CANOPY AND COMMUNITY STRUCTURE OF ROCKWEED BEDS IN NOVA SCOTIA AND NEW BRUNSWICK: REGIONAL VARIATION AND EFFECTS OF COMMERCIAL HARVEST AND PROXIMITY TO AQUACULTURE

by

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Abstract

Ascophyllum nodosum (rockweed) is a significant component of intertidal rocky shore communities in Atlantic Canada. In Nova Scotia and Southwest New Brunswick, rockweed and other fucoids cover 80-90% of the intertidal zone, maintaining high biomass and primary productivity. Rockweed plays important roles storing carbon, cycling nutrients and providing habitat and food for associated plant and animal communities. For humans, rockweed has been economically important and commercially harvested in Atlantic Canada since the late 1950s. Considerable monitoring and research efforts have been made to study changes in rockweed plants themselves in response to harvesting; however, the effects of rockweed harvesting on the overall canopy structure and the associated fauna and flora have received much less attention. Additionally, the cumulative effects of harvesting and other human impacts, such as proximity to aquaculture, on the rockweed community have not been well studied. Using large-scale underwater field surveys and multivariate statistics, we quantified regional variation in the canopy and community structure of harvested and unharvested rockweed habitats in Southwest New Brunswick and Nova Scotia and established that canopy structure influences community structure. We conducted an experimental harvest reproducing the current commercial harvest in Yarmouth, Nova Scotia to assess the short-term effects of current harvest intensity. Finally, we demonstrate an effect of proximity to salmon aquaculture in Southwest New Brunswick that interacts with the effects of long-term rockweed harvesting on canopy and community structure. Overall, our results have implications for the spatial and ecosystem-based management of rockweed harvesting.

List of Abbreviations and Symbols Used

δ	Delta - used for isotope notation
AI	Adam Island
B	Biomass
BI	Barnes Island
BN	Beans Island
C	Circumference
CA	Central Argyle
Chl *a*	Chlorophyll *a*
D	Density (m^{-2})
DFO	Department of Fisheries and Oceans (Canada)
DMR	Department of Marine Resources (Maine)
GNATS	Gulf of Maine North Atlantic Time Series
KC	Kelley's Cove
L	Length
M	Mass
N	Nitrogen
NB	New Brunswick
NS	Nova Scotia
O.TPM	% Organic Content of Total Particulate Matter
PIM	Particulate Organic Matter
POM	Particulate Inorganic Matter
SI	Simpson Island
SST	Sea Surface Temperature
TPM	Total Particulate Matter

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Chapter 1: Introduction

Perennial seaweeds such as fucoids and laminarians are dominant primary producers along rocky shores (Vadas et al. 2004, Worm and Lotze 2006). The rockweed *Ascophyllum nodosum* (L.) Le Jol., along with other fucoids, covers 80-90% of the intertidal zone in Southwest Nova Scotia and New Brunswick and forms dense three-dimensional canopies up to 2 m high when submerged. Rockweed canopies, thus, play an important role in storing carbon, cycling nutrients and providing habitat and food for an abundant and diverse associated flora and fauna (Thompson et al. 2002, Vadas et al. 2004, Worm and Lotze 2006, Schmidt et al. 2011). *A. nodosum* is also an economically important seaweed in Atlantic Canada and has been harvested for the production of alginates as well as for use in animal food and fertilizer since the 1960s (Chopin et al. 1996, Sharp 1987). Given the variety and importance of the ecological services rockweed provides, it is listed as a "high-priority" species for protection in the United States (Wippelhauser 1996), a "priority species" in Northern Ireland (Morton 2011) and a "high-sensitivity species" in the UK (Hill and White 2008).

Despite their ecological importance, rockweed habitats are facing increasing anthropogenic impacts, such as direct harvesting, coastal eutrophication and climate change (Lotze et al. 2006, Worm and Lotze 2006, Schmidt et al. 2011). Although some research has been conducted in recent years on the cumulative effects of multiple stressors to aquatic ecosystems (see review by Crain et al. 2008), there are still major knowledge gaps concerning the combined and interactive effects of multiple human activities and changes in environmental conditions on the growth and function of foundation species in general, as well as on rockweed habitats in particular (Lotze and

Worm 2002). The effects of rockweed harvesting on habitat structure and composition of the associated fauna and flora have not been well studied (Rangeley and Davies 2000), nor have the cumulative effects of harvesting and nutrient loading on the rockweed community (Rangeley and Davies 2000, Worm and Lotze 2006). These knowledge gaps are of particular concern given plans to expand the commercial harvest of rockweed in the Maritimes and increasing nutrient loading into coastal waters in recent decades (Chambers et al. 2001, Lotze et al. 2006, Schmidt et al. 2011).

In this thesis, I address important knowledge gaps in the ecological study of rockweed habitat that require attention in order to strengthen the management of rockweed harvest in Canada and beyond.

1.1 Brief background on the rockweed *Ascophyllum nodosum*

Ascophyllum nodosum is an intertidal brown seaweed from the Family Fucaceae, Order Fucales (Villalard-Bohnsack 2003). In Canada, common names include rockweed, bottle kelp and goémon de roche.[1] *A. nodosum* is found along rocky shores throughout the North Atlantic and up into parts of the Arctic Ocean (Sharp 1987, Kerin 1998). In Atlantic Canada, rockweed dominates the intertidal region of the rocky coastline where it is present (Vadas et al. 2004, DFO 2013). *A. nodosum* extends from the upper intertidal to the mean low tide level, but also grows subtidally in shallow water (Baardseth 1970). It has bioenginnering effects on understory species richness, diversity and composiotion in the high and middle intertidal zones (Watt and Scorsati 2013a, 2013b). This seaweed

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[1] *A. nodosum* will be refered to either by its scientific name or as rockweed throughout this thesis.

grows best with periods of exposure to air and is most abundant in regions with large tidal amplitudes, such as the Bay of Fundy (Kerin 1998, Vadas et al. 2004).

Due to its high phenotypic plasticity, *Ascophyllum nodosum* is able to adapt to a range of different environments (Sharp 1987, Kerin 1998). It exists across gradients of several environmental parameters including wave exposure, salinity, and temperature (Sharp 1987). Wave exposure, in particular, plays a key role shaping the distribution of rockweed (Kerin 1998). Oldest plants, highest coverage, highest growth and relative abundance are all found at wave-sheltered locations; however, biomass is highest at sites of intermediate exposure where the ice-scouring that occurs at sheltered sites is prevented (Vadas and Wright 1986, Vadas et al. 2004). *A. nodosum* is an euryhaline species and grows best at salinities near 32‰, however, it will tolerate temporary changes in salinity to as low as 0.0‰ and is found at the mouths of rivers (Baardseth 1970). Rockweed is a cold water species, and growth increases as sea surface temperature (SST) rises to 20°C, but decreases sharply thereafter (Keser et al. 2005). Surface temperatures of 27-28°C are lethal to rockweed (Keser et al. 2005).

Ascophyllum nodosum is attached to the substratum by a discoid holdfast; often, several linear shoots emerge from the holdfast (David 1943, Moss 1970). Shoots lengthen by apical growth and branch dichotomously, usually once each year. Lateral branches emerge from pits along the primary shoot and can be vegetative or reproductive; if reproductive, the shoots bear receptacles at their apices (Cousens 1982). Rockweed returns slowly after any disturbance that removes holdfasts, such as ice-scouring or overharvesting (Sharp 1987). When holdfasts are intact, however, rockweed biomass is able to regenerate; beds harvested at rates of 20% of the harvestable biomass can recover within the year (DFO 2013). However, beds subjected to harvest rates of 35% take up to three years to recover and those harvested at 50% harvest rates may need more than three years (DFO 2013).

Seasonal changes in the biomass of *A. nodosum* change with latitude (David 1943). Generally, higher growth rates occur in spring with rising water temperatures and increased irradiance (Mathieson et al. 1976). Growth decreases into the summer and fall and there is minimal growth throughout winter (Baardseth 1970, Chock and Mathieson 1983). In Northern Ireland, Stengel and Dring (1997) observed lower growth rates in November and December and highest growth in late spring and early summer with a decrease in growth by mid-summer.

1.2 Thesis outline

Following this general introduction, this thesis consists of three data chapters and a general conclusion. In Chapter 2, I establish the relationship between canopy structure of rockweed habitats and the structure of the associated floral and faunal community. Field surveys in southwest Nova Scotia and New Brunswick were used to quantify the regional variation in the canopy and community structure of rockweed habitats. Multivariate statistical analyses demonstrate that the canopy and community structure are linked.

In Chapter 3, I examine the short-term effects of an experimental rockweed harvest on canopy and associated community structure, and contextualize our findings within a review of previous monitoring and experimental harvest studies. A regularly harvested site in Yarmouth, Nova Scotia was surveyed immediately before and one month after the commercial hand harvest and compared to an unharvested control. Multivariate statistics were used to analyse changes in canopy structure and different components of the associated species community.

In Chapter 4, I investigate how organic loading in the coastal zone influences canopy and community structure and interacts with the effects of long-term rockweed harvesting. A subset of four similar and adjacent study sites in Southwest New Brunswick provided the opportunity to examine the effects of proximity to salmon aquaculture operations in the presence (regularly harvested sites) or absence (harvest exclusion zones) of long-term rockweed harvesting. Using the same field survey design as in previous chapters and multivariate statistical analyses, I investigated the single and combined effects of these two human activities.

In the general conclusion, I discuss the implications of my thesis findings for the management of rockweed harvesting and make recommendations for future research.

Chapter 2: Regional differences and linkage between canopy structure and community composition of rockweed habitats in Atlantic Canada

2.0 Abstract

Ascophyllum nodosum (rockweed) is a dominant, habitat-forming seaweed on intertidal rocky shores in the North Atlantic and commercially harvested in Canada, Maine and Europe. Rockweed plant structure varies regionally and several morphotypes have been identified in Atlantic Canada alone. Yet the regionality of canopy structure, associated communities and the link between the two have not been well understood. Using large-scale field surveys and multivariate statistical approaches, we establish regionally distinct canopy structures in southwest Nova Scotia and southwest New Brunswick as well as distinct associated mobile and sessile species communities. We then demonstrate significant links between canopy and community structure using generalized linear and additive models as well as PERMANOVA+'s BIOENV, a non-parametric matrix linking procedure. Interestingly, plant and canopy structure (e.g length, circumference, density) were always better predictors of associated community structure than simply rockweed biomass, and adding region or site as predictors further improved model fits. Therefore, although rockweed biomass may be a sufficient monitoring measure in a single-species context, plant or canopy structure would strongly improve insight regarding ecosystem changes. Moreover, incorporating information about regional differences in canopy structure and the dependence of associated communities on those canopies is critical for spatially refined, ecosystem-based management of the rockweed harvest.

2.1 Introduction

Rockweed (*Ascophyllum nodosum*) is a significant ecological component of intertidal rocky shore communities in Atlantic Canada and other coasts of the North Atlantic Ocean. In Nova Scotia and southwest New Brunswick, rockweed and other fucoids cover 80-90% of the intertidal zone maintaining high biomass and primary productivity (Chopin et al. 1996, DFO 1998, Worm and Lotze 2006). Thereby, rockweed plays important roles in biochemical cycles by storing carbon and cycling nutrients (Schmidt et al. 2011). With their long fronds and branching structure rockweed plants also create a 3-dimensional forest-like canopy that provides habitat and food for associated plant and animal communities, both at high and low tide (Schmidt et al. 2011, Seeley and Schlesinger 2012). A variety of species, some of commercial importance and others of conservation interest, use rockweed canopies: more than 100 taxa of invertebrates (including lobster, clams and snails), 34 species of fish (including pollock, flounder, herring and cod), many species of shorebirds and waterfowl, and a number of algal species live in rockweed habitats (Larsen 2010, Schmidt et al. 2011, Seeley and Schlesinger 2012).

In addition to its ecological importance, rockweed has also been an commercially important seaweed in Atlantic Canada since the 1960s for production of alginates, fertilizer and animal feed (Chopin et al. 1996). In New Brunswick, commercial harvest of rockweed only began in 1995 and has been regulated during this time using a single species management approach. Considerable monitoring and research efforts have been made to study changes in rockweed plants themselves in response to harvesting; however, the effects of rockweed harvesting on the overall canopy or habitat structure and the associated fauna and flora have received much less attention (see chapter 2 for a full account) (DFO 1998, Rangeley and Davies 2000). Management of rockweed varies by Canadian province and new regulations for rockweed harvesting have recently been developed for Maine (Seeley and Schlesinger 2012, DMR 2013). Notably, differences in management regimes across political boundaries are unrelated to the biological make-up or hydrographic conditions of the rockweed habitat in different regions.

Rockweed shows high phenotypic plasticity, allowing it to adapt to a range of different environments and persisting across gradients of wave exposure, salinity, and temperature (Sharp 1987, Kerin 1998). Wave exposure plays a key role shaping the distribution of rockweed (Vadas and Wright 1986, Kerin 1998). Oldest plants, greatest coverage, highest growth and relative abundance are all found at wave-sheltered locations; however, biomass is highest at sites of intermediate exposure where ice-scouring seen at sheltered sites is prevented (Vadas and Wright 1986, Vadas et al. 2004). As an euryhaline species rockweed grows best at salinities near 32‰; however, it will tolerate temporary salinity changes to as low as 0.0‰ (Baardseth 1970). Rockweed is also a cold water species and growth increases as sea surface temperature (SST) rises to 20°C, but declines sharply thereafter with temperatures of 27-28°C being lethal (Keser et al. 2005).

Vegetated coastal habitats, including rockweed beds, have been shown to shift in structure at regional scales because of environmental differences, including hydrography, temperature, irradiance, salinity, storminess, substrate type, slope and wave exposure (David 1943, Baardseth 1970, Mathieson et al. 1976, Keser et al. 1981, Mathieson et al. 1982, Archamibault and Bourget 1983, Vadas and Wright 1986, Sharp 1987, McCook and Chapman 1993, Keser et al. 2005) as well as in response to human impact~~s~~ such as nutrient exposure (White et al. 2011). Yet so far, few studies have examined whether community composition of rockweed habitats varies by region (see Heaven and Scrosati 2008), although regional differences in community composition are documented in terrestrial vegetated areas (see Karr and Roth 1971, Wilson 1974, Mills et al. 1991, Halaj et al. 2000, Kornan and Adamik 2007, Hinsley et al. 2009, for examples). Moreover, given the dependence of associated fauna and flora on habitat provided by rockweed (Johnson and Scheibling 1987, Bertness et al. 1999, Ingólfsson and Hawkins 2008), we hypothesize that changes in community composition might be associated in part with changes in canopy structure. Determining the linkages between canopy structure and community composition will provide insight into how structural changes in the foundation plants and thus canopy or habitat structure might affect the associated plants and animals.

The goals of the present study are to (1) quantify regional variation in the canopy structure and community composition of rockweed habitats and (2) investigate the link between the two. Knowledge of regional differences and the linkage between canopy structure and community composition could help inform a spatially sustainable and ecosystem-based approach to the management of the rockweed harvest. This knowledge is particularly relevant at this time given that Acadian Seaplants Limited (ASL), the company that has near exclusivity in the harvest of rockweed in southwest New Brunswick and southwest Nova Scotia has intentions to expand its harvest both in the Canadian Maritimes and into Maine (The Canadian Press 2014, Erskine 2014). Large-scale field surveys and a multivariate statistical approach were used to address the objectives of this study.

2.2 Methods

2.2.1 Study sites

In July 2012, intensive field surveys were performed at six study sites within two major areas of rockweed harvesting: southwest Nova Scotia (NS) and southwest New Brunswick (NB) (Ugarte and Sharp 2012). In collaboration with ASL, the main harvester in those regions, we sampled all sites before the annual rockweed harvest took place (R. Ugarte, personal communication). All sites had rockweed beds with consistent cover over at least 150 m of shoreline. We selected two sites in NS: Kelley's Cove (KC), Yarmouth and Eagle Island, Central Argyle (CA), both of which are commercially harvested on a regular basis (Table 1). In NB, we selected four study sites in the outer Bay of Fundy near Deer Island, with two sites (Adam (AI) and Bean Islands (BN)) subject to a commercial rockweed harvest and another two sites (Barnes (BI) and Simpson Islands (SI)) established as harvest exclusion or no-take zones (Table 1). Moreover, two of these sites (BN and SI) have been exposed to finfish aquaculture operations since at least 2002, although the Simpson Island farm was not operating from 2009-2011. All four NB sites were previously classified in the same geographic and hydrographic region (MacKay et al. 1979a-c, Robinson et al. 1996) and as having the same "narrow passage" (Buzeta 2008) geomorphology. All six sites had gravel-boulder sediment.

Table 1. Survey sites, the provinces to which they belong, ID abbreviation, site coordinates, and human activities conducted at each site.

Location	Province	ID	Coordinates	Human activities
Central Argyle	NS	CA	43° 45' 02.68"N 65° 51' 07.83"W	Harvest
Kelley's Cove	NS	KC	43° 46' 57.47"N 66° 07' 39.49"W	Harvest
Adam Island	NB	AI	45° 00' 40.96"N 66° 54' 23.05"W	Harvest
Barnes Island	NB	BI	45° 00' 21.02"N 66° 54' 12.57"W	Harvest exclusion
Simpson Island	NB	SI	45° 00' 07.52"N 66° 54' 27.64"W	Harvest exclusion Aquaculture
Beans Island	NB	BN	45° 00' 00.49"N 66° 56' 01.38"W	Harvest Aquaculture

2.2.2 Sampling methods

2.2.2.i Rockweed canopy

At each study site, four 50 m transect lines were laid out parallel to the shore at low tide. Two sets of transects were laid 4 m apart, 2 m above and 2 m below the approximate center of the bed, with 20-50 m separating the two sets of transects. A weight was attached to each line end to keep it at the bottom and a buoy to locate it at high tide. The maximum transect depth was 1.85 ± 0.35 m at all sites.

Canopy structure measurements were taken at the daytime low tide using five 50 x 50 cm quadrats (every 10 m) along each transect, for a total of 20 quadrats per site. In each quadrat, the number of rockweed plants (i.e. all fronds belonging to a common holdfast) was counted. Since multiple fronds can emerge from each holdfast, we counted plants as separate when holdfasts had at least 0.5 cm distance from each other (or a finger's width). Each rockweed plant was then measured for its maximum length (cm) and maximum circumference (cm) (at the widest portion of the plant) with a measuring tape, and was weighed (g wet weight) on a portable field scale. Whereas small plants were directly placed on the scale, larger plants were placed in a bucket that had one side cut open as described by Ugarte et al. (2006). The weight of individual plants (mass in g) was summed up for each quadrat to gain a biomass estimate (g m^{-2}).

In addition, we collected five tissue samples per site from the tips of haphazardly selected rockweed plants situated below or above the transects to gain insight into the nutrient content of the plants themselves and their environment, with the tips reflecting the last year's growth (i.e., cut just below the previous year's air vesicle). The tips were dried for 48 hours at 80°C, ground to a powder and analyzed for tissue nitrogen (N) and carbon (C) content (%) and stable isotopes ($\delta^{15}N$ (‰), $\delta^{13}C$ (‰)) at the University of California Davis Stable Isotope Facility.

2.2.2.ii Associated communities

At high tide, two surveyors swam parallel to each other along the transect lines and recorded the species name, size, and abundance of all fish and mobile macrofauna observed within 1 m of each side of the transect (100 m^2 surveyed area for each transect). Fish counts were performed during both day and night high tides.

The same 50 m transects were used to survey benthic and epiphytic invertebrates and algae during the daytime high tide. Ten 50 x 50 cm (0.25 m^2) quadrats were placed along each transect at 5 m intervals (for a total of 40 quadrats per site) and all mobile and certain sessile (macrofaunal) invertebrate species were identified and counted. We also identified and estimated the percent cover of sessile benthic and epiphytic macroalgae and the remaining invertebrates.

2.2.2.iii Environmental parameters

To gain long-term insight into environmental conditions in the study regions, seasonal sea surface temperature (SST), salinity, chlorophyll *a* (Chl *a*) and nutrient data were acquired from nearby monitoring stations: the Gulf of Maine North Atlantic Time Series (GNATS) (Balch et al. 2008, 2012, http://seabass.gsfc.nasa.gov/) data set for Yarmouth, NS and the Department of Fisheries and Ocean (DFO) Buoy Prince 5 directly outside Passamaquoddy Bay, NB (Drinkwater 1987, http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/hydro/station/yearly-annuelle-eng.html?a=2andy=2013) as well as SST from Advanced Very High Resolution Radiometer (AVHRR) satellite data from NOAA (http://www.seatemperature.org/north-america/canada/nova-scotia/).

To directly compare the six study sites while sampling in the field, we recorded water temperatures of our dive computers and collected three 1 Liter water samples during the incoming tide, at high tide and during the outgoing tide with a pipe-sampler reflecting an average sample of the water column. We repeated the temperature measurements and water collection in August, approximately one month after surveys were conducted, in order to obtain better average summer values for each study site (by averaging July and August measurements).

For each water sample, three replicates were analyzed to quantify Chl *a* concentrations and total particulate matter (TPM) to gain insight into primary productivity and water turbidity levels. For each Chl α replicate, 100 ml of water were filtered through a Whatman GF/F (25 mm) filter using a 50 ml syringe and filter holder. The filters were then placed in labeled cryovials and transferred to a liquid nitrogen-cooled Dewar. Filtration was carried out in a darkened tent, away from light exposure. In the laboratory, filters were transferred to vials containing 10 ml of cooled acetone and were stored in the dark at -20°C for 24 hours or more. A Turner fluorometer was used to measure the voltage associated with each replicate and an acetone blank following both the Acidification Technique and the Welschmeyer Technique. GF/F filters used for the TPM replicates were initially washed to remove impurities and dried for six hours at 450°C before being weighed (pre-ash weight). Sample water was filtered with a syringe and filter holder until the filtrate just visibly stained the filter, after which the filters were rinsed twice with 5 ml of isotonic (2%) ammonium formate to expel salt. Filters were stored in foil inside cryovials placed in a liquid nitrogen-cooled Dewar while in the field. In the laboratory, filters were dried at 60°C for 24 hours, reweighed (dry weight), and combusted at 450°C for six hours before the final weighing (combusted weight) to determine particulate inorganic and organic matter (PIM, POM).

2.2.3 Data analysis

2.2.3.i Canopy structure

Averages and standard errors were calculated across 20 quadrats at each site for individual plant length (cm), circumference (cm) and mass (g) as well as plant density (# m^{-2}) and biomass (kg m^{-2}). Next, different combinations of these morphometric variables were used to assess differences in canopy structure between sites and regions. To do so, we first tested for correlations among all variables. Because of high (>0.8) correlation, biomass, plant mass and circumference were never included in a measure of canopy structure at the same time.

We then conducted multivariate permutational analysis of variances (perMANOVAs) to determine whether there were significant differences in overall canopy structure between regions (fixed factor: province; NS or NB) or study sites (fixed factor: site) using PRIMER (version 6.1.11) with PERMANOVA+ (version 1.0.1, PRIMER-E, Plymouth). We also used permutational analysis of variance (perANOVAs) to assess whether there was a site or regional effect on each plant or canopy parameter individually. All morphometric variables were normalized prior to computation of Euclidean distance-based similarity matrices. Transect location (shore-ward or seaward of the middle of the bed) was found to be insignificant in initial two-factorial perMANOVAs with site or region, therefore, quadrats from parallel high and low transects were subsequently pooled. Given that site was found to have a significant effect, we also performed post-hoc pairwise tests to determine which sites were significantly different from each other.

In order to improve visualization of the data and corroborate perMANOVA results, centroids (i.e. arithmetic means) for the canopy structure at each site were computed and cluster analysis performed using the centroids. An MDS plot displaying the centroids and overlaid with Euclidean distances from the cluster analysis using group averages was produced.

2.2.3.ii Associated community composition

We analysed three separate components of the community: count macrofauna seen within the quadrats (abundance m^{-2}), mobile macrofauna counted along transects (abundance m^{-2}), and sessile fauna and flora seen within quadrats (% cover).

Additionally, the sessile species were further divided and analysed as benthic and epiphytic assemblages. We first calculated average abundance and % cover of individual species across 4 transects or 40 quadrats per site. Next, we calculated species richness for each community component per site, and used perANOVAs to identify significant differences in abundance, % cover and richness between sites and regions.

PerMANOVAs were used to assess the effects of site or region on each component of community composition. Species-level abundance data for each component were square-root transformed in order to down-weight the influence of abundant species and allow for a contribution to the resemblance matrix from rarer species. The resemblance matrices were based on Bray-Curtis similarities and a dummy variable (value = 1) were added before computation of similarities in order to zero-adjust the coefficients. Where site was found to have a significant effect, we also performed post-hoc pairwise tests to determine which sites were significantly different.

To visualize the data and corroborate perMANOVA results, centroids were computed for each community component and group average cluster analysis performed for the centroids. MDS plots displaying the centroids and overlaid with Euclidean distances from the cluster analysis were produced.

To determine which species contributed most consistently to regional or site differences a similarity percentages (SIMPER) analysis was performed on each community component (Anderson et al. 2008).

2.2.3.iii Linking canopy structure to community composition

First, the BEST/BIOENV procedure in PRIMER was used to identify possible correlations between sets of variables for plant or canopy structure to similarity matrices for each community component. The BIOENV procedure is non-parametric and looks for best rank-order matches between point-to-point dissimilarities of the species resemblances and the point-to-point distances derived from sets of environmental (in our case plant and canopy) variables (version 1.0.1, PRIMER-E, Plymouth). BIOENV provides a non-parametric index rho (ranging from 0 to 1) that indicates how closely the environmental variables explain the multivariate pattern of the species. From there, a permutation test to determine the significance level of the sample statistic (rho) can be run. Several combinations of morphometric variables (plant length, mass or circumference, biomass and density) were used to try to explain the species composition of each community component. Subsequently, the procedure was run using similarity matrices for the centroids for each community component and averaged morphometric variables for each site.

Second, to determine the relationship between plant or canopy structure and aggregated community measures (abundance, richness) or individual species (SIMPER-identified species or other species of interest) we first used generalized linear models (GLMs). In cases where residuals were overdispersed and, or data contained many zeros, generalized additive models (GAMs) or hurdle, which were developed to handle zero-inflated data, were subsequently used (Wood 2006). Models were fitted to (1) total species richness, (2) richness of each community component, (3) abundance or % cover of each community component, and (4) abundance or % cover of individual species using various sets of plant and canopy variables as predictors. Site or region was also added as predictors to increase the model fit. We began by fitting either normally-distributed or Poisson-distributed GLMs to the data, after examining histograms of the species abundances in quadrats. When seeing evidence of overdispersion in several residuals, we also fitted the data to GLMs with quasi-poisson and negative binomial distributions, with little improvement in the overall fit. Subsequently, GAMs were fitted to the data using a Poisson distribution, for which the residuals and deviance explained by the model sometimes improved. In an attempt to further improve the residuals and the fit of the models, we also used hurdle models to fit the data where large numbers of quadrats showed an absence (zero) of species.

2.3 Results

2.3.1 Environmental parameters

Long-term SST readings at the two monitoring locations demonstrated that annual minimum and maximum SST, and July average and maximum SST did not differ greatly between regions over the past decade (Table 2); however the yearly average was 2°C lower in NS (8.3°C) than NB (10.3°C). Although some minimum temperatures appear lower in NB this could be due to the fact that NS readings until 2006 did not include the coldest winter months (Nov-Apr) and that NB's lowest value (1.9°C) comes from a much earlier monitoring period (1950-1981). Interestingly, all SST values (min, max, avg) in NB are higher in the recent (2005-2012) compared to the earlier period, possibly linked to climate warming. Temperature readings from the dive computers at the NB (12 ± 1°C) and NS (13 ± 1°C) sites in July did not differ and were consistent with July values for the two regions from the previous decade (Table 2). Similarly, salinity measures did not differ between the regions (Table 2). Average Chl *a* values appear to be slightly higher in long-term monitoring series NB than NS (Table 2); however, Chl *a* for our water samples averaged over July and August were similar with 1.3 ± 0.1 µg l^{-1} in NB and 1.4 ± 0.1 µg l^{-1} in NS (Figure 1A). Moreover, our TPM samples did not differ between NS and NB (Figure 1B), although the % organic content was significantly higher in NB (51.46 ± 4.32 %) when compared to NS (40.89 ± 2.73 %) (Figure 1C).

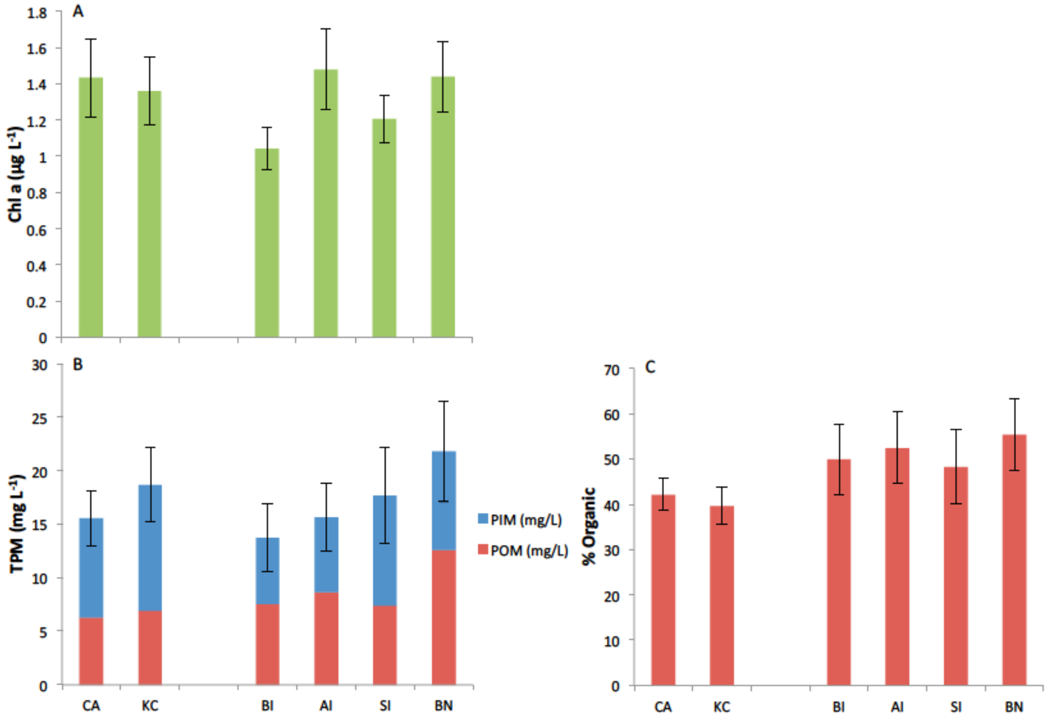


Figure 1. (A) Average chlorophyll *a* (µg L^{-1}) values for July (n=9) and August (n=9)), (B) stacked average particulate inorganic matter (PIM) and particulate organic mater (POM), and (C) average percent organic matter of TPM with SE for all six study sites (CA = Central Argyle, KC = Kelley's Cove, BI = Barnes Island, AI = Adam Island, SI = Simpson Island, BN = Beans Island).

Long-term nutrient measurements indicate higher background nutrient levels in NB relative to NS (Table 2), and this is reflected in significantly higher % tissue nitrogen content measured in plants from NB compared to NS (p= 0.0003, Figure 2A) (see Appendix 2A for pairwise comparisons between sites). Interestingly, nitrogen stable-isotope ratios ($\delta^{15}N$) were significantly lower in NB than NS ($p < 0.0001$, Figure 2C). % tissue carbon (Figure 2B) and carbon stable-isotope ratios (δ13C) were similar across regions.

Table 2. Environmental attributes of the studied regions (NB, NS) sourced from the literature including: sea surface temperature (SST), salinity, chlorophyll *a*, and dissolved inorganic nitrate (DIN) and phosphate (PO_4^{3-}).

Region	**Time span**	**Sampling**	**Measures**	**SST (°C)**	**Salinity ($^0/_{00}$)**	**Chl *a* (µg l^{-1})**	**DIN (µM)**	**PO_4^{3-} (µM)**	**Source**
NB	2005-2012	Monthly	Avg min-max	2.9-13.3	30.5-33.0	-	1.5-10.9	0.5-1.2	DFO Prince 5 (Data retrieved 2014)
			Yearly avg	10.3	32	-	7.4	0.9	
			July avg	11.8	-	-	4.2	0.7	
			July max	14.1	-	-	-	-	
	1951-1980	Monthly	Avg min-max	1.9-11.6	30.5-32.3	3.4 ± 0.2	-	-	Drinkwater 1987
			Yearly avg	6.9	-	3.5 ± 0.7	-	-	
			July avg	9.7	-	2.3 ± 1.1	-	-	
			July max	-	-		-	-	
NS	1999-2010	Monthly (May to October up to 2006)	Avg min-max	5-13	31-32.5	1-2.5	-	-	Balch et al. 2012 (GNATS transect)
			Yearly avg	-		-	-	-	
			July avg	-		-	-	-	
			July max	-		-	-	-	
	2003-2010	Monthly	Avg min-max	3-13.5	-	-	1-3	0.40	Balch et al. 2008
			Yearly avg	-	-	-	-	-	
			July avg	-	-	-	-	-	
			July max	-	-	-	-	-	
	Several years of archived NOAA AVHRR data	-	Avg min-max	-	-	-	-	-	NOAA (Data retrieved 2014)
			Yearly avg	8.3	-	-	-	-	
			July avg	11.9	-	-	-	-	
			July max	14.6	-	-	-	-	

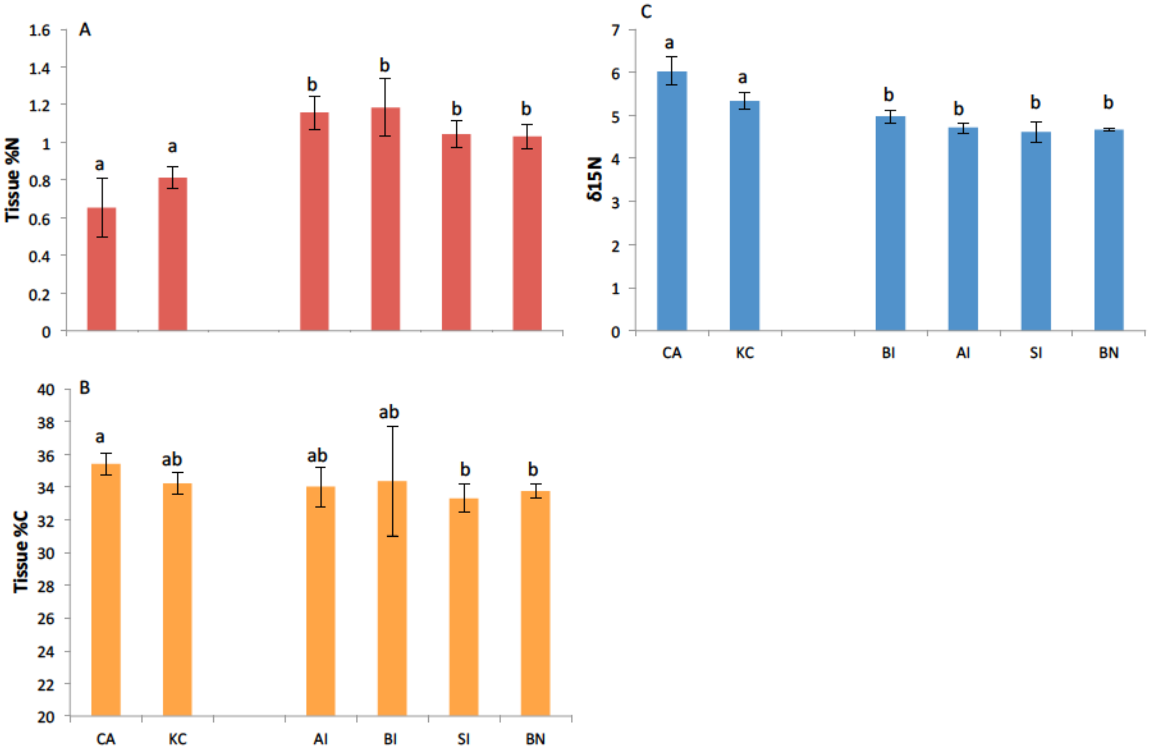


Figure 2. (A) Average tissue percent nitrogen, (B) carbon and (C) δ15N isotope signature with standard errors (SE, n=5) for all six study sites. Lowercase letters indicate significant differences between sites.

2.3.2 Plant and canopy structure

There was a clear difference in plant structure between regions, with plants having significantly greater length (L) (PerANOVA, Pseudo-F = 46.820, p = 0.0001), circumference (C) (Pseudo-F = 156.13, p = 0.0001) and mass (M) (Pseudo-F = 8.187, p = 0.0001) at our study sites in NS than NB (Figure 3A-C). In turn, the density (D) of rockweed plants per unit area was significantly higher (Pseudo-F = 30.613, p=0.0001) in NB (Figure 3D), while overall biomass (B) of rockweed per unit area was lower in NB (Pseudo-F = 2.33, p = 0.044) (Figure 3E).

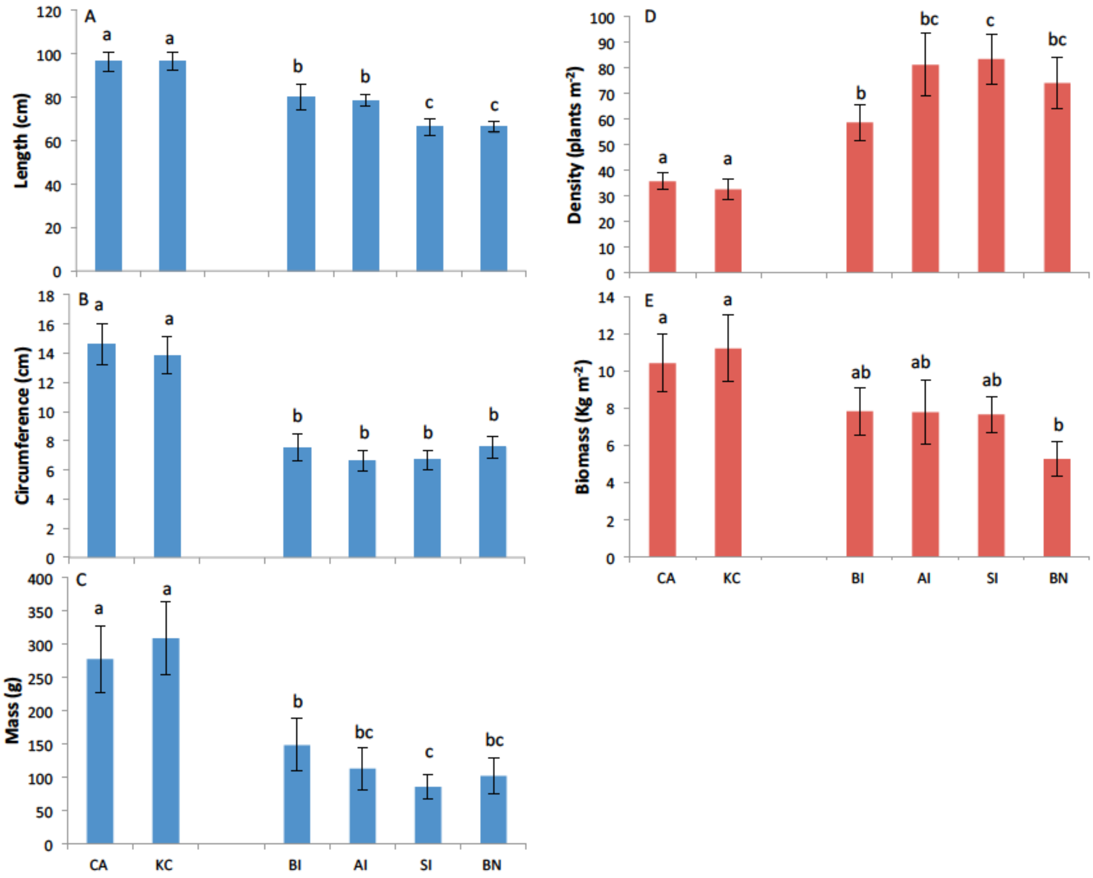


Figure 3. Averages and standard errors (SE, n = 20) for rockweed plant and canopy parameters: (A) plant length (cm), (B) plant circumference (cm), (C) plant mass (g), (D) density (plants m^{-2}), and (E) biomass (kg m^{-2}) across two NS and four NB study sites. Lowercase letters indicate significant differences between sites.

Differences between regions and among study sites were similar regardless of the combination chosen as a measure of canopy structure (e.g. {L,M or L,C}, {L,M,D or L,C,D}, {D,B}, {L,B}), indicating the robustness of the results. Given that region and site explained the most variance when {L, C, D} was used as a measure of canopy structure and that {L. C, D} showed the strongest correlation between canopy structure and abundances of associated species, multivariate results for canopy structure are described for this combination. Two one-factor perMANOVAs (Factor: site and region, respectively) detected a significant effect of region and site on canopy structure {L,C,D} (Tables 3). Region explained 35.3% and site 41.5% of the variation, respectively. The canopy structures of CA and KC in NS were not different from each other but significantly different from all NB sites ($p \leq 0.0021$ for all eight comparisons, see Appendix 2B). Within NB, the only significant difference was seen between BI and BN ($p=0.027$). The MDS plot (Figure 4) illustrates the two distinct clusters for the centroids of canopy structure: one tighter cluster for the NS sites and a second for the NB sites in which Bean Island is distanced from the remaining three sites.

Table 3. One-factor perMANOVA results for the effect of Region or Site on canopy structure {L, C, D}. Sqrt-V values are unbiased estimates of the contribution to variance of Region or Site and the residuals in the model. Variance explained is given by [(SS Factor/SS Total) x 100] and, while more biased than sqrt-V, is included since it is a more intuitive measure of relative effect size (Howell 2002). The degrees of freedom (df) total to 119. See Appendix B for perMANOVA output for pairwise comparisons of sites.

	Source	**Region**	**Residuals**	**Site**	**Residuals**
	df	**1**	**118**	**5**	**114**
{L, C, D}	Pseudo-F	64.438		16.200	
	P	**0.0001**		**0.0001**	
	sqrt-V	2.328	1.957	1.391	1.831
	Variance explained	35.3%	64.7%	41.5	58.5

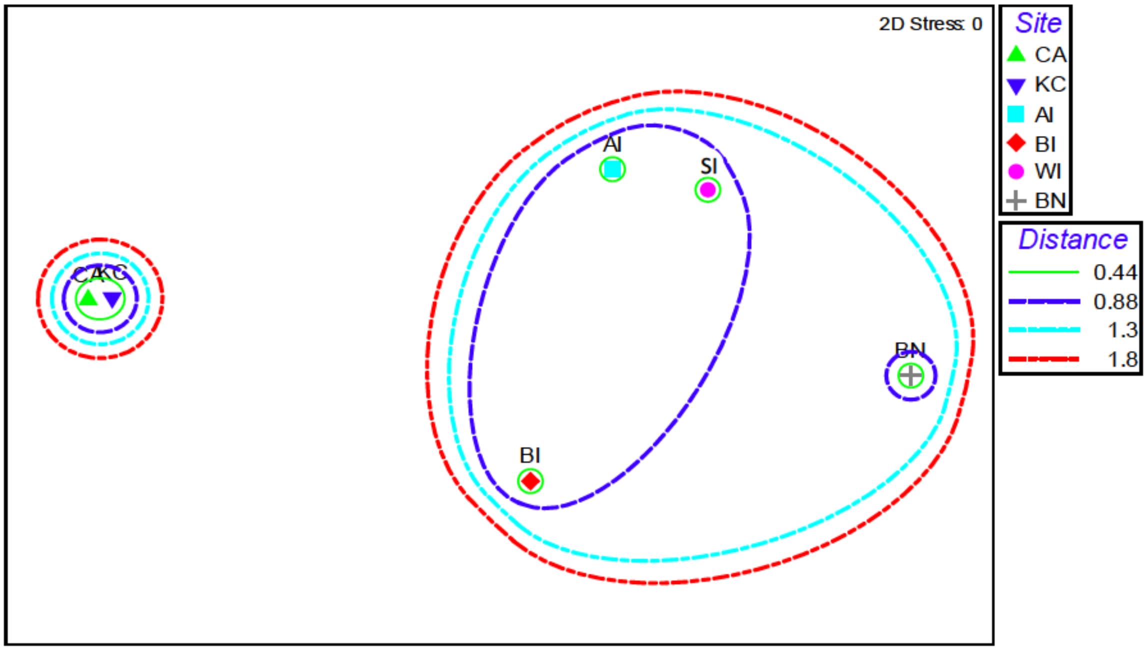


Figure 4. Multidimentsional scaling (MDS) plot showing centroids for similarities matrices using Euclidean distances for canopy structure {L, C, D} from quadrats (n=20) at each of the six study sites. The solid and broken lines encircling the sites indicate Euclidean distances that were derived from a cluster analysis also conducted on centroids of canopy structure. These lines help quantify the relatedness of the structure across sites.

2.3.3 Associated species abundance and richness

Total species richness of all faunal components at three of the four NB sites (AI, BI and SI) was higher than species richness at the two NS sites. All NB sites had a greater number of sessile species (AI, BI and SI 13 species at each; BN 10 species) than KC (8 species) or CA (6 species). However, there were fewer mobile quadrat species at BN, therefore, the total richness of this site was similar to NS sites. Richness of mobile fauna seen along transects was low across all sites (particularly when species also seen in quadrats were eliminated for total species richness estimates to avoid double counting).

Looking at average species richness for each community component, region did not significantly affect count quadrat fauna, however, richness at BN was significantly lower than all other sites (Figure 5A). Sessile species richness did not differ significantly by region, however, richness at CA was significantly lower than all remaining sites (Figure 5B), There was a significant difference in mobile transect species richness between NS and NB (Figure 5C), with lower values in NS. Patterns in species abundances across sites were more varied (Figures 6-8). For mobile quadrat fauna abundance, there was a significant effect of site (Figure 6, Appendix 2A) and region ($p = 0.0001$), with BN demonstrating the significantly lowest abundance (Figure 6). *Littorina littorea* and *L. saxitilis* were more abundant at the two NS sites and AI, while *L. obtusata* was most abundant at SI. For sessile species cover, there was a significant effect of site (Figure 7, Appendix 2A) and region ($p = 0.0004$), with highest cover at KC and lowest at SI and BN (Figure 7). These differences are caused by the high cover of *Semibalanus balanoides* at KC, and low cover of *Hildenbrandia rubra* at SI and BN (Figure 7). The abundance of mobile transect fauna was significantly lower in NS (Figure 8), as indicated by a significant region ($p < 0.0001$) and site effect (Figure 8, Appendix 2A). This was largely caused by *Carcinus maenus* being more abundant at NB than NS sites, as well as *Gasterosteus aculeatus* and ctenophores (*Pleurobrachia pileus* and a large unidentified ctenophore). Fish abundances were low across sites.

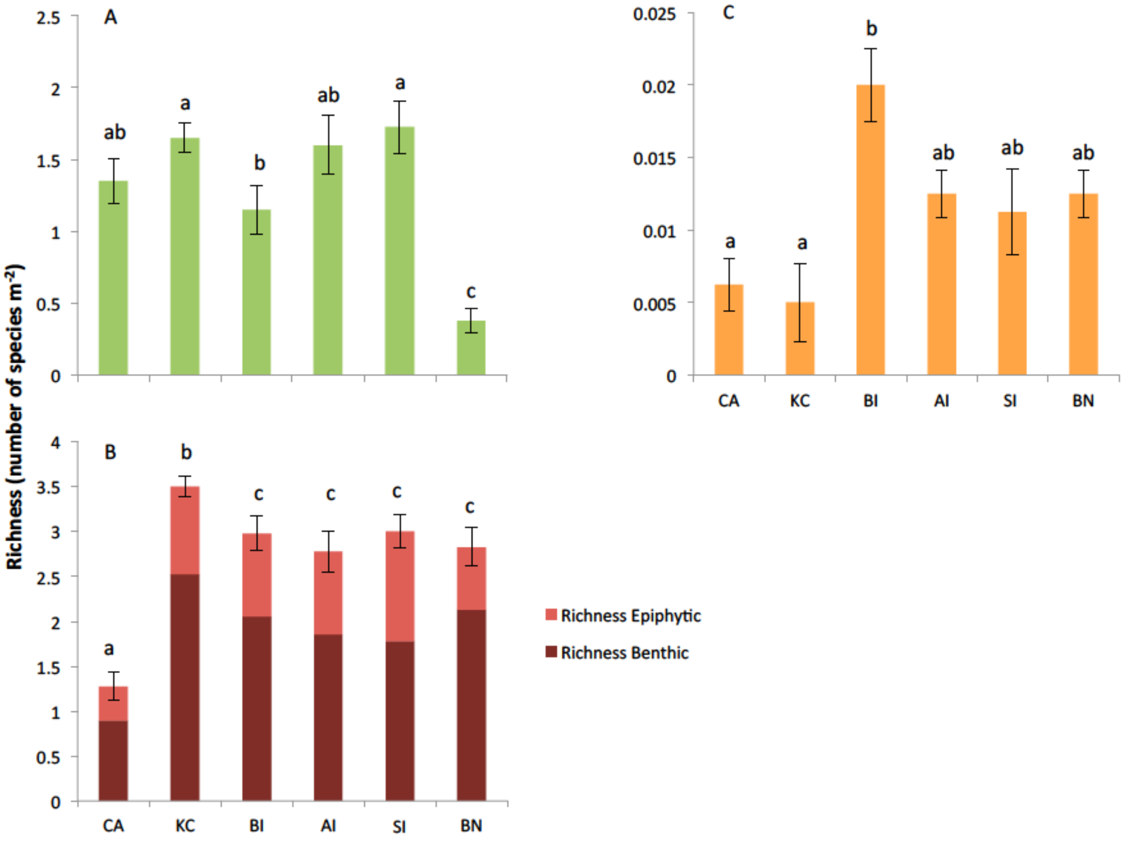


Figure 5. **Average richness m^{-2} and standard error (SE) of (A) count quadrat species, (B) sessile benthic and epiphytic species, and (C) mobile transect species at each of the six study sites. Lowercase letters indicate significant differences between sites.**

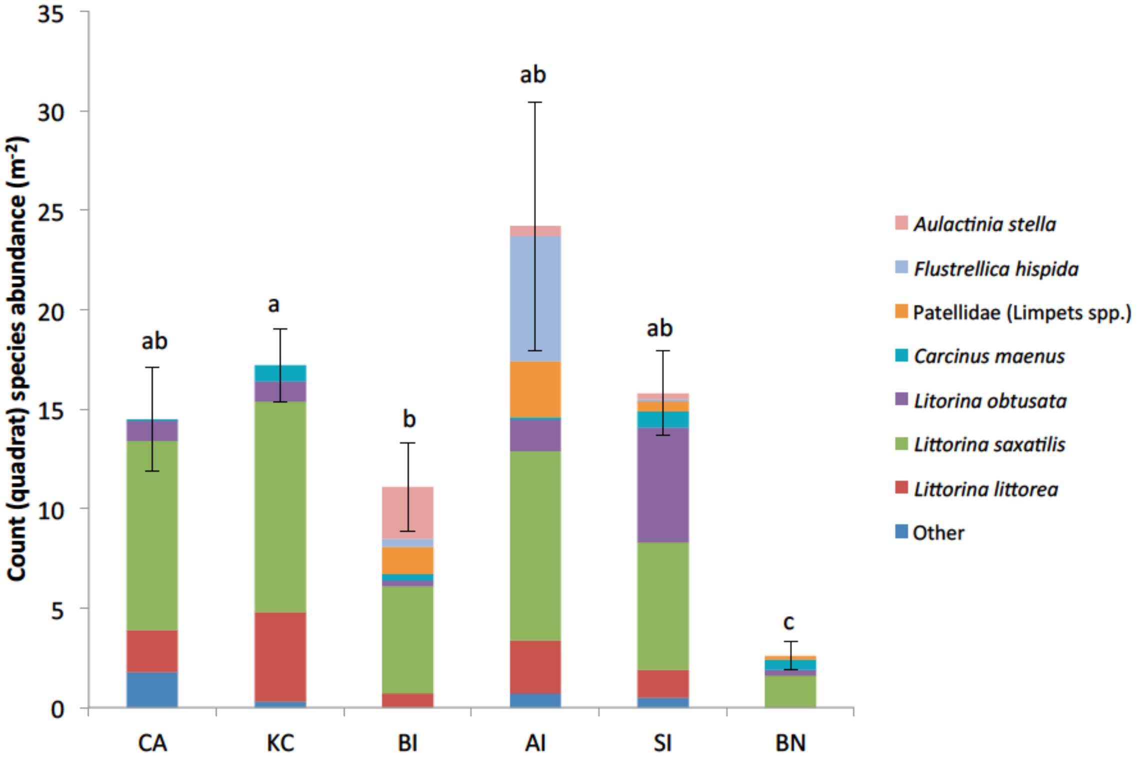


Figure 6. Average abundance and standard error (SE, n = 20) of count quadrat species at each of the six study sites. Lowercase letters indicate significant differences between sites.

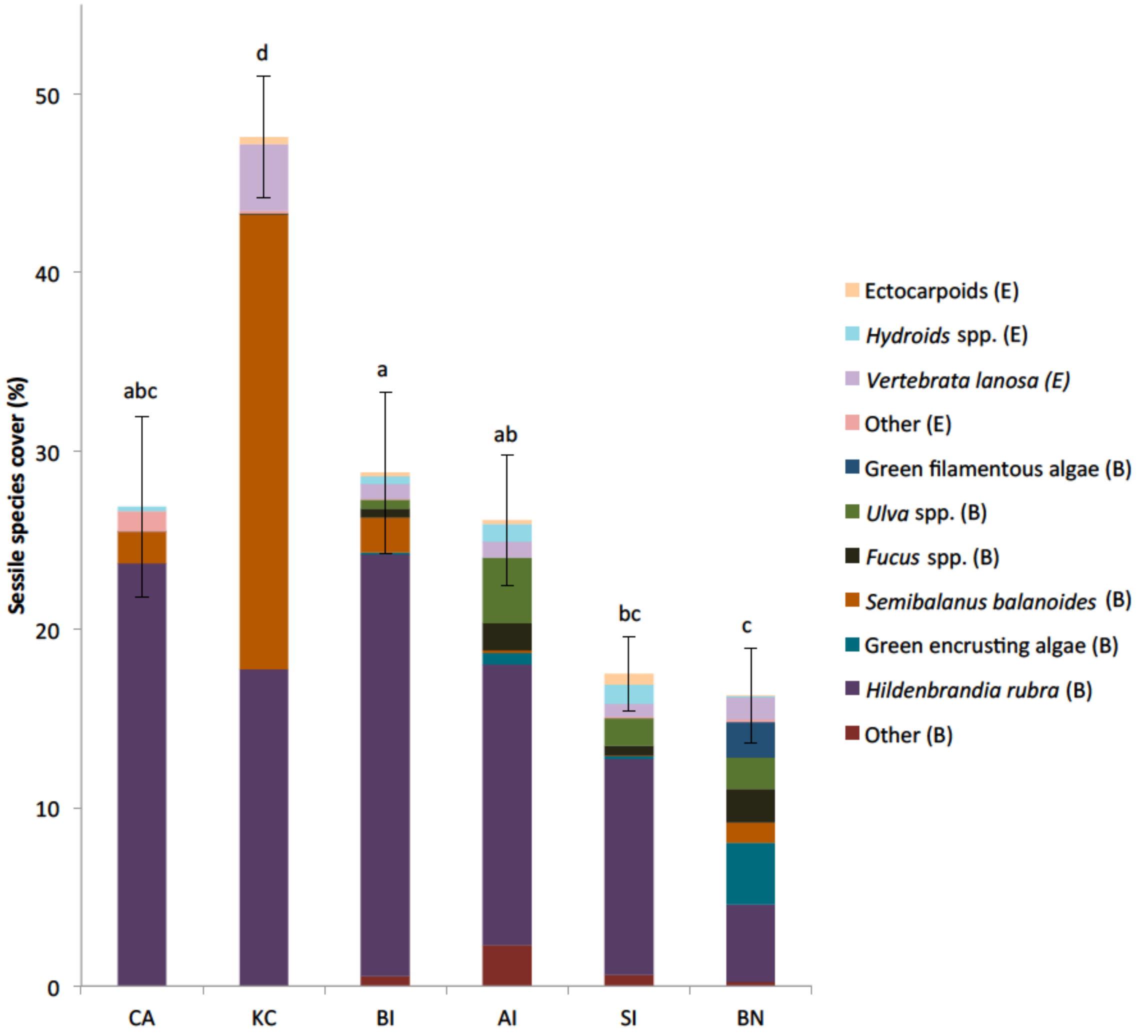


Figure 7. Average percent cover and standard error (SE, n = 20) of sessile benthic (B) and epiphytic (E) species at each of the six study sites. Lowercase letters indicate significant differences between sites.

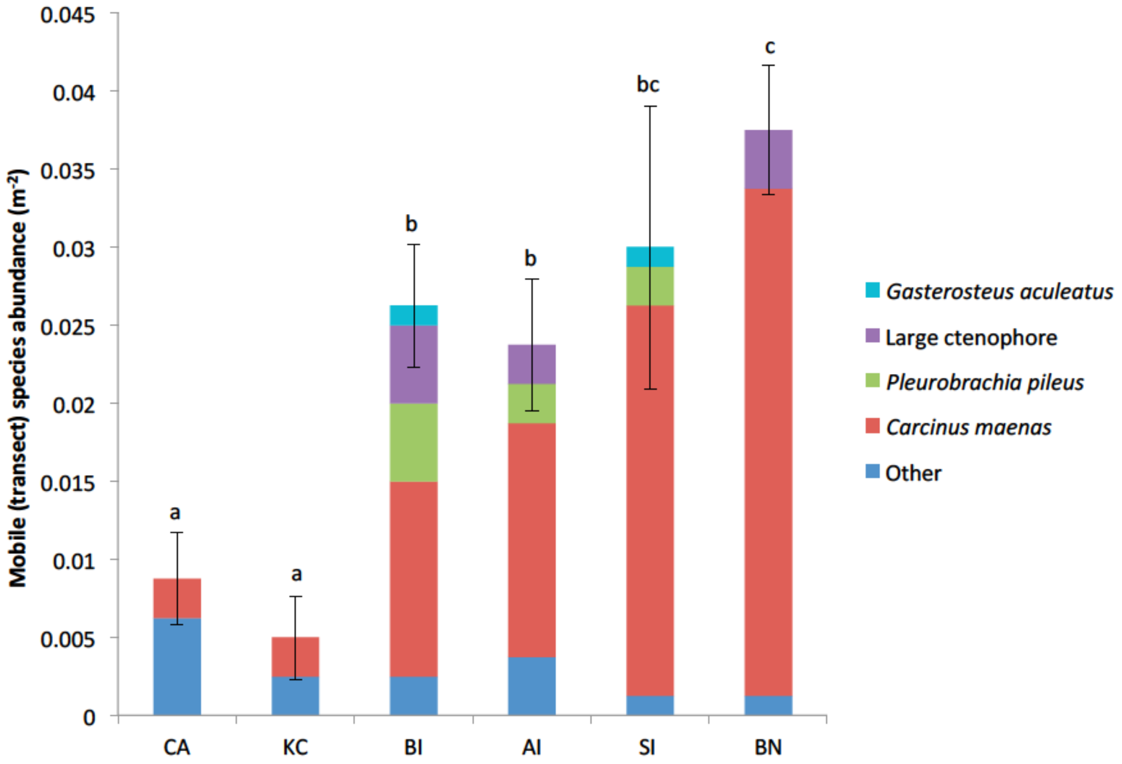


Figure 8. Average abundance and standard error (SE, n = 8) of transect species at each of the six study sites. Lowercase letters indicate significant differences between sites.

2.3.4 Associated community composition

2.3.4.i Count (quadrat) species

One-factor perMANOVAs detected a significant effect of site and region, respectively, on the composition of mobile quadrat species (Table 4), with site explaining 15.1% and region 11.4% of the variation. The composition of quadrat species did not differ significantly between the NS sites, but most pairwise comparisons between NS and NB sites were significantly different ($p \leq 0.0015$, see Appendix 2B for pairwise comparisons between sites), except AI and BI did not differ from CA. In NB, species composition did significantly differ between BI and SI ($p=0.0075$), and BN was significantly different from the other three NB sites ($p \leq 0.0002$). The MDS plot (Figure

9A) corroborates that BI is segregated from all other sites, whereas the NS sites – CA in particular – are more similar to the NB sites. The main species identified by SIMPER contributing >10% to differences among sites include Littorinids (*Littorina littorea, L. obtusata*) as well as limpets and *Carcinus maenas* in some cases (see Appendix C, Figure 8).

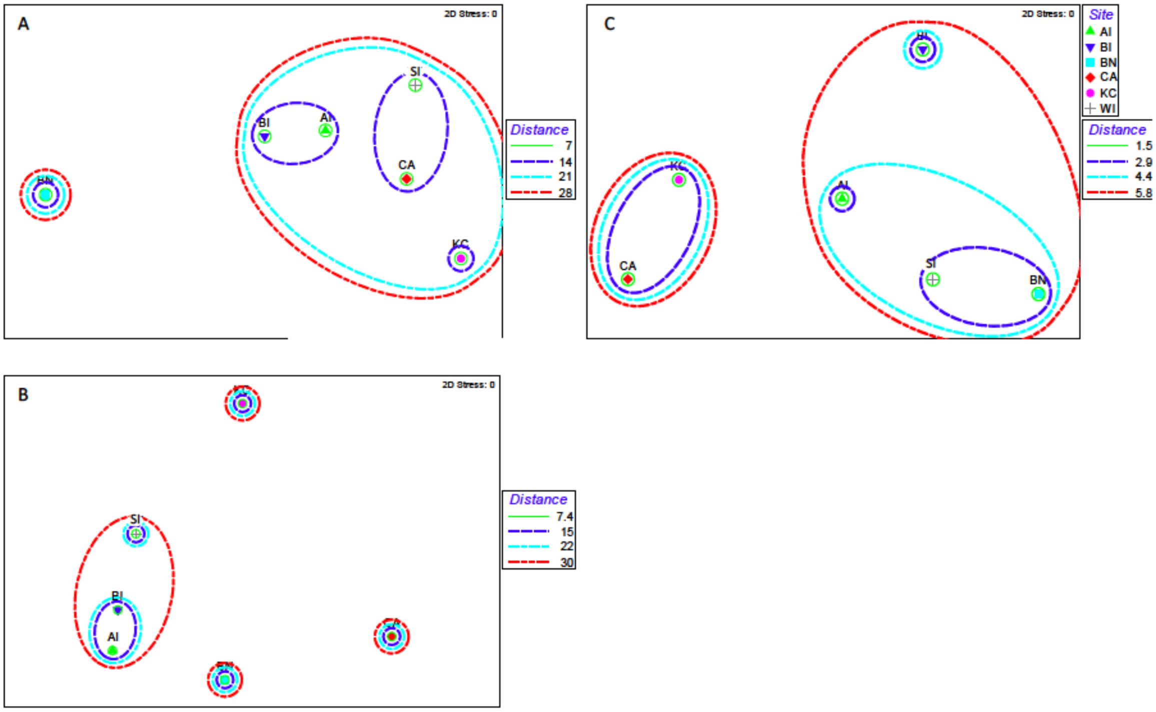


Figure 9. Multidimensional scaling (MDS) plot showing centroids derived from Bray-Curtis similarity matrices for (A) Mobile (quadrat) species composition (quadrats=20), (B) Sessile species (quadrats = 20), and (C) Mobile (transect) species (transects = 8) at each of the six study sites. The solid and broken lines encircling the sites indicate Bray-Curtis similarities that were derived from a cluster analysis also conducted on centroids of canopy structure. These lines help quantify the relatedness of the structure across sites.

2.3.4.ii Sessile species

One-factor perMANOVAs detected a significant effect of site and region, respectively, on the composition of sessile species (Table 4). Site explained 25% of the variation and region explained 15.7% of the variation. The percent cover of sessile species does not differ between three of the sites in NB: AI, BI and SI; all other combinations of sites were significantly different (p = 0.0001, see Appendix 2B). Figure 9B shows a cluster of the NB sites that is similar to that seen for the canopy structure (Figure 4); however, the distances separating the sites are greater and BN is further removed from the other three sites. There is no cluster for the NS sites; however, they are more removed from the NB sites than any of these are from each other. The main species identified by SIMPER contributing >10% to differences among sites include *Hildenbrandia rubra*, and *Semibalanus balanoides*, as well as *Fucus* spp., *Ulva* spp., and green encrusting algae (likely a cyanobactial or cyanobacteria-algal mat) in some cases (see Appendix C, Figure 7).

One-factor perMANOVAs also detected significant effects of site and region on benthic and epiphytic sessile species separately (Table 4); however, the patterns of similarities and dissimilarities (see MDS plots in Appendix D) as well as SIMPER species (Appendix C) are similar to those seen for all sessile species.

Table 4. One-factor perMANOVA results for the effect of Region or Site on the species composition of different community components. Sqrt-V values are unbiased estimates of the contribution to variance of Region or Site and the residuals in the models. Variance explained (Var) is given by [(SS Factor/SS Total) x 100] and, while more biased than sqrt-V, is included since it is a more intuitive measure of relative effect size (Howell 2002). The degrees of freedom (df) total to 239. Post-hoc pairwise comparisons of sites are found in Appendix B. Significant p-values are shown in bold.

	Source	**Region**	**Residuals**	**Site**	**Residuals**
	Df	**1**	**238**	**5**	**234**
Mobile (quadrat) species	**Pseudo-F**	14.676		8.1381	
	P	**0.0001**		**0.0001**	
	sqrt-V	14.705	41.066	16.638	39.386
	Var	11.4%	88.6%	15.1%	84.9%
Sessile (quadrat) species	**Pseudo-F**	20.867		14.299	
	P	**0.0001**		**0.0001**	
	sqrt-V	19.656	45.546	24.175	41.927
	Var	15.7%	84.3%	25%	75%
Epiphytic (sessile) species	**Pseudo-F**	9.539		10.09	
	P	**0.0002**		**0.0001**	
	sqrt-V	7.196	25.433	11.31	23.726
	Var	3.9	96.1	18.5%	81.5%
Benthic (sessile) species	**Pseudo-F**	31.159		16.407	
	P	**0.0001**		**0.0001**	
	sqrt-V	16.437	30.912	17.705	28.527
	Var	11.6	88.4	27.8%	72.2%
Mobile (transect) species	**Pseudo-F**	13.219		4.4985	
	P	**0.0001**		**0.0001**	
	sqrt-V	4.6407	6.1319	3.8857	5.8758
	Var	36.4%	63.6%	30.4%	69.6%

2.3.4.iii Mobile (transect) species

Two separate two-factorial perMANOVAs (site and region, respectively; time of day) detected a significant effect of site (p = 0.0001) and region (p = 0.0001) on the composition of transect species; yet there was no effect of time of day. Night and day transects were, therefore, pooled and one-factor perMANOVAs (site and region, respectively) were performed (Table 4). Site explained 30.4 % and region explained

36.4% of variation. There was no difference between the NS sites, and most NB were significantly different from the NS sites (all $p<0.016$), with the exception that AI was not significantly different from KC. Within NB, BN and BI were significantly different from one another ($p=0.0024$). The MDS plots (Figure 9C) demonstrate two distinct clusters for NS and NB sites, as seen for the canopy structure (Figure 4). Within the NB sites, SI and BI cluster most closely together. The two principal species (for which Sim/SD ≥ 1) identified by SIMPER that contributed to differences among sites were *Carcinus maenas* and *Pleurobrachia pileus*, with a few other species identified in some cases (see Appendix 2C, Figure 8).

2.3.5 Linking canopy structure to community composition

The PRIMER BEST/BIOENV procedure established an association between plant structure {L, C} as well as canopy structure {L, D} and the count quadrat species composition at a significance level of 3.3% (or $p = 0.033$) and 8.4% ($p=0.084$), respectively. There was also an association between canopy structure {L, D} and the sessile species assemblage at a significance level of 6.9% ($p = 0.069$); yet, no combination of morphometric variables captured the pattern of variation in the transect species assemblage or the epiphytic or benthic sessile assemblages. However, the sample statistic rho (ρ), which ranges between 0 and 1, was very low for these associations ($\rho= 0.07$, $\rho= 0.063$ and $\rho= 0.063$, respectively) when individual quadrats for each site were used. When community component centroids were used (i.e. arithmetic means per site), the associationsbetween canopy structure and count quadrat and sessile species composition strengthened $\rho= 0.63$, and $\rho= 0.53$, respectively) while the significance levels remained similar (p= 0.069 and p= 0.07, respectively (Table 4). Moreover, additional relationships between different combinations of morphometric variables and community components were revealed when centroids for community components were used (Table 5). The association between canopy structure {L, C, D} and mobile transect species assemblage had a sample statistic of ρ=0.811 with a significance level of 2.2% (p = 0.022); while the association between density (ρ=0.571) and canopy structure {L, C, D} (ρ=0.446) and sessile benthic species assemblage had a significance level of 7% or less (p = 0.07); and the association between circumference (ρ=0.55) and canopy structure {L, C, D} (ρ=0.389) and sessile epiphytic species assemblage had a significance level of 8.5% or less (p = 0.085). Finally, and the association between length (ρ=0.521) and canopy structure {L, C, D} (ρ=0.296) and mobile quadrat species assemblage had a significance level of 12.9% or less (p = 0.129). The association between biomass and mobile quadrat species assemblage had a sample statistic of ρ=0.675 with a significance level of 5.9% (p=0.059), and the association between density (ρ=0.582) and density and biomass (ρ=0.564) and sessile benthic species assemblage had a significance level of 5.8% or less (p=0.058). It is important to note that there is no clear cutoff for a significant p-value discussed in the literature for the BEST/BIOENV procedure.

Table 5. Rho and p-values from BIOENV analyses associating similarity matrices for community composition centroids with select plant and canopy measures.

Community component	Plant/Canopy structure	Rho	P
Mobile quadrat community	**L**	0.521	≥0.129
	L, D	0.63	0.069
	L, C, D	0.296	≥0.129
	B	0.675	0.059
Sessile community	**L, D**	0.53	0.07
	L, C, D	-	-
Benthic sessile community	**D**	0.571	≥0.07
	L, C, D	0.446	≥0.07
	D, B	0.564	≥0.058
Epiphytic sessile community	**C**	0.55	≥0.085
	L, C, D	0.389	≥0.085
Mobile transect community	**L, C, D**	0.811	0.022

We then used GLMs, GAMs and Hurdle models to identify which structural variables best described the aggregated abundance and richness of each community component as well as the abundance of SIMPER species. Species counts from transects (i.e. nearly all the fish sighted) were not fitted using these models because of the low level of replication (eight transects per site).

GLMs were the first models employed; however, in a number of cases – namely those with overdispersed residuals - GAMs or Hurdle models provided a better fit for the data. Where there was clearly only one appropriate model type, results are recorded for that type only (see Appendix E). Plant structure {L, C} was nearly always a better predictor for patterns in the richness or abundance of community components and SIMPER species than was biomass {B}. Canopy structure {L, C, D} generally predicted more deviation in species patterns than plant structure alone, explaining 10-70% and in some cases as much as 90% of the deviance overall. Canopy structure {L, C, D} had some of its highest predictive power for certain of the benthic and epiphytic sessile species. Adding both region (NB, NS) and especially site into a model as a predictive factor often helped explain an additional 20-30% of deviance. The models did not perform well for *Carcinus maenus*, and the 100% deviance explained by some of the GAMs for certain sessile species almost certainly indicates that the models were over-fitting the data, likely because data are so scarce for these species. Where appropriate, a predictor was removed from the model to reduce over-fitting and deviance explained is also reported for these reduced models (see Appendix E).

Summarizing patterns of change in species richness, abundance or cover with individual plant or canopy metrics, the models suggest we should expect greater mobile quadrat species abundance and richness, and greater cover of *Semibalanus balanoides* and in NS, which has less a densely packed rockweed canopy with larger plants and greater biomass than NB (see Appendix F for all model output). In turn, the models suggest more *Littorina obtusata* and greater cover of pink encrusting algae, *Ulva* spp. and *Dynamina pumila* in NB, which has a more densely packed canopy with smaller plants and lower biomass. *Elachista* sp. and *Fucus* spp. prefer an intermediate canopy of less dense, smaller plants and red foliose algae should be found in denser or intermediate canopies with larger plants. Inconclusive patterns were arrived at for Littorinids, *Carcinus maenus,* green encrusting algae and *Hildenbrandia rubra*.

2.4 Discussion

Using field surveys and multivariate statistics, we established clear regional differences in canopy structure of rockweed beds in southwest Nova Scotia and southwest New Brunswick as well as regional differences in the composition of associated communities. Additionally, rank-order comparisons of plant and canopy structure and community resemblance matrices denote a significant dependence of associated communities on the three-dimensional structure of rockweed habitats. Individual general linear and additive models further showed that plant and canopy structure explained a sizable degree of the pattern in aggregated community abundance and richness as well as the abundance of individual species. While environmental parameters likely explain some of the underlying regional differences in canopy and community structure, the significant link between the two has important resource management implications.

2.4.1 Environmental parameters

Regional differences in plant and canopy structure between our sites in Southwest NB and Southwest NS were likely attributable to differences in underlying environmental factors. Although sea surface temperatures (SST) at our study sites in July were quite similar, the lower average SST in Yarmouth, NS (8.3°C) relative to NB (10.3°C, Table 2) would be expected to influence rockweed growth and thus canopy structure (Mathieson et al. 1976). Growth rate of *Ascophyllum nodosum* is temperature dependent and a substantial amount of its growth occurs in late spring and summer during periods of exposure to air at low tide (Baardseth 1970, Mathieson et al. 1976). Therefore, summer water and air temperatures likely have a greater impact on rockweed growth than average annual SST, which may account for higher growth and larger rockweed plants in NS. Salinity is also known to influence rockweed abundance and growth (Baardseth 1970, Sharp 1987), but long-term averages were also quite similar in NS and NB (Table 2).

Several other physical factors are known to affect rockweed abundance and growth, including hydrology, wave exposure, local storminess, ice scouring, tidal height and sediment type (Baardseth 1970, Keser et al. 1981, Mathieson et al. 1982, Archamibault and Bourget 1983, Vadas and Wright 1986, McCook and Chapman 1993, Vadas et al. 2004). Sediment type was similar across our study sites but wave exposure and tidal height differed. Our NB sites are nestled in among other islands (e.g. Deer Island) in the outer Bay of Fundy that create a narrow passage geomorphology (Buzeta 2008), slowing water movement around the island sites. Modelled current speeds around these sites do not exceed 1 m/s on rising or falling tides (Durand et al. 2008). Our NS sites, on the other hand, while located in embayments, are on the open Atlantic coast and wave exposure was likely highest at KC. Tidal range was lower in Yarmouth, NS (4.5 m) than near Deer Island, NB (5.6 m) (Durand et al. 2008), creating different water movements in NB than NS.

Long-term nutrient concentrations indicate higher levels of nitrate and phosphate in NB (Balch et al. 2012, DFO retrieved 2014), and this was reflected in significantly higher % tissue nitrogen content in our rockweed plants from NB than NS sites. Nutrient loading can directly and indirectly affect rockweed's abundance and morphology (Worm and Lotze 2006, White et al. 2011). While rockweed plants near finfish aquaculture sites in southwest Nova Scotia were larger (more massive) than rockweed at control sites

(White et al. 2011), rockweed cover on rocky shores has been lower at sites exposed to point and non-point nutrient loading (Worm and Lotze 2006). In addition to our tissue content data, we also found significantly higher % organic TPM in NB compared to NS, and higher long-term Chl *a* measurements in NB (although direct field measures of Chl *a* in July and August were comparable). These results indicate generally higher nutrient availability, primary productivity and turbidity in NB.

2.4.2 Canopy structure and community composition

Individual morphometrics such as plant length, circumference and mass or plant density clearly illustrate that there are structural differences between rockweed beds in the two studied regions (Figure 5). Plants are significantly smaller and more densely packed in NB than in NS and distinct clusters for canopy structure are seen for the two regions (Figure 6). Interestingly, site-specific human activities among the NB sites (Table 1) appeared to have some influence on plant and canopy structure, with Bean Island, which is experiencing both regular rockweed harvest and finfish aquaculture, having more distinct canopy structure compared to the other NB sites (Figure 6) (see Chapter 3 for a more thorough investigation).

One guiding hypothesis of this chapter was that there would also be a shift in the community of associated fauna and flora between regions. Overall, species richness (Figure 7) and the abundance of mobile transect fauna (Figure 10) was higher at the NB sites and the community composition in NB differed from that at the NS sites (Figure 11). As with canopy structure, BN separates from the other NB sites, especially for the mobile quadrat fauna and sessile species (Figure 11), possibly due to the combined influence of multiple human activities (see Chapter 4).

While some of these regional differences can certainly be attributable to differences in the above-mentioned environmental factors, we hypothesized that some of it could be attributed to changes in the structure of the rockweed beds themselves. So far, no studies have focused on the relationship between rockweed canopy structure and community composition; however, extensive work has been done on terrestrial canopies and associated species assemblages (see Karr and Roth 1971, Wilson 1974, Mills et al. 1991, Halaj et al. 2000, Kornan and Adamik 2007, Hinsley et al. 2009 for examples) as well as some work relating some structural elements (but not three-dimensional canopy structure) of eelgrass and kelp beds to species assemblages (e.g. Kennelly 1989, Hyndes et al. 2003). For example, canopy cover and height are both important for bird species composition while branch density and arrangement influence arthropods (i.e. spiders) species composition (Halaj et al. 2000, Hinsley et al. 2009). Under-canopy assemblages have also been related to canopy structure. A logical extension for rockweed beds would suggest that plant and canopy structure might affect associated mobile and sessile benthic and epiphytic assemblges. And indeed, using the BIOENV procedure in PRIMER that tests associations between resemblance matrices we found that rockweed plant structure {length, circumference} accounted for a significant degree of the multivariate pattern in the composition of mobile (quadrat) macrofauna ($p = 0.033$). Additionally, plant structure also accounted for a degree of the pattern seen in the sessile (floral and faunal) species ($p = 0.068$); with a larger sample size, this association may become significant.

Investigating the link between rockweed canopy structure and associated species more closely using GLMs, GAMs, and Hurdle models, we established that plant structure {L, C} and even more strongly canopy structure ({L,C,D} routinely outperformed biomass {B} as a predictor of species abundance and richness. This is of particular interest because biomass is regularly used as a metric for monitoring rockweed beds and for assessing bed recovery after harvesting (Ugarte et al. 2006, Trott and Larsen 2012, DFO 2013). Adding region or site as predictors in the models was a way of including environmental variability and, not surprisingly, this further improved the explanation of the pattern or variation for most species of rockweed. Nevertheless, plant or canopy structural variables on their own were able to account for upwards of 50% and in some cases up to 90% of the pattern in nine species of interest, while region or site could add an additional 20-30% of the variance explained. These results strongly emphasize the importance of canopy structure for associated community structure.

Using these canopy measures may help identify areas of ecological importance or interest for conservation and management. Regions with a canopy structure associated with higher species diversity or greater abundance of vulnerable species, for instance, might warrant greater protection. Our field sampling and model results suggest higher abundance of smaller, slow-moving mobile and sessile (quadrat) species in less dense canopies with larger plants as in NS, compared to higher abundance of larger mobile (transect) fauna in dense canopies with smaller plants as in NB.

Unfortunately, we did not encounter a great variety or abundance of larger, commercially important fish or invertebrates, except a few herring (*Clupea harengus*), pollock (*Pollachius pollachius*) and rock crab (*Cancer irroratus*) in NB. This low abundance and diversity of fish in rockweed beds in these regions, where historically juvenile and adult fish have been abundant (e.g. Rangeley and Kramer 1995a, 1995b, Lotze and Milewski 2004), will make any examination of fish communities in these habitats and the effect of the commercial rockweed harvest on fish communities challenging. Interestingly, the most abundant large mobile species was the invasive green crab *Carcinus maenas*, which was introduced to North America in the early 1800s, and which was much more abundant in the dense canopies in NB than NS (Figure 8) (Grosholz and Ruiz 2002).

Greater numbers of *Littorina littorea* and *L. saxatilis* were found in NS as well as at AI, yet more L. obtusata at the two NB sites with the densest canopies (AI and SI). While the periwinkle *Littorina littorea* is commercially harvested in NB (Lotze and Milewski 2004) it is also affected as a bycatch species in the rockweed harvest together with *L. obtusata* (Uguarte et al. 2010a).

Another species of interest amongst the sessile species studied is the annual green alga *Ulva* spp., for which the models suggested greater abundance in denser canopies with smaller plants in NB, which is also the region with higher nutrient availability (e.g. % tissue N, Figure 2A). Whereas the contribution of nutrient exposure is captured in ~~our~~ the predictor variables “Region” or “Site”, even before either of these is added to the models, canopy structure {L, C, D} alone explains 86% of the deviance explained for *Ulva* spp. (Appendix D). The regional difference in nutrient exposure could be affecting canopy structure itself (e.g. Worm and Lotze 2006), thereby constituting an indirect nutrient effect on community structure. The epiphytic hydroid *Dynamena pumila* and brown alga *Elachista* sp. also appear more abundant in canopies with smaller, more densely packed plants in NB.

2.4.3 Management implications

This work has two important implications for resource management. First, the link between canopy structure and associated community structure should be considered in an ecosystem-based management approach. A number of studies mapping relationships between terrestrial canopies and species assemblages discuss these relationships in the context of the management implications, such as for forestry (e.g. Dellasala et al. 1996, Annand and Thompson 1997, Fuller and Green 1998, Robinson and Robinson 1999, Ishii et al. 2004). Given that the structural complexity of canopies influences the forested stand's productivity and biodiversity, including an assessment of the three-dimensional structure into management plans is needed in order to maintain ecosystem functions and biodiversity (Ishii et al. 2004). The same case can be made for the management of rockweed harvesting. Regulation of the rockweed harvest in North America remains a single-species approach (Seeley and Schlesinger 2012) despite long-standing discussion about possible ecosystem effects (DFO 1998, Davies and Rangely 2000). Concern surrounding the rockweed harvest has been focused on the effects of cutting and removing the plants themselves, as evidenced by existing harvest regulations and monitoring efforts by industry mainly consider rockweed biomass (Seeley and Schlesinger 2012, DFO 2013, DMR 2013). While this may be appropriate from a single-species management perspective that aims at keeping rockweed biomass and harvest constant, it does not provide insight into changes in canopy structure and associated species communities. Importantly, the work described here has demonstrated significant relationships between plant and canopy structure and the abundance and composition of associated species. Thus, plant and canopy metrics, like length and circumference combined with plant density, not only give a better indication of the canopy structure of the rockweed bed than biomass alone, they also provide a much stronger predictor of the associated community assemblage. Therefore, including plant and canopy measures into monitoring and management efforts would strongly improve our ability to apply ecosystem-based management.

Second, the strong regional differences documented in canopy and community structure suggest that management strategies should include a spatially refined management framework. Although current harvest regulations slightly differ among the major harvest regions in NS, NB and Maine (Seeley and Schlesinger 2012), they are related to political boundaries rather than environmental differences. The work described here indicates that differences exist in canopy structure and community composition among NS, NB and possibly Maine, which should be recognized in a spatial management framework.

Chapter 3: Effects of commercial rockweed harvesting on canopy and community structure: case study and review

3.0 Abstract

Rockweed (*Ascophyllum nodosum*) has been commercially harvested in Atlantic Canada since the 1960s, yet landings have increased over time and the harvest is currently expanding into the US state of Maine. Existing regulations aim to ensure a sustainable harvest of rockweed plants, while the broader ecosystem effects are neither well-understood nor considered in management actions. Using an experimental field survey and a literature review, this study aimed to (i) understand the effects of the commercial harvest on canopy and community structure of rockweed habitats in Nova Scotia and (ii) place our results in the context of other relevant studies to assess the broader ecosystem consequences of rockweed harvesting. Our field survey found a truncation and lower average values of length, circumference and mass of harvested compared to unharvested rockweed plants. Although biomass per m^2 was also lower, multivariate combinations of plant length and circumference better tracked changes in canopy structure. Species richness of the associated community was little affected, but the abundance of sessile and slow-moving benthic species was lower in harvested than unharvested areas and some shifts in species composition occurred. Highly mobile species (fish, crabs) were only encountered in very low and variable abundances. Our results were comparable but not entirely consistent with other studies on the effects of a moderate commercial hand harvest, and some effects on associated species could be explained by bycatch (e.g. littorinids) and altered light conditions (e.g. encrusting algae). Overall, the literature revealed that more intense harvests result in more substantial and longer-lasting alterations of canopy and community structure that may take from years to over a decade to recover. Yet many studies, particularly on lighter harvest intensities, have encountered difficulties determining community-wide changes because the commercial hand harvest is irregular and patchy difficult to sample, most areas have already been harvested (and altered) for decades, effective exclusion zones for comparison are largely lacking, and detecting changes in very depleted fish communities is largely impossible. Implications for monitoring rockweed habitats and an ecosystem-based management approach are discussed. Importantly, we suggest that rockweed biomass, a common monitoring measure, might not be a good metric to detect changes in canopy structure which is better described by a combination of plant length and circumference.

3.1 Introduction

Extensive rockweed beds are a dominant feature along rocky shores throughout the North Atlantic (Kerin 1998, Seeley and Schlesinger 2012). The primary foundation species *Ascophyllum nodosum* (hearafter rockweed) along with other fucoids cover upwards of 80% of the intertidal zone in Nova Scotia and Southwest New Brunswick (Chopin et al. 1996, DFO 1998, Worm and Lotze 2006). Thus, rockweed is responsible for maintaining high biomass and primary productivity and consequently plays important roles storing carbon and cycling nutrients (Schmidt et al. 2011). Moreover, with plants of 1.5-2.0 m or higher (MacFarlane 1952, Uguarte 2006, Vandermeulen 2013, Kay et al. Chapter 2), and multiple branched fronds per holdfast, rockweed also creates complex, three-dimensional habitat for a wide range of associated plants and animals (Schmidt et al. 2011, Seeley and Schlesinger 2012). Numerous species, some of commercial and others of conservation interest, use rockweed canopies. Over 100 taxa of invertebrates (including lobster, clams and snails), 34 species of fish (including pollock, flounder, herring and cod), shorebirds and waterfowl (including the eider duck), and a number of algal species have been observed interacting with rockweed habitat (Larsen 2010, Schmidt et al. 2011, Seeley and Schlesinger 2012).

Rockweed has also been a commercially important seaweed in Atlantic Canada since the 1960s for the production of alginates, fertilizer and animal feed (Chopin et al. 1996, DFO 2013). Commercial exploitation of rockweed in Nova Scotia began in 1959 as a manual harvest and became mechanized in the 1970s (Ugarte 2007, Seeley and Schlesinger 2012, DFO 2013). However, it was recognized that rockweed was being overharvested, and from 1992 until the present, all harvesting has been conducted manually, mostly with hand-held cutter rakes from small, open boats (DFO 1998, 2013, Seeley and Schlesinger 2012). The harvest expanded to New Brunswick in 1995 and landings within the Maritimes have increased from roughly 15,000 metric tonnes in 1996 to over 40,000 metric tonnes in 2011 (Ugarte and Sharp 2012). Recently, the harvest also expanded into Maine, USA (Seeley and Schlesinger 2012, DMR 2013). Harvest regulations in Canada include a minimum cutting height of 12.7 cm, although recently a change to 25.4 cm has been recommended in Nova Scotia to improve regrowth of rockweed plants after the harvest (DFO 2013). Average harvest rates are 25% of the harvestable biomass per year in Nova Scotia compared to 17% in New Brunswick (Ugarte and Sharp 2001, DFO 2013).

Considerable monitoring and research efforts have been made to study changes in rockweed plants themselves in response to harvesting (DFO 1998, Rangeley and Davies 2000). This research indicates that biomass depletion depends on harvest intensity and recovery time (e.g. Thomas 1994, Ang 1996, Cervin et al. 2004, Jenkins et al. 2004, Uguarte et al. 2006, DFO 2013); however, harvested plants become shorter and bushier over time (Baardseth 1955, Baardseth 1970,Vandermeulen 2013). Much less effort has been directed toward the effects on the associated floral and faunal communities that reside within or use the rockweed beds. Several studies that have looked for effects of harvesting on associated communities have focused on clear-cutting the rockweed bed or very intensive harvests (e.g. Boaden and Dring 1980, Thomas 1994, Fegley 2001, Kelly et al. 2001, Cervin et al. 2004, Jenkins et al. 2004), yet the effect of current harvest practices on the canopy structure of rockweed beds and their associated communities is largely unclear (DFO 2013). Despite this, there are plans to further expand the commercial harvest of rockweed in the Maritimes under the current, single-species management regime (The Canadian Press 2014, Erskine 2014).

A clear understanding of the effects of rockweed harvesting on the canopy structure as well as associated community composition is essential to inform conservation and ecosystem-based management of rockweed habitats. Effects can be immediate and short-term, affecting the canopy and community within the harvesting season itself, or they can be long-term with effects lasting several years or longer (DFO 2013). The goal of this study was to (i) determine the short-term effects of commercial rockweed harvesting on canopy structure and community composition within a major rockweed harvesting area in southwest Nova Scotia, and (ii) compare our results with those of other studies to evaluate the broader ecosystem effects of rockweed harvesting. We also discuss the difficulties of detecting the ecosystem effects of the commercial hand-harvest, which is often irregular and patchy and occurring in already long-term altered rockweed habitats.

3.2 Methods

3.2.1 Case study

3.2.1.i Study site

During the summer of 2012, we established an experimental study site at Kelley's Cove (43° 46' 57.47"N, 66° 07' 39.49"W), Yarmouth, Nova Scotia, which is within the major rockweed harvesting area (District 12) of southwest Nova Scotia (DFO 2013). The study site had a rockweed bed with consistent cover over >150 m of shoreline and gravel-boulder sediment. Originally, we had established five other study sites in southwest Nova

Scotia and southern New Brunswick; however, our harvest treatment - which consisted of regular harvesting practices performed by commercial harvesters (see below) - largely missed our experimental study areas leaving no freshly cut plants in our sampling transects and, thus, effectively no harvest treatment. These other sites were, therefore, not analyzed for harvesting effects; instead, the difficulties of performing this type of work are discussed.

Annual average sea surface temperature for Yarmouth is 8.3 °C and yearly miminum and maximum average temperatures are 3-5°C and 13-13.5°C respectively (Balch et al. 2007, 2012, http://www.seatemperature.org/north-america/canada/nova-scotia/). Maximum tidal range in Yarmouth is approximately 4.5 meters (Durand et al. 2008). The slope at Kelley's Cove was shallow and roughly 50 m width of rockweed bed was exposed at low tide. The cove is exposed to waves when prevailing wind is from the northeast, but a headland protects the site from exposure to south or southeasterly winds. A ridge leading down to the shore at the study site limited access to the study area, decreasing direct human influence (i.e., no houses and fewer beach walkers).

3.2.1.ii Experimental design

In July 2012, we established two treatments – harvested and non-harvested – by dividing the rockweed bed into two halves with permanent markings onshore and buoys in the intertidal. We surveyed both halves of the bed prior to the commercial harvest in July (pre-harvest survey), and re-surveyed both the harvested and non-harvested areas after the commercial harvest 4 weeks later in August (post-harvest survey). In collaboration with industry (Dr. R. Ugarte, Acadian Seaplants Limited [ASL]), licensed commercial harvesters had been asked to postpone their annual harvest at our study site until after our July survey had taken place, after which they were instructed to only harvest half of the bed marked ‘harvested’ using their regular harvesting procedure.

In each half of the rockweed bed, two 50 m transect lines were laid out parallel to the shore at low tide, anchored with weights at either end and marked with floating buoys. Pairs of transects were laid 4 m apart, 2 m above and 2 m below the approximate center of the exposed bed at low tide. At least 20 meters separated the end of one set of transects from the start of the next, which was our buffer zone between the harvested and unharvested half of the bed. Ideally, sampling units assigned to harvested or unharvested treatments would be randomly interspersed; however, given the logistical difficulty of marking harvesting and non-harvesting areas for harvesters and the physical constraint of the length of uninterrupted rockweed bed at our study sites, we opted to divide the beds into harvested and unharvested areas to avoid misapplied treatments. We compared both sides of the bed pre-harvest to rule out differences in canopy structure and identify any differences in community structure between treatment groups.

3.2.1.iii Sampling methods

At low tide, plant and canopy structure were measured in five 50 x 50 cm (0.25 m^2) quadrats placed along each transect at 10 m intervals. In each quadrat, the number of rockweed plants (density) was counted and each plant was measured for its length (cm) and maximum circumference (cm) with a measuring tape, and mass (g wet weight) on a portable scale. Small plants were directly placed on the scale, however, larger plants were placed in a scale-zeroed bucket that had one side cut open (see Ugarte et al. 2006).

Multiple fronds (i.e. genetic individuals) can grow from one coalesced holdfast; we determined that fronds belonged to one plant if their holdfasts touched or were less than a finger width apart, while a larger distance among holdfasts indicated separate plants (pers. comm. R. Ugarte, ASL).

To assess the associated communities, two divers swam at high tide in tandem along the 50 m long by 2 m wide transects (100 m^2 surveyed area for each transect) in each half of the experimental plot and recorded species name, size, and abundance of all fish and large mobile invertebrate species observed. Transect surveys were performed during both day and night high tides. During the day high tide, all mobile and sessile (macrofaunal) invertebrate species were identified and counted in ten 50 x 50 cm (0.25 m^2) quadrats placed along each transect at 5 m intervals. Sizes of larger, commercially important crustaceans (e.g. crabs) were recorded. Percent cover of benthic and epiphytic algae and encrusting invertebrates were also estimated in each quadrat.

3.2.1.iv Data Analysis

Plant and canopy structure were analyzed in several ways. First, we used histograms to compare the length, circumference and mass of individual plants for freshly cut versus unharvested plants post-harvest in the harvested half of the bed. We also used histograms to compare plant metrics between the harvested and unharvested sides of the bed. Second, we calculated average values for individual plant parameters (length, circumference, mass) for each sampling quadrat and summed the mass of individual plants to gain overall biomass (kg m^{-2}) per quadrat. For these and plant density (number m^{-2}) we then computed the mean (± SE) across quadrats for each half of the bed pre- and again post-harvest. Third, several combinations of plant metrics (plant length, circumference, mass, biomass m^{-2}, density m^{-2}) were used to assess differences in canopy structure between the two halves of the bed pre- and post-harvest. Because they had >0.8 correlation, plant mass and circumference were never both included in a measure of canopy structure; 0.7 (Tabachnick and Fidell 1996) correlation is a standard cutoff points for high correlation. To test for significant differences in multi-variate canopy structure between the two sides of the bed pre-harvest and post-harvest, respectively, we conducted two permutational multi-variate analyses of variance (perMANOVAs, fixed factor: side of bed) using PRIMER (version 6.1.11) with PERMANOVA+ (version 1.0.1, PRIMER-E, Plymouth). We also used permutational uni-variate analysis of variance (perANOVAs) to assess whether there was a harvesting effect on average plant length, mass, circumference, density and biomass, seen as a significant difference post-harvest in August that was not present pre-harvest in July. All morphometric variables were normalized prior to computation of Euclidean distance-based similarity matrices.

The associated communities were analysed as three distinct components: mobile macrofauna (and other count species) seen within the quadrats (abundance m^{-2}), mobile macrofauna counted along the transects (abundance m^{-2}), and sessile fauna and flora seen within quadrats (% cover). The sessile species were further divided as benthic and epiphytic assemblages. We calculated average species richness, diversity (Shannon index), and abundance or cover of each component for each half of the rockweed bed in July (pre-harvest) and August (post-harvest), and overall species richness across all community components. Sides of the bed were compared for differences in species richness, diversity and abundance for both July and August using uni-variate perANOVAs. Where of interest, the same side of the bed was also compared pre- and post-harvest (repeated measures, fixed effect: month).

Possible effects of the rockweed harvest on species composition (for each component of the community) were investigated using separate perMANOVAs (Fixed factor: Side of Bed) for July and August. Community composition data for each component was square-root transformed in order to down-weight the influence of abundant species and allow for a contribution to the resemblance matrix from rarer species. PerMANOVAs were also used to assess the effect of harvest on overall quadrat species richness (presence/absence of all species not including species counted along the transects). Community composition data was first transformed to presence/absence before the resemblance matrix was produced. Similarity percentages (SIMPER) tests were performed to determine which species contribute most consistently to differences among harvested and unharvested communities (Anderson et al. 2008).

3.2.2 Literature review

The literature search to find studies evaluating the effects of rockweed harvesting at a range of intensities was conducted through Google Scholar. Key words searched included: *Ascophyllum nodosum*, rockweed, harvest, hand-harvest, mechanical harvest, ice scour, Norwegian suction cutter, intertidal macroalgae, rockweed community, rocky intertidal community, rockweed ecosystem, *Ascophyllum* population structure, short-term changes, long-term changes, recovery after harvesting. Additionally, relevant references cited by articles that were uncovered during the literature search were also sought. In particular, unpublished documents submitted to DFO and DMR during recent government reviews (DFO 2013, DMR, 2013) were identified after reading these reports.

3.3 Results

3.3.1 Case Study

3.3.1.i Plant and Canopy Structure

After completing our pre-harvest survey in July, we were able to observe the commercial hand harvesting of rockweed at our study site without influencing it. The harvest was not regularly patterned, but opportunistic and patchy throughout the bed, following the drift of the harvesting boat and the tides. Returning to the study site 4 weeks later, we found freshly cut plants in seven out of ten sampling quadrats on the harvested side compared to zero out of ten quadrats on the unharvested side. 28% of all measured plants on the harvested side showed signs of fresh cuts to varying degrees; while some plants had all or most fronds cut short, the majority only had a few tips cut off.

Histograms depict plant length, circumference and mass of all measured plants on the harvested compared to the unharvested side of the bed in July (pre-harvest) and August (post-harvest) (Figure 1). While the histograms are similar in shape in July, there is a shift towards higher frequencies of smaller plants on the harvested compared to the unharvested side in August. Larger plants with >160 cm length, >30 cm circumference and >2000 g mass are missing among harvested plants in August, indicating a truncation of harvested plants (Figure 1).

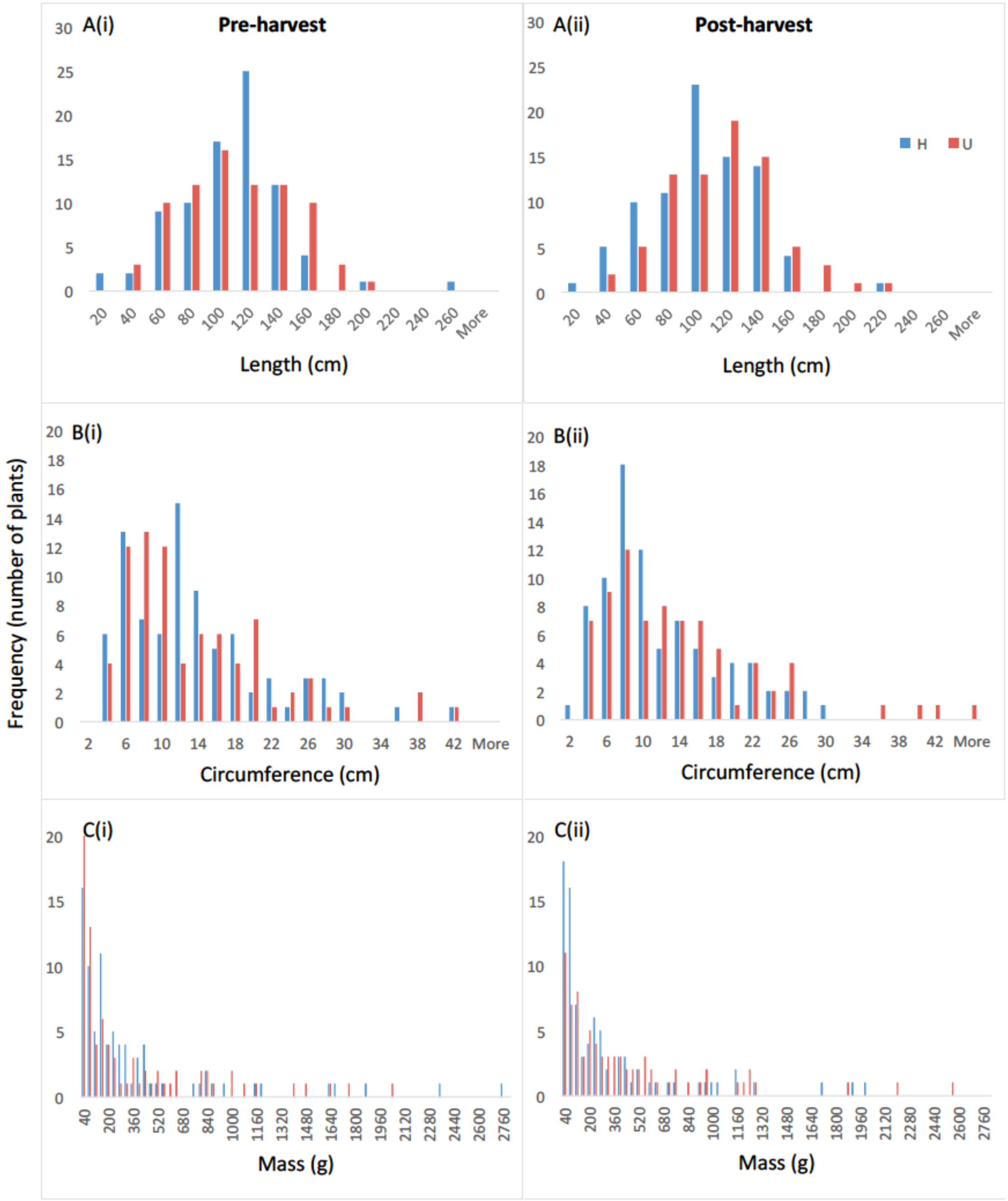


Figure 1. Frequency distribution of plant (A) length (cm), (B) circumference (cm), and (C) mass (g) (Pre-harvest n = 162, Post-harvest n = 161) immediately (i) pre-harvest and one month (ii) post-harvest. Harvested (H) plants are represented by the blue data series and unharvested (U) plants are represented by the red data series.

Comparing average values per quadrat, there was little difference in individual plant parameters between both sides of the rockweed bed in July (pre-harvest), while plants were on average longer, wider and heavier on the unharvested than harvested side in August (post-harvest) (Figure 2A-C). Although these differences in August were not statistically significant when using average values per quadrat, side of bed explained 10-13% of the variation in average plant length and circumference (Appendix 3C Table 1). However, when using individual plant measures side of bed in August became significantly different for plant length (Pseudo-F = 5.330, p = 0.002) and marginally non-significant for circumference (Pseudo-F = 3.370, p = 0.070) (Appendix 3C Table 1). These shifts in plant parameters are reflected in slightly lower average biomass in the harvested compared to the unharvested side in August (Figure 2D), although not statistically significant (Table Appendix). In contrast, plant density did not differ between both sides of the bed pre- or post-harvest (Figure 2E), but since plants are not removed by the harvest this was to be expected.

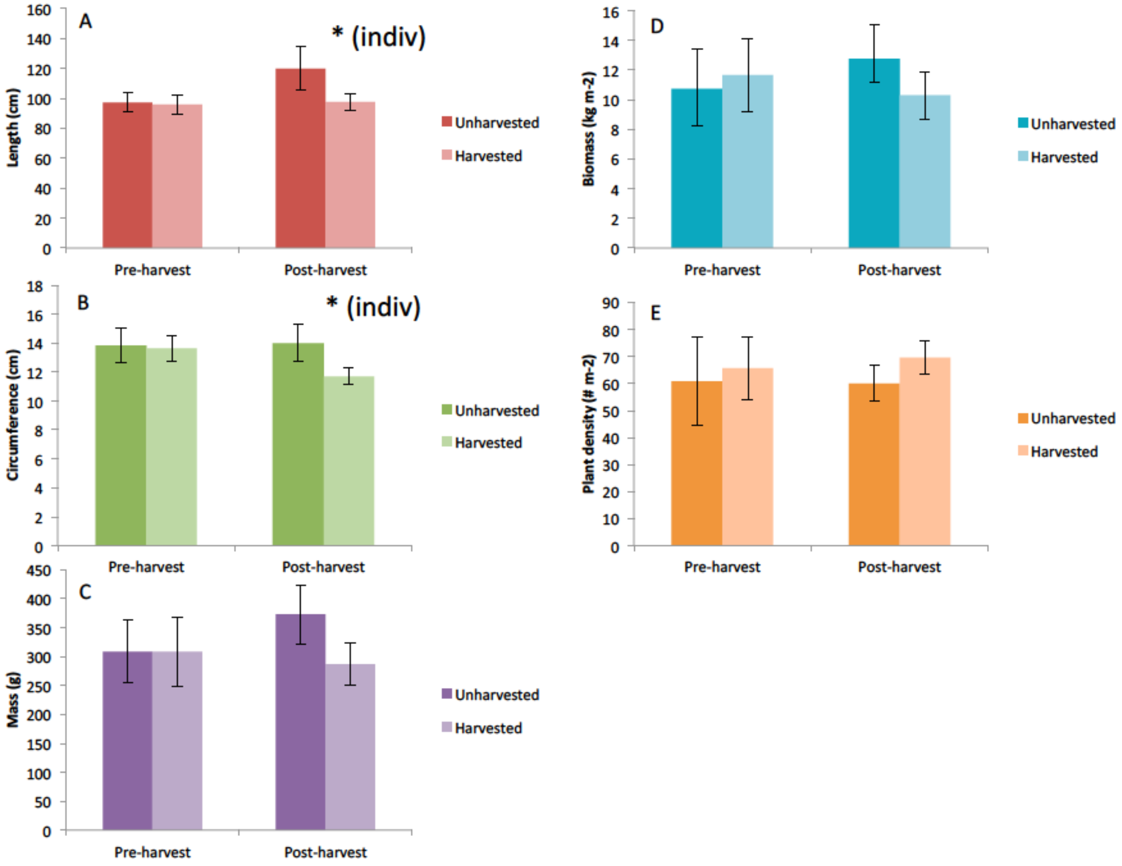


Figure 2. Averages and standard errors (SE, n = 20) for rockweed plant and canopy parameters: (A) plant length (cm), (B) plant circumference (cm), (C) plant mass (g), (D) density (plants m^{-2}), and (E) biomass (kg m^{-2}) for unharvested and harvested sides of the bed, pre-harvest and post-harvest. Significant differences between harvested and unharvested sides of the bed when individual plant metrics were used (Pre-harvest unharvested n = 79, harvested n = 83; Post-harvest harvest unharvested n = 77, harvested n = 84) indicated by *(indiv).

Results of perMANOVAs investigating multi-variate combinations of plant and canopy parameters revealed that the combination of plant length and circumference best reflected the difference between the harvested and unharvested plot in August (p = 0.028 for individual measures, p = 0.080 for quadrat averages) compared to a non-existing difference in July (both p=0.970, Table 1). Using the combination of plant length and mass pointed in the same direction, but less strongly (p = 0.7 in July, p = 0.1147 in August for individual measures), while the combination of plant length and biomass was even weaker. Adding density to any combinations further reduced the signal between harvested and unharvested plots, which is no surprise since plant density is not expected to be affected by the hand-harvest.

Table 1. One-factor perMANOVA results for the effect of Side of bed (in July and again in August) on Plant structure {L, C}. Sqrt-V values are unbiased estimates of the contribution to variance of Site and the residuals in the model. Variance explained (Var) is given by [(SS Factor/SS Total) x 100] and, while more biased than sqrt-V, is included since it is a more intuitive measure of relative effect size (Howell 2002). The degrees of freedom (df) total to 19. Significant p-values are shown in bold.

	Source	**Fixed factor: Side of bed (July)**	**Res**	**Fixed factor: Side of bed (August)**	**Res**
	Df	**1**	**18**	**1**	**18**
Canopy structure {L, C} for quadrats	**Pseudo-F**	5.710 e-2		2.430	
	P	0.970		0.080	
	sqrt-V	-0.450	1.450	0.520	1.360
	Var	<0.1	98.5	11.9	88.90
Canopy structure {L, C} for individual plants	**Pseudo-F**	2.200e-2		4.120	
	P	0.970		**0.028**	
	sqrt-V	-0.160	1.420	0.280	1.400
	Var	0.001	99.9	2.5	97.50

3.3.1.ii Associated communities

Overall, we encountered a total of 19 species associated with rockweed habitats. For mobile fauna, we found two species of fish (alewife *Alosa pseudoharengus*, and an unspecified flounder), three crustaceans (the invasive green crab *Carcinus maenas*, *Cancer irroratus*, and mysid shrimp), and four species of gastropods (*Littorina littorea*, *L. saxatilis*, *L. obtusata* and *Nucella* sp.). For sessile fauna, we found one species of crustacean (the barnacle *Semibalanus balanoides*).

The flora consisted of five benthic (*Chondrus crispus*, green encrusting algae, *Lithothamnion* sp., *Hildenbrandia rubra*, and *Fucus vesiculosus* and *F. spiralis*) and three epiphytic macroalgae (*Vertebrata lanosa*, *Ectocarpus* sp., and *Elachista fucicola*). Overall abundances of larger mobile species, particularly for fish, were extremely low.

In the sessile community, species richness was not significantly different between the harvested and unharvested sides of the bed either pre-harvest (p = 0.170) or post-harvest (p = 0.180) (Appendix 3C Table 2); however, richness on the harvested side was significantly lower after than before the harvest (F =5.020, p= 0.045), while richness on the unharvested side increased from July to August (Figure 3A). A similar pattern was observed for overall sessile diversity (Figure 3B) and just benthic sessile diversity (Figure 3D). In both cases, diversity was significantly higher for the harvested half of the bed pre-harvest (sessile diversity, p = 0.010; benthic diversity, p=0.003), and lower, though non-significantly, than the unharvested half post-harvest (Appendix 3C Table 3) (Figure 3B, D). In fact, sessile and benthic diversity on the harvested half decreased significantly from their pre- to post-harvest values (sessile diversity, F = 4.998, p= 0.034 benthic diversity, F = 4.610, p= 0.037), while it increased non-significantly on the unharvested half of the bed from July to August (sessile diversity, F = 1.446 , p= 0.247; benthic diversity, F = 1.51, p= 0.23) . In contrast, diversity of epiphytic species was higher on the harvested half of the bed post-harvest (p = 0.040), though not pre-harvest (Figure 3C).

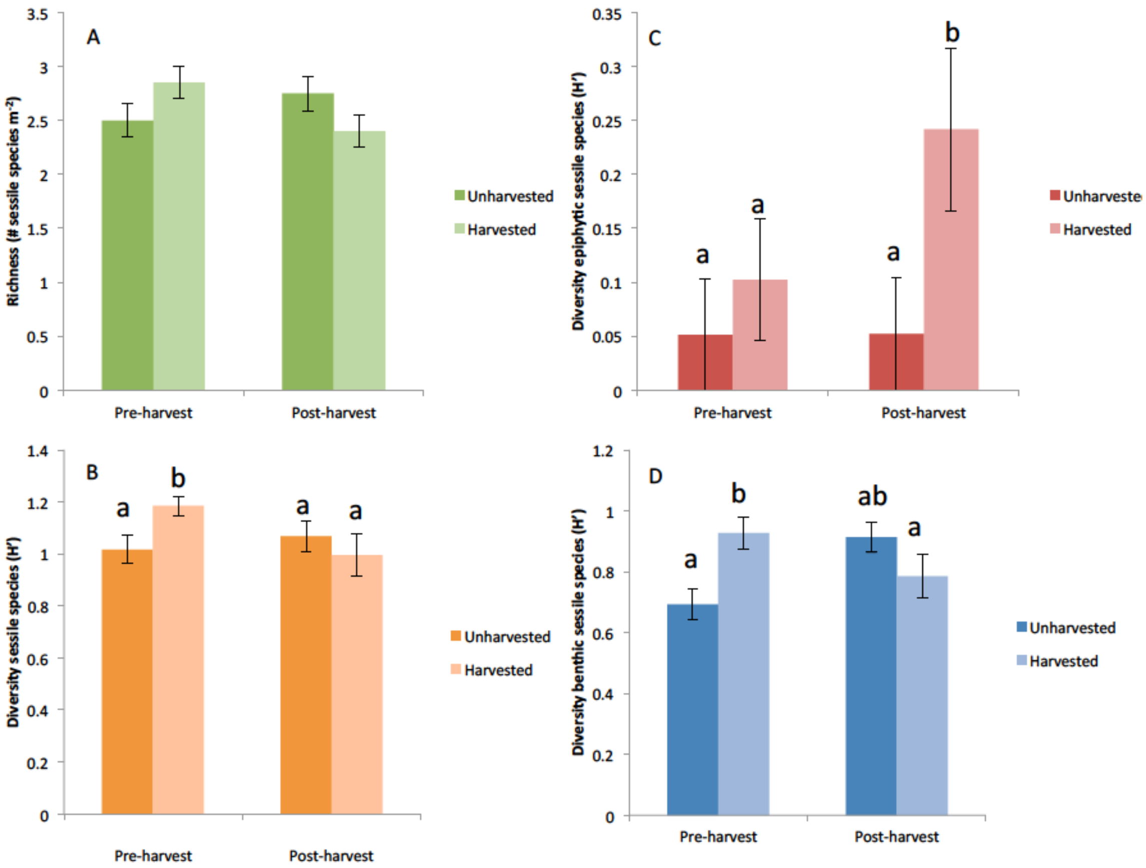


Figure 3. (A) Average richness m^{-2} and standard error (SE, n= 40) of sessile species as well as average diversity (H') and SE of (A) sessile species, (B) sessile benthic and epiphytic species, (C) epiphytic sessile species, and (D) benthic sessile species for unharvested and harvested sides of the bed, pre-harvest and post-harvest. Lower case letters indicate significant differences between sides of the bed within month as well as differences within side of bed across months.

Total cover of sessile fauna and algae was significantly lower on the harvested side pre-harvest (p= 0.006), and this difference increased and became more significant in August (p =0.0006) (Figure 4). Results of perMANOVAs indicate a significant effect of side of bed on the composition of sessile species in July (p = 0.003), which became weaker in August (p = 0.048) (Table 2). Separating the epiphytic and benthic component of the sessile species revealed similar results. SIMPER analysis identified the benthic *Semibalanosus balanoides, Hildenbrandia* *rubra* and green encrusting algae and the epiphytic *Vertebrata lanosa* as contributing strongly to the differences between the two sides of the bed in July, and *S. balanoides* and *H. rubra* post-harvest (Appendix 3A). In both, months, *S. balanoides, H. rubra* and *V. lanosa* were more abundant on the unharvested side, while green encrusting algae were more abundant on the harvested side (Figure 4). The strongest change was observed in the percent cover of *H. rubra*, which was the lowest on the harvested side post-harvest (Figure 4). Also post-harvest, *Elachista fucicola* was more abundant and *Ectocarpus* sp. absent on the harvested side (Figure 4).

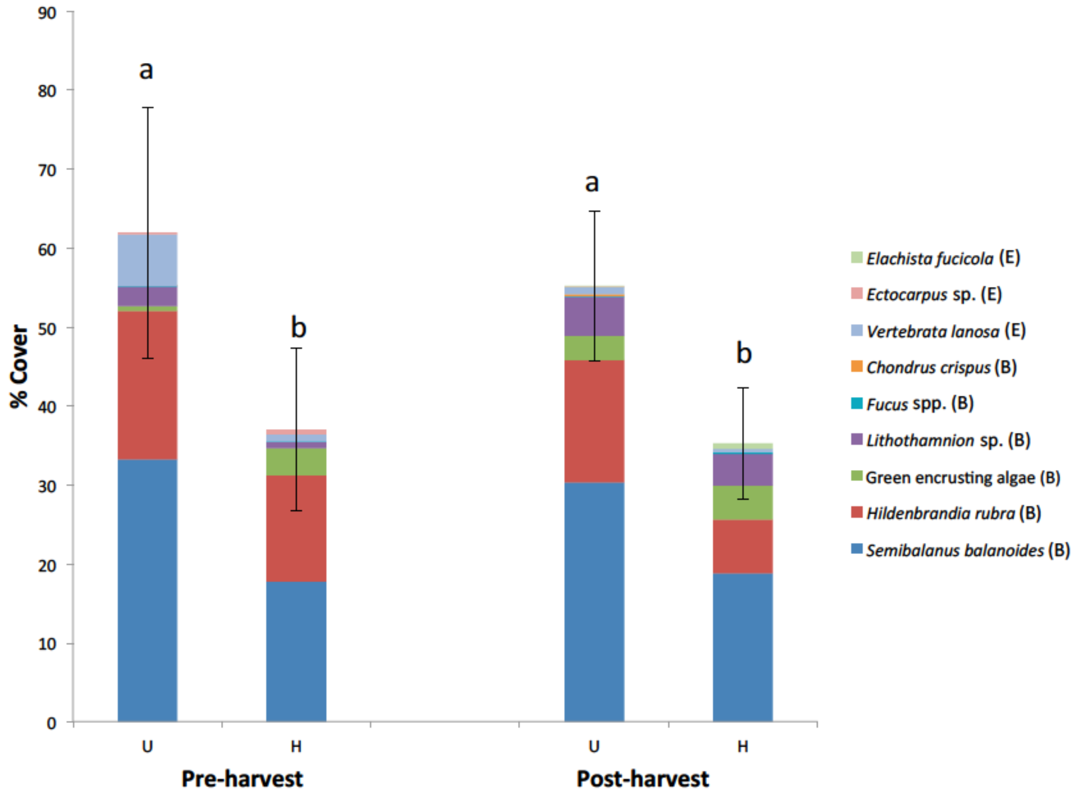


Figure 4. Average percent cover and standard error (SE, n = 20) of sessile benthic (B) and epiphytic (E) species for unharvested and harvested sides of the bed, pre-harvest and post-harvest. Lower case letters indicate significant differences between sides of the bed within month as well as differences within side of bed across months.

For mobile quadrat species, there was no significant difference between species richness or diversity for the sides of the bed either pre-harvest (p=0.170) or post-harvest (p=0.280), but again both richness and diversity were higher on harvested side pre-harvest and lower post-harvest (Figure 5). Moreover, both richness and diversity were significantly lower on both sides of the bed post-harvest than pre-harvest (richness, pseudo-F = 23.841, p = 0.0005 unharvested, pseudo-F = 23.841, p = 0.0002 harvested; diversity, pseudo-F = 10.800, p = 0.006 unharvested, pseudo-F = 31.000, p=0.001 harvested); the most likely explanation for this is that the August (post-harvest) survey took place during a storm and wave action over the bed was more turbulent than in July.

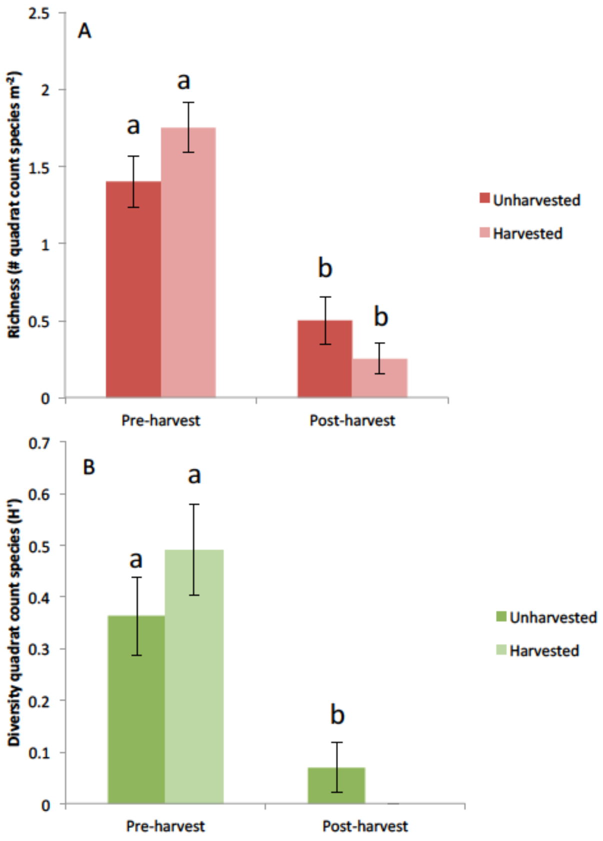


Figure 5. (A) Average richness and standard error (SE, n = 20) and (B) average diversity and SE of count quadrat species for unharvested and harvested sides of the bed, pre-harvest and post-harvest. Lower case letters indicate significant differences between sides of the bed within month as well as differences within side of bed across months.

Total quadrat species abundance was not significantly different between the sides of the bed in either July (p =0.200) or August (p = 0.380) (Figure 6). However, while the average total abundance was higher on the harvested side in July, this pattern reversed in August, with lowest abundance on the harvested side. A strong drop in littorinids, especially *Littorina littorea*, which is a common bycatch species of the commercial rockweed harvest (Sharp et al. 2006, Ugarte et al. 2010a), helps explain the reversal of this trend. Lower overall abundances in August compared to

July are, again, partially attributable to the storminess on our sampling date in August; mobile fauna likely sought shelter.

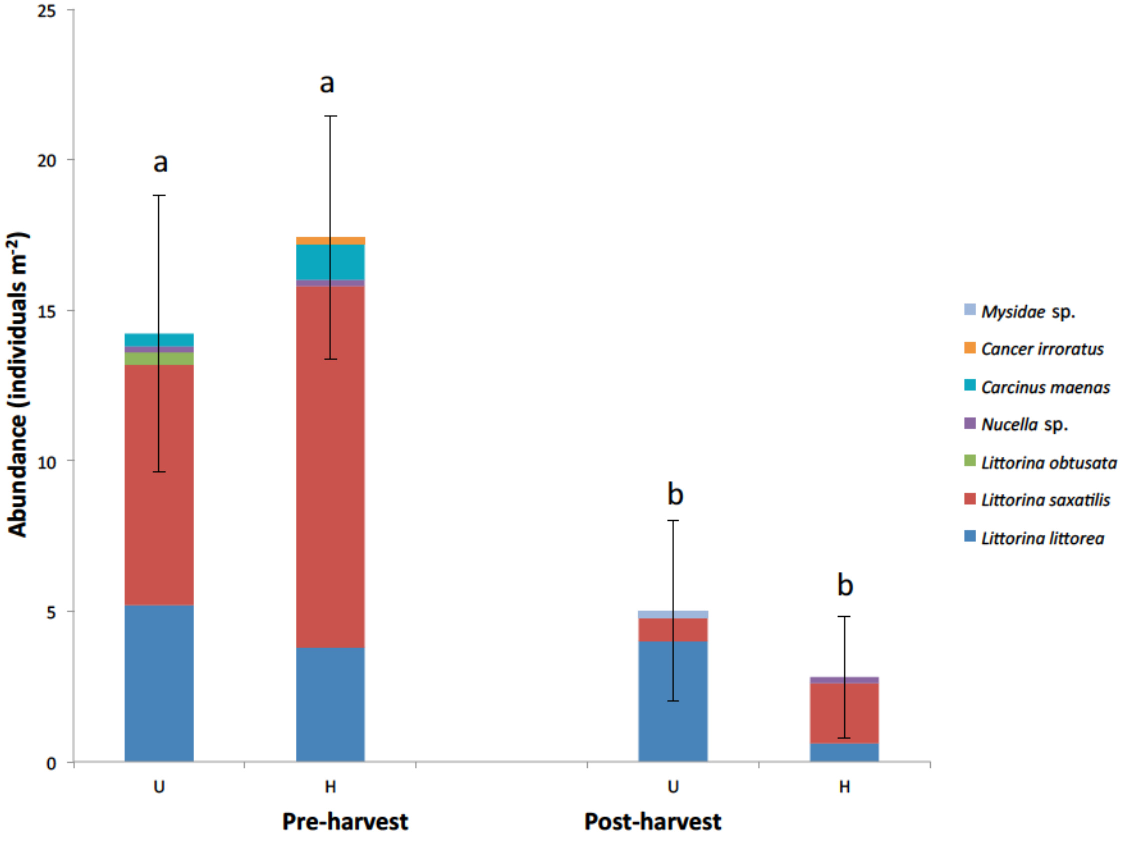


Figure 6. Average abundance and standard error (SE, n = 20) of count (quadrat) species for unharvested and harvested sides of the bed, pre-harvest and post-harvest. Lower case letters indicate significant differences between sides of the bed within month as well as differences within side of bed across months.

PerMANOVAs identified a non-significant effect of side of bed in July ($p = 0.067$) that remained non-significant in August ($p = 0.373$) (Table 2). No species were identified as good discriminators between the sides in either July or August; however, both *Littorina saxatilis* and *L. littorea* contribute most to the dissimilarity (Appendix 3A).

Time of day did not have a significant effect on transect species composition, therefore, night and day-time transects were pooled. Almost no larger mobile species were encountered in our transects, either during the day or night surveys, and those seen - alewife, flounder, rock crab, green crab and mysid shrimp - were present at very low abundance (Figure 7, 8). The results are highly variable and no significant effect of side of bed was seen for richness, diversity, abundance or species composition (Table 2, Appendix 3C Tables 2, 3).

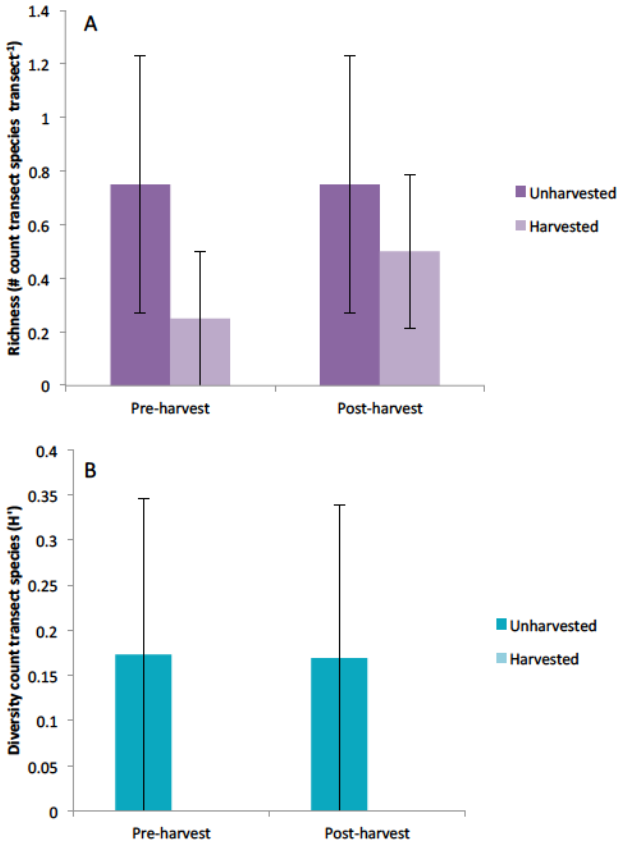


Figure 7. (A) Average richness and standard error (SE, n = 20) and (B) average diversity and SE of mobile transect species for unharvested and harvested sides of the bed, pre-harvest and post-harvest.

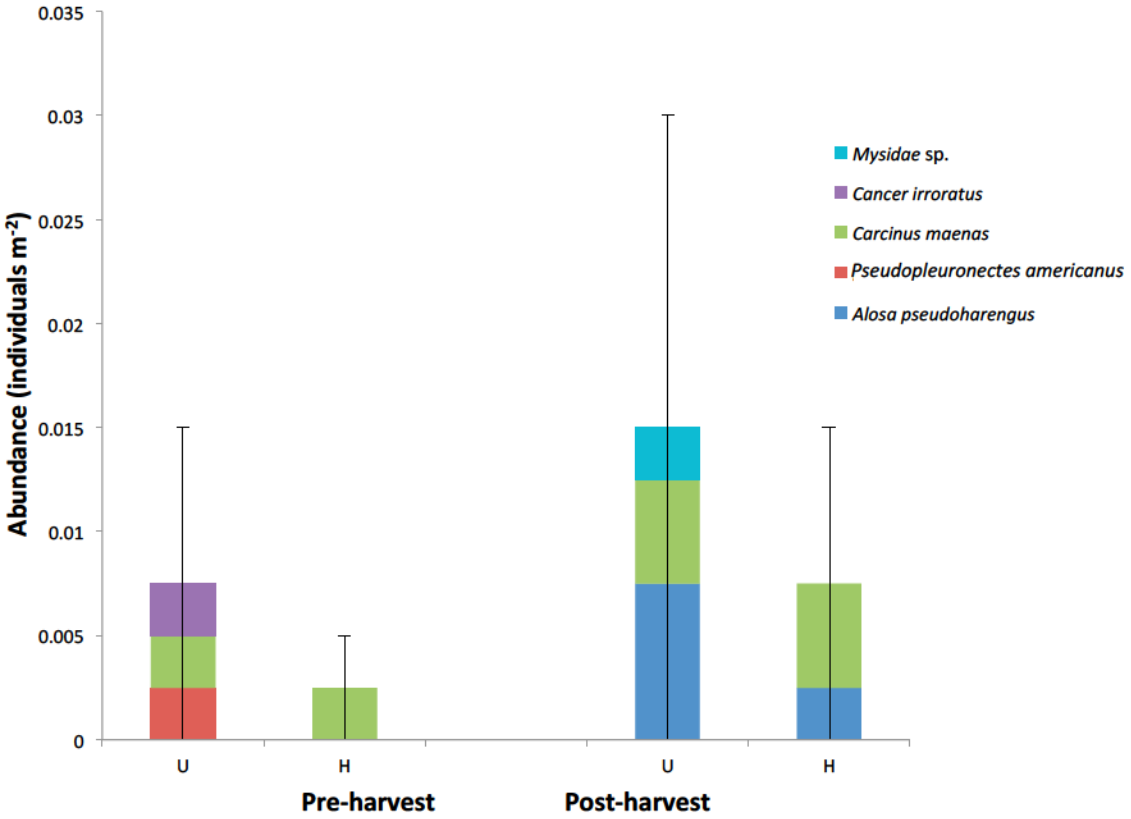


Figure 8. Average abundance and standard error (SE, n = 20) of mobile transect species for unharvested and harvested sides of the bed, pre-harvest and post-harvest.

Table 2. One-factor perMANOVA results for the effect of Side of bed (in July and again in August) on diversity (H') of each community component (benthic, epiphytic, total sessile, mobile (quadrat), and mobile (transect) species). Sqrt-V values are unbiased estimates of the contribution to variance of Site and the residuals in the model. Variance explained (Var) is given by [(SS Factor/SS Total) x 100] and, while more biased than sqrt-V, is included since it is a more intuitive measure of relative effect size (Howell 2002). The degrees of freedom (df) total to 39. Significant p-values are shown in bold.

	Source	**Side of bed (July)**	**Res**	**Side of bed (August)**	**Res**
	df	**1**	**38**	**1**	**38**
Benthic composition	**Pseudo-F**	4.910		2.50	
	P	**0.013**		0.08	
	sqrt-V	12.050	27.240	7.270	26.580
	Var	11.5	88.500	6.2	93.8
Epiphytic composition	**Pseudo-F**	8.26		5.07	
	P	**0.0006**		**0.013**	
	sqrt-V	15.330	25.450	11.390	25.270
	Var	17.9	82.1	11.8	88.2
Sessile species composition	**Pseudo-F**	5.950		2.990	
	P	**0.003**		**0.048**	
	sqrt-V	14.050	28.260	8.930	28.300
	Var	13.5	6.5	7.3	92.7
Mobile (quadrat) species composition	**Pseudo-F**	2.660		1.030	
	P	0.067		0.370	
	sqrt-V	9.750	33.890	1.290	32.460
	Var	6.5	93.5	2.6	97.4
Mobile (transect) species composition	**Pseudo-F**	0.530		9.12 e-2	
	P	1		0.831	
	sqrt-V	-8.330	24.290	-14.91	31.280
	Var	8.1	91.9	1.5	98.5

3.3.2 Literature Review

3.3.2.i Biomass removal

A number of long-term studies that followed clear-cut plots with 100% biomass removal noted that the largely monospecific rockweed canopy was replaced by a *Fucus vesiculosus* dominated canopy or a mixed canopy of *Fucus* spp. and *Ascophyllum nodosum* four to twelve years after the clearing event (Thomas 1994, Cervin et al. 2004, Jenkins et al. 2004) (Table 3; Appendix 3B). Related alterations of the intertidal communities – including increased abundance of opportunistic algae, and decreased abundance of sessile fauna and grazers – in these clearing experiments were observed to last between 2.5 years (Cervin et al. 2004) to >10 years (Thomas 1994).

Mechanical harvesting with a Norwegian suction cutter (an instrument that removes much more of the plant than the current hand harvest and often the holdfast) changed canopy structure in Southwestern Nova Scotia, with the bimodal length distribution becoming unimodal for two years after harvest (Table 3, Ang 1996). Lazo and Chapman (1996) also conducted a study using mechanical harvesting in SW Nova Scotia and saw no effect of harvest intensity (comparing four levels of intensity) on plant growth; however, they noted increased growth of *Ascophyllum* in harvested plots compared to controls. The authors note that, while the increased growth can be attributed to the harvest, their findings do not indicate that there are no negative effects of harvesting on bed productivity; since they did not assess whether biomass of harvested plots returned to pre-harvest levels the authors stressed that they had not enough data to support the idea that cut plots produce more biomass (Lazo and Chapman 1996). While analyzing fronds individually, Lazo and Chapman (1996) noted no significant differences between cut and uncut fronds in terms of growth, reproduction or survival.

After an intensive hand harvest in Ireland (70% cover reduced to 30%), recovery of *Ascophyllum* cover took between 11 and 17 months (Kelly et al. 2001) (Table 3). While there was no marked effect of the harvest on associated species richness, an increase in ephemeral algae was noted at the midshore, possibly attributable to the removal of *Ascophyllum*. The harvest also led to a significant decrease in associated sessile fauna such as sponges and bryozoans and reduced numbers of *Littorina obtusata*.

Similarly, after a 50% exploitation rate by hand harvest in SW New Brunswick, rockweed biomass was reduced by 22% and regrowth of *Ascophyllum* length took from one to over two years (Ugarte et al. 2006) (Table 3). Uguarte (2011) quantified removal of rockweed biomass in the commercial harvest in SW New Brunswick and reported that it was similar to storm removal from a bed. It should be noted, however, that what is being removed by the harvest is additional to what is lost in the storm and is lost all at once, not over the course of a season as is the case with storm-cast rockweed. Additionally, Seeley and Schlesinger (2012) point out that storm-cast *Ascophyllum* contains substantially less area of holdfast and decomposes in the marine ecosystem, providing nutrients and food, while harvested *Ascophyllum* is lost to the system.

Beal et al. (2011) and Trott and Larsen (2012) conducted similar studies to assess the impact of the current rockweed harvesting regime; the results of their studies were presented to the Department of Fisheries and Oceans (DFO, Canada) and the Department of Marine Resources (DMR, Maine, USA) respectively while each governing body was reviewing rockweed harvesting management for their jurisdictions (Table 3). Beal et al. (2011 - unpublished report available at http://www2.mar.dfo-mpo.gc.ca/science/rap/internet/Background_Plants_2012_B.pdf) simulated a commercial hand harvest in Maine at a 17-23% exploitation rate, sampling the study site before and 38 days after the harvest. They noted a non-significant 44% decrease in the biomass of *Ascophyllum* on middle and lower transects of the harvested treatment. Similarly, there was not a significant effect of cutting on the biomass of *L. littorea* or *L obtusata*, the two most abundant macro-invertebrates present at their site; however, *L.littorea* biomass increased on the lowest transect, where the most rockweed biomass was removed, which was also observed by Phillippi et al. (2014). Trott and Larsen (2012 - available online at http://www2.mar.dfo-mpo.gc.ca/science/rap/internet/Background_Plants_2012_D.pdf) conducted their experiment in Maine with the assistance of a professional harvester employed by Acadian Seaplants Limited (ASL) and noted a significant increase in biomass of *Ascophyllum* in the harvested plot, no significant effect on abundance of littorinids (*Littorina littorea, L. obtusata* and *L. saxatilus*), but a significant difference in epiphytic richness between the experimental and control treatments (lower for experimental).

3.3.2.ii Cutting height

Rather than quantifying biomass removal, a set of other studies evaluated the effects of different cutting heights. In the following, we review the results of studies, which evaluated cutting heights that relate to current minimum (12.7 cm) or recommended (25.4 cm) cutting height regulations for Atlantic Canada (DFO 2013). Boaden and Dring (1980) harvested plots within 10-15 cm of the holdfast in Northern Ireland (Table 3). After 2.5 years, plants showed longer internodal length and increased branching, while cover of *Ascophyllum* was reduced by 20% and there was slightly more *Fucus* spp. present. The composition of the associated species remained altered after 2.5 years, with lower densities of *Mytilus* and higher limpet densities, ~60% lower abundance of under-boulder fauna (e.g. barnacles and sponges), and significantly more *Ulva* sp. (Boaden and Dring 1980).

Sharp (1987) noted that when harvesting to 15-25 cm from the holdfast, 2.5 to 3 years are needed for recovery to pre-harvest biomass, meaning that yearly harvests at this intensity will leave lower and lower biomass in successive years. Keser et al. (1981) conducted three successive annual harvests at this cutting height and also recorded decreased biomass. In a personal communication to Sharp and Pringle (1990), Gendron noted that beds harvested to between 15 and 30 cm every two to three years in the Gulf of Saint Lawrence recovered roughly 90% of biomass after three years if harvesting occurred every two to three years rather than annually. In a study conducted in Maine, plants harvested to heights of 18 and 36 cm branched more and were significantly shorter than control plants after a period of two years (Fegley 2001). Short term effects (1-2 years) of the 18 cm harvesting regime included decreases in associated species in both species- and community-level analyses: decreases were seen in the cover of *Fucus vesiculosus, Hildenbrandia rubra* and *Phymatolithon lenormundii*, and abundances of *Carcinus maenas, Dynamena pumila, Halichondria* sp., and *Littorina obtusata*, while *Nucella lapillus* abundance increased.

Table 3. Summary of canopy and community effects resulting from different harvest types. For a more detailed description of each study and additional studies see Appendix 3B.

Harvest type	Canopy effects	Community effects	References
Clear cut			
100% biomass removal	(Not assessed)	No adverse effects on fishes	Black and Miller 1986 Black and Miller 1991
	Strong, long-term (4-12 years) alteration of plant and canopy structure	Replacement with or encroachment by *Fucus* spp., Restoration of understory community took 1.5 years to >10 years (depending on size of areas cleared; for Thomas 1994, Cervin et al. 2004)	Keser et al. 1981 Keser and Larson 1984 Vadas and Wright 1986 Thomas 1994 Cervin et al. 2004 Jenkins et al. 2004
Mechanical harvest			
(Norwegian suction cutter) Ca 80% biomass removal	Bimodal population structure (plant length) became unimodal for two years	(Not assessed)	Ang et al. 1993 Ang et al. 1996
Ca 18%, 60% and 70% biomass removal	Non-significantly increased growth of *Ascophyllum*, however, insufficient data to say cut plots produce more biomass; zygote recruitment possibly affected	(Not assessed)	Lazo et al.1994 Lazo and Chapman 1996
Intense hand harvest			
Cover reduced from 70% to 30%	1-1.5 years for return of cover	Reduction in associated sessile animals and *L. obtusata*, more ephemeral algae, more *F. vesiculosus* in some cases	Kelly et al. 2001
50% biomass removal	Large plants reduced length (45%) and biomass (22%) for 2 years	(Not assessed)	Ugarte et al. 2006
Commercial hand-harvest (ASL)			
Unharvested and pre-commercially harvested (Not sure where to put MacFarlane, if in table at all)	In unharvested areas of Yarmouth, max standing stocks ca 32 wet kg m^{-2}, plants often 180-210 cm long	More *F. vesiculosus* in overharvested areas	MacFarlane 1952
17-25% biomass removal	Ca 17% of holdfast area removed if holdfast is affected (≤ 10% of plants), rockweed cover not	<1% littorinids lost as bycatch	Sharp et al. 2006 Ugarte et al. 2010 a Ugarte 2011

	effected		
	20% of harvest sample by weight was holdfast or basal tissue	Minor impact from loss of littorinids as bycatch	McEachreon 1999
	Biomass lower at half of harvested sectors compared to values from six years earlier	(Not assessed)	Sutherland 2005
	No landscape level effects of harvest	Minor impact from loss of littorinids as bycatch	Sharp et al. 2006
Experimental replication of commercial hand-harvest (ASL)			
17-25% biomass removal	Non-significant decrease in biomass	No effect on *L. littorea, L. obtusata*	Beal et al. 2011
	Increase in biomass	Low level effect on species assemblage	Trott and Larsen 2012
	Decreased plant length, mass circumference	Species assemblage affected, *L. littorea* reduced	This study
Experimental cutting heights			
5.1, 12.7, 20.3, and 27.9 cm	After 2 years, best yield from plants cut at 27.9 cm	(Not assessed)	Walker 1948
Above holdfast (surface cut), 5, 15 and 25 cm	No recovery of biomass at surface or 5 cm cuts, some recovery at 15, some to full recovery at 25 cm after 3 years	More *F. vesiculosus* with surface cuts	Printz 1956 Keser et al. 1981
Surface cut	Mortality, more sporelings, greater internodal length	*F. vesiculosus* and *Ulva* spp. cover significantly higher	Tyler 1994
15-30 cm	Decreased plant length, increased branching	Decrease in 7 species (*L. obtusata*), 1 increased	Fegley 2001
10-15 cm	Recovery of biomass takes 2.5 to 3 years, yearly experimental harvests leave successively lower biomass	(Not assessed)	Gendron (pers com to Sharp) Sharp 1987
	Decreased cover after 2.5 years, increased branching	Decreased densities of several species, significantly more *Ulva* spp. and *F. vesiculosus*	Boaden and Dring 1980
20.3 and 40.6 cm	(Not assessed)	Decease in *C. maenus*, increase in *L. littorea*, no impact on infauna	Philippi et al. 2014

3.4 Discussion

Understanding the ecosystem effects of the commercial rockweed harvest is essential for an ecosystem-based management approach. This includes a clear understanding of the alteration of the rockweed canopy, which provides important habitat structure, as well as changes in the abundance and composition of associated faunal and floral species. So far, not many harvesting studies have attempted to replicate the intensity or spatial distribution of the commercial harvest conducted in Atlantic Canada, and those that do show variable results. Our case study provides more detailed insight into changes in canopy structure and community composition, which we place in the context of other studies along a gradient of harvest intensities. However, our study also points to the difficulty of detecting significant changes in areas that have been harvested and potentially altered for decades without baseline comparison.

3.4.1 Current Case Study

Our case study attempted to replicate the commercial harvest as currently practiced in Atlantic Canada, similar to previous studies by Beal et al. (2011) and Trott and Larsen (2012). Our results reveal some significant harvest effects, but more often trends in changed canopy and community structure.

Beal et al. (2011), Trott and Larsen (2012), and the present experimental harvest were all conducted by, or under the supervision of, harvesters licensed by Acadian Seaplants Limited (ASL), with 17-23% and 17% of the harvested plot's biomass was removed in Beal et al. (2011) and Trott and Larsen (2012) respectively. While we do not have an estimate of the biomass removed in our study, 28% of the plants in our harvested plot showed signs of harvesting, and average biomass in our sampling quadrats on the harvested side of the rockweed bed was 19% lower compared to those on the unharvested side (whereas pre-harvest, average biomass on the harvested side was 4.3% higher than on the unharvested side). It is, therefore, reasonable to assume that the harvesting impact of our study was similar to the previous two studies.

Despite similar harvest impact, we found a significant decrease in plant length, circumference and their combined canopy structure {plant L, C} as well as a non-significant decrease in biomass in the harvested treatment. In comparison, Beal et al. (2011) measured a non-significant decrease and Trott and Larsen (2012) a significant increase in rockweed biomass. These results suggest that measuring biomass of harvested areas alone, as commonly done in both scientific studies and monitoring, may not capture changes in canopy structure, which is better described by a combination of plant length and circumference.

When harvested and unharvested sides of the bed were compared to assess potential effects on the associated community structure, results were variable. Diversity of epiphytic sessile species increased significantly for the harvested side post-harvest, while the diversity of benthic and of all sessile species decreased non-significantly. Among epiphytic species, the greater abundance of *Elachista fucicola* on the harvested side helps explain the higher epiphyte diversity post-harvest. *Ectocarpus* sp. tends to grow near the top of rockweed fronds, together with *Vertebrata lanosa* (Longtin et al. 2009, personal observation). The absence of *Ectocarpus* sp. on the harvested side post-harvest may be explained by it being bycatch of the harvest, given how high up on the *Ascophyllum* frond it attaches. *E. fucicola*, on the other hand, has a tendency to attach to lower portions of the frond than *Ectocarpus* sp. (Longtin et al. 2009). The higher percent cover of *Elachista* sp. on the harvested side post-harvest could be due to faster growth once *Ectocarpus* sp. was removed.

Regarding benthic sessile species, the lower cover of *Hildenbrandia rubra* on the harvested side post-harvest explains the reversal of trends seen in sessile (and benthic sessile alone) species richness and diversity. *Hildenbrandia* spp. have very slow growth rates and low metabolic demands and, therefore, do well in the light-limited understory of macroalgal canopies (Dethier and Steneck 2001, Kwang and Garbary 2006). However, their slow growth rate makes them poor competitors and it is possible that harvesting opened up the canopy enough to favour other species helping explain the lower abundance of *H. rubra* on the harvested side post-harvest (Cervin et al. 2004).

The marked lower richness, diversity and abundance of mobile (quadrat) species on both sides of the bed post-harvest are largely attributable to the storminess of the post-harvest sampling day. However, all three metrics were lower on the unharvested side pre-harvest and this trend was reversed post-harvest (Figures 5, 6). This is primarily explained by the fact that *Littorina littorea* was significantly less abundant in harvested compared to unharvested plots post-harvest. *L. littorea* has been reported as a common bycatch species of the commercial rockweed harvest by a number of sources (McEachreon 1999, Sharp et al. 2006, Ugarte et al. 2010a, Ugarte 2011).

For effects on the associated community, Beal et al. (2011) limited their analysis to the abundance of the most common littorinids seen in the rockweed habitat in question and noted no effect of the rockweed harvest. Similarly, Trott and Larsen (2012) found no effect on the abundance of *Littorina* spp. In addition, these authors did conduct an analysis on community composition and found a shift in the species assemblage with harvesting (see Appendix 3B for details). Yet they did not look at the contribution of sessile (e.g. coverage) species to any element of community composition, which showed some of the most significant effects of harvest in our study. It appears that many standard analyses for assessing immediate effects of harvesting are not capturing the entire associated species community, thereby missing part of the picture. Our approach, which looked at species composition and richness for each community component, may provide a more complete idea of harvesting effects. A further step might be to establish the link between canopy and community structure (see Chapter 2) for both harvested and unharvested treatments.

3.4.2 Broader context of harvesting studies

The majority of harvesting studies to date have not attempted to replicate the intensity or spatial distribution of the commercial hand harvest conducted in Atlantic Canada (see Table 3; Appendix 3B). Higher intensities of harvest and even clear-cutting of plots are more common and the resulting effects on rockweed plants, canopy structure and the associated community are often substantial and long-lasting with recovery requiring several years to decades. Although these studies provide limited insight into the impact of the actual harvest that takes place in Nova Scotia, New Brunswick and Maine, they allow us to locate our results along an impact gradient. The literature shows, as expected, that more intense harvests produce stronger and a greater number of long-lasting effects. Less intense harvests like the commercial harvest in NB and NS often lead to less-pronounced and not always statistically significant effects. Nevertheless, they show the same trends in plant, canopy and community alterations that are seen with more intense harvests.

3.4.3 Challenges in detecting ecosystem effects

3.4.3.i Detecting canopy effects

We encountered a number of difficulties when it came to detecting canopy effects of harvesting at current commercial harvest intensity. Originally, we established our sampling design at six study sites: two in SW Nova Scotia and four in SW New Brunswick. Kelley's Cove, however, was the only site at which we found signs of harvesting (i.e. freshly cut plants) in our quadrats. An examination of the rockweed beds at the level of our sampling transects at the remaining sites did not reveal any harvested patches. We had to search seaward of our transects in order to locate freshly cut plants; generally, harvested sections were not obvious and took time to find. Our transects were laid at the midpoint of the rockweed bed, which is generally the lushest and presumably the most profitable harvesting region. We assumed (based on personal communication with Dr. Raul Ugarte, ASL) that harvesting vessels travelling the length of a rockweed bed would venture into the bed in order to harvest large, visible portions of the bed. Yet based on our experience, harvesters appear to harvest within the lowest third of the rockweed bed.

The patchiness and irregularity of the harvest impedes the detection of its effects on canopy and community structure. While monitoring compliance with regulations in the rockweed harvest from 1996 to 1998, McEachreon (1999) noted that the median number of cut clumps in any sampling quadrat that contained rockweed was zero, with only two exceptions. At Adam's Island, NB, we sampled five quadrats below the level of our transects, for which we targeted patches with signs of harvesting. We observed some patches of plants where only the tips of a few fronds were cut off and others where the entire quarter m^2 was harvested between 8-12 cm of the holdfast. The number of quadrats per transect we used (ten for fauna and flora, five for canopy structure) was selected after consulting species accumulation curves from previous surveys of rockweed beds in the region (Schmidt et al. 2011, A. Schmidt, unpublished data). We considered that ten quadrats per harvesting treatment (five per transect) was sufficient to capture the average canopy structure; however, the challenges we faced with our sampling design suggest that a greater number of quadrats spread out from the middle to the lower end of the bed may be necessary to capture the canopy effects of a irregular and patchy hand-harvest.

Apart from issues arising from the design and execution of this type of work, the absence of real harvest exclusion zones for comparison is highly problematic. Rockweed beds in SW Nova Scotia have some of the highest biomass in the Canadian Maritimes and have been commercially harvested at varying intensities, by hand and mechanically, since the late 1950s. No exclusion zones have been established in this region. While biomass and maximum plant height for a number of locations are available for one time point in the early 1950s (MacFarlene 1952), there has not been a pristine canopy structure against which to compare the ever-changing leased beds. Exclusion zones were established in New Brunswick in the mid-1990s when the hand-harvest expanded there. However, there were clear signs of recent harvesting at the two exclusion zones we visited in New Brunswick (see Chapter 3).

3.4.3.ii Detecting community effects

The absence of exclusion zones is as much an impediment for assessing harvesting impacts on community as it is for detecting effects on canopy. Sites in Nova Scotia have been harvested for more than 50 years and associated species communities have likely adapted and been altered for decades. While we can still detect alterations in community structure immediately after a harvest, we are seeing the difference between a regularly harvested bed and a regularly harvested bed with one additional cut.

Perhaps the greatest challenge we faced when trying to assess the impact of harvesting on the associated community – an issue that holds true at the additional five sites we surveyed – was the marked scarcity of fish (see Chapters 1 and 3). Rockweed beds are known habitat for 34 species of fish and particularly for juvenile fish (Seeley and Schlesinger 2012). Studies by Rangley and Kramer (1995a, 1995b) using both dive surveys and beach seines noted substantial numbers of juvenile pollock in rockweed beds in NB near our sampling sites 20 years ago. However, our dive surveys revealed very low fish counts across sites and the absence of exclusion zones makes it impossible to know whether this is attributable to rockweed harvesting effects, general long-term declines in fish stocks due to overexploitation, or some combination of these factors. Discouragingly, the most abundant and only consistently encountered large mobile species was the invasive green crab *Carcinus maenus*.

3.4.4 Conclusions and Management Implications

Given that the commercial harvest in NS and NB show less-pronounced, but nonetheless similar trends in plant, canopy and community changes that are seen with more intense harvests and that harvests occur on an annual basis in NS and NB, these lower intensity harvests have likely already altered rockweed habitats in the long-term. Without exclusion zones, these long-term effects cannot be resolved. Although exclusion zones were included in the regulation of rockweed harvesting in NB when it began in the mid-1990's, these zones are being poached (see Chapter 4), although hopefully at a lower harvesting intensity than the surrounding beds. Clearly, stronger enforcement is needed to protect harvest exclusion zones which would provide managers and scientists with proper reference sites (DFO 2013).

Monitoring of the effects on canopy by industry and government continues to focus on biomass, which is the least significant and most variable (high error bars) of the measures we investigated for canopy structure (also see Chapter 1). Instead, the use of plant length and circumference would help in identifying subtler changes in canopy structure.

Many of the high impact harvesting studies were conducted when more intense harvesting practices were typical or were being suggested for previously hand-exploited or non-exploited areas (e.g. Walker 1948, Printz 1956, Keser et al. 1981, Keser and Larson 1984, Black and Miller 1986, 1991, Vadas and Wright 1986). These studies allowed for the recognition of the many potential negative effects of high impact harvesting and have supported the implementation of harvesting regulations such as those used in Canada and the USA (DFO 2013, DMR 2013). However, while there has been broad agreement that regulations are necessary, the restrictions on cutting height, intensity and schedule/rate of exploitation are largely extrapolations from studies or practices of overexploitation for acceptable levels of disruption; what's more, the regulations are usually watered-down versions of these scientifically-based recommendations. For example, according to Baardseth (1955), Baardseth (1970), Keser et al., 1981 and Tyler (1994), plants cut between 10 to 20 cm should be left 3-6 years to recover before the subsequent harvest yet it is common practice to harvest the same bed on a yearly or bi-yearly basis. Also, several lines of evidence suggest that recovery of the bed is enhanced if plants are not cut below 25-30 cm, (e.g., Walker 1948, Printz 1956, Keser et al. 1981, Sharp 1987); however, the mandated minimum cutting height in Nova Scotia and New Brunswick remains 12.7 cm with a recommended minimum of 25.4 cm (Seeley and Schlesinger 2012, DFO 2013), while it is 40.6 cm in Maine (DMR 2013).

Industry self-monitoring (e.g. Ugarte et al. 2009, 2010a-b, Ugarte 2011), compliance monitoring by government (e.g. McEachreon 1999) and studies such as Beal et al. (2011), Trott and Larsen (2012), and the present study are among the first to test the effectiveness of the practiced current regulations. Although the results from these three studies vary, we suggest this is largely due to the difficulties associated with monitoring a low-impact harvesting regime in complex and variable natural environments that have been affected and altered by harvesting for a long time. These difficulties are discussed in the following section.

In addition to the direct harvest, rockweed habitats face multiple other human-induced threats, such as sedimentation from land and nearby aquaculture sites that may prevent zygote attachment, and nutrient runoff that could lead to an overgrowth with annual algae (Sharp 1987, Worm and Lotze 2006). Increased storminess and more severe physical disturbance are expected as a result of climate change; this is expected to favour the replacement of *A. nodosum* with *Fucus* spp. patches (Ugarte 2010). Increased sea surface temperatures (SST) are also expected in Eastern Canada as a result of climate change which will decrease rockweed growth if SST exceeds 20°C (Keser et al. 2005, Solomon et al. 2007). These additional stresses will likely persist or increase in the coming decades; thus, rockweed management needs to consider the resilience and persistence of rockweed habitats in addition to providing economic benefit.

Cumulative effects of long-term rockweed (*Ascophyllum nodosum*) harvest and proximity to finfish aquaculture on canopy structure and community composition of rockweed beds in New Brunswick, Canada

4.0 Abstract

Rockweed habitats face multiple human-induced threats including organic loading from nearby finfish aquaculture operations and direct commercial harvesting. However, the impact of culmulative stressors on these habitats remains poorly understood. We surveyed four sites in the Outer Bay of Fundy to evaluate the effects of long-term rockweed harvesting (harvest versus exclusion zones) and finfish aquaculture (presence/absence) in isolation from other land-based human impacts. Minor changes in canopy structure and species assemblage resulted from long-term harvesting alone. Typical signs of low-medium levels of eutrophication, including increased coverage by opportunistic algae and filter feeders, were detected as a result of proximity to aquaculture alone. Finally, significantly smaller *Ascophyllum nodosum* (rockweed) plants and reduced species richness, abundance and diversity resulted from the cumulative impact of harvesting and exposure to finfish aquaculture. The management implication of these findngs for Canada's rockweed harvest is that accommodation should be made for sites with known, pre-existing stressors.

4.1 Introduction

Globally, coastal ecosystems are facing increasing pressure from anthropogenic activities, including nutrient loading, over-harvesting, species invasions, climate change related alterations in water temperature, acidity and storminess, and increased development of shorelines (Lotze et al. 2006, Worm and Lotze 2006, Airoldi and Beck 2007). Moreover, coastal ecosystems are often exposed to multiple concurrent man-made pressures, underscoring the importance of studies that examine the cumulative effects of two or more impacts (Crain et al. 2008). Rockweed (*Ascophyllum nodosum*) beds are a prime example of intertidal ecosystems facing multiple pressures; two significant pressures in southwest New Brunswick are the commercial rockweed harvest and nutrient inputs and organic loading from finfish (mostly salmon) aquaculture operations (Rangeley and Davies 2000, Worm and Lotze 2000, 2006).

Rockweed has been a commercially important seaweed in Atlantic Canada for production of alginates, fertilizer and animal feed for over fifty years (Chopin et al. 1996). Commercial harvest of rockweed in New Brunswick only began in 1995 and has been regulated using a single species management approach since the start (DFO 1998, 2013, Ugarte and Sharp 2001, 2012). Combined landings in Nova Scotia and New Brunswick have increased from about 15,000 metric tonnes in 1996 to over 40,000 metric tonnes in 2011 (Ugarte and Sharp 2012).

While monitoring and research efforts have been made to study the effects of commercial harvesting on rockweed plants themselves, the harvesting effects on habitat function and the associated fauna and flora have received much less attention (DFO 1998, Rangeley and Davies 2000; see Chapter 2 for a more extensive review). Existing studies that have looked at associated species have focused on the effects of canopy clearance (see Thomas 1994, Bertness et al. 1999, Cervin et al. 2004, Jenkins et al. 2004, Ingólfsson and Hawkins 2008, for examples), the effects of high intensity experimental harvests that do not mimic the patchy pattern of the commercial hand-harvest (see Boaden and Dring 1980, Keser et al. 1981, Fegley 2001, Kelly et al. 2001, Guiry and Morrison 2013, for examples), and the effects of the commercial harvest on a limited number of associated species (see Beal et al. 2011), but most lack an understanding of current harvest impacts on the associated species community as a whole (Rangeley and Davies 2000, Seeley and Schlesinger 2012). While management plans restrict the amount of biomass landed and the minimum cutting height of plants, and industry monitors the biomass of rockweed beds, this alone is insufficient to meet the existing management goal of an ecosystem-based approach (Ugarte et al. 2006, Ugarte and Sharp 2012, DFO 2013, DMR 2013).

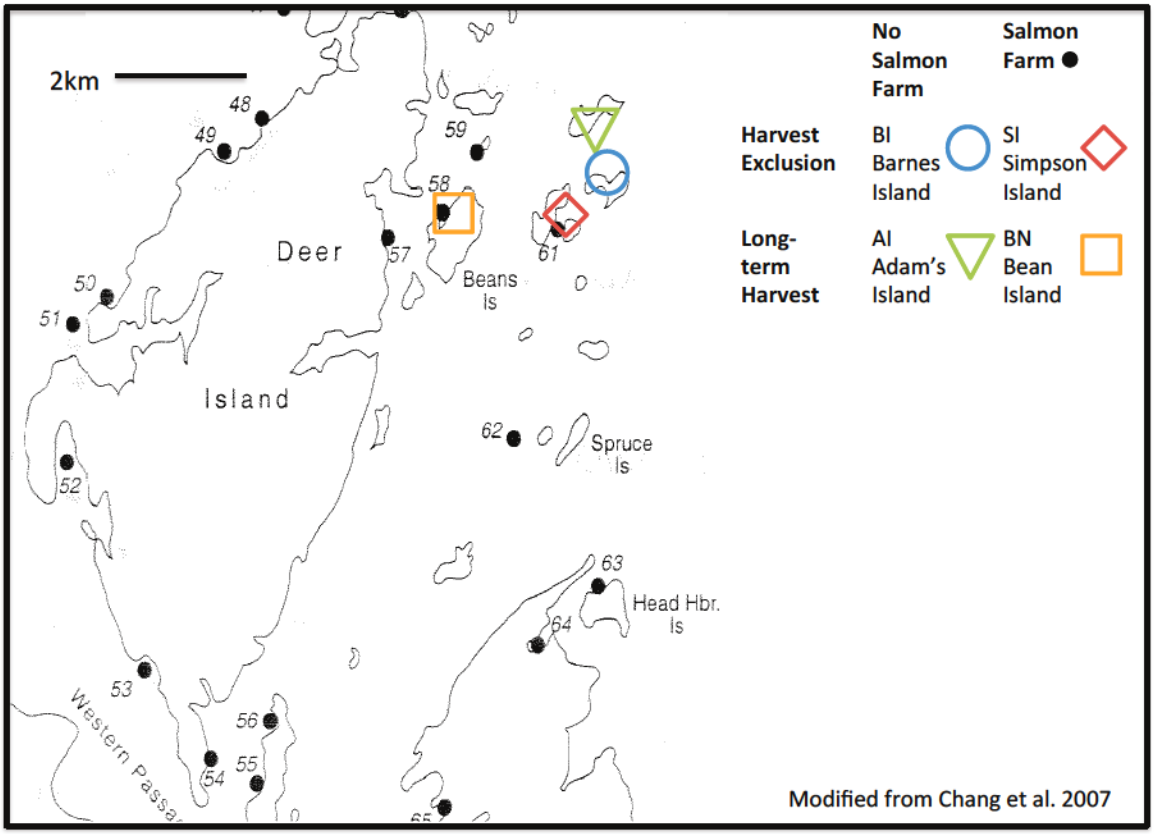
The phenotype of rockweed plants is highly plastic (Sharp 1987, Kerin 1998) and, among a large range of environmental factors, nutrient and organic loading has been shown to affect rockweed's morphology (White et al. 2011). White et al. (2011) found that rockweed near finfish aquaculture sites in Southwest Nova Scotia is larger (more massive) than rockweed at control sites, has a greater number of starting receptacles, greater frond width and greater maximum length of airbladders. These differences were attributed to nutrient enrichment rather than natural environmental differences between the aquaculture and control sites. However, higher nutrient and organic input places rockweed at a disadvantage vis-à-vis faster growing species (Rueness 1973, Kerin 1998, Worm and Lotze 2000, 2006). In the sewage polluted Oslofjord in Norway, rockweed became increasingly less common in the inner fjord and was eventually entirely excluded, possibly because germlings could not compete with the carpet of *Ulva* spp. (Rueness 1973). Severe disturbances of intertidal seaweed communities by point-source (e.g. sewage, fish farms, seafood processing plants) or non-point source (e.g. agricultural run-off) pollution has been shown to reduce species diversity and lead to an increase in opportunistic seaweeds or filter-feeders benefiting from enhanced phytoplankton growth or organic loading (e.g., Littler and Murray 1975, Murray and Littler 1978, Worm and Lotze 2006). However, localized disturbance of intertidal communities has also been shown to cause patches at different stages of succession, which can temporarily increase overall diversity (Sousa 1979).

Although it is well established that both top-down (consumption, exploitation) and bottom-up (nutrient enrichment) effects structure the diversity and functions of coastal ecosystems (Worm et al. 2002), it is less clear how these two opposing factors play out when exploitation directly targets the habitat-building foundation plants. Rockweed habitats face multiple human-induced threats such as sedimentation from land and nearby aquaculture sites that may prevent zygote attachment, nutrient runoff that could lead to an overgrowth of annual algae and direct commercial harvesting The four sites were exposed respectively to (1) no point-source anthropogenic impacts, (2) commercial harvesting only, (3) proximity to fish farm only, and (4) both commercial harvesting and proximity to fish farm. The West Isles in the outer Bay of Fundy provided the necessary conditions for this survey (MacKay et al. 1979, Robinson et al. 1996, Buzeta 2003, Buzeta and Singh 2008). Since the beginning of the commercial rockweed harvest in SW New Brunswick in 1995, certain sites have been reserved as harvest exclusion areas, providing sites that can serve as harvesting controls. In addition, the presence of salmon aquaculture in the region provided easily observable nutrient/organic input sources. The pre-existence of impacted and control sites allowed us to describe the individual and cumulative effects of harvesting and salmon farms both qualitatively and using multivariate statistics. This work constitutes an important baseline study in the context of the proposed continued expansion of both rockweed harvest and finfish aquaculture in Atlantic Canada.

4.2 Methods

4.2.1 Study sites

In July and August of 2012, we performed intensive field surveys at four study sites in the outer Bay of Fundy within the main area of rockweed harvesting in southwest New Brunswick. Two sites, Adam Island (AI) and Bean Island (BN), are subject to a regular commercial rockweed harvest while the remaining two sites, Barnes (BI) and Simpson Island (SI), are established as harvest exclusion or no-take zones (Figure 1, Table 1). Two of the sites, SI and BN, were proximate to salmon aquaculture pens while the other two sites, AI and BI, were not (>1km away). Pens had been installed at BN for two years preceding the summer of 2012; our surveys took place during the fallow year. The fallow year at SI had been 2011 and pens were reinstalled a few months prior to our surveys. We, therefore, had one study site with no human impacts (BI), one that is only regularly harvested (AI), one that is only proximate to salmon aquaculture (SI) and one that is subject to both anthropogenic impacts (BN). While all four islands are uninhabited, a few residential houses can be seen from the study site at BN on nearby Deer Island. These four sites were previously classified in the same geography region (MacKay et al. 1979 a-c), same hydrographic region (Robinson et al. 1996) and as having the same "narrow passage" geomorphology (Buzeta and Singh 2008). All four sites had gravel-boulder sediment. Modeled mid-tide (i.e. fastest) currents around these islands are between 0.4 and 0.75 m s^{-1} (Durand et al. 2008).



Modified from Chang et al. 2007

Figure 1. Map of study sites in southwest New Brunswick (BI = Barnes Island, AI = Adam Island, SI = Simpson Island, BN = Bean Island, • = finfish (mainly salmon) aquaculture leases).

Table 1. Survey sites, ID abbreviation, site coordinates, and human activities conducted at each site.

Location	ID	Coordinates	Human Impact
Adam Island	AI	45° 00' 40.96"N, 66° 54' 23.05"W	Harvest
Barnes Island	BI	45° 00' 21.02"N, 66° 54' 12.57"W	Harvest exclusion
Simpson Island	SI	45° 00' 07.52"N, 66° 54' 27.64"W	Harvest exclusion Aquaculture
Bean Island	BN	45° 00' 00.49"N, 66° 56' 01.38"W	Harvest Aquaculture

4.2.2 Sampling methods

4.2.2.i Environmental parameters

Water temperatures at the study sites were recorded from our dive computers. Seasonal temperature data were also acquired from a nearby monitoring buoy in the Outer Passamaquoddy Bay (DFO Prince 5 Station - data retrieved 2014).

At each site in both July and August, three 1 liter water samples were collected during the incoming tide, at high tide and during the outgoing tide with a pipe-sampler in order to take an average sample for the water column. For each water sample, three replicates were analyzed to quantify chlorophyll *a* (Chl *a*) concentrations and total particulate matter (TPM) at each site. For each Chl *a* replicate, 100 ml of water were filtered through a Whatman GF/F (25mm) filter using a 50 ml syringe and filter holder. The filters were then placed in labeled cryovials and transferred to a liquid nitrogen-cooled Dewar. Filtration occurred in a darkened tent, away from light exposure. In the laboratory, the filters were transferred to vials containing 10 ml of cooled acetone and were stored in the dark at -20°C for 24 hours or more. A Turner fluorometer was used to measure the voltage difference associated with each replicate (as well as an acetone blank). Both the Acidification Technique and the Welschmeyer Technique were used, however, given that the Welschmeyer Technique is more commonly used for seawater samples and that there was not a great difference in the results of the two techniques, results are reported for the Welschmeyer Technique alone.

GF/F filters used for the TPM replicates were initially washed to remove impurities and dried for six hours at 450°C before being weighed (pre-ash weight). Sample water was then filtered using a syringe and filter holder until filtrate just visibly stained the filter after which point the filters were rinsed twice with 5 ml of isotonic (2%) ammonium formate to expel salt. Filters were stored in foil inside cryovials placed in a liquid nitrogen-cooled Dewar while in the field. Filters were then dried at 60°C for 24 hours, reweighed (dry weight), and combusted at 450°C for six hours before the final weighing (combusted weight) to determine % organic content. This will provide a measure of primary productivity, water turbidity and organic content at each site.

4.2.2.ii Rockweed canopy

Four 50 m transect lines were laid out parallel to the shore at low tide. Two sets of transects were laid 4 m apart, 2 m above and 2 m below the approximate center of the bed, with 20-50 m separating the two sets of transects. A weight was attached to each line end to keep it at anchored and a buoy was added to locate the end of the transect at high tide. The maximum transect depth was 1.95 ± 0.25 m at all sites.

Canopy structure measurements were taken at the daytime low tide; along each transect, we sampled five 50 x 50 cm quadrats placed every 10 m. For each quadrat, the number of rockweed plants (i.e. fronds belonging to a common holdfast, sometimes called clumps) was counted. Since multiple fronds can emerge from each holdfast, we counted plants as separate when holdfasts had at least 0.5 cm distance from each other (or a finger's width). These rockweed plants were then measured for their maximum length and maximum circumference with a measuring tape, and were weighed (wet weight) on a portable field scale. Whereas small plants were directly placed on the scale, larger plants were placed in a scale-zeroed bucket that had a slit cut down one side as described by Ugarte et al. (2006).

We also collected five tissue samples per site from the tips of haphazardly selected rockweed plants situated below or above the transects to gain insight into the nutrient status of the plants and their environment. We removed the tips from the apex of the frond, near which there was generally a newly forming vesicle evident, down to the penultimate vesicle; these tips reflected the previous year's growth. These were dried for 48 hours at 80°C, ground to a powder and analyzed for tissue CN content at the University of California Davis Stable Isotope Facility.

4.2.2.iii Associated communities

At high tide, two surveyors swam parallel along the 50 m transect lines and recorded the species name, size, and abundance of all fish and mobile macrofauna observed within 1 m of each side of the transect (100 m^2 surveyed area for each transect). Fish counts took place during both day and night high tides.

The same transects were used to survey benthic and epiphytic invertebrates and algae during the daytime high tide. Ten 50 x 50 cm (0.25 m^2) quadrats were placed along each transect at 5 m intervals and all mobile and sessile macrofaunal invertebrate species were identified and counted. Sizes of larger, commercially important crustaceans (i.e. crabs) and fish were recorded. We also estimated the percent cover of benthic and epiphytic algae and encrusting invertebrates.

4.2.3 Data analysis

4.2.3.i Environmental parameters

To determine whether there were significant differences in the environmental parameters Chl *a*, TPM, and % organic content between sites and between sampling months we conducted repeated measures multivariate permutational analysis of variances (perMANOVAs) using PRIMER (version 6.1.11) with PERMANOVA+ (version 1.0.1, PRIMER-E, Plymouth) (Anderson et al. 2008). We also used permutational analysis of variance (perANOVAs) to assess whether there is a site or month effect on each of these parameters individually. Percent nitrogen (%N) content of rockweed tissue and isotope δ15N and δ13C signatures where also available for August alone; we conducted one-factor perANOVAs to look for significant differences in these variable among sites.

Centroids (i.e. arithmetic means) for the environmental variables at each site were computed and cluster analysis performed for the centroids using group averages. An MDS plot displaying the centroids and overlaid with Euclidean distances from the cluster analysis was produced. Average values for % tissue N, δ15N and δ13C were also calculated.

4.2.4.ii Rockweed canopy

Average values for individual plant length, circumference, and mass as well as for

for plant density (m^{-2}) and biomass (m^{-2}) were calculated for each site. Several combinations of these plant and canopy parameters were used to assess differences in plant and canopy structure between sites. Because they had >0.8 correlation, plant mass and circumference were never both included at the same time. Differences between sites were similar regardless of the combination chosen as a measure of canopy structure, indicating robustness of the results. Given, however, that site explained the most variation (13%) for the combination {L, C, D}, methods and results related to canopy structure are described for this combination.

To determine whether there were significant differences in both plant structure {L,C} and canopy structure {L, C, D} between sites and between sampling months we conducted repeated measures perMANOVAs. We also used permutational analysis of variance (perANOVAs) to assess whether there is a site and time effect on each of quadrat biomass, quadrat density, plant length, mass, and circumference individually. In PERMANOVA+, a partly-nested model is used to analyse repeated measures data; we established 'site' as a fixed factor and 'quadrat' as a random factor nested within 'site' and fully crossed with the fixed factor 'month'. All morphometric variables were normalized prior to computation of Euclidean distance-based similarity matrices. Transect location was found to be insignificant in initial exploratory four-factorial perMANOVAs with site, quadrat, location and month, therefore, quadrats from high and low transects were subsequently pooled by site. Given that site was found to have a significant effect, we also performed post-hoc pairwise tests to determine which sites were significantly different in July and in August.

In order to improve visualization of data and corroborate perMANOVA results, centroids for the canopy structure at each site were computed and cluster analysis performed for the centroids using group averages. An MDS plot displaying the centroids and overlaid with Euclidean distances from the cluster analysis was produced.

4.2.3.iii Associated community components

We analysed three separate components of the community: count species and mobile macrofauna seen within the quadrats (abundance m^{-2}), mobile macrofauna counted along the transects (abundance m^{-2}), and sessile fauna and flora seen within quadrats (% cover). Additionally, the sessile species were further divided and analysed as benthic and epiphytic assemblages. We first calculated average abundance or % cover of individual species (m^{-2}), average diversity (Shannon index) of species (m^{-2}), and average richness of species (m^{-2}). To determine which species contribute most consistently to site differences, similarity percentages (SIMPER) analysis was performed on each community component (Anderson et al. 2008).

PerMANOVAs were used to assess the effects of site and month on each component of the community. Community composition data for each component was square-root transformed in order to down-weight the influence of abundant species and allow for a contribution to the resemblance matrix from rarer species (Anderson et al. 2008). The resemblance matrices were based on Bray-Curtis similarities and dummy variables (value = 1) were added before computation of similarities in order to zero-adjust the coefficients. Where site and month were found to have significant effects, we also performed post-hoc pairwise tests to determine which sites were significantly different from one another in a given month and which sites changes between months.

To visualize the data and corroborate perMANOVA results, centroids were computed for each community component and group average cluster analysis performed for the centroids.

4.2.3.iv Linking environmental parameters to community composition

The Envfit() function in R's Vegan package was used to explore (1) associations between the environmental variables (TPM, % organic content of TPM, Chl *a*) and canopy structure {L, C, D} as well as associations between (2) environmental variable and canopy structure (predictor variables) and composition of sessile species, quadrat count species, and transect count species (response variables). Envfit() determines the linear correlation between, in this instance, the environmental and canopy parameters and the nMDS ordination of the community component of interest. Average values of environmental variable were calculated for each site. For each site, five averages were computed for canopy variables by averaging the corresponding quadrats along each transect (i.e., quadrats positioned at 5 meters along each transect were averaged together). When all forty quadrats per site were used for species composition, patterns were lost in the noise of variability seen at each site. Therefore, for each site, we averaged the corresponding quadrats on all four transects to compute ten averaged samples that were not from spatially clustered quadrats. Analysis was performed separately for July and August.

4.3 Results

Plant and canopy metrics, species richness, abundance, diversity, and community composition were examined for July and August and using repeated measures perANOVA or perMANOVA. Patterns of species abundances (as well other patterns) across the four study sites were often similar for July and August. Given that this was the case, and that we were more interested in the effects of long-term harvest exclusion and proximity to aquaculture, patterns are sometimes described for July only. Where patterns deviate notably between the two months, both are described. When not included in the Results section, figures showing patterns for August are included in Appendix A.

4.3.1 Environmental parameters

Temperature readings from our dive computers at our sites in both July (12 ± 1°C) and August (13 ± 1°C) were consistent with summer values for the region recorded over the previous decade (DFO Prince 5 Station). Temperature differences between sites were negligible.

Chlorophyll *a* (Chl *a*) concentrations in July and August across sites ranged between 0.82 and 2.05 $\mu g\ l^{-1}$ (Figure 2A). At SI and BN, Chl *a* concentrations were significantly higher in August than in July (SI $t = 3.007$, $p = 0.010$; BN $t = 4.468$, $p = 0.001$) and nearing significantly higher at AI, suggesting a mid-summer bloom (Figure 2A). While Chl *a* concentrations were comparable across the four sites in July, concentrations at BI were significantly lower than the remaining sites in August (BI-AI $t = 2.566$, $p = 0.007$; BI-BN $t = 3.804$, $p = 0.002$; BI-SI $t = 2.796$, $p = 0.016$). Total particulate matter (TPM) on the other hand, was significantly higher in July than in

August at all sites except BN (AI t = 2.460, p = 0.011; BI t = 1.999, p = 0.043; SI t = 3.322, p = 0.003) (Figure 2B). There were no significant differences in TPM among sites in either July or August. % Organic content of the TPM was also significantly higher in July for BI, AI, and bordering on significant for BN (AI t = 3.506, p = 0.006; BI t = 4.905, p = 0.001; BN t = 2.084, p = 0.057) (Figure 2C). While % organic content was significantly lower at SI than the remaining sites in July (SI-AI t = 3.494, p = 0.006; SI-BI t = 3.784, p = 0.004; SI-BN t = 3.217, p = 0.009), it also had the highest % organic content, though non-significantly, in August. Apical tissue samples collected in August from BI and AI had non-significantly higher % tissue N than samples from SI and BN (Figure 2D).

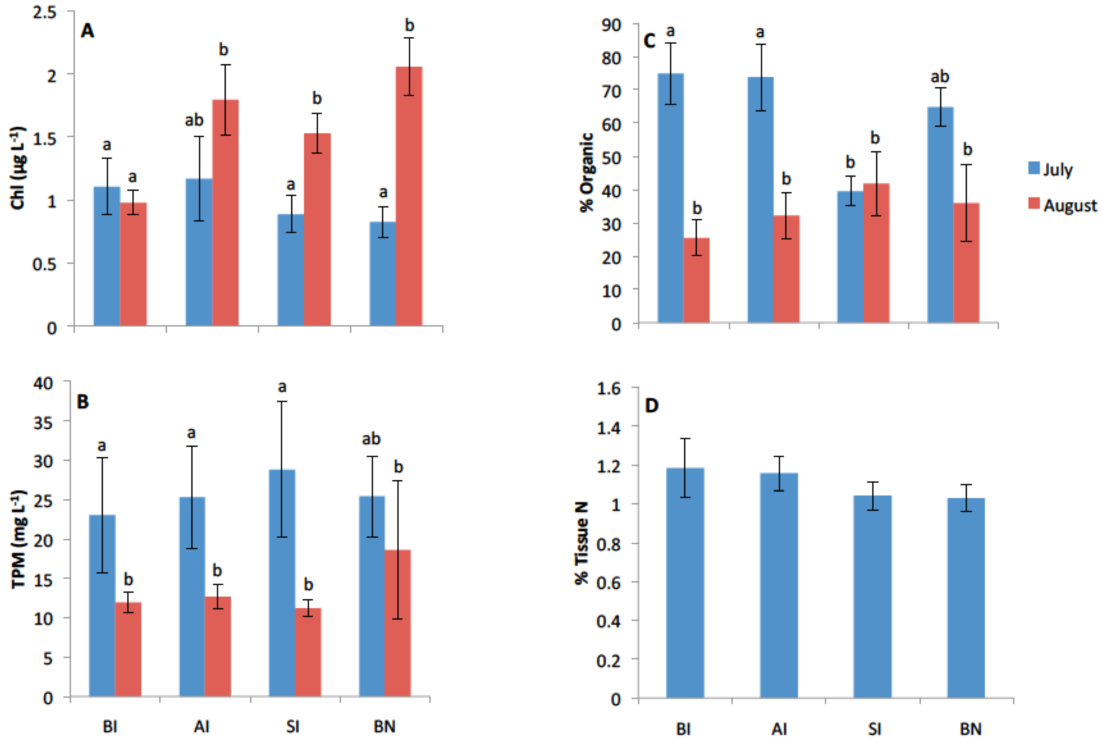


Figure 2. (A) Average chlorophyll *a* (µg L^{-1}) values for July (n=9) and August (n=9), (B) average total particulate matter (TPM), (C) average percent organic matter of TPM, and average rockweed % tissue nitrogen for August (n = 5) with SE for all four study sites. Lower case letters indicate significant differences between site within month as well as within site differences across months.

PerMANOVAs revealed significant differences in multivariate combinations of environmental parameters (Chl *a*, TPM, % organic content of TPM) between sites and within sites across time. In July, SI and AI were marginally non-significantly different (t = 1.694, p = 0.051), while in August, BI differed from all other sites (BI-AI t = 2.133, p = 0.004; BI-BN t = 2.408, p = 0.0001; BI-SI t = 1.970, p = 0.022). All sites differed significantly between July and August (AI t = 2.536, p = 0.004; BI t = 2.923, p = 0.002; BN t = 2.566, p = 0.002; SI t = 1.946, p = 0.012). The MDS plots for the environmental parameters support the presence of these differences (Figure 3).

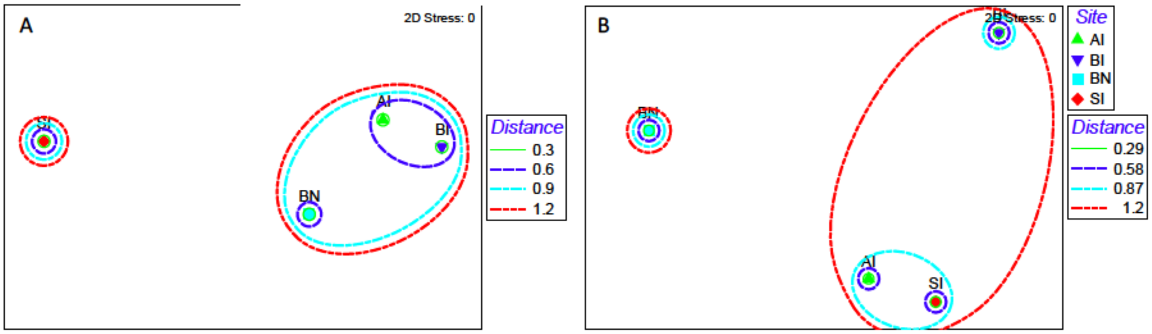


Figure 3. Multidimentsional scaling (MDS) plots showing centroids for similarities matrices using Euclidean distances for environmental parameters (Chl *a*, TPM, % organic content of TPM) for (A) July (n=9) and (B) August (n=9) at each of the four study sites. The solid and broken lines encircling the sites indicate Euclidean distances that were derived from a cluster analysis also conducted on centroids of canopy structure. These lines help quantify the relatedness of the structure across sites.

4.3.2 Rockweed structure

Plants were significantly longer (L) at BI, AI and SI than at BN in both July and August (Figure 4A); plant length at AI was also longer than at SI in July. Plants at BI had significantly greater circumference (C) than at AI in July and non-significantly greater circumference than plants at SI and BN in July (Figure 4B). Plants at BI had also significantly more mass (M) than at SI and non-significantly more mass than at AI or BN in July (Figure 4C). Similar, but non-significant patterns were seen for C and M in August. In July, the density (D) of plants was also significantly lower at BI than at either AI or SI and non-significantly lower than at BN. Recorded density of plants in August was unexpectedly high for BI altering the pattern seen in July. This, however, this was due to the fact that two quadrats fell on very dense patches (Figure 4D). In both July and August, biomass (B) at BN was significantly lower at BN than at all remaining sites (Figure 4E). B was non-significantly higher at all sites in August than in July.

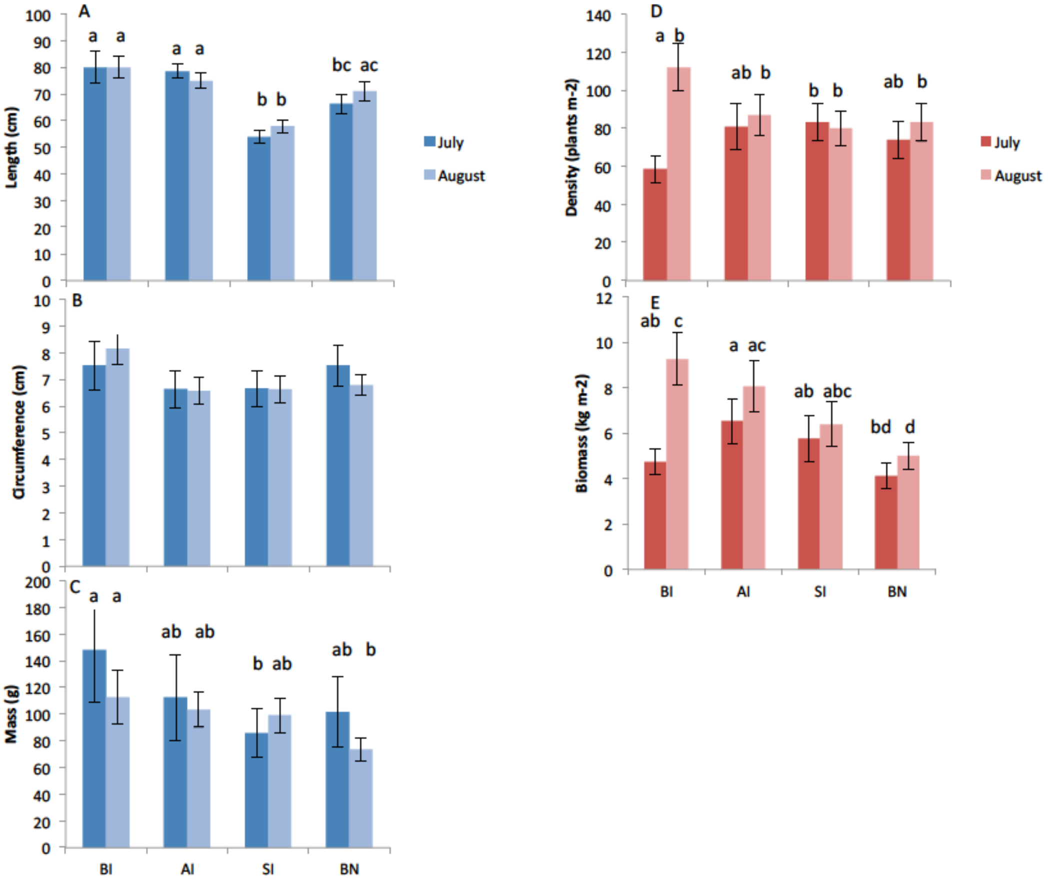


Figure 4. Averages and standard errors (SE, n = 20) for rockweed plant and canopy parameters for July and August: (A) plant length (cm), (B) plant circumference (cm), (C) plant mass (g), (D) density (plants m^{-2}), and (E) biomass (kg m^{-2}) across all four study sites. Lower case letters indicate significant differences between site within month as well as within site differences across months.

In July and August, there was a clear difference in plant structure {L, C} between the aquaculture-exposed site SI and BN and the more distant sites BI and AI (Figure 5, Table 2, Appendix 4B Tables 1 and 2 for post-hoc comparisons). Additionally, plant structure at SI and BN differed significantly in both months (Appendix 4B Tables 1, 2). Canopy structure {L, C, D} at BN was once again significantly different from the structure at all other sites in July and from AI and BI in August (Appendix 4B Table 1).

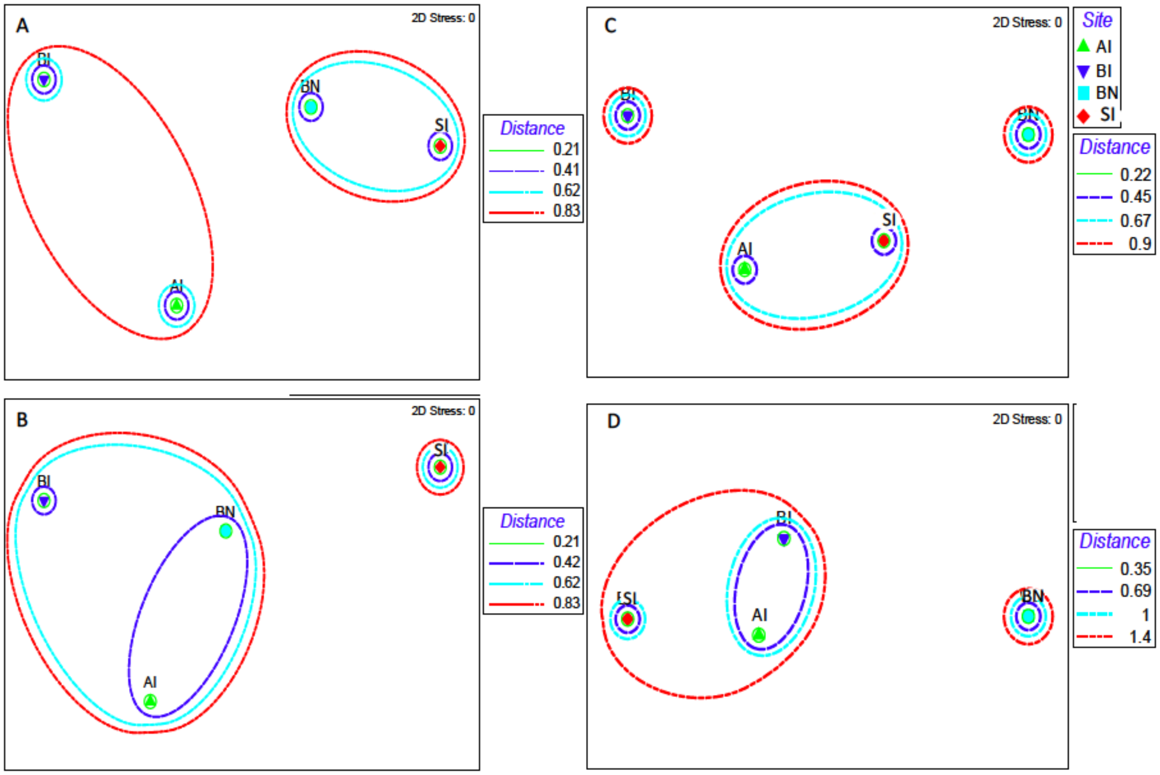


Figure 5. Multidimentsional scaling (MDS) plots showing centroids for similarities matrices using Euclidean distances for plant structure {L, C} in (A) July (n=20) and (B) August (n=20) and plant canopy {L, C, D} in (C) July (n=20) and (D) August (n=20) at each of the four study sites. The solid and broken lines encircling the sites indicate Euclidean distances that were derived from a cluster analysis also conducted on centroids of canopy structure. These lines help quantify the relatedness of the structure across sites.

Table 2. Repeated measures perMANOVA results for the effect of Site and Month on plant structure {L,C} and canopy structure {L,C,D}. Sqrt-V values are unbiased estimates of the contribution to variance of Site, Month, their interaction and the residuals in the model. Variance explained (Var) is given by [(SS Factor/SS Total) x 100] and, while more biased than sqrt-V, is included because it is a more intuitive measure of relative effect size (Howell 2002). The degrees of freedom (df) total to 159. See Appendix B for perANOVA output for post hoc pairwise comparisons between (1) pairs of sites with a month and (2) July and August values for a site. Significant p-values are shown in bold.

		Between subjects		***Within subjects***		
	Source	**Site**	**Res**	**Month**	**Si x Mo**	**Res**
	Df	**3**	**76**	**1**	**3**	**76**
Plant	**Pseudo-F**	12.753		10.560	4.437	
structure	**P**	**0.0001**		**0.0001**	**0.0001**	
{L,C}	**sqrt-V**	0.789	-0.343	0.530	0.636	1.534
	Var	17	33.7	5.2	6.6	37.5
Canopy	**Pseudo-F**	6.400		0.268	0.326	
structure	**P**	**0.0002**		0.816	0.947	
{L, C, D}	**sqrt-V**	0.621	0.323	-0.156	-0.299	1.628
	Var	11.5	45.6	0.2	0.5	42.2

4.3.3 Associated species richness, abundance and diversity

Total species richness (all community components) by site was similar at BI, AI and SI (23, 24 and 25 species respectively), but lower at BN (15 species). This difference is mainly accounted for by the lower number of mobile and other count species observed in the quadrats (7, 9, 10, and 3 species respectively). There were 13 sessile species at each of BI, AI and SI and 10 sessile species at BN. Average richness for sessile quadrat species did not differ significantly among sites in July; in August, however, sessile species richness was significantly higher at AI and BI than at SI or BN (Figure 6A, Appendix B Tables 5, 6 and 7). Average richness of quadrat count species is significantly higher at all sites than at BN in both months as well as being higher at BI than SI in July (Figure 7A, Appendix B). Low abundances of mobile transect species decrease confidence in the significant differences observed between sites, however, richness in

August appears to be significantly lower at SI than all other sites as well as lower at BN than BI (Figure 8A, Appendix B).

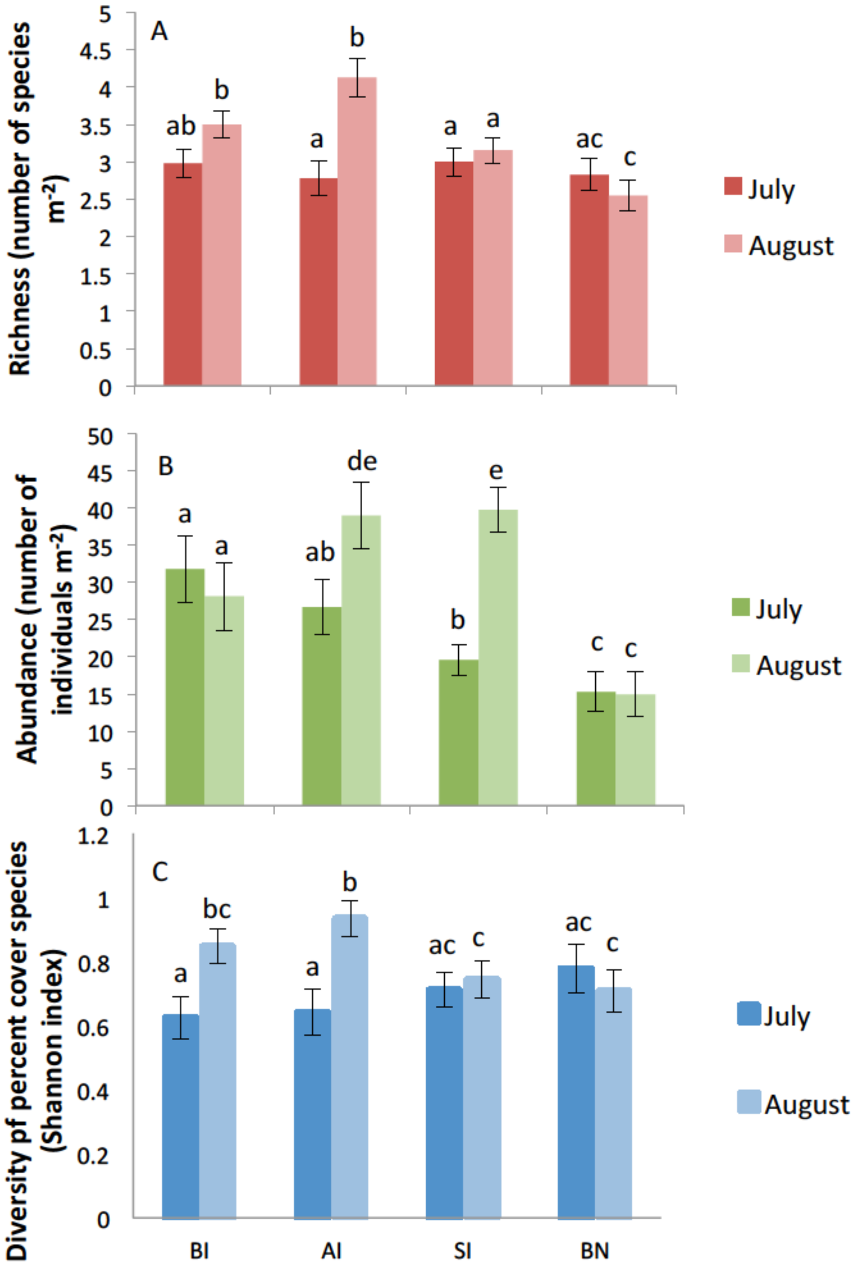


Figure 6. (A) Average richness m^{-2} and standard error (SE, n= 40), (B) average percent cover and SE (n = 40) and (C) average diversity and SE (n=40) of sessile species at all four sites in July and August. Lower case letters indicate significant differences between site within month as well as within site differences across months.

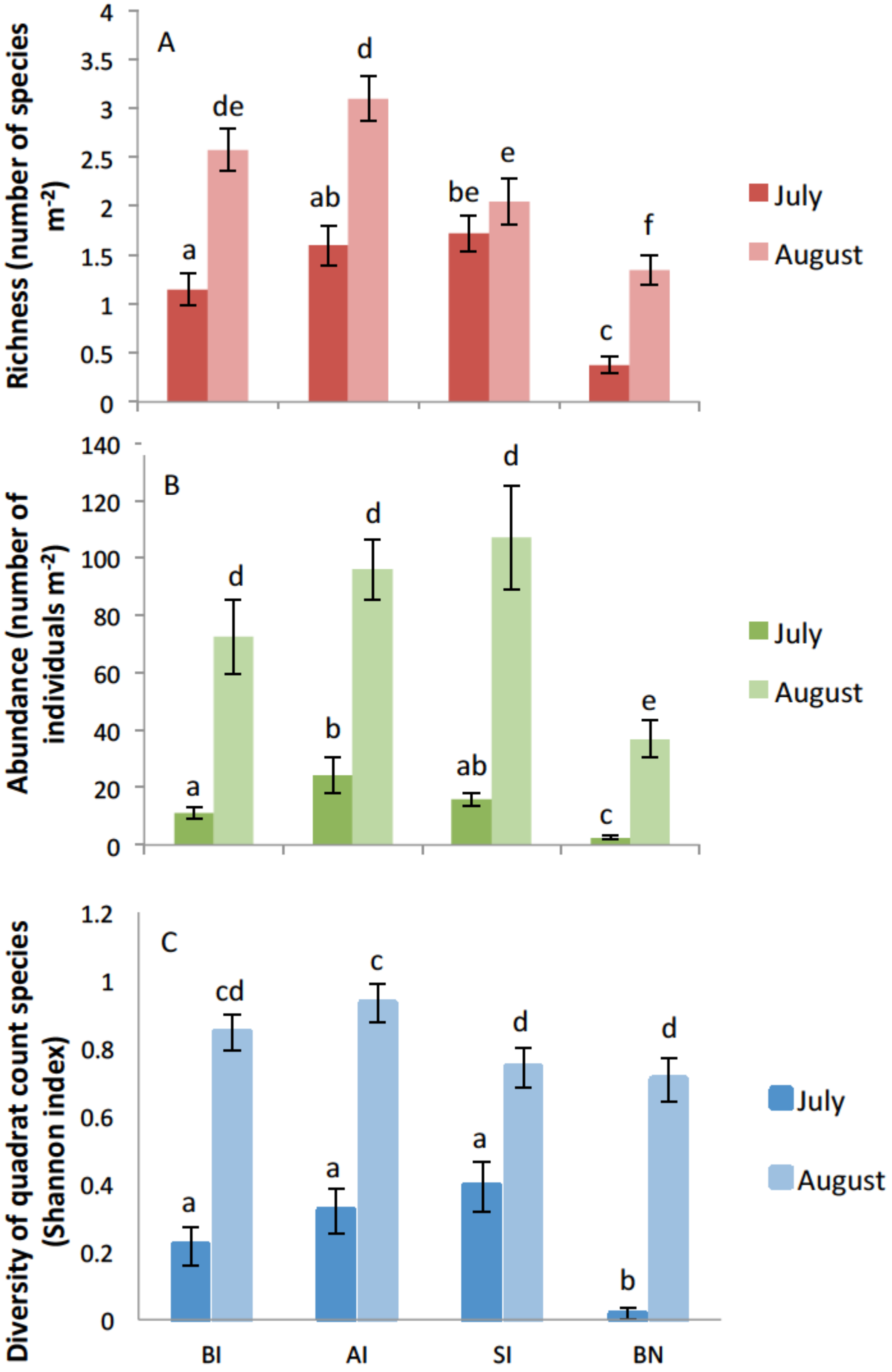


Figure 7. (A) Average richness m^{-2} and standard error (SE, n= 40), (B) average abundance and SE (n = 40) and (C) average diversity and SE (n=40) of count (quadrat) species at all four sites in July and August. Lower case letters indicate significant differences between site within month as well as within site differences across month.

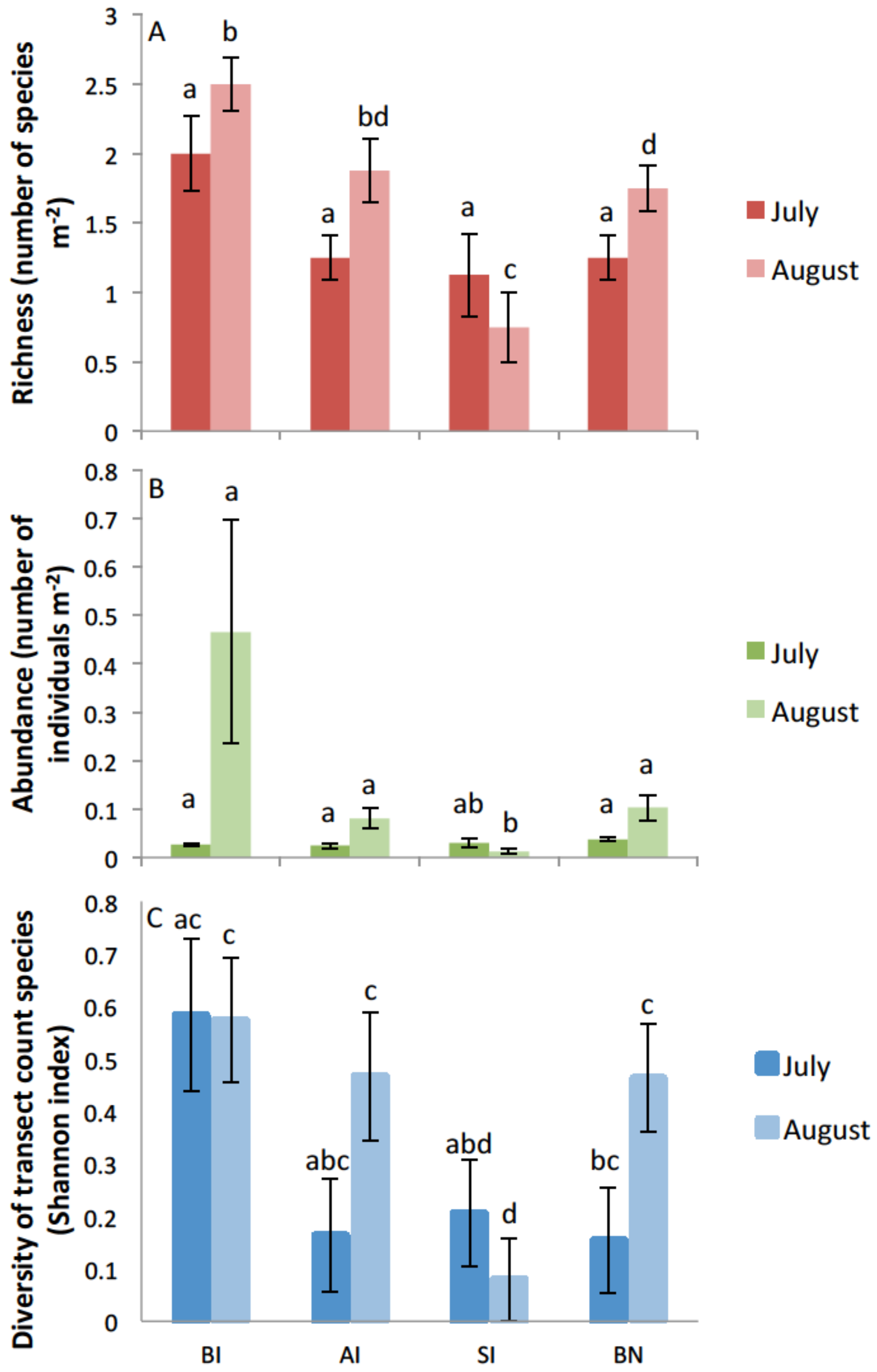


Figure 8. (A) Average richness m^{-2} and standard error (SE, n= 40), (B) average abundance and SE (n = 40) and (C) average diversity and SE (n=40) of mobile (transect) species at all four sites in July and August. Lower case letters indicate significant differences between site within month as well as within site differences across month.

Patterns in average species abundances across the four sites were more varied. In July, sessile species cover was significantly higher at BI and AI than at BN and higher at

BI than S. In August, species cover at SI was also higher than at BN and even became significantly higher than at BI (Figure 6B, Appendix B Tables 8, 9, 10). This switch in pattern was due to increased loads of annual red, green and brown algae and epiphytic filter feeders (hydroids) at SI in August (Figure 9, 10, Appendix A Figures 1-4). Differences in % cover between BN and other sites were largely driven by the % cover of *Hildenbrandia rubra*. Significantly highest cover of *H. rubra* was present at BI and significantly lowest at BN in July (Figure 9A) and remained significantly lower at BN in August (Appendix 4A Figure 1B). In addition, there was significantly more *Chondrus crispus* in the understory at BI and AI than SI or BN in August (Appendix 4A Figure 1B) as well as non-significantly more red foliose algae at AI (Figure 9A, Appendix 4A Figure 1B). Percent cover of filamentous and foliose green algae was highest at BN and lowest at BI in both July and August (Figure 9C); the difference between BI and BN was significant in August (Appendix 4A Figure 3B). Percent cover of the ephemeral algae *Ulva* spp. was significantlyhigher at AI than at BI in July (Figure 9C) and significantly higher at BN than at BI in August (Appendix 4A Figure 3B). There was most cover of *Fucus* spp. at BN in both July and August (Appendix 4A Figure 2B), but in July, the difference was only significant compared to BI and SI (Figure 9B). Epiphytic brown algae cover, driven by cover of *Elachistica fucicola*, was significantly lower at BN than at SI in July (Figure 9B) and significantly lower at BN than all other sites in August (Appendix 4A Figure 2). Cover of epiphytic filter feeders was significantly higher at BI, AI and SI than at BN in July (Figure 9D); the pattern of relative abundance was similar in August when cover at AI and SI became significantly higher than BI in addition to BN (Appendix 4A Figure 4B).

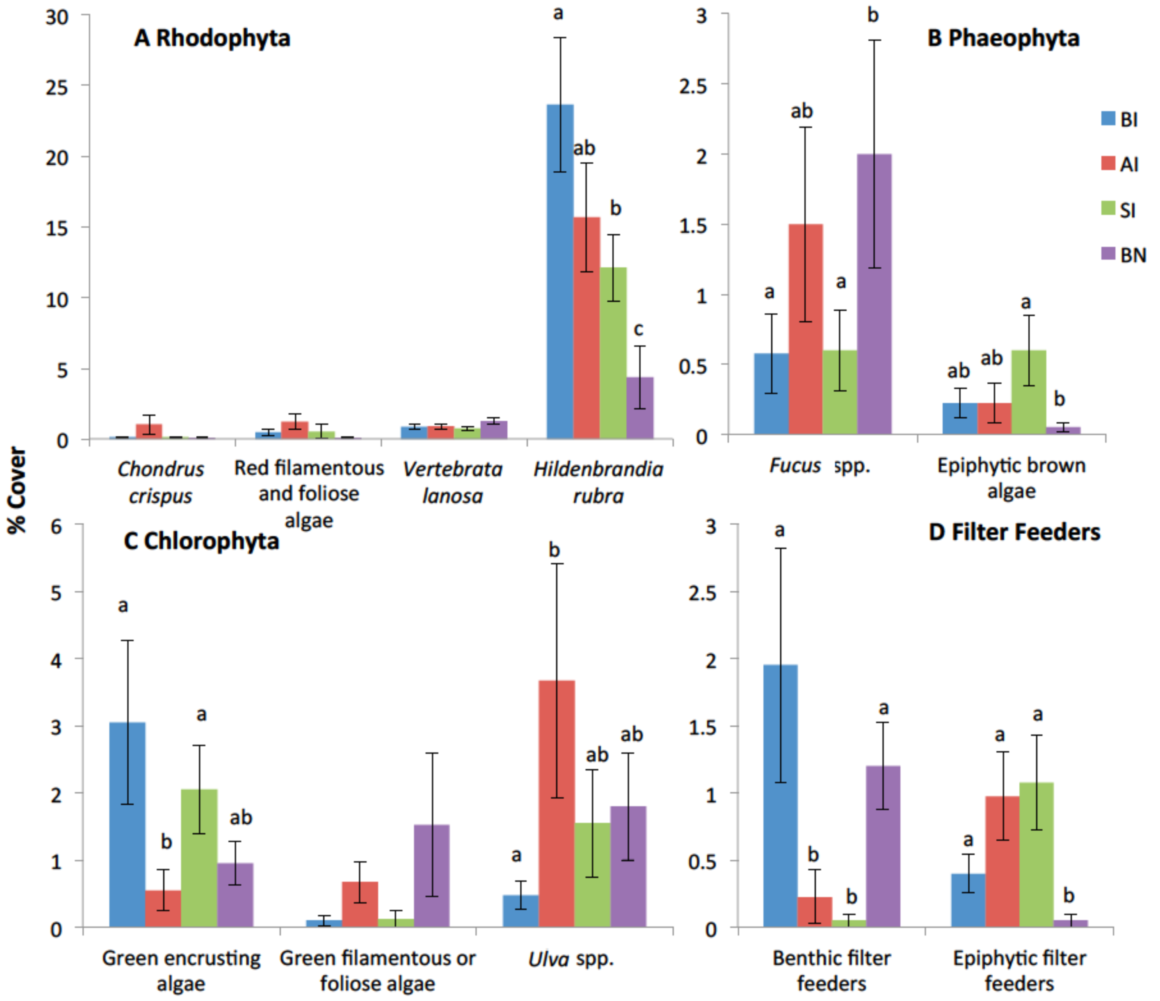


Figure 9. Average coverage (% cover) and standard error (SE, n = 40) of select sessile species or groups of sessile species for July: (A) rhodophyta, (B) phaeophyta, (C) chlorophyta and (D) filter feeders. Lower case letters indicate significant differences between sites. See Appendix 4A for patterns in August.

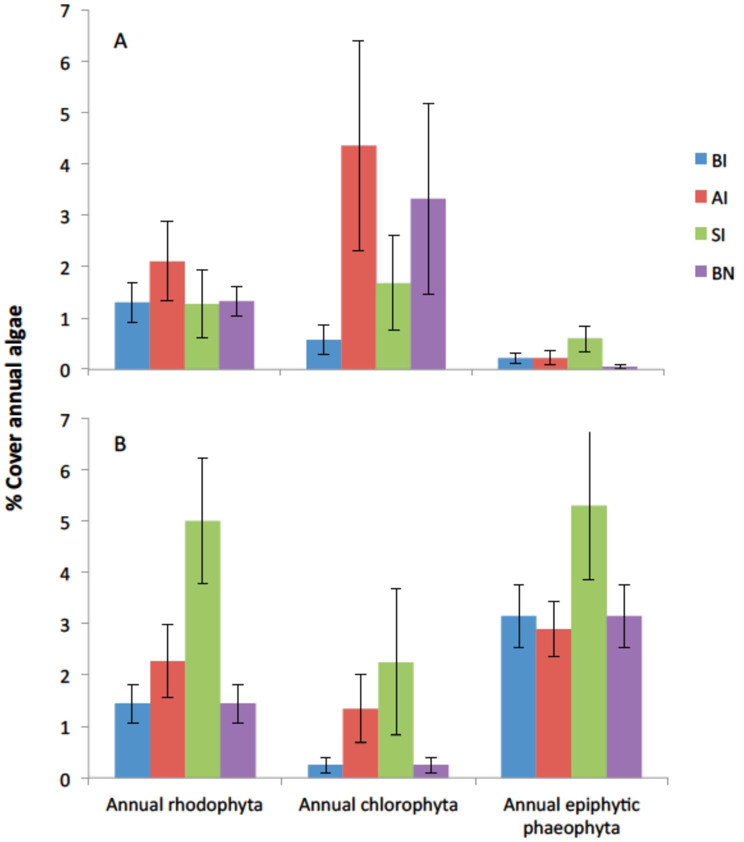


Figure 10. Average coverage (% cover) and standard error (SE, n = 40) of annual rhodophyta, annual chlorophyta and annual epiphytic phaeophyta for (A) July and (B) August. Significant differences between sites are not indicated.

For mobile and count quadrat fauna, abundances at all sites were significantly higher in August (Figure 7B, Figure 11, Appendix B), yet abundance at BN was significantly lower than at the remaining three sites in both months (Appendix B Table 9). Littorinids were the dominant species in July and maintained their levels of abundance in August (Figure 11). *Littorina littorea* and *L. saxitilis* were most abundant at AI, followed by SI and BI, while *L. obtusata* was most abundant at SI (Appendix 4A Figure 5). The appearance of juvenile *Margarites* sp. (snails) in August accounts for the significant increase in abundance.

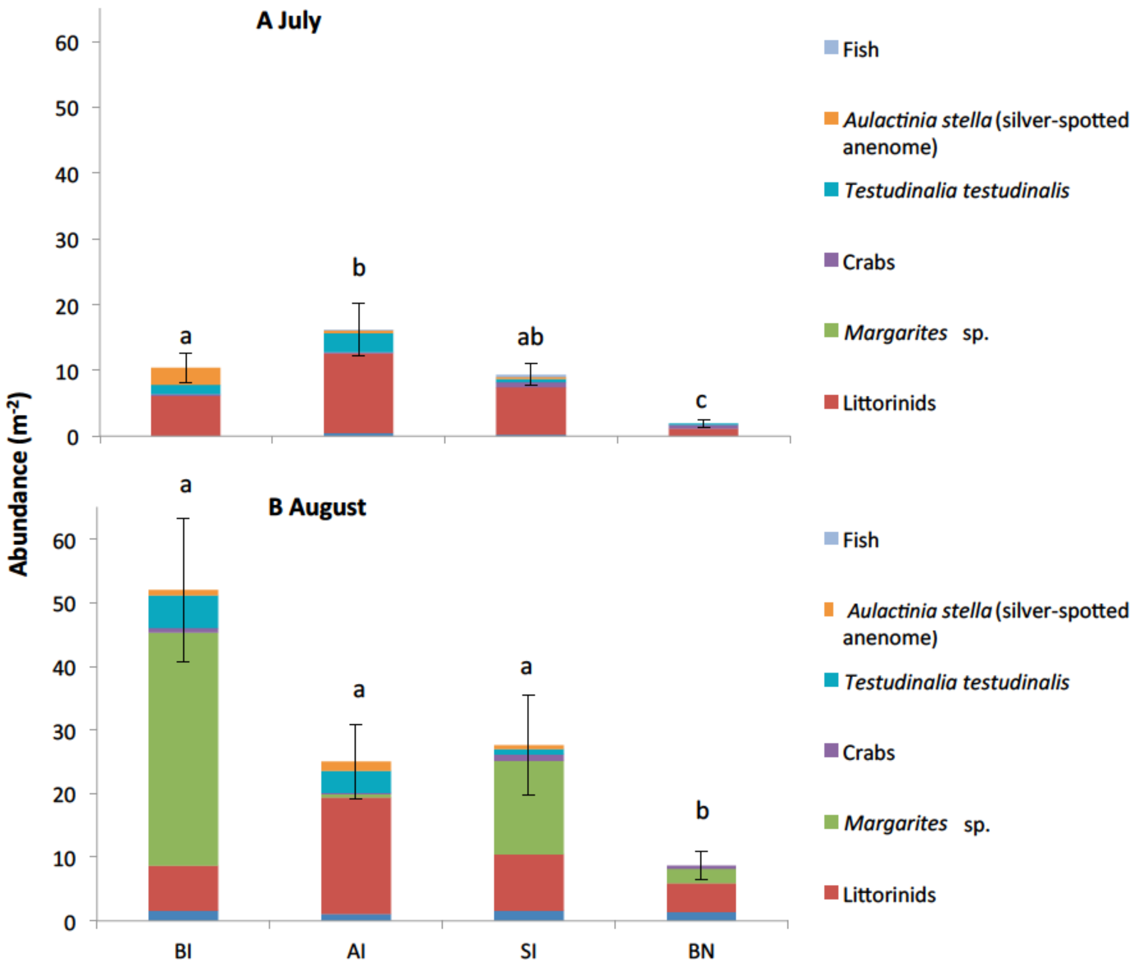


Figure 11. Average abundance and standard error (SE, n = 40) of count (quadrat) species for (A) July and (B) August. Lower case letters indicate significant differences between site within month as well as within site differences across month.

Total abundance of mobile transect species did not differ between sites in July, but was significantly higher at BI than at SI and BN in August and abundance was higher at AI than at BN (Figure 8B, Figure 12, Appendix B Table 9). Large numbers of *Carcinus maenus* were seen at SI and BN in July. Ctenophores (*Pleurobrachia pileus* and a species of large - average length 10 cm - unidentified ctenophore) were present (in blooms) in July, but were rarely seen in August. Fish abundances were low at all sites in

July. A school of >130 juvenile alewife (*Alosa pseudoharengus*) was seen at BI in August and this represented the only deviation from very low transect abundances.

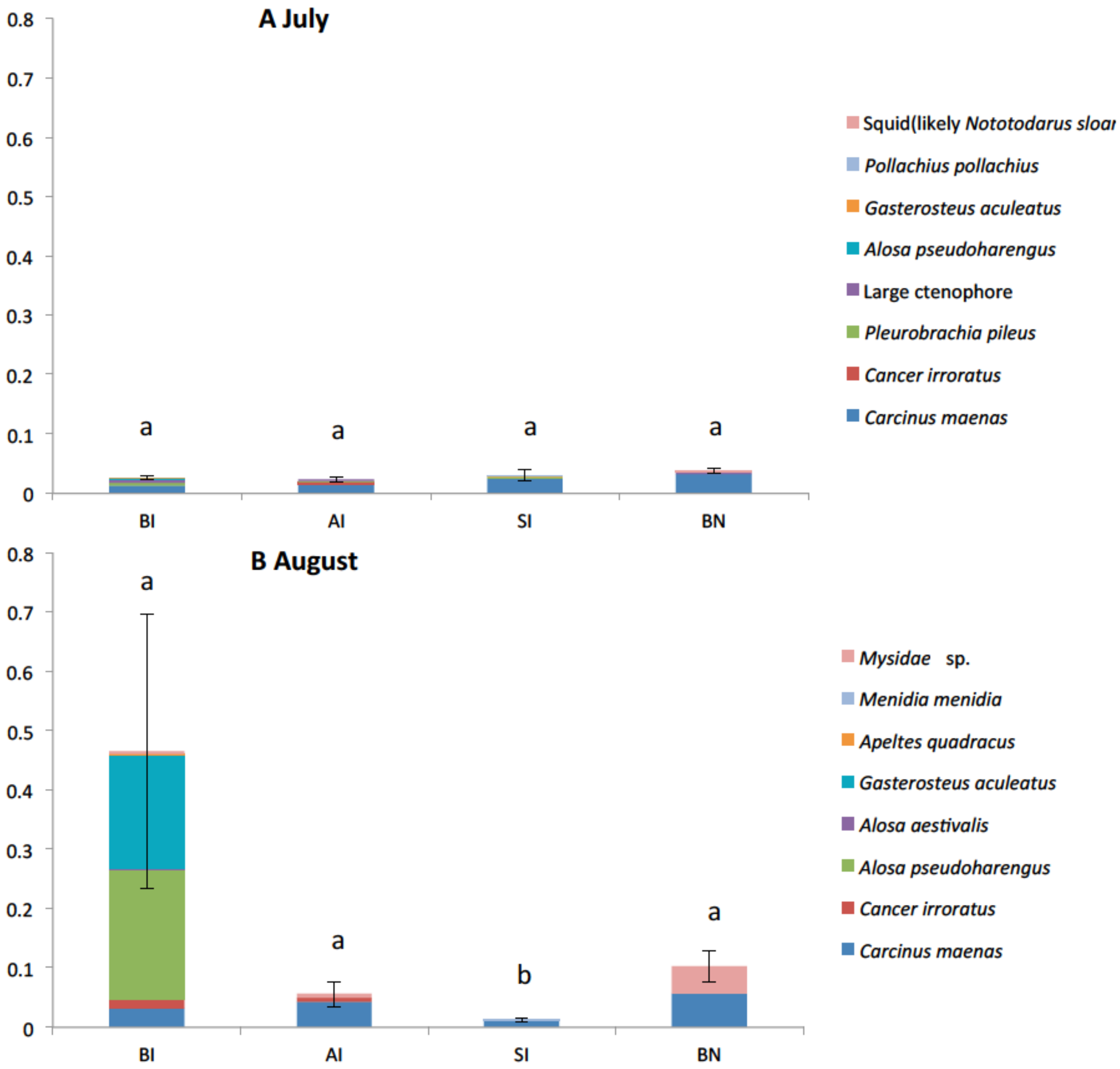


Figure 12. Average abundance and standard error (SE, n = 40) of mobile (transect) species for (A) July and (B) August. Lower case letters indicate significant differences between site within month as well as within site differences across month.

Diversity of sessile (quadrat) species was similar across all four sites in July but was lower at both BN and SI than at AI in August (Figure 6C, Appendix 4B Tables 11, 12). In July, the diversity of count (quadrat) species was lower at BN than at all other sites while in August, diversity of both BN and SI were once again lower than at AI (Figure 7C, Appendix 4B Tables 11, 12). For transect species diversity, BN's diversity was significantly lower than BI's in July (t = 2.426, p = 0.043) and in August, diversity at SI was lower than at all remaining sites (Figure 8C, Appendix 4B Tables 11, 12).

4.3.4 Associated community composition

4.3.4.i Sessile (quadrat) species

Repeated measures perMANOVAs detected a significant effect of the site by month interaction on the composition of sessile species (p = 0.001, Table 3). The interaction accounted for less than 3% of the variation whereas site and month as main effects accounted for 8.8% and 5.5% of variation respectively. In July, sessile species composition was significantly different at BN than at all other sites; in August, species composition at both BN and BI were significantly different from all other sites (Appendix 4B Tables 3, 4).

The MDS plots (Figure 13 A, B) demonstrate a clear separation of BN from the remaining sites in both July and August; the distinctness of BI from the other sites in July is also reflected in the MDS plot. For July, *Hildenbrandia rubra* was identified by SIMPER analysis as an important species for distinguishing between sites (Appendix 4C). For August, *H. rubra* continued to help distinguish between AI and BI as well as AI and BN. Distinguishing species for AI and SI were *H. rubra*, *Dynamena pumila*, *Elachista fucicola* and *Vertebrata lanosa* while BI and BN as well as BI and SI were distinguished by *E. fucicola* and *V. lanosa*. Finally, *V. lanosa* was the only distinguishing species for BN and SI.

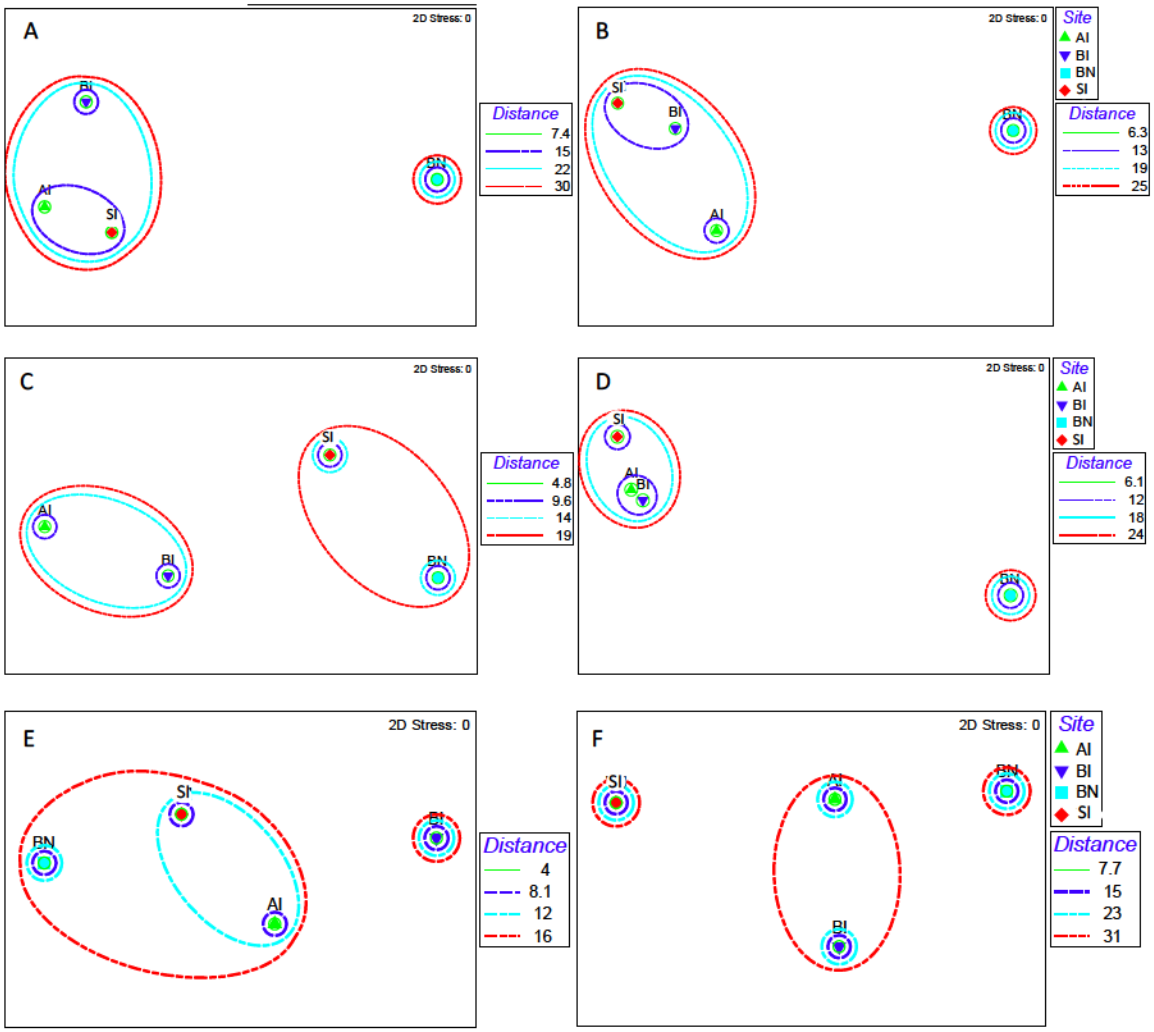


Figure 13. Multidimensional scaling (MDS) plot showing centroids derived from Bray-Curtis similarity matrices for sessile species composition (quadrats=40) in (A) July and (B) August, count (quadrat) species (quadrats = 40) in (C) July and (D) August, and mobile (transect) species (transects = 8) in (E) July and (F) August at each of the four study sites. The solid and broken lines encircling the sites indicate Bray-Curtis similarities that were derived from a cluster analysis also conducted on centroids.

4.3.4.ii Count (quadrat) species

Repeated measures perMANOVAs detected a significant site by month interaction on the composition of mobile (and other count) quadrat species (p = 0.0001, Table 3). The interaction only accounted for 2.3% of the variation while site accounted for 5.5% and month for 17.1% of the variation. In July, species composition was significantly different at BN than at all other sites, and SI and BI were significantly different (Appendix 4B Table 3). These significant differences were also seen in August with the exception of the difference between SI and BN that became non-significant and an additional significant difference between species composition at AI and SI (Appendix 4B Table 3). In both months, BN clearly differs from the other sites. The MDS plots (Figure 13 C, D) support this separation of BN from the other sites as well as the grouping of SI and BN in August. The main species identified by SIMPER contributing strongly (Sim/SD ≥ 1) to differences among sites include *Littorina saxatilis* in July and *Margarites* sp.and *L. obtusata* in August (Appendix C).

Table 3. Repeated measures perMANOVA results for the effect of Site and Month on composition of (i) sessile (quadrat) species, (ii) count (quadrat) species, and (iii) mobile (transect) species. Sqrt-V values are unbiased estimates of the contribution to variance of Site, Month, their interaction and the residuals in the model. Variance explained (Var) is given by [(SS Factor/SS Total) x 100] and, while more biased than sqrt-V, is included because it is a more intuitive measure of relative effect size (Howell 2002). The degrees of freedom (df) total to 319. See Appendix B for perANOVA output for post hoc pairwise comparisons between (1) pairs of sites with a month and (2) July and August values for a site. Significant p-values are shown in bold.

		Between subject		***Within subject***		
	Source	**Site**	**Res**	**Month**	**Si x Mo**	**Res**
	Df	**3**	**156**	**1**	**3**	**156**
Sessile	**Pseudo-F**	10.491	1.123	22.035	3.663	
(quadrat)	**P**	**0.0001**	**0.045**	**0.0001**	**0.0001**	43.148
species	**sqrt-V**	15.747	10.683	15.645	11.134	39.1
	Var	8.8	43.8	5.5	2.8	
Count	**Pseudo-F**	7.035	1.152	76.397	3.347	
(quadrat)	**P**	**0.0001**	**0.025**	**0.0001**	**0.0001**	
species	**sqrt-V**	12.531	11.731	29.174	10.295	42.500
	Var	5.5	40.2	17.1	2.3	34.9
	Df	**3**	**28**	**1**	**3**	**28**
Mobile	**Pseudo-F**	5.515	0.816	3.633	2.215	
(transect)	**P**	**0.0001**	0.907	**0.0042**	**0.007**	
species	**sqrt-V**	14.351	-9.082	8.580	11.658	29.913
	Var	18.1	30.6	4.9	8.9	37.5

4.3.4.iii Mobile (transect) species

Repeated measures perMANOVAs detected a significant site by month interaction on the composition of mobile transect species (p = 0.007, Table 3). 8.9% of the variation was explained by the interaction while site accounted for 18.1% and month for 4.9% of the variation. In July, species composition was significantly different between BI and BN (t = 2.120, p = 0.002) while in August all differences between sites, except AI and BI, were significantly different (Appendix 4B Table 3).

The MDS plots confirm a separation of BI and BN in July (Figure 13 E) and, in August, segregation of both BN and SI while AI and BI cluster together (Figure 13 F).

SIMPER analysis identified *Carcinus maenus* as a species that distinguished between all pairs of sites in both July and August, except between SI and BN in July (Appendix 4C). *Pleurobrachia pileus* also contributed to the dissimilarity between AI and BI in July. In August, the species of mysidae (mysid shrimp was also identified as a distinguishing species for AI vs BN, BI vs BN, and BN vs SI.

4.3.5 Linking environmental parameters to community composition

The Envfit() function from R's Vegan package was used to establish links between environmental parameters, canopy structure and composition of species at the sites. Tissue %N did not help to distinguish between sites close to and distant from fish farms in initial PCA and MDS analyses. We, therefore, removed these proxy environmental factors from multivariate analyses.

The significant multiple linear regressions between the environmental variables and canopy structure {L, C, D} had $R^2 = 0.494$ and $R^2 = 0.363$ for July and August respectively (Tables 4, 5). The R^2 values for the multiple regressions between environmental and canopy variables (predictor variables) and community compositions (response variables) varied from 0.362 to 0.505 (Tables 4, 5). When only one average value per canopy variables per site was used, these R^2 values strengthened to as much as 0.987 (Appendix 4D Tables 1, 2). In both figures 14 and 15 (with the exception of 15E), community samples drawn from each site separate out into two groups with relation to the environmental vectors; samples from AI and BI are associated with lower levels of Chl *a*, TPM, and % organic TPM, while samples from BN and SI are associated with higher values of these environmental metrics. When canopy variables are removed, higher % organic TPM concentrations best correlated with community composition components from SI in August, the only site at which there was active finfish aquaculture during our surveys. Also in August, samples from BN were more closely associated with higher Chl *a* and TPM concentrations than any other sites (Table 15 B, D, F).

Table 4. R^2 and p-values for regressions between individual environmental variables (Chl *a*, TPM, and % organic TPM), canopy variables (L, C and D) and community composition as well as for overall regressions between all predictor variables and components of community composition for July. Significant p-values are shown in bold.

Community component	**Chl**	**TPM**	**% Organic TPM**	**Average Plant L**	**Average Plant C**	**Average D**	**Overall**
Canopy Structure {L, C, D}	R^2 = 0.504 **P = 0.003**	R^2 = 0.458 **P = 0.008**	R^2 = 0.513 **P = 0.006**	NA	NA	NA	R^2 = 0.494 **P = 0.001**
Sessile (quadrat) species	R^2 = 0.660 **P = 0.001**	R^2 = 0.617 **P = 0.001**	R^2 = 0.341 **P = 0.001**	R^2 = 0.799 **P = 0.001**	R^2 = 0.076 P = 0.233	R^2 = 0.980 **P = 0.001**	R^2 = 0.432 **P = 0.001**
Count (quadrat) species	R^2 = 0.567 **P = 0.001**	R^2 = 0.586 **P = 0.001**	R^2 = 0.339 **P = 0.001**	R^2 = 0.923 **P = 0.001**	R^2 = 0.036 P = 0.506	R^2 = 0.988 **P = 0.001**	R^2 = 0.362 **P = 0.001**
Count (transect) species	R^2 = 0.667 **P = 0.001**	R^2 = 0.576 **P = 0.001**	R^2 = 0.407 **P = 0.001**	R^2 = 0.883 **P = 0.001**	R^2 = 0.098 P = 0.223	R^2 = 0.987 **P = 0.001**	R^2 = 0.390 **P = 0.001**

Table 5. R^2 and p-values for regressions between individual environmental variables (Chl *a*, TPM, and % organic TPM), canopy variables (L, C and D) and community composition as well as for overall regressions between all predictor variables and components of community composition for August. Significant p-values are shown in bold.

Community component	Chl	TPM	% Organic TPM	Average Plant L	Average Plant C	Average D	Overall
Canopy Structure {L, C, D}	R^2 = 0.595 **P = 0.003**	R^2 = 0.589 **P = 0.001**	R^2 = 0.336 **P = 0.023**	NA	NA	NA	R^2 = 0.360 P = **0.030**
Sessile (quadrat) species	R^2 = 0.346 **P = 0.002**	R^2 = 0.686 **P = 0.001**	R^2 = 0.110 P = 0.101	R^2 = 0.437 **P = 0.001**	R^2 = 0.024 P = 0.643	R^2 = 0.765 **P = 0.001**	R^2 = 0.437 P = **0.001**
Count (quadrat) species	R^2 = 0.133 P = 0.078	R^2 = 0.371 **P = 0.001**	R^2 = 0.523 **P = 0.001**	R^2 = 0.412 **P = 0.001**	R^2 = 0.058 P = 0.354	R^2 = 0.104 P = 0.125	R^2 = 0.505 **P = 0.001**
Count (transect) species	R^2 = 0.586 **P = 0.001**	R^2 = 0.537 **P = 0.001**	R^2 = 0.391 **P = 0.001**	R^2 = 0.921 **P = 0.001**	R^2 = 0.046 P = 0.535	R^2 = 0.986 **P = 0.001**	R^2 = 0.375 **P = 0.002**

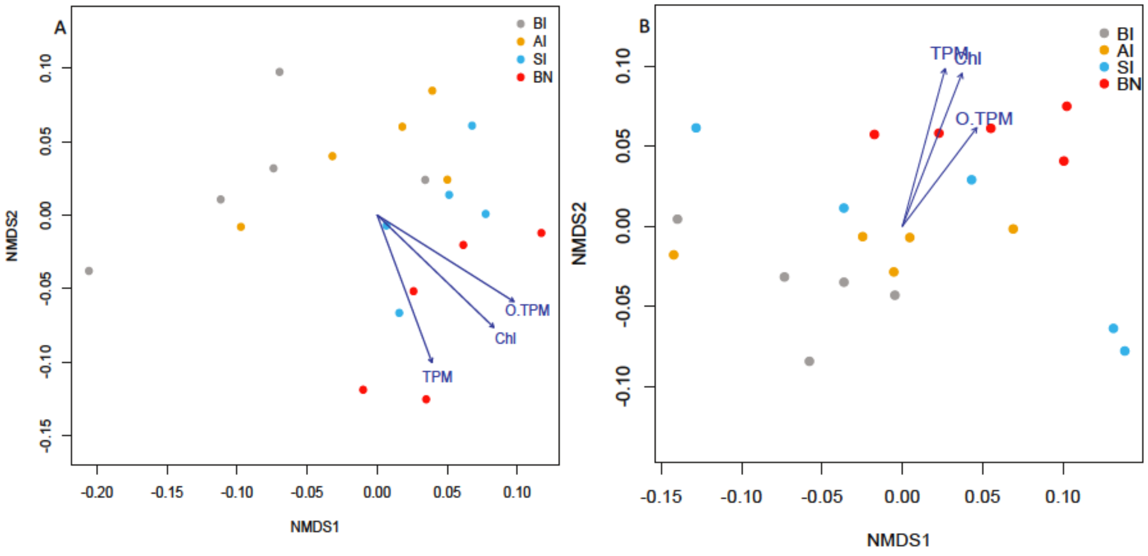


Figure 14. Multidimentsional scaling (MDS) plots showing averages (n=5) for canopy structure {L, C, D} at each of the four sites. Vectors of environmental variables (Chl *a*, TPM, and % organic TPM) that correlate with the ordination axis scores are overlaid.

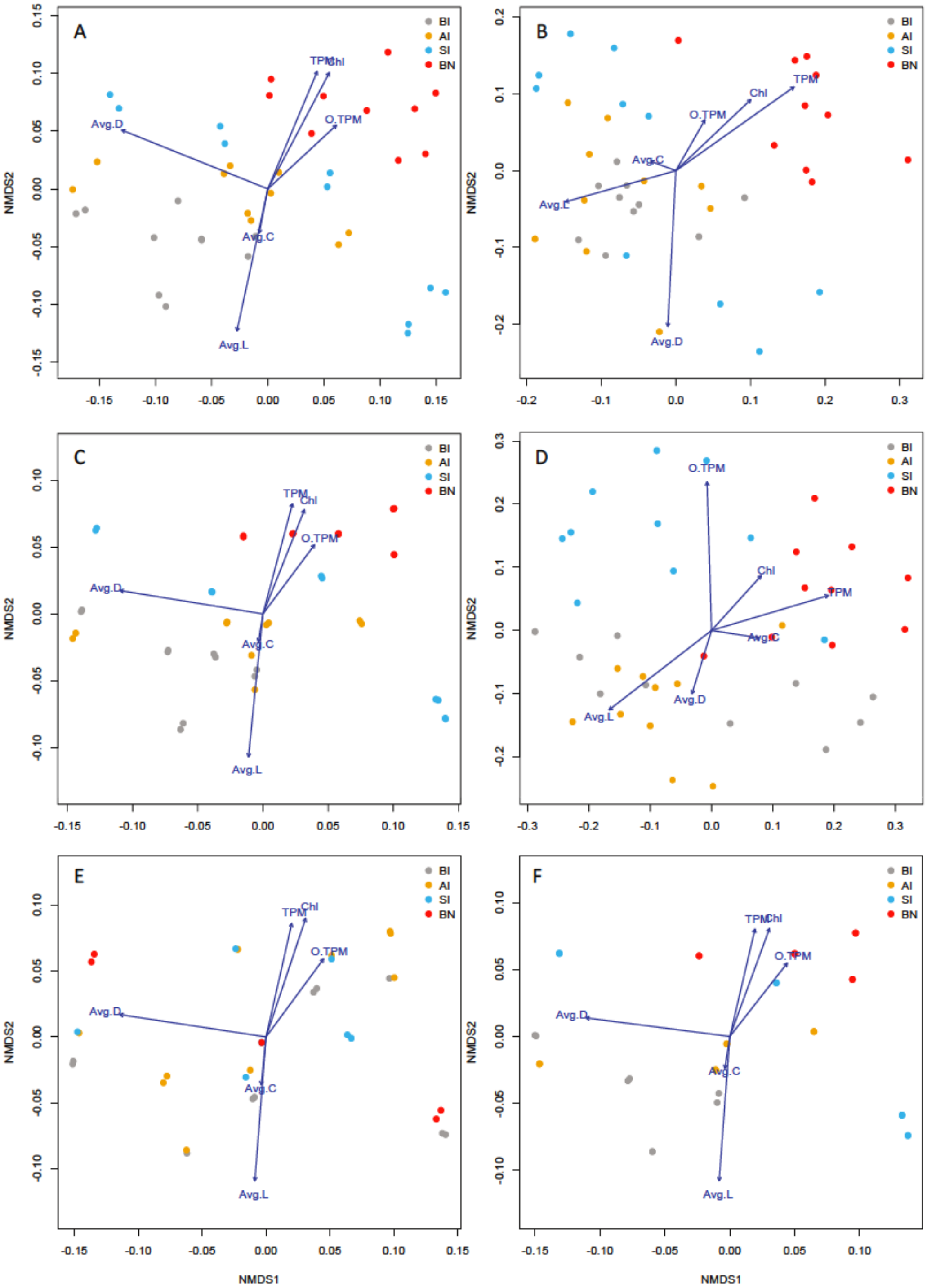


Figure 15. Multidimentsional scaling (MDS) plots showing averages (n=10) for sessile species composition in (A) July and (B) August, count (quadrat) species in (C) July and (D) August, and mobile (transect) species (n = 8) in (E) July and (F) August at each of the four study sites. T. Vectors of environmental and canopy variables (Chl *a*, TPM, and % organic TPM, average plant length, average plant circumference, average density) that correlate with the ordination axis scores are overlaid.

4.4 Discussion

This study addressed two stressors faced by rockweed habitats in the outer Bay of Fundy: long-term rockweed harvesting that can alter plant and canopy structure (e.g. Ang 1993, 1996, Kelly et al. 2001, Ugarte et al. 2006) and finfish aquaculture that enhances nutrient, organic, and chemical loading in its surroundings (Milewski 2001). In the outer Bay of Fundy, we found an ideal group of study sites where we could analyze the individual and combined effects of these two stressors within a region that has otherwise very similar biological, geological and hydrographic characteristics.

The Quoddy region is a noted area of ecological significance and has been subject to substantial monitoring (e.g. MacKay et al. 1978a-c, 1979a-c, Buzeta 2003, Lotze and Milewski 2004, Buzeta and Singh 2008). *A priori* grouping of sites in this region by their habitat characteristics and hydrographic conditions grouped all of our current study sites into a single region; statistical analysis confirmed that species assemblages clustered by these regions (MacKay et al. 1978a-c, 1979a-c, Buzeta and Singh 2008). Hydrographic conditions change from estuarine to oceanic moving from the St. Croix Estuary out to the midbay region; the West Isles area (where our study sites are located) is known to have more stable temperature and salinity and this has been significantly correlated with greater richness of benthic species (Buzeta et al. 2007, Buzeta and Singh 2008). Importantly, the study region presented the opportunity to evaluate the effects of long-term rockweed harvesting (harvest vs exclusion zones) and finfish aquaculture (presence/absence) in relative isolation from other land-based human impacts. There is very little research available to help predict how the effects of rockweed harvesting and aquaculture might interact – the results of this study provide some insight.

4.4.1 Comparison of sites in the context of nutrient and organic loading

Our sampling and survey were not designed in compliance with any pre-existing eutrophication indices; nonetheless, using the criteria of an index as a guide for discussing some of the differences observed across our sites is a useful exercise. When considering the effects of nutrient loading, three indicators for quality of rocky-shore communities are considered in the CFR index (Guinda et al. 2014): coverage of characteristic macroalgae (C), fraction of opportunistic species (F), and richness of characteristic macroalgae (R). We did not assess the percent cover of *Ascophyllum nodosum* at our study sites; however, our biomass, density, and plant measures can provide trends related to the foundation species' abundance. Comparing our two harvest-exclusion sites that are exposed (SI) vs. not-exposed (BI) to aquaculture, neither rockweed biomass nor density was adversely affected at SI compared to BI; however, the plant structure {L, C} – ergo the size of plants – was greater at the un-impacted BI. Similarly, while plant density was similar at the two harvested sites with (BN) and without (AI) aquaculture presence, biomass was marginally non-significantly lower ($p = 0.058$) at BN and plant structure indicated significantly smaller plants at BN than at AI. These results suggest that rockweed plants do not grow better or larger near aquaculture sites, but that nutrient, organic or other (e.g. chemical) loading negatively affect plant growth and canopy structure.

The fraction of opportunistic species cannot be computed relative to the % cover of rockweed, which we did not assess, but relative coverage of opportunists can be compared across sites. Opportunistic annual red, green and brown algae and hydroid epiphytic filter feeders were higher at SI than BI, particularly in August. The opportunistic annual green algae *Ulva* spp. showed significantly higher coverage at SI than at BI. Similarly, coverage of epiphytic brown algae (Ectocarpales and *Elachista fucicola*) was higher at SI than BI in both July and August. Nutrient enrichment and organic loading from aquaculture would account for greater abundance of opportunistic algae and filter feeders respectively (Worm and Lotze 2006). In August, when fish pens had been established for an extra month, there was a strong correlation between the % organic content of TPM and composition of sessile species at SI (Figure 15). In Chopin and Wells (2001), Bates et al. observed signs of nutrient input similar to ours that included blooms of ectocarpoid brown algae, higher percent cover of filter-feeding mussels (while we saw hydroids), and extensive blooms of green algae. Counter to expectation, however, abundances of epiphytic brown algae were lower at BN than AI in both months. This may be due to cumulative effects observed at BN (see *Cumulative impacts* section below).

Site richness (all species) and average abundance of species was markedly low at BN, giving the site a visibly stark appearance. However, the richness of characteristic macroalgae – the third item included in the CFR index – did not vary significantly by site. However, in July, the diversity for quadrat count species at BN was significantly lower than at the other three less impacted sites. Additionally, in August, the Shannon diversity indices for both percent cover and quadrat count species at the non-aquaculture site AI were significantly higher than at both exposed sites SI and BN.

4.4.2 Comparison of sites in the context of commercial harvesting

While BI and SI were designated exclusion zones for the commercial rockweed harvest, there were signs of recent (within the last year) harvesting at both these sites. Despite this illegal harvesting; however, the intensity of poaching at BI and SI was likely lower than the regular commercial harvesting intensity at AI and BN; observations along our sampling transects support this assumption.

Plant and canopy metrics did not differ significantly between the exclusion (BI) and harvested (AI) sites, suggesting that rockweed harvesting at the current commercial harvest intensity has limited effects. However, this could have been influenced by our harvest control site (BI) not being a truly unexploited control due to observed poaching activities. In contrast, rockweed biomass and plant structure {L, C} at BN were significantly lower compared to all other sites, suggesting that significant changes in rockweed canopy structure may be due to multiple concurrent impacts.

Interestingly, more *Fucus* spp. was observed at the two harvested sites AI and BN than at the two exclusion zone sites BI and SI. This is consistent with previous observations of *Fucus* spp. encroachment in harvested areas (MacFarlane 1952, Printz 1956, Boaden and Dring 1980, Keser et al. 1981, Tyler 1994, Kelly et al. 2001). Also in July, coverage of foliose and filamentous benthic green algae was higher at harvested than exclusion sites. Although the harvest of rockweed at current commercial intensities may not be high enough to affect overall coverage of rockweed, it may be possible that a thinning of the canopy in discrete clumps allows for enough additional light penetration to the under-canopy to promote the growth of opportunistic species (Boaden and Dring 1980, Tyler 1994, Kelly et al. 2001, Worm and Lotze 2002, 2006).

Regarding the faunal community, total abundances of count (quadrat) species were significantly lower at BN than SI in both months and lower at AI than BI in July. Moreover, abundances at BN were in fact lower than at all other sites in July and August, and count (quadrat) species in particular appear to avoid BN. Reductions in numbers of *Littorina littorea* and *L. obtusata* lost as bycatch have been reported in a number of studies (McEachreon 1999, Kelly et al. 2001, Sharp et al. 2006, Ugarte et al. 2010, 2011, Philippi et al. 2014, Chapter 3 of this thesis). Decreased densities of other species, including *Carcinus maenus*, *Mytilus* sp., *Semibalanus balanoides*, sponges, bryozoans and hydroids, have been noted in studies simulating more intense harvests than the current commercial practice (Boaden and Dring 1980, Fegley 2001, Cervin et al 2004, Philippi et al. 2014). The added aquaculture impact may be potentiating the effects of harvesting on mobile and other count species in this instance.

4.4.3 Cumulative impacts

There are effects captured at BN that are not simply the addition of effects seen at AI and SI separately. Whereas more typical signs of eutrophication can be seen at SI – for example, increased coverage of annual green and brown algae and filter-feeding hydroids – BN island exhibits its own distinct patterns. Lower rockweed biomass and plant size, lower abundances of all associated community components, lower richness of count (quadrat) species, and lower diversity of count (quadrat) species in August are all markers of a unique, impoverished community at BN. Higher Chl *a* and TPM associated strongly with canopy and all community composition samples from BN. The higher input of organic matter at this site where the foundation species - important for sequestering of carbon and cycling nutrients - is being harvested constitutes a cumulative pressure leading to the degradation of the rockweed bed.

In a series of benthic (intertidal and subtidal) surveys (100 m transect per site), MacKay et al. (1978a-c, 1979a-c) determined species richness at AI, SI and at two locations on BN, one of which was near to our survey site. These surveys were conducted before the introduction of finfish aquaculture to the region in the 1980s and before the start of the commercial harvest of rockweed in 1995. At both BN locations as well as at the SI location, 50 or more species were observed and close to 50 species were seen at AI (MacKay et al. 1978a-c, 1979a-c, Buzeta and Singh 2008). In our survey, however, we encountered significantly lower richness of count (quadrat) species at BN as well as of sessile species in August. Additionally, SI was identified as an island in the region with some of the highest species diversity (MacKay et al. 1978a-c, 1979a-c, Lawton 1992, 1993); our surveys do not corroborate this. Although we did not revisit the exact same sites sampled in the 1970s or 1990s, nor did we survey the subtidal, the data presented in this chapter suggests that the impacts of aquaculture at SI and cumulative human impacts at BN may explain the long-term deterioration of species richness or diversity at these islands.

Stressors other than harvesting and aquaculture are also on the rise with the likely production of more interactive effects for rockweed habitats. Increased storminess and more severe physical disturbance are expected as a result of climate change; this is expected to favour the replacement of *A. nodosum* with *Fucus* spp. patches (Ugarte et al. 2010b). Increased sea surface temperatures (SST) are also expected in Eastern Canada as a result of climate change which will decrease rockweed growth if SST exceeds 20°C (Solomon et al. 2007; Keser et al. 2005).

4.4.4 Conclusion

The take-home message: Given the environmental conditions and high diversity characteristic of the outer Bay of Fundy region where we conducted our study, commercial harvesting at its current intensity alone may have a mild effect on the structure of the rockweed canopy, but does not appear to lead to long-term adverse community effects in the macrofaunal segments of the community that we surveyed. Exposure of beds to runoff from finfish aquaculture conducted with a fallow every third year has led to minor shifts in the structure of the canopy and has produced community alterations that are typical of rocky shores at low-medium levels of eutrophication. The cumulative effects of harvesting and aquaculture runoff, however, resulted in more severe alterations of canopy and community structure at our study site BN. The species community at BN was seemingly not able to absorb the multiple impacts without a resultant loss in species richness, abundance and diversity. The obvious management implication for rockweed harvesting is that it should be of limited intensity or excluded from areas with other known impacts such as aquaculture. Vice versa, aquaculture operations should not be placed in close proximity to areas with commercial rockweed harvesting. Furthermore, with other human-induced stressors such as climate change on the rise, placing more adverse effects on rockweed plants, it is increasingly important to consider the cumulative effects of multiple human activities in coastal and marine management plans (DFO 2013).

Chapter 5: Conclusion

In Chapter 2, I established that structural differences in rockweed canopies exist between Southwest Nova Scotia and Southwest New Brunswick. Additionally, differences in the associated communities of the beds were in part explained by differences in canopy structure.

While both the regional differences and the link between canopy and community may seem intuitive, they have both been largely ignored in the management of rockweed harvest in Canada (DFO 2013). In the current monitoring scheme, there is an over-reliance on biomass measurements of rockweed beds when assessing harvesting effects (DFO 2013, Uguarte et al. 2006, Ugarte and Sharp 2012) and the known impact of harvesting on plant and canopy structure are neglected. Harvested plants grow back shorter and bushier than their original state, but often contribute biomass comparable to the pre-harvested bed because cutting the plants temporarily stimulates growth (Vandermeulen 2013). Based on the results of Chapter 2, we now have evidence to support the hypothesis that this change in the physical structure of the rockweed plants and canopy is affecting the associated species community. Biomass of harvested areas and landings, therefore, should not remain the sole reliably reported measure of harvesting impact.

Our experimental harvest in Chapter 3 highlighted a number of the logistical difficulties involved in trying to replicate the commercial hand harvest of rockweed under more controlled circumstances. Ideally, commercial harvesters would be left to carry out the harvest according to their regular practices; however, it seems that some intervention and direction on the part of the investigator may be necessary in order to ensure sufficient overlap between harvested and sampling areas. Additionally, given the patchy and irregular nature of the rockweed hand harvest, capturing the harvesting effects requires a greater number of sampling units for plant and canopy structure than does describing the more regular structure of an unharvested bed. Moreover, the absence of any long-term unharvested control site in the most heavily harvested areas of Southwest Nova Scotia make in impossible to describe with any certainty what impact 55 years of commercial rockweed harvesting, or 20 years of harvesting under the current management regime, has had on local rockweed habitats. The establishment of no-harvest zones distributed among Nova Scotian rockweed leases would dramatically increase the value of monitoring and research in this area in future. Although no-harvest zones were proposed in the recent assessment report (DFO 2013), so far none have been established.

The results of Chapter 4 suggest that the resilience of rockweed habitats to current levels of harvesting or to exposure to runoff from aquaculture operations can be overwhelmed if these two stressors occur in combination. Although each of these human activities impacts rockweed habitats on their own, their cumulative effect can lead to much stronger alteration of canopy and community structure. Yet to date, Canada's rockweed management strategy includes no mention of accommodation for sites at which other known stressors are present (DFO 2013). My results strongly suggest that this oversight requires amendment.

One major conclusion from this thesis is that ecosystem-based management of rockweed likely requires managing harvested rockweed beds at a smaller scale and monitoring more parameters than rockweed biomass and yield in order to assess changes in canopy and community structure. This thesis demonstrates clear regional differences in canopy and community structure and consequently differences in resilience to stressors. Within regions, there are additional differences between sites with different impact exposure.

Given these inter- and intraregional differences in rockweed canopy, community structure, and resilience, it may be useful to devise management strategies at a smaller scale than is currently the case. Terrestrial forests in Canada already use this approach to some degree (Natural Resources Canada www.nrcan.gc.ca). In Nova Scotia, for example, forests are managed at a landscape level, taking into consideration the spatial pattern and age distribution of forest types, the sizes and shapes of stands, the stage of succession of the various forest types and internal stand structure (NSDNR - Code of Forest Practice, p. 4). While this level of management would present logistical difficulties for coastal vegetated systems, ecosystem-based management of marine macrophyte resources requires a shift towards this level of thinking, taking into consideration the three-dimensional structure of coastal vegetated habitats and their associated species communities.

There is little public and political awareness of the importance of coastal vegetated habitats, despite that this awareness is essential to support their conservation and sustainable management. The non-utility roles that rockweed plays, such as habitat provision and carbon storage, tend to be overlooked, as do the non-charismatic but diverse and fascinating associated flora and fauna. Media coverage – mostly in the form of Chronical Herald articles discussing Acadian Seaplants Ltd. – and my personal communications indicate that the public commonly perceives rockweed as a nuisance, or at best something that provides a marginal amount of utility.

This perception could conceivably be changed; the popular view of wetlands underwent a drastic transformation in the last century, from an image of worthless wastelands to an appreciation of the intrinsic beauty of these ecosystems (Bromberg Gedan et al. 2009, Lotze 2010).

Other marine plants and macrophytes have received more recognition in Atlantic Canada. In 2009, the seagrass *Zostera marina* was designated an Ecologically Significant Species (ESS) by DFO (DFO 2009) and subsequently the threats to this species, and the habitat it forms, were outlined (DFO 2011). Additionally, kelp is not harvested at a large scale in Nova Scotia because of the recognition of its ecological importance (DFO 2013). Rockweed habitats similarly face multiple threats and play significant ecological roles and deserve similar recognition.

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Appendix 2A – PerANOVA output for pairwise comparisons of (1) Chl *a*, TPM, PIM, POM and % organic content of TPM averaged over July and August, (2) abundances of community components, and (3) Richness of community components. T value and associated p-value for pairwise comparisons are reported. Significant p-values (≤0.05) are bolded.

(1) CHL *a* AVERAGED OVER JULY AND AUGUST

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PAIR-WISE TESTS

Term 'Si'
                          Unique
Groups          t P(perm)  perms
AI, BI    1.7281  0.0948    9534
AI, BN   0.13726  0.8893    9586
AI, SI     1.051  0.3052    9547
AI, CA   0.14677  0.8837    9728
AI, KC   0.40718  0.6841    9728
BI, BN    1.7388  0.0908    8057
BI, SI   0.94458   0.352    7572
BI, CA    1.5885  0.1275    8978
BI, KC     1.439  0.1611    9437
BN, SI   0.98641  0.3394    8178
BN, CA 1.6936E-2  0.9866    9129
BN, KC   0.28864  0.7728    9615
SI, CA   0.89646   0.384    9005
SI, KC   0.67197  0.5046    9531
CA, KC   0.25553  0.8008    9666
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TPM AVERAGED OVER JULY AND AUGUST

```
PAIR-WISE TESTS

Term 'Si'
                          Unique
Groups          t P(perm)  perms
AI, BI   0.43121  0.6551     195
AI, BN    1.0506   0.319    1046
AI, CA 2.7498E-2  0.9793    6875
AI, KC   0.62342  0.5488    9503
AI, SI   0.35668  0.7603     363
BI, BN    1.3773    0.18     560
BI, CA    0.4425  0.6586    6223
BI, KC    1.0191  0.3376    9150
BI, SI   0.69808  0.5352     686
BN, CA    1.1737  0.2487    7519
BN, KC   0.54082  0.6007    9573
BN, SI   0.63629   0.532     919
CA, KC   0.70757   0.505    9832
CA, SI   0.41297   0.706    7613
KC, SI   0.18006  0.8609    9699
```

POM AVERAGED OVER JULY AND AUGUST

```
PAIR-WISE TESTS

Term 'Si'
                       Unique
Groups       t P(perm)  perms
AI, BI 0.21883  0.8366    190
AI, BN  1.1728  0.2744   1662
AI, CA 0.85391  0.4036   4376
AI, KC  0.4113  0.6911   6282
AI, SI 0.11758  0.9165    345
BI, BN   0.954  0.3759    702
BI, CA 0.94289  0.3633   3989
BI, KC 0.59155  0.5631   5907
BI, SI 0.30576  0.7685    389
BN, CA  1.7929  0.0634   8401
BN, KC  1.5879  0.1002   9032
BN, SI  1.2351  0.2421   1786
CA, KC 0.57176  0.5904   9557
CA, SI 0.62708  0.5551   4979
KC, SI 0.22212  0.8403   6817
```

PIM AVERAGED OVER JULY AND AUGUST

```
PAIR-WISE TESTS

Term 'Si'
                         Unique
Groups         t P(perm)  perms
AI, BI   0.17809  0.8617    109
AI, BN   0.68868  0.5111   1043
AI, CA   0.92686  0.3693   6085
AI, KC    1.4152  0.1688   8641
AI, SI   0.90232  0.4238    474
BI, BN   0.86841  0.4037    555
BI, CA    1.1584  0.2636   5666
BI, KC    1.5818  0.1176   8123
BI, SI    1.0446  0.3491    458
BN, CA 9.2211E-2  0.9302   7857
BN, KC   0.79463  0.4524   9441
BN, SI   0.35069  0.7567   1855
CA, KC   0.80578  0.4557   9790
CA, SI   0.31776  0.7878   7207
KC, SI   0.34791  0.7293   8930
```

% ORGANIC CONTENT TPM AVERAGED OVER JULY AND AUGUST

```
PAIR-WISE TESTS

Term 'Si'
                             Unique
Groups         t  P(perm)     perms
AI, BI 0.22862       0.82      9480
AI, BN 0.26258     0.7949      9796
AI, CA   1.252     0.2216      9604
AI, KC  1.5328     0.1387      9691
AI, SI 0.37073     0.7235      9142
BI, BN 0.49218     0.6269      9808
BI, CA 0.94989     0.3485      9769
BI, KC  1.2374     0.2219      9830
BI, SI 0.14944      0.889      9809
BN, CA  1.5574     0.1275      9779
BN, KC  1.8383     0.0732      9830
BN, SI 0.63373     0.5405      9810
CA, KC  0.4567     0.6511      9773
CA, SI 0.68755     0.5477      9717
KC, SI 0.96876     0.3614      9790
```

(2) COUNT (QUADRAT) SPECIES ABUNDANCE

```
PAIR-WISE TESTS

Term 'Si'
                             Unique
Groups         t  P(perm)     perms
AI, BI  1.5162     0.1409        77
AI, BN  3.5858     0.0001        70
AI, CA 0.68424     0.5134        81
AI, KC 0.15279     0.9011        73
AI, SI 0.46863     0.6551        76
BI, BN  3.5146     0.0003        42
BI, CA  1.1064     0.2825        61
BI, KC  2.2847     0.0281        53
BI, SI  1.6535     0.1065        51
BN, CA  4.3595     0.0001        50
BN, KC  7.5407     0.0001        44
BN, SI  5.9801     0.0001        43
CA, KC 0.84401      0.424        59
CA, SI 0.35724     0.7474        61
KC, SI 0.54478     0.6067        48
```

SESSILE SPECIES ABUNDANCE

```
PAIR-WISE TESTS

Term 'Si'
                                Unique
Groups         t  P(perm)  perms
AI, BI 0.88622   0.3773      659
AI, BN   2.5091   0.0165      294
AI, CA   0.9217   0.3634      378
AI, KC   4.5862   0.0001      340
AI, SI   1.6862   0.0966      265
BI, BN   3.1424   0.0022      630
BI, CA   1.6024   0.1124      755
BI, KC   3.1329   0.0017      653
BI, SI   2.4592   0.0165      580
BN, CA 0.95776   0.3417      345
BN, KC   7.9359   0.0001      346
BN, SI   1.2679   0.2153      211
CA, KC   4.6645   0.0001      415
CA, SI   0.2299   0.8226      331
KC, SI   7.5394   0.0001      314
```

MOBILE (TRANSECT) SPECIES ABUNDANCE

```
PAIR-WISE TESTS

Term 'Si'
                                Unique
Groups         t  P(perm)  perms
AI, BI 0.42097   0.8409        8
AI, BN   2.3376   0.0505        9
AI, CA   2.9227   0.0147        8
AI, KC   3.7669   0.0028        9
AI, SI   1.8209   0.1364        8
BI, BN   1.9126   0.1234        8
BI, CA   3.4099   0.0103       10
BI, KC   4.2691   0.0033       10
BI, SI   2.2256   0.0041       10
BN, CA   5.6745   0.0006       12
BN, KC   6.6193   0.0004       14
BN, SI   4.0825   0.0675       12
CA, KC 0.94198   0.5306        6
CA, SI 0.69348   0.6428        7
KC, SI   1.4256   0.2624        8
```

(3) COUNT (QUADRAT) SPECIES RICHNESS

```
PAIR-WISE TESTS

Term 'Si'
                           Unique
Groups         t  P(perm)  perms
CA, KC   1.5378   0.1474      27
CA, BI  0.85421   0.4422      33
CA, AI  0.97435   0.3799      19
CA, SI   1.5693   0.1457      19
CA, BN   5.5311   0.0001      15
KC, BI   2.4364   0.0188      31
KC, AI   0.1498   0.9129      36
KC, SI   0.4359   0.7221      31
KC, BN   9.3695   0.0001      29
BI, AI   1.6688     0.11      40
BI, SI   2.2844   0.0292      38
BI, BN   4.1157   0.0001      28
AI, SI  0.45532   0.7196      21
AI, BN   5.5147   0.0001      19
SI, BN   6.6992   0.0001      19
```

SESSILE SPECIES RICHNESS

```
PAIR-WISE TESTS

Term 'Si'
                             Unique
Groups           t  P(perm)  perms
CA, KC      11.746   0.0001     25
CA, BI      6.8907   0.0001     24
CA, AI       5.387   0.0001     24
CA, SI      7.0282   0.0001     25
CA, BN      5.8977   0.0001     25
KC, BI      2.3333    0.031     18
KC, AI      2.7948   0.0099     20
KC, SI      2.2361   0.0412     19
KC, BN      2.7829   0.0084     19
BI, AI     0.65839   0.5737     24
BI, SI  9.1297E-2        1      21
BI, BN     0.51812    0.673     23
AI, SI     0.74322   0.5099     23
AI, BN     0.15774   0.9369     25
SI, BN     0.60674   0.6052     21
```

MOBILE (TRANSECT) SPECIES RICHNESS

```
PAIR-WISE TESTS

Term 'Si'
                              Unique
Groups          t  P(perm)     perms
CA, KC    0.38592        1         5
CA, BI     4.2451   0.0029         6
CA, AI     2.5459   0.0727         3
CA, SI     1.4402   0.3089         5
CA, BN     2.5459   0.0711         3
KC, BI     3.9686   0.0064         8
KC, AI     2.3932   0.0785         5
KC, SI       1.57   0.2291         6
KC, BN     2.3932   0.0761         5
BI, AI     2.3932   0.0773         6
BI, SI      2.198   0.0881         6
BI, BN     2.3932   0.0734         5
AI, SI    0.37048        1         4
AI, BN   Negative
SI, BN    0.37048        1         4
```

Appendix 2B – PerMANOVA output for pairwise comparisons of canopy structure and community composition between sites. T value and associated p-value for pairwise comparisons are reported. Significant p-values (≤0.05) are bolded.

CANOPY STRUCTURE {L, C, D}

```
PAIR-WISE TESTS

Term 'Si'
                                Unique
Groups          t  P(perm)   perms
CA, KC  0.47275   0.8339    9948
CA, AI   4.9508   0.0001    9943
CA, BI    3.726   0.0002    9954
CA, WI   5.7932   0.0001    9947
CA, BN   6.5219   0.0001    9951
KC, AI   4.9919   0.0001    9951
KC, BI   3.6547   0.0001    9949
KC, WI   5.9454   0.0001    9953
KC, BN    6.731   0.0001    9953
AI, BI   1.3652   0.1554    9938
AI, WI   1.1822   0.2376    9946
AI, BN   2.4206    0.005    9936
BI, WI   1.9723   0.0152    9949
BI, BN   2.7622   0.0003    9947
WI, BN   1.3928    0.143    9950
```

MOBILE QUADRAT SPECIES COMPOSITION

```
PAIR-WISE TESTS

Term 'Si'
                                Unique
Groups          t  P(perm)   perms
AI, BI  0.87446   0.5298    9938
AI, BN    3.427   0.0001    9936
AI, CA    1.301   0.1538    9953
AI, KC   2.4801   0.0007    9949
AI, WI    1.403   0.1044    9944
BI, BN   2.8661   0.0002    9948
BI, CA   1.5062   0.0804    9951
BI, KC   3.1435   0.0001    9957
BI, WI    1.978   0.0075    9953
BN, CA   4.5867   0.0001    9948
BN, KC   6.5472   0.0001    9962
BN, WI   4.4113   0.0001    9948
CA, KC   1.6376    0.057    9964
CA, WI   1.4477   0.0929    9956
KC, WI    2.391   0.0015    9957
```

SESSILE SPECIES COMPOSITION

```
PAIR-WISE TESTS

Term 'Si'
                               Unique
Groups       t  P(perm)  perms
AI, BI  1.3167   0.1048   9946
AI, BN  2.9583   0.0001   9949
AI, CA  3.7296   0.0001   9939
AI, KC   5.158   0.0001   9934
AI, WI  1.4179   0.0646   9938
BI, BN  3.0891   0.0001   9955
BI, CA  3.8144   0.0001   9945
BI, KC  4.4671   0.0001   9945
BI, WI  1.2767   0.1401   9946
BN, CA  3.3948   0.0001   9951
BN, KC  5.1805   0.0001   9948
BN, WI  3.5065   0.0001   9931
CA, KC  5.8918   0.0001   9950
CA, WI  4.4158   0.0001   9936
KC, WI  5.5009   0.0001   9944
```

EPIPHYTIC SESSILE SPECIES COMPOSITION

```
PAIR-WISE TESTS

Term 'Si'
                                 Unique
Groups        t  P(perm)  perms
AI, BI  0.60804   0.6942   9565
AI, BN   1.9846   0.0236   7057
AI, CA   4.2024   0.0001   8281
AI, KC   3.0084   0.0003   8142
AI, WI  0.94203    0.431   9625
BI, BN   1.9096   0.0255   8440
BI, CA   3.9935   0.0001   9706
BI, KC   2.8823   0.0005   9556
BI, WI  0.86567   0.4933   9889
BN, CA   5.2227   0.0001   3353
BN, KC   1.7753   0.0513   4566
BN, WI    2.717   0.0009   9584
CA, KC   6.7631   0.0001   7548
CA, WI   4.3597   0.0001   9696
KC, WI      3.4   0.0001   9676
```

BENTHIC SESSILE SPECIES COMPOSITION

```
PAIR-WISE TESTS

Term 'Si'
                       Unique
Groups      t  P(perm)  perms
AI, BI 1.3361   0.1605   9964
AI, BN 3.6103   0.0001   9953
AI, CA 4.5639   0.0001   9960
AI, KC 6.0747   0.0001   9963
AI, WI 1.4915   0.0769   9950
BI, BN 3.1724   0.0001   9957
BI, CA 4.5003   0.0001   9957
BI, KC 5.0132   0.0001   9962
BI, WI 0.9548   0.4717   9959
BN, CA 3.5228   0.0001   9959
BN, KC 4.9308   0.0001   9972
BN, WI 3.6756   0.0001   9960
CA, KC 5.9669   0.0001   9815
CA, WI 5.1749   0.0001   9873
KC, WI 6.0533   0.0001   9953
```

MOBILE TRANSECT SPECIES COMPOSITION

```
PAIR-WISE TESTS

Term 'Si'
                        Unique
Groups       t  P(perm)  perms
AI, BI  1.1605   0.334   1226
AI, BN  1.6015  0.0862    337
AI, CA  1.8044  0.0428    392
AI, KC  1.3028  0.1645    135
AI, WI  1.0074  0.3319    518
BI, BN  2.1353  0.0024   2069
BI, CA  2.6912  0.0033   1349
BI, KC  2.5318  0.0065    450
BI, WI  1.5784   0.074   3120
BN, CA  4.2861  0.0003    755
BN, KC  4.3588  0.0005    250
BN, WI 0.92412  0.4754    561
CA, KC  1.0601  0.3841     40
CA, WI  2.6815  0.0098    453
KC, WI  2.5835  0.0152    125
```

Appendix 2C – SIMPER analysis of square root transformed data for each component of community composition with sessile species combined as well as further divided into benthic and epiphytic subcomponents. SIMPER results reported for between group (i.e. between pairs of Sites). Strongly contributing species (for which Sim/SD ≥ 1) to similarity for within group analyses and dissimilarity for between group analyses are bolded.

COUNT (QUADRAT) SPECIES

```
Groups AI  and  BI
Average dissimilarity = 81.98

                     Group AI Group BI
Species              Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Littorina saxatilis      2.03     1.57   34.26    1.07    41.79 41.79
Littorina littoria       0.82     0.35   13.59    0.60    16.58 58.38
Littorina obtusata       0.45     0.15    8.91    0.43    10.87 69.25
Limpet (checked)         0.68     0.33    8.81    0.56    10.75 80.00
Sea anenome              0.25     0.40    6.43    0.39     7.84 87.84
Limpet (brown)           0.05     0.19    2.89    0.26     3.53 91.36
```

```
Groups AI  and  BN
Average dissimilarity = 92.87

                     Group AI Group BN
Species              Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Littorina saxatilis      2.03     0.48   39.54    1.11    42.58 42.58
Littorina littoria       0.82     0.00   13.42    0.53    14.45 57.03
Littorina obtusata       0.45     0.15   11.16    0.47    12.02 69.05
Limpet (checked)         0.68     0.10   10.06    0.51    10.83 79.89
Carcinus maenus          0.05     0.25    7.45    0.37     8.02 87.90
Sea anenome              0.25     0.00    4.60    0.30     4.95 92.86
```

```
Groups BI  and  BN
Average dissimilarity = 92.08

                     Group BI Group BN
Species              Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Littorina saxatilis      1.57     0.48   43.48    1.13    47.22 47.22
Littorina obtusata       0.15     0.15   12.00    0.41    13.03 60.24
Carcinus maenus          0.15     0.25   10.24    0.45    11.13 71.37
Littorina littoria       0.35     0.00    9.55    0.43    10.37 81.74
Limpet (checked)         0.33     0.10    7.50    0.44     8.15 89.89
Sea anenome              0.40     0.00    4.91    0.30     5.33 95.22
```

```
Groups AI  and  CA
Average dissimilarity = 76.10

                     Group AI  Group CA
Species              Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Littorina saxatilis      2.03      2.31    33.99     1.12     44.67  44.67
Littorina littoria       0.82      0.87    16.83     0.72     22.12  66.79
Littorina obtusata       0.45      0.47     9.05     0.58     11.89  78.68
Limpet (checked)         0.68      0.00     5.53     0.45      7.27  85.95
Sea anenome              0.25      0.00     2.83     0.29      3.72  89.67
Mytilus spp.             0.09      0.20     2.08     0.25      2.73  92.40

Groups BI  and  CA
Average dissimilarity = 76.80

                     Group BI  Group CA
Species              Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Littorina saxatilis      1.57      2.31    37.78     1.14     49.20  49.20
Littorina littoria       0.35      0.87    16.19     0.66     21.08  70.28
Littorina obtusata       0.15      0.47     8.66     0.50     11.28  81.56
Sea anenome              0.40      0.00     3.32     0.27      4.32  85.88
Limpet (checked)         0.33      0.00     3.24     0.35      4.22  90.09

Groups BN  and  CA
Average dissimilarity = 91.41

                     Group BN  Group CA
Species              Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Littorina saxatilis      0.48      2.31    49.60     1.38     54.26  54.26
Littorina littoria       0.00      0.87    19.20     0.65     21.01  75.27
Littorina obtusata       0.15      0.47    10.57     0.55     11.57  86.83
Carcinus maenus          0.25      0.05     6.44     0.36      7.05  93.88

Groups AI  and  KC
Average dissimilarity = 72.60

                     Group AI  Group KC
Species              Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Littorina saxatilis      2.03      2.73    30.44     1.13     41.93  41.93
Littorina littoria       0.82      1.47    18.88     0.88     26.00  67.93
Littorina obtusata       0.45      0.42     8.44     0.47     11.63  79.56
Limpet (checked)         0.68      0.00     4.64     0.47      6.39  85.95
Carcinus maenus          0.05      0.26     3.29     0.34      4.53  90.48

Groups BI  and  KC
Average dissimilarity = 74.05

                     Group BI  Group KC
Species              Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Littorina saxatilis      1.57      2.73    33.28     1.11     44.94  44.94
Littorina littoria       0.35      1.47    19.48     0.85     26.31  71.26
Littorina obtusata       0.15      0.42     7.74     0.41     10.45  81.70
Carcinus maenus          0.15      0.26     4.24     0.41      5.73  87.43
sea anenome              0.40      0.00     2.85     0.26      3.85  91.28
```

```
Groups BN  and  KC
Average dissimilarity = 90.86

                     Group BN  Group KC
Species              Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Littorina saxatilis      0.48      2.73    46.29     1.40     50.94  50.94
Littorina littoria       0.00      1.47    24.50     0.88     26.97  77.91
Littorina obtusata       0.15      0.42     9.39     0.42     10.33  88.24
Carcinus maenus          0.25      0.26     7.09     0.47      7.80  96.04

Groups CA  and  KC
Average dissimilarity = 62.49

                     Group CA  Group KC
Species              Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Littorina saxatilis      2.31      2.73    28.67     1.11     45.88  45.88
Littorina littoria       0.87      1.47    18.25     0.90     29.21  75.08
Littorina obtusata       0.47      0.42     8.53     0.52     13.65  88.73
Carcinus maenus          0.05      0.26     3.09     0.34      4.95  93.69

Groups AI  and  WI
Average dissimilarity = 77.88

                     Group AI  Group WI
Species              Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Littorina saxatilis      2.03      1.90    28.24     1.02     36.26  36.26
Littorina obtusata       0.45      1.22    16.72     0.65     21.46  57.72
Littorina littoria       0.82      0.66    11.89     0.72     15.27  73.00
Limpet (checked)         0.68      0.26     6.62     0.57      8.50  81.50
Carcinus maenus          0.05      0.32     3.67     0.39      4.72  86.22
sea anenome              0.25      0.12     3.49     0.36      4.49  90.70

Groups BI  and  WI
Average dissimilarity = 79.19

                     Group BI  Group WI
Species              Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Littorina saxatilis      1.57      1.90    30.80     1.01     38.89  38.89
Littorina obtusata       0.15      1.22    17.73     0.63     22.38  61.27
Littorina littoria       0.35      0.66    10.18     0.66     12.86  74.13
Limpet (checked)         0.33      0.26     5.03     0.50      6.35  80.48
Carcinus maenus          0.15      0.32     4.69     0.45      5.93  86.41
sea anenome              0.40      0.12     4.26     0.34      5.38  91.79

Groups BN  and  WI
Average dissimilarity = 91.24

                     Group BN  Group WI
Species              Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Littorina saxatilis      0.48      1.90    38.75     1.10     42.47  42.47
Littorina obtusata       0.15      1.22    22.56     0.67     24.73  67.20
Littorina littoria       0.00      0.66     9.59     0.63     10.51  77.71
Carcinus maenus          0.25      0.32     8.32     0.49      9.12  86.83
Limpet (checked)         0.10      0.26     4.55     0.41      4.99  91.82
```

```
Groups CA  and  WI
Average dissimilarity = 71.18

                     Group CA  Group WI
Species              Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Littorina saxatilis      2.31      1.90    28.67     1.04     40.28  40.28
Littorina obtusata       0.47      1.22    16.40     0.69     23.03  63.31
Littorina littoria       0.87      0.66    13.05     0.75     18.33  81.64
Carcinus maenus          0.05      0.32     3.43     0.39      4.82  86.46
Limpet (checked)         0.00      0.26     2.30     0.36      3.23  89.68
Mytilus spp.             0.20      0.00     1.34     0.20      1.88  91.56

Groups KC  and  WI
Average dissimilarity = 66.99

                     Group KC  Group WI
Species              Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Littorina saxatilis      2.73      1.90    24.77     1.09     36.97  36.97
Littorina littoria       1.47      0.66    15.73     0.90     23.48  60.46
Littorina obtusata       0.42      1.22    14.40     0.69     21.50  81.96
Carcinus maenus          0.26      0.32     4.79     0.48      7.14  89.10
Limpet (checked)         0.00      0.26     2.01     0.37      3.00  92.10
```

SESSILE SPECIES

BENTHIC SESSILE SPECIES

```
Groups AI  and  BI
Average dissimilarity = 71.88

                      Group AI Group BI
Species               Av.Abund Av.Abund  Av.Diss  Diss/SD  Contrib% Cum.%
Hildenbrandia rubra       2.77     3.74    30.63     1.23     42.61 42.61
Green encrusting algae   0.23     0.80     7.28     0.57     10.13 52.75
Ulva spp.                 0.74     0.27     6.40     0.57      8.90 61.65
Fucus spp.                0.49     0.36     6.16     0.61      8.57 70.22
Red foliose algae         0.44     0.27     6.10     0.55      8.49 78.71
Semibalanus balanoides   0.08     0.60     5.54     0.41      7.71 86.41
Pink encrusting algae     0.37     0.10     3.76     0.40      5.23 91.65

Groups AI  and  BN
Average dissimilarity = 86.72

                        Group AI  Group BN
Species                 Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib% Cum.%
Hildenbrandia rubra         2.77      1.00    28.78     1.13     33.19 33.19
Fucus spp.                  0.49      0.85    11.84     0.74     13.66 46.84
Ulva spp.                   0.74      0.56    10.43     0.62     12.03 58.87
Semibalanus balanoides      0.08      0.73     9.29     0.68     10.72 69.59
Green filamentous algae    0.32      0.60     8.10     0.47      9.34 78.93
Green encrusting algae      0.23      0.48     6.13     0.60      7.07 86.00
Red foliose algae           0.44      0.06     5.08     0.44      5.86 91.86
```

Groups BI and BN

```
Average dissimilarity = 82.34

                          Group BI Group BN
Species                   Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Hildenbrandia rubra           3.74     1.00   32.40    1.30    39.35 39.35
Semibalanus balanoides        0.60     0.73   11.03    0.77    13.40 52.75
Fucus spp.                    0.36     0.85    9.79    0.76    11.89 64.63
Green encrusting algae        0.80     0.48    9.26    0.72    11.25 75.89
Ulva spp.                     0.27     0.56    7.08    0.59     8.59 84.48
Green filamentous algae       0.07     0.60    5.83    0.39     7.08 91.56
```

Groups AI and CA

```
Average dissimilarity = 86.88

                          Group AI Group CA
Species                   Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Hildenbrandia rubra           2.77     2.29   42.03    1.29    48.38 48.38
Semibalanus balanoides        0.08     0.94   14.48    0.67    16.66 65.05
Ulva spp.                     0.74     0.00    6.06    0.44     6.98 72.02
Red foliose algae             0.44     0.00    5.43    0.43     6.26 78.28
Fucus spp.                    0.49     0.03    5.27    0.42     6.07 84.34
Green filamentous algae       0.32     0.00    4.16    0.34     4.79 89.13
Pink encrusting algae         0.37     0.00    4.11    0.35     4.73 93.87
```

Groups BI and CA

```
Average dissimilarity = 81.96

                           Group BI Group CA
Species                    Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Hildenbrandia rubra            3.74     2.29   42.62    1.40    52.00 52.00
Semibalanus balanoides         0.60     0.94   15.13    0.74    18.46 70.46
Green encrusting algae         0.80     0.00    7.99    0.49     9.75 80.21
Fucus spp.                     0.36     0.03    5.28    0.45     6.45 86.65
Red foliose algae              0.27     0.00    4.69    0.38     5.72 92.37
```

Groups BN and CA

```
Average dissimilarity = 84.81

                          Group BN Group CA
Species                   Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Hildenbrandia rubra           1.00     2.29   25.63    0.90    30.22 30.22
Semibalanus balanoides        0.73     0.94   17.62    0.82    20.78 51.00
Fucus spp.                    0.85     0.03   14.68    0.68    17.31 68.31
Ulva spp.                     0.56     0.00    9.32    0.46    10.99 79.30
Green filamentous algae       0.60     0.00    7.52    0.35     8.87 88.17
Green encrusting algae        0.48     0.00    6.34    0.53     7.47 95.64
```

```
Groups AI  and  KC
Average dissimilarity = 78.34

                        Group AI Group KC
Species                 Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Semibalanus balanoides      0.08     4.65   32.01    2.08    40.86 40.86
Hildenbrandia rubra         2.77     3.12   20.37    1.23    26.00 66.86
Green encrusting algae      0.23     0.90    6.99    0.80     8.93 75.79
Pink encrusting algae       0.37     0.63    5.67    0.69     7.24 83.03
Ulva spp.                   0.74     0.00    3.78    0.43     4.82 87.85
Fucus spp.                  0.49     0.06    2.94    0.48     3.76 91.61

Groups BI  and  KC
Average dissimilarity = 68.80

                        Group BI Group KC
Species                 Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Semibalanus balanoides      0.60     4.65   27.94    1.83    40.61 40.61
Hildenbrandia rubra         3.74     3.12   20.94    1.34    30.43 71.04
Green encrusting algae      0.80     0.90    8.17    0.93    11.88 82.92
Lithothamnion               0.10     0.63    4.45    0.61     6.47 89.39
Fucus spp.                  0.36     0.06    2.58    0.57     3.75 93.13

Groups BN  and  KC
Average dissimilarity = 79.43

                        Group BN Group KC
Species                 Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Semibalanus balanoides      0.73     4.65  29.45     1.83    37.08 37.08
Hildenbrandia rubra         1.00     3.12  22.41     1.20    28.22 65.29
Green encrusting algae      0.48     0.90   7.83     0.90     9.86 75.15
Fucus spp.                  0.85     0.06   6.09     0.82     7.67 82.82
Lithothamnion               0.00     0.63   4.56     0.59     5.74 88.56
Ulva spp.                   0.56     0.00   3.90     0.54     4.92 93.48

Groups CA  and  KC
Average dissimilarity = 74.92

                        Group CA Group KC
Species                 Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Semibalanus balanoides      0.94     4.65  32.38     1.63    43.22 43.22
Hildenbrandia rubra         2.29     3.12  28.31     1.32    37.78 81.00
Green encrusting algae      0.00     0.90   8.19     0.75    10.93 91.93

Groups AI  and  WI
Average dissimilarity = 70.22

                       Group AI Group WI
Species                Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Hildenbrandia rubra        2.77     2.75   29.21    1.13    41.60 41.60
Green encrusting algae     0.23     0.77    8.30    0.68    11.82 53.42
Ulva spp.                  0.74     0.44    8.26    0.56    11.77 65.19
Fucus spp.                 0.49     0.39    6.90    0.63     9.83 75.03
Red foliose algae          0.44     0.14    5.26    0.45     7.50 82.52
Lithothamnion              0.37     0.30    5.24    0.46     7.46 89.98
Green filamentous algae    0.32     0.06    3.36    0.38     4.78 94.76
```

```
Groups BI  and  WI
Average dissimilarity = 66.39

                        Group BI Group WI
Species                 Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Hildenbrandia rubra         3.74     2.75   29.02    1.25    43.72 43.72
Green encrusting algae      0.80     0.77   10.58    0.78    15.94 59.66
Fucus spp.                  0.36     0.39    5.86    0.64     8.83 68.49
Semibalanus balanoides      0.60     0.04    5.61    0.42     8.45 76.94
Ulva spp.                   0.27     0.44    5.41    0.52     8.15 85.09
Red foliose algae           0.27     0.14    4.39     0.42    6.62 91.71

Groups BN  and  WI
Average dissimilarity = 82.67

                       Group BN Group WI
Species                Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Hildenbrandia rubra        1.00     2.75   29.75    1.29    35.99 35.99
Fucus spp.                 0.85     0.39   11.01    0.76    13.32 49.30
Green encrusting algae     0.48     0.77   10.22    0.81    12.37 61.67
Ulva spp.                  0.56     0.44    9.46    0.59    11.44 73.11
Semibalanus balanoides     0.73     0.04    9.28    0.72    11.23 84.33
Green filamentous algae    0.60      0.06    6.01   0.37     7.27 91.60

Groups CA  and  WI
Average dissimilarity = 84.91

                        Group CA Group WI
Species                 Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Hildenbrandia rubra         2.29     2.75   43.22    1.47    50.89 50.89
Semibalanus balanoides      0.94     0.04   14.19    0.70    16.71 67.60
Green encrusting algae      0.00     0.77    9.60    0.64    11.30 78.90
Fucus spp.                  0.03     0.39    6.32    0.48     7.44 86.34
Ulva spp.                   0.00     0.44    5.42    0.36     6.39 92.73

Groups KC  and  WI
Average dissimilarity = 72.73

                        Group KC Group WI
Species                 Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Hildenbrandia rubra         4.65     0.04   32.93    2.29    45.28 45.28
Red encrusting algae        3.12     2.75   18.57    1.21    25.53 70.81
Green encrusting algae      0.90     0.77    8.37    0.96    11.51 82.33
Pink encrusting algae       0.63     0.30    5.49    0.66     7.55 89.88
Fucus spp.                  0.06     0.39    2.84    0.65     3.91 93.79
```

EPIPHYTIC SESSILE SPECIES

```
Groups AI  and  BI
Average dissimilarity = 79.19

                         Group A Group BI
Species                 Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Vertebrata lanosa           0.63     0.59   40.64    1.05    51.31 51.31
Dynamena pumila (hydroid)   0.47     0.30   22.43    0.82    28.32 79.63
Elachista sp.               0.13     0.17   10.97    0.46    13.85 93.49

Groups AI  and  BN
Average dissimilarity = 76.54

                        Group AI Group BN
Species                 Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Vertebrata lanosa           0.63     0.83   45.71    1.14    59.72  59.72
Dynamena pumila (hydroid)   0.47     0.04   16.55    0.61    21.62  81.33
Elachista sp.               0.13     0.05    7.00    0.34     9.15  90.48

Groups BI  and  BN
Average dissimilarity = 77.22

                        Group BI Group BN
Species                 Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Vertebrata lanosa           0.59     0.83   47.19    1.18    61.11 61.11
Dynamena pumila (hydroid)   0.30     0.04   12.52    0.56    16.21 77.33
Elachista sp.               0.17     0.05    9.33    0.43    12.09 89.42
Ulva spp.                   0.03     0.17    4.69    0.33     6.07 95.49

Groups AI  and  CA
Average dissimilarity = 98.61

                        Group AI Group CA
Species                 Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Vertebrata lanosa           0.63     0.00   42.75    1.03    43.36 43.36
Dynamena pumila (hydroid)   0.47     0.14   23.80    0.74    24.13 67.49
Spirorbis sp.               0.00     0.29   14.67    0.51    14.87 82.36
Elachista sp.               0.13     0.00    6.51    0.29     6.60 88.96
Fucus spp. (on rockweed)    0.00     0.17    5.47    0.31     5.55 94.51

Groups BI  and  CA
Average dissimilarity = 98.74

                        Group BI Group CA
Species                 Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Vertebrata lanosa           0.59     0.00   41.66    1.02    42.19 42.19
Dynamena pumila (hydroid)   0.30     0.14   18.97    0.72    19.21 61.40
Spirorbis sp.               0.00     0.29   15.53    0.52    15.73 77.12
Elachista sp.               0.17     0.00   10.23    0.42    10.36 87.48
Fucus spp. (on rockweed)    0.05     0.17    7.61    0.40     7.71 95.19
```

```
Groups BN  and  CA
Average dissimilarity = 99.71

                       Group BN Group CA
Species                Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Vertebrata lanosa          0.83     0.00   58.55    1.45    58.72 58.72
Spirorbis sp.              0.00     0.29   15.21    0.52    15.25 73.97
Dynamena pumila (hydroid)  0.04     0.14    7.29    0.34     7.31 81.28
Fucus spp. (on rockweed)   0.06     0.17    7.02    0.36     7.04 88.32
Ulva spp.                  0.17     0.00    5.21    0.32     5.22 93.54

Groups AI  and  KC
Average dissimilarity = 74.28

                       Group AI Group KC
Species                Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Vertebrata lanosa          0.63     1.47   48.01    1.25    64.63 64.63
Dynamena pumila (hydroid)  0.47     0.00   12.06    0.56    16.23 80.87
Ectocarpus sp.             0.00     0.24    7.19    0.38     9.68 90.55

Groups BI  and  KC
Average dissimilarity = 75.20

                       Group BI Group KC
Species                Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Vertebrata lanosa          0.59     1.47   49.91    1.29    66.37 66.37
Dynamena pumila (hydroid)  0.30     0.00    8.63    0.52    11.48 77.85
Ectocarpus sp.             0.02     0.24    7.92    0.40    10.54 88.38
Elachista sp.              0.17     0.00    5.41    0.37     7.19 95.58

Groups BN  and  KC
Average dissimilarity = 65.87

                   Group BN  Group KC
Species            Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Vertebrata lanosa      0.83      1.47    49.23     1.25     74.74  74.74
Ectocarpus sp.         0.00      0.24     7.43     0.38     11.28  86.02
Ulva spp.              0.17      0.00     3.33     0.28      5.06  91.08

Groups CA  and  KC
Average dissimilarity = 99.83

                       Group CA Group KC
Species                Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Vertebrata lanosa          0.00     1.47   68.98    1.83    69.10 69.10
Spirorbis sp.              0.29     0.00   10.38    0.47    10.40 79.50
Ectocarpus sp.             0.00     0.24    9.33    0.39     9.34 88.85
Fucus spp. (on rockweed)   0.17     0.09    5.82    0.36     5.83 94.67
```

```
Groups AI  and  WI
Average dissimilarity = 78.82

                       Group AI Group WI
Species                Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Vertebrata lanosa          0.63     0.57   36.03    0.95    45.71 45.71
Dynamena pumila (hydroid)  0.47     0.57   23.42    0.92    29.71 75.42
Elachista sp.              0.13     0.33   12.95    0.57    16.43 91.85

Groups BI  and  WI
Average dissimilarity = 79.50

                       Group BI Group WI
Species                Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Vertebrata lanosa          0.59     0.57   36.57    0.97    46.01 46.01
Dynamena pumila (hydroid)  0.30     0.57   20.82    0.93    26.18 72.19
Elachista sp.              0.17     0.33   14.76    0.63    18.57 90.75

Groups BN  and  WI
Average dissimilarity = 78.85

                       Group BN Group WI
Species                Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Vertebrata lanosa          0.83     0.57   41.74    1.06    52.94 52.94
Dynamena pumila (hydroid)  0.04     0.57   15.93    0.75    20.20 73.14
Elachista sp.              0.05     0.33   11.71    0.56    14.85 87.99
Ulva spp.                  0.17     0.00    3.73    0.29     4.73 92.72

Groups CA  and  WI
Average dissimilarity = 98.37

                       Group CA Group WI
Species                Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Vertebrata lanosa          0.00     0.57   36.37    0.90    36.98 36.98
Dynamena pumila (hydroid)  0.14     0.57   21.85    0.92    22.22 59.19
Spirorbis sp.              0.29     0.00   13.56    0.49    13.78 72.98
Elachista sp.              0.00     0.33   13.29    0.57    13.51 86.49
Fucus spp. (on rockweed)   0.17     0.05    6.37    0.37     6.48 92.97

Groups KC  and  WI
Average dissimilarity = 76.91

                       Group KC Group WI
Species                Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Vertebrata lanosa          1.47     0.57  45.03    1.18    58.55 58.55
Dynamena pumila (hydroid)  0.00     0.57  12.15    0.71    15.80 74.34
Ectocarpus sp.             0.24     0.07   8.03    0.42    10.44 84.78
Elachista sp.              0.00     0.33   7.92    0.51    10.30 95.08
```

MOBILE (TRANSECT) SPECIES

```
Groups AI  and  BI
Average dissimilarity = 58.41

                        Group AI  Group BI
Species                 Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Carcinus maenas             0.10      0.10    16.95     1.07     29.02  29.02
Pleurobrachia pileus        0.02      0.05    12.76     1.02     21.84  50.86
Large ctenophore            0.02      0.04    10.15     0.65     17.37  68.23
Cancer irroratus            0.03      0.00     7.90     0.52     13.52  81.75
Alosa pseudoharengus        0.00      0.03     7.56     0.53     12.93  94.69

Groups AI  and  BN
Average dissimilarity = 42.09

                        Group AI  Group BN
Species                 Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Carcinus maenas             0.10      0.18    20.22     1.13     48.04  48.04
Cancer irroratus            0.03      0.00     7.91     0.54     18.80  66.84
Large ctenophore            0.02      0.02     7.70     0.53     18.28  85.12
Pleurobrachia pileus        0.02      0.00     3.39     0.37      8.06  93.18

Groups BI  and  BN
Average dissimilarity = 52.50

                        Group BI Group BN
Species                 Av.Abund Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Carcinus maenas            0.10      0.18    20.25     1.16     38.58  38.58
Pleurobrachia pileus        0.05      0.00    10.44     0.97     19.89  58.47
Large ctenophore            0.04      0.02     9.83     0.67     18.72  77.19
Alosa pseudoharengus        0.03      0.00     6.59     0.54     12.56  89.75
Gasterosteus aculeatus (3SS)0.01      0.00     2.80     0.37      5.32  95.07

Groups AI  and  CA
Average dissimilarity = 85.01

                  Group AI  Group CA
Species           Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Carcinus maenas       0.10      0.03    44.75     1.23     52.64  52.64
Cancer irroratus      0.03      0.00    13.13     0.50     15.44  68.08
Mysidae sp.           0.00      0.03    10.74     0.56     12.63  80.71
Shrimp                0.00      0.02     5.88     0.37      6.92  87.63
Large ctenophore      0.02      0.00     5.84     0.37      6.87  94.50

Groups BI  and  CA
Average dissimilarity = 86.48

                        Group BI  Group CA
Species                 Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Carcinus maenas             0.10      0.03    30.90     1.23     35.73  35.73
Pleurobrachia pileus        0.05      0.00    15.07     0.93     17.43  53.16
Alosa pseudoharengus        0.03      0.00    11.77     0.48     13.61  66.77
Large ctenophore            0.04      0.00    10.20     0.55     11.80  78.56
Mysidae sp.                 0.00      0.03     9.29     0.54     10.74  89.30
Shrimp                      0.00      0.02     5.12     0.36      5.92  95.22
```

```
Groups BN  and  CA
Average dissimilarity = 83.50

                  Group BN Group CA
Species           Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Carcinus maenas       0.18     0.03   59.70    2.04    71.49 71.49
Mysidae sp.           0.00     0.03    9.24    0.56    11.07 82.55
Large ctenophore      0.02     0.00    5.73    0.37     6.86 89.41
Shrimp                0.00     0.02    5.12    0.37     6.13 95.54
```

```
Groups AI  and  KC
Average dissimilarity = 83.39

                      Group AI Group KC
Species               Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Carcinus maenas           0.10     0.03   51.91    1.24    62.24 62.24
Cancer irroratus          0.03     0.01   16.64    0.57    19.95 82.20
Large ctenophore          0.02     0.00    6.37    0.37     7.64 89.84
Pleurobrachia pileus      0.02     0.00    5.01    0.37     6.00 95.84
```

```
Groups BI  and  KC
Average dissimilarity = 86.48

                      Group BI Group KC
Species               Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Carcinus maenas           0.10     0.03   34.87    1.22    40.32 40.32
Pleurobrachia pileus      0.05     0.00   16.35    0.92    18.90 59.23
Alosa pseudoharengus      0.03     0.00   13.59    0.48    15.72 74.95
Large ctenophore          0.04     0.00   11.02    0.55    12.74 87.69
Gasterosteus aculeatus (3SS)0.01    0.00   4.51      0.37      5.21 92.90
```

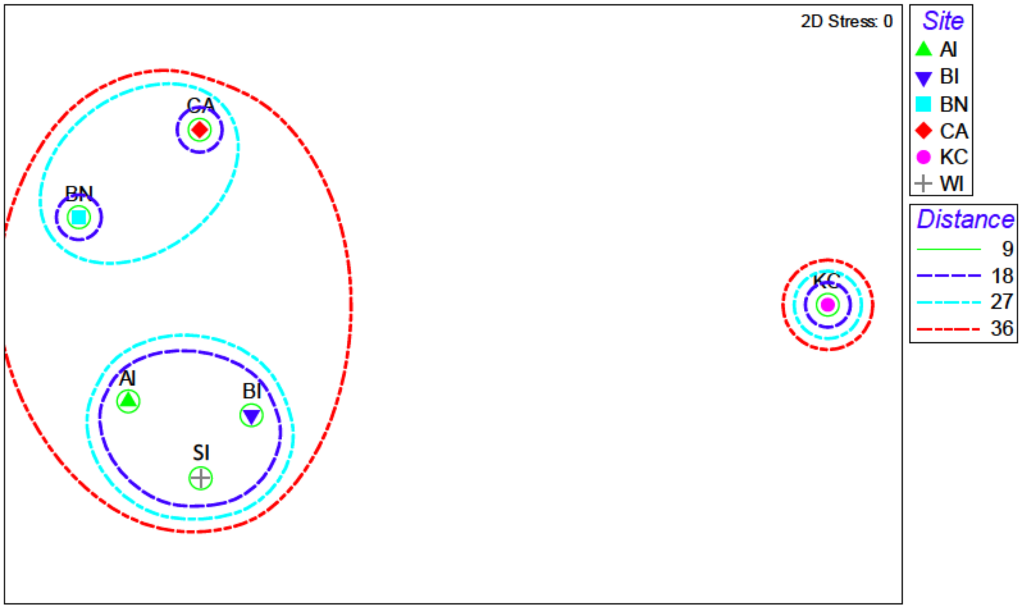
```
Groups BN  and  KC
Average dissimilarity = 83.50

                  Group BN Group KC
Species           Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Carcinus maenas       0.18     0.03   67.17    2.03    80.44 80.44
Large ctenophore      0.02     0.00    6.13    0.37     7.34 87.79
Squid                 0.01     0.00    4.03    0.37     4.82 92.61
```

```
Groups CA  and  KC
Average dissimilarity = 91.84

                 Group CA Group KC
Species          Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Carcinus maenas      0.03     0.03   39.44    0.87    42.94 42.94
Mysidae sp.          0.03     0.00   26.37    0.64    28.71 71.65
Shrimp               0.02     0.00   13.44    0.42    14.64 86.29
Flounder sp.         0.00     0.01    6.30    0.42     6.86 93.14
```

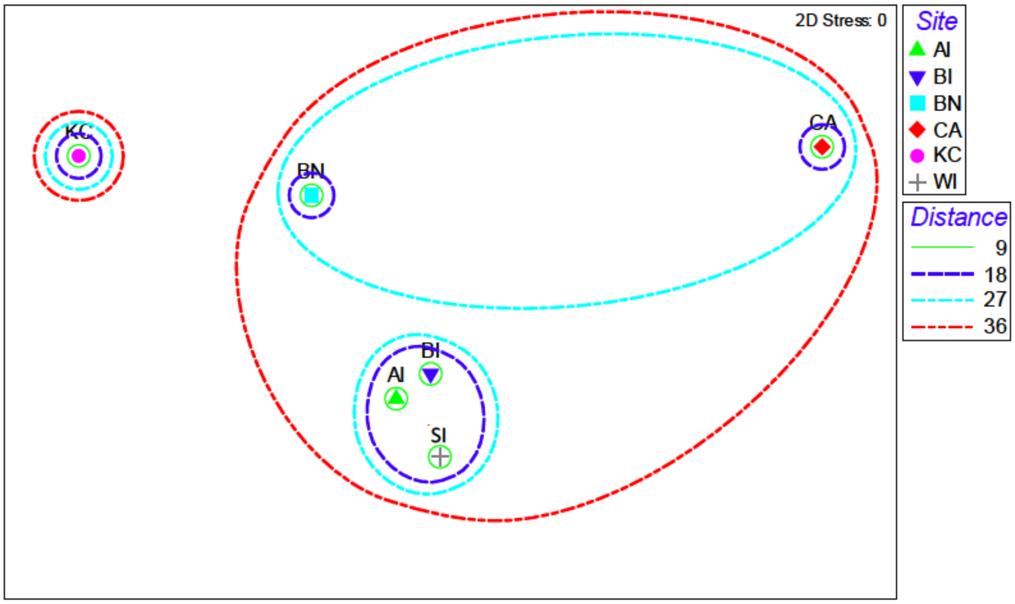
```
Groups AI  and  WI
Average dissimilarity = 59.90

                      Group AI  Group WI
Species               Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Carcinus maenas           0.10      0.13    32.77     0.99     54.71  54.71
Cancer irroratus          0.03      0.00    10.24     0.47     17.09  71.80
Pleurobrachia pileus      0.02      0.02     6.72     0.51     11.22  83.02
Large ctenophore          0.02      0.00     4.73     0.35      7.90  90.91

Groups BI  and  WI
Average dissimilarity = 64.47

                      Group BI Group WI
Species               Av.Abund Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Carcinus maenas           0.10      0.13    25.91     1.12     40.18  40.18
Pleurobrachia pileus      0.05      0.02    13.49     0.94     20.92  61.10
Alosa pseudoharengus      0.03      0.00     9.03     0.44     14.00  75.11
Large ctenophore          0.04      0.00     8.39     0.53     13.01  88.12
Gasterosteus aculeatus (3SS)0.01    0.01    5.32      0.49      8.26  96.38

Groups BN  and  WI
Average dissimilarity = 46.35

                      Group BN Group WI
Species               Av.Abund Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Carcinus maenas           0.18      0.13   30.34      0.83     65.45 65.45
Large ctenophore          0.02      0.00    4.77      0.36     10.28  75.74
Pleurobrachia pileus      0.00      0.02    3.22      0.37      6.96  82.69
Squid                   0.01        0.00    3.06      0.36      6.59  89.29
Gasterosteus aculeatus (3SS)0.00    0.01    2.61      0.37     5.63  94.91

Groups CA  and  WI
Average dissimilarity = 86.53

                      Group CA  Group WI
Species               Av.Abund  Av.Abund  Av.Diss  Diss/SD  Contrib%  Cum.%
Carcinus maenas           0.03      0.13    52.02     1.58     60.12  60.12
Mysidae sp.               0.03      0.00    14.42     0.51     16.67  76.78
Shrimp                    0.02      0.00     7.61     0.35      8.79  85.57
Pleurobrachia pileus      0.00      0.02     4.81     0.39      5.56  91.13

Groups KC  and  WI
Average dissimilarity = 85.53

                      Group KC Group WI
Species               Av.Abund Av.Abund  Av.Diss Diss/SD Contrib%   Cum.%
Carcinus maenas           0.03      0.13    62.09     1.84    72.59   72.59
Pleurobrachia pileus      0.00      0.02     5.51     0.41     6.44   79.03
Gasterosteus aculeatus (3SS)0.00    0.01     4.77     0.41     5.58   84.61
Flounder sp.              0.01      0.00     4.54     0.38     5.30   89.92
Cancer irroratus          0.01      0.00    4.54
```

Appendix 2D – MDS plots illustrating the centroids (i.e. geometric means) of benthic sessile and epiphytic sessile community components. A cluster is present for three of the NB sites (AI, BI, SI) while BN is distanced from the remaining three sites and more similar to CA in NS. KC in NS is farthest removed from all other sites.

BENTHIC SESSILE SPECIES



EPIPYTIC SESSILE SPECIES



Appendix 2E– Output from GLMs, GAMs and Hurdle models explaining the richness or abundance of community components and individual species using structural components of the rockweed canopy and region or site as predictors. Significant factors (indicated by *) and deviance explained (%) by predictor factors are reported for models with best results. Ns (Not significant) indicates that no factors in the model had a significant effect. Results are reported for the following combination of predictors: rockweed biomass (B); plant length (L) and circumference (C) (plant structure); L, C and density (D) (canopy structure); L, C, D and Region (R); and L, C, D and Site (S). Predictor variables are sometimes excluded when the model appears to overfit the data.

	Biomass (B)			**Plant Structure {L, C}**			**Canopy Structure {L, C, D}**			**Canopy Structure and Region**			**Canopy Structure and Site**		
	GLM	**GAM**	**Hurdle**	**GLM**	**GAM**	**Hurdle**	**GLM**	**GAM**	**Hurdle**	**GLM**	**GAM**	**Hurdle**	**GLM**	**GAM**	**Hurdle**
Quadrat richness	Ns 50.7%	-	-	Ns . 50.2%	-	-	Ns 50.4%	-	-	Ns 50.9%	-	-	*C and S 60.0%	-	-
Count (quadrat) species richness	Ns . 50.7%	-	-	Ns 50.8%	-	-	Ns 51.2%	-	-	Ns 50.8%	-	-	*S 50.7%	-	-
Benthic sessile richness	Ns 50.7%	-	-	Ns 50.7%	-	-	*D 51.9%	-	-	*D 51.9%	-	-	*D 56.4%	-	-
Epiphytic sessile richness	Ns 50.4%	-	-	Ns 50.5%	-	-	Ns 50.5%	-	-	*C and R 53.4%	-	-	*C and S 56.1%	-	-
Quadrat fauna abundance	-	*B 6.4 %	-	-	*all 14.9%	-	-	*all 35.3%	-	-	*all 35.9%	-	-	*all 43.4%	-
Benthic % cover	-	*B 6%	-	-	*all 28.7%	-	-	*all 35%	-	-	*all 35.1%	-	-	*all 49.3%	-
Epiphytic % cover	-	*B	-	-	*all	-	-	*all	-	-	*all	-	-	*all	-

		5.3%			7%			19.2%			20.6%			26.2%	
	GLM	**GAM**	**Hurdle**	**GLM**	**GAM**	**Hurdle**	**GLM**	**GAM**	**Hurdle**	**GLM**	**GAM**	**Hurdle**	**GLM**	**GAM**	**Hurdle**
Carcinus maenus	-	-	-	-	-	*all 1.8%	-	-	*L and C 3.3%	-	-	*L, C and R 14.1%	-	-	-
Littorinids (*L. littorina and saxatilis*)	-	*B 7.3%	*B nil	-	*all 20.1%	*all 1.1%	-	*all 43.2 %	*L and C 1.2%	-	*all 45.1 %	*L, C and R 2.6%	-	*all 50.1 %	*L, C and S 13.5%
Littorina obtusata	-	*B 12.2 %	-	-	*all 33.8%	-	-	*all 57.9 %	-	-	*all 59.6 %	-	-	*all 64.6 %	-
Semibalanus balanoides	-	*B 24.2 %	-	-	*all 35.8%	-	-	*all 53.7 %	-	-	all 67.6 %	-	-	*all 85.7 %	-
Chondrus crispus		*B 83.2 %	-	-	*all 100%	-	-	*all 100 %	-	-	-	-	-	…???	-
Green encrusting algae	-	*B 23.4 %	-	-	*all 31.2%	-	-	*all 47.1 %	-	-	*all 52.7 %	-	-	*all 67.2 %	-
Lithothamnion sp.	-	*B 25.8 %	-	-	*all 60.1%	-	-	*all 89.9 %	-	-	*all 93.1 %	-	-	*all except Density - not included) 85.1 %	-

	GLM	GAM	Hurdle	GLM	GAM	Hurdle	GLM	GAM	Hurdle	GLM	GAM	Hurdle	GLM	GAM	Hurdle
Hildenbrandia rubra	-	*B 5.7%	-	-	*all 23.1%	-	-	*all 28.5 %	-	-	*all 28.6 %	-	-	*all 39%	-
Red foliose algae	-	*B 49.0 %	-	-	*all 100% Length alone 42.9%; Circ alone 44.7 %	-	-	*all except Length - not included) 74.9 %	-	-	*all (?) 80.9 %	-	-	NP	-
***Ulva* spp.**	-	*B 20.8 %	-	-	*all 51.8%	-	-	*all 85.9 %	-	-	*all 100 % (overfitting) Density not included 59.8%	-	-	*all except Density - not included) 66.4%	-
Dynamena pumila	-	*B 9.9%	-	-	*all 44.3%	-	-	*all 61.4 %	-	-	*all 100 % Without D 64.7%	-	-	*all (Density not included) 66.4%	-
Vertebrata lanosa	-	*B 14.7 %	-	-	*all 17.6%	-	-	*all 23.6 %	-	-	*all 23.8%	-	-	*all (Density not include	-

d)
45%

	GLM	GAM	Hurdle	GLM	GAM	Hurdle	GLM	GAM	Hurdle	GLM	GAM	Hurdle	GLM	GAM	Hurdle
***Elachista* sp.**	-	*B 21.9 %	-	-	*all 86.2%	-	-	*all 100 % Without length 76.5%	-	-	*all 100 % Without circumference or density 51.3%	-	-	*all (Circumference and density not included) 53%	-
***Fucus* spp.**	-	*B 30.9 %	-	-	*all 40.2%	-	-	*all 61.7 %	-	-	*all 62.4 %	-	-	*all 65.3 %	-

Appendix 3A – Results of SIMPER analysis performed on each component of community composition: Sessile species (further divided into benthic and epiphytic species), mobile (quadrat) species and mobile (transect) species. Groups compared are the unharvested (U) and harvested (H) sides of the bed. SIMPER analysis was performed for each community component both pre-harvest (July) and post-harvest (August). Species reported are those that explained 90% of the dissimilarity between unharvested and harvested sides. Species with Dissimilarity/SD ratios (Diss/SD) greater than 1.3 are considered good discriminating species (Clarke and Warwick 1994); given the relatively low number of species present at our study site and the low number of species that meet the criterion for 'discriminating species', we also considered species with Diss/SD ratios approaching 1.3 (discussed in Chapter 3) and noted all species with Diss/SD ratios ≥ 1.0 (bolded in Appendix).

(1 a) Pre-harvest - Sessile species

```
Groups U  and  H
Average dissimilarity = 45.80

                        Group U Group H
Species                Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Red encrusting algae       3.26     2.98   13.15    1.36   28.71 28.71
Semibalanus balanoides     5.46     3.84   11.27    1.28   24.60 53.32
Vertebrata lanosa          2.16     0.78    7.26    1.43   15.85 69.17
Green encrusting algae     0.34     1.46    6.28    1.27   13.71 82.88
Pink encrusting algae      0.82     0.44    4.51    0.82    9.84 92.72
```

Post-harvest - Sessile species

```
Groups H  and  U
Average dissimilarity = 42.90

                        Group H Group U
Species                Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Hildenbrandia rubra        1.67     2.94   12.49    1.22   29.11 29.11
Lithothamnion sp.          1.12     1.59    8.26    1.08   19.24 48.35
Green encrusting algae     1.30     1.15    7.41    1.04   17.28 65.63
Semibalanus balanoides     4.26     5.38    6.55    1.28   15.26 80.89
Vertebrata lanosa          0.34     0.67    3.00    1.10    6.98 87.88
Elachista sp.              0.58     0.05    2.54    0.97    5.92 93.80
```

(1 b) Pre-harvest - Benthic sessile species

```
Groups U  and  H
Average dissimilarity = 42.53

                        Group U Group H
Species                 Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Hildenbrandia rubra         3.26     2.98   15.64    1.37    36.77 36.77
Semibalanus balanoides      5.46     3.84   13.40    1.29    31.50 68.27
Green encrusting algae      0.34     1.46    7.44    1.25    17.50 85.77
Pink encrusting algae       0.82     0.44    5.19    0.82    12.21 97.98
```

Post-harvest - Benthic sessile species

```
Groups H  and  U
Average dissimilarity = 39.67

                        Group H Group U
Species                 Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Hildenbrandia rubra         1.67     2.94   13.77    1.22    34.72 34.72
Lithothamnion sp.           1.12     1.59    8.94    1.09    22.54 57.26
Green encrusting algae      1.30     1.15    7.96    1.05    20.07 77.33
Semibalanus balanoides      4.26     5.38    7.06    1.30    17.81 95.14
```

(1 c) Pre-harvest - Epiphytic sessile species

```
Groups U  and  H
Average dissimilarity = 62.80

                   Group U  Group H
Species           Av.Abund Av.Abund Av.Diss  Diss/SD  Contrib%  Cum.%
Vertebrata lanosa     2.16     0.78   49.45     1.57     78.74  78.74
Ectocarpus sp.        0.10     0.38   10.70     0.55     17.04  95.78
```

Post-harvest - Epiphytic sessile species

```
Groups H  and  U
Average dissimilarity = 87.03

                        Group H Group U
Species                Av.Abund Av.Abund Av.Diss Diss/SD Contrib% Cum.%
Vertebrata lanosa          0.34     0.67   47.49    1.19    54.57 54.57
Elachista sp.              0.58     0.05   30.20    1.05    34.71 89.28
Fucus spp. (on rockweed)   0.05     0.11    4.84    0.36     5.57 94.84
```

(2) Pre-harvest – Mobile (quadrat) species

```
Groups July U  and  July H
Average dissimilarity = 54.85

                  Group July U Group July H
Species               Av.Abund Av.Abund Av.Diss Diss/SD Contrib%  Cum.%
Littorina saxatilis       2.10     3.36   24.50    1.24    44.66  44.66
Littorina littoria        1.62     1.47   17.10    1.09    31.18  75.84
Littorina obtusata        0.44     0.22    6.22    0.52    11.34  87.18
Carcinus maenus           0.20     0.32    4.42    0.45     8.05  95.23
```

Post-harvest – Mobile (quadrat) species

```
Groups H  and  U
Average dissimilarity = 95.10

                     Group H  Group U
Species             Av.Abund Av.Abund  Av.Diss  Diss/SD  Contrib% Cum.%
Littorina littoria      0.24     0.88    40.69     0.95     42.78 42.78
Littorina saxatilis     0.45     0.40    37.55     0.87     39.48 82.26
Littorina obtusata      0.10     0.00     6.55     0.28      6.88 89.14
Nucella sp.             0.10     0.00     6.55     0.28      6.88 96.03
```

(3) Pre-harvest – Mobile (transect) species

```
Groups U  and  H
Average dissimilarity = 90.00

                  Group U Group H
Species           Av.Abund Av.Abund Av.Diss Diss/SD  Contrib%   Cum.%
Carcinus maenas      0.25     0.25   53.33    1.06    59.26    59.26
Flounder sp.         0.25     0.00   18.33    0.76    20.37    79.63
Cancer irroratus     0.25     0.00   18.33    0.76    20.37   100.00
```

Post-harvest – Mobile (transect) species

```
Groups U  and  H
Average dissimilarity = 87.74

                      Group U  Group H
Species             Av.Abund Av.Abund Av.Diss Diss/SD  Contrib%   Cum.%
Alosa pseudoharengus  0.43     0.25    42.59    0.93     48.54   48.54
Carcinus maenas       0.35     0.35    33.63    0.85     38.32   86.87
Mysidae sp.           0.25     0.00    11.52    0.66     13.13  100.00
```

Appendix 3B – Details of Harvesting Studies from the Literature Review as well as additional studies.

Study	Location	Time of year	Duration	Type of Harvest	Other Factors	Effects of Harvest on plant or bed structure	Effects of Harvest on Community	Effects of other Factors (and cumulative effects)	Note
Fegley 2001 (PhD Thesis)	Mid-coast region of Maine	Harvested in June, sampled every 5-6 weeks	Followed for 2 years post-harvest	1 harvesting event, 3 harvesting regimes (uncut, cut at 18cm, cut at 36 cm); hand shears	-	Increase in number of medium sized shoots (by 108%); increased number of branches at 18cm; increased apical dichotomies; control plants significantly longer (-32%) after 2 years	Short term effects (1-2 years): Decreases in associated species in species and community-level analyses (decreased *Fucus vesiculosus*, *Hildenbrandia rubra* and *Phymutolithon lenormundii and* abundances of *Carcinus maenas*, *Dynamena pumila*, *Halichondria* sp.,and *Littorina obtusata* increased *Nucella lapillus*	-	-
Lazo and Chapman 1996	Southwestern Nova Scotia	Harvest in February or June 1988; plots monitored every 3 months for	Followed for two years post-harvest	Mechanical harvest (Norwegian suction cutter) 4 levels of	Harvesting season (Size class of *Ascophyllum nodosum*)	No significant effect of harvest intensity or duration on growth, but increased growth of *Ascophyllum* in	-	-	Size class specific growth rates provided – authors argue these

		two years		harvesting intensity (biomass estimates): control; low (18 %); medium (60%); high (70%) Mean cut height 20 cm 2 harvesting seasons (summer, winter);		harvested plots; increase in number of reproductive fronds with increased intensity and summer harvest; no effect of harvest on frond breakage or survivorship			will be useful for regulating intervals between harvests Argue for a harvesting regime that targets largest fronds
Ang et al. 1993 Ang et al. 1996	Southwest Nova Scotia	Harvest in September 1991; sampling immediately before and after harvest as well as 1,2 and 3 years after harvest	Monitored for three years after harvest; monitoring of additional sites with varying harvesting histories in summer 1992	Mechanical harvest (Norwegian suction cutter) Ca 80%of the standing stock removed	-	Bimodal population structure (in terms of plant length) became unimodal for two years following harvest, but began returning to bimodal structure in third year; 20-36% plant mortality	-	-	-
Ugarte et al. 2006	Southern New Brunswick	Harvest in summer 2001; monitoring in October 2001, April	Monitoring for two years post-harvest	50% exploitation rate harvest (removal of 50% biomass),	-	Larger plants reduced by up to 55% of their length and 78% of their biomass; Regain of pre-	-	-	-

		2002, August 2002 and August 2003		cutter rake harvest		harvest length took one to >two years			
Ugarte et al. 2010a	Cobscook Bay, Maine	September - October, 2009	One month	ASL contractors, commercial cutter rake hand-harvest		<8% of harvested plants with holdfast; average detached holdfast area was 15.3 mm^2; majority of plants with holgfast weighed <200g	1.32 MT of Littorinids removed as bycatch (Ca 0.044% of littorinids in harvested areas)	-	-
Ugarte 2011	Southern New Brunswick	Harvested samples taken in 2004 from commercially hand-harvested loads; control plants removed between july and August 2004; summer storm inAugust 2004 supplied storm cast plants	Summer 2004	Cutter rake harvest	Storm removal of rockweed	When rake removes part of holdfast (<10% harvested plants), it removes 17.4% of holdfast surface , 63.2 % of the plant biomass and 19.7% of the shoot density	-	Similar effect of storm on clump structure; Coastal storms in New Brunswick have an impact on *Ascophyllum* that is 21 X higher than the annual harvest	Seeley and Schlesinger (2012) point out that storm-cast *Ascophyllum* contains substantially less area of holdfast and decomposes in the marine ecosystem, providing nutrients and food (while harvested *Ascophyllum* is lost to

									the system)
Kelly et al. 2001	Ireland (Connemara and Clew Bay)	Harvested in May 1998, monitored at six time points in 18 months	18 months	Intensive hand harvesting (70% cover reduced to 30% and ca 20cm length left); and mechanical harvesting	-	Recovery of *Ascophyllum* cover after 17 months in Connemara and 11 months in Clew Bay	Significant increase in *Fucus vesiculosus* abundance (Connemara) Increased ephemeral algae in midshore possibly facilitated by removal of *Ascophyllum* No detected effect of harvest on species richness Significant reduction in associated sessile animals (sponges, bryozoans) and *Littorina obtusata* (hand-harvest only) No impact on fish or other large mobile epifaunal species	-	In this trial, hand harvesting was determined to be more efficient and cost effective than mechanical harvesting
Sutherland 2005 (indepen	Southern New Brunswic	May-July, 2005	3 months	Commercial harvest in ASL leased	-	*no statistical testing	-	-	-

dent study by Eastern Charlotte Waterways Inc.)	k			beds		Compared to values from six years earlier: average density of *Ascophyllum* lower in 5 of 6 sectors; average site biomass lower in 3 of 6 sectors; average clump (plant) mass lower in 1, same in 1 and higher in 4 sectors; average length higher in 3 sectors			
Gendron (pers. comm. To Sharp and Pringle 1990)	Gulf of St. Lawrence	-	3 years	Harvested to between 15 and 30 cm every 2 or 3 years	-	Recovered 85 % and 93% of biomass for 2 and 3 year harvesting rates respectively after three years	-	-	-
Thomas 1994	Musquash Head, Bay of Fundy, New Brunswick	Clearing in 1979, monthly monitoring gradually changed to yearl by 1986 and ended in 1988	1979 – 1988; surveyed at least annually	Clearing experiment (cut and sterilized 5 m band through intertidal zone, perpendicular to shore)	-	*Ascophyllum* did not return during this decade, replaced by *Fucus* spp.	After 10 years, community typical of exposed shores in North Atlantic and lacking typical components of *Ascophyllum* understory	-	-
Jenkins et al. 2004	Isle of Man (protecte	Initial clearing in November	12 years	Clearing experiment (canopy	Grazing (by limpets)	*Ascophyllum* slow to return; after 12 years, mixed	-	With removal of Asco, decrease in	-

	d rocky shore)	1991; sampled at 6 week intervals for two years, irregularly for next 4 years; one sampling event after 12 years		removed)		assemblage of *Fucus serratus, Fucus vesiculosus* and *Ascophyllum*		cover by red alga turf and increase in area grazed by limpets; after 12 years, 3-6X increase in limpet population	
Cervin et al. 2004	Swedish west coast, sheltered rocky shores	Clearing of plots in April 1997; sampling in April, July and October 1997; November 1998 and 1999; and September 2001	4 years	Clearing experiment (to mimic ice scouring)	Grazing (Littorina spp.)	*Fucus* spp. encroaching, some recruitment of *Ascophyllum* back (independently of herbivores)	Effect of canopy removal on development of intertidal assemblages lasted for 31 months: Short term increases and decreases in species abundances; short term increase in recruitment of *Semibalanus balanoides* and decrease of red alga *Hildenbrandia rubra*; long term increases in abundances; understory conditions restored within 18 months because	Grazer exclusion and canopy removal: short term increase in ephemeral green algae	-

							of fast recruitment and growth of *Fucus* spp.		
Lazo et al. 1994	Southwestern Nova Scotia	Harvested in February or June 1988 (or control); experiment run from March 1989 to April 1990	1 year	Norwegian suction cutter; Experimental harvest plots (16 x 9m); high intensity harvest relative to normal practice	Grazing	Harvesting may increase *Ascophyllum* zygote production (but not recruitment)	-	Grazing has a highly significant result on zygote recruitment	-
Beal et al. 2011	Jonesport Maine	'Before' and 'After' sampling in June; sampling 38 days after harvest	June-August, 2011	Imitation of commercial harvest, cutter rake harvest; 17-23% biomass removed	-	38 days after harvest, biomass not significantly different in treatment and control plots	No significant effect of harvest on biomass of *L littorea*, *L obtusata* (two most abundant macro-invertebrates)	-	-
Trott and Larsen (2012 report online)	Cobscook Bay, Maine	'Before' assessment in July 2008; 'After' harvest assessment in September 2008	July-September, 2008	Imitation of commercial harvest: professional harvester from Acadian Seaplants Limited (New Brunswick), cutter rake	-	*Ascophyllum* biomass greater after harvest	No effect of harvest on species richness or abundance (except possibly for epifaunal richness); species assemblages affected by harvesting (at level of 65% community similarity);	-	-

				harvest			No effect of harvest on abundance of *Littorina* spp.		
Boaden and Dring 1980	Northern Ireland	Trial harvest in August 1976, Monitoring in 1979	2.5 years	Harvested within 10-15 cm of holdfast	-	Sediment in area was coarser; *Ascophyllum* intermodal length and lateral branching were increased; cut areas have 20% less *Ascophyllum* cover; Significantly more *Fucus spp.* Predict 80% recovery of entire Ascophyllum community within 4 years	After 2.5 years, lower densities of *Mytilus* and higher *Patella* (limpet) densities with smaller mean size; lower under-boulder fauna (e.g. barnacles and sponges) than control area – total number of under-boulder animals reduced by nearly 2/3; significantly more *Ulva* In 1999, differences in algal communities ans limpet numbers between cut and uncut areas (Christine Maggs, pers. comm. in McLaughlin et al. 2006)	-	-
Black and Miller 1991	Lower Argyle, Nova Scotia	Six monthly fish captures between June and	Six months	Cleared areas	-	-	No adverse effects of removal of patches of *Ascophyllum* on	-	Rangeley (1994) critiqued conclusion

(Also Black and Miller 1986)		October					fishes: Number and weight of fish not different between cleared and control areas; Cunner had more food in stomachs when leaving control areas (sculpins did not)		(claiming sampling biases, errors in design of experiment and low statistical power) and Black and Miller (1994) responded
Vadas and Wright 1986	-	-	-	Clearing experiment	-	*Fucus* spp. were first to colonize, but *Ascophyllum* eventually dominated moderately exposed and sheltered shores after six years	-	-	-
Sharp 1987	Review of harvesting in Nova Scotia, Canada	-	Harvest from 1960s to 1980s discussed	Discussion of Aquamarine Harvester, Norwegian suction cutter, and hand rake cutter	-	Recovery to pre-harvest biomass takes 2.5 to 3 years; Yearly experimental harvests (cut to 15-25 cm) leave successively lower biomass; recovery depends on growth of basal shoots and lateral branching on cut shoots	-	-	-

Sharp et al. 1998	Nova Scotia and New Brunswick, Canada	-	Describing commercial harvest regime in Canada in the 1990s	Commercial cutter rake hand-harvest, 17% of standing crop removed annually	-	Average height of stumps 52-57 cm Total cover not affected	Minor impact from removal of *Littorina* spp. as bycatch - <10% of landings for the directed periwinkle harvest and <1% of periwinkle biomass	-	-
Sharp et al. 2006	Nova Scotia and New Brunswick, Canada	-	Describing commercial harvest regime in Canada since the mid 1990s	Commercial cutter rake harvest, 17% of standing crop removed annually	-	No detection of changes in *Ascophyllum* bed structure at a landscape scale <1% annual productivity of the Bay of Fundy removed by this harvest	-Minor impact from removal of annelids and *Littorina spp.* in bycatch -Indirect community effects and ecosystem effects uncertain	-	-
McEachreon 2000	New Brunswick, Canada	-	3 years (1996-1999) of monitoring data	Compliance monitoring for the NB rake cutter Rockweed Fishery	-	20% of harvest sample by weight was holdfast or basal tissue; Cutting height mean of $\geq$ 25cm and min 12.5 cm mostly adhered to	Highly variable bycatch Relatively low levels of *L. littorea* in bycatch	-	-
Printz 1956 (as described by Vandermeulen	-	-	2 years	Experimental sickle hand harvest: left 5, 15 and 25 cm	-	After 2 years, 5 cm – no recovery, eventual mortality; 15 cm – some recovery; 25 cm – full recovery	-	-	-

2013)									
Keser et al. 1981 (as described by Lazo and Chapman 1996 and Vandermeulen 2013)	Maine, USA	-	3 annual harvests, successive years	Experimental harvest: cut at holdfast, 15 or 25 cm	Littorinid grazers	Increased *Fucus vesiculosus* where harvested to holdfast; decreased biomass on 15 and 25 cm treatments; After 3 years, surface cuts recovered 8% or initial biomass and cuts at 15 or 25 cm recovered 62% biomass Yearly harvests result in decreased yields *of Ascophyllum*	-	Grazing by Littorina littorea slowed recovery of *Ascophyllum* after removal	-
Keser and Larson 1984	-	-	-	Clearing experiment	-	After 16 months, more *Fucus* spp., *Ascophyllum* 3-4 cm high covered 52% of the area	-	-	-
MacFarlene (1952)	Shelburne and Yarmouth counties, Nova Scotia (255	Summer 1948, 1949 and 1950	3 consecutive summers	Observations about the 'commercial' harvest in place in Nova Scotia	In non-heavily harvested areas, Yarmouth – Shelburne area has max standing	Observation: *Fucus vesiculosus* encroaches in overharvested areas	-	-	-

	sites)				stocks ca 32 wet kg m^{-2}, plants often 180-210 cm long				
Seip 1980	Computational model	-	-	Modelled a variety of harvest intensities A cut that leaves 10 cm high stumps corresponds to leaving 2% of biomass (intensity of the hand cut harvest in Norway pre-1980)	-	Predicts that harvested every 2, 3 and 4 years require the residual biomass of 20-30%, 8-10% and 3-4% respectively; if the rocks are scraped, could take many more years	-	-	-
Walker 1948 (As described in Burrows et al. 2010)	Orkney, Scotland	August 1946, September 1947, August 1948	Three years (three successive cuts)	Four cutting heights: 5.1 cm, 12.7 cm, 20.3 cm, 27.9 cm	-	Yields after two years greatest for 27.9 cm cutting height (Ca 50% of the plant left unharvested)	-	-	-
Kerin 1998 (Master's Thesis)	Letite, New Brunswick	July 1996, monthly sampling thereafter for 13 months	13 months	Experimental rake cutter hand-harvest	-	N:P, C:N and C:P ratios below cutting points similar to mid-sections of uncut plants (not to	-	-	-

						apical growth areas) – all regrowth due to lateral branching			
Tyler 1994 (as described by Burrows et al. 2010)	Outer Hebrides, Scotland	Harvest in July-August 1996	3-5 years	Hand sickle harvest Cut as close to rock as possible	-	At recently harvested sites, significantly fewer holdfasts than at control sites (*Ascophyllum* mortality); Greater number of sporlings ; significantly lower *Ascophyllum* cover; significantly higher intermodal length	*Fucus vesiculosus* and *Ulva* cover were significantly higher	-	-
Philippi et al. 2014	Maine, USA	May – October 2011 and 2012, point sampling in 2013	2 x six months	Experimental hand-sheared and commercial hand/rake harvest Cut at 20.3 cm, 40.6 cm (Maine legal cut)	-	-	Differences in abundances of mobile macrofauna in experimental but not commercial harvest; No significant effects on infauna; inconsistent significant effects on sediment characteristics	-	-

Appendix 3C – PerMANOVA output for effect of Side of bed on (1) plant metrics, (2) richness and abundance of community components and (3) diversity of community components. Significant p-values (≤0.05) are bolded.

Table 1. One-factor perMANOVA results for the effect of Side of bed (in July and again in August) on quadrat averages of plant Length, Circumference, Mass, Density and Biomass (kg m^{-2}), as well as on individual measures of plant Length, Circumference, and Mass. Sqrt-V values are unbiased estimates of the contribution to variance of Site and the residuals in the model. Variance explained (Var) is given by [(SS Factor/SS Total) x 100] and, while more biased than sqrt-V, is included since it is a more intuitive measure of relative effect size (Howell 2002). The degrees of freedom (df) total to 19 for average metrics and 160 or 161 for individual metrics. Significant p-values are shown in bold.

	Source	**Fixed factor: Side of bed (July)**	**Res**	**Fixed factor: Side of bed (August)**	**Res**
	df	**1**	**18**	**1**	**18**
Average length (cm)	**Pseudo-F**	3.630 e-2		2.150	
	P	0.850		0.120	
	sqrt-V	-0.320	1.030	0.330	0.970
	Var	0.2	99.80	10.6	89.4
Average circumference (cm)	**Pseudo-F**	1.790 e-2		2.730	
	P	0.900		0.130	
	sqrt-V	-0.320	1.030	0.400	0.960
	Var	0.1	99.9	13.2	86.8
Average mass (g)	**Pseudo-F**	3.110e-5		1.840	
	P	1.000		0.210	
	sqrt-V	-0.330	1.03	0.280	0.980
	Var	<0.1	99.99	9.3	90.7
Density (# m^{-2})	**Pseudo-F**	8.100 e-2		0.550	
	P	0.830		0.530	
	sqrt-V	-0.310	1.03	-0.220	1.010
	Var	0.5	99.5	3	97
Biomass (kg m^{-2})	**Pseudo-F**	6.41e-2		0.810	
	P	0.800		0.420	
	sqrt-V	-0.310	1.030	-0.140	1.010
	Var	0.4	99.6	4.3	95.7
	df	**1**	**160**	**1**	**159**
Individual length (cm)	**Pseudo-F**	2.980e-2		5.333	
	P	0.860		**0.0221**	
	sqrt-V	-0.110	1.000	0.230	0.990
	Var	<0.1	99.99	3.2	96.8
Individual circumference (cm)	**Pseudo-F**	1.420e-2		3.370	
	P	0.900		0.070	
	sqrt-V	-0.110	1.000	0.170	0.990
	Var	<0.1	99.9	2.1	97.9
Individual mass (g)	**Pseudo-F**	2.210e-20.880		2.240	
	P	-0.110		0.140	
	sqrt-V	0.0001	1.000	0.120	1.000
	Var		99.99	1.4	98.6

Table 2. One-factor perMANOVA results for the effect of Side of bed (in July and again in August) on richness and abundance of each community component (benthic, epiphytic, total sessile, mobile (quadrat), and mobile (transect) species). Sqrt-V values are unbiased estimates of the contribution to variance of Site and the residuals in the model. Variance explained (Var) is given by [(SS Factor/SS Total) x 100] and, while more biased than sqrt-V, is included since it is a more intuitive measure of relative effect size (Howell 2002). The degrees of freedom (df) total to 39 or 7 for transects. Significant p-values are shown in bold.

	Source	**Fixed factor: Side of bed (July)**	**Res**	**Fixed factor: Side of bed (August)**	**Res**
	df	**1**	**38**	**1**	**38**
Sessile species richness	**Pseudo-F**	2.650		2.510	
	P	0.170		0.180	
	sqrt-V	0.280	0.980	0.270	0.980
	Var	6.5	93.5	6.2	93.8
Sessile species total percent cover (Abundance)	**Pseudo-F**	7.870		17.23	
	P	**0.006**		**0.0006**	
	sqrt-V	6.460	11.02	6.690	7.420
	Var	17.2	82.8	31.2	68.8
Mobile (quadrat) species richness	**Pseudo-F**	1.800		1.860	
	P	0.170		0.280	
	sqrt-V	3.760	18.700	0.210	0.990
	Var	4.6	95.4	4.7	95.3
Mobile (quadrat) species abundance	**Pseudo-F**	2.270		0.800	
	P	0.200		0.380	
	sqrt-V	0.250	0.980	-2.890	28.660
	Var	5.6	94.4	2.1	97.9
	df	**1**	**6**	**1**	**6**
Mobile (transect) species richness	**Pseudo-F**	0.200		0.860	
	P	1.000		0.700	
	sqrt-V	-0.480	1.060	-0.190	1.010
	Var	3.2	96.8	12.5	87.5
Mobile (transect) species abundance	**Pseudo-F**	0.640		0.160	
	P	0.720		0.650	
	sqrt-V	-0.880	2.920	-1.850	4.030
	Var	9.7	90.3	2.6	97.4

Table 3. One-factor perMANOVA results for the effect of Side of bed (in July and again in August) on diversity (H') of each community component (benthic, epiphytic, total sessile, mobile (quadrat), and mobile (transect) species). Sqrt-V values are unbiased estimates of the contribution to variance of Site and the residuals in the model. Variance explained (Var) is given by [(SS Factor/SS Total) x 100] and, while more biased than sqrt-V, is included since it is a more intuitive measure of relative effect size (Howell 2002). The degrees of freedom (df) total to 39. Significant p-values are shown in bold.

	Source	**Fixed factor: Side of bed (July)**	**Res**	**Fixed factor: Side of bed (August)**	**Res**
	df	**1**	**38**	**1**	**38**
Benthic diversity	**Pseudo-F**	10.330		2.150	
	P	**0.003**		0.150	
	sqrt-V	0.610	0.900	0.240	0.990
	Var	21.4	78.6	5.4	94.6
Epiphytic diversity	**Pseudo-F**	0.450		4.260	
	P	0.610		**0.040**	
	sqrt-V	-0.170	1.010	0.390	0.960
	Var	1.2	98.8	10.1	89.9
Sessile species diversity	**Pseudo-F**	6.640		1.330	
	P	**0.010**		0.270	
	sqrt-V	0.500	0.930	0.130	1.000
	Var	14.9	85.1	3.7	96.3
Mobile (quadrat) species diversity	**Pseudo-F**	1.220		2.110	
	P	0.270		0.490	
	sqrt-V	0.110	1.000	0.230	0.990
	Var	3.1	96.9	5.3	94.7
Mobile (transect) species diversity	**Pseudo-F**	1.000		1.000	
	P	1.000		1.000	
	sqrt-V	9.130 e-9	1.000	-1.050 e-8	1.000
	Var	14.3	85.7	14.3	85.7

Appendix 4A – Additional figures for % Cover of epiphytic species broken down by month.

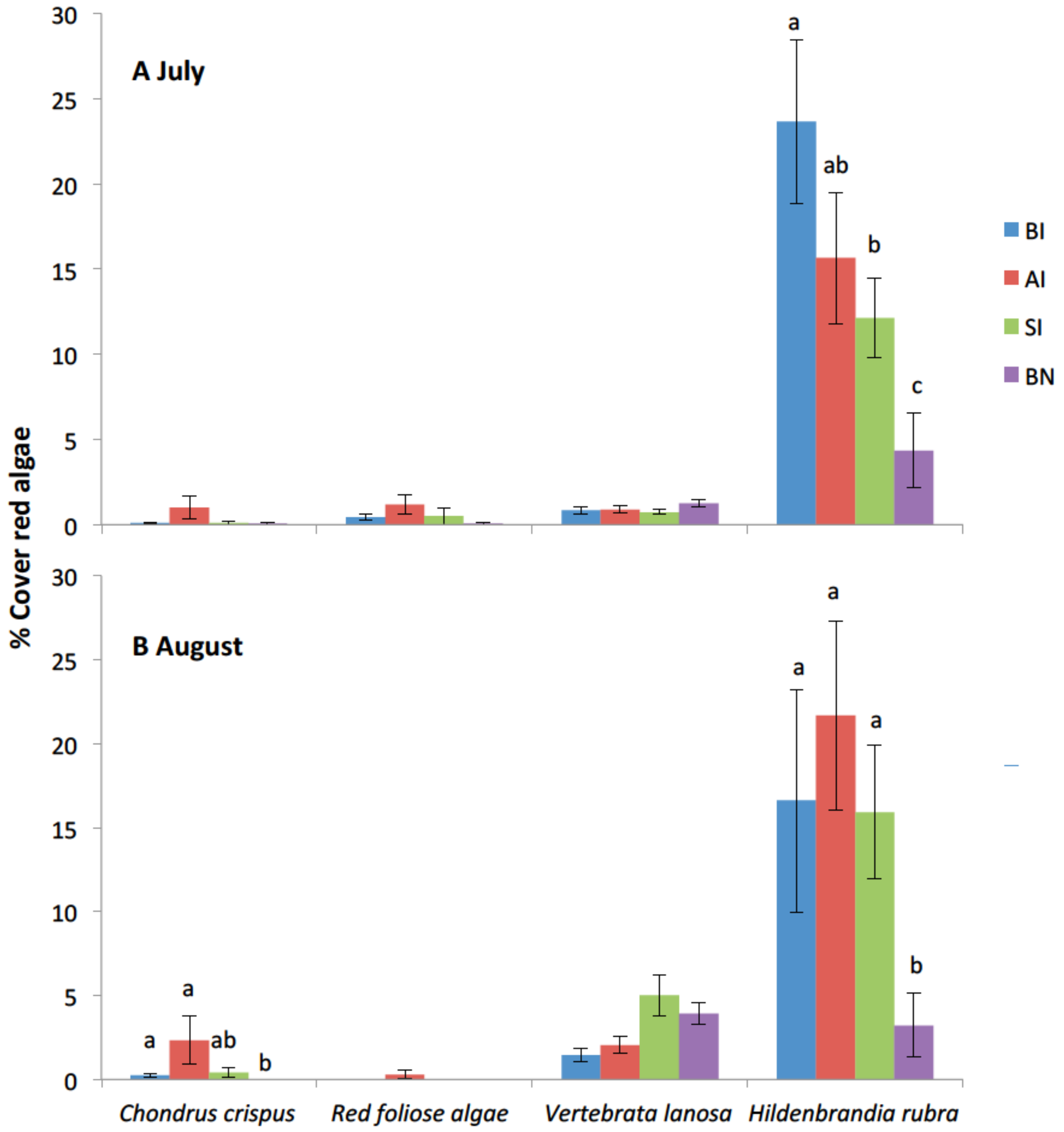


Figure 1. Average abundance and standard error (SE, n = 40) of filter feeders for (A) July and (B) August. Lower case letters indicate significant differences between site within month as well as within site differences across month.

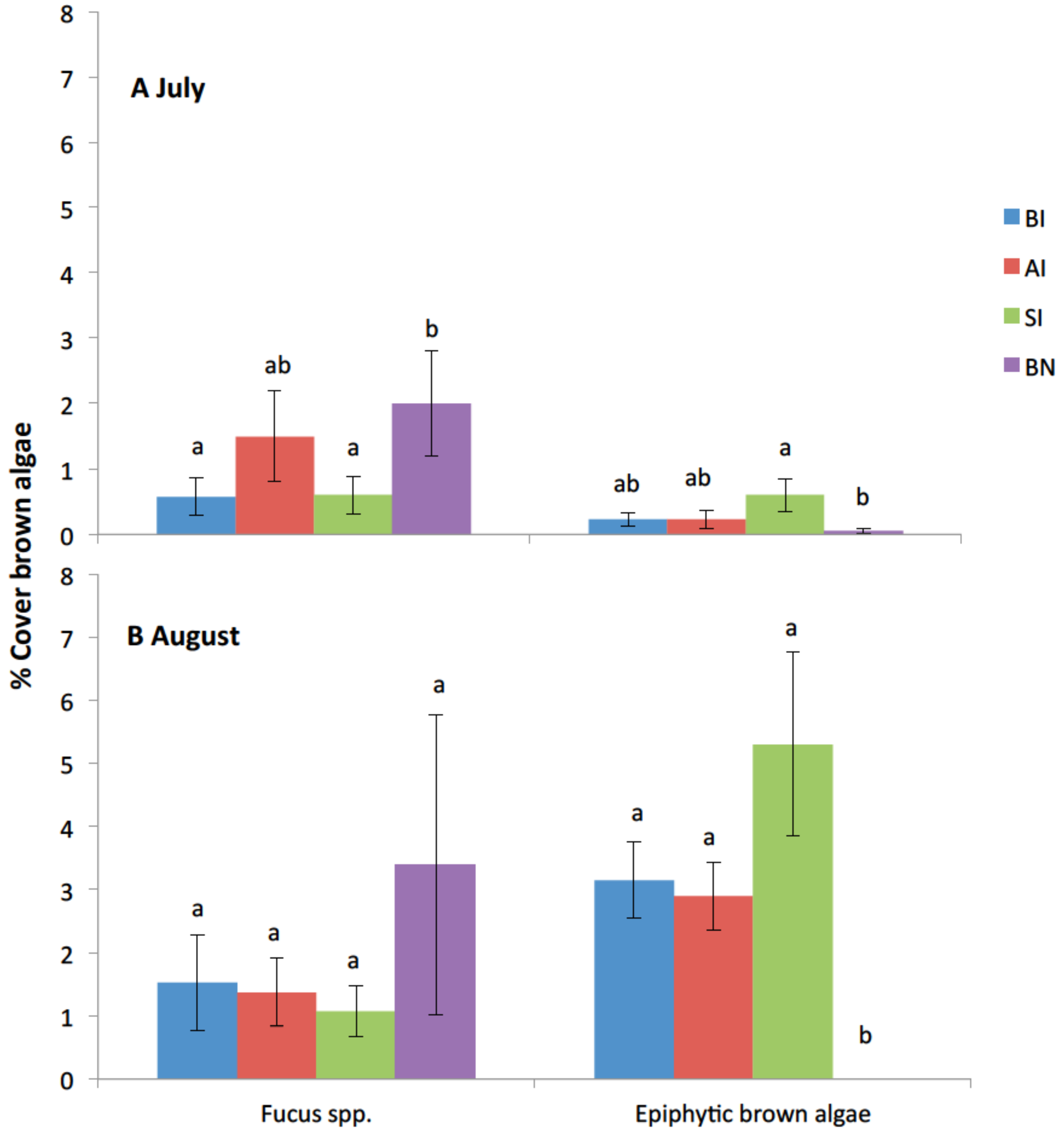


Figure 2. Average abundance and standard error (SE, n = 40) of brown algae for (A) July and (B) August. Lower case letters indicate significant differences between site within month as well as within site differences across month.

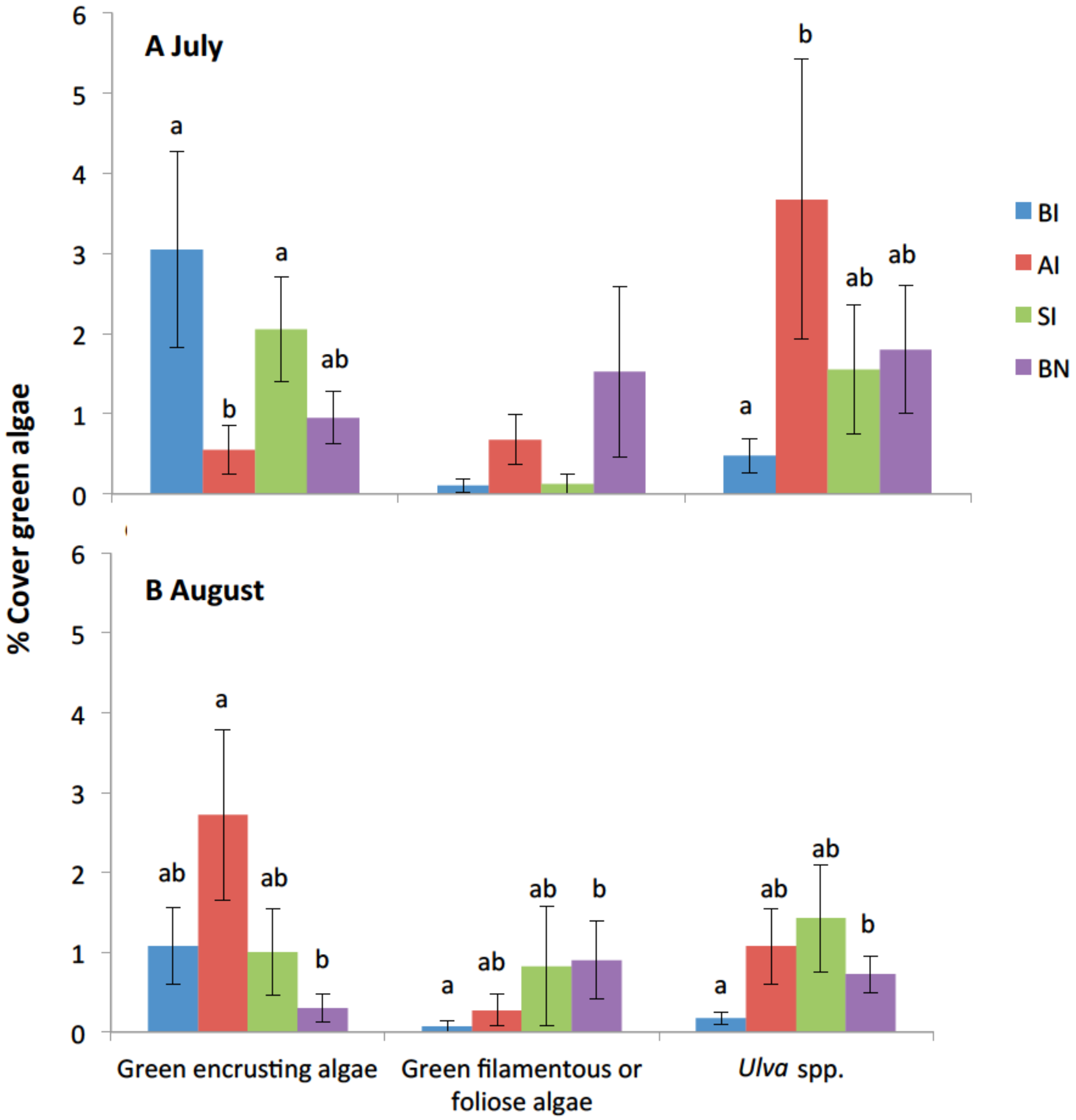


Figure 3. Average abundance and standard error (SE, n = 40) of green algae for (A) July and (B) August. Lower case letters indicate significant differences between site within month as well as within site differences across month.

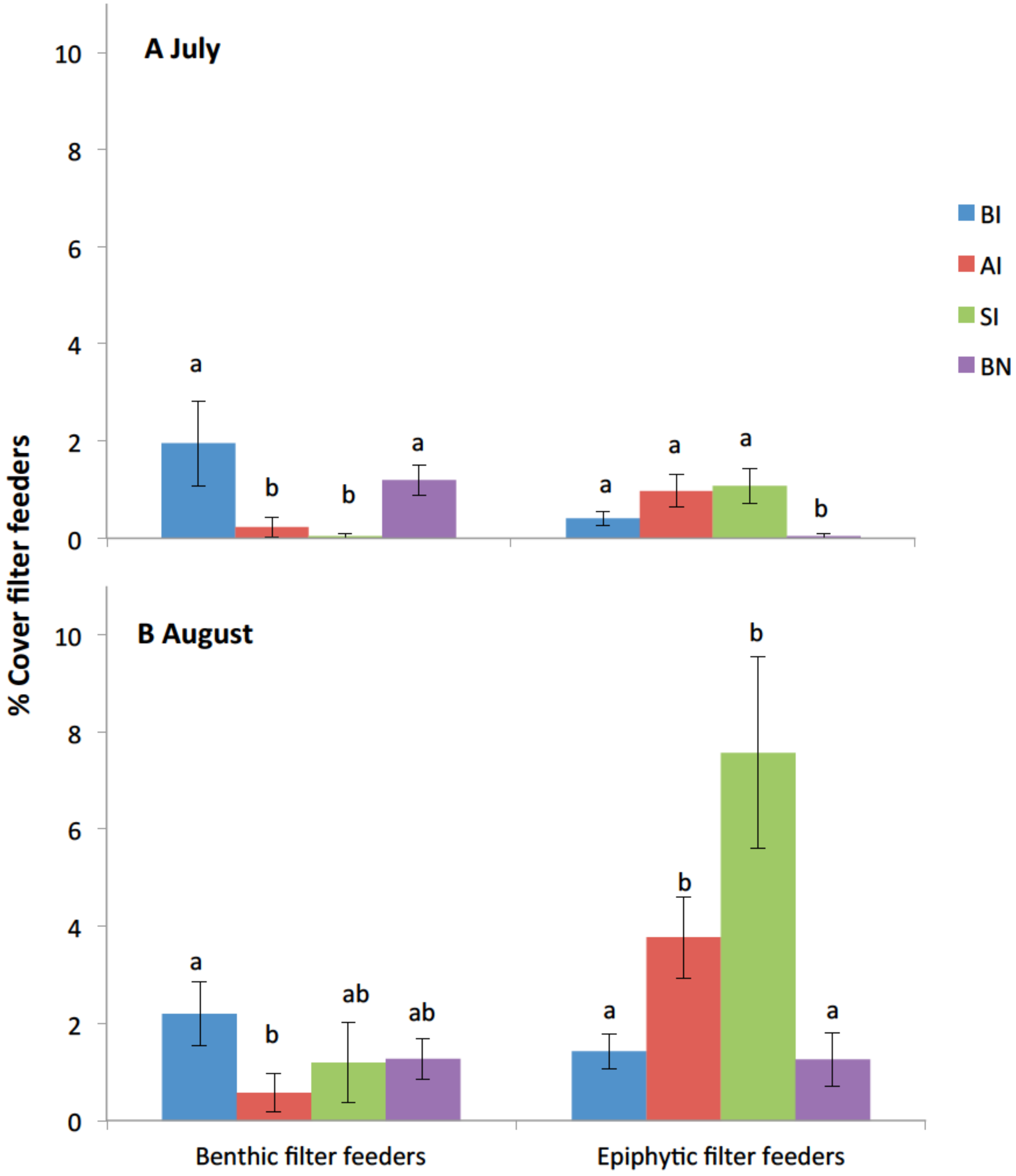


Figure 4. Average abundance and standard error (SE, n = 40) of filter feeders for (A) July and (B) August. Lower case letters indicate significant differences between site within month as well as within site differences across month

Appendix 4B - perMANOVA tables for species richness, abundance, and diversity as well as post-hoc test results for rockweed structure, community composition, richness, abundance, and diversity.

Table 1. Post-hoc inter-site comparisons of (1) plant structure and (2) canopy structure for July and August. Significant p-values are shown in bold.

ROCKWEED	**July**		**August**	
Plant structure {L, C}	**T**	**P**	**T**	**P**
AI-BI	1.211	0.229	1.240	0.165
AI-BN	4.079	**0.0001**	3.005	**0.003**
AI-SI	1.938	**0.027**	4.200	**0.0001**
BI-BN	3.337	**0.0007**	2.136	**0.0015**
BI-SI	1.920	**0.050**	2.898	**0.0002**
BN-SI	1.990	**0.0268**	4.850	**0.0001**
Canopy structure {L, C, D}	**T**	**P**	**T**	**P**
AI-BI	1.139	0.230	1.117	0.276
AI-BN	2.937	**0.001**	2.990	**0.0005**
AI-SI	0.975	0.352	1.508	0.1107
BI-BN	2.076	**0.004**	2.907	**0.002**
BI-SI	0.915	0.470	1.801	0.058
BN-SI	1.990	**0.035**	1.629	0.087

Table 2. Post-hoc intra-site comparisons of (1) plant structure and (2) canopy structure between July and August. Significant p-values are shown in bold.

ROCKWEED	**July-August**	
Plant structure	**T**	**P**
AI-AI	0.944	0.437
BI-BI	0.744	0.613
BN-BN	1.065	0.323
SI-SI	4.765	**0.0001**
Canopy structure	**T**	**P**
AI-AI	0.458	0.815
BI-BI	0.350	0.915
BN-BN	0.818	0.502
SI-SI	0.831	0.431

Table 3. Post-hoc inter-site comparisons of community composition for (1) sessile (quadrat) species, (2) count (quadrat) species, and (3) count (transect) species for July and August. Significant p-values are shown in bold.

COMMUNITY COMPOSITION	**July**		**August**	
Sessile (quadrat) species	**T**	**P**	**T**	**P**
AI-BI	1.317	0.112	1.843	**0.010**
AI-BN	2.958	**0.0001**	4.008	**0.0001**
AI-SI	1.418	0.065	1.204	0.185
BI-BN	3.089	**0.0001**	3.702	**0.0001**
BI-SI	1.277	0.145	2.177	**0.001**
BN-SI	3.507	**0.0001**	3.444	**0.0001**
Count (quadrat) species	**T**	**P**	**T**	**P**
AI-BI	0.875	0.527	1.165	0.254
AI-BN	3.427	**0.0001**	2.983	**0.0001**
AI-SI	1.403	0.0985	2.387	**0.0001**
BI-BN	2.866	**0.00076**	2.026	**0.0029**
BI-SI	1.978	**0.0084**	1.754	**0.0175**
BN-SI	4.411	**0.0001**	1.298	0.151
Mobile (transect) species	**T**	**P**	**T**	**P**
AI-BI	1.088	0.396	1.258	0.162
AI-BN	1.465	0.137	2.210	**0.002**
AI-SI	0.759	0.636	2.576	**0.0007**
BI-BN	2.120	**0.002**	2.136	**0.0003**
BI-SI	1.432	0.119	2.233	**0.0004**
BN-SI	1.192	0.282	4.147	**0.0004**

Table 4. Post-hoc intra-site comparisons of community composition for (1) sessile (quadrat) species, (2) count (quadrat) species, and (3) count (transect) species between July and August. Significant p-values are shown in bold.

COMMUNITY COMPOSITION	**July-August**	
Sessile (quadrat) species	**T**	**P**
AI-AI	3.033	**0.0001**
BI-BI	3.251	**0.0001**
BN-BN	1.875	**0.006**
SI-SI	3.205	**0.0001**
Count (quadrat) species	**T**	**P**
AI-AI	5.381	**0.0001**
BI-BI	4.923	**0.0001**
BN-BN	4.464	**0.0001**
SI-SI	3.695	**0.0001**
Mobile (transect) species	**T**	**P**
AI-AI	0.959	0.407
BI-BI	1.826	**0.018**
BN-BN	3.032	**0.006**
SI-SI	0.979	0.364

Table 5. Repeated measures perMANOVA results for the effect of Site and Month on average richness of (1) sessile (quadrat) species, (2) count (quadrat) species, and (3) count (transect). Sqrt-V values are unbiased estimates of the contribution to variance of Site, Month, their interaction and the residuals in the model. Variance explained (Var) is given by [(SS Factor/SS Total) x 100] and, while more biased than sqrt-V, is included because it is a more intuitive measure of relative effect size (Howell 2002). The degrees of freedom (df) total to 319. Significant p-values are shown in bold.

		Between subject		***Within subject***		
RICHNESS	**Source**	**Site**	**Res**	**Month**	**Si x Mo**	**Residuals**
	Df	**3**	**156**	**1**	**3**	**156**
Sessile (quadrat) species	**Pseudo-F**	5.311		7.987	4.975	
	P	**0.002**		**0.005**	**0.002**	
	sqrt-V	0.210	-0.303	0.209	0.318	0.999
	Var	4.1	39.9	2.5	4.7	48.8
Count (quadrat) species	**Pseudo-F**	18.671		72.608	4.741	
	P	**0.0001**		**0.0001**	**0.003**	
	sqrt-V	0.425	0.333	0.517	0.237	0.773
	Var	14.4	40.1	13.6	2.7	29.2
	Df	**3**	**28**	**1**	**3**	**28**
Mobile (transect) species	**Pseudo-F**	9.333		5.556	3.037	
	P	**0.0002**		**0.026**	**0.047**	
	sqrt-V	0.640	0.412	0.252	0.337	0.668
	Var	34.9	34.9	3.9	6.5	19.8

Table 6. Post-hoc inter-site comparisons of average richness of (1) sessile (quadrat) species, (2) count (quadrat) species, and (3) count (transect) species for July and August. Significant p-values are shown in bold.

RICHNESS	**July**		**August**	
Sessile (quadrat) species	**T**	**P**	**T**	**P**
AI-BI	0.658	0.563	1.937	0.068
AI-BN	0.158	0.940	4.767	**0.0001**
AI-SI	0.743	0.511	3.109	**0.004**
BI-BN	0.518	0.670	3.485	**0.002**
BI-SI	0.091	1	1.389	0.198
BN-SI	0.607	0.599	2.291	**0.031**
Count (quadrat) species	**T**	**P**	**T**	**P**
AI-BI	1.705	0.109	1.643	0.125
AI-BN	5.515	**0.0001**	6.291	**0.0001**
AI-SI	0.455	0.715	3.149	**0.004**
BI-BN	4.147	**0.0001**	4.637	**0.0001**
BI-SI	2.329	**0.031**	1.631	0.122
BN-SI	6.699	**0.0001**	2.493	**0.018**
Mobile (transect) species	**T**	**P**	**T**	**P**
AI-BI	2.393	0.077	2.118	0.124
AI-BN	1.429E-8	1	0.447	1
AI-SI	0.371	1	3.334	**0.015**
BI-BN	2.393	0.075	3	**0.033**
BI-SI	2.198	0.090	5.584	**0.0006**
BN-SI	0.371	1	3.347	**0.018**

Table 7. Post-hoc intra-site comparisons of average richness of (1) sessile (quadrat) species, (2) count (quadrat) species, and (3) count (transect) species between July and August. Significant p-values are shown in bold.

RICHNESS	**July-August**	
Sessile (quadrat) species	**T**	**P**
AI-AI	3.878	**0.0004**
BI-BI	1.693	0.100
BN-BN	1.009	0.325
SI-SI	0.495	0.617
Count (quadrat) species	**T**	**P**
AI-AI	5.810	**0.0001**
BI-BI	5.422	**0.0001**
BN-BN	6.016	**0.0001**
SI-SI	1.123	0.277
Mobile (transect) species	**T**	**P**
AI-AI	2.376	**0.049**
BI-BI	2.646	**0.048**
BN-BN	1.871	0.114
SI-SI	1.158	0.293

Table 8. Repeated measures perMANOVA results for the effect of Site and Month on average abundance of (1) sessile (quadrat) species, (2) count (quadrat) species, and (3) count (transect). Sqrt-V values are unbiased estimates of the contribution to variance of Site, Month, their interaction and the residuals in the model. Variance explained (Var) is given by [(SS Factor/SS Total) x 100] and, while more biased than sqrt-V, is included because it is a more intuitive measure of relative effect size (Howell 2002). The degrees of freedom (df) total to 319. Significant p-values are shown in bold.

		Between subject		***Within subject***		
AVERAGE	**Source**	**Site**	**Res**	**Month**	**Si x Mo**	**Residuals**
ABUNDANCE	**Df**	**3**	**156**	**1**	**3**	**156**
Sessile (quadrat) species	**Pseudo-F**	10.209		7.384	4.474	
	P	**0.0001**		**0.009**	**0.004**	
	sqrt-V	0.310	-0.215	0.192	0.283	0.962
	Var	8	40.7	2.1	3.9	45.3
Count (quadrat) species	**Pseudo-F**	8.170		103.65	3.521	
	P	**0.0002**		**0.0001**	**0.015**	
	sqrt-V	0.263	0.232	0.653	0.205	0.815
	Var	5.9	37.8	21.6	2.2	32.5
	Df	**3**	**28**	**1**	**3**	**28**
Mobile (transect) species	**Pseudo-F**	3.010		5.359	3.055	
	P	**0.015**		**0.022**	**0.027**	
	sqrt-V	0.314	-0.086	0.330	0.453	0.894
	Var	11.2	34.9	6.8	11.6	35.5

Table 9. Post-hoc inter-site comparisons of average abundance of (1) sessile (quadrat) species, (2) count (quadrat) species, and (3) count (transect) species for July and August. Significant p-values are shown in bold.

AVERAGE ABUNDANCE	**July**		**August**	
Sessile (quadrat) species	**T**	**P**	**T**	**P**
AI-BI	0.886	0.380	1.705	0.092
AI-BN	2.509	**0.013**	4.385	**0.0002**
AI-SI	1.686	0.095	0.133	0.896
BI-BN	3.142	**0.001**	2.399	**0.018**
BI-SI	2.459	**0.015**	2.142	**0.036**
BN-SI	1.268	0.217	5.751	**0.0001**
Count (quadrat) species	**T**	**P**	**T**	**P**
AI-BI	1.986	**0.046**	1.414	0.166
AI-BN	3.455	**0.0001**	4.784	**0.0001**
AI-SI	1.283	0.220	0.534	0.599
BI-BN	3.666	**0.0003**	2.463	**0.014**
BI-SI	1.551	0.127	1.562	0.129
BN-SI	6.044	**0.0001**	3.656	**0.0005**
Mobile (transect) species	**T**	**P**	**T**	**P**
AI-BI	0.421	0.837	1.654	0.115
AI-BN	2.337	0.057	0.632	0.587
AI-SI	0.626	0.622	3.188	**0.0004**
BI-BN	1.913	0.116	1.559	0.156
BI-SI	0.375	0.805	1.958	**0.0004**
BN-SI	0.753	0.534	3.389	**0.0001**

Table 10. Post-hoc intra-site comparisons of average abundance of (1) sessile (quadrat) species, (2) count (quadrat) species, and (3) count (transect) species between July and August. Significant p-values are shown in bold.

AVERAGE ABUNDANCE	**July-August**	
Sessile (quadrat) species	**T**	**P**
AI-AI	2.713	**0.011**
BI-BI	0.504	0.622
BN-BN	0.0632	0.946
SI-SI	5.005	**0.0001**
Count (quadrat) species	**T**	**P**
AI-AI	6.341	**0.0001**
BI-BI	4.698	**0.0001**
BN-BN	5.552	**0.0001**
SI-SI	5.197	**0.0001**
Mobile (transect) species	**T**	**P**
AI-AI	2.512	0.034
BI-BI	1.892	0.110
BN-BN	2.340	0.041
SI-SI	1.758	0.125

Table 11. Repeated measures perMANOVA results for the effect of Site and Month on diversity of (1) sessile (quadrat) species, (2) count (quadrat) species, and (3) count (transect). Sqrt-V values are unbiased estimates of the contribution to variance of Site, Month, their interaction and the residuals in the model. Variance explained (Var) is given by [(SS Factor/SS Total) x 100] and, while more biased than sqrt-V, is included because it is a more intuitive measure of relative effect size (Howell 2002). The degrees of freedom (df) total to 319. Significant p-values are shown in bold.

		Between subject		***Within subject***		
DIVERSITY	**Source**	**Site**	**Res**	**Month**	**Si x Mo**	**Residuals**
	Df	**3**	**156**	**1**	**3**	**156**
Sessile	Pseudo-F	0.358		8.081	3.859	
(quadrat)	P	0.786		**0.006**	**0.014**	
species	sqrt-V	-0.090	0.227	0.201	0.255	0.954
	Var	0.3	49.5	2.3	3.3	44.5
Count	Pseudo-F	8.604		173.620	3.013	
(quadrat)	P	**0.0001**		**0.0001**	**0.032**	
species	sqrt-V	0.223	-0.262	0.844	0.182	0.813
	Var	4.2	25.6	36	1.9	32.3
	Df	**3**	**28**	**1**	**3**	**28**
Mobile	Pseudo-F	4.439		2.753	2.380	
(transect)	P	**0.009**		0.110	0.091	
species	sqrt-V	0.446	0.370	0.189	0.336	0.808
	Var	19.6	41.1	2.9	7.4	29

Table 12. Post-hoc inter-site comparisons of diversitye of (1) sessile (quadrat) species, (2) count (quadrat) species, and (3) count (transect) species for July and August. Significant p-values are shown in bold.

DIVERSITY	**July**		**August**	
Sessile (quadrat) species	**T**	**P**	**T**	**P**
AI-BI	0.266	0.793	1.058	0.291
AI-BN	1.309	0.197	2.637	**0.009**
AI-SI	0.782	0.432	2.338	**0.021**
BI-BN	1.615	0.111	1.714	0.091
BI-SI	1.124	0.261	1.357	0.185
BN-SI	0.711	0.481	0.418	0.678
Count (quadrat) species	**T**	**P**	**T**	**P**
AI-BI	1.247	0.210	1.058	0.292
AI-BN	4.421	**0.0001**	2.637	**0.009**
AI-SI	0.706	0.484	2.338	**0.021**
BI-BN	3.275	**0.001**	1.714	0.093
BI-SI	1.912	0.060	1.357	0.180
BN-SI	4.872	**0.0001**	0.418	0.680
Mobile (transect) species	**T**	**P**	**T**	**P**
AI-BI	2.330	0.059	0.624	0.542
AI-BN	0.063	1	0.018	0.986
AI-SI	0.287	1	2.642	**0.018**
BI-BN	2.426	**0.043**	0.695	0.506
BI-SI	2.130	0.053	3.450	**0.006**
BN-SI	0.359	0.933	2.939	**0.022**

Table 13. Post-hoc intra-site comparisons of diversity of (1) sessile (quadrat) species, (2) count (quadrat) species, and (3) count (transect) species between July and August. Significant p-values are shown in bold.

DIVERSITY	**July-August**	
Sessile (quadrat) species	**T**	**P**
AI-AI	3.357	**0.002**
BI-BI	2.832	**0.007**
BN-BN	0.751	0.460
SI-SI	0.395	0.695
Count (quadrat) species	**T**	**P**
AI-AI	6.725	**0.0001**
BI-BI	6.996	**0.0001**
BN-BN	10.375	**0.0001**
SI-SI	3.662	**0.001**
Mobile (transect) species	**T**	**P**
AI-AI	1.893	0.099
BI-BI	0.077	0.935
BN-BN	1.801	0.123
SI-SI	1.196	0.255

Appendix 4C – SIMPER analysis of square root transformed data for each component of community composition. SIMPER results reported for between group only(i.e. between pairs of Sites). Strongly contributing species (for which Sim/SD ≥ 1) to dissimilarity for between group analyses are bolded.

(1a) Sessile (quadrat) species, July

Groups AI and BI
Average dissimilarity = 71.31

	Group AI	Group BI				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Red encrusting algae	**2.77**	**3.74**	**24.32**	**1.26**	**34.10**	**34.10**
Vertebrata lanosa	0.63	0.59	6.17	0.82	8.65	42.75
Green encrusting algae	0.23	0.80	5.90	0.60	8.28	51.03
Ulva spp.	0.74	0.27	5.23	0.56	7.33	58.36
Fucus spp.	0.49	0.36	5.07	0.62	7.11	65.47
Red foliose algae	0.44	0.27	4.93	0.55	6.91	72.38
Semibalanus balanoides	0.08	0.60	4.60	0.43	6.45	78.82
Dynamena pumila (hydroid)	0.47	0.30	4.17	0.72	5.85	84.68
Pink encrusting algae	0.37	0.10	3.26	0.40	4.57	89.25
Green filamentous algae	0.32	0.07	2.50	0.46	3.51	92.76

Groups AI and BN
Average dissimilarity = 82.87

	Group AI	Group BN				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Red encrusting algae	**2.77**	**1.00**	**22.68**	**1.13**	**27.37**	**27.37**
Fucus spp.	0.49	0.85	9.28	0.78	11.20	38.57
Vertebrata lanosa	0.63	0.83	7.85	0.83	9.47	48.04
Ulva spp.	0.74	0.56	7.73	0.67	9.32	57.36
Semibalanus balanoides	0.08	0.73	7.14	0.74	8.62	65.98
Green filamentous algae	0.32	0.60	6.18	0.47	7.45	73.43
Green encrusting algae	0.23	0.48	5.01	0.62	6.05	79.48
Red foliose algae	0.44	0.06	4.22	0.43	5.10	84.58
Dynamena pumila (hydroid)	0.47	0.04	3.76	0.54	4.54	89.12
Pink encrusting algae	0.37	0.00	2.93	0.35	3.53	92.65

Groups BI and BN
Average dissimilarity = 79.68

	Group BI	Group BN				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Red encrusting algae	**3.74**	**1.00**	**26.63**	**1.28**	**33.42**	**33.42**
Semibalanus balanoides	0.60	0.73	8.83	0.80	11.08	44.50
Fucus spp.	0.36	0.85	7.78	0.80	9.77	54.27
Green encrusting algae	0.80	0.48	7.57	0.74	9.50	63.77
Vertebrata lanosa	0.59	0.83	7.11	0.97	8.92	72.69
Ulva spp.	0.27	0.56	5.29	0.65	6.64	79.33
Green filamentous algae	0.07	0.60	4.74	0.38	5.95	85.28
Red foliose algae	0.27	0.06	3.23	0.42	4.06	89.34
Dynamena pumila (hydroid)	0.30	0.04	2.53	0.52	3.18	92.52

Groups AI and WI
Average dissimilarity = 69.97

Species	Group AI Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Red encrusting algae	**2.77**	**2.75**	**20.95**	**1.23**	**29.94**	**29.94**
Green encrusting algae	0.23	0.77	6.93	0.67	9.90	39.84
Ulva spp.	0.74	0.44	6.18	0.57	8.83	48.67
Vertebrata lanosa	0.63	0.57	6.14	0.90	8.77	57.44
Dynamena pumila (hydroid)	0.47	0.57	6.05	0.71	8.65	66.09
Fucus spp.	0.49	0.39	5.32	0.69	7.61	73.69
Pink encrusting algae	0.37	0.30	4.11	0.47	5.88	79.57
Red foliose algae	0.44	0.14	4.06	0.46	5.80	85.37
Elachista sp.	0.13	0.33	3.13	0.54	4.48	89.85
Green filamentous algae	0.32	0.06	2.35	0.45	3.36	93.21

Groups BI and WI
Average dissimilarity = 66.71

Species	Group BI Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Red encrusting algae	**3.74**	**2.75**	**21.85**	**1.35**	**32.75**	**32.75**
Green encrusting algae	0.80	0.77	8.60	0.82	12.90	45.65
Vertebrata lanosa	0.59	0.57	5.71	0.95	8.57	54.22
Dynamena pumila (hydroid)	0.30	0.57	5.02	0.69	7.53	61.74
Semibalanus balanoides	0.60	0.04	4.45	0.45	6.68	68.42
Fucus spp.	0.36	0.39	4.43	0.74	6.64	75.06
Ulva spp.	0.27	0.44	4.07	0.53	6.10	81.16
Red foliose algae	0.27	0.14	3.22	0.44	4.83	85.99
Elachista sp.	0.17	0.33	3.03	0.61	4.55	90.53

Groups BN and WI
Average dissimilarity = 80.27

Species	Group BN Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Red encrusting algae	**1.00**	**2.75**	**22.96**	**1.28**	**28.60**	**28.60**
Green encrusting algae	0.48	0.77	8.39	0.79	10.45	39.05
Fucus spp.	0.85	0.39	7.90	0.89	9.84	48.90
Vertebrata lanosa	0.83	0.57	7.18	1.00	8.95	57.85
Semibalanus balanoides	0.73	0.04	6.58	0.91	8.20	66.05
Ulva spp.	0.56	0.44	6.44	0.65	8.02	74.07
Dynamena pumila (hydroid)	0.04	0.57	5.24	0.58	6.53	80.59
Green filamentous algae	0.60	0.06	4.63	0.37	5.77	86.36
Elachista sp.	0.05	0.33	3.04	0.52	3.79	90.15

(1b) Sessile (quadrat) species, August

Groups AI and BI
Average dissimilarity = 68.94

	Group AI	Group BI				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Red encrusting algae	**3.10**	**2.30**	**18.34**	**1.13**	**26.61**	**26.61**
Dynamena pumila (hydroid)	1.41	0.73	8.42	0.94	12.21	38.82
Elachista sp.	1.35	1.53	6.81	0.97	9.87	48.69
Vertebrata lanosa	0.92	0.84	6.71	0.95	9.74	58.43
Semibalanus balanoides	0.23	0.83	5.18	0.70	7.51	65.94
Green encrusting algae	0.81	0.39	5.09	0.68	7.38	73.31
Fucus spp.	0.50	0.53	5.02	0.64	7.28	80.60
Chondrus crispus	0.53	0.18	3.51	0.51	5.09	85.69
Pink encrusting algae	0.55	0.16	3.42	0.50	4.96	90.65

Groups AI and BN
Average dissimilarity = 83.23

	Group AI	Group BN				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Red encrusting algae	**3.10**	**0.69**	**17.77**	**1.05**	**21.35**	**21.35**
Dynamena pumila (hydroid)	1.41	0.45	10.38	0.93	12.47	33.82
Vertebrata lanosa	0.92	1.55	10.24	0.99	12.31	46.13
Elachista sp.	**1.35**	**0.00**	**10.19**	**1.10**	**12.24**	**58.37**
Fucus spp.	0.50	0.58	5.73	0.60	6.88	65.25
Green encrusting algae	0.81	0.15	5.11	0.63	6.14	71.39
Ulva spp.	0.44	0.41	4.62	0.65	5.55	76.94
Semibalanus balanoides	0.23	0.60	4.45	0.67	5.35	82.29
Green filamentous algae	0.11	0.45	3.34	0.53	4.02	86.31
Pink encrusting algae	0.55	0.00	3.05	0.43	3.66	89.97
Chondrus crispus	0.53	0.00	3.02	0.40	3.63	93.60

Groups BI and BN
Average dissimilarity = 82.04

	Group BI	Group BN				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Red encrusting algae	2.30	0.69	15.41	0.81	18.79	18.79
Elachista sp.	**1.53**	**0.00**	**13.18**	**1.45**	**16.06**	**34.85**
Vertebrata lanosa	**0.84**	**1.55**	**11.58**	**1.08**	**14.11**	**48.96**
Semibalanus balanoides	0.83	0.60	8.39	0.86	10.23	59.19
Fucus spp.	0.53	0.58	7.74	0.62	9.44	68.63
Dynamena pumila (hydroid)	0.73	0.45	7.54	0.80	9.19	77.82
Ulva spp.	0.15	0.41	4.12	0.59	5.02	82.84
Green filamentous algae	0.04	0.45	3.72	0.53	4.54	87.38
Green encrusting algae	0.39	0.15	3.07	0.47	3.74	91.12

Groups AI and WI
Average dissimilarity = 68.18

Species	Group AI Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Red encrusting algae	**3.10**	**2.45**	**17.07**	**1.11**	**25.04**	**25.04**
Dynamena pumila (hydroid)	**1.41**	**1.91**	**9.87**	**1.01**	**14.48**	**39.51**
Elachista sp.	**1.35**	**1.54**	**8.24**	**1.08**	**12.08**	**51.60**
Vertebrata lanosa	**0.92**	**1.55**	**8.21**	**1.07**	**12.04**	**63.63**
Green encrusting algae	0.81	0.34	4.55	0.68	6.68	70.31
Ulva spp.	0.44	0.43	3.81	0.57	5.58	75.89
Fucus spp.	0.50	0.34	3.41	0.69	5.00	80.89
Chondrus crispus	0.53	0.17	3.01	0.47	4.41	85.30
Pink encrusting algae	0.55	0.09	2.76	0.48	4.05	89.35
Semibalanus balanoides	0.23	0.29	2.35	0.38	3.45	92.80

Groups BI and WI
Average dissimilarity = 71.26

Species	Group BI Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Red encrusting algae	2.30	2.45	18.13	0.98	25.44	25.44
Dynamena pumila (hydroid)	0.73	1.91	11.18	0.93	15.69	41.12
Elachista sp.	**1.53**	**1.54**	**9.28**	**1.15**	**13.03**	**54.15**
Vertebrata lanosa	**0.84**	**1.55**	**9.16**	**1.11**	**12.86**	**67.01**
Semibalanus balanoides	0.83	0.29	5.70	0.70	8.00	75.01
Fucus spp.	0.53	0.34	4.33	0.67	6.07	81.08
Ulva spp.	0.15	0.43	3.26	0.47	4.57	85.65
Green encrusting algae	0.39	0.34	3.21	0.53	4.51	90.16

Groups BN and WI
Average dissimilarity = 80.66

Species	Group BN Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Red encrusting algae	0.69	2.45	17.19	0.83	21.31	21.31
Dynamena pumila (hydroid)	0.45	1.91	13.70	0.91	16.98	38.29
Vertebrata lanosa	**1.55**	**1.55**	**11.27**	**1.23**	**13.97**	**52.26**
Elachista sp.	0.00	1.54	10.62	0.87	13.17	65.43
Ulva spp.	0.41	0.43	5.11	0.61	6.33	71.76
Semibalanus balanoides	0.60	0.29	5.08	0.61	6.30	78.06
Fucus spp.	0.58	0.34	5.00	0.59	6.20	84.26
Green filamentous algae	0.45	0.18	3.75	0.52	4.65	88.91
Fucus spp. (on rockweed)	0.31	0.28	3.49	0.58	4.32	93.23

(2a) Count (quadrat) species, July

Groups AI and BI
Average dissimilarity = 81.98

Species	Group AI Av.Abund	Group BI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Littorina saxatilis	**2.03**	**1.57**	**34.26**	**1.07**	**41.79**	**41.79**
Littorina littoria	0.82	0.35	13.59	0.60	16.58	58.38

Littorina obtusata	0.45	0.15	8.91	0.43	10.87	69.25
Limpet (checked)	0.68	0.33	8.81	0.56	10.75	80.00
sea anenome	0.25	0.40	6.43	0.39	7.84	87.84
Limpet (brown)	0.05	0.19	2.89	0.26	3.53	91.36

Groups AI and BN
Average dissimilarity = 92.87

Species	Group AI Av.Abund	Group BN Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Littorina saxatilis	**2.03**	**0.48**	**39.54**	**1.11**	**42.58**	**42.58**
Littorina littoria	0.82	0.00	13.42	0.53	14.45	57.03
Littorina obtusata	0.45	0.15	11.16	0.47	12.02	69.05
Limpet (checked)	0.68	0.10	10.06	0.51	10.83	79.89
Carcinus maenus	0.05	0.25	7.45	0.37	8.02	87.90
sea anenome	0.25	0.00	4.60	0.30	4.95	92.86

Groups BI and BN
Average dissimilarity = 92.08

Species	Group BI Av.Abund	Group BN Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Littorina saxatilis	**1.57**	**0.48**	**43.48**	**1.13**	**47.22**	**47.22**
Littorina obtusata	0.15	0.15	12.00	0.41	13.03	60.24
Carcinus maenus	0.15	0.25	10.24	0.45	11.13	71.37
Littorina littoria	0.35	0.00	9.55	0.43	10.37	81.74
Limpet (checked)	0.33	0.10	7.50	0.44	8.15	89.89
sea anenome	0.40	0.00	4.91	0.30	5.33	95.22

Groups AI and WI
Average dissimilarity = 78.27

Species	Group AI Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Littorina saxatilis	**2.03**	**1.85**	**27.92**	**1.02**	**35.67**	**35.67**
Littorina obtusata	0.45	1.33	17.87	0.67	22.83	58.50
Littorina littoria	0.82	0.64	11.75	0.72	15.01	73.51
Limpet (checked)	0.68	0.25	6.56	0.57	8.38	81.89
Carcinus maenus	0.05	0.31	3.59	0.38	4.59	86.48
sea anenome	0.25	0.12	3.45	0.36	4.41	90.89

Groups BI and WI
Average dissimilarity = 79.63

Species	Group BI Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Littorina saxatilis	**1.57**	**1.85**	**30.38**	**1.00**	**38.16**	**38.16**
Littorina obtusata	0.15	1.33	19.07	0.65	23.95	62.10
Littorina littoria	0.35	0.64	10.01	0.66	12.57	74.67
Limpet (checked)	0.33	0.25	4.96	0.50	6.23	80.91
Carcinus maenus	0.15	0.31	4.61	0.45	5.78	86.69
sea anenome	0.40	0.12	4.22	0.33	5.30	91.99

Groups BN and WI
Average dissimilarity = 91.37

Species	Group BN Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Littorina saxatilis	**0.48**	**1.85**	**37.86**	**1.07**	**41.43**	**41.43**
Littorina obtusata	0.15	1.33	24.27	0.69	26.56	67.99
Littorina littoria	0.00	0.64	9.33	0.61	10.21	78.21
Carcinus maenus	0.25	0.31	8.18	0.48	8.96	87.16
Limpet (checked)	0.10	0.25	4.46	0.41	4.88	92.05

(2b) Count (quadrat) species, August

Groups AI and BI
Average dissimilarity = 66.58

Species	Group AI Av.Abund	Group BI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Margarite	**5.55**	**4.48**	**24.04**	**1.28**	**36.11**	**36.11**
Littorina obtusata	**2.30**	**2.45**	**12.01**	**1.09**	**18.03**	**54.14**
Littorina littoria	2.48	1.46	11.83	0.95	17.76	71.91
Limpet (checked)	0.91	1.08	6.52	0.77	9.79	81.70
Littorina saxatilis	0.76	0.20	4.46	0.52	6.70	88.40
Nucella spp.	0.20	0.27	1.94	0.45	2.91	91.31

Groups AI and BN
Average dissimilarity = 76.89

Species	Group AI Av.Abund	Group BN Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Margarite	**5.55**	**1.68**	**28.52**	**1.24**	**37.10**	**37.10**
Littorina obtusata	**2.30**	**2.66**	**16.56**	**1.07**	**21.54**	**58.64**
Littorina littoria	2.48	1.14	13.29	0.94	17.28	75.92
Littorina saxatilis	0.76	0.00	5.26	0.43	6.85	82.76
Limpet (checked)	0.91	0.00	4.51	0.51	5.86	88.62
Mysidae sp.	0.00	0.44	2.52	0.36	3.28	91.90

Groups BI and BN
Average dissimilarity = 78.70

Species	Group BI Av.Abund	Group BN Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Margarite	**4.48**	**1.68**	**27.13**	**1.07**	**34.47**	**34.47**
Littorina obtusata	**2.45**	**2.66**	**19.75**	**1.06**	**25.09**	**59.56**
Littorina littoria	1.46	1.14	12.63	0.78	16.04	75.61
Limpet (checked)	1.08	0.00	6.29	0.60	7.99	83.60
Carcinus maenus	0.32	0.29	3.19	0.44	4.05	87.65
Mysidae sp.	0.00	0.44	3.14	0.34	3.99	91.64

Groups AI and WI
Average dissimilarity = 73.21

Species	Group AI Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Margarite	**5.55**	**4.19**	**24.91**	**1.13**	**34.03**	**34.03**
Littorina obtusata	**2.30**	**5.25**	**19.36**	**1.21**	**26.44**	**60.47**

Littorina littoria	2.48	1.19	11.30	0.85	15.43	75.90
Littorina saxatilis	0.76	0.46	5.74	0.48	7.84	83.74
Limpet (checked)	0.91	0.29	4.47	0.54	6.11	89.85
Carcinus maenus	0.15	0.44	2.28	0.50	3.12	92.97

Groups BI and WI
Average dissimilarity = 76.52

Species	Group BI Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Margarite	**4.48**	**4.19**	**24.77**	**1.10**	**32.37**	**32.37**
Littorina obtusata	**2.45**	**5.25**	**21.96**	**1.19**	**28.70**	**61.06**
Littorina littoria	1.46	1.19	10.53	0.69	13.77	74.83
Limpet (checked)	1.08	0.29	5.99	0.60	7.83	82.66
Littorina saxatilis	0.20	0.46	4.36	0.42	5.69	88.35
Carcinus maenus	0.32	0.44	3.13	0.55	4.09	92.44

Groups BN and WI
Average dissimilarity = 80.43

Species	Group BN Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Littorina obtusata	**2.66**	**5.25**	**28.74**	**1.15**	**35.73**	**35.73**
Margarite	1.68	4.19	23.22	0.90	28.87	64.60
Littorina littoria	1.14	1.19	11.06	0.64	13.75	78.35
Littorina saxatilis	0.00	0.46	4.63	0.35	5.76	84.11
Carcinus maenus	0.29	0.44	4.38	0.43	5.45	89.56
Mysidae sp.	0.44	0.00	3.65	0.30	4.54	94.10

(3a) Count (transect) species, July

Groups AI and BI
Average dissimilarity = 58.41

Species	Group AI Av.Abund	Group BI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Carcinus maenas	**1.05**	**1.02**	**16.95**	**1.07**	**29.02**	**29.02**
Pleurobrachia pileus	**0.18**	**0.50**	**12.76**	**1.02**	**21.84**	**50.86**
Large ctenophore	0.18	0.35	10.15	0.65	17.37	68.23
Cancer irroratus	0.30	0.00	7.90	0.52	13.52	81.75
Alosa pseudoharengus	0.00	0.25	7.56	0.53	12.93	94.69

Groups AI and BN
Average dissimilarity = 42.09

Species	Group AI Av.Abund	Group BN Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Carcinus maenas	**1.05**	**1.78**	**20.22**	**1.13**	**48.04**	**48.04**
Cancer irroratus	0.30	0.00	7.91	0.54	18.80	66.84
Large ctenophore	0.18	0.22	7.70	0.53	18.28	85.12
Pleurobrachia pileus	0.18	0.00	3.39	0.37	8.06	93.18

Groups BI and BN
Average dissimilarity = 52.50

Species	Group BI Av.Abund	Group BN Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Carcinus maenas	**1.02**	**1.78**	**20.25**	**1.16**	**38.58**	**38.58**
Pleurobrachia pileus	0.50	0.00	10.44	0.97	19.89	58.47
Large ctenophore	0.35	0.22	9.83	0.67	18.72	77.19
Alosa pseudoharengus	0.25	0.00	6.59	0.54	12.56	89.75
Gasterosteus aculeatus (3SS)	0.13	0.00	2.80	0.37	5.32	95.07

Groups AI and WI
Average dissimilarity = 59.90

Species	Group AI Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Carcinus maenas	1.05	1.33	32.77	0.99	54.71	54.71
Cancer irroratus	0.30	0.00	10.24	0.47	17.09	71.80
Pleurobrachia pileus	0.18	0.18	6.72	0.51	11.22	83.02
Large ctenophore	0.18	0.00	4.73	0.35	7.90	90.91

Groups BI and WI
Average dissimilarity = 64.47

Species	Group BI Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Carcinus maenas	**1.02**	**1.33**	**25.91**	**1.12**	**40.18**	**40.18**
Pleurobrachia pileus	0.50	0.18	13.49	0.94	20.92	61.10
Alosa pseudoharengus	0.25	0.00	9.03	0.44	14.00	75.11
Large ctenophore	0.35	0.00	8.39	0.53	13.01	88.12
Gasterosteus aculeatus (3SS)	0.13	0.13	5.32	0.49	8.26	96.38

Groups BN and WI
Average dissimilarity = 46.35

Species	Group BN Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Carcinus maenas	1.78	1.33	30.34	0.83	65.45	65.45
Large ctenophore	0.22	0.00	4.77	0.36	10.28	75.74
Pleurobrachia pileus	0.00	0.18	3.22	0.37	6.96	82.69
Squid	0.13	0.00	3.06	0.36	6.59	89.29
Gasterosteus aculeatus (3SS)	0.00	0.13	2.61	0.37	5.63	94.91

(3b) Count (transect) species, August

Groups AI and BI
Average dissimilarity = 59.14

Species	Group AI Av.Abund	Group BI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Juvenile 3SS	0.00	2.05	13.97	0.57	23.62	23.62
Alosa pseudoharengus	0.00	1.90	12.39	0.52	20.95	44.57
Cancer irroratus	**0.59**	**0.78**	**9.34**	**1.05**	**15.79**	**60.36**
Carcinus maenas	**1.96**	**1.57**	**9.04**	**1.13**	**15.29**	**75.65**
Shrimp	0.25	0.25	5.08	0.50	8.60	84.25
Pollachius sp.	0.56	0.00	4.81	0.36	8.14	92.38

Groups AI and BN
Average dissimilarity = 46.90

Species	Group AI Av.Abund	Group BN Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Mysidae sp.	**0.13**	**1.67**	**19.50**	**1.40**	**41.57**	**41.57**
Carcinus maenas	**1.96**	**2.33**	**9.67**	**1.31**	**20.63**	**62.20**
Cancer irroratus	0.59	0.00	8.61	0.91	18.37	80.56
Pollachius sp.	0.56	0.00	5.77	0.37	12.31	92.87

Groups BI and BN
Average dissimilarity = 66.57

Species	Group BI Av.Abund	Group BN Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Mysidae sp.	**0.00**	**1.67**	**15.79**	**1.24**	**23.72**	**23.72**
Juvenile 3SS	2.05	0.00	13.55	0.56	20.35	44.06
Alosa pseudoharengus	1.90	0.00	12.00	0.51	18.02	62.09
Cancer irroratus	0.78	0.00	9.94	0.91	14.93	77.01
Carcinus maenas	**1.57**	**2.33**	**9.28**	**1.38**	**13.93**	**90.95**

Groups AI and WI
Average dissimilarity = 67.40

Species	Group AI Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Carcinus maenas	**1.96**	**0.82**	**33.22**	**1.14**	**49.28**	**49.28**
Cancer irroratus	0.59	0.00	15.42	0.89	22.87	72.16
Pollachius sp.	0.56	0.00	8.31	0.37	12.32	84.48
Shrimp	0.25	0.00	5.52	0.37	8.19	92.67

Groups BI and WI
Average dissimilarity = 78.12

Species	Group BI Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Carcinus maenas	1.57	0.82	18.82	0.99	24.09	24.09
Juvenile 3SS	2.05	0.00	16.99	0.57	21.75	45.84
Cancer irroratus	0.78	0.00	16.65	0.93	21.32	67.16
Alosa pseudoharengus	1.90	0.00	15.66	0.56	20.05	87.21
Shrimp	0.25	0.00	4.57	0.37	5.85	93.06

Groups BN and WI
Average dissimilarity = 68.44

Species	Group BN Av.Abund	Group WI Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Carcinus maenas	**2.33**	**0.82**	**36.57**	**1.34**	**53.43**	**53.43**
Mysidae sp.	**1.67**	**0.00**	**29.83**	**1.49**	**43.59**	**97.01**

Appendix 4D – Additional output from Envfit analysis when one average of canopy variable is used per site (rather than five).

Table 1. R^2 and p-values for regressions between individual environmental variables (Chl *a*, TPM, and % organic TPM), canopy variables (L, C and D) and community composition as well as for overall regressions between all predictor variables and components of community composition for July. Significant p-values are shown in bold.

Community component	Chl	TPM	% Organic TPM	Average Plant L	Average Plant C	Average D	Overall
Sessile (quadrat) species	R^2 = 0.694 P = **0.001**	R^2 = 0.782 P = **0.001**	R^2 = 0.866 P = **0.001**	R^2 = 0.904 P = **0.001**	R^2 = 0.773 P = **0.001**	R^2 = 0.863 P = **0.001**	R^2 = 0.932 P = **0.001**
Count (quadrat) species	R^2 = 0.696 P = **0.001**	R^2 = 0.893 P = **0.001**	R^2 = 0.944 P = **0.001**	R^2 = 0.942 P = **0.001**	R^2 = 0.775 P = **0.001**	R^2 = 0.923 P = **0.001**	R^2 = 0.987 P = **0.001**
Count (transect) species	R^2 = 0.936 P = **0.001**	R^2 = 0.968 P = **0.001**	R^2 = 0.683 P = **0.001**	R^2 = 0.839 P = **0.001**	R^2 = 0.983 P = **0.001**	R^2 = 0.996 P = **0.001**	R^2 = 1 P = **0.001**

Table 2. Table 4. R^2 and p-values for regressions between individual environmental variables (Chl *a*, TPM, and % organic TPM), canopy variables (L, C and D) and community composition as well as for overall regressions between all predictor variables and components of community composition for July. Significant p-values are shown in bold.

Community component	Chl	TPM	% Organic TPM	Average Plant L	Average Plant C	Average D	Overall
Sessile (quadrat) species	R^2 = 0.389 P = **0.001**	R^2 = 0.858 P = **0.001**	R^2 = 0.463 P = **0.001**	R^2 = 0.786 P = **0.001**	R^2 = 0.191 P = **0.026**	R^2 = 0.821 P = **0.001**	R^2 = 0.796 P = **0.001**
Count (quadrat) species	R^2 = 0.203 P = **0.019**	R^2 = 0.501 P = **0.001**	R^2 = 0.489 P = **0.001**	R^2 = 0.523 P = **0.001**	R^2 = 0.012 P = 0.785	R^2 = 0.198 P = **0.021**	R^2 = 0.570 P = **0.001**
Count (transect) species	R^2 = 0.943 P = **0.001**	R^2 = 0.971 P = **0.001**	R^2 = 0.670 P = **0.001**	R^2 = 0.954 P = **0.001**	R^2 = 0.558 P = **0.001**	R^2 = 0.986 P = **0.001**	R^2 = 1 P = **0.001**