The ecology of sea wrack accumulations across space and time on islands along British Columbia's Central Coast

by

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B.Sc., University of Victoria, 2014

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ABSTRACT

The equilibrium theory of island biogeography provides a useful model for understanding patterns of species richness on island systems and analogous fragmented terrestrial habitats. However, like all models, it is limited in its ability to explain island species richness patterns when nutrients move across ecosystem boundaries. Recently, enhancements to the theory have been proposed, including the subsidized island biogeography hypothesis. This hypothesis suggests that nutrient subsidies from the marine environment may impact the productivity and diversity of small islands. Sea wrack (dead, shore-cast seaweed) is a recognized vector of marine-nutrient subsidies to islands in regions of low *in situ* productivity, but little is known about the mechanisms surrounding sea wrack accumulation in productive, temperate environments.

In this research I explore the spatial and temporal distribution of sea wrack on islands along British Columbia's temperate Central Coast. Through an observational study I investigate three broad factors that could affect sea wrack deposition: climatic patterns, physical characteristics of shorelines, and the amount of nearby donor habitat. I surveyed sea wrack biomass and species composition, as well as the biogeographical characteristics of shorelines across 455 sites on 101 islands. I returned to a subset of sites on a bi-monthly basis to document temporal changes in wrack biomass and species composition. My results demonstrate that sea wrack accumulations were present at sites that were not composed of rock substrate, and that had wide, wave protected shorelines and high amounts of nearby donor ecosystem habitat. Additionally, sea wrack biomass and species composition was ubiquitous throughout all seasons. These results suggest that sea wrack can be considered a press subsidy as it is a consistent vector of nutrients to beaches along the Central Coast.

Ecological research on macrophytes, macroalgae and sea wrack often requires the conversion of wet biomass to dry, to create consistency across investigations. This is a laborious process. Here, I present the results of wet-dry calibrations for 12 common macrophyte and macroalgae species collected from the Northeast Pacific Ocean. Future investigators can use the correction factors derived from these results for estimating dry biomass, reducing the need to conduct wet-dry calibrations for each new macrophyte, macroalgae, or sea wrack study.

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CHAPTER ONE

GENERAL INTRODUCTION

The equilibrium theory of island biogeography (MacArthur and Wilson 1967) is one of the few examples of a general ecological theory that has withstood the test of time and scientific scrutiny (Mittelbach 2012). Island biogeography theory, first proposed by E.O. Wilson and R.H. MacArthur (1963, 1967) predicts equilibrium species richness on islands based on immigration and extinction rates, parameters moderated by island size and isolation from a mainland source. Thus, smaller and more remote islands with less immigration and potentially more extinction would have lower equilibrium species richness than larger islands closer to the mainland, which would have higher immigration and lower extinction rates (Wilson and MacArthur 1967). The success of island biogeography theory in explaining patterns of island species richness on both classic islands surrounded by water (Frick et al. 2008) and island analogs on land (Laurance 2008) has led to many revisions and enhancements of the original theory (Patiño et al. 2017). One interesting empirical observation is that on very small islands (< 3 km^2), species richness may be higher than expected (Anderson and Wait 2001). Several factors may influence the patterns of species richness on small islands, including a higher rate of productivity (Anderson and Polis 1999).

Subsidized island biogeography theory, an extension of the equilibrium theory of island biogeography, links the effects of marine-terrestrial subsidies to the unpredictable patterns of diversity seen on small islands (Barrett et al. 2003). Smaller islands, with more shoreline relative to interior area, have increased amounts of exposure to the adjacent marine environment (Anderson and Wait 2001). This exposes communities on smaller islands to more marine-nutrient subsidies than larger islands, increasing productivity (Anderson and Wait 2001). This could have two potential outcomes in terms of species richness or diversity. Increased productivity may support higher population densities, which in turn could lower extinction rates (Preston 1962), or this increased productivity may lead to the competitive dominance of a few species, thus increasing the extinction rate of the less successful competitors (Wait et al. 2005).

Research has shown that small islands often have higher rates of productivity per unit area than larger ones (Polis and Hurd 1996) and in many cases this is due to the input of allochthonous resources from the adjacent marine environment (Maron et al. 2006). Often referred to as a marine-terrestrial subsidy, this process occurs in many forms. For example, accumulated driftwood can provide important invertebrate habitat (Colombini and Chelazzi 2003). Bird guano has been shown to fertilize soils and increase plant productivity directly (Anderson and Polis 1999, McCauley et al. 2012). Fruit and dune grass seed strandings have aided in species dispersal and dune stabilization (Colombini and Chelazzi 2003, Dugan and Hubbard 2010). Anadromous fish returning to their natal rivers transport marine-derived nitrogen to watersheds (Hocking and Reynolds 2011, Helfield and Naiman 2014). Beach-cast fish, carrion, seaweeds, marine mammal carcasses, and intertidal invertebrates have provided nutrition to numerous vertebrate and invertebrate scavengers, altering nearshore food web structures (Polis et al. 1997, Colombini et al. 2000, Carlton and Hodder 2003). Globally, there exist many examples of subsidization from marine to terrestrial ecosystems.

Sea wrack is another marine subsidy that can alter the productivity of terrestrial plant and animal communities (Cardona and García 2008, Piovia-Scott et al. 2013). Defined as dead, shore-cast seaweeds and seagrasses, sea wrack can modify supralittoral (the area of land between the intertidal and terrestrial edge) and terrestrial habitats (Del Vecchio et al. 2013). Once washed ashore, wrack deposited above the high intertidal zone can act as a direct fertilizer for dune and adjacent forest flora (Cardona and García 2008, Villares et al. 2016). Wrack can also trap sand particles and decrease saltation effects (Dugan and Hubbard 2010). Once wrack traps wind-blown sediment, hummock and embryo dune formations may occur (Hooton et al. 2014), which in turn promotes dune grass colonization (Del Vecchio et al. 2013).When these factors combine, sea wrack accumulations may lead to slowed coastal erosion (Colombini and Chelazzi 2003, Dugan and Hubbard 2010).

Sea wrack deposits may also provide a nutritionally rich and important food supply for a large community of microbe, amphipod, fly, spider, beetle, isopod, and other invertebrate species (Pennings et al. 2000, Ince et al. 2007, Sosik and Simenstad 2013, Lastra et al. 2014). Wrack deposits can also increase beach habitat availability for invertebrates (Olabarria et al. 2007, Rodil et al. 2015). For both reasons, sea wrack accumulations have been shown to significantly increase the abundance and diversity of shoreline invertebrate communities (Dugan et al. 2003, Schlacher et al. 2017). Subsequently, these invertebrate species are ingested by higher trophic-level terrestrial consumers and the presence of sea wrack on a shoreline can affect the diversity and abundance of crabs, lizards, birds, and multiple mammalian omnivores (Dugan et al. 2003, Stapp and Polis 2003, Lewis et al. 2007, Spiller et al. 2010).

Sea wrack is one example of a subsidy that has been shown to alter the productivity and diversity of small islands (Anderson and Polis 1998). However, this process has been demonstrated mainly on islands with low *in situ* terrestrial productivity (such as deserts) (e.g. Polis and Hurd 1996, Hyndes and Lavery 2005, Catenazzi and A. Donnelly 2007). To the best of my knowledge, Paetzold et al. (2008) is the only example of a study considering the effects of sea wrack on a productive, temperate environment. However, only one island was examined (Paetzold et al. 2008).

To begin examining the unknown subsidy effect (if present) of sea wrack to islands with high terrestrial productivity, I first explore the timing and extent of sea wrack accumulations to 100 islands found within the coastal temperate rainforests of the Central Coast of British Columbia (BC). More than 40,000 densely vegetated islands are found on the BC coastline (Sebert and Munroe 1972). These are very productive terrestrial ecosystems, and their forests leech an average of 33,300 kg C km^{-2} yr^{-1} into the surrounding ocean, the highest yields of dissolved organic carbon to be measured to date along a coastal margin (Oliver et al. 2017). Marine productivity is just as impressive: BC has the highest diversity of kelps globally, hosting more than 30 species (Gabrielson et al. 2012). Kelps have high primary productivity, with *Macrocystis pyrifera* alone producing up to 820 g C m^{-2} yr^{-1} (Mann 1973). Like most previous island biogeography studies, this research features a productive marine environment but differs markedly in terrestrial productivity and the number of islands examined.

This research, as a component of the 100 Islands project, is among the first to examine the influence of subsidies from a productive marine environment to productive terrestrial ecosystems on islands. The 100 Islands project is a five-year collaboration between multiple Principle Investigators, Post-doctoral Fellows, Graduate students, and research technicians from three institutions: The University of Victoria, Simon Fraser University, and the Hakai Institute. Project members have surveyed invertebrate, mammal, plant, and songbird communities on 70 – 100 islands along the Central Coast of BC. The Central Coast, exempt from many industrial activities such as logging, host relatively intact ecosystems. Data collected from these surveys will provide baseline information on these taxa that may be useful to marine and land-use planning, understanding influences of climate change, or assessing impacts of industrial development. Additionally, these data will be synthesized in an effort to understand how marine subsidies affect predicted relationships between terrestrial species diversity and island area in a productive, temperate landscape.

The first step in exploring patterns between terrestrial diversity and subsidies is to confirm the presence of nutrient flow from the marine to the terrestrial environment. Several potential forms of marine subsidy are available to the Central Coast islands. Water and nitrogen may enrich soil and plants via fog and sea spray (Whipkey et al. 2000). Feces and detritus deposition from river otters (*Lontra canadensis*), as well as sea wrack deposition, may impact soil and plant communities (Ben-David et al. 1998, Orr et al. 2005). The effects of fog, sea spray, and river otter disturbance are largely confined to the edges of islands (Ben-David et al. 1996, Ewing et al. 2009). Sea wrack-derived nutrients, however, have been shown to penetrate further inland, due to consumption by mobile invertebrate consumers (Paetzold et al. 2008, Mellbrand et al. 2011). Additionally, sea wrack has been proposed to represent a temporally consistent vector (Gómez et al. 2013), although it is unclear if this is the case along the Central Coast of BC Islands.

Nereocystis luetkeana, one of two species that contributes biomass to kelp forests, is a perennial species. In the fall this kelp senesces *en masse*, potentially washing ashore and contributing vast quantities of biomass to terrestrial communities. I hypothesize that seasonal *N. luetkeana* senesces combined with fall storms could lead to significantly larger wrack accumulations, a pattern that has been observed in nearby Oregon (Reimer 2014).

The 100 Islands Project seeks to determine if sea wrack is an important vector of marine-derived nutrients to small island ecosystems on the Central Coast of BC. However, before this can be tested, researchers need to know where, when, and how much sea wrack is washing ashore along this coastline. Therefore, my research seeks to answer the following questions: 1) what environmental variables push and/or trap sea wrack onshore? 2) what are the seasonal changes in wrack biomass and species composition? In Chapter One I address these questions and discuss the results of three years of research that attempts to identify where and when wrack will wash ashore.

In addition to determining spatial and temporal patterns of wrack accumulation, in Chapter Two I discuss a technique for determining the dry biomass of sea wrack, seaweed, and seagrasses from wet biomass measurements. Commonly, sea wrack, seaweed, and seagrass research requires wet to dry biomass conversion to compare measurements across investigators, taxa, and geographical regions. Often, deriving these correction factors is the rate-limiting step in ecological wrack studies, due to the time, labour, and logistics required to transport wet wrack samples. However, the results of wet-dry mass calibrations are rarely (if ever) published, creating the need for each new study to determine a new correction factor. To streamline my own methods and in response to this data discrepancy, I determined the relationship between wet and dry mass for 12 common Northeastern Pacific Ocean seaweeds and seagrasses, with the goal of providing a suite of reliable results that can be incorporated into future research.

Knowing the mechanisms behind a sea wrack subsidy will help us to appreciate the degree to which marine-terrestrial resource subsidies connect ecosystems in British Columbia. Learning how resource subsidies and other processes work synergistically will help us to understand the dynamics that are driving complex ecological systems on islands.

CHAPTER TWO

Site or Storm: Environmental factors that affect sea wrack deposition and accumulation in a coastal temperate rainforest.

2.1 ABSTRACT

Dead, shore-cast seaweeds and seagrasses (commonly called sea wrack) provide an important vector of marine derived nutrients to low productivity terrestrial environments. However, little is known about the processes that facilitate wrack transport, deposition, and accumulation in coastal temperate British Columbia. Three broad factors affect the stock of wrack along a shoreline: climatic events which dislodge seaweeds and move them ashore, physical characteristics which retain wrack at a site, and amount of potential donor habitat nearby. To determine when, where, and what wrack was accumulating on shorelines I surveyed 455 sites across 101 islands to record wrack biomass, species composition, and shoreline biogeographical characteristics. I returned to a subset of sites on a bi-monthly basis to document temporal changes in wrack biomass and species composition. *Zostera marina, Fucus distichus, Macrocystis pyrifera, Nereocystis luetkeana, Pterygophora californica* and *Phyllospadix* spp. were the six dominant species found across spatial and temporal scales. My results indicate that sea wrack can accumulate along any shoreline that is not composed of rock substrate and that the presence of wrack is positively influenced by the amount of donor ecosystem habitat as well as the width and wave exposure of a shoreline. This demonstrates that of the three broad factors considered, physical site characteristics and the amount of donor habitat near a site have more of an influence on wrack accumulations than climate events. Additionally, I found that wrack

biomass and species composition were similar throughout all four seasons. My results suggest that sea wrack is a consistent vector of potential nutrients from the marine to the terrestrial environment in British Columbia.

2.2 INTRODUCTION

The equilibrium theory of island biogeography seeks to explain the structure of species communities on islands (MacArthur and Wilson 1967) and has also been used in analogous fragmented landscapes (Patiño et al. 2017). The original theory has been refined many times, including through subsidized island biogeography theory (Anderson and Wait 2001). Subsidized island biogeography theory attempts to reconcile the patterns of diversity seen on small islands with the effects of bidirectional flow of energy and nutrients across environmental boundaries. These nutrient flows can influence the population and community dynamics of neighboring ecosystems and create connectivity between environments (Polis et al. 1997), with strong effects on marine and terrestrial food web functioning (Anderson and Polis 1998, Oliver et al. 2017). Shorelines are a habitat margin that facilitate movement of nutrients across ecosystem boundaries. These ocean-to-land (and vice versa) resource transfers are widely referred to as marine-terrestrial subsidies.

Sea wrack (a term for dead, shore-cast seaweeds and seagrasses) is one example of a marine subsidy that directly and indirectly affects terrestrial ecosystems (Spiller et al. 2010, Del Vecchio et al. 2013). Sea wrack is generally deposited on a beach in a strip or in patches that run parallel to the water and mark the high, spring, or storm tide line (Suursaar et al. 2014). While decomposing, wrack that has been washed above the high intertidal zone can act as a direct fertilizer, enriching sand and terrestrial flora (Cardona and García 2008, Villares et al. 2016). Wrack deposits also provide a nutritionally rich and important food resource for a large community of microbes, and semi-terrestrial or terrestrial invertebrate decomposers (Pennings et al. 2000, Ince et al. 2007, Sosik and Simenstad 2013, Lastra et al. 2014), which can significantly increase both the abundance and diversity of invertebrate communities along shorelines (Dugan et al. 2003, Schlacher et al. 2017). Subsequently, these invertebrate species are ingested by higher trophic level terrestrial consumers, and the presence or absence of sea wrack on a shoreline can affect the diversity and abundance of crabs, lizards, birds, and multiple mammalian omnivores (Dugan et al. 2003, Stapp and Polis 2003, Lewis et al. 2007, Spiller et al. 2010).

Generally, wrack biomass deposition is thought to be consistent throughout the year (Gómez et al. 2013). The standing stock of wrack on shorelines, however, may significantly fluctuate due to several factors: seasonal senescence, herbivore grazing, or dislodgement and erosion due to tidal and climate events (Seymour et al. 1989, Chapman and Johnson 1990, Krumhansl and Scheibling 2011). Many seaweed species have annual life histories, such as *Nereocystis luetkeana*, which grows from late spring to early fall, then senesces *en masse*, often dislodging during the first large winter storm (Mann 1973). Kelps are also the preferred target of herbivore grazers such as sea urchins, chitons, and marine gastropods, and rapid colonization of a kelp forest by these consumers can negatively affect the abundance and diversity of sub-tidal macroalgae (Bakker et al. 2015). It is unknown whether or not these events significantly affect the volume and species composition of sea wrack washing ashore and in order to understand wracks impact to terrestrial communities it is important to determine if sea wrack is ubiquitous temporally, or deposited in seasonal surges.

Nutrient subsidies can be delivered in two forms: press or pulse (Fong and Fong 2017). Pulsed subsidies from one ecosystem cause perturbations to an adjacent ecosystem, which can cause an initial response in the density of species in the subsidized ecosystem (Bender et al. 1984). After the pulsed subsidy recedes the perturbed communities ease back into a pre-perturbed state (Spiller et al. 2010). Press subsidies from one ecosystem cause perturbations to adjacent ecosystems, which also changes the densities of species in the adjacent ecosystem (Bender et al. 1984). However, press subsidies maintain their perturbations and can force the subsidized ecosystem into a new state of balance if the perturbation pressure is strong enough (Savage et al. 2012). Confirming the timing and extent of sea wrack accumulations will clarify whether or not sea wrack is a pressed or pulsed nutrient subsidy.

Despite the wealth of research on sea wrack subsidies, there are few studies on the spatial and temporal patterns of wrack deposition and accumulation, especially where the marine and terrestrial environments are both highly productive (Reimer 2014). Coastal BC rainforests produce some the of the largest coniferous forest biomass in the world (Alaback 1991). Adjacent to this terrestrial ecosystem is an equally productive marine environment. Coastal upwelling draws cool, nutrient rich waters to the ocean surface, which supports the growth of much life, including large amounts of macroalgae (Thomson 1981). Over 530 macroalgae species have been recorded in BC waters (Druehl and Clarkston 2016). As with many previous studies, this research features a productive marine environment as a source of sea wrack nutrients, but differs in terrestrial productivity. In this study, I explore the timing and distribution of sea wrack accumulations along the temperate Central Coast of British Columbia (BC). This research is among the first to examine the influence of biophysical variables on sea wrack subsidies from a productive marine to temperate island archipelagoes.

Three broad factors are potentially responsible for macrophyte and macroalgal wrack abundance and distribution along the Central Coast of British Columbia: climate, physical shoreline characteristics, and donor ecosystem habitat. Climate factors such as winds, tides, swell, and the interactions between these conditions can detach macroalgae and macrophytes from their anchorages and push them ashore (Krumhansl and Scheibling 2011), creating areas with predictable wrack depositions (Oldham et al. 2010). Elsewhere, strong wind events cause increased seagrass deposits in the northwest Mediterranean (Jiménez et al. 2017). Higher than normal tides increased wrack accumulations along Estonian shorelines (Suursaar et al. 2014), and along the Pacific coastline of the U.S.A. wave events caused by swell increase wrack biomass (Reimer 2014). No clear global pattern has emerged that is capable of predicting wrack deposition due to climate factors, but clearly climate effects are important.

Physical shoreline characteristics such as slope, substrate, aspect, width, and wave exposure may contribute to the capacity of a shoreline to retain and accumulate wrack (Liebowitz et al. 2016). Interactions between beach length and exposure to waves impacted wrack accruals in Spain (Barreiro et al. 2011), and on shorelines in Barkley Sound, British Columbia, beaches composed of cobble substrates retained significantly more wrack than those of sand or gravel (Orr et al. 2005). In California, sloped beaches were positively correlated with the retention of *Phyllospadix* spp., suggesting that steeper beaches can retain greater amounts of specific wrack species (Liebowitz et al. 2016). Intuitively, one would except that slope, substrate, aspect, width, wave exposure and other physical characteristics would significantly affect a shoreline's ability to retain wrack.

The third broad factor potentially responsible for sea wrack accumulations is the contribution of donor ecosystem habitat, which can be a strong indicator of wrack biomass and species composition (Liebowitz et al. 2016). In BC waters, vast quantities of sea wrack originate from several donor habitats: macroalgae beds on rocky intertidal shorelines, kelp forests, and seagrass meadows. On the Pacific coast of Canada the dominant species *Macrocystis pyrifera* forms kelp forests that produce up to 900 g C m^{-2} yr^{-1} (Wilmers et al. 2012), which dislodge and/or erode at a rate of up to 650 g C m^{-2} yr^{-1} (Druehl and Wheeler 1986, Krumhansl and Scheibling 2012). Eelgrass beds of *Zostera* species are estimated to cover 423 km^2 of the coastline of the Central Coast (Reshitnyk et al. 2016), and reach up 1450 g C $m^{-2}yr^{1}$ of primary productivity (Mann 1973), but dislodgement rates have not yet been reported. Aside from these species the rate of productivity is unknown for most marine macroalgae and macrophytes, nor is it known how much of these dislodged kelps and macrophytes are being exported to the open ocean. However, BC's convoluted coastline extends for over 29,000 km (including islands) and seaweed communities comprise a lush band that encompass this complex coastline (Zacharias and Howes 1998). There is potential for a large amount of biomass from this band to be washed ashore.

Globally, sea wrack as a vector of marine to terrestrial nutrient transfer is a well-studied phenomenon, but little research exists on the mechanisms of wrack depositions and accumulations to shorelines over an extended spatial and temporal scale in British Columbia or in any other temperate environment, especially in regions of both high marine and terrestrial productivity. In this study, I aim to distinguish when and where sea wrack is most likely to accumulate along the coast of BC by asking the following questions: 1) what are the biophysical environmental variables that have the capacity to push and/or trap sea wrack onshore? And 2) what are the seasonal changes in wrack biomass and species composition? Informed by the results of this study ecologists can begin to understand the processes driving sea wrack accumulations on the Central Coast of British Columbia.

2.3 METHODS

2.3.1 Study region

The Central Coast of British Columbia encompasses the region between the northern tip of Vancouver Island (50.7865 ° N, 128.2324 ° W) and the southern tip of Haida Gwaii (51.8711 ° N, 131.0010 ° W). My study area spanned ~ 2000 km^2 area within the Central Coast (Fig. 1) and contains ~1500 islands. This region is located within the very wet hypermaritime subzone of the Coastal Western Hemlock biogeoclimatic classification (Meidinger and Pojar 1991) and is characterized by cool summers (mean warmest month 14.0 °C), warm winters (mean coldest month 2.3 °C), and large amounts of precipitation (mean annual precipitation 3254 mm) (Meidinger and Pojar 1991). The majority of sites in the study area were located in either the Hakai Lúxvbálís Conservancy or the Penrose Island Marine Provincial Park.

2.3.2 Spatial surveys

Island Selection. Cluster analysis was used to identify study islands. Clustering is an unsupervised, multivariate technique that can be used to group observations or sample units (i.e. islands), that are similar with respect to the variables used to define them (Hill and Lewicki n.d.).

Cluster analysis provides a method of data reduction that ensures that a range of island characteristics are sampled.

Cluster variables were selected for their relevance to Island Biogeography theory (e.g., island size and distance to mainland, Wilson and MacArthur (1967)) and subsidized island biogeography theory (i.e. isolation and perimeter to area ratio, Polis and Hurd (1996), Appendix, Table 3). Five biogeographical descriptors for all islands within the study region (n = 1470) were derived. Biogeographical characteristics were extrapolated from the British Columbia (BC) ShoreZone dataset (Howes et al. 1994). The results of cluster analysis identified several clusters (Appendix, Table 4) where multiple islands were located within close proximity to each other (i.e. within a 'node'), and for logistical reasons I chose to sample these nodes. Within a node, islands were selected to maximize variation across a range of island sizes and shoreline structure. The final dataset consisted of 101 islands within nine nodes (Fig. 1).

Wrack Biomass and Composition Measurements. During May, June, July and August of 2015, 2016, and 2017, I visited each island once, conducting four surveys per island, one at each of predetermined coordinates representing the furthest North, East, South, and West aspect of each island. Additionally, because different substrates have varying abilities to trap and hold wrack (Orr et al. 2005), extra surveys were performed on islands that had beaches with either a sand, gravel, cobble, or boulder substrate outside of the cardinal direction surveys. Therefore, each island had either a minimum of four or a maximum of ten survey sites for a total of 455 sites in the study area. Each survey entailed three 20 meter transects, centered on the pre-determined cardinal direction coordinates. To account for tidal range flux, transects were focused in and around the supralittoral zone which I could access during all tidal cycles. For each survey, one transect was placed at the most recent high tide wrack line, one at the spring/storm/surge wrack line (the highest wrack line visible on the shore), and one was placed just inside the shoreline's terrestrial edge (towards the island interior).

I used a random number generator to determine three locations along each transect line (n = 9 across three transects at each cardinal direction) to place a 1 m^2 quadrat. All wrack that was visible within the quadrat was identified to the functional group (as per Steneck and Dethier 1994), genus, or species level, sorted, and weighed. Wrack that was unidentifiable was categorized as such and weighed. Wrack that was partially buried but still had a portion visible was uncovered, rinsed or wiped of sand, sorted, and weighed. Wrack was weighed with either a kitchen diet scale with accuracy (+/-) 2 g or a hanging spring scale with accuracy (+/-) 1 kg attached to a tarp.

Prior to weighing I also assigned a wet/dry category to each species pile (desiccated = air or sun dried and fully desiccated, damp = partially air or sun dried but still retaining some moisture content, wet = appearing to be freshly washed ashore, wet, full moisture content). Following methods outlined in chapter three, I took subsamples from twelve of the most common seaweed species of each wet/dry scale category and dried them in a Fisher Scientific Isotemp drying oven at 80 degrees Celsius until the samples each reached a constant mass (weight within +/- 0.005 g for three consecutive measurements). Wet to dry mass calibrations were performed by deriving a correction factor from each species' linear relationship between wet and dry conditions. The correction factor was applied to all wet and damp biomass measurements. Subsequently all biomass results for both spatial and temporal data are reported in dry estimates.

Biophysical and Environmental Measurements. In addition to the wrack biomass and composition surveys, I also collected site data as per protocols outlined in the ShoreZone Coastal Habitat Mapping Protocol (Harper and Morris 2014). The ShoreZone Mapping Protocol describes methods to catalog geomorphic and biological coastal features of the Pacific Northwest (including BC, Alaska, Washington and Oregon). Site data I collected included shoreline slope, aspect, substrate, width, and biobands, which are patterns of identifiable biota observable in the intertidal and supralittoral zone (Howes et al. 1994). Biobands were used to classify the wave exposure of a site as per the ShoreZone Mapping protocol. Substrate categories were adapted from the Wentworth scale of grain size and included sand, gravel, cobble, boulder, and rock (Wentworth 1922). Shoreline slope, aspect, and width measurements were used to ground-truth the results of a shore zone morphology dataset generated by Unmanned Aerial Vehicle (UAV) imagery (Nijland *et al. unpublished data).* The UAV dataset generated slope, aspect, and width measurements at every five meters along every islands shoreline. These measurements were similar but more precise than my on the ground measurements (Nijland *et al. unpublished data).* Therefore, in my models I used the mean slope, aspect, and width measurements from the UAV dataset for each site. Methods of imagery analysis are outlined in Nijland et al. (2016) and are used with UAV imagery and elevation models at ten centimeter resolution.

Wind direction, wind speed, wave height, and wave period measurements from the time period of six hours before every site visit were accessed from Environment Canada West Sea Otter

Buoy archives ("West Sea Otter Archive Plot" n.d.). If data were unavailable for that specific time period a measurement was used from within +/- 2 hours.

A site's proximity to a source seaweed habitat was calculated by identifying the three main donor ecosystems: 1) kelp forests as donors of *M. pyrifera* and *N. luetkeana*, 2) eelgrass beds as donors of *Z. marina*, and 3) rocky intertidal shorelines as a donor of *F. distichus*. To determine the relative contribution of each ecosystem in explaining biomass measurements, I analyzed UAV and World View 2 satellite imagery in ArcGIS and estimated the extent of all forest/bed/rocky intertidal habitats. With the understanding that kelps such as *M. pyrifera* commonly wash ashore within a five kilometer radius of their detachment sites (Jenifer E. Dugan *unpublished data*), I positioned a set of radii around each survey site (length of radii = 25 m, 50 m, 100 m, 500 m, 1km, 2 km, 3 km, 4 km, 5 km, 7.5 km) and analyzed the strength of the relationship between the summed area of forest/bed/rocky intertidal habitat and kelp/eelgrass/*F. distichus* biomass using Spearman's correlation analysis for non-normally distributed data in R Version 3.3.3 (R Core Team 2017). Following methods established by Leibowitz *et al.* (2016), the radius with the strongest relationship (from my analysis: 2 km) was used for subsequent analysis.

2.3.3 Temporal surveys

Site Selection. Strong winter wind storm and swell events on the Central Coast can limit boat access. For this reason, a small subset of easily approachable sites was chosen on which to conduct temporal surveys. These included North Beach (51.6628 ° N, 128.1401 ° W), West Beach (51.6558 ° N, 128.120 ° W) and Fourth Beach (51.6431 ° N, 128.1510 ° W) on Calvert island, all of which are classified as flat (<5°), sandy, semi-exposed shorelines as per the BC ShoreZone dataset (Howes et al. 1994). Surveys were conducted once every two months starting in July 2016 and ending in April 2017, with one three-month period elapsing between November 2016 and February 2017 survey dates.

Wrack Biomass and Composition Measurements. In an effort to establish a finer-scaled resolution of the shift in wrack biomass and species composition throughout a seasonal interval, transects were surveyed at each site during each monthly low tide window (less than 1.0 meter). Power analysis results suggested 12 transects per site to achieve 80% power. However, this proved physically impossible to do within one day so we visited each site twice (two days apart) and performed six transects per visit. The three beaches' terrestrial edges were divided into 100 meter intervals and six transect locations were randomly generated. One transect per 100 meters was completed to avoid overlap along the beach. Transects were run perpendicular to the water, starting at the terrestrial edge and marked permanently with flagging tape. A compass bearing was measured along the perpendicular direction, and this bearing was followed for each survey creating a repeatable transect. I collected wrack starting at the daily high tide wrack line and ending at the lowest water level experienced during the daily low tide. All wrack within 0.5 meters of either side of the transect line was collected, identified, and weighed. Collected and weighed wrack was placed far above the highest tidal line to prevent it from being redeposited in the transect during the next survey (two days following).

A wet-to-dry mass calibration was established using previously collected data (Wickham et al. under review).

2.3.4 Statistical analysis

Spatial surveys. UAV data from the 2017 field season was not available at the time of this manuscript's writing. Therefore, my models examining the effects of biophysical variables were based on data from 2015 and 2016 (388 sites across 91 islands). However, any results that only rely on wrack biomass and/or species composition were generated using the complete dataset (455 sites across 101 islands).

Prior to modeling, continuous predictor variables (wind direction, wind speed, wave period, wave height, high tide, aspect, slope, width, and donor habitat), were standardized by subtracting the mean and dividing by the standard deviation. One extreme outlier was removed from the dataset as I suspected it was a data entry mistake. The response variable (dry biomass) was log-transformed to normalize distribution. Collinearity and correlation between predictor variables was examined using pairplots with Spearman correlation coefficients (Zuur et al. 2010). Wave height was correlated with wind speed and wind direction and was subsequently removed. Dry wrack biomass was compared across nodes using analysis of variance (ANOVA), and differences in biomass accumulations between nodes were explored via Tukey's HSD test.

I used hurdle modeling to help with zero inflated data (Zuur et al. 2009). This required two steps. First, the data were considered as zero or non-zero and a presence/absence dataset was created. Second, a normally distributed non-zero observation (biomass) dataset was created. Using a generalized linear model (GLM) with binomial distribution, I used the presence/absence dataset to model the probability that a zero value was observed. The biomass dataset was used to explore what drives biomass accumulation with linear mixed-effect modelling using the R package nlme (Pinheiro et al. 2017). I expected baseline biomass in the biomass dataset to be different spatially so I included node as a random intercept in the linear mixed-effect models and site as a fixed effect.

Wrack accumulation is understood to be determined by biophysical forces (represented by my predictor variables), not the influence of latitude or longitude (Barreiro et al. 2011). However, because of the spatial nature of my dataset, I qualitatively assessed *a priori* whether any additional spatial component was necessary. For the initial arrival of wrack (presence/absence model), I found no evidence of a spatial relationship. Biomass accumulation showed no relationship to individual or island or coordinate location. Therefore, I used a mixed-effects structure for the biomass models, where the node was included as a random intercept. For both the presence/absence and the biomass model I thoroughly examined the residuals of each best model for signals that I violated assumptions of independence in my linear model. I also mapped residuals against their spatial coordinates to check for any patterns that may indicate spatial correlation issues (Appendix, Fig. 8 & 9), using the package gstat in R (Pebesma 2004, Graler et al. 2016).

I developed multiple models *a priori* (listed in Tables 1 and 2), for both datasets and ranked them using the Akaike Information Criterion (AIC) (Burnham and Anderson 2003). The model with the lowest AIC value was considered to be the best option to explain the data, though I did consider any models that ranked four or less AIC points from the top model as having a similar level of support.

Temporal surveys. Dry wrack biomass was compared using the Kruskal-Wallis test for non-parametric data with month and site as fixed factors. To test the variability in wrack species composition and biomass through time I analyzed the relative biomass of each wrack taxon per month and per site using analysis of similarities (ANOSIM). ANOSIM routines are based on a Bray-Curtis dissimilarity matrix of species occurrences using the species' logged dry biomass data. Non-metric Multidimensional Scaling (NMDS) using Bray-Curtis dissimilarity matrix techniques was also used to assess whether composition changed with seasons or between sites. A similarity percentage (SIMPER) routine was performed to find the species with the highest contribution to the similarity/dissimilarity of each month or site. All data were analyzed using the Vegan package in R (Oksanen et al. 2017).

2.4 RESULTS

Spatial surveys. A total of 52 genus, functional group, or species representatives were recorded throughout the study region (Appendix, Table 5). Calvert node had the highest number of species (35) and Stirling node had the least (8 species, Fig. 2). Of these 52 species, six dominated the wrack biomass: *Z. marina* (40 % of total wrack biomass), *F. distichus* (26 %), *P. californica* (10 %), *M. pyrifera* (4 %), as well as *N. luetkeana,* and *Phyllospadix* spp., (each contributing 2 % to the sum of the total wrack biomass) (Appendix Table 5). The other 46 species each contributed to 1% or less of total wrack biomass (Appendix Table 5). Species composition was similar between nodes (ANOSIM; factor = node, R = 0.08, $p < 0.02$, Fig. 2 & 3).

Accumulated wrack varied widely across the study region (Fig. 1, panels A-F), ranging from a mean of 0 g/m^2 on many islands to a mean of 6952 g/m^2 at one small island in the Goose node. Average wrack accumulations per site differed between nodes (ANOVA; $p = 0.03$). These differences were largely driven by wrack accumulations in the Goose node, which were significantly different from many of the nodes located to the south of it, the exception being South Calvert node (Tukey multiple comparison of means; Triquet $p < 0.03$, Stirling $p < 0.05$, Calvert $p < 0.04$, Penrose $p < 0.03$, South Calvert $p > 0.1$).

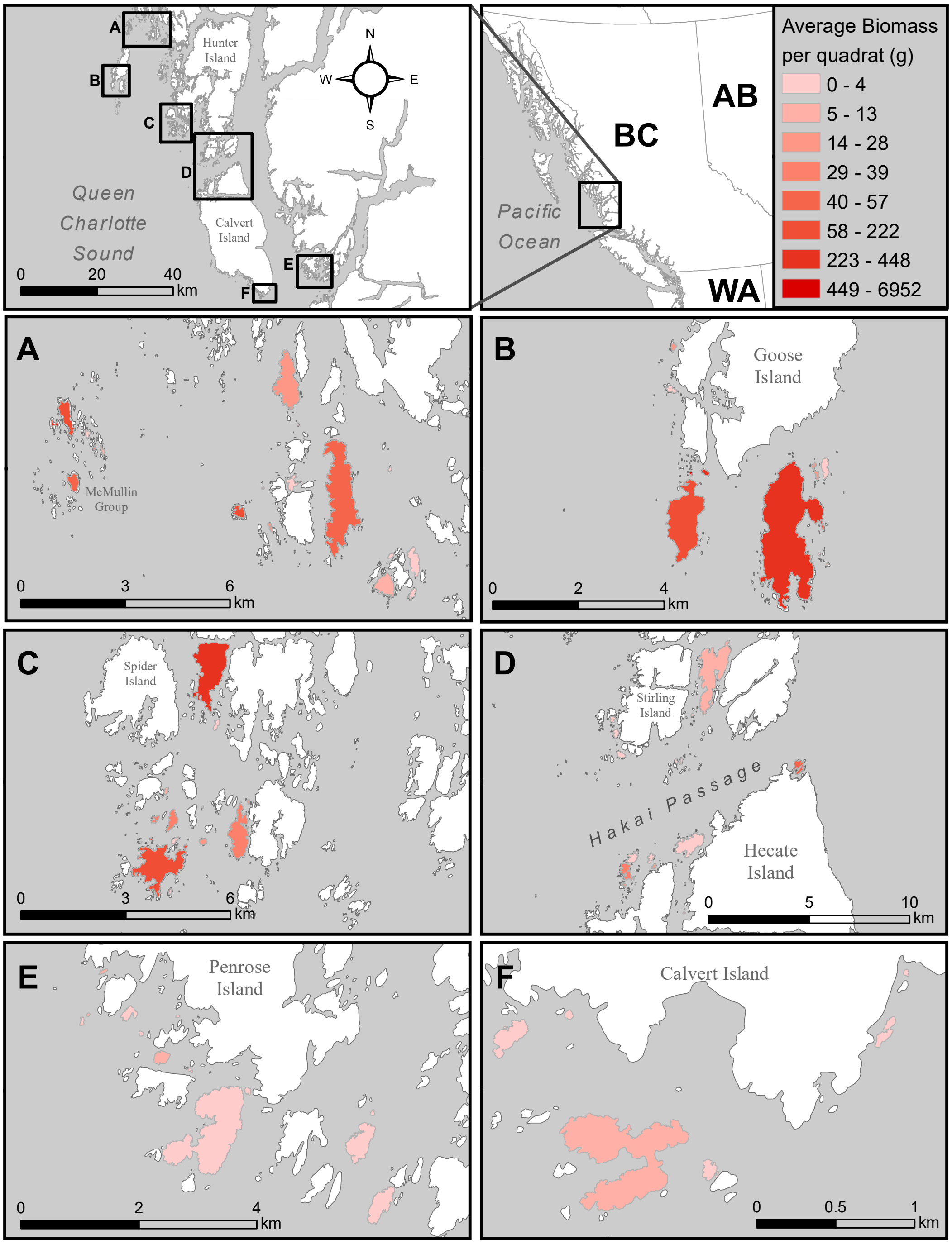

Figure 1. British Columbia's Central Coast (top right). The study region and location of nodes of study islands as chosen by cluster analysis (top left). All study islands are coloured in red according to their dry biomass accumulations. (A) McMullin, Tribal, and Admiral nodes. (B) Goose node. (C) Triquet node. (D) Calvert and Stirling nodes. (E) Penrose node. (F) South Calvert node.

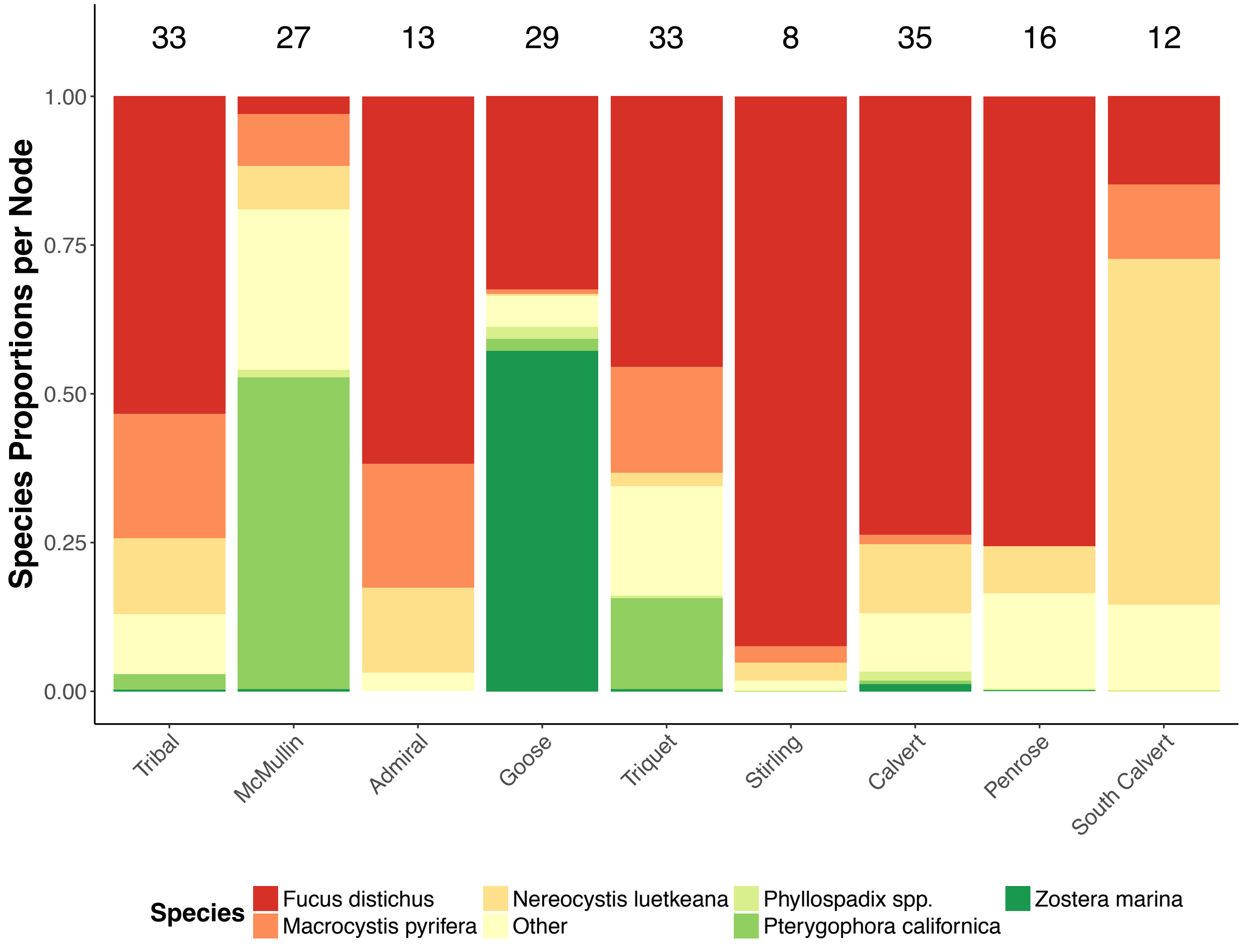

Figure 2. Proportion of species for each node, of the six dominant species seen throughout the study area. Other is the combined total of all other species recorded in that node. Proportions are calculated from summed dry biomass. Total number of species of seaweeds recorded in the wrack deposits for each node is displayed above the bar.

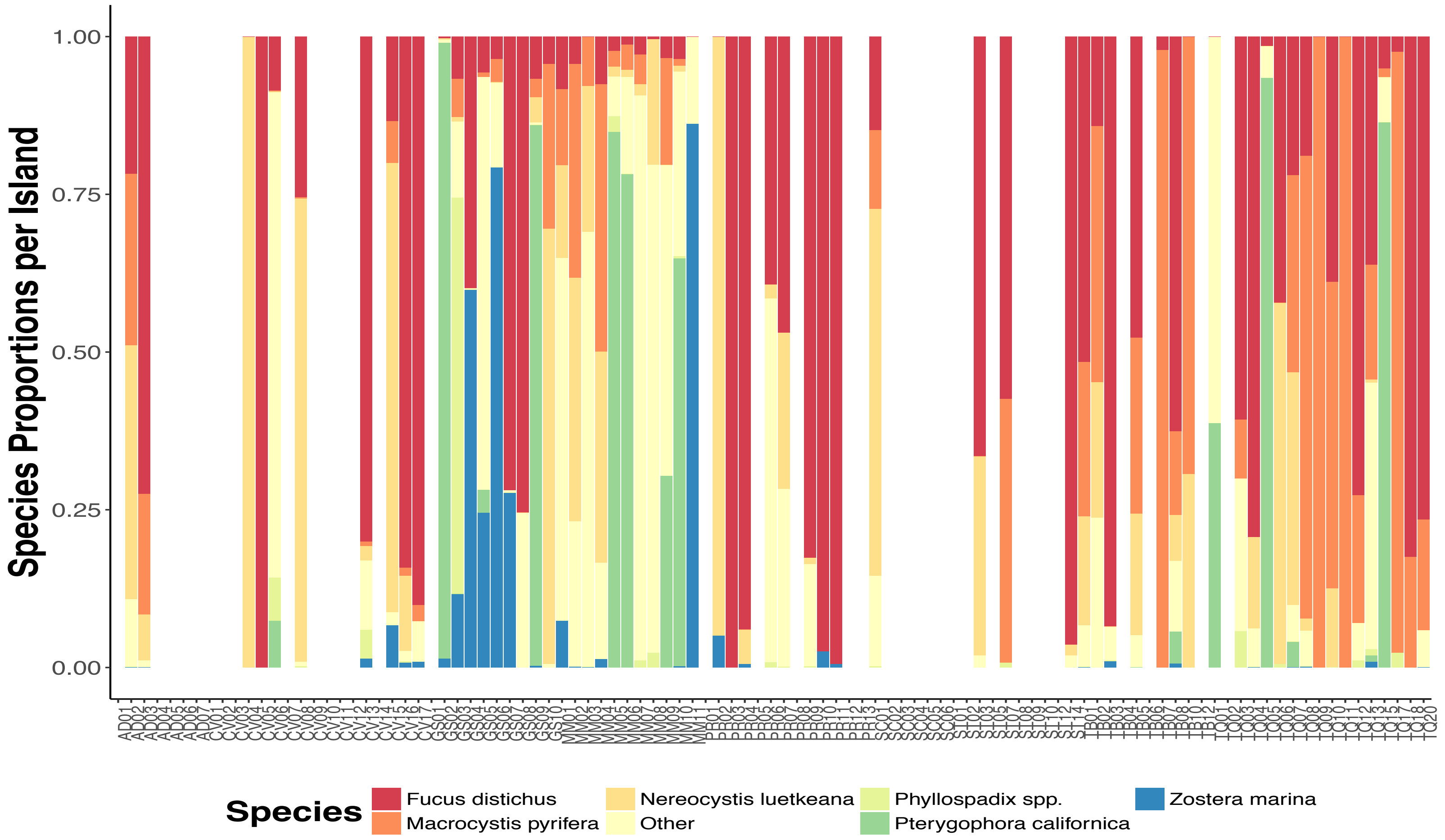

Figure 3. Proportion of species for each island, showing the six dominant species seen throughout the study area. Other is the combined total of all other species recorded in that node. Proportions are calculated from summed dry biomass. Islands with no bar displayed had zero biomass recorded for all sites. See Appendix Table 6 for island node and number abbreviations.

In tests for the presence/absence of wrack with all three parameters (site, climate, and donor habitat), the model comprised of site and donor habitat parameters indicated that the combination of aspect, slope, width, substrate, wave exposure, and donor habitat best predicted whether or not a site would have wrack presence (Table 1a). Upon closer inspection of the relative influence of each factor in the top model, it was revealed that substrate, donor habitat, wave exposure, and width had significant influences. Of the five substrate types (sand, gravel, cobble, boulder, and rock), rock had a strong negative influence when predicting presence or absence of wrack on shorelines (Table 1b, Fig. 4). None of the other four substrates significantly influenced wrack presence. The amount of donor habitat within a two-kilometer radius had a positive influence on wrack presence (Table 1b, Fig. 4) as did the width of the shoreline (Table 1b, Fig. 4). Of the six categories of wave exposure (very protected, protected, semi-protected, semi-exposed, exposed, and very exposed), very protected exposures were positively correlated with wrack presence (Table 1b, Fig. 4).

For the biomass data set, which tested the predictors of accumulated wrack biomass at a site, the best model was the same combination of aspect, slope, width, substrate, wave exposure, and donor habitat variables (Table 2a). However, rock substrate was the only term to significantly influence the amount of wrack located at a site (Table 2b, Fig. 4). Aspect, slope, width, substrate and donor habitat had no significant influence on the biomass of wrack deposits at a site.

For both presence/absence and biomass there was one other combination of variables that scored within four AIC points of the top model. Site and donor habitat parameters, which combined aspect, slope, width, substrate, and donor habitat variables to explain both wrack presence and biomass, scored exactly four points more than the top presence/absence model (Table 1a), and within two points of the top biomass model (Table 2a). The exclusion of wave exposure from this model was the only factor distinguishing it from the top model. Rock substrate, donor habitat, and width were the most significant variables explaining presence/absence in the site and donor habitat (minus wave exposure) model, with p – values of < 0.001, < 0.001, and 0.04, respectively. Rock substrate was the only significant variable for the biomass dataset (p – value $<$ 0.001).

Table 1. (a) AIC values from model testing performed to determine the best predictors of sea wrack presence/absence. AIC denotes Aikake Information criterion score; Δ AIC is the difference between the current and best model; (*) denotes interaction terms. (b) Coefficient estimate, standard error (SE), and *p* - value for each significant term in the top model, as determined by the lowest AIC score.

Table 1a

Parameters	**Variables**	**AIC**	**Δ AIC**
Site + Habitat	Aspect + Slope + Width + Wave Exposure + Substrate + Donor habitat	250.8	0
Site + Habitat	Aspect + Slope + Width + Substrate + Donor Habitat	254.9	4.1
Site + Habitat + Climate	Wind Direction + Wave Height + Wave Period + High Tide + Aspect + Slope + Width + Wave Exposure + Substrate + Donor Habitat	256.3	55.5
Site + Habitat + Climate	Wind Direction*Wave Height + Wave Period + High Tide + Wind Direction*Aspect + Slope*Substrate + Width + Wave Exposure + Donor Habitat	259.8	9
Site + Habitat	Aspect + Slope*Substrate + Width + Wave Exposure + Donor Habitat	360.3	109.5
Site + Habitat + Climate	Wind Direction*Wave Height + Wave Period + High Tide + Wave Exposure + Donor habitat	421.6	170.8
Climate + Site	Wind Direction + Wave Height + Wave Period + High Tide + Wave Exposure	511	261.1
Climate	Wind Direction + Wave Height + Wave Period + High Tide	526.4	275.6

Table 1b

Variables	**Estimate**	**SE**	***p* - value**
Width	0.87	0.36	0.02
Wave exposure - very protected	1.97	0.91	0.03
Substrate - rock	-4.15	0.68	< 0.001
Donor habitat	1.45	0.27	< 0.001

Table 2. (a) AIC values from model testing performed to determine the best predictors of accumulated sea wrack biomass. AIC denotes Aikake Information criterion score; Δ AIC is the difference between the current and best model; (*) denote interaction terms. (b) Coefficient estimate, standard error (SE), and *p* - value for each significant term in the top model, as determined by the lowest AIC score.

Table 2a

Parameter	**Variables**	**AIC**	**Δ AIC**
Site + Habitat	Aspect + Slope + Width + Wave Exposure + Substrate + Donor Habitat	718.5	0
Site + Habitat	Aspect + Slope + Width + Substrate + Donor Habitat	720.3	1.8
Site + Habitat + Climate	Wind Direction + Wave Height + Wave period + High tide + Aspect + Slope + Width + Wave Exposure + Substrate + Donor Habitat	726.3	7.8
Site + Habitat	Aspect + Slope*Substrate + Width + Wave Exposure + Donor Habitat	729.4	10.9
Site + Habitat + Climate	Wind Direction*Wave Height + Wave Period + High Tide + Wind Direction*Aspect + Slope*Substrate + Width + Wave Exposure + Donor Habitat	731.5	13
Climate	Wind Direction + Wave Height + Wave Period + High Tide + Wave Exposure	752.8	34.3
Site + Climate + Habitat	Wind Direction*Wave Height + Wave Period + High Tide + Wave Exposure + Donor habitat	753.3	34.8
Climate	Wind Direction + Wave Height + Wave Period + High Tide	755.8	37.3

Table 2b

Variables	**Estimate**	**SE**	***p* – value**
Substrate - rock	-2.05	0.62	0.002

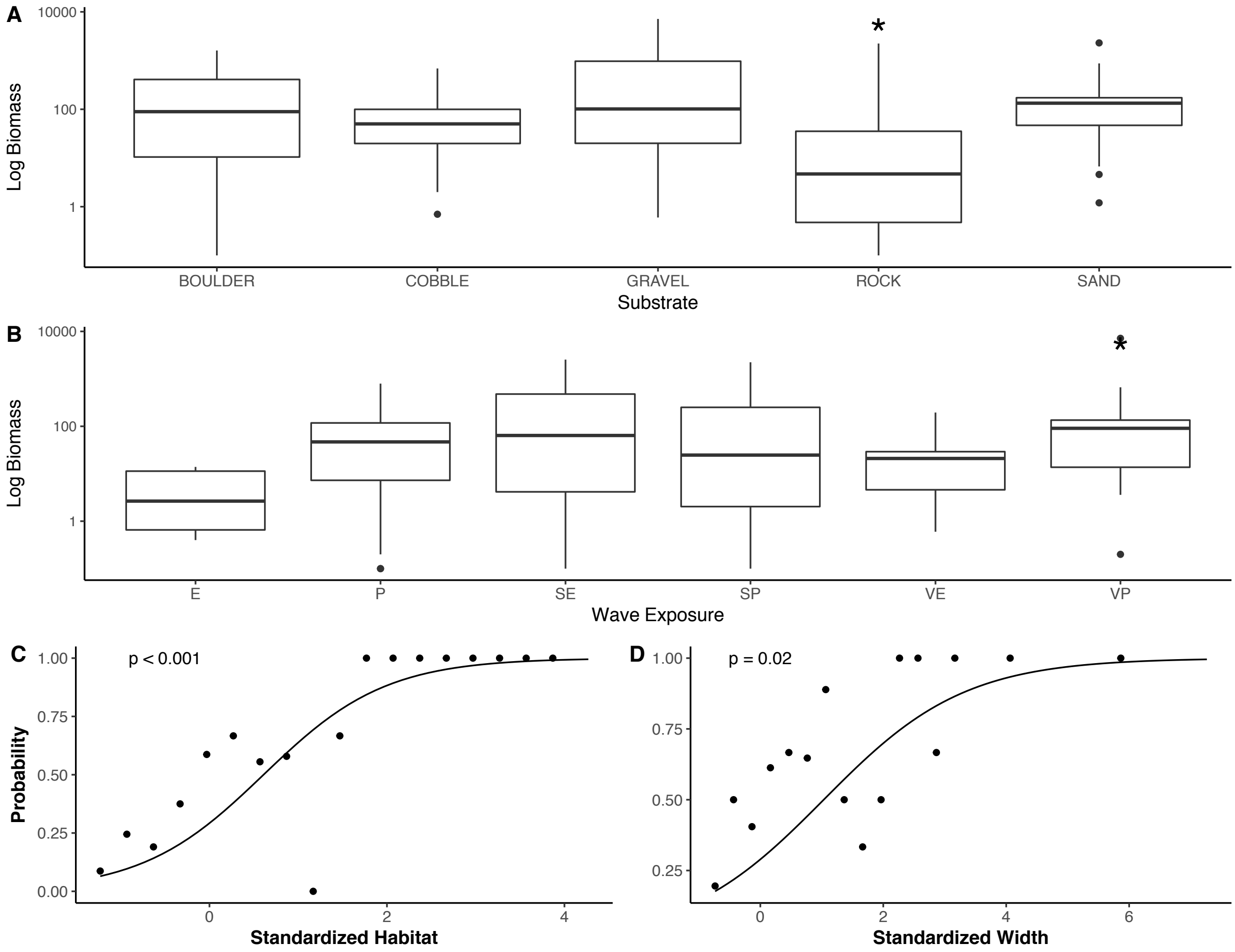

Figure 4. Wrack presence as a function of the significant terms; (A) substrate, (B) wave exposure, (C) donor habitat, and (D) width, from the top-ranking model predicting the presence or absence of wrack at 388 sites on 91 islands on the Central Coast of British Columbia. Categorizations for the wave exposure are: E for exposed, P for protected, SE for semi-exposed, SP for semi-protected, VE for very exposed, and VP for very protected. (*) denotes significance between categories. For rock substrate $p < 0.001$ and for very protected wave exposures $p = 0.03$. The p-values for the continuous variables of habitat (the amount of m^2 of donor habitat per 2 km radius of site), and width (m) are displayed in the top corner of each plot. Rock substrate is also the only significant term from the top-ranking model predicting wrack biomass accumulations (it is negatively related to wrack biomass, $p < 0.001$).

Temporal Surveys. Wrack was present at all sites in all seasons (Fig. 5). There was no significant difference in the amount of wrack deposited on a monthly basis (ANOVA; $p > 0.5$), nor was there any significant difference between the amount of wrack deposited at each site (ANOVA; $p > 0.1$). There were likely differences in species composition between months, though because our ANOSIM R value was low (R = 0.23 or 0.24) and our number of replicates relatively low, I have chosen to interpret these results conservatively. Thus, I consider there to be general overlap in species composition for both month and site (Fig. 6, ANOSIM; factor = month, R = 0.24, $p < 0.001$; factor = site, R = 0.23, $p < 0.05$). North Beach had the most distinct biomass and species composition for each survey, driving what little amount of variation there was between sites in the ANOSIM results.

The top contributors to the similarities between all sites were *N. luetkeana* and *Phyllospadix* spp., (SIMPER; *N. luetkeana* average similarity = 48%, *Phyllospadix* spp. average similarity = 64%). *F. distichus* was also a top contributor in explaining North Beach's similarities to West and Fourth Beaches (SIMPER; average similarity = 24%). *N. luetkeana* and *Phyllospadix* spp. were again the driving forces in explaining similarities between months (SIMPER; *N. luetkeana* average similarity = 38%, *Phyllospadix* spp. average similarity = 62%). In addition, *F. distichus* was a top contributor in July (SIMPER; average similarity = 56%), and *P. californica* was a top contributor in February (SIMPER; average similarity = 29%). All SIMPER results for the cumulative contribution of the most influential species summarized in the Appendix, Figure 10 & 11.

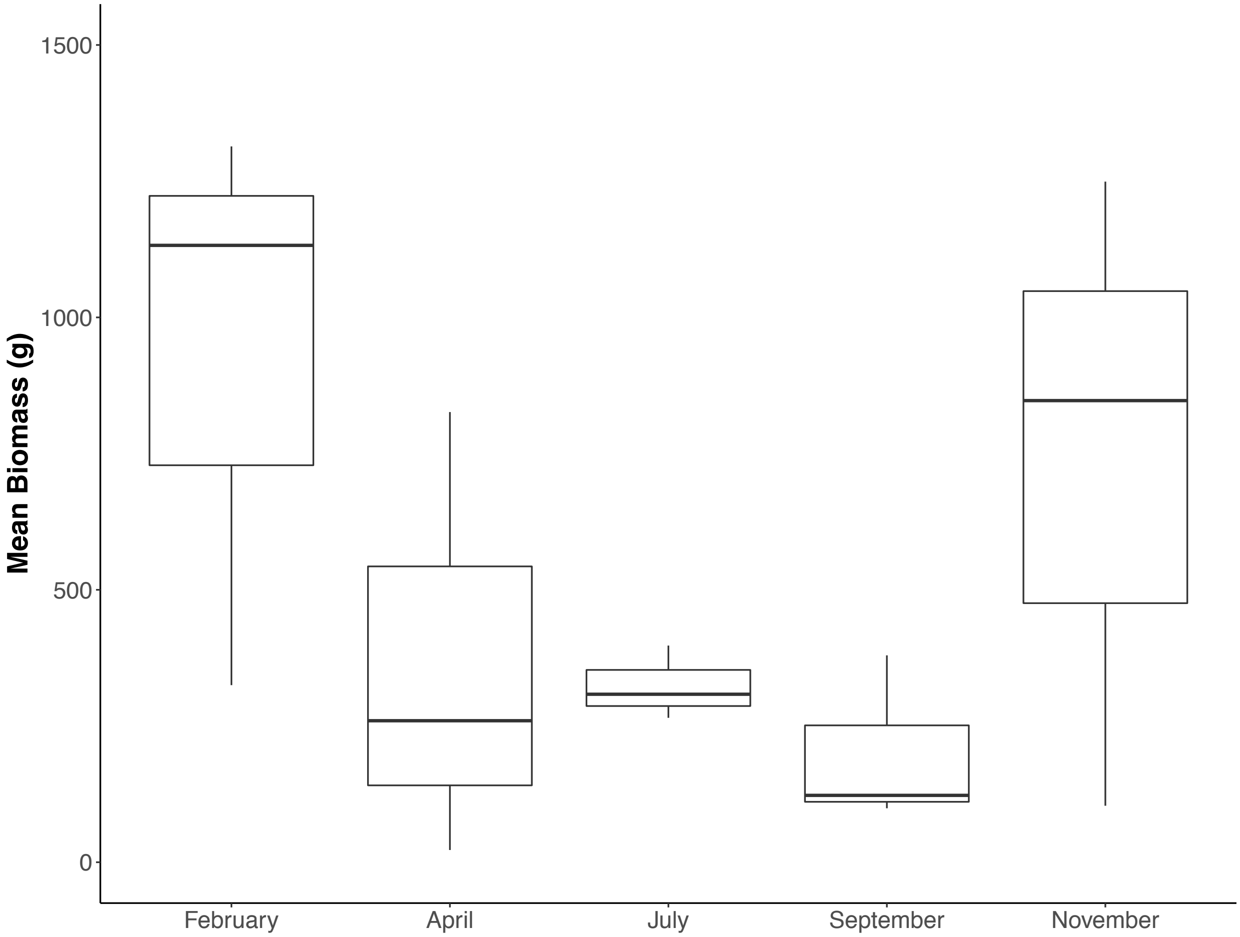

Figure 5. Mean dry wrack biomass per site at five different seasonal intervals. Box plots show median value (solid horizontal line), upper and lower quartiles (box), and maximum and minimum values recorded (whiskers). No significant differences in biomass between months were detected.

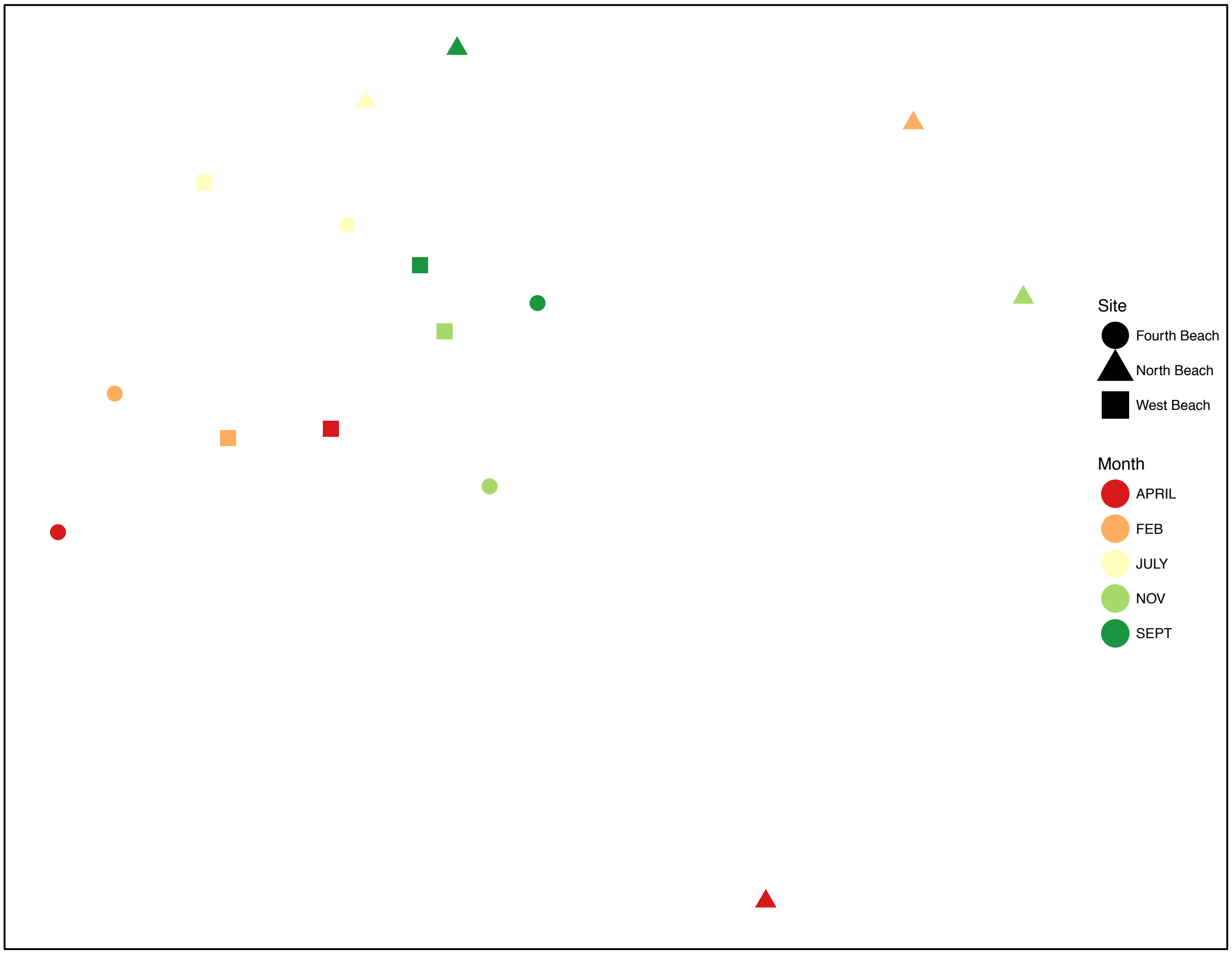

Figure 6. Wrack species composition among three different sites and throughout five different months (NMDS ordination). Stress = 0.12.

2.5 DISCUSSION

I conducted a comprehensive survey of wrack deposits on the Central Coast of British Columbia to explain patterns of wrack presence and accumulation. Of the three broad factors considered, (climatic events, physical site characteristics, and nearby donor ecosystem habitat) wrack presence was most influenced by physical site characteristics, followed by donor ecosystem habitat. The third factor, climate events (i.e., wind, tides, swell), had no significant effect on wrack accumulations. My results suggest that sea wrack can accumulate along any shoreline that is not composed of rock substrate (i.e., a rocky bench or cliff face) and that presence of wrack is positively influenced by the amount of donor ecosystem habitat (i.e., kelp beds, seagrass meadows) nearby as well as the width and wave exposure of the shoreline. Additionally, I determined that along these shorelines, wrack accumulations do not differ significantly in biomass or species composition throughout the year. These results indicate that sea wrack deposits can be considered a consistent vector (both spatially and temporally) of potential nutrients to the terrestrial environment in coastal British Columbia.

Temporal variation in sea wrack biomass is a localized phenomenon and not all coastal regions experience the consistency displayed on the Central Coast in terms of wrack biomass and species composition. Some studies have measured higher mass accumulations in the winter months (Koop and Field 1980, Ochieng and Erftemeijer 1999), while others found more in the summer and fall (Piriz et al. 2003, Reimer 2014, Liebowitz et al. 2016). In the Bahamas during the hurricane season, storms deliver significant quantities of sea wrack to shorelines, which initiates a rapid response from detritivorous amphipods (which consume wrack) and lizards (which consume the amphipods) (Spiller et al. 2010). Shortly after wrack removal, however, amphipod densities decline and lizards return to eating other invertebrates (Spiller et al. 2010). This low frequency and high-density transfer of nutrients from marine to terrestrial communities is one example of a pulsed nutrient subsidy (Fong and Fong 2017). In contrast, the high frequency, continuous density delivery of sea wrack to beaches on the Central Coast can be considered an example of a pressed nutrient subsidy.

Research contrasting the effects of pulse versus press subsidies in the same environment is limited (but see Murphy et al. 2012), though it has been shown that either process can affect species' abundances and the structure of communities (Fong and Fong 2017). Pulse subsidies from one ecosystem cause perturbations to an adjacent ecosystem, which can quickly alter the density of species in the adjacent ecosystem (Bender et al. 1984). This causes an initial response from the adjacent ecosystems' community, however, the community quickly eases back to a pre-perturbation state after the pulsed subsidy recedes (Spiller et al. 2010). Press subsidies cause perturbations to adjacent ecosystems that also effect several species' densities, however, press subsidies maintain their perturbations (Bender et al. 1984). The constant pressure from the perturbation effects the community structure of the adjacent ecosystem and if it's strong enough, can eventually force the community to attain a new state of balance (Savage et al. 2012). It is unknown whether sea wrack inputs on Central Coast beaches have affected the equilibrium of terrestrial communities.

Aside from sea wrack deposition, marine-terrestrial subsidies on the Central Coast commonly occur in the form of pulse events. For example, once every one-to-four years (depending on the species), anadromous salmon (*Oncorhynchus* spp.) will return to their natal rivers to spawn

(Simenstad et al. 1982). These events transport significant amounts of marine derived nitrogen to watersheds and watershed inhabitants (Hocking and Reynolds 2011, Helfield and Naiman 2014). Dead fish, bird, or marine mammal carcasses can wash ashore and provide nutrient pulses to vertebrate and invertebrate scavengers (Polis and Hurd 1996). Yet shore cast carrion is an unpredictable and unreliable event. These examples and many other such forms of marine terrestrial subsidies (e.g., forage fish spawning events, fruit and seed strandings, intertidal foraging of maritime mammals) are also highly seasonal or stochastic events (Carlton and Hodder 2003, Colombini and Chelazzi 2003, Fox et al. 2015), and do not display regularity on a daily basis. Sea wrack may be one of the very few press subsidies available to terrestrial consumers.

Wrack deposits provide a nutritionally rich and important food resource for a large community of semi-terrestrial and terrestrial invertebrates that have adapted their feeding preferences to exploit this consistent subsidy (Colombini et al. 2000). For example, upon being washed ashore, the brown kelp *N. luetkeana* quickly loses most of its mass by secreting mucosal alginate, the main structural component of its cell walls (Mews et al. 2006). This structural decay is rapid and amphipods will respond to and degrade kelp blades within one day of stranding (Mews et al. 2006, Pelletier et al. 2011). However, *Fucus* rockweeds contain high levels of phenolic compounds and do not appear to structurally degrade until 30 days after stranding (Mews et al. 2006). Therefore, the variation in amphipod preference of aged wrack is both species dependent and time dependent. This preference affords these detritivores a range of diet opportunities, an adaptation that allows for flexibility in their dependence on sea wrack depositions, despite the species composition of the wrack.

Secondary consumers such as birds, spiders, scorpions, geckos, lizards, and rodents also benefit from sea wrack nutrient subsidies (Polis and Hurd 1996, Stapp and Polis 2003, Catenazzi and A. Donnelly 2007, Piovia-Scott et al. 2013), as they take advantage of the increased abundances of amphipods, isopods, and other macroinvertebrate near wrack depositions (Dugan et al. 2003). Some larger mammals, such as coyotes (*Canus latrans*), and black bears (*Ursus americanus*), have also been observed to opportunistically ingest wrack as a food source (Rose and Polis 1998), although it is possible that the intended target is the invertebrate community utilizing the wrack (Fox et al. 2015). Regardless of the intended target, it is clear that sea wrack biomass subsidizes a diverse array of terrestrial consumers.

The effects of wrack on food web structure have been shown to be especially important where the terrestrial environment has low *in situ* productivity, such as the arid deserts of Baja California, the Atacama Desert, and the west coast of Australia (Anderson and Polis 1998, Catenazzi and Donnelly 2007, Ince et al. 2007). These deserts can generate as little as 50 g C m^{-2} yr^{-1} of terrestrial productivity while the marine habitat may produce up to 5000 g C m^{-2} yr^{-1} (Rose and Polis 1998). In Baja California, terrestrial study sites with access to wrack supported 2 to 100 times as many invertebrate consumers as their inland counterparts did (Anderson and Polis 1998). Flies (*Diptera* spp.) captured in and around sea wrack in Western Australia show almost exclusive use of marine carbon derived from seaweeds (Ince et al. 2007). Even in temperate regions such as Scotland and the Pacific Northwest of America, most research focuses on the effects generated at exposed, bare, sandy beach environments, that have low *in situ* productivity (e.g. Orr et al. 2014, Reimer 2014, but see Mellbrand et al. 2011). Coastal British Columbia, in contrast, has high terrestrial productivity. It is not yet clear what the magnitude of subsidy is on receiving communities when wrack washes ashore at productive temperate coastal landscapes.

My research reveals that on British Columbia's temperate Central Coast, sea wrack is present on all wide sand, gravel, cobble, and boulder shorelines that have protected wave exposures and large amounts of nearby donor habitat. Additionally, six dominant species of seaweeds (*F. distichus, M. pyrifera, N. luetkeana, Phyllospadix* spp., *P. californica,* and *Z. marina)* were washed ashore as sea wrack on a consistent basis though out the year, which suggests that sea wrack is an important press subsidy. Confirming the spatial and temporal patterns of wrack accumulations can help to infer which types of shorelines accumulate sea wrack and therefore facilitate the movement of marine nutrients to the terrestrial ecosystems of oceanic islands. These marine-terrestrial nutrient subsidies may affect the productivity of terrestrial consumers on islands, as they have been shown to do in low-productivity terrestrial environments (Polis and Hurd 1996). Further research investigating terrestrial species diversity and abundance at these sites can determine the effects, if any, sea wrack has on temperate terrestrial communities in high productivity environments. Comparing the impacts of marine-terrestrial subsidies in high and low productivity terrestrial island environments could have interesting implications for island biogeography theory (Wilson and MacArthur 1967) in the unique context of the subsidized island biogeography hypothesis (Anderson and Wait 2001).

CHAPTER THREE

Species specific wet-dry mass calibrations for dominant Northeastern Pacific Ocean macroalgae and macrophytes

3.1 ABSTRACT

Macroalgae and macrophytes form the base of productive ecosystems in the Northeastern Pacific Ocean. Often, ecological research on macrophytes, macroalgae, and sea wrack requires the conversion of biomass from wet to dry to create consistency across investigations. This process, however, can be impractical, time consuming, and labour intensive. In this research, I collected samples of 12 common Northeastern Pacific Ocean seaweed species (*Alaria marginata*, *Codium fragile*, *Egregia menziesii*, *Fucus distichus*, *Macrocystis pyrifera*, *Mazzaella* spp., *Nereocystis luetkeana*, *Pterygophora californica*, *Pyropia* spp., *Ulva* spp., and the seagrasses *Zostera marina* and *Phyllospadix* spp.) in two states: wet and fresh, or aged and partially desiccated. I weighed, dried, and compared samples, finding that all species displayed a strong ($R^2 > 0.5$) and predictable ($p < 0.05$) linear relationship between wet and dried conditions. Half of the aged samples did not have a significant relationship between partially desiccated and dried conditions. My results offer a reliable set of species-specific standardized correction factors for wet samples that can be used in future macrophyte, macroalgae, and sea wrack research, reducing the need to conduct extensive wet-dry calibrations in future studies.

3.2 INTRODUCTION

In the Northeastern Pacific Ocean, subtidal and intertidal biomass is dominated by various species of macroalgae and macrophytes. Some, including Bull Kelp (*Nereocystis luetkeana*) and Giant Kelp (*Macrocystis pyrifera*) are among the fastest growing algae in the world, and form vast and ecologically important underwater forests (Duggins et al., 1989, Krumhansl et al., 2016). Others, like Eelgrass (*Zostera* spp.) comprise extensive mats across the shallow subtidal zone that provide key nursery habitats for species of ecological, cultural, and economic value, such as salmon (*Oncorhynchus* spp.) (Simenstad et al. 1982) and rockfish (*Sebastes* spp.) (Olson 2017). Marine mammal activity, storms, and annual senesce cycles all cause these macrophytes and macroalgae to detach from the seafloor and be cast ashore in large quantities as sea wrack (Krumhansl and Scheibling 2012). This accumulated wrack can influence intertidal and terrestrial food webs (Piovia-Scott et al. 2013).

The role of sea wrack in ecological processes has attracted research interest globally, and live macrophyte and macroalgae ecological research is fundamental in understanding ecosystem function, habitat connectivity, and coastal invasive species (Polis and Hurd 1996, Krumhansl and Scheibling 2011). For example, macrophytes have been shown to increase nearshore productivity in both North Atlantic and tropical locations (Mann 1973, Duggins et al. 1989) and studies in countries as disparate as Kenya, Scotland, Spain, Peru, and the USA have demonstrated the importance of shore-cast macroalgae as a food and habitat matrix for both marine and terrestrial invertebrates (Olabarria et al. 2007, Dugan et al. 2011, MacMillan and Quijón 2012, Orr et al. 2014). Investigations into marine-terrestrial subsidies in Sweden, Australia, Canada, and Mexico have highlighted the importance of sea wrack as a vector of nutrient transfer between ecosystems

(Polis and Hurd 1996, Orr et al. 2005, Mellbrand et al. 2011). Additionally, studies done in Australia and Canada have quantified the difficulty of attempting to control invasive and disruptive macrophyte species (Bickel 2014, Holden et al. 2016).

As a product of all this research, well-developed survey methods and practical applications have emerged. Shoreline sea wrack surveys can serve as a proxy measurement for species composition and biomass of nearby subtidal macroalgae and/or macrophyte communities and these surveys act as a more accessible, safe, and cost-efficient method than underwater dive surveys (Torn et al. 2016). Furthermore, with combined wrack and underwater macroalgae/macrophyte biomass data attempts can be made to calculate the biomass exported to the open ocean (Krumhansl and Scheibling 2011) and its implications for marine productivity (Krumhansl and Scheibling 2012). Although work on macrophytes, macroalgae, and sea wrack has well-established methods for sampling and surveying techniques and equipment, a gap in knowledge remains in understanding the relationship between wet and dry biomass. Estimating wet-dry calibrations for dominant Northeastern Pacific macrophyte and macroalgae would facilitate simplified future research on these ecologically important species.

Dry mass measurement is considered the most reliable method for precise biomass estimates of sea wrack, marine macrophytes, and macroalgae (these three groups hereafter referred to as seaweeds) (Bickel and Perrett 2015). Typically, a subsample of a mixture of several seaweed species is oven dried to a constant weight where no further mass loss is recorded (Madsen 1993). This method, which creates a determined end point, enables consistent results across all investigations (Bickel & Perrett, 2015). Dry mass can also account for the ecological variation in the water content of different seaweed species (Bickel and Perrett 2015), or the variation in desiccation level of sea wrack depositions along shorelines. After dry mass determination, the most commonly used approach is to regress wet vs dry mass and use the slope as a wet-dry correction factor (e.g., Fox et al., 2014; Orr et al., 2005).

Obtaining dry mass measurements is labour intensive and time consuming. For field studies with large amounts of seaweeds (often hundreds of kg), which is often the case in invasive species research (e.g., Holden et al., 2016), dry mass measurements can be unfeasible. Performing wet-dry calibration work in remote field locations without power can be impractical (Madsen 1993). Additionally, one common genus of marine macroalgae (*Desmarestia* spp.) contains sulphuric acid in its tissue that will rapidly disintegrate itself and any co-occurring specimens after collection (Druehl and Clarkston 2016). Many dry mass determinations are performed with a combination of species within a subsample and are not species specific (Orr et al. 2005, Reimer 2014). Most importantly, dry mass determination also renders the organism unsuitable for further research and may remove large amounts of seaweeds from natural settings, which can disturb ecological processes (Dugan et al. 2003).

Despite the substantial amount of information available regarding seaweed survey and sampling techniques across the globe, I found little information on standardized regression coefficients obtained from dry mass determination. Therefore, each study that requires dry seaweed biomass measurements must perform the time consuming and labour intensive step of dry mass determination. In this paper, I present the results of wet-dry calibrations for 12 common macrophyte and macroalgae species collected from the Northeastern Pacific with the goal of providing a suite of standardized correction factors for use in estimating the dry biomass of macroalgae, macrophytes, and wrack in western North America.

3.3 METHODS

I collected 251 macrophyte and macroalgae specimens from three sandy beaches and two rocky outcrops located along the northwest end of Calvert Island, British Columbia, Canada (51.6536° N, 128.1301° W) in July and September 2016. These specimens included *Alaria marginata*, *Codium fragile*, *Egregia menziesii*, *Fucus distichus*, *Macrocystis pyrifera*, *Mazzaella* spp., *Nereocystis luetkeana*, *Pterygophora californica*, *Pyropia* spp., *Ulva* spp., and the seagrasses *Zostera marina* and *Phyllospadix* spp. Samples of various weights (27 - 265 grams) were collected indiscriminately from shoreline wrack accumulations and harvested live from rocky intertidal shorelines. Samples were sorted into two categories based on their moisture saturation levels; aged or wet. Aged samples were collected from wrack lines that had been stagnant on the beach for over 24 hours and contained seaweed species that had partially desiccated. Wet samples were collected from samples that had been deposited recently on the shoreline (confirmed visually) or from samples that were harvested live from rocky outcrops.

Blades, stipes, and (when applicable) pneumatocysts were collected. Samples were sorted and separated into species and for kelp some samples were processed as “blade only” or “stipe only”. However, because most researchers may not separate kelp blades from stipes, I also processed samples that were random combinations of blade and stipe (“mixed”). Wet weights of all samples were measured on a Denver Instrument MXX-612 balance and transferred into a Fisher Scientific Isotemp drying oven within one hour of collection. Samples were dried at 80° C until their dry weight reached a constant mass (+/- 0.005g) for three consecutive measurements (typically this took about 72 hours).

I performed linear regressions in RStudio Version 1.0.136 (RStudio Team 2015). The slope of the linear equation was used to generate correction factors. From three species (*Ulva* spp., *Pyropia* spp. and *F. distichus*) I compared regression slopes (Analysis of Covariance: ANCOVA) of wet, fresh samples that were harvested live against wet, fresh samples that were collected from wrack lines. I also compared regression slopes for the mixed, blade only, and stipe only categories of the three kelps *M. pyrifera, N. luetkeana*, and *P. californica* with ANCOVA.

3.4 RESULTS

All 12 species exhibited strong and significant linear relationships between wet and dry mass when dried from fresh, wet samples (Fig. 7). Four species out of eight (*C. fragile*, *E. menziesii*, *N. luetkeana*, and *Phyllospadix* spp.) also exhibited significant linear relationships between aged and dry mass (Fig. 8). For the species *Ulva* spp., *Pyropia* spp., and *F. distichus*, wet samples that were harvested live from rocky outcrops displayed the same strong and significant linear relationships as the wet samples that were collected from freshly deposited wrack lines (ANCOVA, all *p*-values < 0.09).

For the kelps *M. pyrifera*, *N. luetkeana*, and *P. californica* I dried three combinations of samples (blade only, stipe only, and mixed). For each species, there was no statistically significant difference between the slopes of the relationships between wet and dry weight for blade, stipe, and mixed samples (ANCOVA, all *p*-values > 0.1).

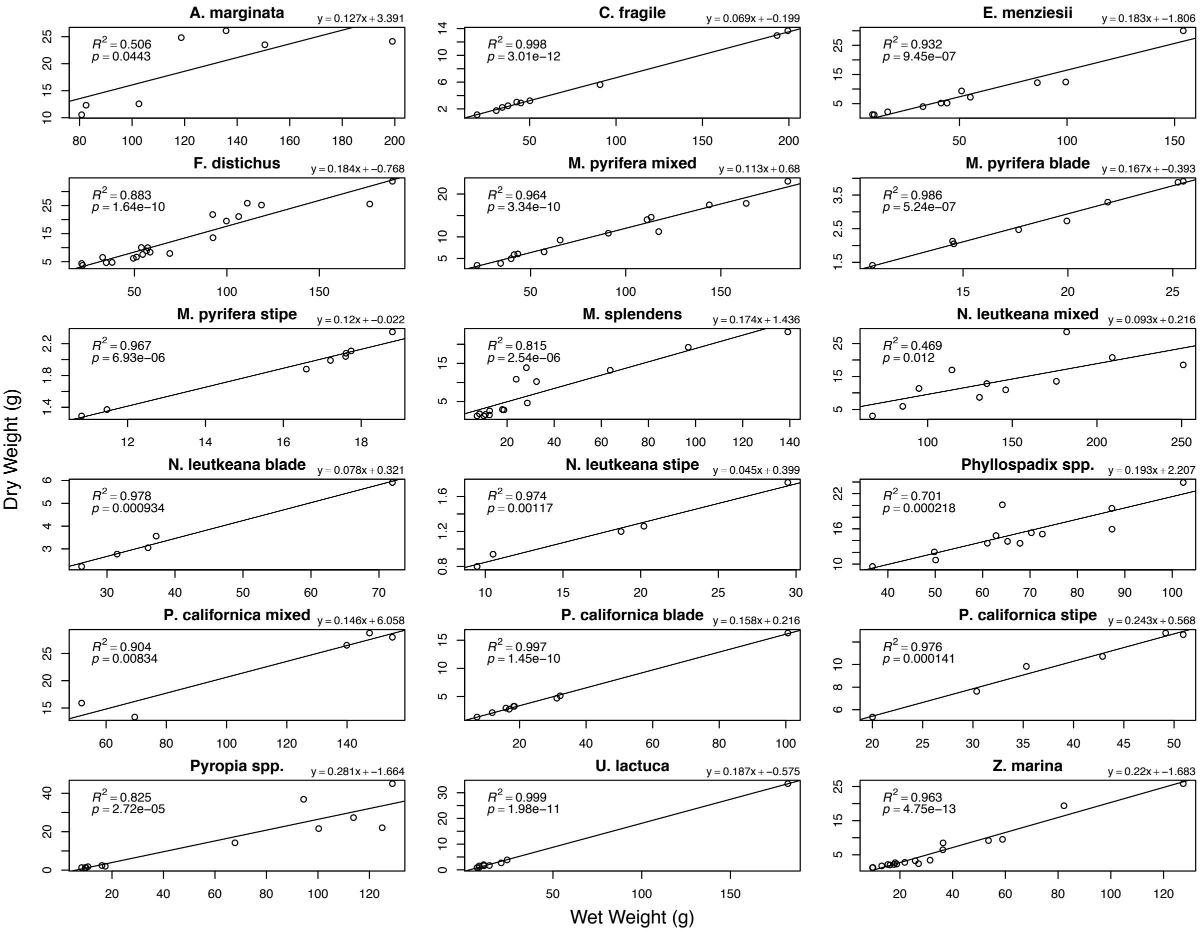

Figure 7. Relationships between wet and dry mass for twelve species of marine macrophytes and macroalgae commonly found in the Northeastern Pacific Ocean. All samples were collected fresh from recently deposited wrack lines or harvested live. The species-specific correction factor is the slope of the linear equation, displayed in the top right corner of each plot.

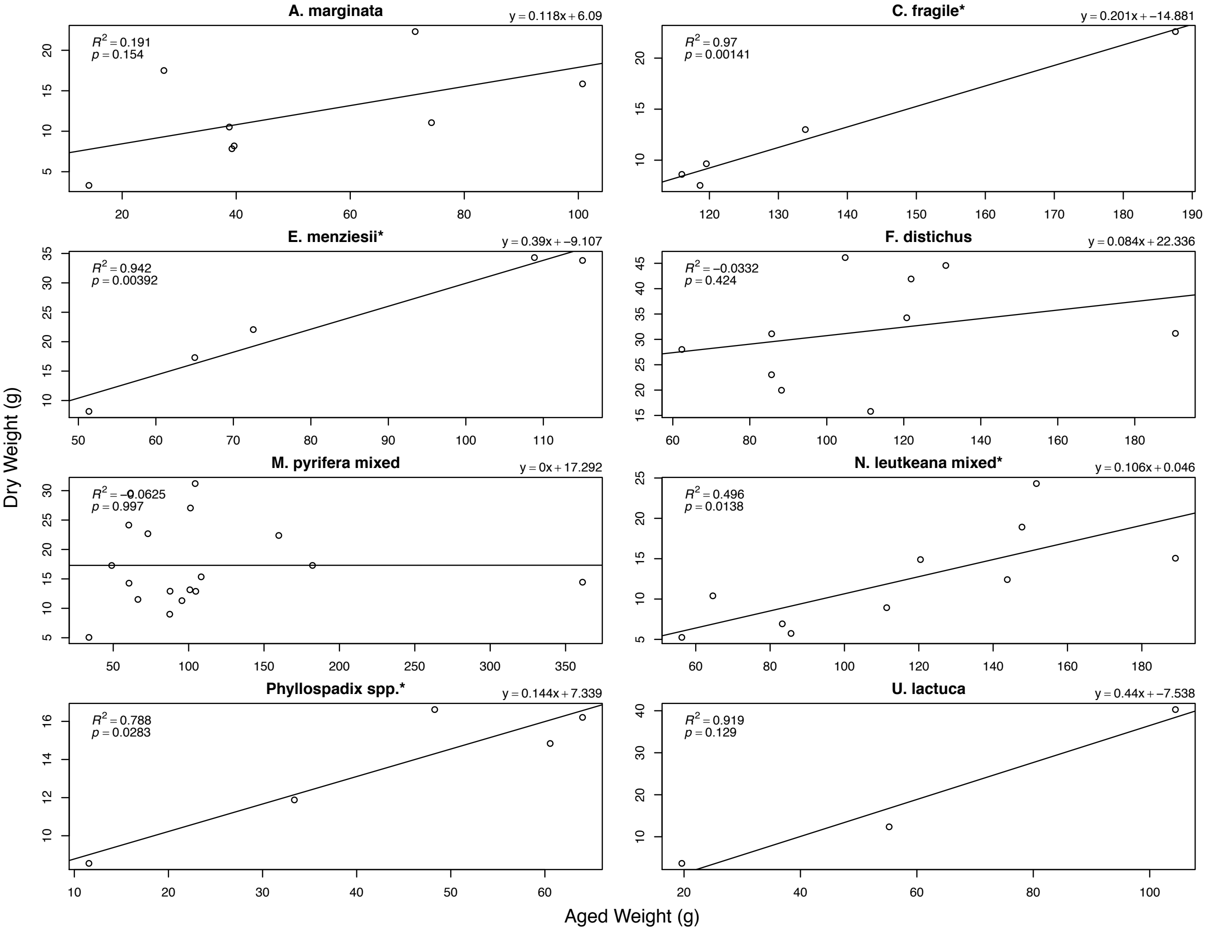

Figure 8. Relationships between aged and dry mass for eight species of marine macrophytes and macroalgae commonly found in the Northeastern Pacific Ocean. All samples were collected from aged wrack lines and had signs of some desiccation. The species-specific correction factor is the slope of the linear equation, displayed in the top right corner of each plot. Statistically significant results (*Codium fragile*, *Egregia menziesii*, *Nereocystis luetkeana*, and *Phyllospadix* spp.), are marked by (*).

3.5 DISCUSSION

I found that water content loss from live collected and shore-cast marine seaweed species displayed strong and predictable relationships. Using these calibrations, researchers in coastal areas of the Northeastern Pacific can estimate the dry biomass of these 12 dominant macrophyte and macroalgae species. I am not aware of any data that show differences in water content amounts between local areas within the region these species are found. As a consequence, these results may offer a first estimation for correction factors across their ranges until more local-scale data are available.

The reliable water content loss relationships only existed for recently deposited seaweed samples and ones that had been collected live. Establishing a relationship between aged (partially desiccated) to dry ratios was less dependable. Only four of the eight species demonstrated significant relationships between aged and dry masses, and the relationships were considerably weaker. From the aged samples collected along wrack lines, *A. marginata*, *F. distichus*, *M. pyrifera*, and Ulva spp. did not display significant water content loss relationships. This could be due to variation in how desiccated individual samples were at time of collection and a lack of precision in recording moisture saturation categories. In the future, it would be helpful to develop several more specific categories of desiccation in sea wrack. These categories could be based on the time the seaweeds were deposited along a shoreline, inferred from tidal information.

For the kelps *M. pyrifera*, *N. luetkeana*, and *P. californica* I dried three combinations of wet samples: blade only, stipe only, and blade and stipe together (mixed). For each species, neither the blade, stipe, or mixed categories had any significant effect on the relationship between wet and dry weight, indicating that the blades and stipes of these kelps have similar water content loss potentials and the correction factor for ‘mixed’ samples can be utilized. However, if possible, separating the blades from the stipes would yield more precise estimates as the relationships displayed by the blade only and stipe only categories were stronger than those of the mixed category.

Each species demonstrated its own particular wet-dry mass relationship. This variability could be due to the fact that each species has different chemical compositions. For example, the kelps *M. pyrifera* and *N. luetkeana* contain high amounts of alginate which leaches quickly and increases mass loss (Mews et al. 2006). The seagrasses *Z. marina* and *Phyllospadix* spp. contain higher amounts of lignin and cellulose, which do not leach upon drying and may contribute to relatively decreased amounts of mass loss in these species (Mews et al. 2006). The confirmation of these differences should encourage investigators to apply species-specific correction factors to their research.

Seaweed productivity is commonly reported in dry biomass. Recently, precise techniques for reporting wet biomass have emerged (Bickel and Perrett 2015), and are helpful in simplifying fieldwork regimes. However, the wet biomass estimations generated by these techniques are not directly comparable to the volume of literature that already reports dry mass approximations. Applying pre-determined, species-species correction factors to wet biomass estimations from the field will enable researchers to directly compare all seaweed biomass findings, past and present.

CHAPTER FOUR

GENERAL DISCUSSION

Over three years and in an area of 2000 km^2 I surveyed 101 islands and 455 sites on British Columbia’s Central Coast, recording sea wrack biomass, species composition, and shoreline site characteristics. In Chapter One I discussed how my surveys revealed that wrack had the capacity to accumulate biomass on any sand, gravel, cobble, and boulder shorelines, suggesting it has a ubiquitous presence on beaches along the Central Coast. Wrack was, however, absent at sites composed of rock substrate. Sea wrack was also consistently detected at sites that had wide, wave protected shores, and high amount of nearby donor ecosystem habitat. Additionally, sea wrack species composition and biomass washed ashore in relatively uniform quantities throughout the year. The spatial and temporal consistency of sea wrack implies it would be appropriate to consider wrack a press nutrient subsidy. In Chapter Two I outlined how and why I established correction factors for 12 common northeastern Pacific Ocean macrophytes and macroalgae species. These correction factors can be applied to wet biomass measurements in order to estimate dry biomass, a step that can simplify future research requiring seaweed dry mass determinations.

My results emphasized that the presence and accumulation of sea wrack was lower at sites that were composed of rock, compared to sand, gravel, cobble or boulder substrates. The Central Coast is well known for its dramatic rock and cliff shorelines (Appendix, Fig. 10). In fact, 75% of sites I surveyed were classified as rock (Appendix, Fig. 11). These rock shorelines created a boundary that separated sea wrack from the terrestrial environment. Boundary dynamics, a framework for investigating how boundaries affect flow of materials over adjacent ecosystems, describes permeability as an important factor in regulating the transport of nutrients and energy vectors across ecosystems (Wiens et al. 1985). Permeability, the degree to which a boundary may deflect the movement of vectors, is dependent on the boundary characteristics and the nature of the vector (Wiens et al. 1985). In the context of boundary dynamics, my data reveal that rocky shorelines are impermeable to a sea wrack vector, while sand, gravel, cobble, or boulder shorelines are permeable.

Anecdotally, it seemed that most of the smaller islands along the Central Coast had steep, rocky shores whereas larger islands had more convoluted shorelines and more beaches composed of sand, gravel, cobble or boulder. If the smaller islands are generally comprised of rocky shores, then less wrack would be accumulating along their shorelines and permeating into the islands' interiors. Productivity would not be affected by sea wrack, and there would be no evidence of a small island effect in the context of the subsidized island biogeography hypothesis. On the other hand, larger islands, with more beaches and therefore more wrack, would be permeable, despite the fact they have less shoreline relative to interior area. Productivity on these larger islands could be affected by a wrack subsidy. If this is the case, then boundary dynamics and permeability may have more of an effect on terrestrial diversity then perimeter to area ratios for islands on the Central Coast.

However, sea wrack is not the only vector delivering marine nutrients to these island ecosystems. Fog, sea spray, and river otters are three potential vectors that seemed ubiquitous in the study region. Other vectors such as salmon streams or seabird colonies, which are common elsewhere on this coastline (Reimchen et al. 2003, Maron et al. 2006) were not present on my study islands. Fog, sea spray, and river otters each have their own specific boundaries that would affect their ability to permeate into island interiors and are not deflected by rocky shorelines. Trees and shrubs create an relatively impermeable boundary for fog and sea spray (Ewing et al. 2009), and river otters tend to latrine and den near the terrestrial edges of coastlines (Ben-David et al. 1998), limiting the direct effects of these vectors to the edges of islands. Nevertheless, communities on rocky islands would still be able to accept these vectors of nutrient flow. These vectors could increase productivity and result in patterns of diversity more closely linked to subsidized island biogeography hypotheses or the equilibrium theory of island biogeography.

Members of the 100 Islands project, who have collected diversity data on invertebrates, mammals, plants, and songbirds across 70 – 100 islands on the Central Coast of BC, will use my wrack biomass measurements in their own respective research. The sea wrack measurements will enable project members to detect if terrestrial species are being affected by marine nutrient flow, permeability, species-area relationships or a complex interaction between all three variables.

Determining that sea wrack is a temporally consistent vector of nutrients to beaches on the Central Coast was an unanticipated result. Globally, there are no accurate predictions of which season contributes the most sea wrack. I hypothesized that seasonal senesces after the summer growing season combined with early winter storms would lead to significantly larger wrack accumulations in the fall, a pattern that had been observed in nearby Oregon (Reimer 2014). And while storm disturbances and seasonal senescence may cause localized pulses in wrack depositions, my data reflect that shoreline wrack accumulations on beaches are temporally consistent.

These results highlight that sea wrack is a press subsidy to islands on the Central Coast of British Columbia, and wrack can supply food and habitat to semi-terrestrial and terrestrial invertebrate consumers in all seasons. The main avenue facilitating the transfer of seaweed-derived nutrients to the terrestrial environment is the direct consumption of wrack by invertebrates such as amphipods (Lastra et al. 2008). Amphipods are considered one of the most abundant and ecologically important residents of beach ecosystems, comprising almost 90% of the total macrofauna found in these habitats (Colombini and Chelazzi 2003). Anecdotally, I noticed amphipods were present throughout all of the temporal beach surveys, although populations appeared reduced in the winter. These observations are consistent with the known life histories of amphipods, which suspend reproduction from December to March (Slattery 1985).

Broadly, amphipods are not selective in their dietary preferences for seaweeds and a wealth of research has shown amphipods incorporate many different species of kelp, brown algae, and seagrasses into their diets (Crawley et al. 2009, Duarte et al. 2011, Olson 2017). Amphipods, in turn, are predated on by many higher level trophic consumers (Hyndes et al. 2014), and can be an important source of nutrients for mammals as large as bears (Fox et al. 2014). In arid, unproductive environments all over the world, sea wrack depositions have increased amphipod abundances and amphipod consumer abundances and diversity (Dugan et al. 2003, Stapp and Polis 2003, Catenazzi and A. Donnelly 2007). However, wrack-amphipod-bird/mammal food web dynamics have not yet been comprehensively explored in productive environments. To determine the significance of a sea wrack subsidy to temperate islands, the response of amphipods and amphipod consumers to wrack needs to be tested.

During this research, I demonstrated that seaweeds display a predictable relationship between wet and dry biomass conditions, allowing for a detailed estimation of water loss within a species. Ecological investigations often report seaweed measurements in dry biomass, requiring researchers to perform the laborious step of dry mass determination. The species-specific correction factors from the linear regressions for each of the 12 species I sampled can be used to apply to future research on seaweeds from the northeast Pacific Ocean.

Determining that sea wrack is present at beaches along the Central Coast on a consistent spatial and temporal scale, and knowing the mechanisms that contribute to this process, is the first step in confirming that sea wrack is an available source of nutrients from the marine environment to terrestrial consumers. These data may be useful to test theory on habitat boundary dynamics, marine-terrestrial subsidies, and island biogeography theory. Additionally, knowing when and where sea wrack is washing ashore will contribute to understanding the complex ecological processes that connect the marine environment to terrestrial habitats on temperate coastal islands.

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APPENDIX

Table 3. List of island biogeographical characteristics as derived from Island Biogeography and subsidized island biogeography theory used for clustering analysis.

Variable name	**Units**	**Description**
Distance from mainland	km	Shortest linear distance from edge of island to mainland BC
Area	m^2	Terrestrial area of island
Normalized perimeter to area (P:A) ratio (McGarigal 2015).	n/a	A normalized P:A where the complexity of a shape (i.e. island) is compared to a standard shape (circle) which accounts for the size dependence displayed by calculating perimeter/area.
Exposure (Howes et al. 1994)	Categorical	Score derived by proportion of each island's coastline that is within exposure categories: very protected, protected, semi-protected, semi-exposed, exposed, very-exposed.
Neighbouring land	n/a	The percentage of area occupied by surrounding landmasses within a 5<1<1m distance of each island.

Table 4. Results of Clustering Analysis.

Cluster number	Number of Islands	Description
1	134	high exposure, close to mainland, few neighbouring islands
2	264	low exposure, close to mainland
3	432	high exposure, far from mainland, few neighbouring islands
4	426	low exposure, far from mainland, many neighbouring islands
5	197	low exposure, very close to mainland, neighbouring many islands, low P:A

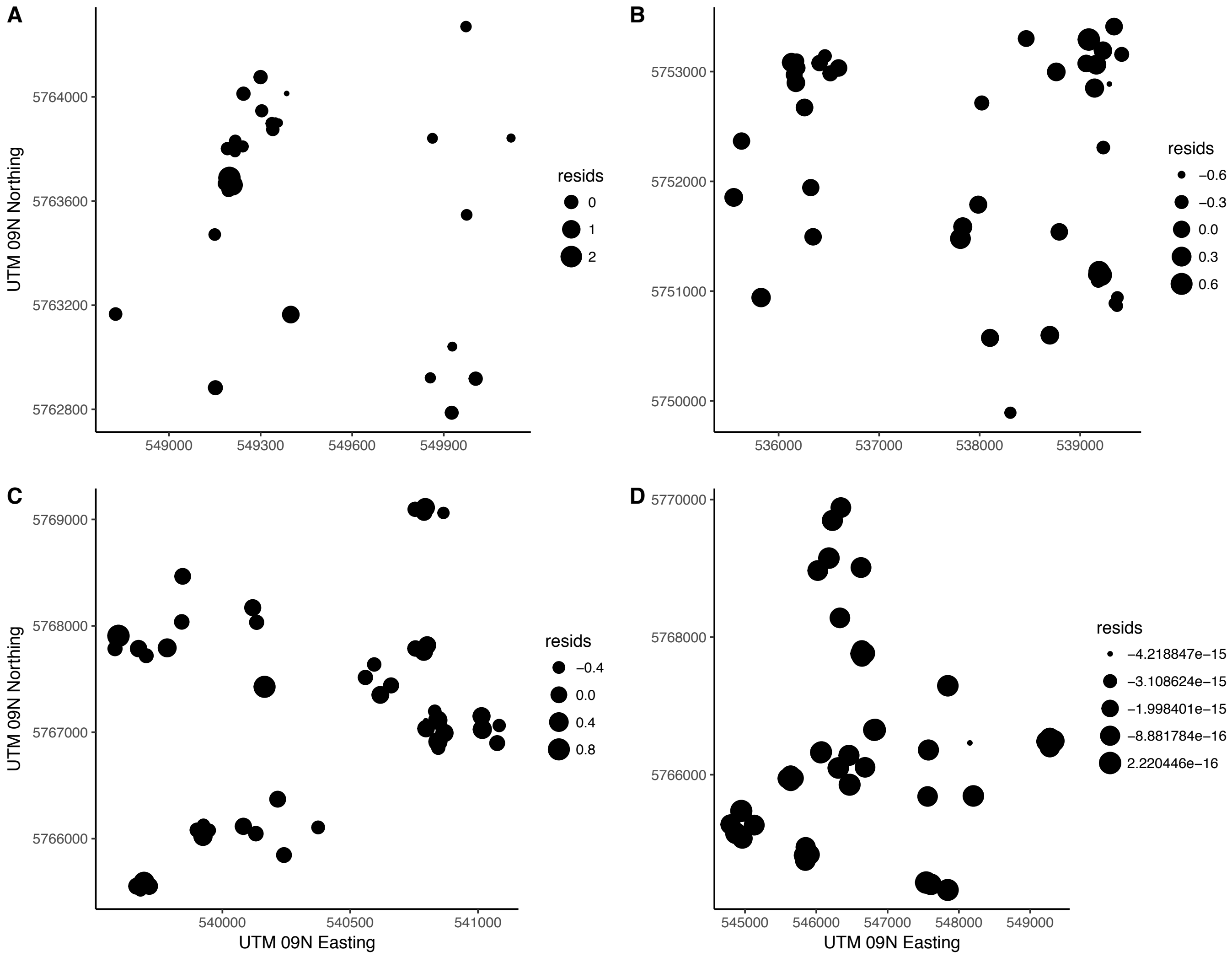

Figure 9. Bubble plot of residuals for the presence/absence dataset (sites = 388, islands = 91) mapped against their spatial coordinates to check for any patterns that may indicate spatial correlation issues. None were detected. A - Admiral node, B – Goose node, C – McMullin node, D – Tribal node.

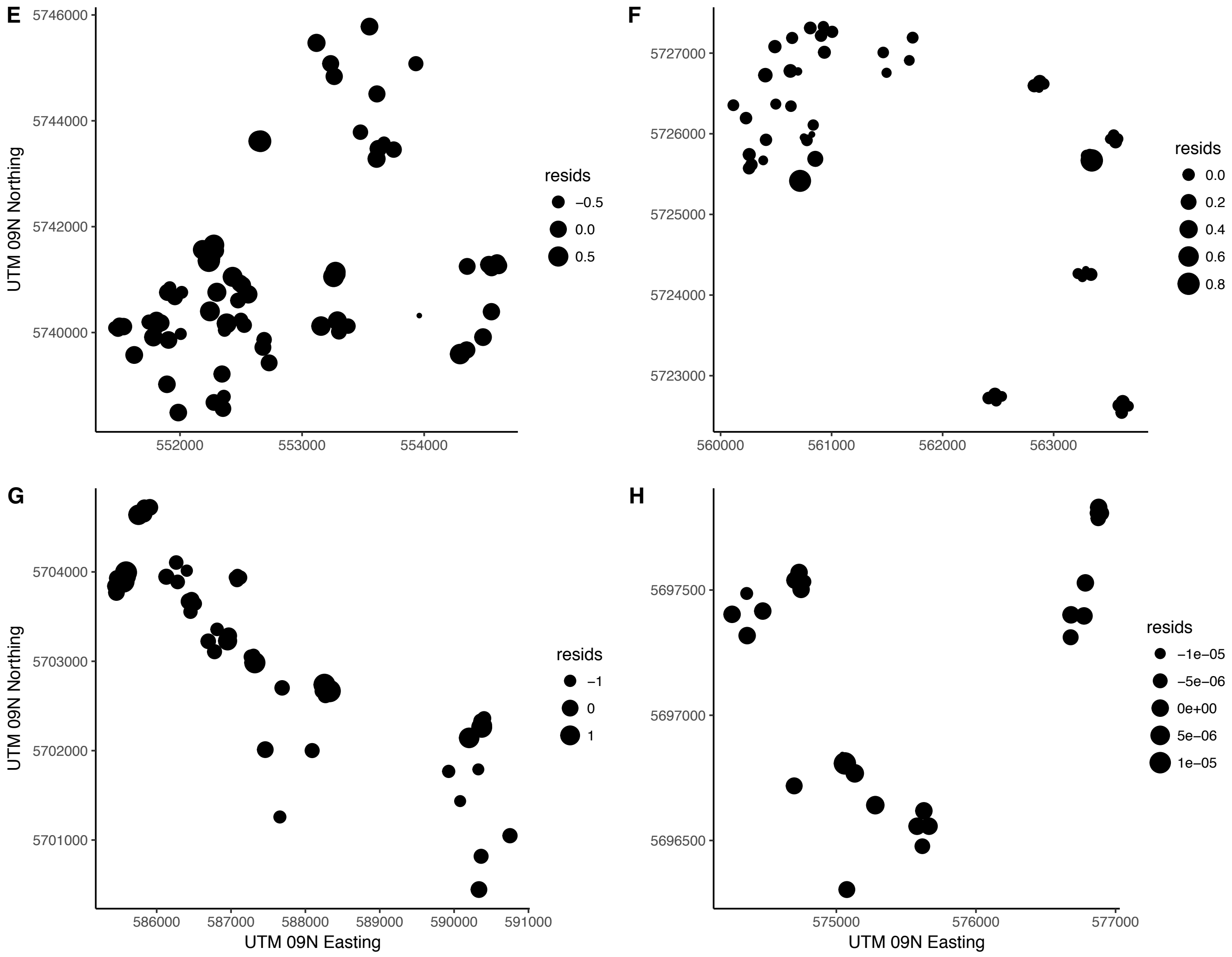

Figure 10. Bubble plot of residuals for the presence/absence dataset (sites = 388, islands = 91) mapped against their spatial coordinates to check for any patterns that may indicate spatial correlation issues. None were detected. E – Triquet node, F – Calvert node, G – Penrose node, H – South Calvert node.

Table 5. Species recorded in surveys from 455 sites across 101 islands and their percent contribution to the total biomass. % cont. denotes the percent contribution each functional group, genus, or species made to the total biomass.

Spatial Surveys		**Temporal Surveys**	
Species	**% cont.**	**Species**	**% cont.**
Acrosiphonia spp.	<1	*Acrosiphonia* spp.	<1
Alaria marginata	<1	*Ahnfeltia fastigiata*	<1
Articulated calcalreous corallines	<1	*Ecklonia arborea*	<1
Callithamnion spp.	<1	*Callophyllis* spp.	<1
Chondracanthus spp. (bladed form)	<1	*Alaria marginata*	1
Cladophora spp.	<1	*Chondracanthus* spp. (bladed form)	<1
Codium fragile	<1	*Codium fragile*	1
Costaria costata	<1	*Codium setchellii*	<1
Cryptopleura spp.	<1	*Colpomenia* spp.	<1
Cymathaere triplicata	<1	*Constantinea sublifera*	<1
Desmarestia (cylindrical form)	<1	*Cryptopleura* spp.	<1
Desmarestia ligulata	<1	*Stephanocystis* spp.	<1
Egregia menziesii	1	*Costaria costata*	<1
Filamentous reds	<1	*Desmarestia* (cylindrical form)	1
Fucus distichus	26	*Desmarestia ligulata*	1
Halosaccion glandiforme	<1	*Egregia menziesii*	1
Laminaria setchellii	<1	*Endocladia muricata*	<1
Leathesia marina	<1	*Fucus distichus*	8
Lessoniopsis littoralis	<1	Articulated calcareous corallines	<1
Macrocystis pyrifera	4	*Halosaccion glandiforme*	<1
Mastocarpus spp.	<1	*Gracilaria* spp.	<1
Mazzaella spp.	<1	*Laminaria setchellii*	1
Microcladia spp.	<1	*Leathesia marina*	<1
Neorhodomela acuelata	<1	*Lessoniopsis littoralis*	1
Neorhodomela larix	<1	*Mastocarpus* spp.	<1
Neorhodomela oregana	<1	*Macrocystis pyrifera*	8
Nereocystis luetkeana	2	*Mazzaella* spp.	<1
Osmundea spectabilis	<1	*Neorhodomela acuelata*	<1
Phyllospadix spp.	2	*Neorhodomela larix*	<1
Pleurophycus gardneri	<1	*Neorhodomela oregona*	<1
Prionitis spp.	<1	*Nereocystis luetkeana*	14
Pterygophora californica	10	*Osmundea spectabilis*	<1
Ptilota spp.	<1	*Palmaria* spp.	<1
Pyropia spp.	<1	*Phyllospadix* spp.	43
Saccharina groenlandica	<1	*Pleurophycus gardneri*	<1
Saccharina latissima	<1	*Prionitis* spp.	<1
Saccharina sessilis	<1	*Pterygophora californica*	7
Sargassuim muticum	<1	*Ptilota* spp.	<1
Ulva spp.	<1	*Pyropia* spp.	<1

Table 5. (continued) Species recorded in surveys from 455 sites across 101 islands and their percent contribution to the total biomass. % cont. denotes the percent contribution each functional group, genus, or species made to the total biomass.

Spatial Surveys		Temporal Surveys	
Species	**% cont.**	**Species**	**% cont.**
Unidentifiable brown kelps	3	*Saccharina groenlandica*	<1
Unidentifiable red seaweeds	<1	*Saccharina latissima*	<1
Unidentifiable seagrasses	4	*Saccharina sessilis*	<1
Zostera marina	40	*Scytosiphon* spp.	<1
		Ulva spp.	<1
		Unidentifiable brown kelps	8
		Unidentifiable red seaweeds	<1
		Unidentifiable seagrasses	<1
		Zostera marina	<1

```
Fourth Beach_North Beach
      PHY   NER.LUE    UNK.BK       FUC 
0.4427955 0.5779957 0.6903339 0.7773377 

Fourth Beach_West Beach
      PHY   NER.LUE    UNK.BK   MAC.INT 
0.3815503 0.5157184 0.6269417 0.7352643 

North Beach_West Beach
      PHY   NER.LUE   MAC.INT       FUC 
0.2582436 0.4791348 0.6607349 0.7473772 
```

Figure 11. Results from similarity percentages analysis (SIMPER) for the most influential species on similarities between sites. FUC = *Fucus distichus*, NER.LUE = *Nereocystis luetkeana*, UNK.BK = Unidentifiable brown kelps, PHY = *Phyllospadix* spp., MAC.INT = *Macrocystis pyrifera*.

```
APRIL_FEB
      PHY   NER.LUE   PTE.CAL    UNK.BK
0.3239517 0.5651997 0.6953094 0.8132855

APRIL_JULY
      FUC       PHY    UNK.BK   MAC.INT   NER.LUE
0.1993053 0.3820819 0.5351546 0.6620293 0.7487430

APRIL_NOV
      PHY   NER.LUE    UNK.BK
0.4225081 0.6573931 0.7834557

APRIL_SEPT
      PHY    UNK.BK   NER.LUE   MAC.INT
0.2516059 0.4470207 0.6108728 0.7570158

FEB_JULY
      PHY   NER.LUE   PTE.CAL       FUC
0.3207653 0.5107384 0.6370126 0.7172475

FEB_NOV
      PHY   NER.LUE   PTE.CAL
0.4278513 0.6257951 0.7555644

FEB_SEPT
      PHY   NER.LUE   PTE.CAL
0.3554897 0.6001086 0.7405947

JULY_NOV
      PHY       FUC   NER.LUE
0.4203072 0.5744571 0.7250968

JULY_SEPT
      FUC   NER.LUE   MAC.INT       PHY   DES.LIG
0.2689970 0.4360706 0.5900019 0.6733492 0.7430870

NOV_SEPT
      PHY   NER.LUE
0.5114044 0.7585423
```

Figure 12. Results from similarity percentages analysis (SIMPER) for the most influential species on similarities between months. FUC = *Fucus distichus*., NER.LUE = *Nereocystis luetkeana*, PTE.CAL = *Pterygophora californica*, UNK.BK = Unidentifiable brown kelps, PHY = *Phyllospadix* spp., MAC.INT = *Macrocystis pyrifera*, DES.LIG = *Desmarestia ligulata*.

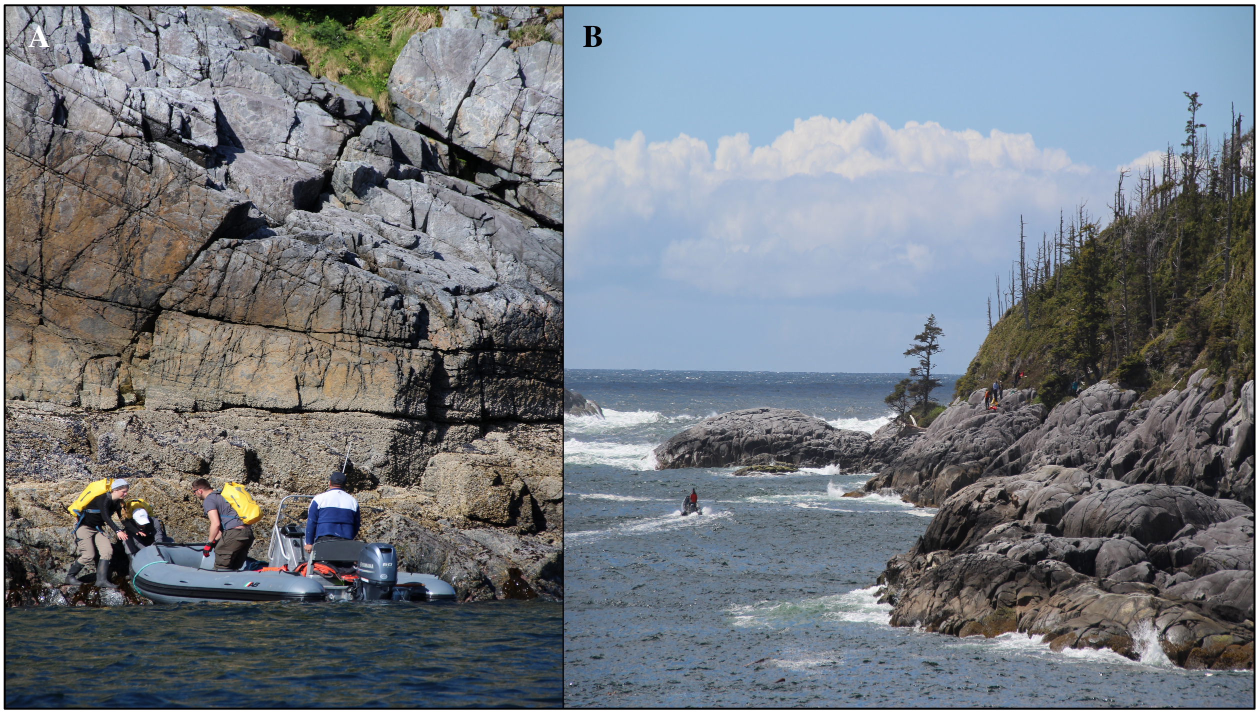

Figure 13. Examples of the rocky shorelines commonly found on the Central Coast of British Columbia. (A) Rock cliffs on island SC04 (51.4241 ° N, 127.9250 ° W). (B) Rock benches on island SC01 (51.4160 ° N, 127.9204 ° W). See Appendix Table 6 for island node and number abbreviations.

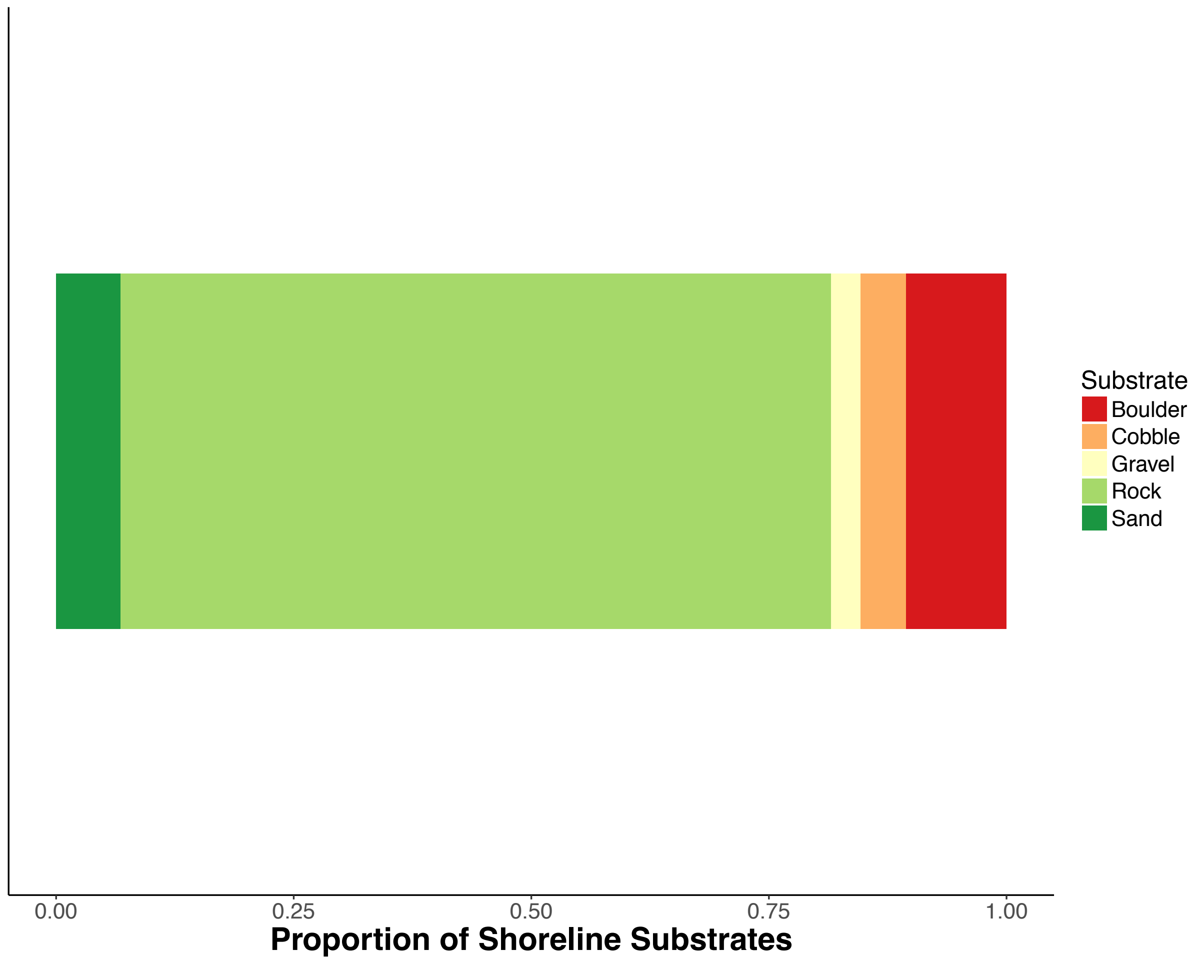

Figure 14. A bar plot depicting the proportion of sites (n = 455) with shoreline substrates that were classified with sand (n = 31), gravel (n = 14), cobble (n = 22), boulder (n = 48), or rock (n = 340) substrate.

Table 6. Node names, island numbers, and island codes for the 101 islands that were surveyed for sea wrack along the Central Coast of British Columbia during the summers of 2015, 2016, and 2017.

Node	Island	Island code	Node	Island	Island code
Admiral	01	AD01	Penrose	06	PR06
Admiral	02	AD02	Penrose	07	PR07
Admiral	03	AD03	Penrose	08	PR08
Admiral	04	AD04	Penrose	09	PR09
Admiral	05	AD05	Penrose	10	PR10
Admiral	06	AD06	Penrose	11	PR11
Admiral	07	AD07	Penrose	12	PR12
Calvert	01	CV01	Penrose	13	PR13
Calvert	02	CV02	South Calvert	01	SC01
Calvert	03	CV03	South Calvert	02	SC02
Calvert	04	CV04	South Calvert	03	SC03
Calvert	05	CV05	South Calvert	04	SC04
Calvert	06	CV06	South Calvert	05	SC05
Calvert	07	CV07	South Calvert	06	SC06
Calvert	08	CV08	Stirling	01	ST01
Calvert	09	CV09	Stirling	02	ST02
Calvert	10	CV10	Stirling	03	ST03
Calvert	11	CV11	Stirling	05	ST05
Calvert	12	CV12	Stirling	07	ST07
Calvert	13	CV13	Stirling	08	ST08
Calvert	14	CV14	Stirling	09	ST09
Calvert	15	CV15	Stirling	10	ST10
Calvert	16	CV16	Stirling	12	ST12
Calvert	17	CV17	Stirling	14	ST14
Goose	01	GS01	Tribal	01	TB01
Goose	02	GS02	Tribal	02	TB02
Goose	03	GS03	Tribal	03	TB03
Goose	04	GS04	Tribal	04	TB04
Goose	05	GS05	Tribal	05	TB05
Goose	06	GS06	Tribal	06	TB06
Goose	07	GS07	Tribal	07	TB07
Goose	08	GS08	Tribal	08	TB08
Goose	09	GS09	Tribal	10	TB10
Goose	10	GS10	Tribal	12	TB12

Table 6. (continued) Node names, island numbers, and island codes for the 101 islands that were surveyed for sea wrack along the Central Coast of British Columbia during the summers of 2015, 2016, and 2017.

Node	Island	Island code	Node	Island	Island code
McMullin	01	MM01	Triquet	01	TQ01
McMullin	02	MM02	Triquet	02	TQ02
McMullin	03	MM03	Triquet	03	TQ03
McMullin	04	MM04	Triquet	04	TQ04
McMullin	05	MM05	Triquet	05	TQ05
McMullin	06	MM06	Triquet	06	TQ06
McMullin	07	MM07	Triquet	07	TQ07
McMullin	08	MM08	Triquet	08	TQ08
McMullin	09	MM09	Triquet	09	TQ09
McMullin	10	MM10	Triquet	10	TQ10
McMullin	11	MM11	Triquet	11	TQ11
Penrose	01	PR01	Triquet	12	TQ12
Penrose	02	PR02	Triquet	13	TQ13
Penrose	03	PR03	Triquet	15	TQ15
Penrose	04	PR04	Triquet	17	TQ17
Penrose	05	PR05	Triquet	18	TQ18
			Triquet	20	TQ20