

Beach-cast deposition and commercial harvesting of a non-indigenous alga, *Mazzaella japonica*: Implications for macrofauna communities in Baynes Sound, British Columbia

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ARTICLE INFO

Keywords:

Spatial subsidy
Biomass
Species richness
Abundance
Wrack
Marine macrophytes

ABSTRACT

Accumulations of beach-cast seaweeds and other debris, collectively known as wrack, are a common and ecologically important occurrence along coastal regions worldwide. As the rate of seaweed introductions continues to increase, so too does their beach-cast collection for aesthetic or commercial purposes. The ecological effects of these harvests are poorly characterized in the literature, especially for nutrient-rich regions such as the Northeast Pacific. Within the southern extremity of Baynes Sound, British Columbia, beach wrack contains an introduced species of red alga called *Mazzaella japonica*, which became the target of a commercial beach-cast harvest in 2007. The objectives of this research were threefold: 1) to quantify the contribution of *M. japonica* to wrack inputs within the harvest region; 2) to explore how wrack characteristics influence macrofauna communities; and 3) to determine if the commercial removal of beach-cast seaweeds has a detectable effect on wrack characteristics and macrofauna communities. To answer these questions we monitored a series of permanent transects at six sites across the harvest region from November 2014 until March 2015. We recorded as much as 853 kg (± 173 SD) of wrack per meter of shoreline, approximately 90% of which was *M. japonica*. Despite the removal of 675 tonnes of beach-cast seaweeds, we found that the trends in wrack biomass were similar between both harvested and unharvested locations. Macrofauna communities differed between study sites, as well as with the age class, and depth of the wrack from which they were sampled. These findings contribute to the limited literature on beach-cast seaweed harvesting and provide an important record of *M. japonica* wrack inputs for future research or monitoring of this non-indigenous seaweed.

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

infaunal 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

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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* in Baynes Sound. 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 other marine macrophytes (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). On the other hand, non-indigenous seaweeds may also provide an un-palatable food source (Wright et al., 2014), with consequences for the fitness of native consumers (Scheibling and Anthony, 2001). 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. Given *M. japonica*'s dominance in the marine environment (Pawluk, 2016), we anticipated that this non-indigenous species would also be the most abundant macrophyte present in the wrack. Based on findings in the literature, we expected that macrofauna communities would differ among sites and levels of wrack decomposition (Zemke-White et al., 2005), as well as with the biomass of wrack depositions (Ince et al., 2007). If there was an effect of harvesting, we anticipated that wrack characteristics and macrofauna communities would be most similar among harvested sites. This research 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. Methods

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 (Fig. 1). Three of these were harvest sites, located at the Deep Bay RV Park (RVH), Shoreline Drive (SH), and Buccaneer Beach (BC). These harvest sites were the only three locations within the harvest region from which licence holders planned to collect

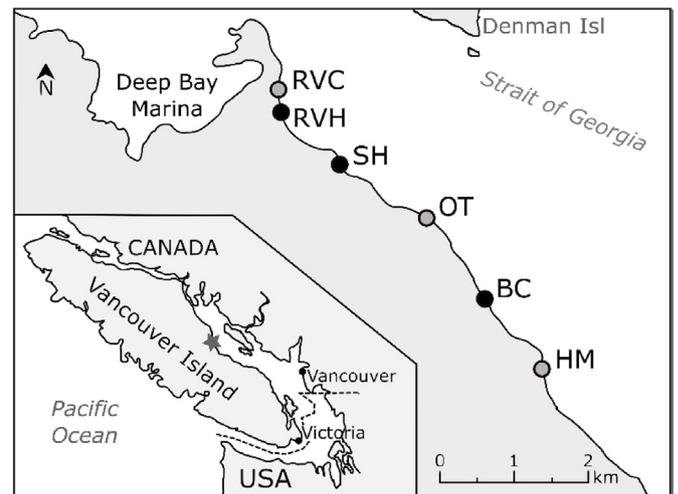


Fig. 1. Map of study area in Baynes Sound, British Columbia. Licensed harvest region extended from RVH to BC in the 2014–2015 season. Harvest sites are indicated by black circles (●), un-harvested comparison sites indicated by grey circles (○). RVC = Deep Bay RV Park comparison site, RVH = Deep Bay RV Park harvest site, SH = Shoreline Drive, OT = Ocean Trail, BC = Buccaneer Beach, and HM = Henry Morgan.

beach-cast seaweeds. The three remaining sites, located just north of the Deep Bay RV Park (RVC), at Ocean Trail (OT), and at Henry Morgan Road (HM), were selected as comparison sites, from which no seaweeds would be harvested. The resulting study design placed one study site at six southeast-facing portions of shoreline within the 4.24 km harvest region, with approximately 1 km or less between sites.

Three permanent transects were established within each study site on the first day of sampling following Dugan et al. (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 m was left between permanent transects within each site to minimize potential effects of monitoring activities on adjacent transects. This method, including the number of transects per site, has previously been used by Dugan et al. (Dugan et al., 2003) to identify significant differences in macrofauna community and shorebird abundance in response to macrophyte inputs on sandy beaches. Furthermore, using three transects per site allowed us to visit all 18 permanent transects within a single low tide.

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 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 (Electronic Supplement A, Table A.1). Presence of terrestrial vegetation and anthropogenic modifications to the landward boundaries of each site were also noted (Electronic Supplement A, Table A.2).

2.3. Harvest data

Harvest records, including the location of harvesting activity, the number of baskets hauled, and the wet weight of seaweed collected for each day were obtained from the licence holders.

2.4. Permanent transect monitoring

Permanent transects were visited at low tide once a week from November 14, 2014, until February 5, then every two weeks until March 5, 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 2 m wide, 1 m was excluded from either end of the band's range in order to minimize edge effects. If the band was less than 2 m wide, the centre 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 six point age class scale created at the outset of the study, modelled after Large Woody Debris classification by [Wooster and Hilton \(2004\)](#). 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 (Electronic Supplement B). 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 m³, determined from the 1 L 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.

2.5. 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 section 2.6). An additional 83 samples were randomly selected from various age classes across the six sites to ensure that all levels of decomposition were represented. These samples were rinsed under fresh water in a 3 mm sieve to remove macrofauna, salt, and sediment, and dried at 60 °C for 48 h. 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.

2.6. 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 h then weighed to the nearest 0.01 g. The proportion represented by each macrophyte group was calculated for every sample, then averaged across all samples for a given site and date.

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 × 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. Some specimens could not be identified to this taxonomic resolution due to decomposition, or the difficulty associated with distinguishing among families (e.g. larval stages). Specimens were therefore grouped by Order or a broader grouping, such as larvae, as required. The resulting nine taxonomic groupings were: Amphipoda, Araneae, Acari, Diptera, Coleoptera, Collembola, Hymenoptera, Nematoda and larvae. This level of taxonomic resolution has also been used in other studies examining macrofauna communities in beach wrack, facilitating comparison between our findings and other research in the literature (e.g. [Ince et al., 2007](#)).

Beta diversity of the dataset ([Whittaker, 1960](#)) was used to gauge the amount of compositional heterogeneity in samples and evaluate which ordination methods would be appropriate for community analysis. Beta diversity was calculated as follows:

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

Where: β = Beta diversity. γ = Gamma diversity (total number of species groups in all samples). α = Alpha diversity (mean number of species groups per sample).

Overall, macrofauna samples had a beta diversity of 1.63, indicating an appropriate level of community diversity for the use of ordination methods (beta diversity < 5; [McCune and Grace, 2002](#)).

A Constrained Analysis of Principal Coordinates, or CAP ([Anderson and Willis, 2003](#)), was run on macrofauna composition including transect of collection, age class, mean depth, percent cover, and biomass of the band from which the sample was taken as environmental variables. 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 CAP 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% 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.

Because we also wanted to know how the characteristics of the wrack influenced macrofauna communities, independent of the location from which they were collected, we repeated the CAP using wrack age class, mean depth, biomass, and percent cover as environmental variables, as before, but with the effects of transect and date of collection partialled out. The Dufrene-Legendre indicator (DLI) value for each taxonomic grouping was estimated (from 1000 iterations) to identify the macrofauna important in delineating the wrack age class from which samples were collected (Dufrene and Legendre, 1997).

All statistical analyses were performed using R (R Core Team, 2016). The CAP, and Detrended Correspondence Analysis were performed using the vegan package (Oksanen et al., 2015), while the DLI analysis was done with labdsv (Roberts, 2015).

3. Results

3.1. Site characterization

Site characterization according to the ShoreZone protocol (Harper and Morris, 2014) indicated that all six study sites shared similar characteristics (Electronic Supplement A, Table A.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 $< 5^\circ$, a width of > 30 m 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 (Electronic Supplement A, Table A.2).

3.2. Harvesting activity

A total of 675 tonnes of wet beach-cast seaweeds were harvested from the licensed region during the 2014–2015 season (Table 1). Harvesting began October 10, 2014, at BC, shifting north to SH on October 17. Harvesting moved to RVH on October 30, 2014, where it continued for the remainder of the harvesting period. 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 15, 2015, the collection of beach-cast seaweeds was concluded by January 9. Licence holders cited the declining quality of wrack as the reason they stopped.

Table 1

Total metric tonnes of beach-cast seaweeds (wet weight) harvested by location and month during the 2014–2015 harvest season. Site abbreviations are as they appear in Fig. 1.

Month	Site			Total
	BC	SH	RVH	
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

3.3. Wrack biomass

Peak biomass was observed in December at BC, SH, RVC, and RVH study sites (Fig. 2a). 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 22 and December 29, 2014. 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.

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 (Fig. 2b). The average area of beach substrate covered by wrack at a given site reached as much as 34.7 m² (± 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 (Fig. 2c). Wrack tended to cover a greater area of substrate at RVH than at RVC and other sites, which was offset by lower mean depth values. On the second day of sampling (November 20, 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 m² (± 3.4 SD) per meter of shoreline, but only 7.3 m² (± 0.8 SD) per meter of shoreline at RVC.

3.4. Age classes

Averaged over the entire monitoring period, the majority of wrack belonged to the freshest age classes one through three (Fig. 3). Older age classes (four through six) represented less than 25% of average 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 (four through six) on average.

3.5. Macrophyte composition

Unidentifiable material, which was too degraded for identification, represented 12%–30% of average sample dry weights among locations, and was removed from subsequent calculations to facilitate comparisons. The non-indigenous red seaweed, *M. japonica*, was the dominant macrophyte species present in wrack samples across all six study sites (Electronic Supplement C). The average proportion of sample dry weight represented by this introduced species ranged from 87% at RVH, to 94% at SH. Terrestrial debris accounted for 3%–7% of average sample weight across sites, while *Sargassum muticum*, *Fucus* spp., and *Zostera marina* contributed less than 5% combined. Several rarer macroalgae species (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

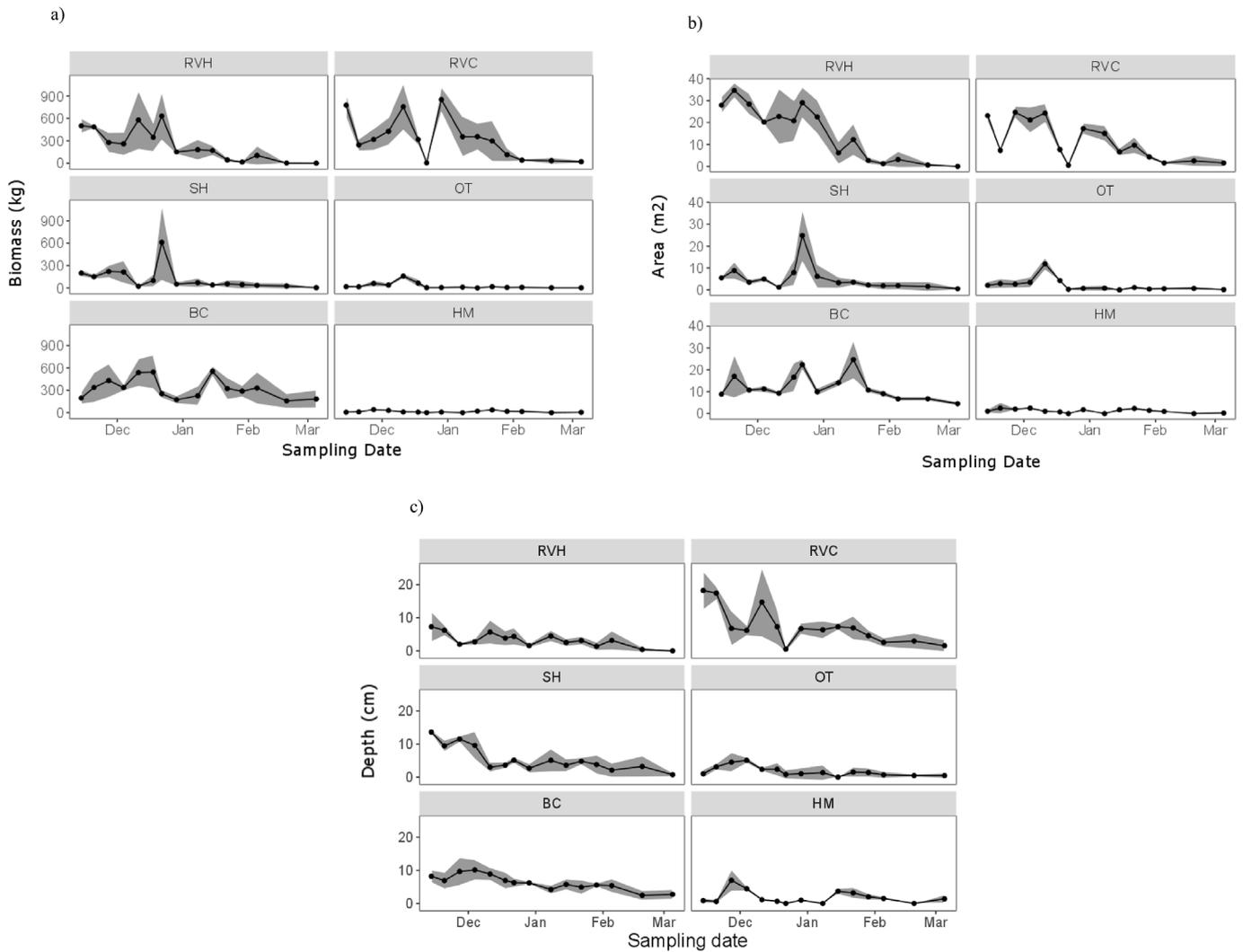


Fig. 2. a) Mean biomass of wrack (kg) in wet weight, b) mean area of beach substrate covered by wrack (m²), and c) mean depth of the wrack (cm) where present. Shaded interval represents one standard deviation around the mean (n = 3 transects per site). Potential harvest sites are aligned on the left and un-harvested comparison sites are aligned on the right. Site definitions are as they appear in Fig. 1. 78% of beach-cast seaweeds were collected from RVH during the entirety of the licensed harvesting period.

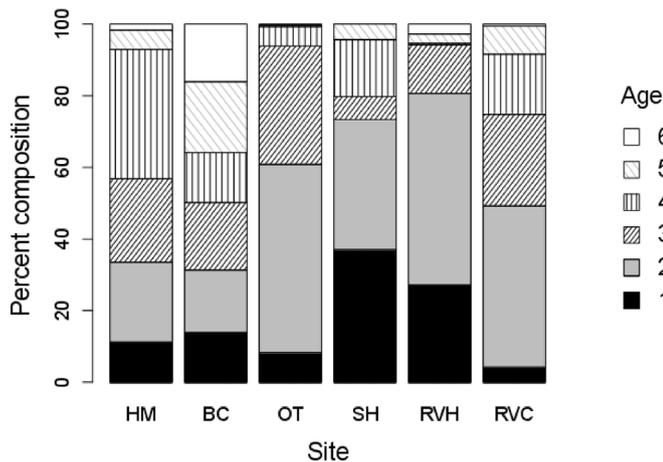


Fig. 3. Average proportion of dry wrack biomass belonging to each age class for the monitoring period (November 14, 2014 to March 5, 2015). Age class was designated according to a six point scale, where 1 represents the freshest wrack and 6 represents the highest level of decomposition observed in the field. Site definitions are as they appear in Fig. 1 and arranged from south to north.

species accumulation curves reaching an asymptote (Electronic Supplement D, Figure D.1a).

3.6. Macrofauna communities

Categorized by the nine taxonomic groupings, macrofauna species accumulation curves for the six sites (Electronic Supplement D, Figure D.1b), as well as the five age classes of wrack (Electronic Supplement D, Figure D.1c) all reached an asymptote, indicating that sampling was sufficient. Macrofauna communities appeared to be largely composed of nematodes at OT, SH, RVH, and RC, where they accounted for 35%–57% of sample composition (Fig. 4). 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, while 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.

With transect of collection, as well as wrack age class, biomass, depth, and percent cover included as explanatory variables in the CAP, constrained variation comprised 35.7% of the total variation in

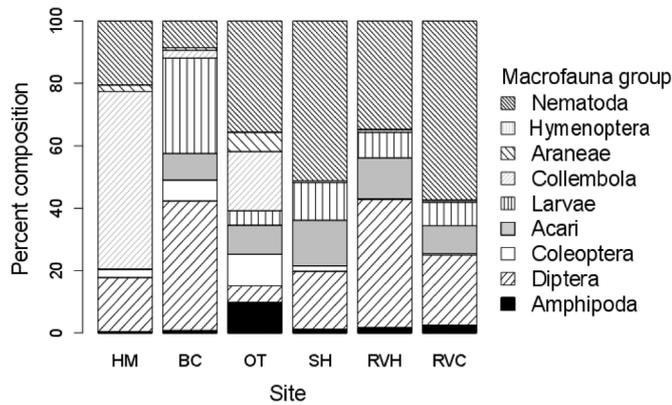


Fig. 4. Mean proportion of macrofauna abundance belonging to each macrofauna group collected from 1 L samples of wrack. Samples were collected from three transects per site on four dates (n = 93 samples total). Site definitions are as they appear in Fig. 1 and arranged from south to north.

macrofauna assemblages. The first canonical axis explained 22.8% of the constrained variation, but only 8.2% of the total variation in macrofauna composition. This axis largely separated OT and HM transects, which had mean positive scores, from BC transects, which had mean negative scores (Fig. 5a). Macrofauna groups that loaded negatively on the first axis were: larvae, Diptera, Acari, and Coleoptera (Fig. 5b). Collembola, on the other hand, loaded strongly and positively on this axis.

The second axis, which explained 21.5% of the constrained variation and 7.8% of total variation, largely separated RVC and SH transects (Fig. 5a). Nematodes loaded strongly and negatively onto this axis, while Collembola loaded positively (Fig. 5b). Older age classes were associated with larvae, Diptera, Acari, and Coleoptera, which loaded negatively on the first canonical axes. Increasing depth, percent cover, and biomass of the wrack band were more strongly associated with Nematoda and Acari, which loaded negatively on the both the first and second canonical axes.

Mean site scores for transects at RVH, the primary harvest site, spanned both the first and the second canonical axes, forming no clear cluster within the CAP. Mean site scores for RVH transects overlapped with samples collected from BC and, to a lesser extent, RVC, SH, and OT.

When the CAP was repeated, with the effects of transect partialled out, wrack characteristics (age class, depth, percent cover, and band biomass) explained 7.5% of the total variation in macrofauna community composition. Wrack age class was strongly and negatively associated with the first axis, which explained 58.1% of the constrained variation, but only 6.1% of total variation (Fig. 6a). Wrack depth was also negatively associated with the first axis, though not as strongly as age class. Larvae loaded most strongly on this axis, followed by Collembola, Acari, Diptera, Coleoptera, Araneae, Amphipoda, and Nematoda in ascending order of mean species scores (Fig. 6b). Amphipoda and Nematoda were the only taxonomic groups that loaded positively on this axis. Wrack age class was also strongly and negatively associated with the second axis, which explained 23.4% of the constrained variation and 2.5% of total variation (Fig. 6a). 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 second axis (Fig. 6b).

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

4. Discussion

4.1. Wrack characteristics

The non-indigenous seaweed *M. japonica*, made a substantial contribution to wrack inputs in Baynes Sound, accounting for ~90% of dried macrophyte biomass across all six study sites. During peak

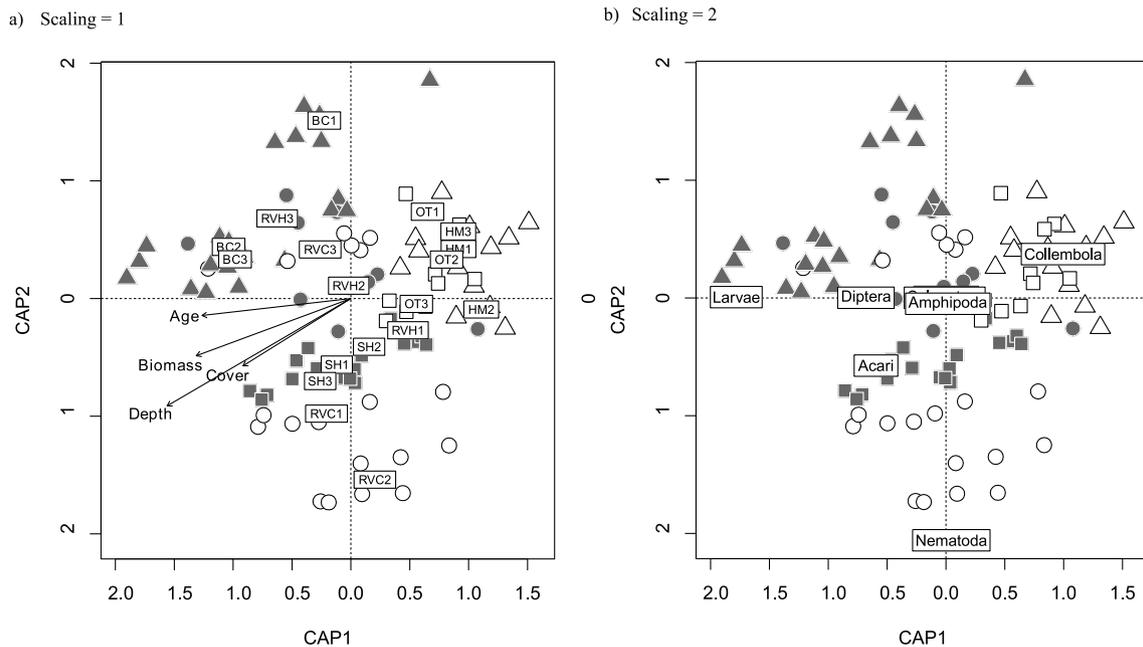


Fig. 5. Results of the constrained analysis of principal coordinates (CAP) using Bray-Curtis dissimilarity. a) Scaling = 1 biplot of the collection sites on the first two axes of the CAP, tip of the arrow heads indicate the biplot scores for the constraining variable lengths. c) Scaling = 2 biplot plotting the macrofauna species scores for the CAP on the first two axes. Site abbreviations are as they appear in Fig. 1. Harvest sites: ● RVH, ■ SH, ▲ BC; Comparison sites: ○ RVC, □ OT, △ HM. Numbers represent transect identification number within the site of collection. 78% of harvested beach-cast seaweed biomass was collected from RVH.

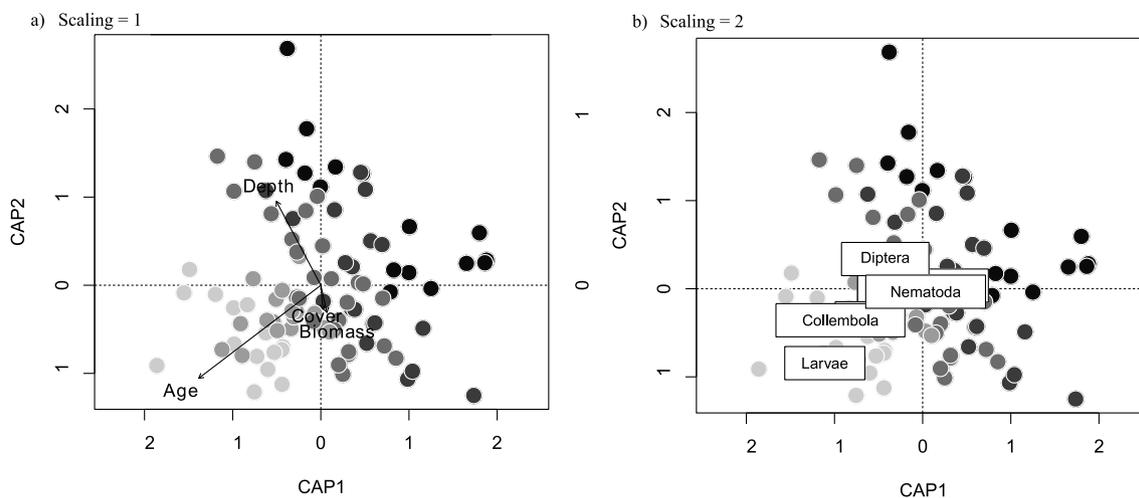


Fig. 6. Results of the constrained analysis of principal coordinates (CAP) using Bray-Curtis dissimilarity, with the effects of collection site partialled out. Sample points are shaded from freshest wrack age class (● = age class 1) to oldest wrack age class (● = age class 6). a) Scaling = 1 biplot of 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 species scores.

Table 2

The Dufren re-Legendre indicator (DLI) values of each taxonomic grouping (Group) for the wrack age classes 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	Age Class	DLI	<i>p</i>
Amphipoda	2	0.163	0.198
Diptera	3	0.318	0.235
Coleoptera	5	0.298	0.009
Acari	5	0.311	0.031
Larvae	5	0.443	0.001
Collembola	4	0.536	0.003
Araneae	5	0.133	0.091
Nematoda	4	0.254	0.418

biomass (November through December), these inputs covered the study sites in an extensive ‘blanket’ of seaweed, reaching as much as 853 kg (± 173 SD) of wrack per meter of shoreline and covering up to 35 m² (± 3 SD) of beach substrate per meter of shoreline. These findings are highly consistent with wrack biomass measurements in a concurrent study of the harvest region (Holden et al., 2017), which reported 497 to 1,350 kg of wrack per meter of shoreline in this area on December 31, 2014.

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 Vancouver 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 (B land, 2012). The highest wrack loadings observed in our study were closer to reports of 1–3 tonnes of wrack per meter of shoreline in the Gulf of California (Polis and Hurd, 1996), South Africa (Koop and Field, 1980), and Australia (Kirkman and Kendrick, 1997). As the number of eutrophication events and seaweed introductions continue to increase across the globe, the deposition of large wrack accumulations may become increasingly common (Smetacek and Zingone, 2013).

Large depositions of non-indigenous seaweeds, such as those observed in this study, could have an array of implications for recipient beaches and their communities. Differences in physical structure,

decomposition rates, and nutritional values could alter habitat provision and nutrient cycling (Rossi et al., 2011). *M. japonica*, for example, 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 colonisation studies have indicated that other macrophytes, such as, *S. muticum* are preferred over *M. japonica* in Baynes Sound (Pawluk, 2016). Non-indigenous macrophytes can also attract associated fauna by providing a new food source, while others may cause physiological damage to native generalist herbivores (Rodil et al., 2008). More research is needed to evaluate how changes in habitat and food provision associated with the introduction of *M. japonica* influence macrofauna communities.

4.2. Variation in macrofauna communities

In contrast with other studies on wrack-associated invertebrates, macrofauna communities across all six study sites were numerically dominated by dipterans and nematodes. Previous research has reported talitrid amphipods (Behbehani and Croker, 1982; Griffiths and Stenton-Dozey, 1981; Stenton-Dozey and Griffiths, 1983) or coleopterans (Ince et al., 2007) as the dominant components of wrack-associated macrofauna communities. 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, creating an unfavourable habitat for invertebrates that prefer dry beach-cast seaweeds (Ince et al., 2007). The substantial presence of larvae, strongly associated with older age classes of wrack, indicates that these beach-cast seaweeds provide 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 may 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, are known to feed on intertidal amphipods and insects (Colwell and Landrum, 1993; Yasu , 2005). Invertebrate prey densities can have consequences for feeding rates and fitness during these critical stages in migration (Yasu , 2005). 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). Understanding the influence of wrack characteristics and harvesting activity on macrofauna communities could therefore have far reaching implications for coastal and terrestrial ecosystems.

Despite differences in the composition of macrofauna communities reported here, explanatory variables important in delineating variation were consistent with findings in the literature. Combined, transect, mean depth, percent cover, band biomass, and age class of the wrack explained 35.7% of the total variation in macrofauna composition according to the CAP. Of these, transect emerged as the most important environmental variable (explaining 28.2% of total variation), with mean transect site scores generally clustering by collection site. Variation in macrofauna communities among sites have previously been attributed to 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 et al., 2010). With the effects of transect partialled out, wrack characteristics (mean depth, percent cover, biomass, and age class) explained only 7.5% of the total variation in macrofauna community composition.

Age class and mean depth emerged as the strongest wrack characteristics explaining the variation in macrofauna communities. Other studies have similarly 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 are often 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 the DLI values of taxonomic groups across wrack age classes in our study, 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 three and four respectively. Coleoptera, Acari, larvae, Collembola, and Araneae all had maximum DLI values for age class five, which was the highest level of decomposition sampled.

Wrack belonging to older age classes (four through six), with which most macrofauna groups were associated, 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 in other systems (e.g. by Inglis (1989) and Colombini et al. (2000)), where it was noted 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).

4.3. Effects of commercial harvesting

Despite the concentration of harvesting efforts at RVH, from which 78% of the harvested biomass was collected, 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 (Fig. 2a), indicating that harvesting activity did not deplete wrack availability below naturally occurring quantities. Furthermore, the area of substrate covered by wrack was often greatest at RVH suggesting that harvesting activity may spread the wrack, so that it covers a greater area with reduced mean depth.

Harvesting activity did not appear to explain substantial variation in macrofauna communities, though our ability to distinguish the effects

of harvesting was limited by a concentration of effort at RVH. Given their spatial proximity, it was expected that macrofauna samples collected from transects at RVH and RVC would be the most similar if there was no effect of harvesting activity. RVH samples, however, tended to cluster more closely with those collected from BC, though they did not form an independent cluster in 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.

These findings contrast with other studies on the removal of beach-cast seaweeds, which have reported large effects on macrofauna communities. The complete removal of wrack by beach grooming for aesthetic purposes has been repeatedly associated with negative impacts on the biomass and diversity of macrofauna (Dugan et al., 2003; Lavry et al., 1999; Llewellyn and Shackley, 1996; McLachlan, 1985). 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 impacts infauna and accelerates erosion (Defeo et al., 2009). Dissimilarities in the effects of beach-cast seaweed removal could, however, be attributable to differences in beach grooming and commercial harvesting practices.

Though it is used as a proxy for commercial harvesting in the literature, beach grooming practices are often very different from those employed by commercial harvesters. Grooming 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). Harvesting licence conditions, such as those in Baynes Sound (British Columbia Ministry of Agriculture, 2014), typically require that a proportion of the available wrack biomass be left behind; prohibit the removal of any sediment; and ban the mechanized collection of beach-cast seaweeds. Unlike beach grooming, the commercial harvesting of beach-cast seaweeds is also regulated by quotas. 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).

Compared to other commercial beach-cast seaweed harvests, the quantity of wrack removed by Baynes Sound licence holders was relatively low. A concurrent study of the 2014–2015 Vancouver Island harvest by Holden et al. (2017) 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 countries such as Australia. The total biomass harvested (675 tonnes) was also much lower than harvest quotas in Ireland, where hundreds to thousands of tons of beach-cast seaweeds can be collected daily per commercial licence (McLaughlin et al., 2006).

5. Conclusions

Understanding the effects of large non-indigenous wrack inputs and their removal will be increasingly important as the number of seaweed introductions continues to grow worldwide (Schaffelke et al., 2006). This study 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 habitat provision of a non-indigenous seaweed within the marine-terrestrial ecotone.

The effects of commercial beach-cast harvesting observed in this study differed substantially from those of beach grooming, which is often used as a proxy in the literature (Kirkman and Kendrick, 1997). 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 this study 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, CAP did not indicate that harvesting explained any substantial variation in macrofauna communities. Differences between beach grooming and commercial harvesting practices may be responsible for these dissimilarities in the effects of wrack removal. Based on these findings, we recommend that future research and management decisions refrain from using beach grooming studies as a proxy for commercial harvesting, or do so with caution.

Potential impacts associated with the removal of beach-cast seaweeds on macrofauna communities could be minimized in Baynes Sound by limiting harvest interactions with older wrack age classes. All taxonomic groups examined, with the exception of talitrid amphipods and dipterans, were strong indicators for highly decomposed beach-cast seaweeds (age classes four and five). This decomposing wrack, found within the supralittoral zone, represented only 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 harvesters could help minimize interactions with wrack-associated macrofauna groups. 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).

Further research will be required to determine the influence of *M. japonica*'s introduction on intertidal and subtidal ecosystems in Baynes Sound. The decomposition of such large accumulations could lead to the creation of anoxic conditions, with negative impacts on infauna communities (Gamenick et al., 1996; Rodil et al., 2008), and littoral vegetation (Den Hartog, 1994). 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 (deGraaf, personal communication). 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, the majority of which does not decompose on the beach. While this study provides an important record of *M. japonica*'s beach-cast biomass and distribution, continued monitoring will help inform the management of this non-indigenous species and its removal by commercial harvesting.

Acknowledgements

We would like to thank Dr. Kylee Pawluk for her valuable input on this study. A special thanks to Dr. Michael Hawkes and Dr. Rick Harbo as well, for their assistance with species identification. We gratefully acknowledge the help of volunteers from Vancouver Island University with field work and sample processing. Finally, we would like to thank the harvest licence holders and crew for their co-operation. This research was funded by the Natural Sciences and Engineering Research Council of Canada, and the British Columbia Ministry of Agriculture, with logistic support from Vancouver Island University's Deep Bay Marine Field Station, and Centre for Shellfish Research.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.ecss.2018.06.008>.

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