Beach-cast deposition, food provision, and commercial harvesting of a non-indigenous seaweed, *Mazzaella japonica*, in Baynes Sound, British Columbia

by

Jessica Holden
B.Sc., University of Victoria, 2014

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Biology

Supervisory Committee

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Abstract

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This thesis examines the contribution of a non-indigenous red alga, *Mazzaella japonica*, to wrack subsidies in Baynes Sound, British Columbia, and the effects of its removal by a commercial beach-cast harvest. Field and laboratory work was conducted to determine: 1) How large wrack inputs are in terms of biomass and spatial extent within the harvest region, and what proportion of this is comprised of *M. japonica*; 2) how wrack characteristics influence associated macrofauna communities; 3) if there is any detectable effect of beach-cast harvesting on either the wrack characteristics or macrofauna communities; and 4) if *M. japonica* provides a food source for native invertebrate consumers within the subtidal and supralittoral zones.

Field surveys conducted from November 2014 through March 2015 found that wrack biomass within the harvest region could reach as much as 853 kg (±173 SD) per meter of shoreline, and cover up to 35 m^2 (± 3 SD) of beach surface within this area. The macrophyte composition of the wrack was dominated by *M. japonica*, which accounted for 90% of the identifiable macrophyte biomass on average. Wrack in the later stages of decomposition hosted the most speciose and diverse assemblages of macrofauna, though community composition also differed among collection sites and with depth of the wrack.

Though we were limited in our ability to disentangle the effects of beach-cast harvesting due to a concentration of effort at one site, we failed to detect any large influence on wrack biomass or macrofauna communities. Harvesting does, however, appear to be associated with a greater area of wrack cover and decreased mean depth.

Stable isotope mixing models estimated that *M. japonica* contributed no more than 22% and 17% on average to the diets of supralittoral and subtidal consumers respectively, despite its overwhelming dominance in both environments. These results suggest that the non-indigenous red alga may experience a reprieve from herbivory within the subtidal environment. A lack of consumption within the supralittoral zone could influence nutrient cycling on recipient beaches and increase propagule pressure in the surrounding regions.

Results from these studies are intended to help inform the management of *M. japonica* and its commercial harvesting. Combined, they indicate that this non-indigenous seaweed does not provide a substantial subsidy in the form of food provision for resident invertebrates. Furthermore, the commercial removal of *M. japonica* is small compared to the total biomass available, and had no detectable effect on the wrack-associated macrofauna communities examined.

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Acknowledgments

I would like to start by thanking my supervisor, Francis Juanes, and committee members, Sarah Dudas, and Rana El-Sabaawi, for their guidance and advice over the past two years. I was truly blessed to have had the help of such a supportive, kind, and insightful group of scientists. Sarah, you went above and beyond the role of a committee member, contributing to every stage of this thesis, from its design and development to the final manuscript revisions. Your mentorship and generosity with your time has been greatly appreciated.

This work could not have been completed without the following funders: National Sciences and Engineering Research Council of Canada, University of Victoria, British Columbia Ministry of Agriculture, and TD Friends of the Environment. Thanks also to VIU's Centre for Shellfish Research and the Deep Bay Marine Field Station for logistic support, including the use of their facilities and equipment.

This research benefited tremendously from discussions and collaboration with Kylee Pawluk, whose knowledge of *Mazzaella japonica* and this system is unparalleled. Thanks to Shaun MacNeill for your company and good humour during our five months of winter sampling. I could not have finished this chapter without your help during all those nights of field work and weekends spent in the lab. Thanks also to Lily Campbell for all of your help on the stable isotopes project. Your enthusiasm in both the field and the lab made this project so much more fun. I'm sorry we couldn't get you more nematodes, and will genuinely miss my morning "disruptions".

Thanks to the Fisheries Ecology lab at UVic, and Ecological Interactions Research Program at VIU for your helpful advice, insight, and discussion. I cannot name everyone, and for that I am sorry, but a special thanks to Geoff Osgood, Laura Kennedy, Mary Toews, and Aharon Fleury, I so enjoyed being a part of this cohort with you. Eric Hertz and Angeleen Olson, thank you for patiently answering all my questions about stable isotopes and seaweeds.

Finally, a special thanks to my friends and family for their love and support. Ryan Dyck, Gord and Colleen Holden, you've been my biggest supporters in every aspect of this, thank you also for tolerating seaweed in your freezers.

Chapter 1: Introduction

1.1 The ecological role of beach wrack

Subtidal macrophytes detached by natural senescence or storm action are often transported to coastlines by oceanic currents, tides, winds, or surf, where they may become stranded on the beach (Kersen and Martin, 2007; Suursaar et al., 2014). Accumulations of these beach-cast seaweeds, seagrasses, and other debris, collectively known as wrack, play an important role within the marine-terrestrial ecotone (Orr et al., 2005; Rodil et al., 2008). These inputs can be very high; in South Africa (Koop and Griffiths, 1982) and Western Australia (Lenanton et al., 1982), for example, it is estimated that each year as much as 2000 kg of beach-cast seaweeds are deposited per meter of shoreline. Decomposition by physical processes and beach-dwelling organisms releases nutrients, such as nitrogen and phosphorous, which contribute to nutrient cycling (Mews et al., 2006), enhance macroalgae and bacterial growth within the intertidal zone (Rodil et al., 2008), and promote the establishment of coastal vegetation (Nordstrom et al., 2000). Wrack deposits also provide refuge from desiccation and predation for many species of intertidal macrofauna (Inglis, 1989). Within the supralittoral zone, it is a main source of food for many terrestrial invertebrates (Colombini et al., 2000; Dugan et al., 2003). Beach wrack enters terrestrial food webs through direct consumption (Fox et al., 2015; Orr et al., 2005), or through predation on wrack-dwelling macrofauna by birds and terrestrial mammals (Carlton and Hodder, 2003; Dugan et al., 2003; Mellbrand et al., 2011). The nature and complexity of these processes depends on the biomass, distribution and species composition of the wrack (Valiela et al., 1997).

Several factors can drive temporal and spatial variability in the characteristics of wrack. Increased wind speeds, surface waves, and swell during storm activity may detach and cast ashore large quantities of macrophytes (Milligan and DeWreede, 2000; Orr et al., 2005). Natural senescence of macroalgae or variation in breakage rates between life cycle stages can result in seasonality in the supply of beach-cast seaweeds. In the red seaweed *Mazzaella splendens*, for example, female gametophytes break more easily than male gametophytes or other life history stages (Mach, 2009). Temporal patterns in the biomass and composition of beach-cast seaweeds may therefore reflect changing hydrodynamic forces (e.g. strong winter storms), seasonality in life history stages, or a combination thereof (Dyck and DeWreede, 2006). Wrack deposits may also vary considerably among locations due to the properties of recipient beaches. Algal community composition differs, for instance, between catchment areas of wave-exposed and sheltered beaches (Orr et al., 2005). Moderately exposed beaches also tend to accumulate higher wrack inputs than sites with extreme shelter from waves or extreme exposure (Orr et al., 2005). Furthermore, exposure is linked to the substratum composition of a beach, with high energy beaches and increased grain size being associated with increased mass of retained wrack (Orr et al., 2005).

Wrack biomass has a strong influence on the abundance of macrofauna, such as semi-terrestrial amphipods, dipterans, coleopterans and collembolans, which begin to colonise these accumulations shortly after deposition (Colombini and Chelazzi, 2003; Inglis, 1989). Numerous studies have reported positive correlations between wrack biomass and total macrofaunal biomass (Dugan et al., 2003; Kirkman and Kendrick, 1997; Koop and Field, 1980; Stenton-Dozey and Griffiths, 1983; Zemke-White et al., 2005), as well as species richness (Dugan et al., 2003). Increased supply of macrofauna associated with larger wrack inputs can, in turn, increase the abundance of predators. Winter shorebird densities in California (Bradley and Bradley, 1993), and Herring Gull nest densities in New York Harbour (Maccarone et al., 2016), for example, are higher during periods of greater wrack deposition. Although increased wrack biomass is generally considered beneficial to the marine-terrestrial ecotone, the deposition of very large quantities can also have severe economic and ecological consequences (Charlier et al., 2008; Smetacek and Zingone, 2013). The decomposition of very large accumulations can lead to the formation of hypoxic conditions and the production of hydrogen sulphide gas, which have adverse effects on infauna communities (Gamenick et al., 1996; McLachlan and McGwynne, 1986; Smetacek and Zingone, 2013).

The spatial distribution of wrack within the foreshore influences its ultimate fate (Rodil et al., 2008). Wrack within the lower intertidal zone is often freshly deposited and highly transient, returning to the offshore marine environment with the movement of outgoing tides, waves, or sediment (Rodil et al., 2008). Here, drifting seaweeds can form habitat for juvenile fishes, while sunken seaweeds may provide food for subtidal herbivores or be further decomposed by marine detritivores (Lenanton et al., 1982; Norkko, 1998; Zemke-White et al., 2005). In oligotrophic systems, nutrients released by re-suspended wrack may contribute to nearshore and subtidal productivity (Hansen, 1984; Lenanton et al., 1982), as well as the growth rates of benthic filter feeders (Duggins et al., 1989). Such contributions, however, may not be significant in nutrient-rich systems, such as those off the coast of South Africa or the Northeast Pacific (Koop and Griffiths, 1982). Wrack deposits in the supralittoral zone typically remain in place for longer periods of time, undergoing dehydration and decomposition (Rodil et al., 2008). These accumulations are more likely to be incorporated in terrestrial food webs as they undergo successional changes in macrofauna species composition (Zemke-White et al., 2005). Amphipods and isopods, for instance, are typically succeeded by terrestrial insects, such as dipterans and coleopterans, as microclimatic conditions change with the loss of moisture content and progressive decomposition (Colombini and Chelazzi, 2003). In the latest stages of decomposition these communities often become dominated by nematodes, oligochaetes, mites, and springtails (Inglis, 1989).

The species composition of wrack also influences its role as a source of habitat, food, and nutrients (Rodil et al., 2008). Different seaweeds will have unique decomposition rates (Mews et al., 2006) and nutritional values (Rossi et al., 2011). Dissimilarities in physical structure, such as branching or toughness, influence palatability and the microclimatic conditions (e.g. habitat complexity, temperature, and humidity) created by the wrack (Rodil et al., 2008). These properties, in turn, have the potential to affect the composition of associated macrofauna assemblages, as well as the biomass and turnover of these species (Colombini et al., 2000; Pennings et al., 2000; Rodil et al., 2008). The unique properties of some seaweed species, such as the production of phycocolloids in their cell walls, also make them commercially valuable and have led to the development of beach-cast harvests (Kirkman and Kendrick, 1997).

1.2 Harvesting of beach-cast seaweeds

Worldwide, wrack is collected for aesthetic purposes (Dugan and Hubbard, 2010; Dugan et al., 2003; Gilburn, 2012), or as a commercial resource (Kirkman and Kendrick, 1997). Beach grooming, or cleaning, is common on populated shorelines and tourist beaches, where wrack might impede aesthetic appeal, recreational use, or enjoyment of the beach (Defeo et al., 2009). The commercial collection of beach-cast seaweeds is less widespread, and largely restricted to regions such as Australia and South Africa (Kirkman and Kendrick, 1997; Zemke-White et al., 2005), though smaller industries also operate in countries including New Zealand (Luxton and Courtney, 1987), Ireland (McLaughlin et al., 2006), and Canada (Chopin and Ugarte, 2005). Commercial uses of beach-cast seaweeds include fertilizers, livestock and mariculture feeds, the production of biofuels, and phycocolloids (agar, carrageenan, and alginates) (FAO, 2014; McHugh, 2003). Phycocolloids, found in the cell walls of seaweeds, are used in a variety of processed foods, pharmaceuticals, and cosmetic products (Bixler and Porse, 2011; McHugh, 2003; Valderrama et al., 2013).

Given the lack of research on commercial beach-cast harvests, studies on the impacts of mechanized beach grooming are often used as a proxy (Kirkman and Kendrick, 1997). Grooming typically involves the complete removal of all beach-cast material using rakes, sieving, and mechanized vehicles, over spatially extensive lengths of shoreline (Dugan et al., 2003). Thorough removal of wrack has been repeatedly associated with negative impacts on the biomass and diversity of macrofauna (Dugan et al., 2003; Lavery et al., 1999; Llewellyn and Shackley, 1996; McLachlan, 1985). Grooming has also been linked to declines in shorebird abundance (Dugan et al., 2003) and fish densities (Lavery et al., 1999). In addition to eliminating the spatial subsidy provided by beach-cast seaweeds, beach grooming can result in the disruption and removal of large quantities of sediment, which accelerates erosion, impacts infauna, and can cause direct mortality of beach-nesting shorebird, turtle, and fish eggs (Defeo et al., 2009).

Though it is the closest substitute in the literature, the ecological effects of beach grooming could be quite different from those of commercial harvesting. Harvesting licence conditions, for instance, often require that a proportion of the available wrack biomass be left behind, prohibit the removal of any sediment, and in many cases ban the mechanized collection of beach-cast seaweeds (e.g. PIRSA, 2014). Unlike grooming, the commercial harvesting of beach-cast seaweeds is often regulated by quotas, though management practices vary. Kelp harvests on King Island, Australia, for example, permit the removal of up to 50% of the available beach-cast bull kelp (*Durvillaea potatorum*) (PIRSA, 2014). Similarly, a harvest in South Australia allows the collection of up to 75% of the estimated beach-cast biomass, but requires that 25% of the 102 km of coastline licensed for harvesting be set aside as ‘exclusion zones’ (PIRSA, 2014). In Ireland, quotas are set by fixed biomass rather than proportion, permitting the collection of hundreds to thousands of tons of drift seaweeds daily per commercial licence (McLaughlin et al., 2006).

Two reviews of commercial beach-cast harvests have identified several key research gaps which should be addressed when examining the effects of removal and making resource management decisions (Kirkman and Kendrick, 1997; Zemke-White et al., 2005). These include: quantitative assessments of the distribution of beach-cast seaweeds and its species composition; assessments of harvesting effects on beach invertebrate community structure and trophodynamics; and research on the fate of un-harvested seaweeds. Given that the majority of previous research has taken place in oligotrophic systems, filling these knowledge gaps is of particular importance in nutrient-rich waters such as those of the Northeast Pacific (Kirkman and Kendrick, 1997).

As the rate of seaweed introductions continues to increase, so too does the collection of non-indigenous beach-cast algae for both aesthetic and commercial purposes (Pickering et al., 2007; Smith et al., 2004; Villanueva et al., 2010). Intensified maritime traffic and aquaculture have facilitated the global spread of seaweeds (Ruiz et al., 2000; Schaffelke et al., 2006), with more than 400 introductions reported world-wide (Williams and Smith, 2007). In the case of invasive species, such as *Hypnea musiformis* in Hawaii, beach-cast removal for aesthetic reasons can be very expensive (Van Beukering and Cesar, 2004). In Australia and New Zealand, on the other hand, the accidental introduction of the economically valuable *Undaria pinnatifida* has yielded a profitable commercial harvest, which doubles as a potential management tool to limit further dispersal (Kirkman and Kendrick, 1997; Ministry of Agriculture and Forestry, 2010). Although the harvest of an introduced species is generally perceived positively (Pickering et al., 2007), little is known about the effects of such removal on wrack-associated fauna (Kirkman and Kendrick, 1997).

Non-indigenous seaweeds often have negative impacts on the abundance and biodiversity of sympatric native primary producers, but may have negligible or even positive effects on herbivores and higher trophic levels (Maggi et al., 2015). The invasive red seaweed *Gracilaria vermiculophylla*, for example, provides gammarid amphipods with protection from desiccation and predation, thereby increasing their abundance in Georgia mudflats of the United States (Wright et al., 2014). Similarly, in the San Juan Islands, *Sargassum muticum* supports more abundant and diverse epibiont communities than the native kelp *Laminaria saccharina* (Giver, 1999). This invasive seaweed has also been documented as a novel food source for the semi-terrestrial amphipod *Talitrus saltator*, especially during the winter (Rossi et al., 2010). On the other hand, non-indigenous seaweeds can outcompete native macrophytes which provide a preferred food source (Engelen et al., 2011; Gollan and Wright, 2006; Maggi et al., 2015; Tomas et al., 2011); alter carbon, nitrogen and phosphorous provision (Rossi et al., 2011); cause physiological damage to generalist herbivores; or create anoxic conditions (Rodil et al., 2008).

On the east coast of central Vancouver Island, a species of non-indigenous red seaweed called *Mazzaella japonica* washes ashore in conspicuous quantities during the late fall and early winter. Like many red algae, *M. japonica* is rich in carrageenan, a valuable global commodity used as a gelling and thickening agent in a variety of processed foods, pharmaceuticals, and cosmetics (McHugh, 2003; Valderrama et al., 2013). The abundance of this seaweed, and its valuable phycocolloid content, prompted interest in a commercial harvest.

1.3 Baynes Sound harvest

In 2007, the British Columbia Ministry of Agriculture began issuing licences for the beach-cast harvest of *M. japonica* from the southern end of Baynes Sound (Figure 1.1). Native to Korea, Japan, and Russia, *M. japonica* was first recognized in the region about 10 years ago, and confirmed to be non-indigenous by genetic identification (Saunders, 2009). Likely transported along with Pacific oyster (*Crassostrea gigas*) seed from Japan for aquaculture purposes, it may have been introduced 45 to 80 years ago (Saunders, 2009). In the marine environment it accounts for 67 to 99% of macrophyte cover, outcompeting native primary producers and the notoriously invasive *Sargassum muticum* (Pawluk, 2016). While its complete subtidal distribution remains to be determined, reports of *M. japonica* suggest that it is concentrated in the area south from Deep Bay and north of Qualicum, where detached specimens wash ashore in the greatest volumes.

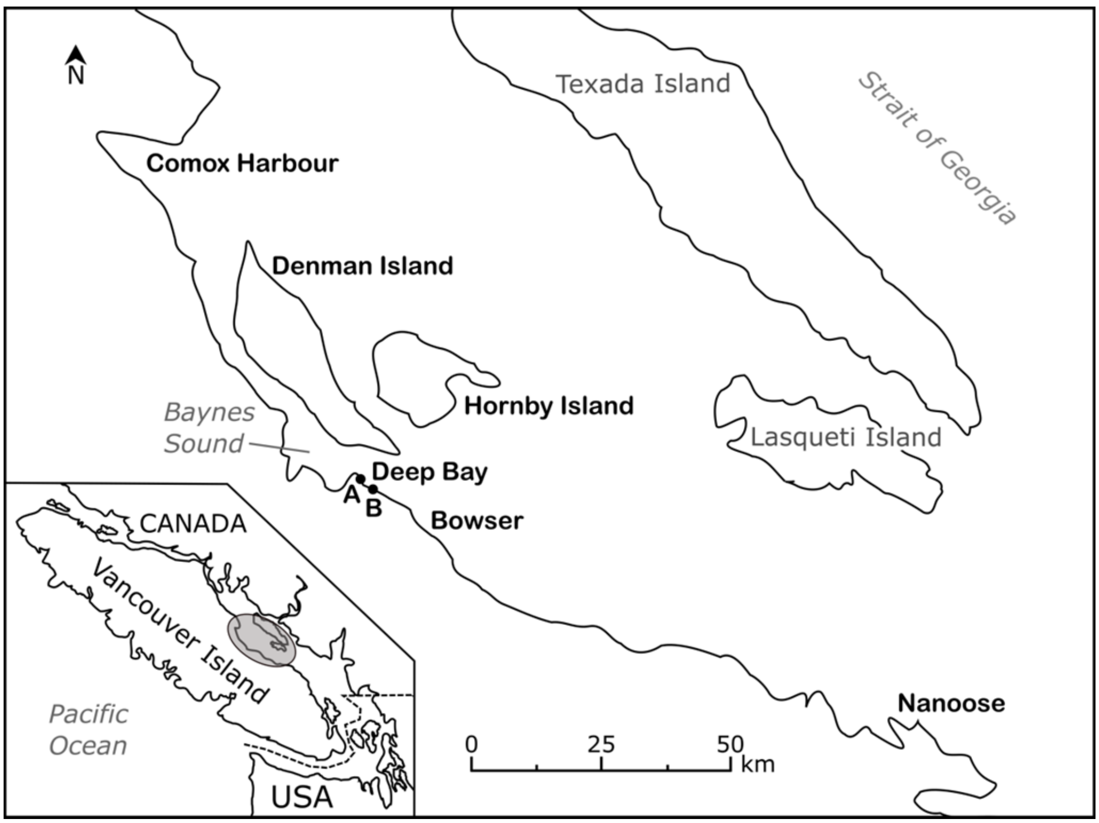


Figure 1.1 Study region - Baynes Sound, British Columbia. Research took place between the unincorporated communities of Deep Bay and Bowser, which are located at the southern end of Baynes Sound.

In the 2014-2015 harvest season, three licence holders were granted quotas of 300 tonnes (wet-weight) each, which they were permitted to collect from September 15, 2014 to February 15, 2015. The area open to harvesting was restricted to approximately 5 km extending from the RV Park in Deep Bay, south to Buccaneer Beach in the neighbouring community of Bowser (Figure 1.1). Licencing conditions stipulated that harvesting activities were limited to the upper intertidal zone, and must be done by hand using pitch-forks so as not to disturb the substrate (BC Ministry of Agriculture, 2014). Mechanical harvesting was prohibited, as was removal of substrate from the beach, or harvesting from the water. Harvesters were also required to leave behind a layer of wrack sufficient to cover the sediment. Access to the harvest area was limited to one tracked vehicle, which was permitted to travel bi-directionally above the high tide mark only. Furthermore, in the event that herring eggs were observed on the beach during the licensed term, harvesters were required to cease their collections immediately. Similarly, harvesting would stop in the event of annual bird migrations.

The beach-cast harvest was a source of contention within adjacent communities, where some called for a moratorium until the ecological effects of *M. japonica* removal were better understood (Birtwell et al., 2013). Among their concerns, critics of the harvest felt that it may be removing an important source of habitat, food, and nutrients (Birtwell et al., 2013; Brusse, 2013). Baynes Sound is an Ecologically and Biologically Significant Marine Area (Levesque and Jamieson, 2014), also globally recognized as an Important Bird Area (Booth, 2001). It hosts spawning sites for forage fish, including Pacific Sand Lance (*Ammodytes hexapterus*), and Surf Smelt (*Hypomesus pretiosus*) (de Graaf, 2015), as well as Pacific Herring (*Clupea pallasii*) (Hay and McCarter, 2001). The Sound is also a rearing habitat for commercially valuable juvenile Pacific salmon (*Oncorhynchus* spp.) (Jenkins et al., 2000). With a long history of shellfish aquaculture, beginning in the early 1900s, Baynes Sound now produces approximately 50% of the province’s farmed shellfish (Jamieson et al., 2001). Concerns within the community were therefore wide-ranging and garnered a great deal of local media coverage. Conflict culminated in the planting of protest gardens at three main access points in an attempt to block harvesters from the beach at the opening of the 2014-2015 season.

1.4 Research objectives

The primary objective of this thesis was to begin documenting the habitat and food provision subsidies provided by beach-cast *M. japonica* within the harvest region, while investigating the potential effects of commercial removal. Specifically I asked:

1. How large, in terms of biomass and spatial extent, are wrack inputs within the harvest region, and what proportion of this is comprised of the non-indigenous seaweed *M. japonica*?
2. How do wrack characteristics influence associated macrofauna communities?
3. Does the commercial beach-cast harvest of *M. japonica* have any detectable effect on wrack characteristics and macrofauna communities?
4. Does *M. japonica* provide a food source for resident invertebrates of the subtidal and supralittoral zones?

In Chapter two, I document the trends in available wrack biomass within the harvest region, its distribution, and species composition. Evaluating the variation in wrack-dwelling invertebrate assemblages, I describe how the characteristics of this subsidy influence macrofauna communities. Finally, by comparing harvested and un-harvested sites I discuss the potential effects of beach-cast harvesting on wrack characteristics and macrofauna composition. In Chapter three, I investigate the role of *M. japonica* as a potential food source in subtidal and intertidal food webs using stable isotope analysis. Comparing stable isotope carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) ratios of invertebrate consumers from both environments with those of the seven most abundant macrophytes, I evaluate what proportion of their diets can be attributed to non-indigenous seaweeds in Baynes Sound. Chapter four summarizes the ecological significance of this research, potential implications for the management of *M. japonica*, and social considerations. The results of this research program are intended to provide a record of *M. japonica*'s beach-cast biomass and distribution, as well as information for the basis of management decisions. Furthermore, this research fills important knowledge gaps regarding the commercial harvesting of beach-cast seaweeds, advances our understanding of wrack subsidies, and contributes to limited literature on the beach-cast ecology of non-indigenous seaweeds.

Chapter 2: The commercial harvesting of a non-indigenous red alga, *Mazzaella japonica*, and implications for beach wrack communities in Baynes Sound, British Columbia

2.1 Introduction

Accumulation of beach-cast seaweeds, seagrasses, and other debris, collectively known as wrack, are a common occurrence on coastlines worldwide where they link marine and terrestrial environments (Mellbrand et al., 2011). On beaches with little *in situ* primary productivity, this marine-derived subsidy provides food and habitat for a diverse array of organisms (Brown and McLachlan, 1990; Colombini and Chelazzi, 2003; Inglis, 1989). Greater wrack biomass is often associated with an increased abundance of primary consumers such as amphipods, isopods and insects (Dugan et al., 2003; Ince et al., 2007). These benefits extend to higher trophic levels as wrack-associated organisms fall prey to terrestrial predators, including birds and terrestrial mammals (Dugan et al., 2003; Fox et al., 2015; Mellbrand et al., 2011). The decomposition of very large accumulations, however, can lead to the creation of anoxic conditions with negative consequences for infauna communities (Gamenick et al., 1996; Smetacek and Zingone, 2013). The effects of wrack on community dynamics can also vary with species composition, as seaweeds differ in their nutritional value, decomposition rates, and structure, creating unique micro-habitat and micro-climatic conditions (Rossi et al., 2011).

In areas with high marine macrophyte inputs, the harvesting of beach-cast seaweeds has become increasingly widespread. Beach grooming, for aesthetic purposes, typically involves the mechanized removal of all beach-cast material (Dugan et al., 2003). Common in populated regions and tourist beaches, grooming has been associated with decreased biodiversity and abundance of wrack-associated macrofauna, such as talitrid amphipods (commonly known as "beach hoppers" or "sand fleas") and flies (Dugan et al., 2003). The collection of beach-cast seaweeds for commercial purposes, on the other hand, typically involves quotas and regulations that preclude the complete removal of wrack. In Australia, for example, harvesters are permitted to collect up to 50% of available beach-cast bull kelp (*Durvillaea potatorum*) (Kirkman and Kendrick, 1997; PIRSA, 2014). Other countries such as Ireland, permit larger harvests by biomass rather than proportion, allowing commercial businesses to collect hundreds to thousands of tonnes of drift seaweeds per licence daily (McLaughlin et al., 2006). Knowledge about the effects of commercial beach-cast harvests on macrofauna (macroscopic animals greater than 1 mm in size) communities is limited, however, especially for nutrient rich systems such as coastlines of the Northeast Pacific (Kirkman and Kendrick, 1997).

On the east coast of Vancouver Island, British Columbia, a pilot harvest of beach-cast seaweeds began in 2007, targeting the non-indigenous red alga *Mazzaella japonica*. With the collapse of Irish moss (*Chondrus crispus*) fisheries on the east coast of Canada, *M. japonica* has become a valuable alternative source of carrageenan. Native to Korea, Japan, and Russia, *M. japonica's* complete distribution in the area remains unknown, but appears to be concentrated in the southern end of Baynes Sound (Pawluk, 2016). In the subtidal environment this non-indigenous seaweed outcompetes native primary producers, as well as the notoriously invasive brown alga *Sargassum muticum* (Pawluk, 2016). On adjacent beaches, detached seaweeds, including *M. japonica*, wash ashore in large quantities during the fall and early winter, blanketing extensive portions of the shoreline in a thick layer of wrack.

While the harvest of an introduced or invasive seaweed is often perceived positively (Pickering et al., 2007), little is known about the effects of removal on wrack-associated fauna. Some invasive seaweeds can have negligible or even positive effects on native herbivores and higher trophic levels (Maggi et al., 2015). By providing a novel habitat or food source these species may increase the biodiversity and abundance of associated fauna (Crooks, 2002; Rodriguez, 2006; Wright et al., 2014). It is therefore important to understand the ecological implications of a non-indigenous species when making management decisions regarding its removal (Bergstrom et al., 2009; Vermeij et al., 2009).

The objectives of this study were threefold: 1) to determine how large, in terms of biomass and spatial extent, wrack inputs are in the harvest region and what proportion of this is comprised of *M. japonica*; 2) to explore how wrack characteristics influence macrofauna assemblages; and 3) to determine if the commercial removal of beach-cast seaweeds has a detectable effect on wrack characteristics and macrofauna assemblages. Meeting these objectives will not only help inform local management practices, but will contribute to limited literature on the effects of beach-cast harvesting. Furthermore, this research will serve as an important record of wrack composition and *M. japonica* biomass, as well as a basis for future studies on the ecology of this non-indigenous species.

2.2 Methods

2.2.1 Study site selection

Six sites within the 4.24 km harvest region were selected based on their similarity in beach characteristics, accessibility, and potential exposure to harvesting (Figure 2.1). Three of these were harvest sites, located at the Deep Bay RV Park (RVH), Shoreline Drive (SH), and Buccaneer Beach (BC), from which licence holders had consistently collected beach-cast seaweeds in previous years and anticipated accessing again. The three remaining sites were selected as comparison sites, from which no seaweeds would be harvested, and were located just north of the Deep Bay RV Park (RVC), at Ocean Trail (OT), and at Henry Morgan Road (HM). Three permanent transects were established within each study site on the first day of sampling following Dugan et al.'s (1990) protocol. The positions of these permanent transects were determined using a random number generator to select three points within an initial 50 m transect, parallel to the water, at the landward boundary of the supralittoral zone. This method yielded three transects per site, at six sites, for a total of 18 permanent transects within the harvest region. A minimum distance of 10 meters was left between permanent transects within each site to minimize potential effects of monitoring activities on adjacent transects. The coordinates of permanent transects were recorded with a hand-held GPS at the outset of the study, and marked with flagging tape so that they could be revisited throughout the monitoring period.

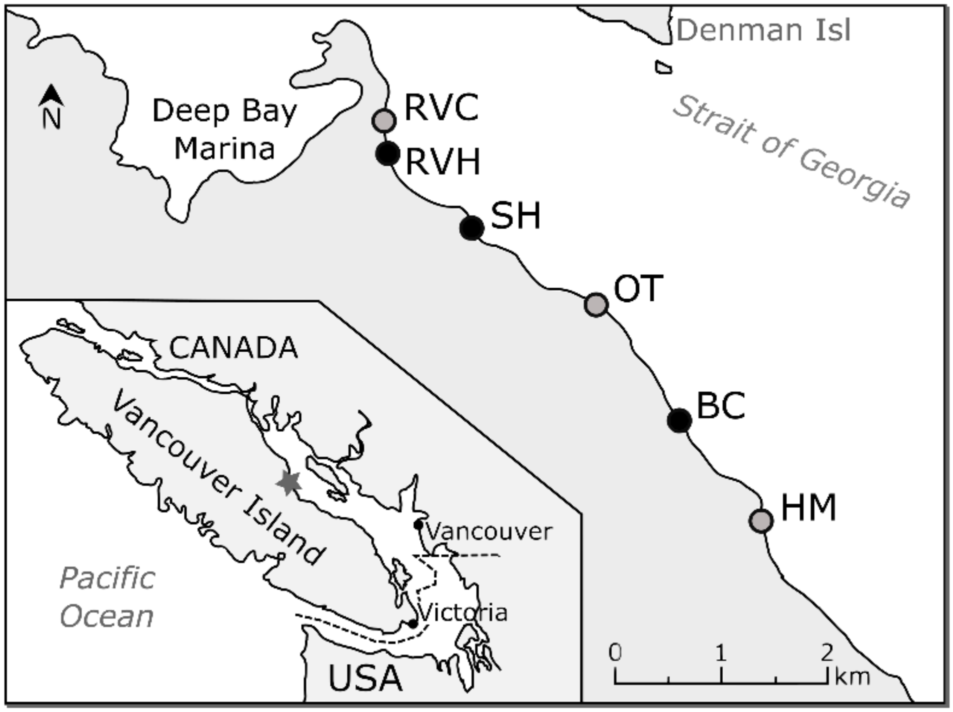


Figure 2.1 Map of study area in Baynes Sound, British Columbia. Licensed harvest region extended from RVH to BC in the 2014-2015 season. Harvest sites are indicated by black circles (●), un-harvested comparison sites indicated by grey circles (○). RVC = Deep Bay RV Park comparison site, RVH = Deep Bay RV Park harvest site, SH = Shoreline Drive, OT = Ocean Trail, BC = Buccaneer Beach, and HM = Henry Morgan.

2.2.2 Site characterization

Each permanent transect was characterized according to the ShoreZone Coastal Habitat Mapping Protocol (Harper and Morris, 2014). Substrate type and sediment composition were estimated visually, widths of the supratidal and the intertidal zones (up to 30 m) were recorded from the transect tape, and three slope measurements were recorded within upper and lower components of both intertidal and supratidal zones. Averages of the three transects per beach were used to assign shore type to each study site (supplementary material, Table S2.1). Presence of terrestrial vegetation and anthropogenic modifications to the landward boundaries of each site were also noted (supplementary material, Table S2.2).

2.2.3 Environmental conditions and harvest data

Weather data were obtained from the Department of Fisheries and Oceans (Department of Fisheries and Oceans Canada, 2014). The Halibut Bank weather buoy was chosen for its location (open water in the Strait of Georgia, approximately 70 km from the harvest region) and its abundance and consistency of data. Average hourly wind speed was calculated as the arithmetic mean. Hourly wind direction was calculated using vector averaging, consistent with procedures used by the National Oceanic and Atmospheric Administration's National Data Buoy Center (NOAA, 2012). Hourly averages were used to generate a wind rose using the openair package (Carslaw and Ropkins, 2012) in R (R Core Team, 2016). Harvest records, including the location of harvesting activity, the number of baskets hailed, and the wet weight of beach-cast seaweed collected for each day were obtained from the licence holders.

2.2.4 Permanent transect monitoring

Permanent transects were visited at low tide once a week from November 14th, 2014, until February 5th, 2015, then bi-weekly until March 5th, 2015. On each sampling date a transect tape was run from the landward boundary of the transect locations to the water line. For each of these point-contact transects we recorded the first and last position of every distinct band of wrack that intersected the transect tape, as well as the position of any gaps. Bands were distinguished based on their level of decomposition, depth, and spatial separation.

A random number generator was used to select one point along the transect within each distinct band of wrack. If the band was greater than two meters wide, one meter was excluded from either end of the band's range in order to minimize edge effects. If the band was less than two meters wide, the center point of the band was selected. A 0.25 m by 0.25 m quadrat was placed directly next to the transect tape at the selected point. For each quadrat we recorded a visual estimate of percent wrack cover of the beach substrate, three depth measurements, and the level of wrack decomposition. Level of decomposition was rated according to a 6 point age class scale created at the outset of the study. Age classes were distinguished based on the colouration and texture of *M. japonica*, which transitioned from a uniform deep red when fresh, becoming increasingly bleached, fragmented, and gelatinous as it decomposed. Percent cover and wrack age class were recorded by the same individual throughout the study to maintain consistency. Once these wrack characteristics had been measured, a 1 L sample of wrack was collected from the centre of each quadrat and weighed in the field using a hand-held spring scale. For wrack accumulations deeper than the 1 L vessel, one sample was taken from the top, a second from the centre, and a final sample from the bottom of the wrack accumulation. These were mixed in a plastic tote and a single 1 L subsample was retained. Collected samples were transferred to labeled Ziploc bags, sealed, and frozen for later analysis.

The volume of wrack within a meter-wide transect of each distinct band was estimated as the product of mean wrack depth multiplied by the length of the band (excluding any gaps). Volume was multiplied by the wet weight of wrack per m^3, determined from the 1L sample, to yield an estimate of biomass. The total biomass within a given transect was calculated as the sum of each distinct band at that location.

2.2.5 Age class composition

Water retention within the wrack varied with level of decomposition, therefore the proportion of biomass belonging to each age class was calculated using dry weights. Dried weights were obtained from a subset of 176 samples, 93 of which were samples analyzed for their macrophyte and macrofauna composition (see below). An additional 83 samples were randomly selected from various age classes across the six sites to ensure that all were represented. These samples were rinsed under fresh water in a 3 mm sieve to remove macrofauna, salt, and sediment, and dried at 60ºC for 48 hours. The total biomass of wrack within distinct bands was multiplied by the mean ratio of sample field weight to sample dry weight for the corresponding age class. This allowed us to estimate dry weight biomass, and calculate the proportion of wrack belonging to each age class, while controlling for differences in water retention.

2.2.6 Macrophyte composition

Macrophyte composition was analyzed for samples from four of the fifteen collection dates, each three weeks apart: November 27th, December 18th, January 8th, and January 29th. Samples were rinsed under fresh water in a 1 mm sieve, and transferred to a tray for sorting. Where possible, macrophytes were identified to species. Terrestrial plant material was grouped collectively as “terrestrial debris”, and macrophyte fragments too small or degraded to identify with confidence were grouped collectively as “unidentifiable”. Sorted groups were dried at 60°C for 48 hours then weighed to the nearest 0.01g. The proportion represented by each macrophyte group was calculated for every sample, then averaged across all samples for a given site and date.

2.2.7 Macrofauna communities

Concurrent with macrophyte sorting, all macrofauna were removed from wrack samples using forceps, and stored in vials containing 75% ethanol. Nematodes, larvae (belonging to various taxa, likely Diptera and Coleoptera), and mites occasionally occurred in numbers too great to remove by hand. In these cases, the number of individuals was counted in three randomly selected squares of the sorting tray, which had a 2 x 6 grid on the bottom. The number of individuals belonging to each taxa was then averaged across the three squares and multiplied by 12, generating an estimate of their total abundance within the sample. Macrofauna were identified to family where possible, then grouped by order. Mites (Acari), nematodes (Nematoda), and larvae (assorted taxa), however, were not identified to such taxonomic resolution, resulting in nine taxonomic groupings: Amphipoda, Araneae, Acari, Diptera, Coleoptera, Collembola, Hymenoptera, Nematoda and larvae. Alpha, beta, and gamma diversity (*sensu* Whittaker 1960) were calculated using these taxonomic groups. Alpha diversity represents local diversity, and was calculated as the mean number of species groups per sample. Gamma diversity represents landscape diversity and was the total number of groups recorded (i.e. all samples aggregated). While there are numerous measures of beta diversity, we used a measure established by Whittaker (1960), which is suitable for ecological analysis of community data (Wilson and Shmida, 1984). This was calculated as follows:

$$\beta = (\gamma / \alpha) - 1$$

Where: β = Beta diversity

γ = Gamma diversity (total number of groups in all samples)

α = Alpha diversity (mean number of groups per sample)

Beta diversity can be thought of as the number of distinct communities, and was used to gauge the amount of compositional heterogeneity in samples. This was later used to evaluate which ordination methods would be appropriate for community analysis. Ordination methods are increasingly challenged when beta diversity is high. As a general rule of thumb, $\beta > 5$ is considered high for ordination (McCune and Grace, 2002).

The true diversity, or the effective number of species, refers to the number of equally abundant species which would be required to obtain the same average proportional abundance as that observed in the dataset (Jost, 2006). True diversity of macrofauna groups was calculated by exponentiation of the Shannon entropy value, also known as the Shannon-Wiener index (Jost, 2006). Overall difference in true diversity was compared among seven fixed factors: age class, mean depth, percent cover, biomass of the band, collection site, transect, and date using a univariate permutation analysis of variance (PERMANOVA) (Euclidean distance, 999 permutations). This was repeated independently for group richness. Bray-Curtis dissimilarity indices were also calculated to compare mean macrofauna composition among collection sites and wrack age classes. The Bray-Curtis dissimilarity index ranges from 0 to 1, where 0 indicates that all species are shared (no dissimilarity) and 1 indicates that there are no species in common (high dissimilarity).

A distance-based multivariate regression tree analysis (MRT), using Bray-Curtis dissimilarity, was used to search for clustering in macrofauna composition. MRTs form clusters by repeated splitting of the data, where each split is defined by a rule based on an environmental variable. The goal is to identify the series of splits which minimizes the dissimilarity between samples within the same cluster. Environmental variables included were site of collection, age class, mean depth, percent cover, and biomass of the band from which the sample was taken. The most parsimonious tree within 1 standard error of the overall best tree was selected; this was replicated 1000 times before picking the tree that was most consistently produced. The Dufrêne-Legendre indicator (DLI) value for each taxonomic grouping was estimated (from 1000 iterations) at every node of the tree to determine the macrofauna group important in delineating each cluster (Dufrêne and Legendre, 1997).

A Constrained Analysis of Principal Coordinates, or CAP (Anderson and Willis, 2003), was run on macrofauna composition including the same explanatory variables as the MRT. In contrast with unconstrained ordination methods (e.g. principal coordinate analysis, or nonmetric multidimensional scaling), constrained ordinations can be used to relate the response variables (species abundance) with predictor variables, such as environmental conditions (Anderson and Willis, 2003). Constrained ordinations may also be used to examine the amount of total variation in the response variables explained by the predictor variables (constrained variation). This particular constrained ordination method was chosen based on the gradient axis lengths of a Detrended Correspondence Analysis and the rank correlation index of distance measures. Detrended Correspondence Analysis involves rescaling, or shifting the positions of samples, along the ordination axis so that a given distance between samples in ordination space represents the same difference in beta diversity regardless of position. A by-product of this process is gradient length, the length of the first axis expressed in standard deviations of species turnover (SD units). If sampling takes place over a gradient length of > 4 SD, unimodal ordination methods should be applied. Linear methods are preferred for gradient lengths < 3 SD, and either method may be appropriate for gradient lengths between these values (Lepš and Šmilauer, 2003). Length of the first axis for our data was 3.2, suggesting that relationships between community composition and environmental factors are likely to be linear, but that either method could be appropriate. Rank correlations between dissimilarity indices and gradient separation were used to evaluate which index was most appropriate, given that a good dissimilarity index will have high rank-order similarity with gradient separation. Compared to Euclidean, Kulczynski, Chao, and Horn-Morisita distances, Bray-Curtis dissimilarity had the highest rank correlation index. This distance measure also has the advantage of being easy and intuitive to interpret when analyzing ecological data (McCune and Grace, 2002). Because CAPs use linear relationships and allow for the use of Bray-Curtis distance measures, this method was selected for ordination.

Prior to ordination, Hymenoptera was dropped from the dataset due to its rarity (occurred in only 2.2% of sample units). Deleting rare species, typically defined as those found in fewer than 5% of sample units, enhances the detection of relationships between community composition and environmental factors for multivariate analysis of correlation structure, and is in accordance with the goals of this analysis (McCune and Grace, 2002). Date of collection was partialled out (removed) for this analysis, as we were specifically interested in the influence of wrack characteristics and site of collection on macrofauna communities. Sample points on the resulting ordination plot were coloured based on the MRT cluster to which they belonged.

Because we also wanted to know how the characteristics of the wrack influenced macrofauna communities, independent of site, we repeated the CAP using the same explanatory variables as before, but with both site and date of collection partialled out. The colour of each sample point was filled according to the age class of wrack from which it was collected. The DLI values of each macrofauna group were calculated for all wrack age classes (number of iterations = 1000).

All statistical analyses were performed using R (R Core Team, 2016). The MRTs were run using the package mvpart (Therneau and Atkinson, 2014), while the DLI analysis was done with labdsv (Roberts, 2015). The PERMANOVA, CAPs, and Detrended Correspondence Analysis were performed using the vegan package (Oksanen et al., 2015).

2.3 Results

2.3.1 Site characterization

Site characterization according to the ShoreZone protocol (Harper and Morris, 2014) indicated that all six study sites shared similar characteristics (supplementary material, Table S2.1). HM and BC were identified as wide gravel flats, while the remaining four sites were classified as wide gravel and sand flats. All sites had a mean slope of < 5°, a width of > 30 meters and were composed of boulders, cobble, pebbles, and sand. Anthropogenic modifications to the landward boundaries included hardened shorelines at RVC and RVH, roads at SH, and houses at BC, RVC, and HM (supplementary material, Table S2.2).

2.3.2 Harvesting activity

A total of 674.5 tonnes of wet beach-cast seaweeds were harvested from the licensed region during the 2014-2015 season (Table 2.1). Harvesting began October 10th

at BC, moving north to SH on October 17th. Harvesting began at RVH on October 30th, where it continued for the remainder of the harvesting period, with the exception of two days spent at SH in November. The three harvest sites therefore experienced very different levels of harvesting activity over the course of the season, with the greatest proportion of total biomass (78%) collected from RVH. RVH was the only site harvested during the monitoring period of this study, with the exception of two days spent at SH in November. Though licensing conditions permitted harvesting until February 15th, 2015, the collection of beach-cast seaweeds was concluded by January 9th. Licence holders cited the declining quality of wrack as the reason they stopped.

Table 2.1 Total metric tonnes of beach-cast seaweeds (wet weight) harvested by location and month during the 2014-2015 harvest season. SH = Shoreline Drive, BC = Buccaneer Beach, RVH = Deep Bay RV Park harvest site.

	Site			
Month	**BC**	**SH**	**RVH**	**Total**
October	10.4	127.0	42.3	179.7
November	0	12.8	372.9	385.7
December	0	0	96.3	96.3
January	0	0	12.8	12.8
Total	10.4	139.8	524.3	674.5

2.3.3 Environmental Data

The strongest winds, ranging from 30-53 km/h, came primarily from the South-East and East (Figure 2.2). A smaller proportion of strong winds came from the North-West, while almost exclusively weaker winds (<15 km/h) came from North to North-East, and South to South-West directions. Strongest winds were more prevalent from November to December, and decreased from January through March.

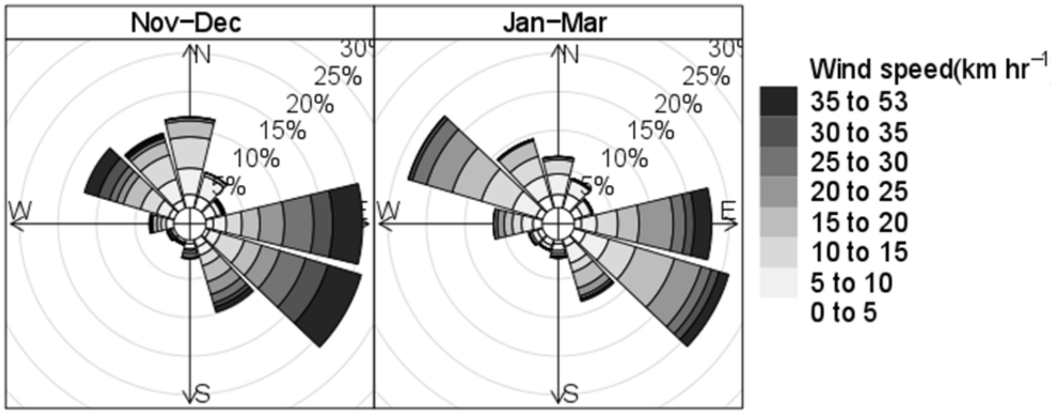
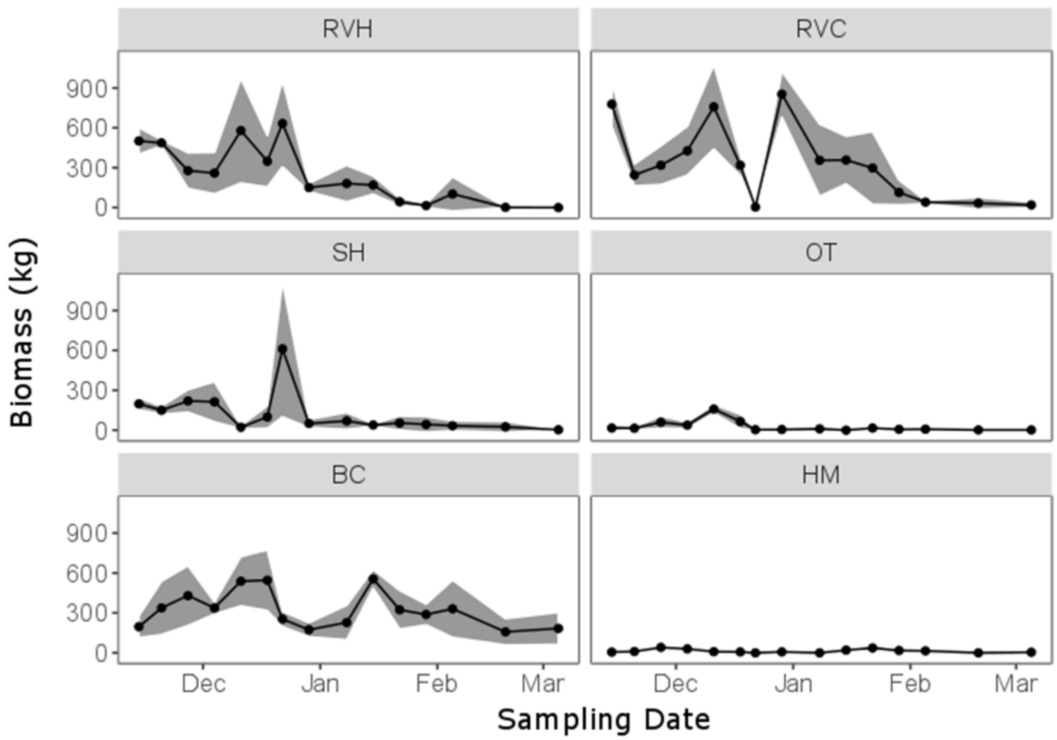


Figure 2.2 Wind speeds (km/h) and wind direction for November through December and January through March of 2014-2015. Wind data were downloaded from the Halibut Bank Weather buoy. Average hourly wind speed was calculated as the arithmetic mean and hourly wind direction was calculated using vector averaging.

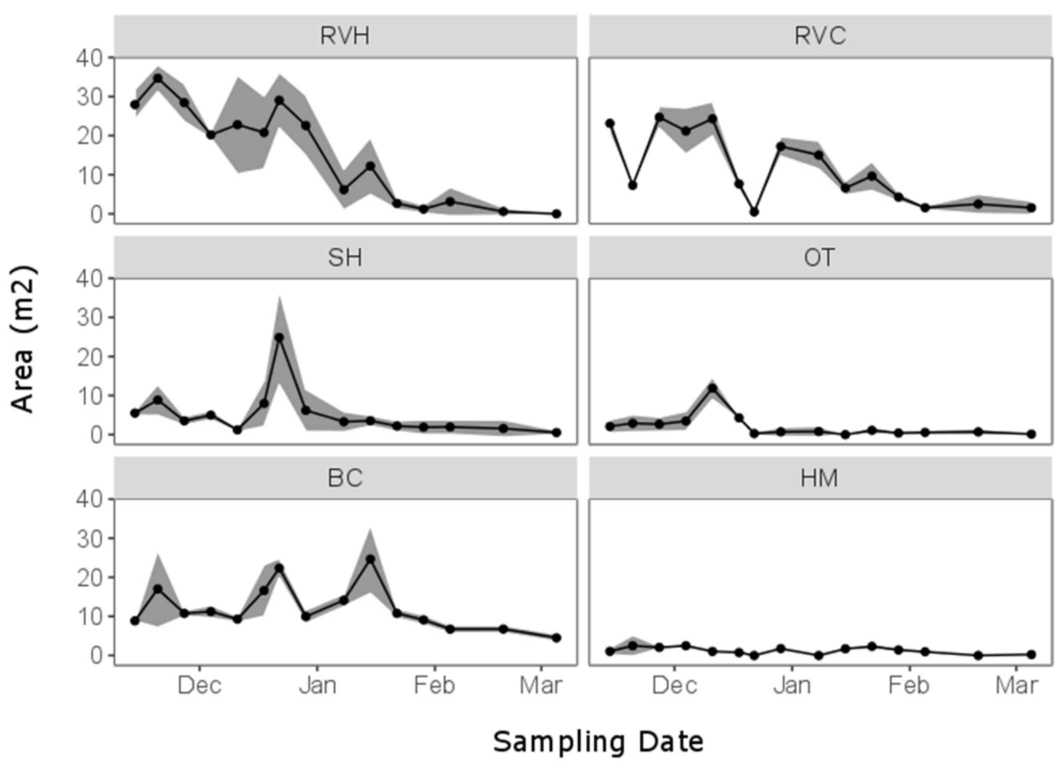
2.3.4 Wrack biomass

Peak biomass was observed in December at BC, SH, RVC, and RVH study sites (Figure 2.3A). For example, as much as 853 kg of wrack (±173 SD) per meter-wide transect was recorded at RVC during this month. All four of these locations, however, experienced rapid declines and influxes of wrack biomass. RVC went from a mean of 4 kg (±7 SD) per transect to 853 kg of wrack (±173 SD) in a single week between December 22nd and December 29th. Wrack biomass generally declined in late December and early January at RVH, RVC, BC, and SH. HM and OT study sites, on the other hand, remained consistently low in wrack biomass throughout the entire monitoring period.

A)


RVH
RVC
SH
OT
BC
HM
900
600
300
0
Biomass (kg)
Dec
Jan
Feb
Mar
Sampling Date

B)


RVH
RVC
SH
OT
BC
HM
40
30
20
10
0
Area (m2)
Dec
Jan
Feb
Mar
Sampling Date

C)

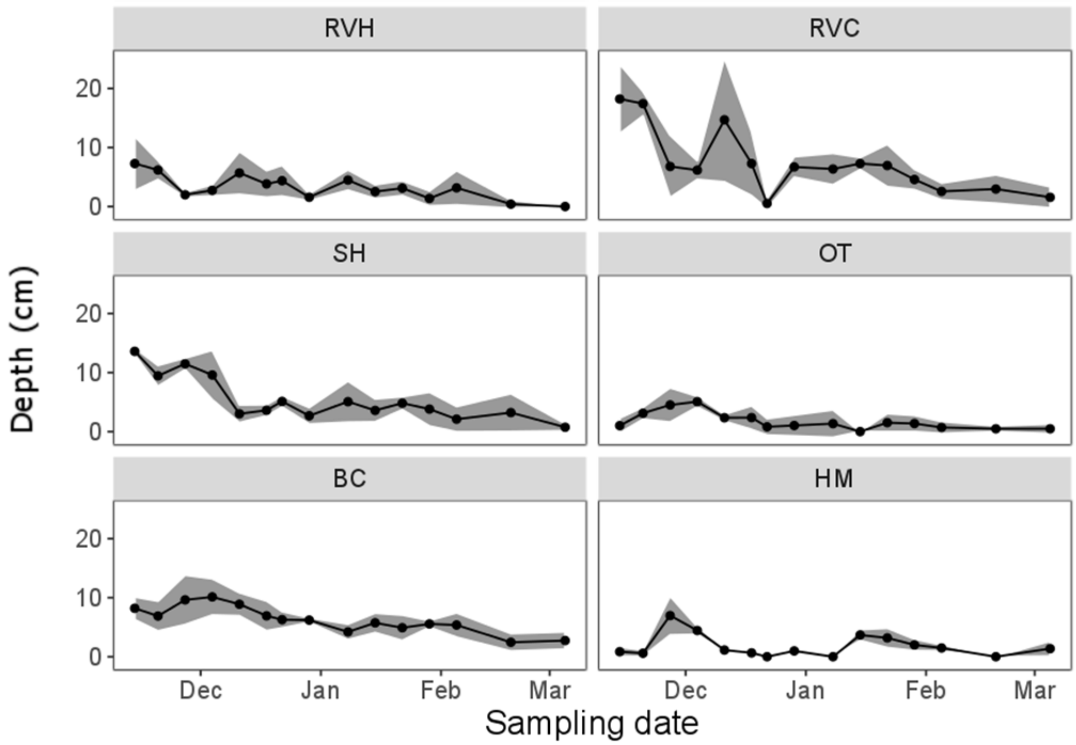


Figure 2.3 A) Mean biomass of wrack (kg) in wet weight, B) mean area of beach substrate covered by wrack (m^2), and C) mean depth of the wrack (cm) where present. Shaded interval represents one standard deviation around the mean (n = 3 transects per site). Potential harvest sites are aligned on the left and un-harvested comparison sites are aligned on the right. 78% of beach-cast seaweeds were collected from RVH during the entirety of the licensed harvesting period.

Wrack area and mean depth followed similar temporal trends as average biomass; peaking in November and December, then declining for the remainder of the monitoring period (Figure 2.3B). The average area of beach substrate covered by wrack at a given site reached as much as 34.7 m^2 (± 3.4 SD) per meter of shoreline. Where wrack was present, average depth across transects ranged from 1.1 cm (±0.3 SD) to 18.2 cm (±5.9 SD), with a maximum depth of 55.0 cm recorded in the field (Figure 2.3C). Wrack tended to cover a greater area of substrate at RVH than at RVC and other sites, which was offset by lower average depth values. On the second day of sampling (November

20th, 2014), for example, mean wrack depth at RVH was only 6.2 cm (±1.6 SD) compared to 17.4 cm (± 2.1 SD) at RVC. Wrack area, on the other hand, at RVH averaged 34.7 m^2 (± 3.4 SD) per meter of shoreline, but only 7.3 m^2 (± 0.8 SD) per meter of shoreline at RVC.

2.3.5 Age classes

Averaged over the entire monitoring period, the majority of wrack biomass belonged to the freshest age classes 1 through 3 (Figure 2.4). Older age classes (4 through 6) represented less than 25% of average dry wrack biomass present at OT, SH, RVH, and RVC study sites. BC and HM, however, had distinctly higher proportions (> 43%) of these older age classes (4 through 6) on average.

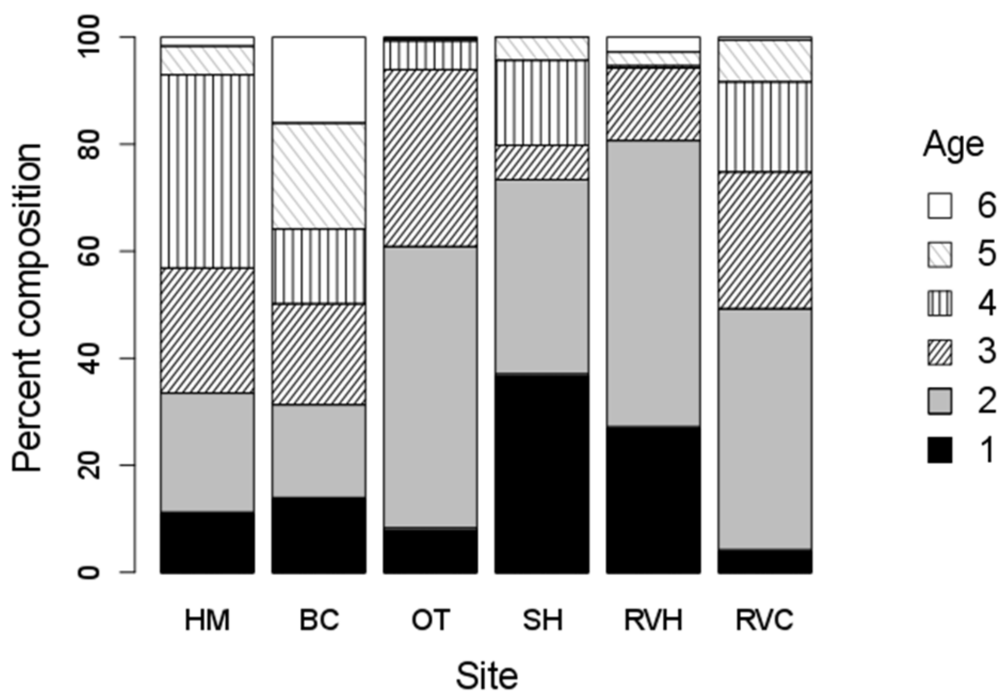


Figure 2.4 Average proportion of dry wrack biomass belonging to each age class for the monitoring period (November 14, 2014 to March 5, 2015). Age class was designated according to a six point scale, where 1 represents the freshest wrack and 6 represents the highest level of decomposition observed in the field.

2.3.6 Macrophyte composition

Unidentifiable material, which was too degraded for identification, represented 12% to 30% of average sample dry weights among locations, and was therefore removed from subsequent calculations to facilitate comparisons. *M. japonica* was the dominant macrophyte species present in wrack samples across all six study sites (Figure 2.5). The average proportion of sample dry weight represented by this non-indigenous species ranged from 87% at RVH, to 94% at SH. Terrestrial debris accounted for 3% to 7% of average sample weight, while *Sargassum muticum*, *Fucus* spp., and *Zostera marina* contributed less than 5% combined. Several rarer species of seaweed (e.g. *Ulva* spp., *Chondracanthus* spp., *Gracilaria* spp., and *Neorhodomela* spp.) were also present in the wrack, but only accounted for a small proportion (< 2% collectively) of average sample weight. All six sites appear to have been sufficiently sampled, with macrophyte species accumulation curves reaching an asymptote (supplementary material, Figure S2.1A).

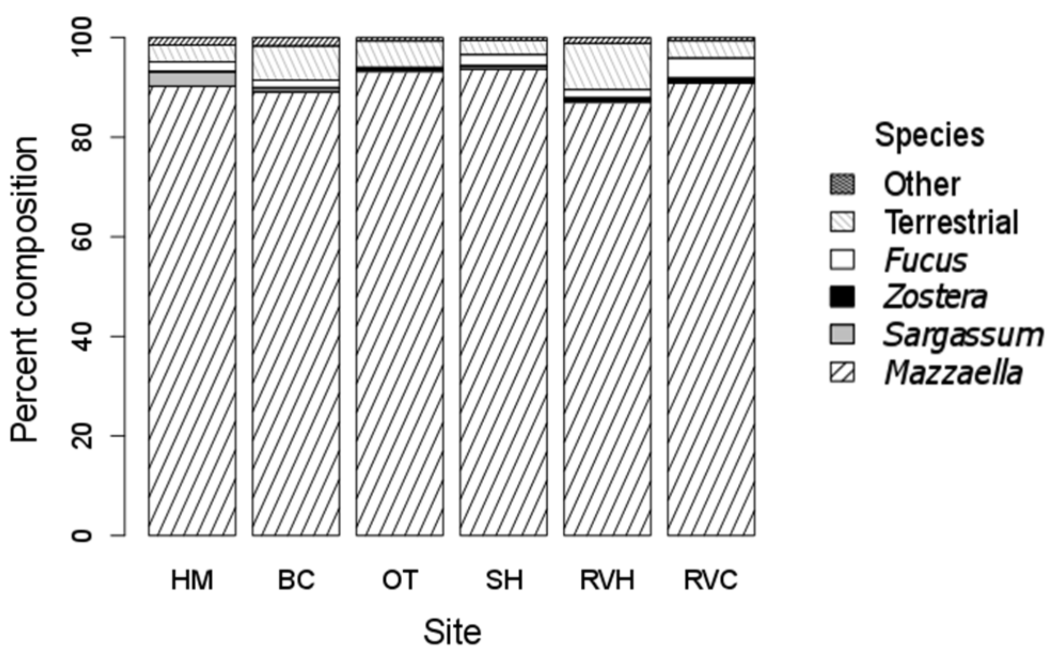


Figure 2.5 Average proportion of identifiable wrack biomass (dry weight) belonging to each macrophyte group within a 1 L sample. Samples were collected from three transects per site on four sampling dates (n = 93 samples total).

2.3.7 Macrofauna communities

Categorized by the nine taxonomic groupings, macrofauna species accumulation curves for the six sites (supplementary material, Figure S2.1B), as well as the five age classes of wrack (supplementary material, Figure S2.1 C) all reached an asymptote, indicating that sampling was sufficient. Macrofauna communities were largely composed of nematodes at OT, SH, RVH, and RC, where they accounted for 35% to 57% of sample composition (Figure 2.6). Dipterans also represented a large proportion of the macrofauna communities, especially at BC (42%) and RVH (41%). HM had a notably higher proportion of collembolans (57%) and an absence of both mites and larvae. OT had the highest proportion of amphipods (10%), coleopterans (10%) and spiders (6%) compared to other sites. The primary harvest site, RVH, appeared to have relatively similar proportions of each macrofauna group compared to the nearby RVC and SH sites.

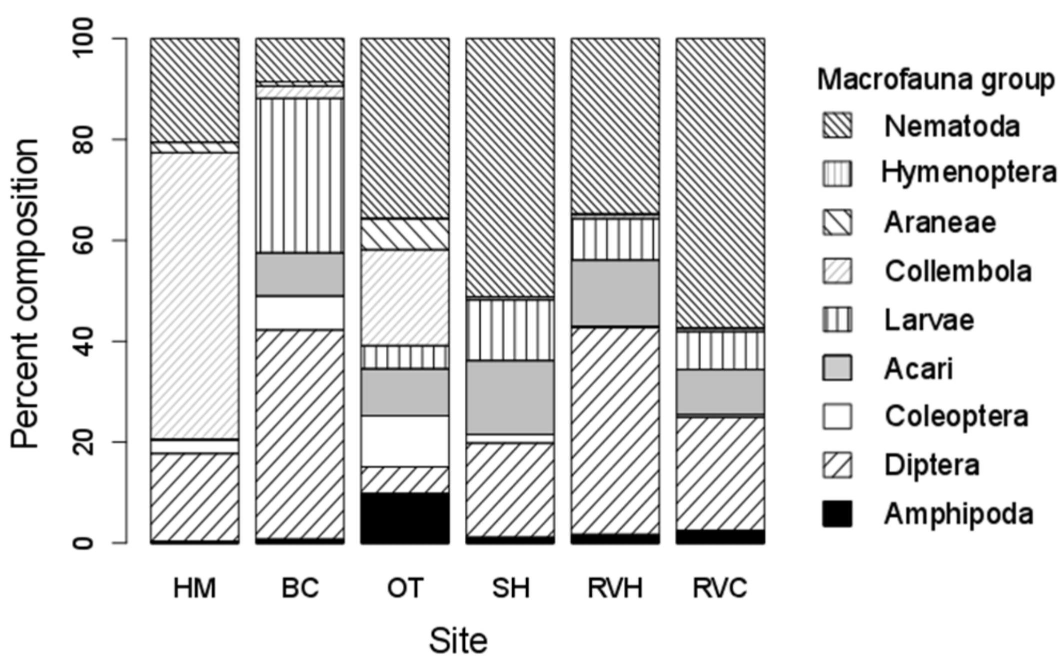


Figure 2.6 Mean proportion of macrofauna abundance belonging to each macrofauna group collected from 1 L samples of wrack. Samples were collected from three transects per site on four dates (n = 93samples total).

Based on frequency of occurrence, the presence of most macrofauna groups increased with the age class of the wrack (Table 2.2). Collembolans, larvae and coleopterans, for example, were found in only 6%, 25%, and 19% of age class 1 samples respectively, but occurred in 73%, 93%, and 80% of age class 5 samples. Dipterans and nematodes occurred frequently in all age classes; while amphipod frequency appeared to decrease from age class 1 (25%) to age class 5 (13%).

Table 2.2 Percentage of samples in which each macrofauna group was present among wrack age classes. Samples were aggregated across six study sites and four collection dates (n = 93 total). Age class was designated according to a six point scale of decomposition where 1 represents the freshest wrack and 6 represents the greatest level of decomposition. Wrack of age class 6 was not present during the dates sampled.

	Age Class				
Group	**1**	**2**	**3**	**4**	**5**
Acari	12.5	50.0	44.4	52.9	66.7
Amphipoda	25.0	38.9	29.6	23.5	13.3
Araneae	6.3	0	11.1	5.9	20.0
Coleoptera	18.8	0	22.2	52.9	80.0
Collembola	6.3	33.3	44.4	70.6	73.3
Diptera	68.8	72.2	85.2	76.5	100.0
Hymenoptera	0	0	0	5.9	6.7
Larvae	25.0	22.2	22.2	52.9	93.3
Nematoda	50.0	55.6	77.8	76.5	33.3

2.3.8 Sample diversity, richness, and dissimilarity

Overall, macrofauna samples had a beta diversity of 1.63 (Table 2.3), indicating an appropriate level of community diversity for the use of ordination methods (beta diversity < 5). The alpha diversity of macrofauna groups across sites ranged from 2.5 at RVH to 3.9 at BC, and increased with increasing age class of the wrack (Table 2.3).

Table 2.3 Sample size (n), alpha, beta, and gamma diversity by site and wrack age class based on the nine taxonomic groupings of macrofauna used in this study (Amphipoda, Diptera, Coleoptera, Acari, larvae, Collembola, Araneae, Hymenoptera, and Nematoda). Age class was designated according to a six point scale of decomposition where 1 represents the freshest wrack.

			Diversity		
		n	**Alpha**	**Beta**	**Gamma**
Site	RVC	20	3.4	1.1	7
	RVH	10	2.5	2.2	8
	SH	17	3.8	0.9	7
	OT	11	3.7	1.2	8
	BC	21	3.9	1.3	9
	HM	14	2.7	2.0	8
Age class	1	16	2.1	2.8	8
	2	18	2.7	1.2	6
	3	27	3.37	1.37	8
	4	17	4.18	1.15	9
	5	15	4.87	0.85	9
Total		93	3.42	1.63	9

Mean group richness (Figure 2.7A) and true diversity, representing the effective number of groups (Figure 2.7B), generally increased with increasing age class of the wrack. Differences among age classes were significant in the univariate PERMANOVAs for both dependent variables (Table 2.4). In addition to wrack age class, macrofauna group richness differed significantly among sites, with the mean depth of wrack, and the total biomass (Table 2.4). True diversity also varied significantly with the total biomass of wrack, but not among sites or depths (Table 2.4).

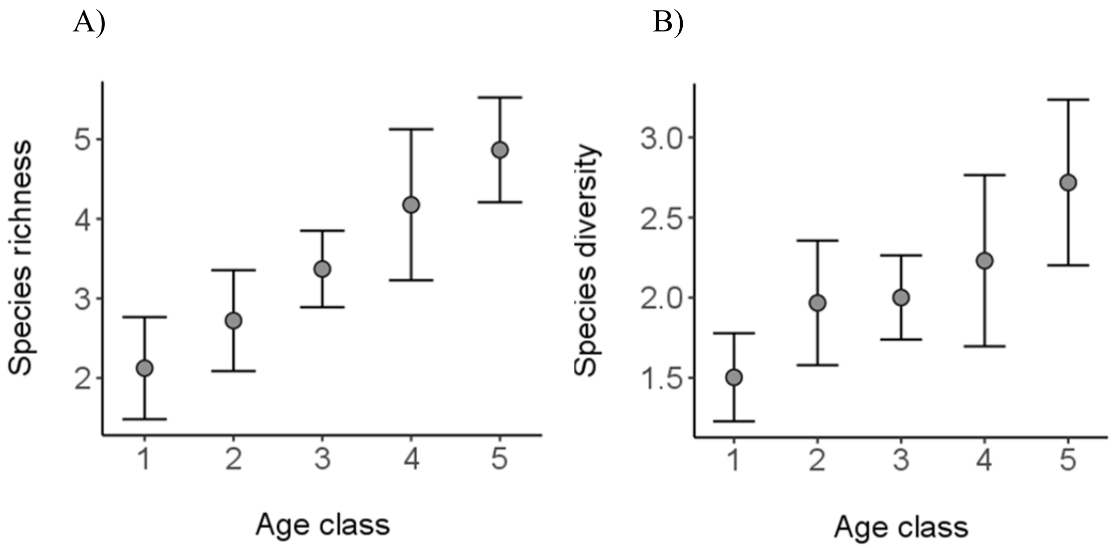


Figure 2.7 Mean macrofauna A) group richness and B) diversity (effective number of groups) from 1 L samples of wrack, with increasing age class of the wrack. Error bars represent a 95% confidence interval around the mean. Samples were aggregated among six collection sites and four sampling dates (n = 93 samples total). Age class was designated according to a six point scale of decomposition where 1 represents the freshest wrack.

Table 2.4 Univariate PERMANOVA (Euclidean distance, 999 permutations) results comparing the effects of: wrack age class (Age), mean depth (Depth), total biomass of the wrack band (Biomass), percent cover (Cover), site of collection (Site), permanent transect (Transect), and date, on the dependent variables: macrofauna group richness and true diversity. Df = degrees of freedom; MS = mean sum of squares; F = Pseudo-F, R^2 = R-squared, p = P-value by permutation. Bold values indicate statistical significance ($p < 0.05$).

Source of variation	df	Group richness				Group diversity			
		MS	F	R^2	p	MS	F	R^2	p
Age	4	19.20	13.02	0.32	**0.001**	3.05	5.37	0.18	**0.003**
Depth	1	13.16	8.92	0.06	**0.005**	0.27	0.48	0.00	0.495
Biomass	1	7.31	5.00	0.03	**0.022**	3.93	6.92	0.06	**0.009**
Cover	1	1.43	0.97	0.01	0.347	0.48	0.85	0.01	0.354
Site	5	4.65	3.16	0.10	**0.015**	0.93	1.64	0.07	0.151
Transect	12	1.41	0.96	0.07	0.464	0.01	0.02	0.00	0.898
Date	1	0.91	0.62	0.00	0.442	0.66	1.16	0.12	0.307
Residuals	80	1.47		0.41		0.57		0.56	
Total	92			1.00				1.00	

Bray-Curtis dissimilarity was lowest between macrofauna assemblages from RVC and SH (Bray-Curtis dissimilarity index = 0.28), as well as RVH and OT (Bray-Curtis dissimilarity index = 0.44) (Table 2.5A). When Bray-Curtis dissimilarity was calculated using data pooled by wrack age class, index values were generally lower (Table 2.5B). Assemblages from adjacent age classes (e.g. 1 and 2, 2 and 3, etc.), were most similar, with Bray-Curtis dissimilarity index values of 0.24 to 0.46. Macrofauna assemblages separated by more than one age class, on the other hand, had index values ranging from 0.5 to 0.71.

Table 2.5 Bray-Curtis dissimilarity index values based on mean macrofauna composition among A) collection sites and B) wrack age classes. Age class was designated according to a six point scale, where 1 represents the freshest wrack. Age class 6 was not present on the dates sampled.

A) Site	**BC**	**HM**	**OT**	**RVC**	**RVH**
HM	0.92				
OT	0.76	0.76			
RVC	0.64	0.76	0.76		
RVH	0.73	0.78	0.44	0.68	
SH	0.56	0.68	0.65	0.28	0.57
B) Age Class	**1**	**2**	**3**	**4**	
2	0.24				
3	0.50	0.46			
4	0.65	0.68	0.44		
5	0.59	0.64	0.71	0.36	

2.3.9 Multivariate regression tree

When site of collection and wrack characteristics were included as explanatory variables, the most parsimonious tree had three terminal leaves, and explained 13.6% of the total variation in macrofauna communities. Site of collection was the only variable defining the nodes of the MRT (Figure 2.8). The first node explained 8% of the variation, separating RVC and SH collection sites from the others. The remaining four sites were further divided, explaining 5.6% of the total variation, with one leaf containing BC and

RVH collection sites and the other HM and OT. The cross-validated relative error was 1.01, indicating that these explanatory variables are generally poor predictors of macrofauna community composition. All macrofauna groups, with the exception of Araneae and Coleoptera, were strong indicators (DLI values ≥ 0.2; DeVantier et al., 2006) for terminal leaves of the MRT (Table 2.6). Nematoda was the primary indicator group for the cluster comprising RVC and SH collection sites, though Amphipoda and Acari were also strong indicators for this terminal leaf. Diptera and larvae were indicative of BC and RVH collection sites. Finally, Collembola was a strong and significant indicator for HM and OT sites.

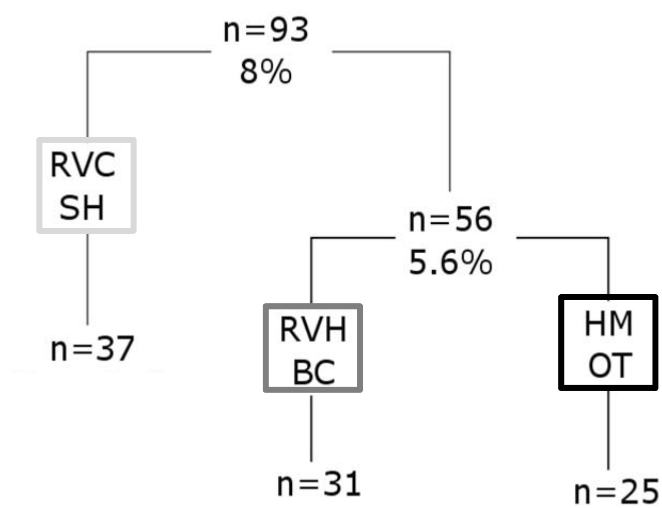


Figure 2.8 Distance-based multivariate regression tree showing discriminating explanatory variables for macrofauna communities using Bray-Curtis dissimilarity. Percentages under each node represent percentage of total variation explained by the split. Sample size (n) is also given for each group produced by the splits.

Table 2.6 The Dufrêne-Legendre indicator (DLI) values of each taxonomic grouping (Group) for the MRT cluster (Sites) in which it has the maximum indicator value. DLI values ≥ 0.2 are considered strong and are indicated in bold face. P-values (*p*) are estimated from 1000 iterations, significance ($p < 0.05$) is indicated in bold face.

Group	Sites	DLI	*p*
Acari	RVC & SH	**0.260**	0.257
Amphipoda	RVC & SH	**0.219**	0.079
Nematoda	RVC & SH	**0.589**	**0.001**
Coleoptera	BC & RVH	0.127	0.891
Diptera	BC & RVH	**0.583**	**0.002**
Larvae	BC & RVH	**0.362**	**0.021**
Collembola	HM & OT	**0.785**	**0.001**
Araneae	HM & OT	0.130	0.073

2.3.10 Constrained analysis of principal coordinates

With site of collection included as an explanatory variable in the CAP, constrained variation comprised 23.8% of the total variation in macrofauna assemblages (Figure 2.9). Clustering within the CAP was largely consistent with the results of the MRT. The first canonical axis, for example, separated RVH and BC collection sites from OT and HM, which had mean positive scores (Figure 2.9A). Macrofauna groups that loaded negatively on this axis were: larvae, Diptera, Acari, Nematoda and Coleoptera (Figure 2.9B). Collembola, on the other hand, loaded strongly and positively on this axis, followed by Amphipoda and Araneae, which loaded near the center. This axis explained 31.1% of the constrained variation, but only 7.5% of the total variation in macrofauna composition. The second axis, which explained 23.2% of the constrained variation, and 5.6% of total variation, largely separated RVC and SH collection sites (which had mean positive scores) from BC, RVH, OT, and HM (Figure 2.9A). Nematodes loaded strongly and positively onto the second axis, while larvae and Collembola loaded negatively (Figure 2.9B). Older age classes were associated with larvae, Diptera, and Coleoptera, which loaded negatively on both the first and second canonical axes. Increasing depth, percent cover, and biomass of the wrack band were associated with Nematoda and Acari, which loaded negatively on the first canonical axes and positively on the second.

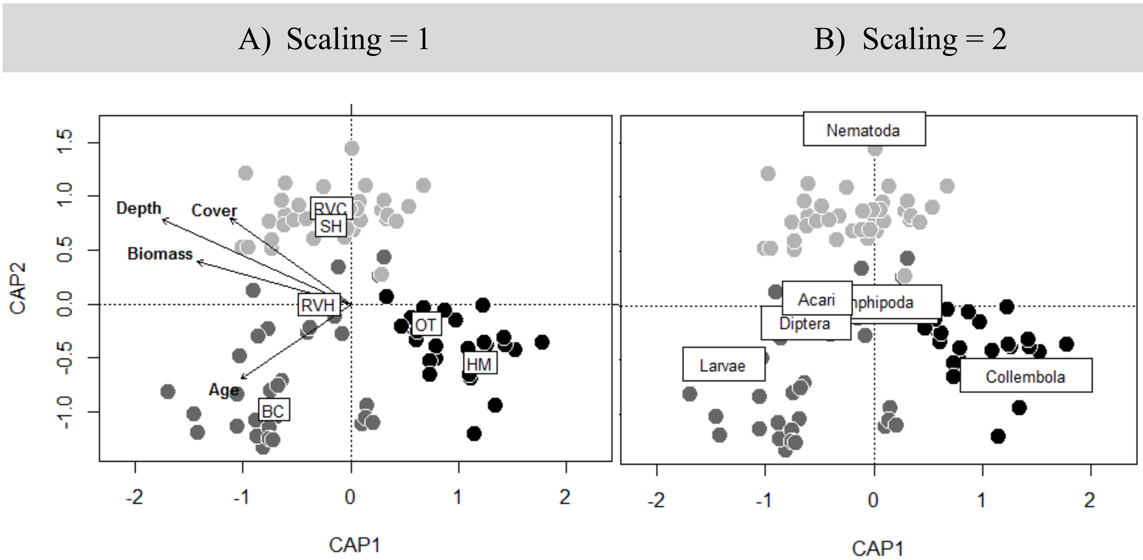


Figure 2.9 Results of the constrained analysis of principal coordinates (CAP) using Bray-Curtis dissimilarity. Sample points in the CAP are shaded according to their corresponding cluster in the MRT (● = HM &OT, ● = BC & RVH, ● = RVC & SH). A) Scaling = 1 biplot of the collection sites on the first two axes of the CAP, tip of the arrow heads indicate the biplot scores for the constraining variable lengths. C) Scaling = 2 biplot plotting the macrofauna group scores for the CAP on the first two axes.

When the CAP was repeated, with the effects of collection site partialled out, wrack characteristics (age class, depth, percent cover, and band biomass) explained 8.1% of the total variation in macrofauna community composition. Wrack age class and mean emerged as important environmental variables explaining the constrained variance in macrofauna communities. Wrack age class was strongly and negatively associated with the first axis, which explained 53.4% of the constrained variation, but only 5.2% of total variation (Figure 2.10A). Wrack depth was also negatively associated with this axis, though not as strongly as age class. Larvae loaded most strongly on this axis, followed by Collembola, Acari, and Diptera in ascending order of mean scores (Figure 2.10B). Wrack age class was also strongly and negatively associated with the second axis, which explained 22.3% of the constrained variation and 2.2% of total variation (Figure 2.10A). Mean wrack depth, on the other hand, was strongly and positively associated with this axis. Amphipoda and Diptera were the only two macrofauna groups that loaded positively on the on the second axis (Figure 2.10B).

A) MRT, scaling = 1	B) MRT, scaling = 2

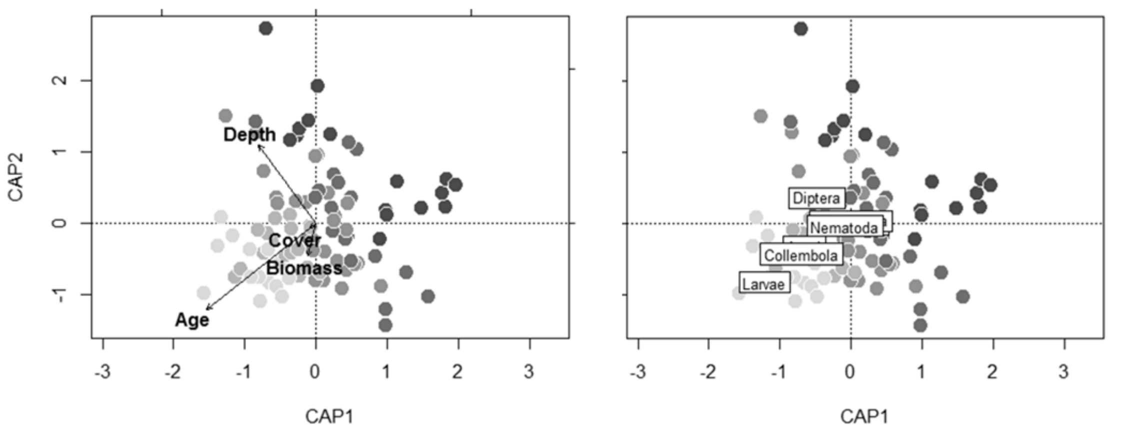


Figure 2.10 Results of the constrained analysis of principal coordinates (CAP) using Bray-Curtis dissimilarity, with the effects of collection site partialled out. Sample points are shaded from freshest wrack age class (● = age class 1) to oldest wrack age class (● = age class 6). A) Scaling = 1 biplot of the wrack characteristics on the first two axes of the CAP, tip of the arrow heads indicate the biplot scores for the constraining variable lengths. B) Scaling = 2 biplot plotting the macrofauna group scores.

Amphipoda had a maximum DLI value within age class 2, but was neither a strong nor a significant indicator for this age class (Table 2.7). Diptera was a strong indicator for age class 3, while Collembola and Nematoda were indicative of age class 4. Coleoptera, Acari, larvae, and Araneae all had maximum DLI values for age class 5. Of these, all but Araneae were strong (DLI > 0.2) and significant ($p < 0.05$) indicators (Table 2.7).

Table 2.7 The Dufrêne-Legendre indicator (DLI) values of each macrofauna group for the wrack age class in which it has the maximum indicator value. DLI values ≥ 0.2 are considered strong and are indicated in bold face. P-values (*p*) are estimated from 1000 iterations, and significance ($p < 0.05$) is indicated in bold face.

Group	Age class	DLI	*p*
Amphipoda	2	0.163	0.198
Diptera	3	**0.318**	0.235
Collembola	4	**0.536**	**0.003**
Nematoda	4	**0.254**	0.418
Coleoptera	5	**0.298**	**0.009**
Acari	5	**0.311**	**0.031**
Larvae	5	**0.443**	**0.001**
Araneae	5	0.133	0.091

2.4 Discussion

Wrack biomass within the harvest region at the southern end of Baynes Sound was very high, reaching as much as 853 kg (±173 SD) of wrack per meter of shoreline. Approximately 90% of this this biomass was attributed to the non-indigenous red alga *Mazzaella japonica*. Despite the commercial removal of 674.5 tonnes of beach-cast seaweeds, we found that the trends in biomass were similar between the harvested and unharvested locations, though harvesting activity may be associated with spreading of the wrack over a greater area of substrate. Macrofauna communities differed between study sites, as well as with the age class and depth of the wrack from which they were sampled. Older age classes of wrack, for example, were more speciose and diverse than fresh age classes. Though there was a concentration of harvesting activity at one location, effects of the harvest on macrofauna communities appear to be small if any.

2.4.1 Wrack biomass, distribution, and composition

During peak biomass (November through December), a significant portion of our study sites were under an extensive ‘blanket’ of seaweed. An average 853 kg of wrack

(±173 SD) per meter of shoreline, for example, was recorded at RVC on December 29th. These findings are highly consistent with wrack biomass reported in a concurrent study of the harvest region (Kingzett et al., 2015). The average area of beach covered by wrack reached as much as 35 m^2 (±3 SD) at RVH on November 20th, and the maximum depth measurement recorded during this period was 55 cm. While knowledge about the deposition of beach-cast seaweeds elsewhere in British Columbia is limited, accumulations of such magnitude and composition may be unique to this region of Vancouver Island. A summer study by Orr et al. (2005), for example, recorded a maximum mean biomass of only 38 kg (±6 mean absolute deviation) of wet wrack per meter of shoreline on the west coast of the island, though the authors noted that wrack loading is likely higher in the winter. Wrack biomass was similarly low in studies of southern California (Revell et al., 2011), as well as on the East Coast of Canada (Béland, 2012). While the highest wrack loadings observed in our study were lower than reports of 1 to 3 tonnes of wrack per meter of shoreline in the Gulf of California (Polis and Hurd, 1996), South Africa (Koop and Field, 1980), and Australia (Hansen, 1984), Kingzett et al. (2015) recorded as much as 1.35 tonnes per meter of shoreline within the harvest region on October 27th, before we began monitoring. Across the globe, non-indigenous seaweeds and eutrophication events have contributed to the deposition of large wrack accumulations, though comparable biomass estimates expressed per meter of shoreline are lacking in the literature (Smetacek and Zingone, 2013).

Within the 5 km harvest region, wrack generally appeared to accumulate in the greatest quantities in late autumn, coinciding with higher wind speeds from the south-east. This suggests that storm activity, perhaps in concert with seasonal cycles in macroalgae reproduction and senescence (Dyck and DeWreede, 2006), may be responsible for the detachment and subsequent deposition of beach-cast seaweeds in Baynes Sound. Sudden changes in wrack biomass and trends in age class composition across the six study sites suggest that the wrack is highly transient. The greatest accumulations of wrack biomass were recorded on south-east facing beaches (RVH, RVC, BC, and SH), which is also supported by patterns in the spatial distribution of wrack biomass across the entirety of the harvest region (Kingzett et al., 2015). Given observations of a strong south-east wind regime, these are the sites where we would expect seaweed biomass to dissipate the slowest under the influence of longshore drift. The small proportion of substantially decomposed wrack (age classes 4-6) and rapidly decreasing total biomass over time, also suggest that the majority of drift seaweeds are exiting the system.

The ultimate fate of drifting *M. japonica* remains unknown, but could have implications for offshore productivity. Drift seaweeds in oligotrophic systems, for example, can increase nutrient availability important for subtidal communities (Lenanton et al., 1982). Their significance as a source of nutrients is less clear, however, for more productive systems (Kirkman and Kendrick, 1997), such as those on the east coast of Vancouver Island. Detached seaweeds are also believed to be an important agent in long-range dispersal of benthic macroalgae; floating *Ascophyllum* plants, for example, have been found up to 5500 km from their nearest potential point of origin (van den Hoek, 1987). Some of the most notorious invasive seaweeds, such as *Gracilaria salicornia*, propagated in recipient systems from drift specimens which had escaped sea farms (Conklin and Smith, 2005; Smith et al., 2004). *M. japonica*, however, lacks floatation structures and has not been observed drifting on the surface offshore, suggesting that it may not disperse as effectively in this manner.

Species diversity of the wrack was very low, with *M. japonica* representing 87% to 94% of identifiable macrophyte dry weight, on average, among the six study sites. Beach wrack typically reflects the macrophyte composition of near-coastal sea areas (Suursaar et al., 2014), suggesting that this non-indigenous species also dominates the neighbouring marine environment. Indeed, these proportions are consistent with observations of the subtidal composition of nearby seaweed beds (Pawluk, 2016). Removal studies have also indicated that the species richness and diversity of subtidal macrophytes increases with the continuous removal of *M. japonica* (Pawluk, 2016). Such impacts on the abundance and diversity of native primary producers is common among invasive seaweeds (Maggi et al., 2015).

The large fraction of non-indigenous seaweed within the wrack could have an array of implications for recipient beaches and their communities. Differences in physical structure, decomposition rates, and nutritional values, for example, could alter habitat provision and nutrient cycling (Rossi et al., 2011). *M. japonica* decays more slowly than *S. muticum* and *Chondracanthus exasperatus*, but faster than the native seaweeds *Fucus* spp. and *Ulva* spp. (Pawluk, 2016). While some non-indigenous seaweeds have a positive effect on the abundance of associated fauna by providing novel habitat (Wright et al., 2014), wrack colonization studies have indicated that *S. muticum* is preferred over *M. japonica* in Baynes Sound (Pawluk, 2016). Some non-indigenous species also attract associated fauna by providing a new food source, while others may cause physiological damage to native generalist herbivores (Rodil et al., 2008). A feeding study involving the green sea urchin, *Strongylocentrotus droebachiensis*, collected from Baynes Sound indicated that urchin growth (wet weight, test diameter, and gonad mass) was greater when fed a diet of *Chondracanthus* sp. compared to *M. japonica* (James, 2016). Urchins fed the non-indigenous red seaweed exclusively, however, appeared to allocate a greater proportion of their growth to gonad mass (James, 2016). More research will be required to understand the ecological role of subtidal and beach-cast *M. japonica* in Baynes Sound food webs.

2.4.2 Macrofauna communities

Macrofauna communities across all six study sites were largely dominated by dipterans and nematodes. This contrasts with other studies in which talitrid amphipods were the dominant component of wrack-associated fauna (Behbehani and Croker, 1982; Griffiths and Stenton-Dozey, 1981; Stenton-Dozey and Griffiths, 1983). Although Ince et al. (2007) also reported low amphipod abundances in wrack samples from south-western Australia, Coleoptera dominated their epifauna assemblages across both the lower and upper intertidal zones. Colder temperatures, rainfall, and the gelatinous nature of decomposing *M. japonica* may have contributed to increased water retention within the wrack sampled in our study, created an unfavourable habitat for coleopterans which prefer dry beach-cast seaweeds (Ince et al., 2007). The substantial presence of larvae at most locations indicates that the wrack provides a habitat for terrestrial invertebrate reproduction and rearing. Rotting seaweed is known to provide shelter, warmth, and a relatively constant environment allowing terrestrial invertebrates to continue breeding during harsh winters (Colombini et al., 2000; Jedrzejczak, 2002).

These wrack-associated macrofauna could provide an important food source for higher trophic levels. Both the Least Sandpiper (*Calidris minutilla*) and the Semipalmated Plover (*Charadrius semipalmatus*), which migrate along coastal Vancouver Island, feed on an array of prey including amphipods and insects (Colwell and Landrum, 1993; Yasué, 2005). Invertebrate prey densities are known to influence shorebird abundance (Colwell and Landrum, 1993), and can have consequences for feeding rates and fitness during critical stages in migration (Yasué, 2005). Furthermore, littoral amphipods, Diptera, Araneae, and Coleoptera have also been found to dominate the diets of shrew populations (*Sorex* spp.), indicating beach foraging by individuals caught as far as 60 m inland (Stewart et al., 1989). The wrack-associated macrofauna populations supported by accumulations of *M. japonica* may therefore have far reaching implications for higher trophic levels, though more work is needed to understand how these communities differ from similar beaches which lack the non-indigenous seaweed.

Site of collection, mean depth, percent cover, band biomass, and age class of the wrack combined explained 24% of the total variation in macrofauna composition according to the CAP. Of these, site was identified as the most important explanatory variable by the MRT. Differences attributed to site could reflect the influence of beach properties, such as finer scale differences in sediment size, exposure, slope, and hydrological processes (Brown and McLachlan, 1990), or anthropogenic modifications (Sobocinski, 2003). With the effects of collection site partialled out, wrack characteristics (mean depth, percent cover, biomass, and age class) explained only 8% of the total variation in macrofauna community composition. Age class and mean depth emerged as two strong environmental variables explaining the variation in macrofauna communities.

Macrofauna group richness (pseudo-F = 13.0, df = 4, $p < 0.01$) and diversity (pseudo-F = 5.4, df = 4, $p < 0.01$) also varied significantly among age classes. Likewise, both of these dependent variables differed with wrack biomass (richness: pseudo-F = 5.0, df = 1, $p < 0.05$; diversity: pseudo-F = 6.9, df = 1, $p < 0.01$). Other studies have reported differences in macrofauna communities between areas of high and low accumulations of wrack (Ince et al., 2007), as well as successional changes in macrofauna community composition with wrack decomposition (Zemke-White et al., 2005). Amphipods tend to be the primary colonisers of freshly deposited macrophytes (Colombini et al., 2000; Griffiths and Stenton-Dozey, 1981). Inglis (1989), for example, reported that talitrid amphipods, as well as adult Diptera and Coleoptera, were the first to colonise wrack, but that nematodes, mites, collembolans, and dipteran larvae dominated the invertebrate community after 18 days. These findings are largely consistent with our results, which indicated that littoral amphipods were associated with fresher wrack. Diptera and Nematoda, on the other hand, were strong indicators for wrack of age class 3 and 4 respectively. Coleoptera, Acari, larvae, Collembola, and Araneae all had maximum DLI values for age class 5, which was the highest level of decomposition sampled.

Overall, both the richness and diversity of macrofauna groups increased with the age class of the wrack (Figure 2.7). These findings are consistent with expectations that older age classes would be more heavily colonised, given their proximity to the terrestrial boundary and their relatively longer duration on the shore. While successive colonisation by dipterans and coleopterans can be very rapid, their abundances peaking after 3-6 days (Jedrzejczak, 2002), colonization in this study region appears to be slower and lasts longer (Pawluk, 2016). These differences may be attributable to decreased activity and productivity during the winter months when wrack biomass peaks in Baynes Sound.

The more heavily colonised wrack, belonging to older age classes (4-6), represented a relatively small proportion of the total biomass (e.g. < 25% at OT, SH, RVH, and RVC study sites). This is consistent with observations made by Inglis (1989) and Colombini et al. (2000) who concluded that only a small proportion of deposited material remains on the beach long enough to reach an advanced state of decomposition. Others have also noted the highly transient nature of wrack inputs (Ince et al., 2007; Kirkman and Kendrick, 1997), and have suggested that this movement may prevent the accumulation of organic matter in sediments, regardless of wrack biomass (Ince et al., 2007).

2.4.3 Effects of commercial harvesting

The collection of beach-cast seaweeds within the harvest region was limited to three locations with suitable access points (RVH, SH, and BC). During the 2014-2015 season however, 78% of the 674.5 tonnes of beach-cast seaweeds were removed from only one of these locations (RVH). Given that our monitoring began in mid-November, we essentially had one primary harvest site and 5 comparison sites, as opposed to three of each. This limited our ability to separate the effects of site, wrack characteristics and harvesting activity. Despite the concentration of harvesting efforts at RVH, however, both the quantity of wrack and the temporal trends in biomass were similar between this site and the nearby RVC comparison site. Throughout the monitoring period, this primary harvest site had consistently higher mean wrack biomass than SH, OT, and HM (Figure 2.3A), indicating that harvesting activity did not deplete wrack availability below naturally occurring quantities. The area of substrate covered by wrack was often greatest at RVH, reaching as much as 35 m^2 (± 3 SD) per meter of shoreline (Figure 2.3B). Mean wrack depth, on the other hand tended to be lower at RVH than at RVC, BC, and SH (Figure 2.3C). This suggests that harvesting activity may be spreading the wrack around, so that it covers a greater area with reduced mean depth, compared to sites of similar biomass.

Compared to other commercial beach-cast seaweed harvests, the quantity of wrack removed by Baynes Sound licence holders was relatively low. In Ireland, for example, commercial harvesters are permitted to collect hundreds to thousands of tonnes of beach-cast seaweeds daily (McLaughlin et al., 2006). On King Island Australia and Southern Australia, drift seaweed harvests are limited to 50% and 75% of total available biomass respectively (Kirkman and Kendrick, 1997; PIRSA, 2014). A concurrent study of the 2014-2015 Vancouver Island harvest by Kingzett et al. (2015) estimated that, on average, only 15% of the available wrack biomass within the harvest region was collected each week, falling well below the proportion permitted by other countries.

Given their spatial proximity, it was expected that macrofauna communities collected from RVH and RVC would be most similar if there was no effect of harvesting activity. Bray-Curtis dissimilarity, however, was lowest between SH and RVC. RVH samples clustered with those collected from BC in the MRT, and were not unique enough to form an independent cluster. Spatial proximity among sites failed to explain any of the clustering observed in both the MRT and the CAP. Whether or not harvesting activity has an influence on macrofauna community composition therefore remains unclear but effects, if any, appear to be small. Given that wrack belonging to older age classes tended to contain the most speciose and diverse macrofauna assemblages, harvesting of highly transient fresh wrack from the lower intertidal zone may have fewer consequences for wrack-dwelling macrofauna, so long as decomposing bands are still permitted to form within the supralittoral zone. Such harvesting practices align with the interests of the licence holders, who target the freshest *M. japonica* for its higher economic value (Kingzett et al., 2015).

2.4.4 Conclusions

The non-indigenous *M. japonica* made a substantial contribution to wrack inputs within the harvest region, accounting for ~90% of dried macrophyte biomass across all six study sites. These inputs could be very large, reaching as much as 853 kg of wrack per meter of shoreline. Wrack age class and depth emerged as important characteristics explaining variation in macrofauna communities. Increasing age class, in particular, was associated with an increase in macrofauna group richness and diversity, though these bands represented a relatively small proportion (< 25%) of total wrack biomass at most sites. While our ability to discern the effects of harvesting were limited by a concentration of activity at one location, the commercial removal of beach-cast *M. japonica* did not reduce wrack biomass below quantities recorded at un-harvested sites. The area of beach substrate covered by wrack was, in fact, consistently higher at the primary harvest site, though this was offset by a decrease in mean wrack depth.

Wrack inputs as large as those within the Baynes Sound harvest region have yet to be observed in neighbouring shorelines which lack *M. japonica* (personal observation) or elsewhere in British Columbia (e.g. Orr et al. 2005). Present wrack characteristics could therefore be very different from historical conditions prior to the introduction of this species, which outcompetes native marine macrophytes (Pawluk, 2016). Given the association between greater wrack biomass and increased abundances of wrack-associated invertebrates (e.g. Dugan et al. 2003), it is possible that this system now supports a larger faunal community than it did before (Crooks, 2002; Rossi et al., 2010; Wright et al., 2014). If *M. japonica* provides an unfavourable habitat or food source, however, it could have negative implications for resident fauna. The decomposition of large wrack accumulations has, for example, been associated with the smothering of macrophytes and infauna communities (den Hartog, 1994; Gamenick et al., 1996; Raffaelli, 2000). A lack of herbivory on beach-cast *M. japonica* could reduce the amount of wrack recycled in the food web (Rossi et al., 2010). Furthermore, limited or absent herbivory in the subtidal environment could contribute to this seaweed's invasive potential via enemy release (Elton 1958).

2.5 Supplementary Material

Table S2.1 Shore types for each of the six permanent transect sites characterized according to the ShoreZone Coastal Habitat Mapping Protocol (Harper and Morris, 2014).

Site name	Substrate	Sediment	Width (m)	Slope (degrees)	Shore Type
RVC	Sediment	Gravels and sand: Pebbles, cobble, boulders and >10% sand	>30	3.6	Sand and Gravel flat, wide
RVH	Sediment	Gravels and sand: Pebbles, cobble, boulders and >10% sand	>30	4.3	Sand and Gravel flat, wide
SH	Sediment	Gravels and sand: Pebbles, cobble, boulders and >10% sand	>30	2.7	Sand and Gravel flat, wide
OT	Sediment	Gravels and sand: Pebbles, cobble, boulders and >10% sand	>30	2.86	Sand and Gravel flat, wide
BC	Sediment	Gravels: Boulder, cobble and pebbles (<10% sand)	>30	3.88	Gravel flat, wide
HM	Sediment	Gravels: Boulder, cobble and pebbles (<10% sand)	>30	4.9	Gravel flat, wide

Table S2.2 Natural characteristics and anthropogenic modifications to the landward boundaries of the six permanent transect sites.

Site	Terrestrial vegetation of landward boundary	Anthropogenic modifications to landward boundary
RVC	Some grasses, no other terrestrial vegetation.	Hardened: rock wall, fences and homes lined all three transects within site.
RVH	No terrestrial vegetation.	Hardened: rock wall lined all three transects, parking lot and viewing gazebo located above first two transects, and a home located above the third.
SH	Some grass, sparse trees and shrubs on an exposed bank of sediment.	A paved road runs the length of the site along the top bank (~3 m up and ~3 m back from landward boundary).
OT	Entirely trees with a narrow foot path leading to access point.	Narrow footpath within the trees leading to site, no other modifications to landward boundary of the site, though homes line the upper banks.
BC	Terrestrial vegetation including grass and a few shrubs, transitioning into primarily trees growing up a steep ridge.	Cabin located at sea level at landward boundary of first transect, some debris at landward boundary of second transect, no visible modifications at third transect.
HM	Terrestrial vegetation including grass and a few shrubs, transitioning into primarily trees growing up a steep bank.	Home located to the left of first transect.

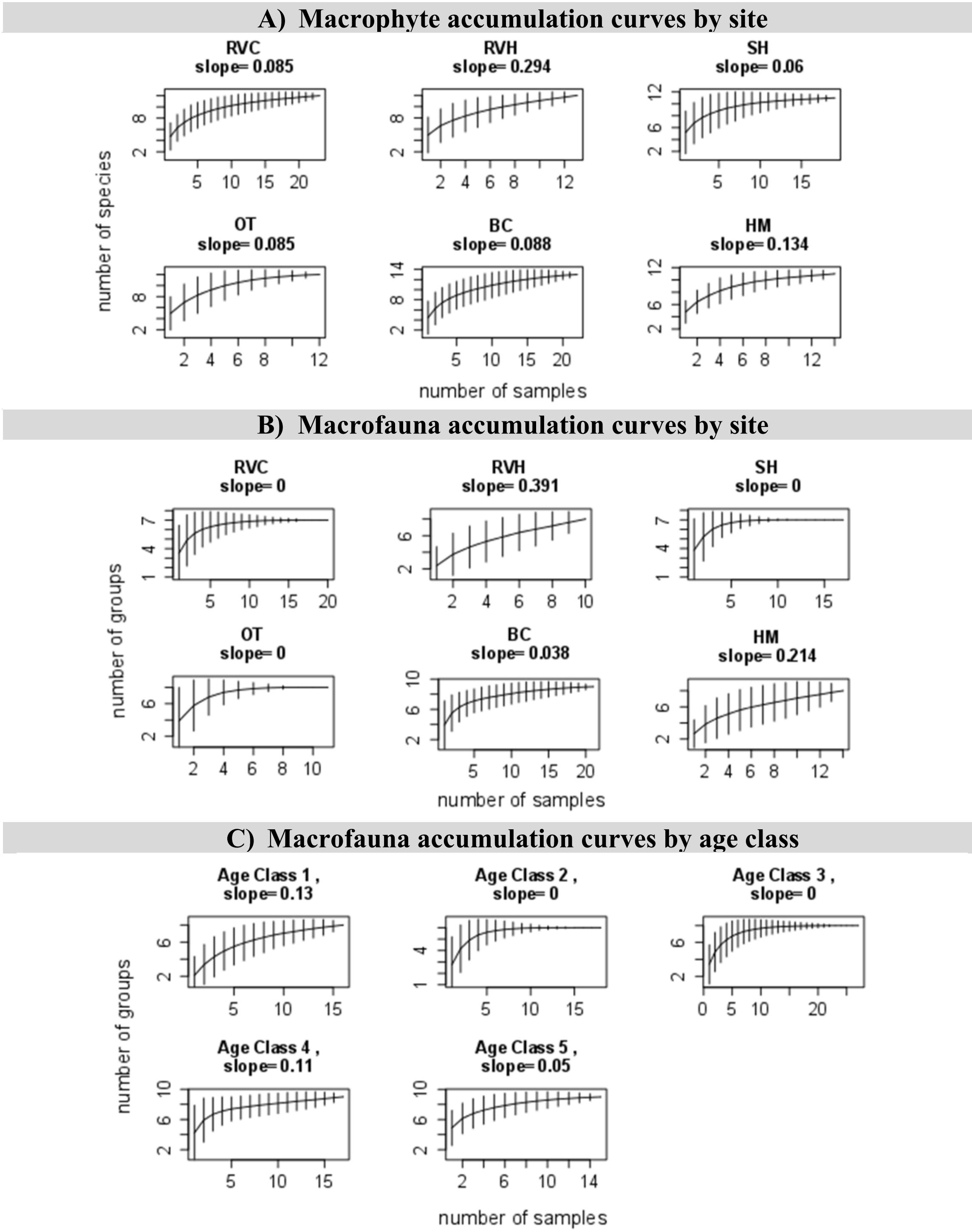


Figure S2.1 A) Macrophyte species and B) macrofauna group accumulation curves for each collection site. C) macrofauna group accumulation curves by wrack age class. Slope represents the slope between the last two points. Produced using the specaccum function from the BiodiversityR package (Kindt and Coe, 2005; method = random, number of permutations = 1000) in R (R Core Team, 2016). All accumulation curves reached an asymptote, with a slope of less than 0.5 between the last two points.

Chapter 3: Dietary contributions of non-indigenous seaweeds to subtidal and supralittoral food webs of Baynes Sound, British Columbia

3.1 Introduction

Non-indigenous species are widely recognized as a threat to native biodiversity, as well as the structure and functioning of ecosystems (Carlton and Geller, 1993; Czech and Krausman, 1997; Molnar et al., 2008; Ruiz et al., 2015). With more than 400 seaweed introductions reported world-wide (Williams and Smith, 2007), the global spread of macroalgae constitutes a substantial change to marine and coastal habitats (Grosholz, 2002; Lotze et al., 2006; Schaffelke et al., 2006). The effects of non-indigenous seaweeds on recipient biodiversity and ecosystem functioning vary among species, trophic levels, and recipient habitats (Maggi et al., 2015). Consequences of non-indigenous seaweed invasions include: a reduction in the abundance and biodiversity of native primary producers (Maggi et al., 2015), the provision of unpalatable food sources (Wright et al., 2014), and decreased fitness of native consumers (Scheibling and Anthony, 2001). When non-indigenous species provide a novel habitat or food source, however, positive effects on resident herbivores and higher trophic levels are frequently observed (Crooks, 2002; Wright et al., 2014).

The success of a non-indigenous species in a recipient habitat may be influenced by a combination of factors including: species intrinsic properties (e.g. growth rate, the ability to monopolize space, and tolerance range), propagule pressure, and the abiotic or biological (e.g. absence of predators, herbivores, parasites, or disease) characteristics of the recipient ecosystem (Britton-Simmons and Abbott, 2008; Engelen and Santos, 2009; Monteiro et al., 2009). Herbivory, for example, is understood to play an important role in seaweed community structure (Duffy and Hay, 2000). One leading hypothesis for why some macrophytes become abundant in an introduced range is the enemy release hypothesis (Engelen et al., 2011; Parker et al., 2006), whereby non-indigenous species thrive because they lack co-evolved consumers, pathogens, or other regulators in the new habitat (Elton, 1958; Keane and Crawley, 2002; Maron and Vilà, 2001; Mitchell and Power, 2003). Studies have reported that native herbivores, including sea urchins (Scheibling and Anthony, 2001; Tomas et al., 2011), fish (Gollan and Wright, 2006), and a variety of mesograzers (Engelen et al., 2011; Gollan and Wright, 2006; Wright et al., 2014), consume less biomass of non-indigenous seaweeds compared to native algae. In other cases, however, non-indigenous species can provide a new or even preferred food source for native herbivores (Parker et al., 2006). In multiple-choice feeding assays, for example, the invasive kelp *Undaria pinnatifida* was consumed by subtidal grazers at rates comparable to most native macroalgae (Jiménez et al., 2015). A preference for non-indigenous species over native macrophytes would support the biotic resistance hypothesis, which suggests that introduced species may be poorly adapted to deter native consumers, thereby limiting their invasive potential in the recipient habitat (Elton, 1958).

Non-indigenous seaweeds not only influence trophic relationships in the marine environment, but can have far-reaching implications for intertidal and terrestrial ecosystems (Rodil et al., 2008; Rossi et al., 2011, 2010). Once senesced or detached by wave action, drift seaweeds, seagrasses, and other debris, may be washed ashore, forming accumulations known as wrack (Orr et al., 2005). Wrack provides an important 'spatial subsidy' (Polis et al. 1997), or transfer of resources across habitat boundaries, from the marine environment to beaches where *in situ* productivity is often low (Brown and

McLachlan, 1990; Colombini and Chelazzi, 2003; Inglis, 1989). This allochthonous material is an important habitat and source of food for many species of intertidal and supralittoral macrofauna (Colombini and Chelazzi, 2003; Colombini et al., 2000; Dugan et al., 2003; Inglis, 1989). Furthermore, wrack decomposition by terrestrial or semi-terrestrial invertebrates, bacteria, and physical processes contributes to the release of nitrogen, carbon, and phosphorous important in local nutrient cycling (Mews et al., 2006). The macrofauna communities supported by wrack inputs are, in turn, an important food source for a variety of marine and terrestrial animals including fish (Crawley et al., 2006), shorebirds (Dugan et al., 2003), and mammals (Carlton and Hodder, 2003; Fox et al., 2015; Mellbrand et al., 2011). If non-indigenous seaweeds provide a novel food source, they may support wrack-associated populations that would otherwise be absent or reduced (Rossi et al., 2010). Alternatively, a lack of herbivory on non-indigenous beach-cast seaweeds could reduce the proportion or total amount of wrack recycled in marine and terrestrial food webs (Rossi et al., 2010).

Baynes Sound, British Columbia, is a unique system in which to study two overlapping non-indigenous seaweeds and their contribution to the diets of resident invertebrates. Likely introduced as hitchhikers along with Pacific oysters (*Crassostrea gigas*) from the East coast of Asia for aquaculture purposes, *Mazzaella japonica* and *Sargassum muticum* coexist within the southern end of the Sound (Pawluk, 2016; Saunders and Millar, 2014). The red alga, *M. japonica*, is the predominant subtidal macrophyte in this region, where it accounts for ~88% of macrophyte cover in areas where it grows and outcompetes both native primary producers and *S. muticum* (Pawluk, 2016). *M. japonica* also constitutes ~90% of wrack biomass during fall and winter months, when it washes ashore in quantities of up to 853 kg per meter of shoreline (Chapter 2). Despite its apparent success in Baynes Sound, there have been no reports of other *M. japonica* introduction events in the literature. *S. muticum*, on the other hand, is a notoriously invasive brown seaweed, with a near-global distribution (Critchley et al., 1990). Where it overlaps with *M. japonica* in Baynes Sound, *S. muticum* represents ~15% of the subtidal macrophyte cover (Pawluk, 2016) and less than 1% of average wrack biomass (Chapter 2; Pawluk, 2016). Multiple-choice feeding studies involving non-indigenous *S. muticum* and native herbivores have revealed mixed results; in some marine food webs *S. muticum* is preferred over native seaweeds (Strong et al., 2009), while in others it is not (Engelen et al., 2011; Monteiro et al., 2009). A stable isotope analysis of beach-cast *S. muticum* use by talitrid amphipods on the Galician coast indicated that it can provide an important food source, especially during the winter (Rossi et al., 2010). The incorporation of either non-indigenous macrophyte in subtidal and supralittoral food webs has yet to be assessed for Baynes Sound.

Natural stable isotope distributions provide a powerful tool for investigating the trophic significance of potential food sources, and have been used to examine the role non-indigenous seaweeds in recipient food webs (Rossi et al., 2010; Wright et al., 2014). The stable nitrogen isotope ratio ($\delta^{15}N$), for example, provides a measure of trophic level because it becomes enriched between prey and predator tissues (DeNiro and Epstein, 1981). The stable carbon isotope ratios ($\delta^{13}C$), on the other hand, exhibits little or no change with trophic level, but varies between primary producers due to differences in photosynthesis or physiological processes (DeNiro and Epstein, 1978). The goal of this study was to investigate the importance of the non-indigenous *M. japonica* and *S.*

muticum in the diets of subtidal and supralittoral invertebrates of Baynes Sound using nitrogen and carbon stable isotope ratios. Specifically, we wanted to know what proportion of resident invertebrate diets originates from each of the non-indigenous seaweeds, how this compares to the dietary contribution of native macrophytes, and finally, how characteristics of the macrophyte food sources, such as percent nitrogen content or palatability, may explain differences in their contribution to the diets of resident consumers.

3.2 Methods

3.2.1 Study system

Our study was conducted in the southern end of Baynes Sound at three sites: Deep Bay RV Park, Shoreline Drive, and Buccaneer Beach (Figure 3.1). All three locations are characterized as wide sand and gravel flats, composed of boulders, cobble, pebbles, and sand (Chapter 2; GeoBC, 2015). The subtidal environments at all three locations were primarily cobble and sand, and contained both *Mazzaella japonica* and *Sargassum muticum*. Supralittoral and subtidal samples were collected from January 8th to 10th, 2016.

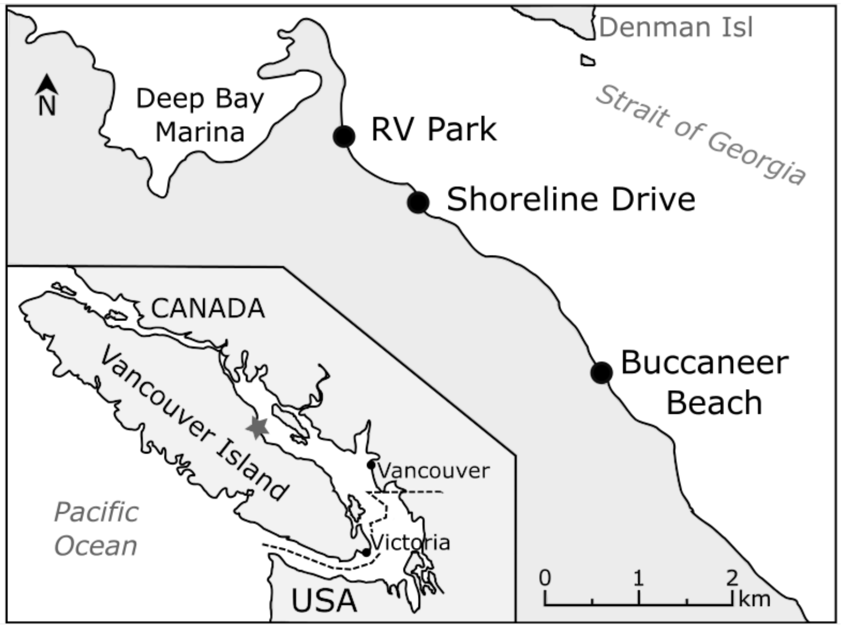


Figure 3.1 Map of the study region located at the southern end of Baynes Sound, British Columbia. Points indicate collection sites, where samples were collected from both the subtidal and supralittoral environments.

3.2.2 Subtidal sampling

Seaweeds were collected subtidally by SCUBA divers. Five species of seaweeds were chosen for this study: the two non-indigenous seaweeds *M. japonica*, and *S. muticucm*; as well as the three most abundant native species: *Chondracanthus exasperatus, Fucus* spp., and *Ulva* spp. At each of the three sites a total of five samples per species were selected haphazardly from different plants. Samples for each species were collected from the depth at which it was most abundant, but no deeper than 20 meters. *Ulva* spp. were absent from the RV Park site, therefore only four species of seaweed were collected from this location.

Subtidal invertebrates were collected opportunistically, along with the seaweeds, at the three sampling locations. Five samples for each of the following three species were collected: kelp crabs (*Pugettia producta*), subtidal snails (*Neptunea* sp.), and subtidal gammarid amphipods. Only three subtidal snails could be found at the RV Park, resulting in a smaller sample size at this site. For the kelp crab and subtidal snail, one individual constituted one sample. Due to their smaller size, a single sample of gammarid amphipods was composed of 10-20 individuals collected within close proximity.

3.2.3 Supralittoral sampling

Wrack availability was measured from three point-contact transects at each of the three study sites, following the methods outlined in Chapter 2. Transect locations were selected using a random number generator to determine their starting points along a 90 m transect tape, running parallel to the water line. This section of shoreline also delineated the area in which supralittoral invertebrates and macrophytes were collected. The three transects extended from their starting points, along the landward boundary, down to the last band of wrack within the supralittoral zone, running perpendicular to the water line. For each distinct band of wrack that came into contact with the transect we recorded its beginning and end position (length), mean depth, percent cover within a 0.5 m x 0.5 m quadrat, level of decomposition (on a scale of 1 to 6, where 1 represents the freshest wrack), and the weight of a 1 L sample, according to the methods in Chapter 2. Average wrack biomass from the three transects was used as a measure of wrack resource availability for each site.

Terrestrial macrophyte samples were collected haphazardly from the most abundant plant at the landward boundary of each site. *Zostera marina*, which was absent in the adjacent subtidal sampling sites, was collected from the wrack. Supralittoral macrofauna were collected from the same 90 m stretch of shoreline at each location using pitfall traps. Ten pitfall traps were buried, flush with the sediment, amongst accumulations of wrack at low tide. These were left out overnight and collected the following day. Multiple individuals of each macrofauna group from the same pitfall trap were pooled per sample, but specimens from the same trap were not split into multiple samples. Supralittoral amphipods were a mix of *Traskorchestia georgiana* and *T. traskiana*; both species were combined for stable isotope analysis. For the supralittoral amphipods and beetles, one replicate was composed of three to five individuals. For the smaller shore flies (family ephydridae) and beetle larvae (not identified to species), approximately five to seven individuals were combined per replicate. Collembola and nematode samples required a volume of approximately 1 mL of individuals per replicate. Due to the low abundance of adult beetles and the difficulty associated with collecting a sufficient quantity of nematodes, these consumers had fewer than three replicates within each site and were not included in subsequent statistical analyses.

3.2.4 Sample preparation

Following collection, all seaweed and invertebrate samples were frozen for transportation and storage. Samples were processed one at a time so that they were only thawed once. Macrophytes were scraped clean of epiphytes and biofilm using scalpels, and rinsed twice with deionized water. A sample of muscular foot tissue from the subtidal snail was removed, and rinsed with deionized water. Due to the small size of some kelp crab individuals, we were unable to collect a sufficient quantity of muscle tissue for analysis, thus we were required to use entire legs. One to four legs were collected from each crab, depending on its size, scraped clean of biofilm using a scalpel, and rinsed in deionized water. Marine amphipods and all wrack macrofauna were rinsed twice in deionized water before drying.

All samples were dried at 60°C for 48 hours, and ground into a fine homogeneous powder using an amalgamator. A digital Wig-L-Bug amalgamator was used for seaweed samples, while the smaller invertebrates were ground in a Retch grinder, using an Eppendorf tube adapter, to minimize sample loss. To dissolve excess carbonate from the kelp crab carapace, 10% HCl was added to the ground samples approximately 1 mL at a time, until bubbles stopped forming. Though the use of an acid wash to eliminate non-dietary carbon has been questioned due to potential effects on $\delta^{15}N$ and $\delta^{13}C$ values, acidification is generally recommended for invertebrates with calcareous structures (Schlacher & Connolly 2014). Jaschinski et al. (2008), for example, found that *in situ* acidification with 10% HCl did not significantly influence the $\delta^{15}N$ values of crustaceans and gastropods. Crab leg samples were then placed in the drying oven at 60°C for at least 48 hours, or until completely dry.

Subsamples (5-7 mg per sample of seaweed, 2-3 mg per sample of terrestrial plant, and ~1 mg per sample of each invertebrate species) were packaged in tin capsules and analyzed for total and isotope ratios of nitrogen and carbon by the University of Victoria's Water and Aquatic Sciences Research Program, using Isotope Ratio Mass Spectrometry. Natural abundances of ^{15}N and ^{13}C were expressed in parts per thousand (‰), as deviation from international standards (N_2 and Pee Dee Belemnite), calculated by $(R_{sample} / R_{standard} - 1) \times 1000$, where R is the ratio of the heavy:light isotope.

3.2.5 Statistical analysis

Overall differences in the $\delta^{13}C$ and $\delta^{15}N$ values among source species were compared independently using univariate permutation analysis of variance (PERMANOVA; Euclidean distance measure, 999 permutations). Each dependent variable was compared among the two fixed factors: site (RV Park, Shoreline Drive, and Buccaneer Beach), and species (consumers and food sources). Similarly, we tested for significant differences in percent carbon (%C), percent nitrogen (%N), and C:N ratios among the fixed factors site and species among macrophyte food sources. All PERMANOVAs were done in R (R Core Team, 2015) using the vegan package (Oksanen et al., 2015).

We used a Bayesian mixing model (MixSIAR v3.1; Moore & Semmens 2008; Stock & Semmens 2013) to estimate probability distributions for the proportional contribution of each macrophyte source to consumer diets. Subtidal and supralittoral habitat mixing models for each site were run independently. Terrestrial plant matter was included as a potential food source in supralittoral mixing models only, and consumers with fewer than three replicates per site were not included. Informative priors, which allow for the incorporation of previous knowledge (e.g. dietary contributions based on gut content analyses or feeding studies), were not specified. Like other mixing models, MixSIAR requires specification of trophic enrichment factors (TEFs), also known as consumer-diet discrimination values, to account for differences in $\delta^{13}C$ and $\delta^{15}N$ values between consumers and their food sources. These differences arise due to fractionation, resulting in the preferential incorporation of one dietary isotope over the other (DeNiro and Epstein, 1981, 1978). Researchers have reported considerable variation in TEFs (e.g. McCutchan Jr et al. 2003; Vanderklift & Ponsard 2003; Dalerum & Angerbjörn 2005). Although Bayesian mixing models such as MixSIAR incorporate uncertainty around the estimate for this parameter, model results are still sensitive to the TEFs used (Phillips et al., 2014). For the consumers in our MixSIAR models, we used fixed TEFs of -0.41 ‰

(± 1.14 SD) and +2.52 ‰ (±2.5 SD) for $\delta^{13}C$ and $\delta^{15}N$ respectively, based on the results of a meta-analysis of herbivore fractionation (Zanden and Rasmussen, 2001). We acknowledge, however, that these generalized TEFs and standard deviations have not been demonstrated for each of the individual species used in our mixing model.

3.3 Results

3.3.1 Site characteristics

The three collection sites shared similar shore type characteristics but varied in their degree of anthropogenic modification (Table 3.1). Wrack biomass within the supralittoral zone was greatest at the RV Park site, where there was an estimated 23.8 kg (± 12.0 SD, wet weight) of wrack per meter of shoreline, covering an area of 2.0 m^2 (± 0.7 SD). Buccaneer Beach had the next highest biomass (5.2 kg ± 5.0 SD), followed by Shoreline Drive (2.8 kg ± 2.8 SD). Wrack decomposition within the supralittoral zone was greatest at the Buccaneer Beach site. This site had a mean age class of 4.0 (± 0 SD) based on the six point age class scale established in Chapter 2, where age class one represented the freshest wrack, and six the oldest. Wrack at Shoreline Drive was slightly more fresh, with a mean age class of 3.3 (± 0.6 SD), followed by the RV Park site (2.7 ± 0.6 SD).

Table 3.1 Supralittoral characteristics of each collection site, including wrack biomass and the area of substrate covered per meter of shoreline. Data were recorded January 8th to 10th, 2016, concurrent with the collection of supralittoral consumers from each site. Level of wrack decomposition was assigned on a six point scale, where age class 1 represents the freshest wrack and 6 is the most decomposed.

	Site		
	RV Park	**Shoreline Drive**	**Buccaneer Beach**
Landward boundary	Cement wall ~0.5m tall, lined by houses	Some vegetation, < 5m from a road	Vegetation
Wrack cover m^2 (±1 SD)	1.96 (0.74)	0.35 (0.40)	0.66 (0.56)
Wrack biomass kg (±1 SD)	23.78 (11.98)	2.76 (2.79)	5.15 (5.01)
Wrack age class (±1 SD)	2.67 (0.58)	3.33 (0.58)	4.0 (0)

3.3.2 Food sources

The terrestrial plant $\delta^{13}C$ and $\delta^{15}N$ values were more depleted than those of the other food items at all three sites (Figure 3.2, and supplementary material Table S3.1). On average, *Z. marina* $\delta^{13}C$ values were more enriched than those of any other food source, while mean *S. muticum* and *M. japonica* $\delta^{13}C$ values were the most depleted of the seaweeds. The mean $\delta^{13}C$ values obtained from subtidal and terrestrial primary producers varied significantly among species and among sites (Table 3.2). The mean $\delta^{15}N$ values of primary producers, on the other hand, varied significantly among species only (Table 3.2).

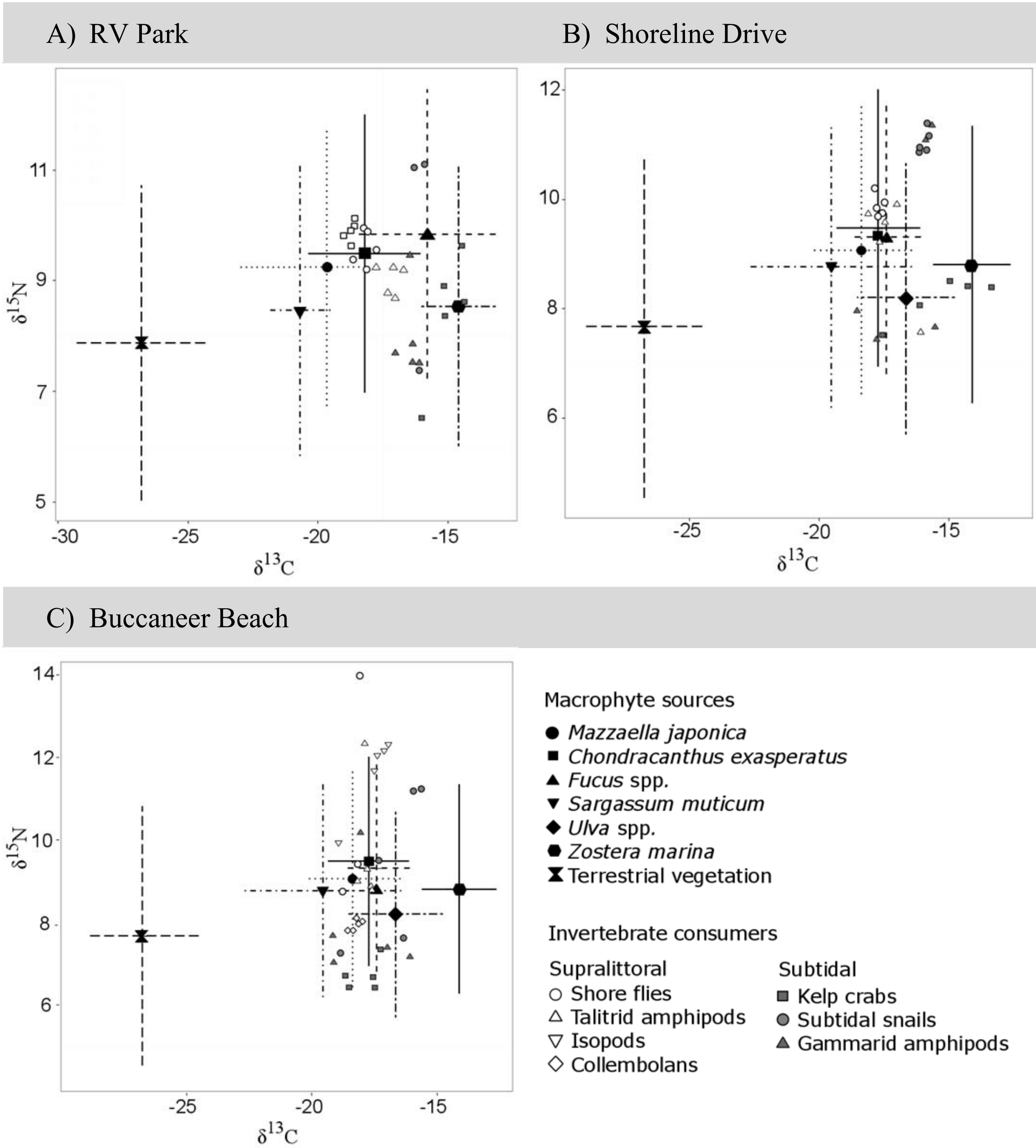


Figure 3.2 $\delta^{13}C$ and $\delta^{15}N$ values of macrophyte food sources (mean ± 1 SD), and individual subtidal and supralittoral macroinvertebrate consumers. Macrophyte values were adjusted using trophic enrichment factors from Zanden and Rasmussen (2001): corrected $\delta^{13}C = \delta^{13}C - 0.41$ ‰ (± 1.14 SD), corrected $\delta^{15}N = \delta^{15}N + 2.52$ ‰ (± 2.5 SD). Samples were collected from A) Deep Bay RV Park, B) Shoreline Drive, and C) Buccaneer Beach sites.

Table 3.2 Results of a univariate PERMANOVA (Euclidian distance, 999 permutations) testing for differences in δ^{13}C and δ^{15}N values among macrophyte food sources (Species) and sites (RV Park, Shoreline Drive and Buccaneer Beach). Df = degrees of freedom; MS = mean sum of squares; F = Pseudo-F, *p* = P-value by permutation. Bold values indicate statistical significance ($p < 0.05$).

Source of variation	**df**	**δ^{13}C**			**δ^{15}N**		
		MS	**F**	***p***	**MS**	**F**	***p***
Species (Sp)	6	264.55	74.93	**0.001**	6.32	7.42	**0.001**
Site (S)	2	18.45	5.23	**0.004**	0.79	0.93	0.377
Sp x S	11	4.99	1.41	1.68	0.48	0.56	0.849
Residuals	79	3.53					
Total	98						

Primary producers varied significantly in percent carbon, percent nitrogen, and C:N among species, but not among sites (Table 3.3 and Table 3.4). Terrestrial plant material typically had the highest mean percent carbon content (45% C) followed by *Z. marina* (43% C) across all three sites. *M. japonica* (28% C) and *C. exasperatus* (31% C), on the other hand, had the lowest mean percent carbon content. Trends in mean percent nitrogen content were less consistent among sites (Table 3.3). At the RV Park site, for example, *M. japonica* had the highest percent nitrogen (3.0% N), and *Fucus* spp. had the lowest (1.8% N), while at Shoreline Drive *C. exasperatus* had the highest mean value (3.0% N) and *S. muticum* had the lowest (1.5% N). *C. exasperatus*, *M. japonica*, and *Ulva* spp., when present, had the lowest mean C:N values of all the macrophyte sources, ranging from 9.1 to 13.4, though their relative order varied among sites (Table 3.3).

Table 3.3 Average percent carbon content (%C), percent nitrogen content (%N), and the ratio of carbon to nitrogen (C:N) (±1 SD) for potential food sources at the RV Park, Shoreline Drive, and Buccaneer Beach.

	RV Park				Shoreline Drive				Buccaneer Beach			
Source	**n**	**%C**	**%N**	**C:N**	**n**	**%C**	**%N**	**C:N**	**n**	**%C**	**%N**	**C:N**
Chondracanthus	5	32.36 (2.83)	2.75 (0.23)	11.78 (0.89)	5	31.32 (20.87)	3.02 (1.52)	11.32 (1.60)	5	28.0o (0.22)	2.60 (0.37)	10.95 (1.64)
Fucus	5	34.22 (3.68)	1.75 (0.13)	18.22 (6.07)	5	36.81 (11.01)	1.98 (0.27)	18.97 (8.88)	5	35.89 (3.45)	1.80 (0.17)	20.07 (1.67)
Mazzaella	5	27.14 (0.60)	3.0 (0.36)	9.13 (1.03)	5	30.97 (6.91)	2.56 (0.04)	13.36 (2.86)	5	27.14 (2.42)	2.38 (0.53)	11.82 (2.47)
Sargassum	5	37.85 (1.32)	1.87 (0.55)	21.73 (6.14)	5	35.74 (3.64)	1.50 (0.43)	25.54 (7.58)	5	41.21 (6.71)	2.48 (1.09)	18.09 (4.54)
Ulva	0	-	-	-	5	40.96 (6.30)	4.43 (1.06)	9.44 (1.03)	5	36.46 (5.97)	3.27 (0.93)	11.73 (2.76)
Zostera	5	43.57 (0.83)	2.58 (0.17)	16.94 (1.01)	5	42.28 (0.69)	2.29 (0.39)	18.86 (2.88)	4	41.94 (0.90)	1.92 (0.41)	22.77 (5.39)
Terrestrial	5	44.61 (0.57)	2.14 (0.40)	21.42 (4.27)	5	44.76 (0.79)	2.27 (0.92)	22.17 (8.15)	5	44.87 (1.05)	1.80 (0.43)	26.16 (6.90)

Table 3.4 Results of univariate PERMANOVAs (Euclidian distance, 999 permutations) testing for differences in percent carbon content (%C), percent nitrogen (%N) and the carbon to nitrogen ratio (C:N) among potential food sources (Species), and sites (RV Park, Shoreline Drive, and Buccaneer Beach). Df = degrees of freedom; MS = mean sum of squares; F =Pseudo-F, *p* = P-value by permutation. Bold values indicate statistical significance ($p < 0.05$).

Source of variation	df	%C			%N			C:N		
		MS	**F**	***p***	**MS**	**F**	***p***	**MS**	**F**	***p***
Species (Sp)	6	471.05	11.88	**0.001**	5.62	13.51	**0.001**	403.97	18.66	**0.001**
Site (S)	2	35.41	0.89	0.430	0.71	1.70	0.167	30.99	1.43	0.234
Sp x S	11	31.57	0.80	0.658	0.70	1.68	0.091	26.17	1.21	0.300
Residuals	79	39.67			0.42			21.65		
Total	98									

3.3.3 Consumers

The δ^{13}C and δ^{15}N values obtained from subtidal and supralittoral macrofauna showed significant differences among species and sites (Table 3.5). The three taxa of subtidal consumers were generally more enriched in δ^{13}C than invertebrates collected from the supralittoral zone at all three sites (Figure 3.2 and supplementary material, Table S3.1). These organisms also tended to be depleted in δ^{15}N relative to their terrestrial counterparts, with the exception of subtidal snails (*Neptunea* sp.). The snails consistently had the highest average δ^{15}N value of the marine invertebrates, as well as the greatest variability in this stable isotope ratio at the RV Park (9.8 ‰ ± 2.1 SD) and Buccaneer Beach (9.4 ‰ ± 2.0 SD) sites. Both δ^{13}C and δ^{15}N values for the gammarid amphipods were highly variable at all three sites (Figure 3.2). The kelp crabs were, on average, the most depleted in δ^{13}C, with the exception of crabs from Buccaneer Beach. At the RV Park site, shore flies and beetle larvae had relatively similar δ^{13}C and δ^{15}N values, while the supralittoral amphipods were more enriched in δ^{13}C, but depleted in δ^{15}N.

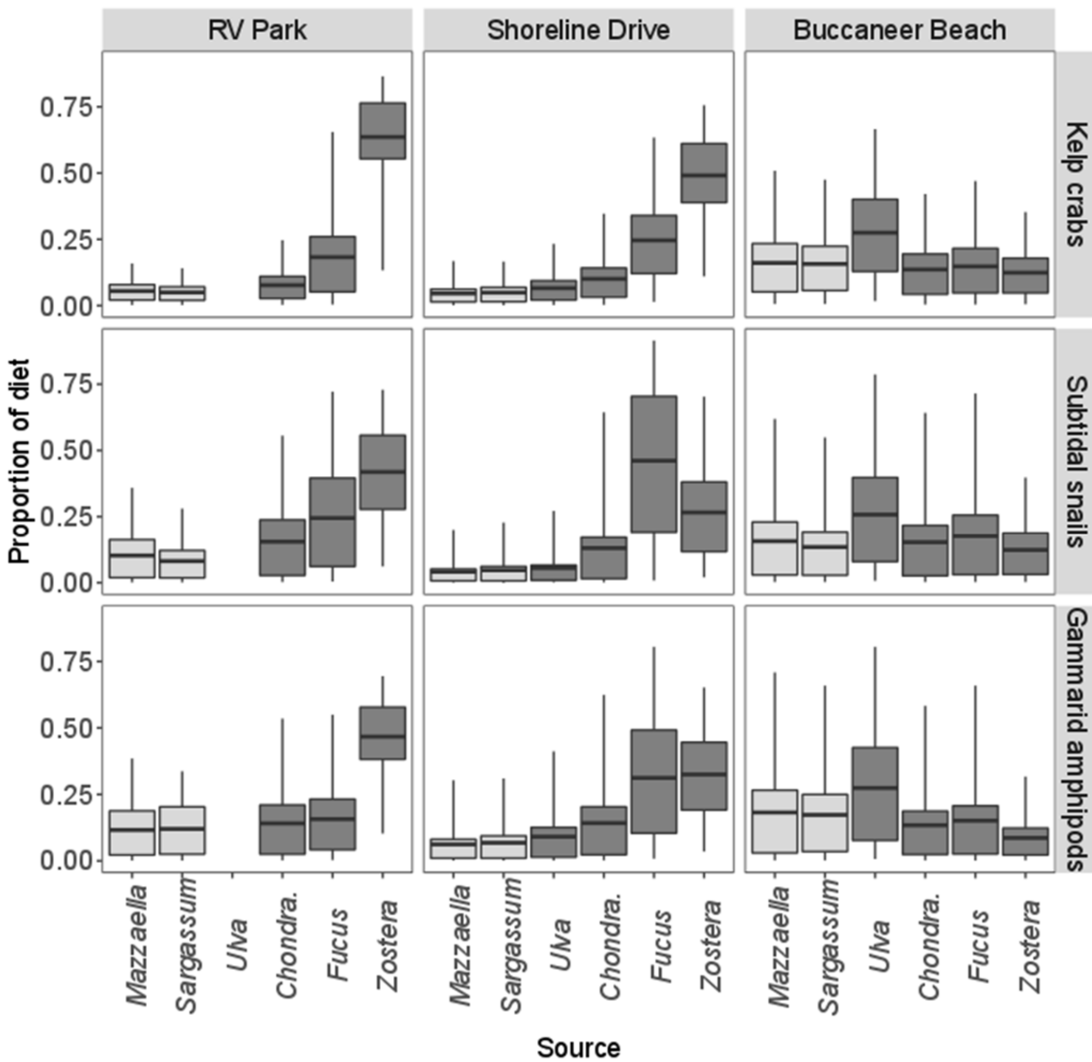
Table 3.5 Results of a univariate PERMANOVA (Euclidian distance, 999 permutations) testing for differences in $\delta^{13}C$ and $\delta^{15}N$ values among consumer species and sites (RV Park, Shoreline Drive and Buccaneer Beach). Df = degrees of freedom; MS = mean sum of squares; F = Pseudo-F, *p* = P-value by permutation. Bold values indicate statistical significance ($p < 0.05$).

Source of variation	**df**	**$\delta^{13}C$ MS**	**F**	***p***	**$\delta^{15}N$ MS**	**F**	***p***
Species (Sp)	11	6.07	9.18	**0.001**	13.15	9.63	**0.001**
Site (S)	2	11.16	16.87	**0.001**	4.27	3.13	**0.049**
Sp x S	9	1.47	2.22	**0.028**	2.19	1.60	0.126
Residuals	69	0.66			1.36		
Total	91						

3.3.4 Mixing model outputs

Statistical comparisons of the contribution made by potential food sources to consumer diets estimated by MixSIAR were performed independently for supralittoral and subtidal habitats at each of the three sites (Figure 3.3). *Z. marina* made the largest contribution in the diets of subtidal invertebrates at the RV Park (Figure 3.3A) and Shoreline Drive sites (Figure 3.3B), where it represented an estimated 27% to 64% of dietary biomass. *Fucus* spp. were also a large component of these consumers' diets, especially for gammarid amphipods (RV Park: 16%, Shoreline Drive: 31%) and subtidal snails (RV Park: 25%, Shoreline Drive: 46%). *Fucus* spp. and *C. exasperatus* tended to dominate supralittoral diets, accounting for 17% to 43% and 19% to 30% respectively. Supralittoral invertebrates also tended to consume higher proportions of *M. japonica*, which accounted for as much as 15% in the diets of shore flies from the RV Park site.

A) Subtidal Consumers



B) Supralittoral consumers

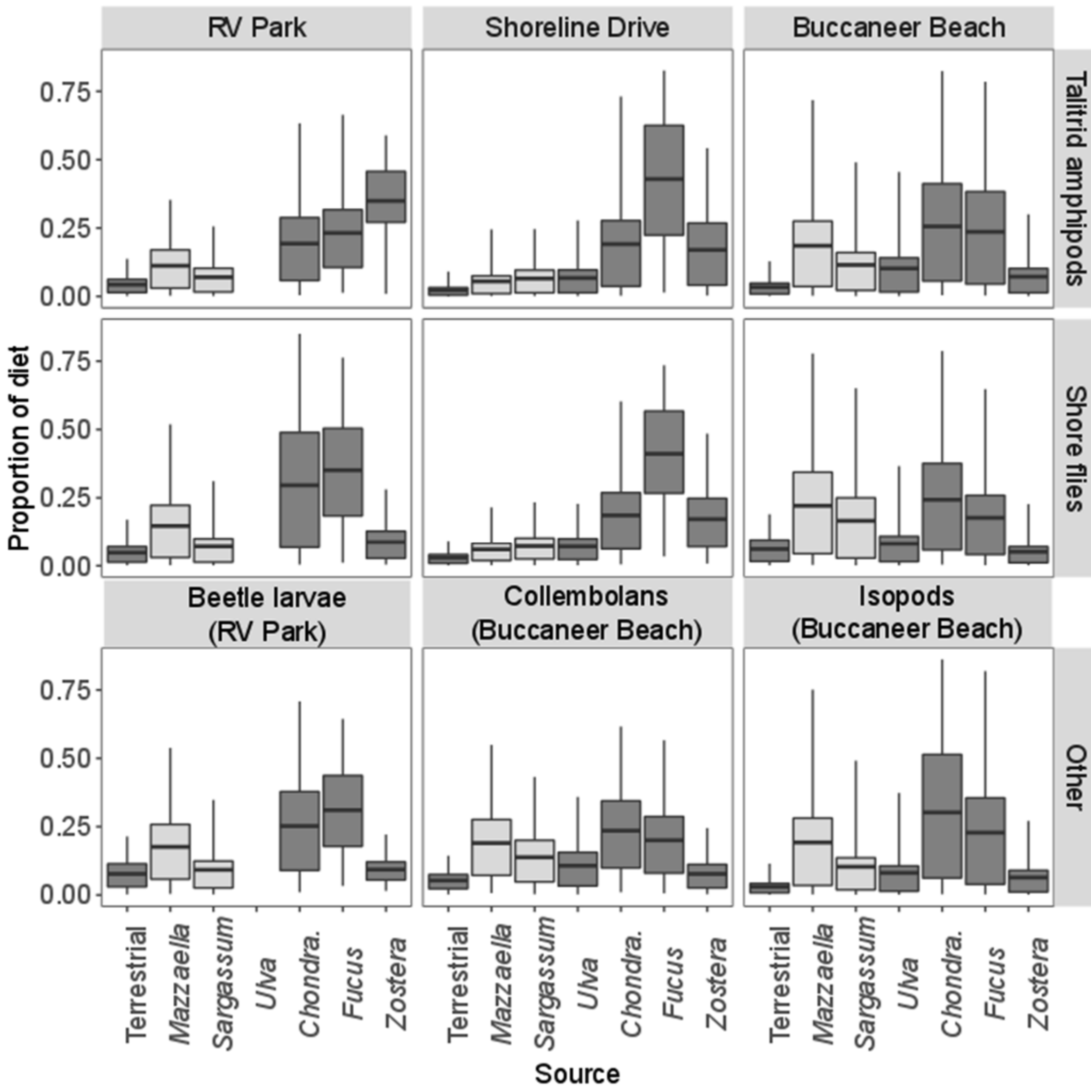


Figure 3.3 Dietary contribution made by macrophyte food sources to A) subtidal and B) supralittoral consumer diets at the Deep Bay RV Park, Shoreline Drive, and Buccaneer Beach sites, estimated by MixSIAR. Food sources include two non-indigenous seaweeds (indicated in light grey): *Mazzaella japonica* and *Sargassum muticum*, as well as the most common native macrophytes (indicated in dark grey): *Ulva* spp., *Chondracanthus exasperatus, Fucus* spp., and *Zostera marina*. Terrestrial plant samples were included in the mixing models for supralittoral species only. *Ulva* spp. were absent from the RV Park collection site. The dark bar represents the estimated mean, boxes contain the 50% credibility interval and whiskers represent the 95% credibility interval based on the posterior probability distributions (supplementary material, Table S3.2).

The dietary contributions of macrophyte species were notably different for consumers collected at Buccaneer Beach (Figure 3.3C). *Ulva* spp. made the largest dietary contribution in subtidal invertebrates (accounting for 26% to 28% of their diets), while *C. exasperatus* consistently made the greatest contribution to supralittoral invertebrate diets (accounting for 24% to 26% of their diets). Consumers from both environments also consumed higher proportions of *M. japonica* and *S. muticum* at the Buccaneer Beach site compared to the other two locations, but very little *Z. marina* (5% to 12%).

Correlation among macrophyte species was low in all mixing models, with the exception of *Z. marina* and *Fucus* spp. There were strong negative correlation values (ranging from -0.63 to -0.93), for these species in the subtidal and supralittoral mixing models for the RV Park and Shoreline Drive sites, indicating difficulty distinguishing the contributions of these two macrophyte sources.

3.4 Discussion

Overall, native macrophytes, especially *Zostera marina* and *Fucus* spp., made the greatest contributions to the diets of consumers in both the subtidal and supralittoral environments. The invasive brown alga *Sargassum muticum* accounted for no more than 17% of estimated invertebrate diets, while the non-indigenous *Mazzaella japonica* accounted for no more than 22%, despite representing ~ 88% of the subtidal cover and 90% of wrack biomass within this region of Baynes Sound. Such a low dietary contribution may suggest that a reprieve from herbivory (enemy release) contributed to this species' success in the subtidal environment, where it outcompetes native macrophytes (Pawluk, 2016). Reduced consumption relative to native species within the supralittoral zone could decrease the amount of macrophyte biomass recycled in the food web, have consequences for nutrient cycling, and increase propagule pressure in adjacent regions resulting from drift seaweeds.

3.4.1 Dietary contribution of non-indigenous seaweeds

The non-indigenous *M. japonica* and invasive brown seaweed *S. muticum* contributed a relatively small proportion to the diets of supralittoral invertebrates (≤ 18% and ≤ 9% respectively) and subtidal consumers (≤ 12% for both), at the RV Park (Figure 3.3A) and Shoreline Drive sites (Figure 3.3B). These proportions were slightly higher at the Buccaneer Beach site (Figure 3.3C), where *M. japonica* and *S. muticum* accounted for as much as 22% and 17% of supralittoral and subtidal diets respectively. The low dietary contribution of *M. japonica* is surprising given its abundance; accounting for ~90% of identifiable wrack material (Chapter 2) and ~88% of subtidal cover in areas of high density (Pawluk, 2016). Such findings are consistent, however, with feeding studies on *Traskorchestia* spp. amphipods from Baynes Sound, which found that they avoid consuming this red alga (Pawluk, 2016). While no other *M. japonica* introductions have been reported in the literature, native herbivores are known to avoid feeding on various non-indigenous red seaweeds within introduced ranges (Vermeij et al., 2009; Wright et al., 2014). Low feeding preference for the more widely studied *S. muticum* has been reported for numerous herbivorous species across its near-global introduced distribution (Engelen et al., 2011; Monteiro et al., 2009; White, 2010). Others, however, have reported indiscriminate feeding on *S. muticum* and native seaweeds alike (Britton-Simmons et al., 2011; Cacabelos et al., 2010). Rossi et al. (2010) found that *S. muticum* was one of the main food sources for the semi-terrestrial amphipod *Talitrus saltator*, especially during the fall and winter when the availability of native macrophytes decreased. Feeding choice studies in Baynes Sound have also indicated that semi-terrestrial amphipods (*Traskorchestia* spp.) prefer *S. muticum* over native seaweeds (Pawluk, 2016).

Herbivory plays an important role in seaweed community structure (Duffy and Hay, 2000), and small marine herbivores are a large component of these assemblages (Gollan and Wright, 2006). The small dietary contribution of *M. japonica* and *S. muticum* could therefore indicate a reprieve from this regulatory pressure, which may have contributed to their successful colonization (Elton, 1958; Keane and Crawley, 2002; Maron and Vilà, 2001). Given that the two seaweeds represent similar proportions of consumer diets, other intrinsic properties may be responsible for the notable disparity in their relative abundance. Differences in reproductive strategies, growth rates, tolerance ranges, and ability to monopolize space (Nyberg and Wallentinus, 2005; Schaffelke et al., 2006; Valentine et al., 2008), for example, could have contributed to *M. japonica's* greater success in this region. Within the intertidal and supralittoral environment, low consumption of *M. japonica* and *S. muticum* could increase propagule pressure in surrounding areas, as a large biomass of beach-cast seaweeds remains available for transportation via longshore drift (Chapter 2). Furthermore, low herbivory on *M. japonica* could have consequences for the flux of allochthonous organic matter in beach food webs due to its abundance.

3.4.2 Dietary contribution of native macrophytes

Among subtidal and supralittoral consumers from all three sites, native macrophytes made the largest contribution to estimated dietary biomass (Figure 3.3).

Native seaweeds are often consumed in greater quantities than non-indigenous species (Gollan and Wright, 2006; Wright et al., 2014), consistent with the enemy release hypothesis which states that herbivores should prefer species with which they have co-evolved (Elton, 1958; Keane and Crawley, 2002; Maron and Vilà, 2001).

Subtidal consumers tended to favour the native seagrass *Z. marina* and brown alga *Fucus* spp. at the RV Park (Figure 3.3A) and Shoreline Drive sites (Figure 3.3B). Kelp crab (*Pugettia producta*) diets, on average, were primarily composed of *Z. marina* (50% to 64%) and *Fucus* spp. (18% to 25%), with no other macrophytes contributing more than 10%. *Z. marina* is widely recognized as an important food source in estuarine systems (Kharlamenko et al., 2001; McConnaughey and McRoy, 1979), and *Fucus* spp. has also been reported as a preferred food source for various marine gastropods and arthropods in British Columbia (White, 2010). Subtidal snails (*Neptunea* sp.) and subtidal gammarid amphipods also consumed more *Z. marina* and *Fucus* spp. than other macrophytes at these sites, but their diets included a higher proportion of *Chondracanthus exasperatus* (13% to 15%) than kelp crabs. At the Buccaneer Beach site (Figure 3.3C), on the other hand, *Ulva* spp. accounted for the greatest proportion of subtidal consumer diets (26% to 28% among species), while the estimated contributions of other macrophytes ranged from 9% to 18%.

The diets of supralittoral consumers appeared to be more generalist than those of the marine species, especially at the RV Park (Figure 3.3A) and Buccaneer Beach sites (Figure 3.3C). *Fucus* spp. frequently made the greatest dietary contribution, though considerable proportions of *C. exasperatus* (> 25%) were recorded in the diets of beetle larvae, shore flies (ephydridae), terrestrial isopods, and semi-terrestrial talitrid amphipods

(*Traskorchestia* spp.). These differences could reflect the mixed nature of wrack, where invertebrates may be in closer proximity to multiple food sources simultaneously. Terrestrial plant material contributed very little to supralittoral invertebrate diets (≤ 5%), regardless of differences in wrack availability between sites. These results indicate that marine macrophytes provide a substantial food source for supralittoral invertebrates. A positive association between semi-terrestrial and terrestrial arthropod abundance and wrack biomass is well documented within the literature (Colombini and Chelazzi, 2003; Dugan et al., 2003; Ince et al., 2007). Our findings further contribute to evidence that wrack is not only an important habitat, but also a substantial trophic component in the marine-terrestrial ecotone (Adin and Riera, 2003; Rossi et al., 2010).

3.4.3 Characteristics of the macrophyte sources

The relative abundance of macrophyte food sources, based on previous studies (Chapter 2, Pawluk, 2016), couldn't explain their dietary contributions to both the subtidal and supralittoral environments. While *M. japonica* is the most abundant macrophyte in both environments, this non-indigenous seaweed contributed no more than 22% to supralittoral invertebrate diets on average, and less than 18% to subtidal consumer diets at all three sites. *Z. marina* and *Fucus* spp. often emerged as the predominant macrophytes in invertebrate diets. *Z. marina* was present but scarce in the wrack (< 1%, Chapter 2), and rare within the subtidal regions sampled (Pawluk, 2016). Correlation values were high for *Z. marina* and *Fucus* spp. at the RV Park and Shoreline Drive sites (-0.63 to -0.93), indicating that the mixing models had difficulty distinguishing between them. *Z. marina*'s contribution to some invertebrate diets could therefore actually belong to, at least in part, the relatively more abundant *Fucus* spp., or vice versa.

Brown seaweeds are often preferred by consumers over other macroalgae and seagrasses, regardless of relative abundance (Adin and Riera, 2003; Duffy and Hay, 2000; Pennings et al., 2000). Various species belonging to the genus *Fucus*, specifically, have been reported as the preferred food source of invertebrates in both the supralittoral and subtidal environments (Adin and Riera, 2003; White, 2010). This is surprising given their production of polyphenolic compounds, which are known to deter herbivores (Geiselman and McConnell, 1981; Paul et al., 2001; Steinberg, 1988). Some herbivores, however, may preferentially feed on chemically defended seaweeds to decrease their own risk of predation (Duffy and Hay, 1994; Hay et al., 1987). Associations with chemically defended seaweeds has been found to reduce predation by omnivorous fishes on amphipods (Duffy and Hay, 1994) and crabs (Hay et al., 1990). The benefit of this association would be greatest for mesograzers that develop a tolerance for the plant's chemical defenses and are not required to leave to forage (Duffy and Hay, 1994).

Nutritional preferences can also influence the feeding choices of consumers. The generalist herbivorous snail, *Littorina sitkana,* for example, preferentially consumes two species of nitrogen-rich ulvoid green algae despite their high concentrations of defense compounds (Van Alstyne et al., 2009). These findings are well supported in the literature, with numerous reports of preferential feeding on more palatable (low C:N) and nutritious (high nitrogen content) food sources (Barile et al., 2004; Cruz-Rivera and Hay, 2009; Quadros et al., 2014). Contrary to this hypothesis, however, the seaweeds with the lowest C:N values in our study (*M. japonica*, *Ulva* spp., and *C. exasperatus*) did not comprise the majority of any species' diet at the RV Park or Shoreline Drive sites. At the Buccaneer Beach site, on the other hand, these macrophytes often made a similar or greater contribution to consumer diets, compared to the less palatable *Fucus* spp. and *Z. marina.* Percent nitrogen content also failed to explain the dietary contributions of macrophytes for most consumers. *Ulva* spp., for example, consistently had the highest mean percent nitrogen, followed by *C. exasperatus* and *M. japonica*. *Ulva* spp., however, made relatively small dietary contributions (< 10%) for all consumers, with the exception of subtidal invertebrates from the Buccaneer Beach site.

Decomposition can increase the palatability of primary producers and reduce concentrations of anti-herbivory compounds (Agnew and Moore, 1986; Pennings et al., 2000). Indeed, wrack-associated macrofauna often prefer decomposing specimens over fresh macroalgae of the same species (Pennings et al., 2000). *S. muticum* and *C. exasperatus* undergo faster decay and decomposition than *M .japonica*, *Ulva* spp., and *Fucus* spp. (Pawluk, 2016). This may explain, at least in part, the larger contribution of *C. exasperatus* in supralittoral diets compared to those of subtidal invertebrates, though *S. muticum* accounted for a similar proportion of consumer diets in both environments. Diets could also differ between the supralittoral and subtidal environments due to features of the consumers, such as differences in their feeding apparatus or gut characteristics (Targett et al., 1995).

3.4.4 Sources of error

There are numerous sources of variation in the natural abundances of $\delta^{13}C$ and $\delta^{15}N$ in marine macrophytes. Within the same plant, for instance, isotope ratios may differ between tissue types or ontogenetic stages (Cronin and Hay, 1996). Consumers often feed selectively on specific parts of a plant (e.g. Vergés et al. 2007), which can have consequences for the conclusions of stable isotope studies if a different tissue, or an aggregate, is sampled. Natural abundances of $\delta^{13}C$ and $\delta^{15}N$ within a macrophyte can also vary due to environmental variables such as temperature, light exposure, wave exposure, and grazing intensity, which may give rise to significant differences in isotope ratios among sites (Dethier et al., 2013; Wiencke and Fischer, 1990). The movement of consumers among locations can therefore lead to discrepancies between their isotopic ratios and those of the food sources at their location of collection. The mixing of seaweeds originating from different sites could also yield greater variation in $\delta^{13}C$ and $\delta^{15}N$ values for beach-cast seaweeds within the wrack than was captured with our study design, as we only sampled the seaweeds subtidally. Furthermore, the $\delta^{13}C$ and $\delta^{15}N$ values of macrophytes can change during the processes of decay and decomposition, though previous studies have found these differences to be very small (Crawley et al., 2007; Stephenson et al., 1986; Zieman et al., 1984).

Epiphytes, microbial communities, and particulate organic matter are other potential food sources which were not accounted for in this study. Epiphytes of *Z. marina*, for example, are known to be preferred by consumers over the marine macrophyte itself (Kitting et al., 1984). Beach-cast seaweeds are also colonised by bacteria and fungi that may themselves be more digestible and nutritious, adding another fractionation step to the food chain (Agnew and Moore, 1986). Some of the consumer groups in this study, such as the gammarid amphipods, could include detritivores and/or scavengers that may be opportunistically consuming mixed material originating from multiple primary producers or other animals. This could explain the variation in $\delta^{13}C$ and $\delta^{15}N$ values, which was especially high for kelp crabs and gammarid amphipods.

In the mixing model we first assumed fixed isotopic trophic enrichment factors (TEF) of -0.41 ‰ (± 1.14 SD) and +2.52 ‰ (±2.50 SD) for $\delta^{13}C$ and $\delta^{15}N$ respectively, based on a meta-analysis of herbivore fractionation (Zanden and Rasmussen, 2001). The differences in $\delta^{13}C$ and $\delta^{15}N$ between consumers and their diets, however, are known to vary considerably among taxa, environments, tissue types, and food sources, as well as with the consumer's diet quality, size and age (Caut et al., 2009; Crawley et al., 2007; France and Peters, 1997; Vanderklift and Ponsard, 2003). By allowing for the specification of variance in TEF values, Bayesian mixing models incorporate this uncertainty in their estimates of source proportions, but are still sensitive to TEF selection (Phillips et al., 2014).

To test the robustness of our conclusions we re-ran the mixing models with another set of TEFs from the literature. A meta-analysis investigating differences in TEFs of carbon ($\Delta^{13}C$) and nitrogen ($\Delta^{15}N$) stable isotopes among taxonomic groups, environments, and tissue types determined that the $\delta^{13}C$ and $\delta^{15}N$ values of the food source were the only significant factors influencing TEFs (Δ) in invertebrates (Caut et al., 2009). Based on Caut et al.'s relationship between food source stable isotope ratios and trophic enrichment factors ($\Delta^{13}C = -0.113\ \delta^{13}C - 1.916$; $\Delta^{15}N = -0.311\delta^{15}N + 4.065$), we calculated unique TEFs for the primary producers at each site (supplementary material, Table S3.3). The results of these mixing models also indicated that native macrophytes, especially *Fucus* spp. and *Z. marina*, made a greater contribution to the diets of resident invertebrates than the non-indigenous *M. japonica* and *S. muticum*, with the exception of some consumers from the Buccaneer Beach site (supplementary material, Table S3.4). Because these alternative mixing models had slightly higher DIC values on average (supplementary material, Table S3.5), we retained the original results based on TEF values from Zanden and Rasmussen (2001). Although our conclusions were consistent across both sets of trophic enrichment factors, they would benefit from *ad hoc* experiments to identify TEFs for each combination of consumer species and food source.

3.4.5 Conclusions

Overall, *Z. marina* and *Fucus* spp. constitute the greatest contributions to both subtidal and supralittoral invertebrate diets within the southern end of Baynes Sound, despite their relatively low palatability, nitrogen content, and abundance. Compared to subtidal consumers, the diets of supralittoral invertebrates tended to include greater proportions of multiple macrophyte species, which could be due to the mixed nature of wrack, changes in macrophyte characteristics during decomposition, or differences in consumer preferences and traits. The non-indigenous red alga *M. japonica* and invasive brown alga *S. muticum* contributed less than native macrophytes to the estimated diets of resident consumers, representing no more than 22% and 17% of their diets respectively. Given that *M. japonica* is considerably more abundant than any other macrophyte within this region, these results suggest that it may experience a reprieve from herbivory, consistent with the enemy release hypothesis (Elton, 1958). Lack of herbivory by resident consumers may not only contribute to its successful proliferation in the subtidal environment, but could have implications for food webs and nutrient cycling within the marine-terrestrial ecotone (Rossi, 2006; Rossi et al., 2010). These non-indigenous seaweeds may be acting as nutrient sinks rather than a source. Furthermore, large accumulations of *M. japonica* which go uneaten could increase the propagule pressure from drift seaweeds in surrounding regions, thus furthering the spread of this species. This research supports previous studies which have indicated that marine macrophytes provide an important food source for terrestrial invertebrates (Bessa et al., 2014; Ince et al., 2007), and contributes to very limited literature on the trophic significance of beach-cast non-indigenous seaweeds within the supralittoral environment.

3.5 Supplementary material

Table S3.1 Average $\delta^{13}C$ and $\delta^{15}N$ values in ‰ (±SD) of consumers and food sources at RV Park, Shoreline Drive, and Buccaneer Beach sites. n represents sample size.

	RV Park			Shoreline Drive			Buccaneer Beach		
Sources	**n**	**$\delta^{13}C$**	**$\delta^{15}N$**	**n**	**$\delta^{13}C$**	**$\delta^{15}N$**	**n**	**$\delta^{13}C$**	**$\delta^{15}N$**
Chondracanthus	5	-17.81 (1.83)	6.97 (0.29)	5	-17.84 (2.17)	6.58 (0.98)	5	-17.32 (1.14)	6.96 (0.46)
Fucus	5	-15.39 (2.39)	7.32 (0.77)	5	-15.94 (1.04)	7.22 (0.42)	5	-17.01 (0.72)	6.79 (0.19)
Mazzaella	5	-19.24 (0.92)	6.73 (0.23)	5	-21.59 (4.11)	5.46 (1.45)	5	-17.96 (1.55)	6.54 (0.84)
Sargassum	5	-20.28 (0.20)	5.94 (0.82)	5	-20.17 (0.82)	5.90 (1.05)	5	-19.14 (2.90)	6.25 (0.64)
Ulva	0	-	-	5	-18.89 (1.45)	5.57 (0.37)	5	-16.24 (1.5)	5.68 (0.23)
Zostera	5	-14.20 (0.89)	6.02 (0.40)	5	-13.92 (0.94)	6.29 (0.62)	4	-13.70 (0.97)	6.29 (0.47)
Terrestrial	5	-26.39 (2.21)	5.35 (1.37)	5	-29.28 (2.88)	5.02 (1.81)	5	-26.34 (1.93)	5.16 (1.90)
Subtidal consumers									
Gammarid amphipods	5	-16.48 (0.33)	8.02 (0.82)	5	-16.70 (1.38)	9.11 (1.94)	5	-17.88 (1.35)	7.90 (1.30)
Subtidal snail	3	-16.11 (0.20)	9.84 (2.13)	5	-15.98 (0.16)	11.06 (0.21)	5	-16.90 (1.34)	9.36 (1.89)
Kelp crabs	5	-15.06 (0.64)	8.41 (1.16)	5	-15.27 (1.64)	8.18 (0.39)	5	-17.91 (0.64)	6.71 (0.37)
Supralittoral consumers									
Talitrid amphipods	5	-17.20 (0.40)	9.03 (0.28)	5	-17.26 (0.77)	9.21 (0.95)	5	-17.81 (0.24)	9.67 (1.50)
Shore flies	5	-18.17 (0.32)	9.6 (0.32)	5	-17.70 (0.13)	9.89 (0.20)	3	-18.35 (0.37)	10.71 (2.86)
Beetles - larvae	5	-18.75 (0.16)	9.9 (0.19)	0	-	-	0	-	-
Beetles - adults	0	-	-	1	-17.93 (na)	12.81 (na)	2	-17.69 (1.48)	10.28 (2.38)
Isopods	0	-	-	0	-	-	5	-17.59 (0.79)	11.63 (0.97)
Collembola	0	-	-	0	-	-	5	-18.28 (0.20)	7.94 (0.13)
Nematodes	0	-	-	1	-19.26 (na)	9.99 (na)	0	-	-

Table S3.2 Estimated mean proportion of diet attributed to each macrophyte food source for invertebrate consumers by MixSIAR mixing models, with standard deviation (SD) and quantiles based on the posterior probability distribution. Potential food sources included two non-indigenous seaweeds: *Mazzaella japonica* and *Sargassum muticum*, and native macrophytes: *Ulva* spp., *Chondracanthus exasperatus, Fucus* spp., and *Zostera marina*. Terrestrial plant samples were included in mixing models for supralittoral species only. Collection sites included: A) Deep Bay RV Park, B) Shoreline Drive and C) Buccaneer Beach.

A) Deep Bay RV Park

				Quantiles						
Consumer	**Source**	**Mean**	**SD**	**2.5**	**5**	**25**	**50**	**75**	**95**	**97.5**
Kelp crab	*Chondra.*	0.077	0.066	0.003	0.005	0.027	0.061	0.11	0.203	0.247
	Fucus	0.183	0.173	0.004	0.01	0.052	0.126	0.26	0.563	0.655
	Mazzaella	0.055	0.043	0.002	0.004	0.021	0.045	0.079	0.138	0.159
	Sargassum	0.05	0.038	0.002	0.004	0.02	0.041	0.071	0.123	0.141
	Zostera	0.636	0.185	0.133	0.221	0.554	0.689	0.764	0.843	0.865
Subtidal amphipod	*Chondra.*	0.141	0.153	0.002	0.003	0.025	0.081	0.21	0.459	0.535
	Fucus	0.157	0.151	0.003	0.007	0.042	0.108	0.232	0.471	0.55
	Mazzaella	0.116	0.113	0.001	0.003	0.022	0.076	0.188	0.343	0.385
	Sargassum	0.12	0.103	0.001	0.003	0.025	0.095	0.203	0.308	0.337
	Zostera	0.467	0.152	0.103	0.162	0.382	0.491	0.578	0.669	0.695
Subtidal snail	*Chondra.*	0.154	0.16	0.002	0.004	0.027	0.096	0.238	0.484	0.556
	Fucus	0.245	0.21	0.004	0.008	0.061	0.188	0.396	0.647	0.722
	Mazzaella	0.102	0.103	0.001	0.003	0.019	0.064	0.162	0.318	0.359
	Sargassum	0.081	0.081	0.001	0.003	0.018	0.051	0.121	0.251	0.281
	Zostera	0.419	0.184	0.061	0.093	0.278	0.439	0.557	0.69	0.729
Beetle larvae	*Chondra.*	0.252	0.193	0.01	0.019	0.09	0.21	0.378	0.629	0.708
	Fucus	0.31	0.168	0.033	0.052	0.178	0.296	0.437	0.601	0.644
	Mazzaella	0.176	0.146	0.004	0.01	0.058	0.137	0.258	0.469	0.538
	Sargassum	0.092	0.093	0.002	0.004	0.026	0.064	0.124	0.286	0.348
	Terrestrial	0.077	0.058	0.002	0.005	0.03	0.067	0.114	0.184	0.214
	Zostera	0.093	0.053	0.015	0.023	0.055	0.083	0.121	0.193	0.221
Shore flies	*Chondra.*	0.296	0.256	0.004	0.009	0.068	0.227	0.489	0.779	0.85
	Fucus	0.351	0.207	0.011	0.028	0.184	0.345	0.504	0.707	0.763
	Mazzaella	0.147	0.147	0.002	0.004	0.03	0.095	0.223	0.458	0.519
	Sargassum	0.071	0.085	0.001	0.002	0.013	0.038	0.1	0.253	0.311
	Terrestrial	0.048	0.047	0.001	0.002	0.013	0.033	0.07	0.146	0.17
	Zostera	0.087	0.077	0.004	0.007	0.027	0.061	0.128	0.241	0.281
Talitrid amphipods	*Chondra.*	0.193	0.173	0.004	0.009	0.058	0.14	0.288	0.548	0.633
	Fucus	0.232	0.167	0.013	0.027	0.106	0.199	0.317	0.571	0.664
	Mazzaella	0.112	0.1	0.002	0.005	0.03	0.085	0.17	0.309	0.353
	Sargassum	0.07	0.071	0.001	0.002	0.016	0.046	0.103	0.221	0.256
	Terrestrial	0.043	0.038	0.001	0.003	0.014	0.033	0.062	0.12	0.137
	Zostera	0.349	0.151	0.009	0.027	0.271	0.378	0.457	0.55	0.589

B) Shoreline Drive

Consumer	Source	Mean	SD	Quantiles 2.5	5	25	50	75	95	97.5
Kelp crab	*Chondra.*	0.101	0.097	0.003	0.006	0.032	0.073	0.142	0.291	0.347
	Fucus	0.246	0.165	0.014	0.025	0.121	0.214	0.34	0.566	0.634
	Mazzaella	0.046	0.049	0.001	0.003	0.014	0.032	0.062	0.136	0.168
	Sargassum	0.049	0.045	0.001	0.003	0.015	0.036	0.069	0.139	0.166
	Ulva	0.066	0.062	0.002	0.004	0.021	0.048	0.094	0.189	0.233
	Zostera	0.491	0.165	0.11	0.175	0.389	0.512	0.611	0.728	0.756
Gammarid amphipods	*Chondra.*	0.142	0.165	0.002	0.003	0.023	0.077	0.203	0.496	0.624
	Fucus	0.312	0.236	0.008	0.017	0.104	0.266	0.492	0.743	0.805
	Mazzaella	0.062	0.084	0.001	0.002	0.01	0.029	0.081	0.234	0.303
	Sargassum	0.068	0.083	0.001	0.001	0.01	0.033	0.094	0.251	0.31
	Ulva	0.091	0.112	0.001	0.002	0.014	0.046	0.126	0.326	0.412
	Zostera	0.325	0.17	0.035	0.058	0.191	0.321	0.446	0.61	0.652
Subtidal snail	*Chondra.*	0.13	0.173	0.001	0.002	0.015	0.054	0.171	0.527	0.644
	Fucus	0.461	0.286	0.008	0.017	0.191	0.496	0.704	0.883	0.915
	Mazzaella	0.041	0.061	0.001	0.001	0.007	0.019	0.051	0.152	0.2
	Sargassum	0.047	0.062	0	0.001	0.007	0.023	0.061	0.182	0.228
	Ulva	0.055	0.077	0.001	0.002	0.009	0.028	0.066	0.208	0.272
	Zostera	0.266	0.187	0.02	0.034	0.117	0.227	0.381	0.633	0.703
Shore flies	*Chondra.*	0.186	0.16	0.005	0.011	0.062	0.142	0.269	0.522	0.603
	Fucus	0.411	0.196	0.034	0.063	0.267	0.427	0.567	0.704	0.735
	Mazzaella	0.06	0.06	0.002	0.003	0.019	0.043	0.082	0.171	0.215
	Sargassum	0.072	0.063	0.002	0.004	0.025	0.057	0.102	0.192	0.234
	Terrestrial	0.029	0.025	0.001	0.002	0.009	0.022	0.041	0.077	0.091
	Ulva	0.071	0.063	0.002	0.004	0.023	0.052	0.1	0.195	0.228
	Zostera	0.172	0.128	0.008	0.016	0.07	0.146	0.248	0.422	0.485
Talitrid amphipods	*Chondra.*	0.191	0.202	0.002	0.006	0.037	0.116	0.277	0.635	0.731
	Fucus	0.429	0.241	0.014	0.033	0.224	0.457	0.625	0.783	0.826
	Mazzaella	0.055	0.069	0.001	0.001	0.01	0.031	0.075	0.188	0.245
	Sargassum	0.065	0.068	0.001	0.002	0.013	0.04	0.096	0.208	0.246
	Terrestrial	0.023	0.025	0	0.001	0.005	0.014	0.032	0.075	0.091
	Ulva	0.067	0.076	0.001	0.002	0.013	0.038	0.097	0.228	0.278
	Zostera	0.17	0.155	0.003	0.006	0.041	0.12	0.268	0.478	0.542

C) Buccaneer Beach

Consumer	Source	Mean	SD	Quantiles 2.5	5	25	50	75	95	97.5
Kelp crab	*Chondra.*	0.136	0.117	0.004	0.009	0.043	0.105	0.195	0.369	0.421
	Fucus	0.148	0.128	0.004	0.008	0.048	0.115	0.216	0.406	0.47
	Mazzaella	0.161	0.137	0.006	0.01	0.052	0.123	0.234	0.434	0.509
	Sargassum	0.157	0.128	0.006	0.011	0.057	0.125	0.224	0.409	0.475
	Ulva	0.275	0.179	0.017	0.032	0.129	0.248	0.401	0.601	0.666
	Zostera	0.124	0.095	0.005	0.01	0.048	0.103	0.179	0.311	0.353
Gammarid amphipods	*Chondra.*	0.134	0.156	0.002	0.003	0.024	0.075	0.187	0.478	0.583
	Fucus	0.151	0.178	0.001	0.003	0.026	0.08	0.207	0.547	0.659
	Mazzaella	0.182	0.197	0.002	0.004	0.03	0.108	0.266	0.624	0.709
	Sargassum	0.173	0.181	0.002	0.005	0.035	0.11	0.25	0.564	0.659
	Ulva	0.274	0.231	0.007	0.013	0.077	0.209	0.426	0.733	0.805
	Zostera	0.086	0.087	0.002	0.004	0.022	0.057	0.123	0.268	0.317
Subtidal snail	*Chondra.*	0.152	0.175	0.002	0.003	0.026	0.082	0.217	0.539	0.642
	Fucus	0.176	0.196	0.002	0.004	0.03	0.1	0.256	0.615	0.715
	Mazzaella	0.156	0.169	0.002	0.005	0.029	0.095	0.23	0.522	0.619
	Sargassum	0.134	0.147	0.002	0.005	0.028	0.08	0.192	0.444	0.549
	Ulva	0.258	0.218	0.007	0.012	0.079	0.196	0.398	0.691	0.787
	Zostera	0.123	0.113	0.002	0.004	0.031	0.088	0.188	0.35	0.398
Shore flies	*Chondra.*	0.243	0.226	0.004	0.009	0.058	0.171	0.376	0.715	0.787
	Fucus	0.177	0.178	0.002	0.005	0.041	0.114	0.259	0.562	0.648
	Mazzaella	0.221	0.222	0.003	0.006	0.044	0.14	0.344	0.699	0.778
	Sargassum	0.166	0.181	0.001	0.003	0.028	0.095	0.25	0.543	0.651
	Terrestrial	0.061	0.054	0.001	0.002	0.016	0.046	0.095	0.165	0.19
	Ulva	0.081	0.098	0.001	0.002	0.015	0.045	0.109	0.271	0.366
	Zostera	0.051	0.062	0.001	0.002	0.011	0.029	0.07	0.178	0.227
Talitrid amphipods	*Chondra.*	0.256	0.239	0.004	0.007	0.056	0.178	0.412	0.755	0.824
	Fucus	0.236	0.231	0.003	0.006	0.045	0.152	0.383	0.705	0.785
	Mazzaella	0.185	0.196	0.002	0.005	0.036	0.113	0.275	0.609	0.718
	Sargassum	0.115	0.135	0.001	0.003	0.022	0.064	0.16	0.408	0.49
	Terrestrial	0.034	0.035	0.001	0.001	0.009	0.022	0.048	0.11	0.128
	Ulva	0.102	0.124	0.001	0.002	0.016	0.052	0.141	0.37	0.455
	Zostera	0.072	0.082	0.001	0.002	0.013	0.04	0.102	0.244	0.3
Collembola	*Chondra.*	0.235	0.167	0.01	0.02	0.099	0.207	0.344	0.549	0.616
	Fucus	0.2	0.152	0.006	0.014	0.08	0.165	0.287	0.505	0.566
	Mazzaella	0.19	0.149	0.007	0.013	0.072	0.154	0.276	0.494	0.549
	Sargassum	0.138	0.116	0.003	0.008	0.048	0.107	0.2	0.372	0.432
	Terrestrial	0.053	0.038	0.002	0.005	0.023	0.046	0.075	0.126	0.144
	Ulva	0.107	0.096	0.002	0.006	0.033	0.081	0.156	0.307	0.359
	Zostera	0.077	0.067	0.003	0.005	0.026	0.059	0.112	0.208	0.245
Isopods	*Chondra.*	0.302	0.267	0.003	0.007	0.062	0.217	0.514	0.815	0.862
	Fucus	0.228	0.235	0.002	0.005	0.039	0.138	0.355	0.725	0.819
	Mazzaella	0.192	0.21	0.002	0.004	0.035	0.108	0.281	0.658	0.751
	Sargassum	0.103	0.129	0.001	0.003	0.019	0.054	0.136	0.375	0.491

Terrestrial	0.03	0.033	0.001	0.002	0.008	0.019	0.042	0.097	0.115
Ulva	0.081	0.103	0.001	0.002	0.014	0.042	0.106	0.299	0.373
Zostera	0.064	0.075	0.001	0.002	0.011	0.036	0.09	0.224	0.271

Table S3.3 Trophic enrichment factors for each primary producer at the three collection sites, calculated using the relationship between food source stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) and trophic enrichment factors ($\Delta^{13}C$ and $\Delta^{15}N$) for invertebrates from Caut et al. (2009): $\Delta^{13}C = -0.113\ \delta^{13}C - 1.916$; $\Delta^{15}N = -0.311\delta^{15}N + 4.065$.

	Site					
	RV Park		**Shoreline Drive**		**Buccaneer Beach**	
Species	**$\Delta^{13}C$**	**$\Delta^{15}N$**	**$\Delta^{13}C$**	**$\Delta^{15}N$**	**$\Delta^{13}C$**	**$\Delta^{15}N$**
Chondracanthus	0.096	1.898	0.099	2.018	0.042	1.902
Fucus	-0.176	1.787	-0.114	1.818	0.007	1.953
Mazzaella	0.259	1.973	0.524	2.366	0.113	2.030
Sargassum	0.375	2.216	0.363	2.229	0.247	2.121
Terrestrial	1.066	2.400	1.392	2.502	1.060	2.461
Ulva	NA	NA	0.219	2.334	-0.080	2.297
Zostera	-0.312	2.194	-0.343	2.108	-0.368	2.110

Table S3.4 Estimated mean proportion, and standard deviation (SD), of diet attributed to each macrophyte food source for invertebrate consumers by MixSIAR mixing models, using the trophic enrichment factors from Table S3.2. Potential food sources included two non-indigenous seaweeds: *Mazzaella japonica* and *Sargassum muticum*, and native macrophytes: *Ulva* spp., *Chondracanthus exasperatus, Fucus* spp., and *Zostera marina*. Terrestrial plant samples were included in mixing models for supralittoral species only. Collection sites included: Deep Bay RV Park, Shoreline Drive and Buccaneer Beach. Bold values represent the macrophyte source with the highest estimated proportion for a given consumer from a given site.

		Site					
		RV Park		**Shoreline Drive**		**Buccaneer Beach**	
Consumer	**Source**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Kelp crab	*Chondra.*	0.107	0.09	0.056	0.169	0.166	0.138
	Fucus	0.265	0.206	0.105	0.25	0.173	0.142
	Mazzaella	0.068	0.055	0.024	0.096	**0.198**	**0.152**
	Sargassum	0.056	0.044	0.018	0.049	0.194	0.143
	Ulva	na	na	0.026	0.074	0.178	0.144
	Zostera	**0.503**	**0.221**	**0.772**	**0.299**	0.091	0.077
Gammarid amphipods	*Chondra.*	0.191	0.196	0.292	0.411	0.163	0.18
	Fucus	0.211	0.174	**0.549**	**0.44**	0.172	0.191
	Mazzaella	0.144	0.142	0.032	0.119	0.223	0.217
	Sargassum	0.122	0.115	0.025	0.074	**0.224**	**0.207**
	Ulva	na	na	0.056	0.173	0.155	0.169
	Zostera	**0.331**	**0.163**	0.047	0.124	0.063	0.067
Subtidal snail	*Chondra.*	0.204	0.201	0.341	0.444	0.193	0.204
	Fucus	0.285	0.214	**0.577**	**0.452**	**0.207**	**0.214**
	Mazzaella	0.124	0.127	0.024	0.111	0.192	0.192
	Sargassum	0.091	0.095	0.019	0.074	0.167	0.166
	Ulva	na	na	0.017	0.083	0.158	0.171
	Zostera	**0.297**	**0.179**	0.022	0.083	0.082	0.09
Shore flies	*Chondra.*	0.133	0.128	**0.235**	**0.198**	0.206	0.16
	Fucus	**0.459**	**0.172**	0.35	0.205	0.157	0.127
	Mazzaella	0.107	0.108	0.079	0.086	**0.222**	**0.166**
	Sargassum	0.091	0.114	0.081	0.073	0.175	0.139
	Terrestrial	0.15	0.087	0.034	0.029	0.083	0.052
	Ulva	na	na	0.069	0.066	0.092	0.086
	Zostera	0.059	0.048	0.151	0.125	0.065	0.061

Talitrid amphipods	*Chondra.*	0.136	0.174	0.255	0.254	0.192	0.196
	Fucus	**0.544**	**0.212**	**0.384**	**0.256**	0.134	0.145
	Mazzaella	0.095	0.123	0.066	0.092	**0.247**	**0.236**
	Sargassum	0.075	0.107	0.072	0.08	0.213	0.214
	Terrestrial	0.105	0.08	0.026	0.028	0.097	0.074
	Ulva	na	na	0.063	0.077	0.072	0.091
	Zostera	0.046	0.055	0.135	0.143	0.045	0.056
Beetle larvae	*Chondra.*	0.172	0.205	na	na	na	na
	Fucus	**0.47**	**0.215**	na	na	na	na
	Mazzaella	0.083	0.092	na	na	na	na
	Sargassum	0.061	0.072	na	na	na	na
	Terrestrial	0.059	0.047	na	na	na	na
	Ulva	na	na	na	na	na	na
	Zostera	0.155	0.152	na	na	na	na
Collembola	*Chondra.*	na	na	na	na	0.231	0.228
	Fucus	na	na	na	na	0.17	0.186
	Mazzaella	na	na	na	na	**0.237**	**0.229**
	Sargassum	na	na	na	na	0.159	0.168
	Terrestrial	na	na	na	na	0.055	0.048
	Ulva	na	na	na	na	0.089	0.113
	Zostera	na	na	na	na	0.059	0.074
Isopods	*Chondra.*	na	na	na	na	**0.248**	**0.246**
	Fucus	na	na	na	na	0.169	0.191
	Mazzaella	na	na	na	na	0.25	0.245
	Sargassum	na	na	na	na	0.149	0.166
	Terrestrial	na	na	na	na	0.053	0.049
	Ulva	na	na	na	na	0.075	0.099
	Zostera	na	na	na	na	0.056	0.073

Table S3.5 DIC values from MixSIAR mixing models using A) trophic enrichment factors for herbivore fractionation from Zanden and Rasmussen (2001): $\Delta^{13}C$ = –0.41 ‰ ± 1.14 SD and $\Delta^{15}N$ = +2.52 ‰ ±2.5 SD) and B) trophic enrichment factors calculated based on the relationship between food source stable isotope values and invertebrate fractionation from Caut et al. (2009): $\Delta^{13}C = -0.113\ \delta^{13}C - 1.916$; $\Delta^{15}N = -0.311\delta^{15}N + 4.065$ (Table S3.2).

		Source of trophic enrichment factors	
Site	**Environment**	**A) Zanden and Rasmussen (2001)**	**B) Caut et al. (2009)**
RV Park	Subtidal	77.89	75.84
	Supralittoral	51.13	79.64
Shoreline	Subtidal	117.24	112.67
Drive	Supralittoral	45.05	52.89
Buccaneer	Subtidal	111.59	108.59
Beach	Supralittoral	109.22	114.17

Chapter 4: Conclusions

Baynes Sound provides a unique system in which to study the ecological role of a non-indigenous red alga, *Mazzaella japonica*, and the effects of its removal by a commercial beach-cast harvest. As the number of seaweed introductions continues to rise worldwide, the collection of non-indigenous species for aesthetic or commercial purposes has become increasingly common (Andreakis and Schaffelke, 2012; Pickering et al., 2007). Commercial harvests of detached seaweeds, however, are poorly characterized in the literature and can be contentious given their well-documented ecological role as wrack (Kirkman and Kendrick, 1997; Zemke-White et al., 2005). The objective of this thesis was to study the contribution of *M. japonica* to beach wrack subsidies in terms of biomass, distribution, and food provision, as well as potential effects of harvesting activity. Chapter 2 provided the first record of trends in wrack biomass, distribution, and species composition for this harvest region throughout the duration of the licensed season. Harvested and un-harvested locations were compared to evaluate the effects of commercial removal on both wrack characteristics and macrofauna communities, which were minimal. Finally, in Chapter 3, this non-indigenous seaweed was found to make a small contribution ($\leq$ 22%) to the diets of subtidal and supralittoral invertebrate consumers despite its abundance. Combined, these findings can help inform decisions regarding the management of *M. japonica* as a non-indigenous and commercially harvested species.

3.6 Ecological considerations of *Mazzaella japonica*'s introduction

Accounting for approximately 90% of wrack biomass (Chapter 2), and 88% of subtidal macrophyte cover (Pawluk, 2016), the successful proliferation of *M. japonica* in Baynes Sound likely has significant ecological implications. With no historical records of wrack characteristics, subtidal macrophyte cover, or invertebrate communities for this region, it is difficult to evaluate what these effects are; however, comparisons with nearby coastlines, the results of removal experiments, and the effects of other seaweed introductions in the literature provide some insight.

Wrack accumulations at the southern extremity of Baynes Sound were unprecedentedly large compared to surrounding areas beyond *M. japonica*'s introduced range (personal observation), and reports from elsewhere in British Columbia (e.g. Orr et al. 2005). During peak biomass (November through December), for example, we recorded as much as 853 kg of wrack per meter of shoreline. This substantial biomass of beach-cast seaweeds could support macrofauna communities that would otherwise be absent or reduced (Rossi et al., 2010). Greater macrofauna abundance and biodiversity are often positively correlated with increasing wrack biomass (Dugan et al., 2003; Stenton-Dozey and Griffiths, 1983). This, in turn, could benefit higher trophic levels such as shorebirds (Bradley and Bradley, 1993; Dugan et al., 2003), fish (Crawley et al., 2006), and mammals (Carlton and Hodder, 2003). Large accumulations of detached seaweeds, however, can also have deleterious ecological effects (Smetacek and Zingone, 2013; Ye et al., 2011). Macroalgal mats and wrack deposits have been associated with the smothering of seagrass beds (den Hartog, 1994), the mortality of cultured animals (Ye et al., 2011), the creation of anoxic conditions (Gamenick et al., 1996), and deleterious impacts on sediment-dwelling fauna (Raffaelli, 2000).

Differences in physical structure, decomposition rates, and nutrient values between *M. japonica* and displaced subtidal species could alter habitat and food provision within the intertidal and supralittoral zones (Rossi et al., 2011). *M. japonica* contributed less than 22%, on average, to the diets of supralittoral consumers (Chapter 3). These findings suggest that native macrophytes provide a more substantial food source than this non-indigenous seaweed, despite its abundance in the supralittoral environment. Low consumption of *M. japonica* could reduce the proportion of detrital material recycled in the food web. Furthermore, the biomass of remaining beach-cast *M. japonica* could have consequences for the flux of allochthonous organic matter, and increase propagule pressure in surrounding areas (Rossi et al., 2011).

The relatively small contribution of *M. japonica* (< 17%) in the diets of subtidal consumers (Chapter 3) may have contributed to this species' success in Baynes Sound. Herbivory plays an important role in the structuring of seaweed communities (Duffy and Hay, 2000), and a lack of such regulatory pressure can contribute to the proliferation of a non-indigenous species (Elton, 1958). Given that *M. japonica* displaces native primary producers (Pawluk, 2016), its propagation also reduces the availability of potentially preferred food sources for invertebrate consumers in both the subtidal and supralittoral environments.

Whether the ecological effects of *M. japonica*'s introduction are viewed as positive or negative also depends on how they are valued by local stakeholders. If the services provided by a non-indigenous seaweed, such as habitat heterogeneity or food provision, for example, are greater than those provided by the 'natural' state, changes to ecosystem services may be considered positive. Though *M. japonica* supplies a large biomass of wrack within the supralittoral zone (Chapter 2), this does not appear to provide a preferred habitat (Pawluk, 2016), nor a substantial food source (Chapter 3). While much more research is required to understand what the ecological effects of *M. japonica*'s introduction are, the perceived nature of these impacts will be contingent on management goals and social considerations.

3.7 Implications for harvest management

The effects of commercial beach-cast harvesting observed in this study differed substantially from those of beach grooming for aesthetic purposes, which is often used as a proxy in the literature (Kirkman and Kendrick, 1997) and in discussions of harvest management (e.g. Birtwell et al. 2013; Brusse 2013). Grooming, for example, involves the complete removal of all wrack using mechanized vehicles, rakes, and/or sieves (Defeo et al., 2009; Dugan et al., 2003), all of which are practices commonly prohibited by the licensing conditions of beach-cast harvests (BC Ministry of Agriculture, 2014; PIRSA, 2014). While groomed beaches have significantly reduced wrack biomass compared to un-groomed beaches (Dugan and Hubbard, 2010; Dugan et al., 2003), the primary harvest site in Chapter 2 maintained similar or greater accumulations of wrack compared to un-harvested sites. Grooming has also been associated with negative impacts on macrofauna abundance, species richness, and diversity (Dugan and Hubbard, 2010; Dugan et al., 2003; Ince et al., 2007). Though we were limited in our ability to isolate the effects of harvesting on macrofauna communities due to a concentration of effort at one site, we failed to detect such an impact. Based on these findings, we recommend that future research and management decisions refrain from using beach grooming studies as a proxy for commercial harvesting.

If managers wish to maintain the collection of *M. japonica* as a continued, sustainable harvest, current harvesting intensity appears consistent with these goals for the intertidal and supralittoral zones, though effects on subtidal productivity have not yet been studied. Current levels of beach-cast harvesting in the southern end of Baynes Sound yielded little difference in mean biomass between harvested and un-harvested locations, nor was there a detectable impact on macrofauna communities (Chapter 2). Furthermore, native primary producers made a greater contribution to the diets of invertebrate consumers compared to the non-indigenous red alga targeted by harvesting (Chapter 3). Our findings, however, have led us to make two recommendations which could minimize potential effects within the marine-terrestrial ecotone:

1) *Minimize interactions with decomposing wrack in the supralittoral zone:* Older bands of wrack, located in the supralittoral zone, contained the most speciose and diverse assemblages of macrofauna (Chapter 2). This decomposing wrack represented a small proportion of the total biomass during the late fall and early winter, when harvesting was most intense. Ensuring that decomposing bands are permitted to form, and limiting their disturbance by harvesting activity could help minimize potential effects on these communities. Such goals align well with the interests of the licence holders, who target the freshest *M. japonica* for its higher economic value (Kingzett et al., 2015).
2) *Minimize bycatch of native macrophytes*: Mixing models comparing the $\delta^{13}C$ and $\delta^{15}N$ values of macrophyte sources and invertebrate consumers estimated that *M.*

japonica contributed no more than 22 % to the diets of supralittoral macrofauna (Chapter 3), despite accounting for ~ 90% of dried wrack biomass (Chapter 2). Semi-terrestrial amphipods, shore flies, and other consumers tended to prefer the native *Fucus* spp. and *Chondracanthus exasperatus*. Given that native primary producers appear to be a more important food source for intertidal and supralittoral macrofauna, we recommend that *M. japonica* harvesting practices should minimize the bycatch (accidental collection) of these macrophytes. This is also in the best interest of licence holders, who would benefit economically from maximizing the purity of their product.

Rather than managing *M. japonica* as a continued, sustainable harvest, this non-indigenous species could be managed as an invasive seaweed. Increased harvesting of beach-cast *M. japonica* could help reduce propagule pressure in the surrounding areas. In Australia and New Zealand, for example, beach-cast harvesting of the invasive *Undaria pinnatifida* is used as a management tool to limit its dispersal (Kirkman and Kendrick, 1997; Ministry of Agriculture and Forestry, 2010). Given the biomass of wrack within this region, however, the complete removal of beach-cast *M. japonica* may not be a viable option. Large-scale removal of beach-cast seaweeds could also have negative impacts on wrack-associated macrofauna (Chapter 2), which feed on the small fraction of native macrophytes (Chapter 3). An increase in harvesting activity on the beach could also contribute to tension with other beach users. A subtidal hand-harvest of *M. japonica* may circumvent such issues (Pawluk, 2016). The long-lasting holdfast from which this species re-grows suggests that fronds could be cut sustainably (Pawluk, 2016; Vásquez et al., 2012), while mitigating the release of propagules to un-invaded environments and reducing the bycatch of native seaweeds. Complete eradication of *M. japonica* from the subtidal environment is unlikely, but would allow for an increase the biodiversity of native primary producers (Pawluk, 2016). This, in turn, would likely benefit herbivorous invertebrates, who consume higher proportions of native macrophytes than *M. japonica* (Chapter 3). Such an endeavor would require a thorough collection of plant fragments and the removal of holdfasts (Pawluk, 2016). This would be an expensive, and potentially ineffectual venture, that may not result in any ecological advantage (Anderson, 2007; Bergstrom et al., 2009; Myers et al., 2000).

Another option available to managers is the cessation of *M. japonica* harvesting. If native macrophyte biodiversity is not necessary or valued, managers may wish to maintain this flourishing seaweed population and the large quantity of wrack that it provides for adjacent beaches. More research is required, however, to determine if a subtidal environment dominated by *M. japonica* is functionally equivalent to an ecosystem with high native biodiversity. There also remain unexplored consequences of the large wrack biomass in this region, such as the potential formation of anoxic conditions (Gamenick et al., 1996; Rodil et al., 2008), sulphide poisoning of macrofauna (Gamenick et al., 1996), smothering of other vegetation (den Hartog 1994), and interactions with forage fish spawning. While ecological and economic considerations are essential, coastal management strategies must also consider societal values and stakeholder perceptions (Weinstein et al., 2007).

3.8 Social considerations

The management of coastal resources involves multiple stakeholders, especially near developed properties (Weinstein et al., 2007). In communities adjacent to Baynes Sound, the beach-cast harvesting of *M. japonica* has been a source of concern for community members, where critics of the harvest have called for a moratorium (Birtwell et al., 2013). A great deal of negative media coverage accompanied the opening of the 2014-2015 season, and protest gardens were erected at all three access points in an attempt to block harvesting equipment from the beach.

Other seaweed harvests have been met with similar controversy. On the east coast of North America, for example, live harvesting of the native alga *Ascophyllum nodosum* was opposed by residents, fishery stakeholders, and other community members in New Brunswick, Nova Scotia, and Maine (Marshall, 1999). Similarly, the harvesting of kelp for aquaculture feed in Monterey Bay, California, led to use conflicts between harvesters and recreational users in the area (King and DeVogelaere, 2000). Where wrack accumulations interfere with water use activities, decrease aesthetic appeal, or create an odor nuisance, on the other hand, removal may be perceived positively (Smetacek and Zingone, 2013). Accumulations of *M. japonica* in Baynes Sound, however, are greatest during the winter, and largely dissipate from the region by the time recreational beach use increases in the spring and summer.

Many of the community concerns in Baynes Sound pertain to the ecological effects of wrack removal (Birtwell et al., 2013), some of which we were able to examine in Chapters 2 and 3. Future research, and its dissemination to the public, may help to address these concerns and improve relationships between industry stakeholders and community members. Uncertainty about the ecological effects of shellfish aquaculture in Baynes Sound, for example, has contributed to a sense of distrust among community stakeholders who would otherwise like to support the local industry (D'Anna and Murray, 2015). A well-attended presentation on the ecology of *M. japonica* and its harvest in Baynes Sound was held in August 2015, including results from studies by Kingzett et al. (2015), Pawluk (2016), and Chapter 2 of this thesis. Though the timing could be coincidental, negative media coverage decreased in the following harvest season, the protest gardens were removed, and the harvesters reported that interactions with community members had become increasingly positive. Continuing such efforts to communicate current scientific knowledge will be important in addressing the social considerations of *M. japonica* management.

3.9 Future research

Much remains to be understood about the ecology of *M. japonica* in Baynes Sound. Creating a map of its current subtidal distribution should be completed to facilitate long-term monitoring and establish whether the population is expanding, remaining constant, or shrinking. Elucidating the abiotic and biotic factors that make the southern end of Baynes Sound such a suitable habitat for *M. japonica* would further contribute to our understanding of its invasive potential. Understanding what makes this region particularly susceptible to the proliferation of *M. japonica* could also help identify other areas of elevated risk. Though the life history characteristics of seaweeds alone are generally poor predictors of invasiveness (Valentine et al., 2008), understanding these properties can help inform the management of a non-indigenous species (Anderson, 2007; Wotton et al., 2004). Important traits, which have yet to be studied in *M. japonica*, include temperature and pH range, life span, growth rate, dispersal distance, number of reproductive episodes, and the ability to propagate vegetatively (Anderson, 2007; Valentine et al., 2008).

M. japonica's ecology within the intertidal and supralittoral zones also warrants further research. Where the decomposition of large accumulations leads to the creation of anoxic conditions, it could have negative impacts on infauna communities (Gamenick et al., 1996; Rodil et al., 2008), and littoral vegetation (den Hartog, 1994). Though fresh wrack was highly transient, we observed the formation of anoxic pockets where seaweeds became buried in the sediment (personal observation). Beaches within the licensed harvest region also provide important spawning habitat for Pacific Sand Lance (*Ammodytes hexapterus*), and Surf Smelt (*Hypomesus pretiosus*), which lay their eggs within the upper intertidal zone during the fall and winter (de Graaf, 2015). These forage fish are small, low-trophic level, schooling species that provide an important food source for piscivorous animals, including other fishes, marine mammals, and seabirds (Brodeur, 1990; Robards et al., 1999; Therriault et al., 2009). Nothing is known, however, about how this unusually large biomass of wrack affects their ability to access suitable spawning substrate, or the survival of buried embryos.

The ultimate fate of beach-cast *M. japonica* in Baynes Sound is yet another unexplored part of this seaweed's ecology. Only a small proportion of wrack decomposed on beaches within the harvest region, yet the biomass of beach-cast seaweeds declined rapidly from January through March, likely swept from the beach by longshore drift (Chapter 2). While detached specimens of *M. japonica* have been recovered from prawn traps set in the deepest portions of Baynes Sound (Kingzett et al., 2015), it is unclear where the majority of re-suspended drift seaweeds settle and how far they may travel. Though drift seaweeds make a significant contribution to offshore productivity in oligotrophic waters (Kirkman and Kendrick, 1997), this may not be the case in nutrient-rich regions (Koop and Griffiths, 1982), such as the Strait of Georgia. Determining if detached seaweeds contribute to the productivity of live *M. japonica* populations will also have important management implications for the harvesting of this non-indigenous species.

One of the main concerns associated with commercial beach-cast harvests is the disturbance caused by harvesting activity (Kirkman and Kendrick, 1997). While *M. japonica* harvesting practices are largely consistent with environmental protection measures outlined by McLaughlin et al. (2006), the use of a tracked vehicle to transport seaweeds from the beach is a source of concern. Though visible disturbance caused by the vehicle appears to be temporary, it is a potential source of beach compaction (Anders and Leatherman, 1987), and mortality for forage fish embryos (de Graaf, 2012), as well as other infauna (Schlacher and Thompson, 2008). The removal of fresh beach-cast *M. japonica* may have a minimal effect on macrofauna communities (Chapter 2), but associated activity could influence their transfer to higher trophic levels. Semipalmated plovers (*Charadrius semipalmatus*), for example, have been found to decrease their feeding rates in response to human activity on the beach, while Least Sandpiper (*Calidris minutilla*) feeding rates may be influenced by a combination of human densities and prey availability (Yasué, 2005). Human densities currently attributable to the Baynes Sound harvest are low, and are limited to four harvesters on the beach at a time per licence (BC

Ministry of Agriculture, 2014). Such effects, however, should be examined if the industry expands in coming years.

This thesis addresses some of the key knowledge gaps pertaining to the effects of commercial beach-cast seaweed harvests (Kirkman and Kendrick, 1997; Zemke-White et al., 2005), advancing our understanding of an activity which is poorly characterized in the literature. Furthermore, it is one of very few studies examining the wrack biomass and food provision of a non-indigenous seaweed within the marine-terrestrial ecotone. Clearly, however, much remains to be learned about the ecological effects of introduced seaweeds and their removal. Future research of this nature is of growing importance as the number of seaweed introductions continues to increase worldwide (Schaffelke et al., 2006).

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