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Sea wrack delivery and accumulation on islands: factors that mediate marine nutrient permeability

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ABSTRACT: Sea wrack provides an important vector of marine-derived nutrients to many terrestrial environments. However, little is known about the processes that facilitate wrack transport, deposition, and accumulation on islands. Three broad factors can affect the stock of wrack along shorelines: the amount of potential donor habitat nearby, climatic events that dislodge seaweeds and transfer them ashore, and physical characteristics of shorelines that retain wrack at a site. To determine when, where, and how wrack accumulates on island shorelines, we surveyed 455 sites across 101 islands in coastal British Columbia, Canada. At each site, we recorded wrack biomass, species composition, and shoreline biogeographical characteristics. Additionally, over a period of 9 mo, we visited a smaller selection of sites ($n = 3$) every 2 mo to document temporal changes in wrack biomass and species composition. Dominant wrack species were *Zostera marina*, *Fucus distichus*, *Macrocystis pyrifera*, *Nereocystis luetkeana*, *Pterygophora californica*, and *Phyllospadix* spp. The amount of donor habitat positively affected the presence of accumulated biomass of sea wrack, whereas rocky substrates and shoreline slope negatively affected the presence of sea wrack biomass. Biomass was higher during winter months, and species diversity was higher during summer months. These results suggest that shorelines with specific characteristics have the capacity to accumulate wrack, thereby facilitating the transfer of marine-derived nutrients to the terrestrial environment.

KEY WORDS: Sea wrack · Marine–terrestrial subsidy · Spatial subsidy · Ecosystem connectivity · Wrack deposition · Wrack accumulation · Macrophyte · British Columbia · Remote sensing

1. INTRODUCTION

Boundary dynamics provide a framework for investigating how ecosystem edges can affect the flow of materials from one environment to another. This framework describes permeability as an important factor in regulating the transport of nutrients and energy vectors across ecosystems (Wiens et al. 1985).

Permeability, the degree to which a boundary may deflect the movement of vectors, depends on the boundary characteristics and the nature of the vector (Wiens et al. 1985). The permeability of marine subsidies at the coastal boundary may be particularly important on small islands that have large perimeter to area ratios, allowing marine resources to penetrate to the island's interior more easily than on larger islands

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and potentially affecting species productivity and diversity (Polis & Hurd 1996, Anderson & Wait 2001).

Marine–terrestrial subsidies can take many forms. Bird guano (derived from marine resources) and discarded marine mollusk shells fertilize soils and increase plant productivity directly through nutrient additions (Anderson & Polis 1999, McCauley et al. 2012, Trant et al. 2016). Beach-cast fish, carrion, marine mammal carcasses, and intertidal invertebrates provide nutrition to numerous vertebrate and invertebrate scavengers, increasing consumer populations (Polis & Hurd 1996, Barrett et al. 2005). Despite fluctuating across both spatial and temporal scales, primary consumers (e.g. amphipods and isopods) will increase in abundance near these vectors of marine subsidy (Polis & Hurd 1996, Colombini et al. 2000, Dugan et al. 2003, Ince et al. 2007, MacMillan & Quijón 2012). Accordingly, secondary consumers such as birds, spiders, scorpions, lizards, and rodents will respond to the increased abundances of macroinvertebrates (Catenazzi & Donnelly 2007, Spiller et al. 2010, Schlacher et al. 2017). Larger mammals, such as coyotes *Canis latrans* and black bears *Ursus americanus*, have also been observed to alter their spatial and temporal distribution in response to marine subsidies (Rose & Polis 1998, Carlton & Hodder 2003, Fox et al. 2015).

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

As with many marine nutrient subsidies, wrack depositions and accumulations vary temporally. In some locations, wrack biomass accumulations are consistent throughout the year (Barreiro et al. 2011). However, seaweed detritus production may fluctuate due to seasonal senescence, water temperature, wave conditions, shoreline dislodgment, or erosion due to tidal and climate events (Koop & Field 1980, Stenton-Dozey & Griffiths 1983, Witman 1987, Seymour et al. 1989, Chapman & Johnson 1990, Krumhansl & Scheibling 2011, de Bettignies et al. 2013). Many seaweed species have annual life histories that influence detritus production. For example, bull kelp *Nereocystis luetkeana* grows from late spring to early fall, then senesces en masse, often dislodging during the first large winter storm (Mann 1973). These seasonal and climatic events can influence the volume and species composition of detrital production, though it is unknown whether this higher availability translates to changes in onshore sea wrack deposition and accumulation. Examining the timing and extent of accumulations may clarify whether sea wrack is ubiquitous temporally or is deposited in seasonal surges, which will help to decipher how resource pulses may affect resource–consumer interactions on islands.

To explore the potential subsidy effect of sea wrack on islands, we first examined the permeability of the coastal boundary by measuring the timing and extent of wrack accumulations on 101 islands within the coastal temperate rainforests of the Central Coast of British Columbia (BC), Canada. We predicted that 3 broad factors may affect macrophyte and macroalgal wrack abundance and distribution: the extent of donor habitats, climate, and physical shoreline characteristics.

The extent and proximity of detrital donor habitats may be a strong indicator of wrack biomass and species composition. On the eastern Pacific coast, vast quantities of sea wrack originate from several donor habitats: intertidal macroalgal beds, subtidal kelp forests, and seagrass meadows. On the Pacific coast of Canada, the dominant canopy-forming kelp species, *Macrocystis pyrifera*, forms kelp forests that produce up to $900 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Wilmers et al. 2012), which produce as much as 650 g C m^{-2} of detritus every year (Druehl & Wheeler 1986). Eelgrass beds of *Zostera* species are estimated to cover 423 km^2 of the coastline of the Central Coast (Reshitnyk et al. 2016), and reach up to $1450 \text{ g C m}^{-2} \text{ yr}^{-1}$ of primary productivity (Mann 1973), but dislodgment rates have not yet been reported. Aside from these species, the rate of productivity and detrital production is not well

known for many of the dominant marine macroalgae and seagrasses found throughout the Central Coast. Additionally, little is known about how many of these dislodged kelps and macrophytes are being exported to the open ocean (but see Harrold & Lisin 1989). Given that BC's convoluted coastline extends for over 29 000 km (including islands) and seaweed communities comprise a lush band that encompasses this complex coastline (Druehl & Clarkson 2016), there is potential for a large amount of biomass from this band to be washed ashore.

Climate can affect wrack depositions. Factors such as winds and swell, and the interactions among these conditions and the tides, can detach macroalgae and macrophytes from their anchorages (Witman 1987, Seymour et al. 1989, Krumhansl & Scheibling 2011), creating areas or times with predictable wrack depositions (Oldham et al. 2010, López et al. 2019), especially where there are consistent winds. For instance, increased seagrass deposits in the northwest Mediterranean are attributed to strong wind events (Jiménez et al. 2017), higher than normal tides have increased wrack accumulation along Estonian shorelines (Suur Saar et al. 2014), and on the Pacific coastline of the USA, wave events caused by swell increased wrack accumulations (Reimer 2014). Additionally, storms can facilitate sporadic long-distance kelp dispersal events, disrupting patterns of connectivity across ecosystem boundaries (Waters et al. 2018).

The third broad factor potentially affecting sea wrack accumulation and retention is a site's physical shoreline characteristics, which are: slope, substrate, aspect, width, and wave exposure. Interactions between beach length and exposure to waves that resulted in greater edge exposures to donor habitats (similar to the large perimeter to area ratios seen on small islands) increased wrack accruals in Spain (Barreiro et al. 2011). Along the coastlines of Vancouver Island, BC, shores composed of cobble substrates retained significantly more wrack than those composed of sand or gravel, as the spaces between cobbles trapped large wrack particles and retained them despite tidal and wave forces (Orr et al. 2005). In California, sloped beaches were positively correlated with the retention of *Phyllospadix* spp., suggesting that steeper beaches can retain greater amounts of specific wrack species when high tides deposit wrack high upon the shoreline (Liebowitz et al. 2016), presumably in part due to the buoyancy of a species (Oldham 2014).

Although globally sea wrack as a vector of marine to terrestrial nutrient transfer is a well-studied phenomenon, little research exists on the mechanisms of

wrack deposition and accumulations on island shorelines across extended spatial and temporal scales. In this study, we aimed to determine the drivers of spatial and temporal wrack variability across large spatial and temporal scales by distinguishing when and where sea wrack is most likely to accumulate along coastlines by asking the following questions: (1) What are the biophysical and environmental variables that best explain patterns in wrack accumulations on-shore? (2) What are the seasonal changes in accumulated wrack biomass and species composition?

2. MATERIALS AND METHODS

2.1. Study region

The Central Coast of BC encompasses the region between the northern tip of Vancouver Island (50.7865°N, 128.2324°W) and the southern tip of Haida Gwaii (51.8711°N, 131.0010°W). The study area spanned ~2000 km² within the Central Coast region (Fig. 1), which contains ~1500 islands. This region is located within the very wet hypermaritime subzone of the Coastal Western Hemlock biogeoclimatic classification (Meidinger & Pojar 1991), which is characterized by cool summers (mean warmest month 14.0°C), warm winters (mean coldest month 2.3°C), and large amounts of precipitation (mean annual precipitation >3000 mm) (Meidinger & Pojar 1991). The sea surface ocean temperatures range from a mean low of 7°C in March to a mean high of 15°C in August (Jackson et al. 2015). Tides in the region fluctuate from 3 to 5 m and are semidiurnal (Thomson 1981). Field work was conducted out of the Hakai Institute on Calvert Island, BC, within the Hakai Lúxvbálís Conservancy, and in the Penrose Island Marine Provincial Park area under a long-term operation BC Parks Use Permit No. 107190. All research was conducted within the territories and with permission of the Heiltsuk and Wuikinuxv First Nations.

2.2. Spatial surveys

2.2.1. Island selection

We selected 101 islands to represent a range of island characteristics and used cluster analysis to provide a method of data reduction that still ensured a range of island characteristics were sampled (Hargrove & Hoffman 2004). Five biogeographical de-

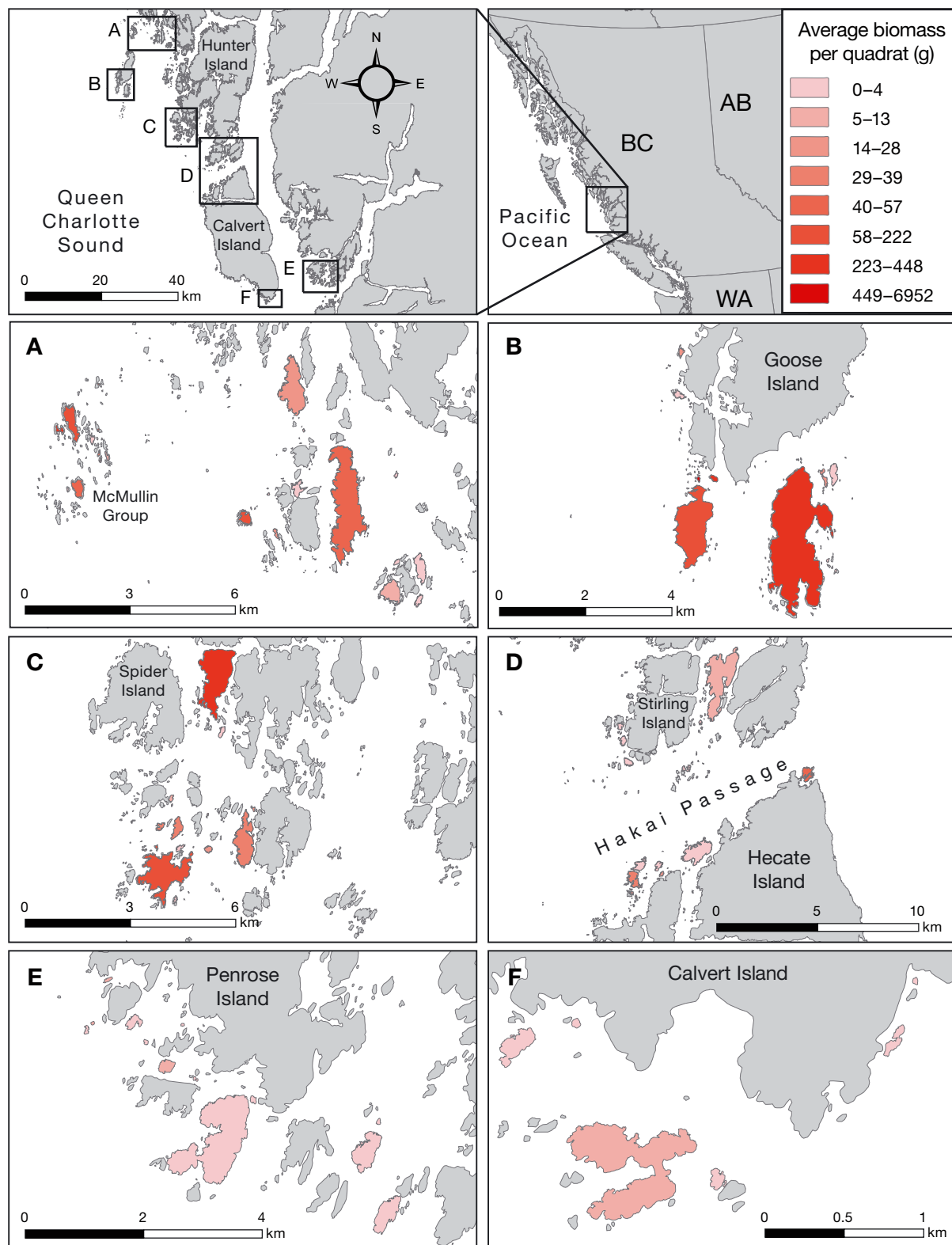


Fig. 1. Central Coast of British Columbia (BC), Canada (top right; WA: Washington State, AB: Alberta). The study region and location of nodes of study islands as selected by cluster analysis (top left). All study islands are colored in red shades according to their average biomass per quadrat (g) dry biomass accumulations. (A) McMullin, Tribal, and Admiral nodes (52.0457°N, 128.3563°W); (B) Goose node (51.9291°N, 128.4524°W); (C) Triquet node (51.8256°N, 128.2132°W); (D) Calvert and Stirling nodes (51.7425°N, 128.0576°W); (E) Penrose node (51.4632°N, 127.7247°W); and (F) South Calvert node (51.4250°N, 127.9108°W). Map reproduced with permission from the Hakai Institute

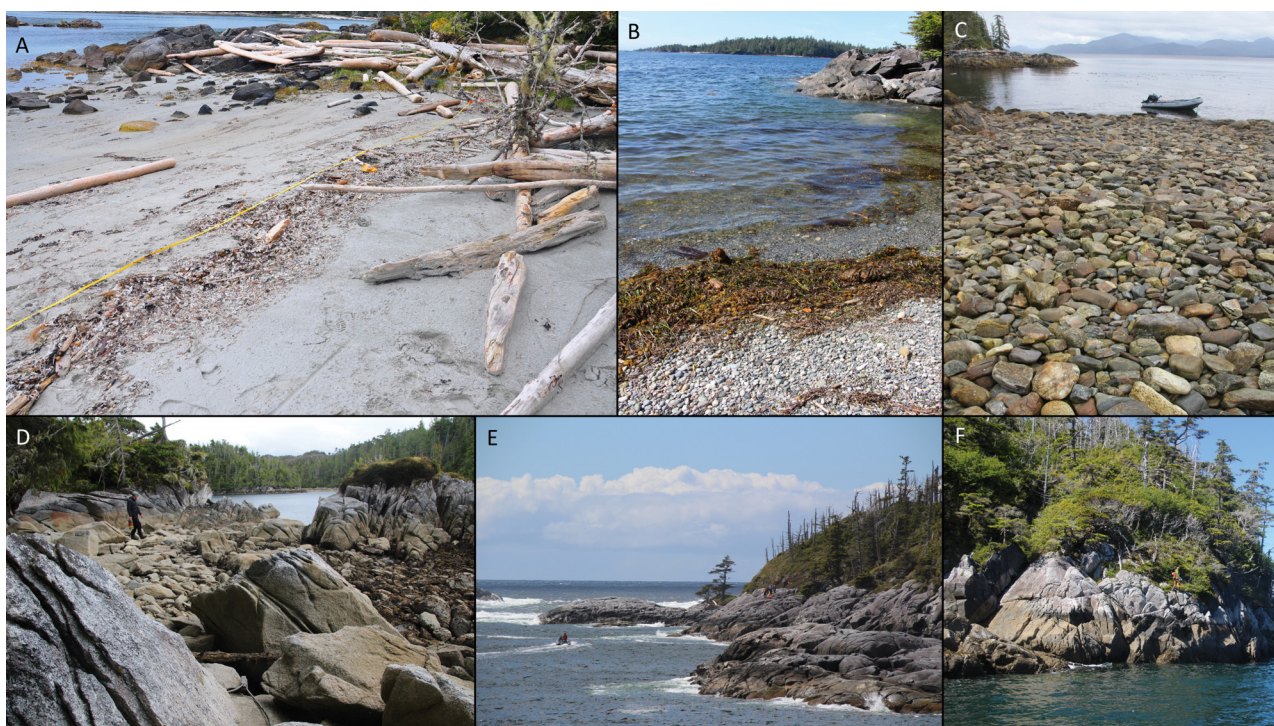


Fig. 2. Examples of the different types of shoreline substrates commonly found on the west coast of British Columbia: (A) sand on island GS05 (51.9271°N, 128.4691°W), (B) gravel on island GS03 (51.9170°N, 128.4763°W), (C) cobble on island CV17 (51.7306°N, 128.0012°W), (D) boulder on island ST14 (51.7729°N, 128.0626°W), (E) rock on island SC01 (51.4160°N, 127.9203°W), and (F) rock on island ST10 (51.7463°N, 128.1323°W). Refer to Supplement Table S3 for island node and number abbreviations

scriptors (distance from mainland, area, normalized perimeter to island ratio, exposure, neighboring land) for all islands within the study region ($n = 1470$) were derived (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m635p037_supp.pdf), and additional biogeographical characteristics were extrapolated from the BC ShoreZone dataset (Howes et al. 1994). The results of cluster analysis identified several nodes (Table S2) where islands with different biogeographical descriptors were located within close proximity to each other. Within a node, islands were selected to maximize variation across a range of island sizes and shoreline structure. The final dataset consisted of 101 islands within 9 nodes (Fig. 1, Table S3).

2.2.2. Wrack biomass and composition measurements

During the spring/summer season (May–August) of 2015–2017, we visited each island one time throughout the 3 yr period. During a visit, we conducted 4 surveys per island, one at each of the predetermined

coordinates representing the furthest north, east, south, and west aspect of each island. Depending on the availability of substrate, additional surveys were conducted on islands that had shorelines with either a sand, gravel, cobble, or boulder substrate (Fig. 2). This allowed us to examine substrate effects on wrack retention. Therefore, each island had a minimum of 4 to a maximum of 10 survey sites resulting in a total of 455 sites in the study area. Each survey entailed one 20 m transect, centered on the most recent high tide wrack line (which ran roughly parallel to the waterline), and beginning at the pre-determined cardinal direction coordinates.

We randomly sampled 1 m² ($n = 3$) quadrats along each transect line. Within each quadrat, we identified and sorted all wrack either to the functional algal group (as per Steneck & Dethier 1994), genus, or species level and then weighed all samples. Wrack that was unidentifiable was categorized as such and weighed. Wrack that was partially buried but still had a portion visible was uncovered, rinsed or wiped of sand, sorted, and weighed. Wrack was weighed with either a small scale with precision of ± 2 g or a hanging spring scale with precision of ± 1 kg at-

tached to a tarp. Following methods outlined by Wickham et al. (2019), we collected subsamples from 12 of the most common seaweed species to derive a correction factor for wet to dry weight conversions. All biomass results for both spatial and temporal data are reported in dry estimates.

2.2.3. Biophysical and environmental measurements

To determine the drivers of wrack accumulation, we included 10 biophysical and environmental measurements as variables in our analysis (wind direction, wind speed, wave height, wave period, high tide, shoreline slope, shoreline width, shoreline wave exposure, shoreline substrate, and extent of nearby donor habitat; Table 1).

To determine the relative contribution of donor habitat in explaining wrack biomass measurements, we first determined each site's proximity to a wrack source. We identified the 3 main wrack donor habitats within our study area: (1) kelp forests as donors of *Macrocystis pyrifera* and *Nereocystis luetkeana*,

(2) eelgrass beds as donors of *Zostera marina*, and (3) rocky intertidal shorelines as donors of *Fucus distichus*. We analyzed remotely piloted aerial system (RPAS)-based digital photogrammetry and WorldView-2 multispectral satellite imagery in ArcGIS and estimated the extent of all donor habitats, then summed these estimates. Kelps such as *M. pyrifera* commonly wash ashore within a 5 km radius of their detachment sites (Dugan & Miller 2019), so we positioned a set of radii around each survey site (length of radii = 50, 100, and 500 m, and 1, 2, 3, 4, 5, and 7.5 km) and analyzed the strength of the relationship between the summed area of donor habitat and the onshore biomass of kelp/eelgrass/*F. distichus* using Spearman's correlation analysis for non-normally distributed data (Fig. S1). Following methods established by Liebowitz et al. (2016), the extent of donor habitat within the radius with the strongest relationship (from our analysis: 2 km) was used for subsequent analysis.

Climate variables such as hourly wind direction, wind speed, wave height, and wave period measurements for the day of a site visit were accessed from Environment Canada West Sea Otter Buoy archives

Table 1. Biophysical and environmental variables used as predictors in the candidate models. VC: variable categories; variables that are continuous are listed as 'na'

Parameter	Variable	VC	Source	Description
Donor habitat	Donor habitat	na	WorldView-2 and RPAS imagery	Extent of summed <i>Zostera marina</i> , <i>Fucus distichus</i> , <i>Nereocystis luetkeana</i> , and <i>Macrocystis pyrifera</i> habitat visible within 2 km of a survey site (m ²)
Climate	Wind direction	na	Environment Canada	Direction from which the wind is blowing (° True)
	Wave height	na	Environment Canada	Wave height as reported by the buoy (m)
	Wave period	na	Environment Canada	Wave peak period as reported by the buoy (s)
	High tide	na	Fisheries and Oceans Canada	Predicted high water associated with vertical movement of tide (m)
Site	Aspect	na	WorldView-2 and RPAS imagery	Mean value of 5 measurements taken at 5 m intervals for 20 m (°)
	Slope	na	WorldView-2 and RPAS imagery	Mean value of 5 measurements taken at 5 m intervals for 20 m (°)
	Substrate	Sand, gravel, cobble, boulder, rock	Recorded at site	Determined via Wentworth scale of grain size
	Width	na	WorldView-2 and RPAS imagery	Mean value of 5 measurements taken at 5 m intervals for 20 m (m)
	Wave exposure	Very protected, protected, semi-protected, semi-exposed, exposed, very exposed	Recorded at site	Classified via biobands (Howes et al. 1994)

(West Sea Otter Archive Plot⁴). Data from 6 h prior to a site visit until the hour of the site visit were averaged (the amount of time for 1 tidal cycle; Fig. S2). We included tide as a climate variable because of the potential for wind and waves to interact with tidal conditions.

We collected data pertaining to a site's physical characteristics following protocols outlined in the ShoreZone Coastal Habitat Mapping Protocol (Harper & Morris 2014). This protocol describes methods to catalog geomorphic and biological coastal features of the Pacific Northwest (including BC, Alaska, Washington, and Oregon). Site data collected included shoreline slope, aspect, substrate, width, and biobands (patterns of identifiable biota observable in the intertidal and supralittoral zone) (Howes et al. 1994). Biobands were used to classify the wave exposure of a site as per the ShoreZone Mapping Protocol (Harper & Morris 2014). Substrate categories were adapted from the Wentworth scale of grain size and included sand, gravel, cobble, boulder, and rock (Wentworth 1922). Shoreline slope, aspect, and width measurements were obtained from RPAS-derived imagery and elevation models, which were produced at 10 cm ground resolution and processed according to the methods outlined by Nijland et al. (2017). This dataset generated slope, aspect, and width measurements at every 5 m along every island's shoreline, which we averaged for each 20 m transect.

2.3. Temporal surveys

2.3.1. Site selection

We chose 3 easily accessible sites for temporal surveys because winter wind, storms, and swells can limit boat access. These included North Beach (51.6628° N, 128.1401° W), West Beach (51.6558° N, 128.120° W), and Fourth Beach (51.6431° N, 128.1510° W) on Calvert Island, all of which are classified as flat (<5°), sandy, semi-exposed shorelines (Howes et al. 1994). Sites with consistent biophysical characteristics were chosen to best gauge temporal rather than biophysical effects. Surveys were conducted during the lowest tide (<1.0 m) once every 2 mo starting in July 2016 and ending in April 2017, with one 3 mo period between the November 2016 and February 2017 survey dates.

2.3.2. Wrack biomass and composition measurements

To establish a finer-scaled resolution of the shift in accumulated wrack biomass and species composition throughout a seasonal interval, we visited each site twice (2 d apart) every 2 mo and performed 6 transects per visit ($n = 12$). The terrestrial edges of each site were divided into 100 m intervals, and 6 transect locations were randomly generated. One transect per 100 m was completed to avoid overlap along the beach. Transects ran perpendicular to the water, starting at the terrestrial edge and marked permanently with flagging tape. A compass bearing was measured along the perpendicular direction, and this bearing was followed for each survey to create a repeatable transect. We collected wrack starting at the daily high tide wrack line and ending at the lowest water level experienced during the daily low tide. All wrack within 0.5 m of either side of the transect line was collected, identified, and weighed. Collected and weighed wrack was placed far above the highest tidal line to prevent it from being redeposited in the transect during the next survey (2 d following). A wet-to-dry mass calibration was established using previously collected data (Wickham et al. 2019).

2.4. Statistical analysis

2.4.1. Spatial surveys

All analyses were performed in R version 3.5.1 (R Core Team 2018). To test the variability in wrack species composition among nodes, we analyzed the relative biomass accumulation of each wrack taxon per site using analysis of similarity (ANOSIM) (Clarke 1993). ANOSIM routines are based on a Bray-Curtis dissimilarity matrix of species occurrences using the species' logged dry biomass data. A similarity percentage (SIMPER) routine was performed to identify the species with the highest contribution to the similarity/dissimilarity of each node. All data were analyzed using the 'vegan' package in R (Oksanen et al. 2017). To determine which nodes accumulated the most wrack, dry biomass per site was compared using ANOVA, with node ($n = 9$) as a fixed factor and island ($n = 101$) as a random variable using the 'lmerTest' package in R (Kuznetsova et al. 2017).

We used a modeling approach to investigate how our potential explanatory variables predicted the presence and biomass of wrack across our study sites. Given that our dataset was heavily inflated with

⁴<http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/waves-vagues/index-eng.htm>

zeros (i.e. no wrack found in a quadrat), we separated the data into 2 datasets (a presence/absence dataset and a biomass dataset) and used hurdle modeling (Zuur et al. 2009). This required 2 steps. First, the data were considered as zero or non-zero to capture the probability of wrack presence on a beach during the surveys. Second, all zero data points were removed and a normally distributed dataset was created that captured wrack biomass accumulations on a beach once wrack was present.

Prior to modeling, the response variable (dry biomass) was log-transformed to normalize distribution. Periodic data (wind direction and aspect variables) were multiplied by sine and cosine to account for cyclical values (Roberts 1986). Wind speed and wave height were correlated and wind speed was subsequently removed because wave height provides a more direct measure of the process we intended to investigate. High and low tides were correlated, so we removed

low tide, given our primary interest in understanding the ability of a high tide to transfer wrack ashore. Continuous predictor variables (wind speed, wave period, wave height, high tide, slope, width, and extent of donor habitat) were standardized by subtracting the mean and dividing by the standard deviation.

To analyze the presence/absence dataset, we used a generalized linear model (GLM) with binomial distribution (Zuur et al. 2009). To analyze the biomass data set, we used a linear mixed effect model with Gaussian distribution and month and year as random effects and our 10 biophysical predictor variables for fixed effects (as described in Table 1) using the R package 'nlme' (Pinheiro et al. 2017). We ranked the multiple candidate models generated for each dataset using Akaike's information criterion (AIC) (Burnham & Anderson 1998). We developed multiple candidate models *a priori* (Tables 2 & 3) for both datasets. All models within 4 points of the lowest AIC

Table 2. Akaike's information criterion (AIC) values from candidate models to predict sea wrack presence/absence. Δ AIC: difference between the current and best model; AIC_w: Akaike weight; DE: proportion of deviance explained by the model; (*) denotes interaction terms. Best performing models are in **bold** text

Parameters	Variables	AIC	Δ AIC	AIC _w	DE
Site + Donor Habitat	Aspect + Slope + Substrate + Width + Wave Exposure + Donor Habitat	236.59	0	0.50	0.64
Site + Climate* + Donor Habitat	Aspect + Slope + Substrate + Width + Wave Exposure + Wind Direction \times Wave Height + Wave Period + High Tide + Donor Habitat	237.01	0.42	0.41	0.66
Site + Climate + Donor Habitat	Aspect + Slope + Substrate + Width + Wave Exposure + Wind Direction + Wave Height + Wave Period + High Tide + Donor Habitat	240.05	3.46	0.09	0.65
Site	Aspect + Slope + Substrate + Width + Wave Exposure	281.01	44.42	0	0.56
Site + Climate	Aspect + Slope + Substrate + Width + Wave Exposure + Wind Direction + Wave Height + Wave Period + High Tide	282.73	46.14	0	0.58
Site* + Climate* + Site \times Climate + Donor Habitat	Aspect \times Wind Direction + Slope \times Substrate + Width + Wave Exposure + Wind Direction \times Wave Height + Wave Period + High Tide + Donor Habitat	361.97	125.38	0	0.44
Site* + Climate + Donor Habitat	Aspect + Slope \times Substrate + Width + Wave Exposure + Wave Height + High Tide + Donor Habitat	366.34	129.75	0	0.44
Site* + Donor Habitat	Aspect + Slope \times Substrate + Width + Wave Exposure + Donor Habitat	369.35	132.76	0	0.41
Site* + Climate*	Aspect + Slope \times Substrate + Width + Wave Exposure + Wind Direction \times Wave Height + High Tide	397.61	161.02	0	0.38
Site*	Aspect + Slope \times Substrate + Width + Wave Exposure	404.04	167.45	0	0.34
Climate* + Donor Habitat	Wind Direction \times Wave Height + Wave Period + High Tide + Donor Habitat	477.52	240.93	0	0.21
Climate + Donor Habitat	Wind Direction + Wave Height + Wave Period + High Tide + Donor Habitat	499.96	263.37	0	0.16
Donor Habitat	Donor Habitat	508.39	271.80	0	0.13
Climate*	Wind Direction \times Wave Height + Wave Period + High Tide	570.33	333.74	0	0.03
Climate	Wind Direction + Wave Height + Wave Period + High Tide	570.79	334.20	0	0.03

Table 3. Akaike's Information criterion (AIC) values from candidate models to predict accumulated sea wrack biomass. AIC: AIC score; Δ AIC: difference between the current and best model; AIC_w: Akaike weight; (*) denotes interaction terms. Best performing models are in **bold** text

Parameters	Variables	AIC	Δ AIC	AIC _w
Site*	Aspect + Slope \times Substrate + Width + Wave Exposure	732.68	0	0.54
Site* + Donor Habitat	Aspect + Slope + Substrate + Width + Wave Exposure + Donor Habitat	734.68	2	0.20
Site	Aspect + Slope + Substrate + Width + Wave Exposure	735.99	3.31	0.10
Site* + Climate*	Aspect + Slope \times Substrate + Width + Wave Exposure + Wind Direction \times Wave Height + Wave Period + High Tide	737.37	4.69	0.05
Site + Donor Habitat	Aspect + Slope + Substrate + Width + Wave Exposure + Donor Habitat	737.86	5.18	0.04
Site + Climate	Aspect + Slope + Substrate + Width + Wave Exposure + Wind Direction + Wave Height + Wave Period + High Tide	739.47	6.79	0.02
Site* + Climate + Donor Habitat	Aspect + Slope \times Substrate + Width + Wave Exposure + Wind Direction + Wave Height + Wave Period + High Tide	739.77	7.09	0.02
Site* + Climate* + Site \times Climate + Donor Habitat	Aspect + Slope \times Substrate + Width + Wave Exposure + Wind Direction \times Wave Height + Wave Period + High Tide + Wind Direction \times Aspect + Donor Habitat	741.26	8.58	0.01
Site + Climate + Donor Habitat	Aspect + Slope + Substrate + Width + Wave Exposure + Wind Direction + Wave Height + Wave Period + High Tide + Donor Habitat	741.47	8.79	0.01
Site + Climate* + Donor Habitat	Aspect + Slope + Substrate + Width + Wave Exposure + Wind Direction \times Wave Height + Wave Period + High Tide + Donor Habitat	741.69	9.01	0.01
Donor Habitat	Donor Habitat	743.24	10.56	0
Climate	Wind Direction + Wave Height + Wave Period + High Tide	744.22	11.54	0
Climate*	Wind Direction \times Wave Height + Wave Period + High Tide	745.92	13.24	0
Climate + Donor Habitat	Wind Direction + Wave Height + Wave Period + High Tide + Donor Habitat	745.95	13.27	0
Climate* + Donor Habitat	Wind Direction \times Wave Height + Wave Period + High Tide + Donor Habitat	747.84	15.16	0

value were considered to have similar levels of support. From the top models, we determined which option best explained the data by calculating the Akaike weight for each model and the proportion of deviance being explained for the presence/absence model (Tables 2 & 3) (Burnham et al. 2011).

For both the presence/absence and the biomass datasets, we checked the models for independence and spatial correlation by examining the residuals of each top model for signals that we violated independence (Fig. S3) and none were detected. Wrack accumulation is understood to be determined by biophysical forces (represented by our predictor variables), not the influence of latitude or longitude (Barreiro et al. 2011). However, for both the presence/absence and the biomass dataset, we examined the residuals of each top model for signals that we violated assumptions of spatial independence in the linear model. We plotted residuals against latitude, longitude, and island node and found no patterns of

concern. We also mapped residuals against their spatial coordinates using the package 'gstat' in R (Pebesma 2004, Graler et al. 2016) to check for any patterns that may indicate spatial correlation issues not captured by plots of latitude or longitude individually (Figs. S4–S7).

2.4.2. Temporal surveys

Dry wrack biomass was log transformed and compared across months ($n = 5$) and sites ($n = 3$) using ANOVA, and significant differences in biomass accumulations among months and sites were explored via Tukey's HSD test. To test the variability in wrack species composition and biomass accumulation through time, we analyzed the relative biomass accumulation of each wrack taxon per month and per site using ANOSIM (Clarke 1993). Non-metric multidimensional scaling using Bray-Curtis dissimilarity

matrix techniques was also used to assess whether composition changed with seasons or between sites. A SIMPER routine was performed to identify the species with the highest contribution to the similarity/dissimilarity of each month or site. The Shannon–Wiener diversity index was used to explore species diversity in the summer (June, July, September) compared to the winter (November, February, April).

3. RESULTS

3.1. Spatial surveys

A total of 52 genus, functional group, or species representatives were recorded throughout the study region (Table S4). Calvert node had the highest number of species ($n = 35$) and Stirling node had the lowest ($n = 8$, Fig. 3). Six species contributed to 84 % of the total biomass accumulations: *Zostera marina* (40 % of total biomass), *Fucus distichus* (26 %), *Pterygophora californica* (10 %), *Macrocystis pyrifera* (4 %), and *Nereocystis luetkeana* and *Phyllospadix* spp. (each contributing 2 % to total biomass) (Table S4). The other 46 species each contributed 1 % or less of total accumulated biomass (Table S4). Species composition was dissimilar among nodes (ANOSIM; factor = node,

$R = 0.08$, $p < 0.02$, Fig. 3; Fig. S8). The top contributors to the dissimilarities among nodes were *Zostera* spp., *F. distichus*, and *P. californica* (SIMPER; *Zostera* spp. average dissimilarity = 69 %, *F. distichus* = 49 %, *P. californica* = 43 %). All SIMPER results for the cumulative contribution of the most influential species can be found in Fig. S9. Driving these dissimilarities are species that appeared dominant in certain nodes: *P. californica* was abundant in the McMullin node, *Z. marina* in the Goose node, *N. luetkeana* in the South Calvert node, and *F. distichus* in all nodes except McMullin (Fig. 3).

Accumulated wrack biomass varied widely across the study region (Fig. 1A–F), ranging from 0 g m⁻² on many islands to a mean of 6952 ± 4325 (SD) g m⁻² at one small island in Goose node. Average wrack accumulations per site did not differ among nodes (ANOVA; $F = 0.42$, $p = 0.9$).

In tests for the presence/absence of wrack, the top model was composed of 2 parameter groups: site and the extent of donor habitat (Table 2). This model indicated that the combination of aspect, slope, width, wave exposure, substrate, and extent of donor habitat best predicted whether a site would have wrack present (Table 2). Examining the relative influence of each factor in the top model, substrate, extent of donor habitat, and slope had significant associations (Table 4). Of the 5 substrate types (sand, gravel, cobble, boulder, and rock), rock had a strong negative

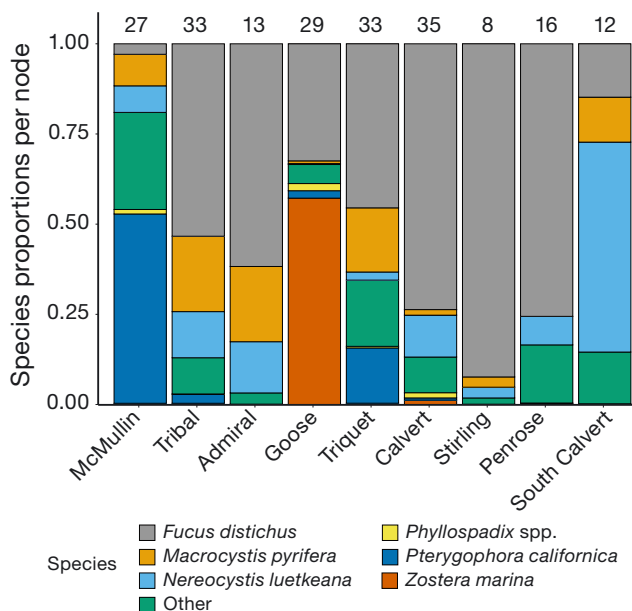


Fig. 3. Proportions for each node of the 6 dominant algal species observed throughout the study area. 'Other' is the combined total of all other species recorded in that node. Proportions are calculated from summed dry biomass. Total number of species of seaweeds recorded in the wrack deposits for each node is displayed above the bar

Table 4. Coefficient estimate, standard error (SE), and p-value for each term in the top model (see Table 2) predicting wrack presence/absence, as determined by the lowest AIC and highest AIC_w scores. Coefficient estimate is standardized for continuous predictor variables (shoreline width, wave period, and donor habitat). The first (alphabetical) term for categorical variables (substrate: boulder and wave exposure: exposed) is the reference/baseline for that category. Significant terms are in **bold text**

Variable	Estimate	SE	p
Sine aspect	0.24	0.28	0.4
Cosine aspect	-0.44	0.27	0.1
Shoreline slope	-0.83	0.32	<0.01
Shoreline width	0.57	0.32	0.8
Wave exposure: very protected	1.85	1.03	0.07
Wave exposure: protected	1.45	0.79	0.06
Wave exposure: semi-protected	0.96	0.82	0.2
Wave exposure: semi-exposed	0.49	0.80	0.5
Wave exposure: very exposed	-0.28	0.98	0.8
Substrate: sand	14.5	1022.67	1
Substrate: gravel	-0.29	1.40	0.8
Substrate: cobble	0.82	1.30	0.5
Substrate: rock	-4.84	0.69	<0.01
Donor habitat	1.42	0.26	<0.01

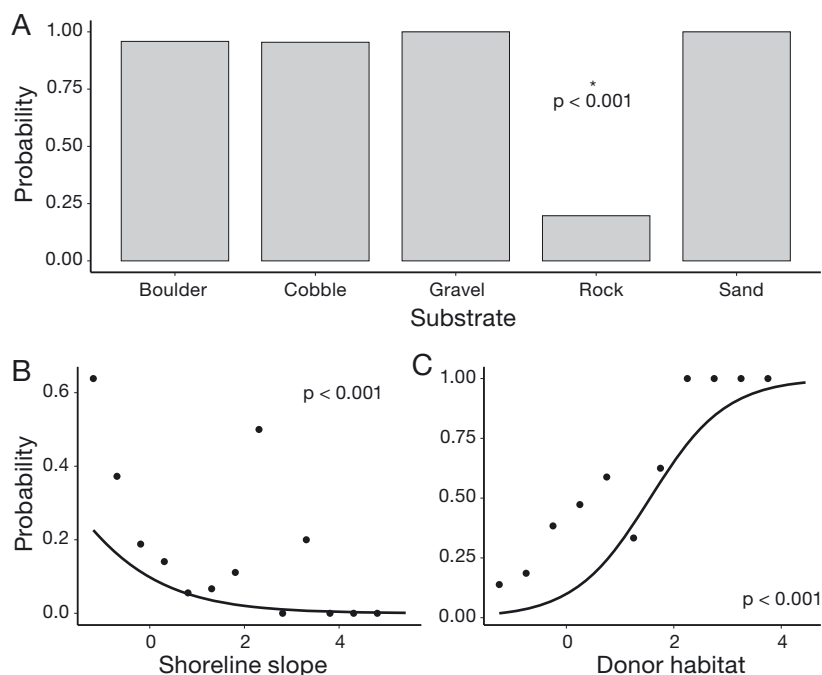


Fig. 4. Probability of wrack presence as a function of the significant terms: (A) substrate, (B) shoreline slope, and (C) extent of donor habitat from the top-ranking model predicting the presence or absence of wrack at 455 sites on 101 islands on the Central Coast of British Columbia. (*) denotes significant difference among categories. Continuous predictor variables (shoreline slope and donor habitat) have been standardized by subtracting the mean and dividing by the standard deviation, and thus have no units

influence when predicting the presence of wrack on shorelines (Table 4, Fig. 4). None of the other 4 substrates significantly influenced wrack presence. Shoreline slope negatively influenced wrack accumulations (Table 4, Fig. 4). The extent of donor habitat within a 2 km radius had a positive influence on wrack presence (Table 4, Fig. 4).

For the biomass data set, which tested the predictors of accumulated wrack biomass at a site, the top model had 1 parameter: site (and the interactions between site variables; Table 3). This model indicated that a combination of aspect, slope, width, substrate, wave exposure, and interactions between slope and substrate best predicted wrack biomass accumulations (Table 3). Wave exposure and width significantly influenced the biomass of wrack accumulations (Table 5). Of the 6 categories of wave exposure (very protected, protected, semi-protected, semi-exposed, exposed, and very exposed), semi-exposed exposures were positively correlated with wrack presence (Table 5, Fig. 5). The width of the shoreline, measured from the terrestrial edge to the water's edge at a consistent tidal height, also had a positive influence on wrack accumulations (Table 5, Fig. 5).

3.2. Temporal surveys

Wrack was present at all sites in all seasons (Fig. 6), but we found a significant difference in the amount of wrack deposited on a monthly basis (ANOVA; $F_{5,174} = 4.07$, $p < 0.002$). These results were driven by differences in wrack accumulations between July and the winter months (Tukey multiple comparison of means; February $p < 0.03$, November $p < 0.009$, Fig. 6). There was a significant difference in wrack accumulation among sites (ANOVA; $F_{2,177} = 4.39$, $p < 0.02$), driven by a difference between North Beach and West Beach (Tukey multiple comparison of means $p < 0.02$). We also found differences in species composition among months. Given the modest ANOSIM R estimate ($R = 0.23$ or 0.24) and the low number of replicates, we interpret these results conservatively and thus we consider there to be only moderate overlap in species composition for both month and site (Fig. S10, ANOSIM; factor = month, $R = 0.24$, $p < 0.001$; factor = site, $R =$

0.23 , $p < 0.05$). North Beach had the most distinct biomass and species composition for each survey, driving the variation among sites in the ANOSIM

Table 5. Coefficient estimate, standard error (SE), and p-value for each significant term in the top model (see Table 3) predicting wrack biomass accumulation as determined by the lowest AIC and highest AIC_w scores. Coefficient estimate is standardized for continuous predictor variables (donor habitat). The first (alphabetical) term for categorical variables (wave exposure: exposed) is the reference/baseline for that category. × denotes interaction terms. Significant terms are in **bold text**

Variable	Estimate	SE	p
Sine aspect	0.21	0.29	0.5
Cosine aspect	0.39	0.31	0.2
Shoreline width	0.46	0.21	0.03
Wave exposure: very protected	2.06	2.06	0.1
Wave exposure: protected	1.73	1.20	0.2
Wave exposure: semi-protected	0.88	1.24	0.5
Wave exposure: semi-exposed	2.73	1.26	0.03
Wave exposure: very exposed	0.30	1.65	0.9
Slope × Substrate: sand	−0.89	0.72	0.2
Slope × Substrate: gravel	−0.19	0.96	0.9
Slope × Substrate: cobble	−0.70	0.49	0.2
Slope × Substrate: boulder	−1.02	0.64	0.1
Slope × Substrate: rock	0.86	0.57	0.1

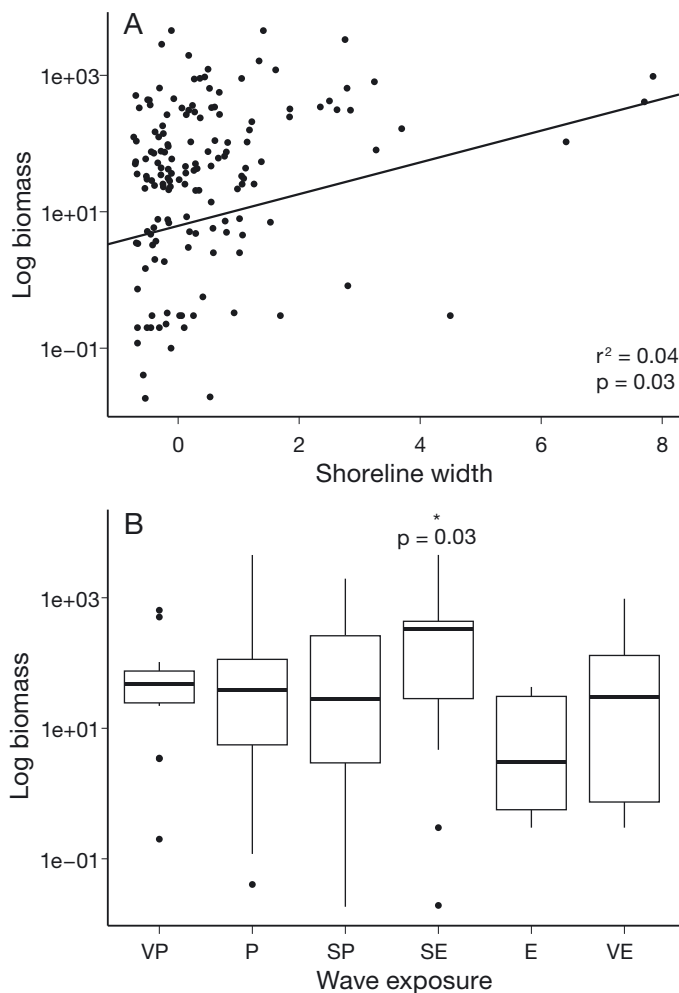


Fig. 5. Log wrack biomass as a function of model parameters with significant ($p < 0.05$) effects; (A) shoreline width and (B) wave exposure from the top-ranking model predicting biomass of wrack at 455 sites on 101 islands on the Central Coast of British Columbia. Categorizations for wave exposure are VP: very protected, P: protected, SP: semi-protected, SE: semi-exposed, E: exposed, and VE: very exposed. (*) denotes significant difference among categories. Continuous predictor variable (shoreline width) has been standardized by subtracting the mean and dividing by the standard deviation, and thus has no units. Box plots show median value (solid horizontal line), upper and lower quartiles (box), and maximum and minimum values recorded (whiskers). Outliers (•) are also shown

results. Species diversity was higher in the summer ($H' = 2.02$) than in the winter ($H' = 1.64$).

The top contributors to the dissimilarities among all sites were *N. luetkeana* and *Phyllospadix* spp., (SIMPER; *N. luetkeana* average dissimilarity = 52%, *Phyllospadix* spp. = 36%). *F. distichus* was also a top contributor in explaining North Beach's dissimilarities to West and Fourth Beaches (SIMPER; average dissimilarity = 76%). *N. luetkeana* and *Phyllospadix* spp. were again responsible for explaining dissimi-

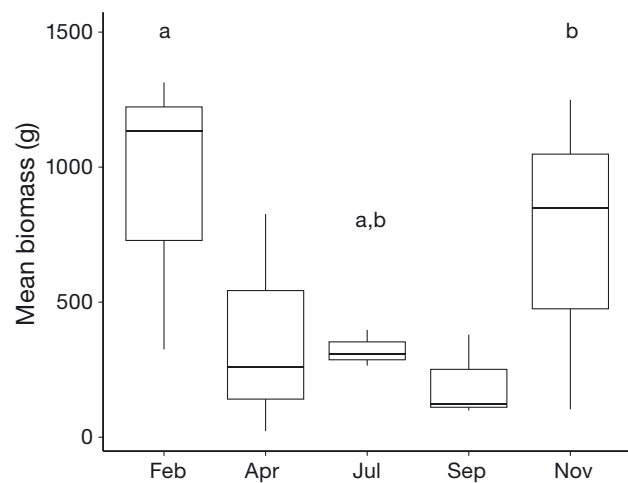


Fig. 6. Total dry wrack biomass per site at 5 different seasonal intervals. Box plots show median value (solid horizontal line), upper and lower quartiles (box), and maximum and minimum values recorded (whiskers). Mean biomass accumulation differed significantly between July and February ($p < 0.03$), and between July and November ($p < 0.009$), as indicated by letters above respective plots

larities among months (SIMPER; *N. luetkeana* average dissimilarity = 62%, *Phyllospadix* spp. = 38%). In addition, *F. distichus* was a top contributor in July (SIMPER; average dissimilarity = 44%), and *P. californica* was a top contributor in February (SIMPER; average dissimilarity = 71%). All SIMPER results for the cumulative contribution of the most influential species are summarized in Figs. S11 & S12.

4. DISCUSSION

We conducted a multi-year survey of wrack deposits on 101 islands to explain patterns of wrack presence and accumulation along shorelines. Of the 3 broad factors considered (extent of nearby donor habitats, climate, and site characteristics) we found strong evidence that wrack accumulations were primarily driven by site characteristics and the donor habitat area. Climate events (i.e. wind, tide, swell) had little influence on wrack accumulation. However, the climate data used for analysis were short term. Further analysis of long-term climate data could provide more evidence for an effect of climate on wrack accumulations. Ocean currents, which we did not include in our models, are another broad factor that may affect wrack accumulations along this coastline, and we recommend this as an avenue for future studies. Finally, we also found that wrack depositions differed significantly temporally and compositionally

(i.e. among species). As seen in other systems, these results indicate that wrack subsidies are varied, pulsed across both space and time, and have the potential to impact terrestrial productivity and diversity (Spiller et al. 2010, Filbee-Dexter et al. 2018, Fong & Fong 2018).

Wrack accumulations varied in biomass across the study region, ranging from 0 to 6952 g m⁻², with an average of 698 g m⁻² in accumulated biomass per site. Previous research on sea wrack performed in Barkley Sound recorded dry biomass accumulations ranging from near 0 to almost 9 kg m⁻¹ of shoreline across 6 sites in 1 season (Orr et al. 2005). A similar study in Oregon recorded wrack biomass accumulations across 12 sites in 2 seasons and found a maximum of 100 g m⁻² in the summer and a maximum of 115 g m⁻² in the fall (Reimer 2014). Notably, our surveys were the only surveys to record sites with zero accumulations and also the only surveys to include sites composed of rock or boulder substrates.

These results demonstrate that patterns in wrack biomass accumulations vary across the Pacific Northwest, which is not surprising as these sites differ in so many factors (i.e. physical characteristics, donor habitat species and productivity, climate). These results highlight the importance in determining accumulation rates specific to local geographies when considering wrack as a potential vector of marine nutrients. Below, we discuss the local factors (shoreline substrate, slope, wave exposure, width, and the extent of donor habitat) that affect the ability of sea wrack to permeate ecosystem boundaries on the Central Coast of BC.

4.1. Spatial and temporal patterns of wrack accumulation

The presence of sea wrack was significantly lower at sites with consolidated rocky substrates compared to sites with sand, gravel, cobble, or boulder substrates. Previous studies have confirmed that the volume of wrack along a shoreline decreases with a substratum's pore size (Valiela & Rietsma 1995, Orr et al. 2005). Rock, having no pores and relatively high surface friction, does not retain wrack detritus to the same extent as sand, gravel, cobble, or boulder substrates do. Like many of the world's temperate coastlines, the Central Coast of BC has abundant rocky shorelines (Alaback & Pojar 1997; Fig. 2). In fact, nearly 75% of the sites surveyed were classified as rock (Fig. S13). These small temperate islands with rocky shores accumulate less wrack along their shorelines, and thus fewer marine resources are available to terrestrial consumers. Therefore, in the context of

boundary dynamics, wrack nutrient subsidy in this system relies on site permeability, which may significantly decrease nutrient arrival and thus dampen the expected relationship between island size and subsidy-enhanced productivity.

Shorelines with steeper slopes (i.e. cliffs, Fig. 2) were negatively correlated with wrack presence. This result aligns with our predictions based on the assumption that cliffs would provide gravity the opportunity to pull wrack off of a shoreline and back into the ocean. These findings are also consistent with results of previous studies from Australia and Spain, which reported negative associations between slope and the rate of wrack accumulations (Oldham et al. 2010, Barreiro et al. 2011). In contrast, Liebowitz et al. (2016) found that the biomass of shore-cast *Phyllospadix* spp. was positively correlated with steeper slopes, and suggested that this genus (which degrades slowly) can persist on steep shorelines when it is cast high up on the beach during peak high tides (Liebowitz et al. 2016). However, Liebowitz et al. (2016), Oldham et al. (2010), and Barreiro et al. (2011) all performed research on sandy beaches, whereas our research was conducted on a variety of shoreline substrates. We suggest that more buoyant seaweeds (i.e. species with pneumatocysts) could be retained on steep slopes when they are cast high upon the shoreline, and when this process does occur, it may permit a wrack subsidy to permeate islands with shorelines comprised of cliffs as either direct fertilization for shoreline flora or indirectly as an invertebrate food source.

The extent of donor habitat was a consistent driver of wrack presence, suggesting that the size and productivity of eelgrass beds, kelp forests, and *Fucus distichus* habitats are important factors when considering island archipelagos and convoluted shorelines, as fetch is reduced in these contexts and wrack is likely to wash ashore close to its site of detachment, creating predictability in marine resource subsidy availability. These results are consistent with similar findings on the coast of California, which tested the relationship between accumulated wrack biomass and extent of donor habitat within a 1 km radius of a site and found the extent of donor habitat to have a positive influence on accumulated wrack biomass (Liebowitz et al. 2016). However, because the coast of California differs geomorphologically from the Central Coast of BC, these results have different implications in the context of rocky islands and the presence and extent of donor wrack species. Islands with permeable shorelines near large, productive donor habitats may receive more consistent wrack input than

islands further away from donor habitats. Alternatively, impermeable islands with rock and cliff shorelines will not be able to accept wrack as a subsidy, regardless of the size or productivity of a donor bed. Additionally, the species composition of the habitat could affect the consistency of the subsidy, as eelgrass and *Macrocystis pyrifera* kelp are perennials and may contribute wrack to shorelines year-round. However, the kelp *Nereocystis luetkeana* is an annual and may contribute the bulk of its biomass as wrack to shorelines when it senesces during the fall/winter storm season. Accordingly, the size, proximity, and species composition of the donor habitat, as well as the permeability of the recipient ecosystem, should be considered when investigating ecosystem connectivity and marine–terrestrial subsidy.

We found that shorelines with semi-exposed wave exposures were significantly positively associated with wrack biomass accumulations. This contrasts with other research, which described how reduced water flow in more protected wave exposures leads to greater wrack accumulations (Howd 2006, Barreiro et al. 2011). However, on the Central Coast, the moderate disturbance of semi-exposed shorelines may create more seaweed erosion and thus more floating wrack. The width of a shoreline was also positively associated with wrack accumulations. When considering these results together, we hypothesize that wider shorelines create a conducive environment for waves to push wrack accumulations on shore.

The processes that drive wrack species composition involve factors that operate at local scales. Although the species comprising wrack accumulations were ubiquitous across the study region, which indicates no influence of a latitudinal gradient on species composition, some species were present in higher abundances in certain nodes (*Pterygophora californica* in McMullin node, *Zostera marina* in Goose node, *N. luetkeana* in South Calvert node, and *F. distichus* in all nodes except McMullin). Abundances for some species can be readily explained; there is a large seagrass bed present in the Goose node, and historical sea otter colonization mediated a recent mass senescence of *P. californica* in the McMullin node (Rechsteiner et al. 2018). Accordingly, rocky intertidal shorelines (habitat for *F. distichus*) may be present throughout the region in relatively similar abundance. Our findings that indicated increased donor habitat adjacent to a site led to the presence of wrack on that same site's shoreline, may be especially important when considering other factors. For example, the physical characteristics of seaweed and kelp species (such as pneumatocysts that create

buoyancy) may also influence the distribution pattern of wrack species to shorelines, allowing some species to travel further than others before being washed ashore or cast higher up the beach (Salomonsen et al. 1999, Hobday 2000, Flindt et al. 2007, Oldham 2014, Liebowitz et al. 2016).

Our results indicate that wrack was consistently present on shorelines throughout the year with pulses in seasonal accumulations. Many seaweeds in the northeast Pacific Ocean are annual species that grow only in the spring and summer (Druehl & Clarkston 2016), which was consistent with our observations of a higher diversity of seaweed species onshore during these seasons. Accumulated biomass was higher in the winter, but with fewer species. Of the top biomass contributors, *N. luetkeana* displayed patterns of seasonal wrack deposition. This is expected for seaweeds with annual life histories. *N. luetkeana* grows from early spring to the fall (Mann 1973) and dislodgment due to winter storms likely accounts for the increased biomass we recorded at our sites. Species with perennial life histories are expected to display less pronounced seasonal signals (Liebowitz et al. 2016); however, our results demonstrated temporal dissimilarities for the perennials *Phyllospadix* spp., *Pterygophora californica*, and *F. distichus*. This suggests that seasonality may not affect patterns of wrack deposition and accumulation on the Central Coast of BC. More frequent temporal surveys could parse out whether seasonal patterns are dominant factors in wrack accumulation.

4.2. Implications for island nutrient subsidies

Our finding that shoreline substrate is a key factor in facilitating the arrival of wrack on islands has implications for the extent of island nutrient subsidies. Globally, the main avenue thought to facilitate the transfer of seaweed-derived nutrients to the terrestrial environment is the direct consumption of wrack by a large community of semi-terrestrial and terrestrial invertebrates (Lastra et al. 2008). Amphipods are considered one of the most abundant and ecologically important residents of beach ecosystems (sand, gravel, or cobble substrates), but are not found on rocky shorelines (Colombini & Chelazzi 2003, Pelletier et al. 2011). On islands composed only of rocky shorelines, amphipods would not be able to facilitate the transfer of seaweed-derived nutrients and permeability would be restricted at these sites.

On islands with sand, gravel, or cobble substrates (capable of hosting amphipod populations), marine

nutrient permeability to the islands' interior would be feasible. This vector of nutrient transfer would likely be intensified during the summer months, which is the active season for amphipods (Pelletier et al. 2011). Amphipods preferentially feed on aged wrack over freshly deposited seaweed material, although there is no clear amphipod preference for a particular seaweed species (Pennings et al. 2000, Mews et al. 2006). Therefore, an amphipod's variation in wrack preferences enables a range of diet opportunities. This is ideal during the summer months because wrack accumulations are lower, but wrack species diversity is higher. This adaptation allows amphipods to exploit this marine resource and enables the subsidy to permeate island shorelines that are composed of sand, gravel, or cobble.

Permeability to subsidies is likely to depend on the specific vector being considered. Other vectors of marine-terrestrial subsidies (such as fog, sea spray, humans, and river otters *Lontra canadensis*) fertilize terrestrial soils with marine-derived nitrogen and other nutrients (Ben-David et al. 1998, Whipkey et al. 2000, Ewing et al. 2009, Trant et al. 2016) and were ubiquitous in the study region. Such vectors could contribute to patterns of productivity in this area and beyond. Fog, sea spray, humans, and river otters each have distinct behaviors that would affect their ability to permeate into island interiors and would likely be less deflected by steep, rocky shorelines than sea wrack is. However, the direct effects of these vectors are limited to the edges of islands: trees and shrubs can create a relatively impermeable boundary for fog and sea spray (Ewing et al. 2009), historical humans created 'shell middens' (large piles of bi-valve shells) at habitation sites in bays and estuaries (Fisher et al. 2019), and river otters tend to create latrines and dens near the terrestrial edges of coastlines (Ben-David et al. 1998). Nevertheless, in contrast to sea wrack, communities on rocky islands would still be able to accept these vectors of nutrient flow. On steep, rocky islands along the BC Central Coast (impermeable to sea wrack penetration into the island interior), these 4 vectors of marine nutrient subsidies (fog, sea spray, humans, and river otters) could affect terrestrial productivity. The specific permeability characteristics of a vector should be considered when evaluating the flow of nutrients across ecosystem boundaries.

4.3. Conclusions

Our research reveals that on BC's Central Coast, sea wrack is present on shorelines close to large

donor habitats and is not present on rocky or steep shorelines. Additionally, wrack accumulates on wide, semi-wave-exposed shorelines. Six dominant species of seaweeds and seagrasses (*F. distichus*, *M. pyrifera*, *N. luetkeana*, *P. californica*, *Zostera marina*, and *Phyllospadix* spp.) had a consistent presence on shorelines throughout the year but displayed pulses in biomass accumulations and species composition. These results confirm the potential of sea wrack as a vector of marine resources to islands with beach shorelines. This marine-terrestrial nutrient subsidy may affect the productivity of terrestrial consumers on permeable islands, as other marine resources have been shown to do in low-productivity terrestrial environments (Polis & Hurd 1996, Stapp & Polis 2003, Maron et al. 2006, Mellbrand et al. 2011, Adame et al. 2015). Further research investigating terrestrial species diversity and abundance at these sites can determine the effects, if any, sea wrack has on temperate terrestrial communities in high productivity environments.

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