.00
%SandMud : Swept Area$_{\text{All Years}}$	6.08E-02	1.95E-02	1.00	8.90E-03	2.86E-03	1.00

Appendix 5

Table A5.1. Model selection statistics for foundation species density using *in situ* continuous substrate (i.e., percent SandMud), observed categorical sand/mud and surficial geology-based sand/gravel. The model set with percent SandMud as substrate shows models within 10 ΔAIC_c units of the top model, ordered by ΔAIC_c. Model sets with *in situ* categorical sand/mud and surficial geology-based sand/gravel show models within 4 ΔAIC_c units of the top model, ordered by ΔAIC_c. The dashed line indicates the cutoff of models within 4 ΔAIC_c units of the top model for model averaging using percent SandMud as substrate. Also shown are the Akaike Information Criteria corrected for small sample sizes (AIC_c), the Akaike Information Criteria differences from the best model (ΔAIC_c), Akaike model weights (w_i) and R^2 values for model fit. The "x" represents the main effects and interactions in the linear model.

Model (Species density)	AICc	ΔAICc	w_i	R^2
Models with substrate as % Sand/Mud				
% Sand/Mud x Depth + % Sand/Mud x Swept $Area_{All\ Years}$	130.67	0.00	0.82	0.81
% Sand/Mud x Depth	135.22	4.55	0.08	0.69
% Sand/Mud + Depth + Swept $Area_{All\ Years}$ + % Sand/Mud x Depth	136.85	6.18	0.04	0.70
% Sand/Mud	138.03	7.36	0.02	0.58
% Sand/Mud + Depth + Swept $Area_{All\ Years}$ + Depth x Swept $Area_{All\ Years}$	139.19	8.52	0.01	0.67
% Sand/Mud + Depth	140.10	9.42	0.01	0.58
% Sand/Mud + Swept $Area_{All\ Years}$	140.11	9.43	0.01	0.59
Models with substrate as In Situ Categorical Sand/Mud				
In Situ Categorical Sand/Mud + Swept $Area_{All\ Years}$ + Depth + Depth x Swept $Area_{All\ Years}$	150.25	0.00	0.38	0.50
In Situ Categorical Sand/Mud x Swept $Area_{All\ Years}$ + Depth x Swept $Area_{All\ Years}$	152.17	1.92	0.14	0.52
In Situ Categorical Sand/Mud	152.74	2.49	0.11	0.30
In Situ Categorical Sand/Mud x Swept $Area_{All\ Years}$	153.11	2.86	0.09	0.40
In Situ Categorical Sand/Mud + Swept $Area_{All\ Years}$	153.27	3.01	0.08	0.34
In Situ Categorical Sand/Mud + Swept $Area_{All\ Years}$ + Depth	153.52	3.27	0.07	0.39
Depth x Swept $Area_{All\ Years}$	153.68	3.42	0.07	0.38
In Situ Categorical Sand/Mud+ Depth	154.22	3.97	0.05	0.32
Models with substrate as Surficial Geology-Based Categorical Sand/Gravel				
Depth x Swept $Area_{All\ Years}$	153.68	0.00	0.62	0.38
Depth + Swept $Area_{All\ Years}$	155.76	2.08	0.22	0.28
Depth + Surficial Geology-Based Categorical Sand/Gravel + Swept $Area_{All\ Years}$ + Depth x Swept $Area_{All\ Years}$	156.29	2.62	0.17	0.38

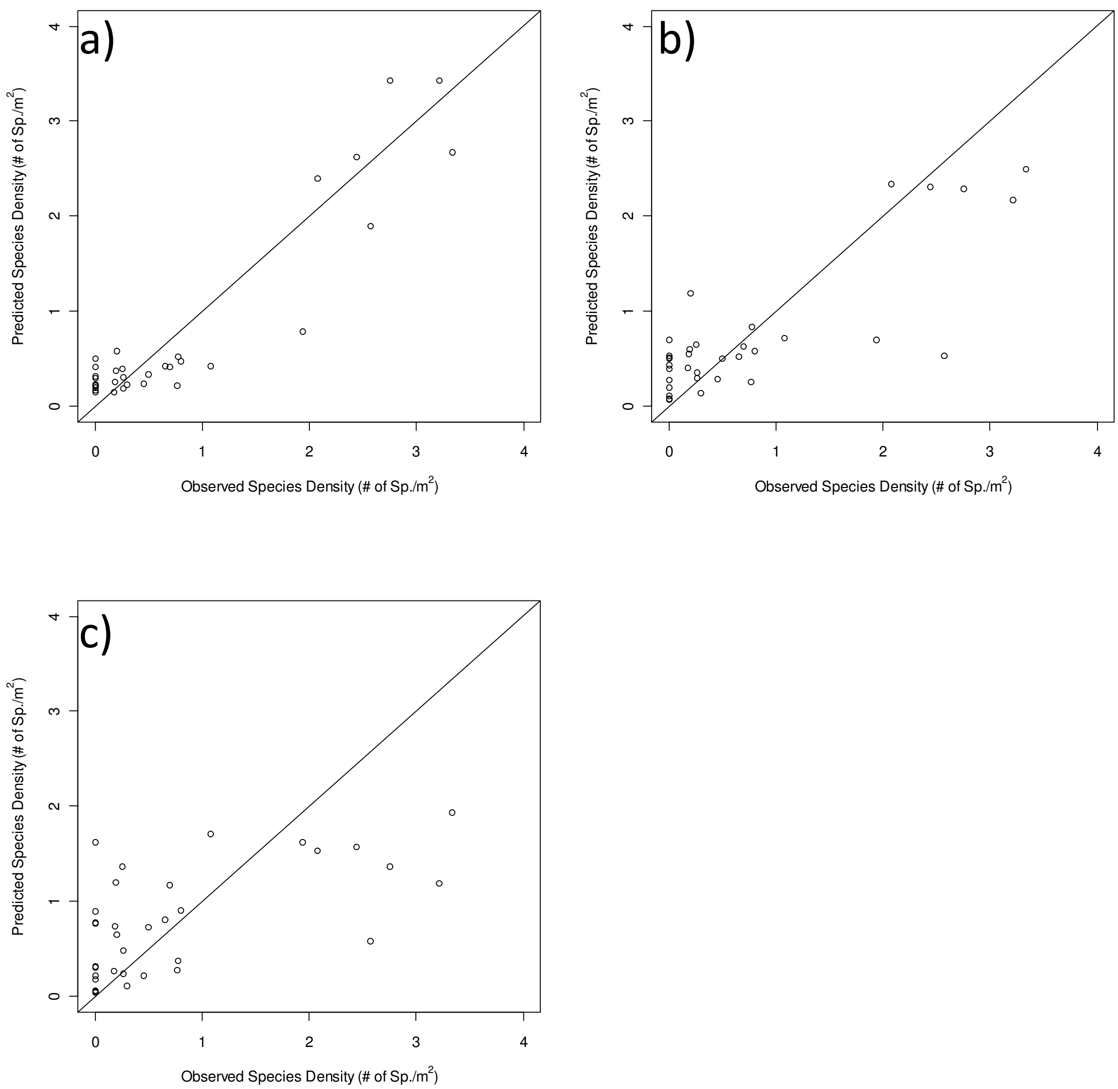

Figure A5.1. Predicted vs. observed species density using the model-averaged regression equation with a) *in situ* continuous substrate (i.e., percent SandMud), b) *in situ* categorical substrate, and c) surficial geology-based categorical substrate.

Table A5.2. Multi-model averaged parameter estimates, unconditional standard errors (SE), and relative variable importance (RVI) of parameters appearing in the top set of models within 4 ΔAIC_c units of the top model for species density using *in situ* continuous substrate (i.e., percent SandMud) (Table A5.1). Only one model had a $\Delta AIC_c<4$, therefore results presented are coefficients of the top model. Parameter estimates are presented for both raw data (Raw) and for depth and *in situ* continuous substrate data in standard deviation units (Standardized). The colon (:) represents an interaction between two variables.

	Standardized			*Raw*		
Parameter	**Estimate (SDUs)**	**SE**	**RVI**	**Estimate (Raw)**	**SE**	**RVI**
Intercept	-4.57E-01	1.82E-01	-	-1.02E+01	5.11E+00	-
Depth	2.64E-02	1.66E-01	1.00	2.26E-01	5.54E-02	1.00
Swept Area$_{All\ Years}$	-9.49E-01	3.43E-01	1.00	-1.99E+01	7.53E+00	1.00
%SandMud	-1.20E+00	1.68E-01	1.00	1.01E-01	5.64E-02	1.00
%SandMud : Depth	-5.07E-01	1.28E-01	1.00	-2.36E-03	5.93E-04	1.00
%SandMud : Swept Area$_{All\ Years}$	1.35E+00	5.16E-01	1.00	1.98E-01	7.56E-02	1.00