

AN ABSTRACT OF THE THESIS OF

Jessica N. Reimer for the degree of Master of Science in Zoology presented on September 19, 2014.

Title: Patterns of Macrophyte Wrack Deposition on Sandy Beaches of the Pacific Northwest Coast, U.S.A.

Abstract approved:

Sally D. Hacker

Bruce A. Menge

Dislodged macroalgae and seagrasses, also known as marine wrack, frequently wash into coastal ecosystems from the ocean and are potentially important ecological resources for biological communities. These nutrient and organic matter subsidies may be especially important on sandy beaches, where little *in situ* primary productivity exists for higher trophic levels. To better understand the prevalence of marine wrack as a coastal subsidy to nutrient-poor sand and beachgrass ecosystems, we investigated the pattern of deposition and composition of wrack that washes onto Pacific Northwest sandy beach ecosystems.

We conducted a large-scale, observational study at 12 coastal sites located from southern Washington to northern California to estimate the patch density, biomass, total biomass, and species composition of wrack on each beach. All sites were surveyed in both early summer and early fall to understand how the temporal patterns of certain processes (e.g., storms and algal senescence) affect wrack presence. Linear mixed-effect

models were used to determine the effect of site location and season, as well as a suite of environmental predictors including cross-shore and alongshore upwelling and shoreline change rate (SCR). At all sites, marine wrack increased in patch density and biomass on beaches in the fall suggesting that productivity over the summer, storm activity, and wave action in the fall may have affected the delivery of wrack. In terms of spatial distribution, wrack patch density (per m²) was greatest in the northern region (Greys Harbor to Sand Lake) and wrack biomass (per m²) was greatest in the southern region (Bandon to Cape Mendocino). However, overall total wrack biomass (per block), an integrative measure of patch density and biomass, was greatest in the south (Bandon to Cape Mendocino), intermediate in the north (Greys Harbor to Sand Lake), and lowest in the central region (South Beach to North Spit), although Greys Harbor and Cape Lookout in the north had similar amounts to sites in the southern region. Further analysis showed that cross-shore upwelling had a positive effect on wrack patch density and wrack biomass, while total biomass was not correlated with the environmental variables we tested.

Composition varied predictably across the coast, with eelgrass present in greater proportions at northern sites and kelp present in greater proportions at central and southern sites. Kelp and eelgrass biomass were also strongly negatively influenced by distance from rocky reefs and estuaries, their respective source habitats (kelp biomass decreased further from rocky reefs, while eelgrass biomass decreased further from estuaries). In addition, kelp biomass was positively affected by SCR, while eelgrass biomass was negatively affected by cross-shore upwelling and positively affected by alongshore upwelling.

This study, one of the first to examine large biogeographic scale patterns of wrack deposition, suggests that upwelling, outwelling (the movement of debris from estuaries to the open coast), proximity to source habitat, and beach geomorphology interact to determine the distribution and abundance of wrack onshore. Wrack plays an important role in structuring beach community and food web dynamics, and may also influence beach grass productivity, and thus dune structure and function. Further research on how wrack subsidies affect beach and dune ecosystems, both as a food resource and a nutrient resource, would provide greater insight to its role in these systems, and could have potential implications for dune restoration and conservation.

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Patterns of Macrophyte Wrack Deposition on Sandy Beaches of the
Pacific Northwest Coast, U.S.A

by
Jessica N. Reimer

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented September 19, 2014
Commencement June 2015

Master of Science thesis of Jessica N. Reimer presented on September 19, 2014.

APPROVED:

Co-major Professor, representing Zoology

Co-major Professor, representing Zoology

Chair of the Department of Integrative Biology

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Jessica N. Reimer, Author

ACKNOWLEDGEMENTS

There are so many who have been influential in getting me through this stage of my education, and I sincerely thank all who have provided support through mentoring, dedication of time and energy, friendship, and their belief in my abilities. First and foremost, I have to thank my advisors, Dr. Sally Hacker and Dr. Bruce Menge, who have played a critical role in helping me both complete my masters' degree and decide the best educational route for my interests. Their unwavering support of my research and my decision to take a different path from where I began has meant so much and allowed me to gain confidence in my abilities as a scientist and researcher. I will always be grateful for their encouragement to build the career that I want.

I have been lucky to be a part of two labs that feel more like family than co-workers. Doing everything from sharing offices and collaborating on projects, to spending countless hours together in the field and never quite understanding "The Game" on endless van rides, to attending numerous happy hours, concerts and taking fun trips – the last three years have been full of many incredible experiences and memories because of all of you. To the graduate students (and former grads) – Allison Barner, Elizabeth Cerny-Chipman, Chenchen Shen, Sarah Close, Jeremy Rose, Jeremy Henderson, Alison Iles, Reuben Biel, and Jenna Sullivan – thank you for your many conversations and advice on both research and life. Your moral support has helped develop me into the graduate student, scientist, and person that I am today, and I am grateful. To the (current and former) lab technicians – Angela Johnson, Shawn Gerrity, Jonathan Robinson, Tully

Rohrer, Jerod Sapp, and Lindy Hunter – thank you for your constant willingness to help in the lab and field, making the countless field trips feel like play and not work, and for always providing friendship. I will greatly miss both working and playing with all of you.

Completing my project would not have been possible without the incredible dedication of Sarah Vojnovich, Ian Maher and, especially, Melanie Ripley, who put in countless hours of sorting icky, mushy, decaying wrack samples. Their always-positive attitude and willingness to sort for hours on end, even during school breaks, not only helped me collect all of my data, but kept me in good spirits as well. To this end, I also have to thank all of those who participated in the “wrack sorting party,” which helped me through the last push of data collection.

My additional committee members provided great insight and guidance on my project. Dr. Francis Chan encouraged me to think critically about my research and taught me to constantly shift the lens through which I viewed my work in order to best interpret and understand the results. My graduate representative, Dr. Selina Heppell, provided productive comments, advice and moral support. All of my committee members, especially Dr. Hacker and Dr. Menge, have helped me develop into a true scientist.

The Oregon State University Department of Zoology (now Integrative Biology) has also been incredibly supportive, especially Torri, Tara, Traci and Trudy, who always seem to have the answer, no matter how obscure.

Finally, I have to thank my family for their love and unconditional support as I have embarked on this new journey of becoming a scientist. Their patience, listening ear, and financial help have allowed for my success, and I could not have done it without

them. To my friends at and outside of OSU, thank you for the dose of reality you always provided and for keeping me sane. To Matt, who entered my world during the midst of my graduate school tenure, thank you for the pep talks and helping me keep it all in perspective. You all have helped me get to where I am today.

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Patterns of Macrophyte Wrack Deposition on Sandy Beaches of the Pacific Northwest Coast, U.S.A

INTRODUCTION

The dynamics of coastal ecosystems are complex and involve the interplay of many processes at various spatial and temporal scales that help to structure communities living along the shoreline. However, research over the past half century, and specifically the last decade, has helped model this complexity through the development of conceptual frameworks which address coastal dynamics at large biogeographic scales. Specifically, meta-ecosystem theory (Loreau et al. 2003) has been proposed as a framework for understanding the flow of ecological subsidies, defined as “energy, materials and organisms that cross ecosystem boundaries,” such as those between nearshore, intertidal, and beach systems. The theory was recently refined by Menge and collaborators (in review) who consider the scales across which these subsidies are transported, and explain the degree of connectivity that exists between local, regional, and macroscales.

Spatial and temporal flows of materials and organisms between ecosystems are increasingly identified as important drivers of local community structure, trophic dynamics, and productivity within and among a variety of ecosystems, particularly at the land-water interface of coastal (Polis and Hurd 1996, Kirkman and Kendrick 1997, Orr et al. 2005, Spiller et al. 2010) and riparian habitats (Vannote et al. 1980, Murakami and Nakano 2001, Sabo and Power 2002). Allochthonous ecological subsidies, or nutrients and organic matter that cross from a “source” ecosystem into an adjacent “sink” habitat, have been shown to directly and indirectly affect local productivity by providing

additional resources to both primary producers and consumers (Wootton 1994, Polis and Hurd 1996, Sears et al. 2004). In coastal ecosystems, empirical work investigating the flow of allochthonous subsidies among different systems was pioneered by Polis and colleagues (Polis and Hurd 1995, 1996, Polis et al. 1997, Rose and Polis 1998, Sanchez-Pinero and Polis 2000) who found strong coupling between the highly productive marine ecosystem and oligotrophic desert islands, particularly during periods of low rainfall. Specifically, their research showed that marine macrophyte wrack (dislodged macroalgae and seagrasses) and carrion of marine animal carcasses that were deposited onshore contributed substantially to the terrestrial productivity of the island (Polis and Hurd 1996). The ecological role of marine wrack has been investigated in tropical regions (e.g., Spiller et al. 2010, Piovia-Scott et al. 2013), but only recently have investigations expanded to temperate zones where both terrestrial and marine systems are highly productive (Dugan et al. 2003, Lastra et al. 2008, Barreiro et al. 2011, Dethier et al. 2014, Nielsen et al. 2013), thus providing insight into the generality of the functional role of wrack in coastal ecosystems.

The ecological role of marine macrophyte wrack has been of interest because of its ubiquity on coastal beaches and the role it plays as a nutrient subsidy (Polis and Hurd 1995, Orr et al. 2005, Spiller et al. 2010, Dugan et al. 2011, Gomez et al. 2013). Wrack is thought to be important habitat and a primary food resource for macroinvertebrate and bird communities that live on beaches and dunes (Holmquist 1997, Dugan et al. 2003, Jaramillo et al. 2006, Dethier et al. 2014), and contributes to the abundance and diversity of beach communities through the enhancement of trophic webs (Ince et al. 2007). For

example, more wrack can support a greater abundance and diversity of macroinvertebrates, which in turn can enhance bird populations. Dugan et al. (2003) demonstrated these connections in southern California when they considered the community structure of groomed versus natural beaches. Natural beaches with high amounts of wrack had greater species richness and abundance of crustaceans and insects compared to beaches with less wrack or those that were groomed. In addition, they found that the abundances of two species of plovers, a small shorebird that uses visual cues to forage, were positively correlated with the standing crop of wrack. Research conducted on beaches and dunes also has revealed that marine wrack increases nutrients, primarily nitrogen (both organic and inorganic forms) and phosphorus, that are available to consumers (Dugan et al. 2011, Barreiro et al. 2013), and is a source of dissolved organic carbon to beaches (Lavery et al. 2013). Moreover, wrack subsidies may be an important source of nutrients to dune vegetation, controlling its abundance and sand capture ability, and ultimately affecting dune geomorphology. Dune structure and function are key to a number of important ecosystem services including coastal protection from overtopping and erosion (Barbier et al. 2008, 2011, Seabloom et al. 2013). However, the influence of wrack on the productivity of dune ecosystems, particularly vegetation, is poorly understood.

Although it is clear that wrack subsidies are ubiquitous and can have important ecosystem level effects for sandy beach habitats, they have only been studied in a few locations around the world and at small, local spatial scales, with the exception of Nielsen et al. (2013), which looked at wrack deposition across the North-Central California coast.

In this study, we investigate the large-scale regional distribution of wrack on sandy beaches of the Pacific Northwest coast of the United States. This is a region characterized by extensive sandy beach habitat (roughly 40% of the coast) and the largest dune sheet in North America (Cooper 1958). The majority of these beaches are backed by dune habitat covered by two congeneric invasive beach grasses (*Ammophila arenaria* and *A. breviligulata*) that, along with sand supply and waves, play a dominant role in shaping the structure and biodiversity of these habitats, and thus coastal protection (Wiedemann and Pickart 2008, Zarnetske et al. 2010, 2013, Hacker et al. 2012, Seabloom et al. 2013). Moreover, these beaches are exposed to the California Current, a highly productive upwelling system that supports large macrophyte communities along the headlands and estuaries of the Pacific coast (Hessing-Lewis and Hacker 2013, Menge et al. in review). To explore this understudied system, we conducted surveys on dune-backed sandy beaches from central Washington to northern California, a 900-km distance along the coast, to determine the distribution and abundance of macrophyte wrack subsidies, their potential origin, and the resulting implications for the management of beach and dune communities.

Three primary factors are likely responsible for macrophyte wrack abundance and distribution: ocean productivity, current and tidal movement, and beach geomorphology. First, ocean productivity determines the amount of the wrack macrophyte standing stock, in conjunction with the availability of rocky substrate and estuarine habitat (source habitats of macrophytes). In our region, primary productivity varies along the coast because of differences in ocean upwelling driven by the California Current (Hessing-

Lewis and Hacker 2013, Menge et al. in review), which spans 3,000 km from the southern coast of British Columbia, Canada to Baja California, Mexico. Upwelling is a coupled ocean-atmosphere phenomenon that occurs during the summer months (in the northern hemisphere) and brings cold, nutrient rich water to the surface when strong winds blow southward across the surface waters of eastern-boundary coastal systems. Upwelling interacts with coastal topography and geomorphology to differentially affect coastal regions, with areas of strongest upwelling around headlands (Morgan et al. 2011, Woodson et al. 2012). Nutrients delivered to headlands, generally characterized by rocky intertidal and subtidal habitat, support large kelp forests and macroalgal communities, especially in the southern extent of the region (Menge et al. in review). Estuaries are also affected by upwelling, with regions of stronger, more persistent upwelling generally characterized by a greater biomass of green ulvoid macroalgae and regions with weaker upwelling characterized by greater eelgrass (*Zostera marina* and *Zostera japonica*) biomass (Hessing-Lewis et al. 2011, Hessing-Lewis and Hacker 2013). Therefore, upwelling plays an important role in structuring local rocky shore and estuarine communities and fueling macrophyte productivity and growth, and together with the habitat types present in the region, may affect the amount and composition of wrack that is delivered to the shore.

Nearshore coastal currents, tidal movement, and wind are likely the mechanisms through which marine wrack is transported from the source habitat to the beach. Although there are two major currents that dominant in this region – the previously mentioned California Current, which flows southward during the upwelling season, and

the Davidson Current, which is closer to shore and flows northward in the winter (Schwartzlose and Reid 1972) – nearshore currents, such that are formed by upwelling, are likely responsible for the movement of wrack alongshore (Nickols et al. 2012). This movement is also partially driven by wind, as upwelling is a wind-driven current. During the upwelling season, when an upwelling event occurs, strong winds from the north push surface waters, and thus potentially wrack, southward and offshore (Kirincich and Barth 2009). When these winds relax and the onshore movement of water, or downwelling, occurs, surface waters are pushed northward and thus potentially shift the direction of wrack movement.

Marine macrophyte wrack patterns may also be influenced by ‘outwelling’ (Teal 1962, Odum 1968), a term that specifically applies to connectivity between estuaries and the open coast. The outwelling hypothesis suggests that material produced within estuaries is transported to the open coast through the tidal movement of water, where it may become a subsidy to other coastal habitats. However, there is considerable debate as to whether this process exports substantial amounts of organic matter or nutrients to the coast, despite the known exchange of tidal water between estuaries and the ocean (Taylor and Allanson 1995, Dame and Allen 1996, Winter et al. 1996, Cai et al. 1999, Lopes et al. 2008, Das et al. 2010). In addition, a majority of outwelling studies have been conducted in east coast estuaries, where upwelling does not play a strong role in fueling macroalgal growth. One of the few studies of outwelling in West Coast estuaries was conducted in Coos Bay, Oregon, and did not find evidence of outwelling, but rather found that chlorophyll a and phytoplankton largely were transported into the estuary, and

that they served as a resource for estuarine suspension feeding organisms (Roegner and Shanks 2001). Nonetheless, based on the outwelling hypothesis, we would predict that eelgrass, salt marsh vegetation, and most ulvoid macroalgae found on coastal beaches is the result of outwelling from estuaries, and the transportation alongshore via currents. If this process is not strong along the California Current, however, we may not expect to find substantial amounts of estuarine material in wrack.

Finally, the physical properties of the beach and wave action may be important to patterns of wrack deposition. Beach geomorphology is highly variable along the Pacific coast because of differences in sand supply and vegetation that affect the shape and width of the beach and the foredune (Wiedemann and Pickart 2008, Hacker et al. 2012). Research on coastal sand movement has shown that shallower, wider beaches allow for more sand deposition and retention than steeper, narrower beaches (Guza et al. 2011). These systems are fed by river-eroded sand, which moves by currents and strong seasonal winds, creating areas of deposition and erosion along the coast. Erosion and deposition is measured by shoreline change rate (SCR), which acts as a proxy for sediment supply to and from the beach. Typically, beaches with positive SCRs are wider, while those with neutral or negative SCRs are narrower (Ruggiero et al. 2010, 2013). Differing beach geomorphology affects wave action, with wider beaches dissipating wave energy offshore (Wright et al. 1979) and thus creating conditions that would favor wrack deposition over a greater area. In contrast, narrower beaches cause waves to break directly onshore, therefore potentially making it more difficult for wrack to be stranded.

To gain insights into the distribution and abundance of wrack, the factors that control its distribution, and its potential role as a subsidy in this system, we surveyed dune-backed sandy beaches adjacent to the major headlands (Cape Meares, Tillamook Head, Cape Foulweather, Cape Perpetua, Cape Arago, Cape Blanco and Cape Mendocino) and large estuaries (Grays Harbor, Willapa Bay, Netarts Bay, Yaquina Bay, Coos Bay, and Humboldt Bay) that have the potential to export significant amounts of organic matter. We postulated that a combination of upwelling, outwelling, and physical beach characteristics interact to determine the patterns of wrack deposition across the coast. We tested four hypotheses:

H₁: Wrack presence will increase in the fall due to algal senescence and increased wave and storm activity;

H₂: Beaches adjacent to weak upwelling regions will have fewer subsidies compared to beaches with strong upwelling due to increased productivity and growth of macrophytes in source habitats;

H₃: Beaches near rocky shores will have greater amounts of macroalgae, while those near estuaries will have increased amounts of eelgrass; and

H₄: Beaches with greater shoreline change rates (i.e., wider beaches) will have more wrack deposition than narrower beaches.

MATERIALS & METHODS

Study Sites

Our study region consisted of twelve sites spanning a distance of 900 kilometers along the coast from central Washington to Northern California, USA (Figure 1, Table 1). We chose beach sites that had been previously surveyed for dune vegetation and geomorphic features (Hacker et al. 2012; Appendix A) and are located within distinct littoral cells, or areas along the coast with the same sediment source and sink. Sampling was conducted twice to capture seasonal differences in wrack distribution - once in summer 2013 (June-July), when winds from the north drive frequent upwelling events, and once in fall 2013 (September-October) when upwelling events subside and storm frequency increases.

Wrack Distribution Surveys

Sites were sampled within a season as close in time as possible. Surveys within a site were conducted within one day. At each site, we established three replicate blocks. Each block was 100 m long (parallel to shore) and as wide as the beach from the base of the dune to the mean higher high water (MHHW) tide line. We used the MHHW tide line to delineate the block at the water's edge because we observed that the vast majority of the wrack was deposited at or above the high tide line. Each block was bisected by one primary transect parallel to the shore that ran through the most dense wrack zone on the beach (determined visually). Within each block, five secondary belt transects, 10 m wide, were established perpendicular to the shore along the primary transect at 0, 25, 50, 75, and 100 meters (Figure 1, inset). The 50 m transect locations for most blocks

corresponded to transect locations used in Hacker et al. (2012) (see Appendix A for details).

Along each of the secondary transects, we counted the total number of individual wrack patches composed of marine macrophytes (defined as marine macroalgae, seagrasses, and salt marsh vegetation). Detailed surveys of wrack patches were then conducted within each block to better understand the variation in patch size and species composition among sites. Along the primary transect that bisected the block we collected all of the wrack patches in 1-m² quadrat at 25 meter intervals. Samples were stored at -80°C until they were processed in the lab. These collection points corresponded with the intersection of the primary (parallel) and secondary (perpendicular) transects described above. In the lab, samples were sorted to the lowest possible taxonomic classification, dried (60°C), and weighed (grams dry weight, gdw).

Environmental characteristics

We obtained data on upwelling intensity, shoreline change rate (SCR), and distance to potential macrophyte sources (estuaries and rocky reefs) for each site to understand how these environmental characteristics and processes affected wrack distribution and biomass across our study region. Upwelling data were obtained from the NOAA Pacific Fisheries Environmental Laboratory database (<http://coastwatch.pfeg.noaa.gov/erddap/griddap/erdlasFnTran6.html>). We used the cross-shore and alongshore components of Ekman transport ($\text{m}^3 \text{s}^{-1} 100 \text{ m}^{-1}$), with positive values indicating upwelling, and negative values indicating downwelling. We

averaged the daily cross-shore and alongshore values for each site from May – October, which encompassed the upwelling season, as a way to characterize upwelling at each site. We averaged over this six-month period to cover the time span during which our surveys took place, and to account for the potential lag time between upwelling events and the integration of the upwelling signal in the macrophytes (i.e., productivity due to nutrients). Further, the process of dislodgement and deposition on the shore is sporadic, and likely represents an integrated measure across time.

To identify potential source habitats for beach wrack, we used Google Earth (version 7.1.2.2041) and Oregon MarineMap (www.oregon.marinemap.org) to measure the distance from our sites to the nearest estuarine and rocky reef habitat (Table 1). Estuaries were visually identified, and the largest, closest estuary was assumed to be the major source habitat for estuarine wrack identified on the beaches. Rocky reef habitat was identified using the “Rock” layer of the Interim Surficial Geologic Habitat Map for the Oregon Territorial Sea (<http://www.activetectonics.coas.oregonstate.edu/data.htm#2>). The reefs generally correlated with major capes along the coast (Cape Meares, Tillamook Head, Cape Foulweather, Cape Perpetua, Cape Arago, Cape Blanco and Cape Mendocino), but smaller intertidal and subtidal regions between the major capes also may be sources of macrophytes. However, we assumed that a majority of the macroalgal wrack found on beaches came from the nearest cape. Ten of our twelve sites were closest to estuaries, while two sites were closest to rocky reefs (Table 1).

Finally, we used SCR to represent beach geomorphology because of its high correlation with beach width, and comprehensive site coverage (Appendix B). We were

also interested in testing the effects of beach slope, but poor coverage of values at our southern sites precluded its use in our models. SCR was obtained at the 50 m-mark along the primary transect for each block within each site from the USGS National Assessment of Shoreline Change Project (<http://coastal.er.usgs.gov/shoreline-change/>). Sites with positive SCRs accrete sand year-to-year and generally are associated with wider beaches (Appendix B), and those with negative SCRs show erosion and are associated with narrower beaches. We used the available short-term SCRs for Washington and Oregon from Ruggiero et al. (2013), and California from Hapke et al. (2006). SCR from these analyses are the calculated change between historical shoreline positions, collected from digitized maps and aerial photographic sources, and the shoreline in 2002, collected using lidar. Historical shorelines are from a variety of time periods, extending from the 1800s to 1980s.

Statistical analyses

Wrack distribution and abundance

We considered the pattern of wrack presence by examining three response variables – wrack patch density, wrack biomass, and total wrack biomass. Wrack patch density (per m²) was calculated by dividing the total number of patches within each transect by the transect area, and then averaged over the block (n=5 transects per block). Wrack biomass (grams dry weight [gdw] per m²) was summed to the quadrat level, and also averaged over each block (n=5 quadrats per block). Total wrack biomass (kilograms dry weight [kgdw] per block) was determined by first calculating an average weight per

patch (g) for each block. We then calculated the total number of patches in a block by extrapolating the average patch density values collected from the secondary transects to the entire block. Finally, we multiplied the average weight per patch by the total number of patches to obtain total biomass within a block (equation 1).

$$total\ biomass = \left(\frac{avg\ \# \ patches}{m^2 * block} \times block\ area\ (m^2) \right) \times average\ patch\ biomass(g) \quad (Eq.\ 1)$$

We did not scale the total biomass response by area because it represents an integrated measure of patch density, patch biomass and beach width, and we were interested in the differences in these values over the study extent.

All responses were log-transformed to normalize the residuals, but were graphed without the transformation. Blocks (three per site, except where noted due to sampling issues) were used as replicates in our analysis (patch density: n=35 for both summer and fall; biomass: n=29 for summer and n=35 for fall; total biomass: n=29 for summer and n=35 for fall). We also grouped sites into three regions, north (n=5 sites), central (n=4 sites) and south (n=3 sites), to determine the broader-scale differences across the coast (Table 1). Regions were primarily determined by proximity to each other, as well as littoral cell and upwelling patterns (Hacker et al. 2012, Menge et al. in review).

All analyses were conducted using R (version 3.0.2). For each response variable, we first fit a linear mixed-effects ANOVA with site, season, and site x season as fixed effects with a block-by-site random effect (lme4 package [Bates et al. 2014]). Random effect structure was determined using criteria for a nested observational design outlined in Bates (2010). To determine the final model output for each response variable, we compared the full model to a reduced additive model (minus interactions) and a null

model using a Chi-squared drop-in-deviance test. Once the appropriate model was chosen, predictor significance was analyzed using a Type II Wald chi-square test ('Anova' function in the car package [Fox and Weisberg 2011]). Post-hoc differences between sites were determined using linear mixed-effect Tukey's contrasts ('glht' function in the multcomp package [Hothorn et al. 2008]). We analyzed patterns occurring at a larger spatial scale by fitting linear mixed models for each response, with region as a fixed effect and a block-within-region random effect. Because season was an overwhelming driver, we decided to focus on spatial patterns across regions only within our fall survey, when patch density and biomass were generally higher and thus the patterns stronger.

To determine how environmental conditions affected wrack patterns (for all responses listed above), we fit linear mixed-effects models with upwelling variables (average alongshore and cross-shore components of Ekman transport, $\text{m}^3 \text{s}^{-1} 100 \text{ m}^{-1}$) and shoreline change rate (log-transformed, m year^{-1}) as fixed effects, and random effects of block-within-site and season to account for repeated measures over time. We again used chi-squared drop-in-deviance tests to test for model significance, and a Type II Wald chi-square test for predictor significance of the final model.

Wrack composition

We analyzed wrack patch composition at each site to gain insight into the primary wrack source, and thus infer whether beach subsidies primarily came from estuaries and/or rocky reefs. Wrack macrophytes were divided into seven functional groups,

including eelgrass, kelp, brown algae, red algae, green algae, surfgrass, and other estuary salt marsh vegetation (Appendix C). We tested for differences in the proportion of wrack functional group biomass (logit-transformed) using a two-way ANOVA, with site and functional group as fixed effects. We also individually analyzed eelgrass and kelp biomass patterns across sites using one-way ANOVAs. We assumed that eelgrass (*Zostera marina* and *Z. japonica*) came strictly from estuaries, because it is the primary source habitat for eelgrass, and that kelp (e.g., *Nereocystis luetkeana*, *Cystoseira osmundacea*, *Macrocystis integrifolia*, and others – see Appendix C) came strictly from offshore, subtidal rocky reef habitats. We were not able to definitely determine the source of surfgrass (*Phyllospadix* spp.) or other macroalgae because they grow in both rocky reef and near-estuarine habitats.

Finally, we tested for relationships between our environmental predictors and kelp and eelgrass biomass across the coast separately to better understand how the local environment affects wrack composition. We fit general linear models for the kelp biomass and eelgrass biomass (individually) with source distance variables (distance to rocky reefs and estuaries), SCR, and upwelling variables (cross-shore and alongshore components of Ekman transport) as predictors.

RESULTS

Wrack distribution and abundance

We found that wrack patch density, wrack biomass, and total wrack biomass all varied by both site and season, with a site by season interaction (linear mixed-effect

ANOVAs; wrack patch density: $\chi^2(11)=44.56$, $p<0.001$; wrack biomass: $\chi^2(10)=26.63$, $p=0.003$; total wrack biomass: $\chi^2(10)=21.57$, $p=0.02$; Figure 2, Table 2a). All responses were equal or greater in the fall than in the summer at all sites except for Cape Lookout, where biomass and total biomass were greater in the summer. However, within each season, there were consistent patterns that held across our sites, and which tended to be more pronounced in the fall. Wrack patch density (patches m^{-2}) was greatest at northern sites (Greys Harbor to Sand Lake), with the exception of Sand Lake, which had densities closer to those in central (South Beach to North Spit) and southern sites (Bandon to Cape Mendocino; Figure 2). North Spit, a central site located furthest south within the region and near Coos Bay, was also more similar to northern sites than those in the central region, while most other central sites were similar to those in the south (Tukey's contrasts for linear mixed-effect models; see Appendix D for detailed analysis table). In contrast to wrack patch density, wrack biomass was greatest at the three southern sites (Bandon, Flora's Lake, and Cape Mendocino). Central sites had greater biomass than sites in the north during the fall, but northern and central sites were comparable and fairly low in the summer (Figure 2, Appendix D). Total wrack biomass ($kg\ block^{-1}$), an integrative measure of patch density and patch biomass, showed variability among sites. Specifically, Greys Harbor and Cape Lookout in the north had similarly high amounts of total biomass as Bandon and Cape Mendocino in the south (average total wrack biomass across season: GH=64.47 +/- 7.99; CL=42.43 +/- 8.44; BAN=65.55 +/- 20.75; CME=33.96 +/- 10.75); Long Beach, North Spit and Flora's Lake had intermediate amounts of total biomass (LB=14.27 +/- 3.69; NS=18.05 +/- 5.30; FL=19.80 +/- 6.06);

and Fort Stevens, Sand Lake, South Beach, Siuslaw South Jetty and Umpqua Dunes had similarly low total biomass (FS=3.10 +/- 0.87; SL=8.53 +/- 4.25; SB=9.89 +/- 2.70; SSJ=4.48 +/- 1.64; UD=4.73 +/- 1.59; Figure 2, Appendix D).

Grouping sites by region helped clarify the spatial patterns. Regional comparisons show that there was greater wrack patch density within the northern region than both the central and southern regions ($\chi^2(2)=29.83$, $p<0.001$); greater wrack biomass within the southern region than either the central or northern regions ($\chi^2(2)=23.84$, $p<0.001$); and that the greatest amount of total wrack biomass was in the south, intermediate in the north, and lowest in the central region, although statistically, the north was similar to the central region ($\chi^2(2)=13.43$, $p=0.007$; Figure 3; Tables 2b, 3).

Our analysis of environmental characteristics (cross-shore and alongshore upwelling, and SCR) helped explain what may be controlling some of the patterns we found. For wrack patch density, only cross-shore and alongshore upwelling were important, indicated by a lack of significance of a model that included SCR ($\chi^2(1)=0.68$, $p=0.41$). Wrack patch density decreased with increases in cross-shore upwelling, while it increased with greater alongshore upwelling (Table 4). The final model for wrack biomass only included cross-shore upwelling, and there was a lack of significance of models with alongshore upwelling and SCR ($\chi^2(2)=2.31$, $p=0.32$). Wrack biomass increased with greater cross-shore upwelling (Table 4). Finally, the model for total wrack biomass showed that none of the environmental factors were important to those patterns, as indicated by comparison with a null model ($\chi^2(3)=5.22$, $p=0.16$). However, alongshore upwelling was marginally significant when all predictors were in the model, but this is

likely a statistical artifact because this variable does not emerge as significant across different models tested.

Wrack composition

We found strong patterns in wrack functional group composition at our sites in the fall, although there was no interaction between site and functional group presence (2-way ANOVA: $F_{17, 225} = 10.15$, $p < 0.0001$, $\text{adj. } R^2 = 0.39$). Sites differed in wrack composition, although kelp and eelgrass were present at every site except for Sand Lake, where the proportion of non-kelp brown algae was highest (Figure 4a). Specifically, the proportion of eelgrass biomass in the north was much higher than in the south or central regions (1-way ANOVA: $F_{2, 32} = 27.74$, $p < 0.0001$, $\text{adj. } R^2 = 0.61$; Figure 4b), and the proportion of kelp biomass was highest in the south, intermediate in the central, and low in the north (1-way ANOVA: $F_{2, 32} = 57.41$, $p < 0.0001$, $\text{adj. } R^2 = 0.77$; Figure 4b). Thus estuaries are the primary source for wrack at the northern sites, while rocky reefs are the primary source of wrack for the southern and most of the central sites (North Spit in the central region is an exception – it sits at the mouth of Coos Bay, a major estuary in the south).

Kelp biomass was predicted primarily by SCR and distance to a rocky reef ($F_{5, 58} = 6.98$, $p < 0.001$, $\text{adj. } R^2 = 0.32$). Kelp biomass increased with SCR, while it decreased at greater distances from rocky reef habitat (Table 5). Eelgrass biomass was primarily predicted by upwelling variables and distance to an estuary ($F_{5, 58} = 7.27$, $p < 0.001$, $\text{adj. } R^2 = 0.33$). Eelgrass biomass decreased with increasing cross-shore upwelling values and

with distance from an estuary, while it increased with increasing alongshore upwelling (Table 5).

DISCUSSION

Patterns of Wrack Distribution Across Latitude

The simplest (i.e., “null”) hypothesis for wrack distribution along sandy beaches is one of homogeneity, with little difference in the onshore deposition pattern of wrack material due to the connections between coastal waters and estuaries, rocky reefs, and sandy beaches. However, we found strong spatial and temporal patterns of macrophyte wrack deposition on sandy beaches of the Pacific Northwest. These patterns were primarily linked to upwelling variables and the proximity of the beaches to particular source habitats (rocky reefs and estuaries). Shoreline change rate was generally not correlated with wrack distribution and abundance.

Our results allow insight into the sources and causes of wrack distributional differences along the Pacific Northwest coast. In the north, upwelling is weak, estuaries are common and large compared to rocky shore habitat, and beaches are wide due to generally positive shoreline change rates (Table 1, Appendix B). Here we found that wrack patches were numerous but small and primarily composed of eelgrass (e.g., Figure 5a, and Figures 3, 4). In the south, upwelling is strong and persistent, rocky shores are common compared to estuaries, and beaches are, on average, narrow due to neutral or negative shoreline change rates (Table 1). Southern sites had fewer wrack patches but greater biomass, and were primarily composed of brown macroalgae, specifically kelp

(e.g., Figure 5b and inset), although we also found small amounts of eelgrass at these sites. In the central region, upwelling is stronger than in the north, estuaries are large, rocky shores are common and beach width varies but is generally narrower (Table 1). In this region (South Beach to North Spit) the wrack patterns on beaches were more heterogeneous, with similar patch densities to the southern region, but which had lower biomass more similar to the north region. This resulted in less overall total wrack biomass per site (Figure 3). Central region composition was also more heterogeneous, although South Beach and Siuslaw South Jetty had high kelp presence.

As predicted by hypothesis H₁, we found strong seasonal patterns, with all response variables greater in the fall than in the summer. There were some sites that did not follow this pattern, specifically Cape Lookout, where biomass and total biomass were less in the fall than summer (Figure 2). Patch density was also similar or lower in the fall at three of the four central sites (South Beach, Siuslaw South Jetty, and Umpqua Dunes). We were initially interested in differences between seasons because they represent a shift in environmental conditions that we did not explicitly incorporate into our analysis, particularly increased storm intensity and wave action, and shifts in prevailing wind direction that occur in the fall (Mendez et al. 2008, Ruggiero et al. 2010). Storms and waves increase ocean turbulence, which causes macrophytes growing on rocky shores and within estuaries to be dislodged and deposited onshore via wave action and wind. In addition, the inherent higher biomass of macrophytes by the end of the growing season may cause wrack patches to be larger in the fall. Regardless, the effect of season is as we expected, though the direct mechanisms are unknown.

Upwelling, Outwelling, and Wrack Deposition

Collectively, the patterns of macrophyte wrack we found provide evidence of three primary factors responsible for determining the distribution of wrack along the coast: upwelling, outwelling, and beach geomorphology. Upwelling is important for fueling macrophyte productivity, outwelling influences the movement of wrack from estuaries to beaches, as well as the wrack composition, and beach morphology influences deposition and retention on the shore.

Our results are partially consistent with hypothesis H₂, which predicts that increased upwelling is associated with increased subsidies. Upwelling, particularly the cross-shore component of Ekman transport, was the only environmental variable that definitively emerged as important for predicting wrack patch density, wrack biomass, and the composition of wrack patches across the coast. Upwelling is a seasonal coastal process that delivers significant amounts of nutrients to the surface from the bottom of the ocean. Pulses of nutrients from upwelling events influence macroalgae, seagrasses, and other primary producer growth on rocky shores and within estuaries, and are important for structuring community composition and dynamics (e.g., Menge et al. 1997; Woodson et al. 2012; Hessing-Lewis and Hacker 2013). Along the California Current, upwelling intensity shifts from weaker and intermittent in the north, to stronger and more persistent in the south (Menge et al. in review). The effect of upwelling on macroalgal growth is especially strong near headlands, where offshore kelp beds and intertidal algae thrive on rocky reefs (e.g., Menge et al. in review), and within estuaries where up to 30x

more ulvoid macroalgae is produced with strong upwelling (Hessing-Lewis and Hacker 2013). Eelgrass biomass, however, is negatively correlated with upwelling in estuaries along the Pacific Northwest (Hessing-Lewis and Hacker 2013). These responses to upwelling are reflected in our results, as we saw a greater proportion of kelp in the south where upwelling is strong, and a greater proportion of eelgrass in the north, where upwelling is weak. We did not see greater amounts of ulvoid macroalgae at central sites, particularly near Coos Bay, as may have been predicted based on its prevalence in southern estuaries (Hessing-Lewis and Hacker 2013). In fact, very little ulvoid macroalgae was present in wrack suggesting that it is less likely to leave the estuary (Figure 4, green algae functional group).

Outwelling is a process that specifically refers to the transfer of ecological subsidies from within estuaries to the open coast through tidal and current movement. We found evidence of this process on all the beaches we sampled, as eelgrass was present at every site regardless of distance to an estuary. In fact, and consistent with hypothesis H₃, estuary distance emerged as an important factor for describing eelgrass biomass (biomass was greater on beaches closer to estuaries), suggesting that eelgrass is outwelled from all the estuaries on the coast and may also be transported long distances before arriving on shore. As noted, eelgrass presence was particularly strong on beaches in the north, where there are numerous large, highly productive estuaries (Greys Harbor, Willapa Bay, and Netarts Bay). Our central region sites also had a relatively high abundance of eelgrass, and were close to major estuaries (Yaquina Bay and Coos Bay), though kelp abundance was greater overall. However, at central sites near Coos Bay (Umpqua Dunes and North

Spit), we saw similar proportions of kelp and eelgrass biomass in wrack, suggesting an influence of both estuaries and rocky shores in this region. Because kelp tissue is much denser than eelgrass tissue, a significant amount of eelgrass would need to be deposited onshore to equal that of kelp (Figure 4). Central sites, though close to rocky shores, did not have as much kelp as southern sites, likely because intermittent upwelling in the central region supports less growth of kelp than the strong, persistent upwelling in the south. In addition, there is less rocky shore habitat for kelp to grow on in this region. Despite strong kelp presence in the south, eelgrass was also present, supporting the hypothesis that material outwelled from estuaries is ubiquitous on beaches, though the magnitude varies across the coast (Figure 4).

These findings support our hypothesis that outwelling from estuaries occurs along the California Current, and potentially contributes subsidies to most, if not all, regions along the coast. This is the first study, as far as we are aware, to show evidence of outwelling as a process in West Coast estuaries. This is also one of the first studies to directly link estuaries to open-coast beaches through the deposition of estuarine matter, though there are many studies of macrophyte deposition and decomposition have occurred on beaches *within* estuaries (Jedrzejczak 2002; Nicastró et al. 2012; Gomez et al. 2013; Lavery et al. 2013). As has been previously shown, eelgrass can contribute a significant amount of dissolved organic carbon to beaches (Lavery et al. 2013). Therefore, our data support the idea that outwelling contributes carbon (and likely other nutrients in eelgrass) to coastal systems, though better characterization of the ecological role of eelgrass wrack on beaches would help to substantiate the importance of this link.

Contrary to hypothesis H₄, we found that SCR, a proxy for beach width, was not an important predictor for wrack patch density, biomass, or total wrack biomass. However, SCR was related to kelp biomass on beaches (where kelp was present, it had greater biomass on wider beaches). We may have found a pattern with kelp because of the way that waves and beach geomorphology (slope and width) interact to deposit wrack. On wide, shallow beaches that dissipate wave energy, waves break 75-300 m seaward of the beach and wash further up the shore (Wright et al. 1979), depositing material floating in the water column. On narrow, steep beaches that reflect wave energy, waves tend to break onshore and create a more turbulent swash zone where wrack is constantly delivered and removed from the beach. Therefore, dissipative beaches, theoretically, create conditions for greater wrack retention, while reflective beaches are less favorable for deposition (Guza et al. 2011). Because this pattern emerged only with kelp, it may be that kelp wrack patches are more susceptible to wave action on narrow beaches due to their size (up to 80 m³, Reimer et al. unpubl. data) and weight, whereas eelgrass may be moved above the tide line more quickly by wind. The lack of significance of SCR could also be another indication of the ubiquity of eelgrass, suggesting that all beaches, regardless of width, accumulate eelgrass.

Implications of Wrack Distributional Patterns

Our study provides some of the first evidence to show that macrophyte subsidies to sandy beaches vary dramatically depending on the upwelling conditions of the region, proximity to estuaries versus rocky reefs, the geomorphology of the beach, and the

season in which it is measured. This variability has implications for the structure, function, and services provided by beach ecosystems.

Prior research has established that wrack plays an important role on beaches as a resource for macroinvertebrate abundance and diversity (Holmquist 1997, Jedrzejczak 2002, Dugan et al. 2003, Orr et al. 2005, Jaramillo et al. 2006, Ince et al. 2007, Bishop and Kelaher 2013, Nielsen et al. 2013) and provides organic matter (Lavery et al. 2013) and nutrients, particularly nitrogen and phosphorous (Schlacher and Connolly 2009, Dugan et al. 2011, Barreiro et al. 2013). Wrack subsidies influence aquatic and terrestrial food webs, reaching secondary consumers such as birds (Sanchez-Pinero and Polis 2000, Dugan et al. 2003, Hubbard and Dugan 2003), spiders (Polis and Hurd 1995), and lizards (Barrett et al. 2005, Spiller et al. 2010, Piovia-Scott et al. 2013) which take advantage of the increased macroinvertebrate densities. Some mammals have even been shown to opportunistically use wrack as food, especially coyotes (Rose and Polis 1998), though they likely target a combination of macrophyte wrack and carcasses that wash onshore (Schlacher et al. 2013). While no studies have been conducted on macroinvertebrate abundance and diversity on beaches in the Pacific Northwest, it seems likely that wrack has a similar effect to that elsewhere. Our results lead to interesting follow-up questions, such as whether or not macroinvertebrates prefer different types of wrack; if differences in wrack distribution, abundance and composition affect the beach macroinvertebrate community; and whether differences in wrack distribution, and potentially macroinvertebrate distribution, influence the coastal food web. There is some evidence of macroinvertebrate preference for kelp and other fleshy macroalgae over seagrasses

(Mews et al. 2006) so based on our findings, we may expect to find greater abundances and diversity of macroinvertebrates at sites in the central and south regions of the Pacific Northwest where more kelp washes onshore.

One of the most important questions arising from this research is if wrack subsidies can influence dune vegetation and thus the structure and protective role of foredunes. In the Pacific Northwest, foredunes were created with the introduction of *Ammophila breviligulata* and *A. arenaria*, two beach grasses that are very efficient at capturing and accreting sand, and spreading along the coast. This introduction has caused a change from open, shifting sand dunes to very tall, spatially stable foredunes. The question remains, though, if wrack deposition and composition influences the growth of beach grasses through increases in the amount or type of nutrients available. If these ocean-derived nutrients affect dune vegetation growth, then areas with more wrack, or with a particular kind of wrack, may influence dune structure. While *A. arenaria* and *A. breviligulata* both cause the formation of foredunes, *A. arenaria* is better at accreting sand than *A. breviligulata* (Hacker et al. 2012, Zarnetske et al. 2012) and is a better competitor (Zarnetske et al. 2013). Taller foredunes create better coastal protection services for development by preventing wave over-topping and flooding (Barbier et al. 2011, Seabloom et al. 2013).

The introduction of *Ammophila*, and the resulting formation of foredunes, has also had negative effects. With foredune formation, much of the habitat for the Western snowy plover (*Charadrius alexandrinus nivosus*), a small, open-ground nesting shorebird, has disappeared. This bird is now endangered and federally protected. Many resources

are applied towards snowy plover habitat restoration, which primarily includes bulldozing foredunes or applying herbicide to kill the beach grasses (Zarnetske et al. 2010). Plovers, and other shorebirds, actively forage in the intertidal and swash zone of the beach, in and around macrophyte wrack where they likely consume the macroinvertebrates that utilize wrack (Dugan et al. 2003, Hubbard and Dugan 2003). If areas with more wrack provide better food resources for plovers, and the composition of the wrack matters to determining macroinvertebrate distributions, then understanding wrack patterns may help inform dune restoration decisions. Because of the important role that dunes play in providing coastal protection, understanding where conservation and development trade-offs can be made is critical for both ecosystem and human well-being.

CONCLUSION

Our study is the first in the Pacific Northwest, and one of few that exist globally, to examine the deposition pattern of a ubiquitous resource, marine macrophyte wrack, on sandy beaches at a large biogeographic scale. Through this investigation, we found evidence of connectivity between rocky reefs, estuaries, and sandy beaches among sites and within regions across the coast. A large and growing body of work suggests that connections between ecosystems are important, and are likely changing with increased coastal development and global change. Already, increases in the intensity of upwelling patterns have been documented (Iles et al. 2012, Sydeman et al. 2014). This intensification has been linked to stronger winds (Sydeman et al. 2014) and increased ocean acidification (Lachkar 2014), which may affect marine macrophyte growth in their

source habitats, thus influencing the supply of macrophytes. If marine macrophyte abundance and diversity changes, there may be knock-on effects for dunes and beach communities that could affect food webs and habitat restoration activity. Thus, this work represents a critical foundation of information on wrack variability that can be used for the design of future studies on wrack nutrient deposition and subsidy of beach ecosystems in the Pacific Northwest.

Addressing issues of connectivity is not easy, especially given the ephemeral and complex nature of the connections. However, as anthropogenic pressure on our coastal ecosystems increases, it is important to consider how ecosystems are connected, and how disruptions of connections might impact the function of a system upon which we rely. Coastal systems provide a number of ecosystem services – from fishery nursery habitat to water filtration to coastal protection (Barbier et al. 2011). Integrating ecosystem connections into ecosystem-based management schemes will help to preserve the important, potentially unknown flows between systems that structure coastal communities. In addition, it provides a reason to approach coastal development conservatively in order to preserve these links that may not be recognized. With climate change and coastal development occurring in tandem, the preservation of these links may be even more important to maintain the important services provided by coastal systems in the Pacific Northwest.

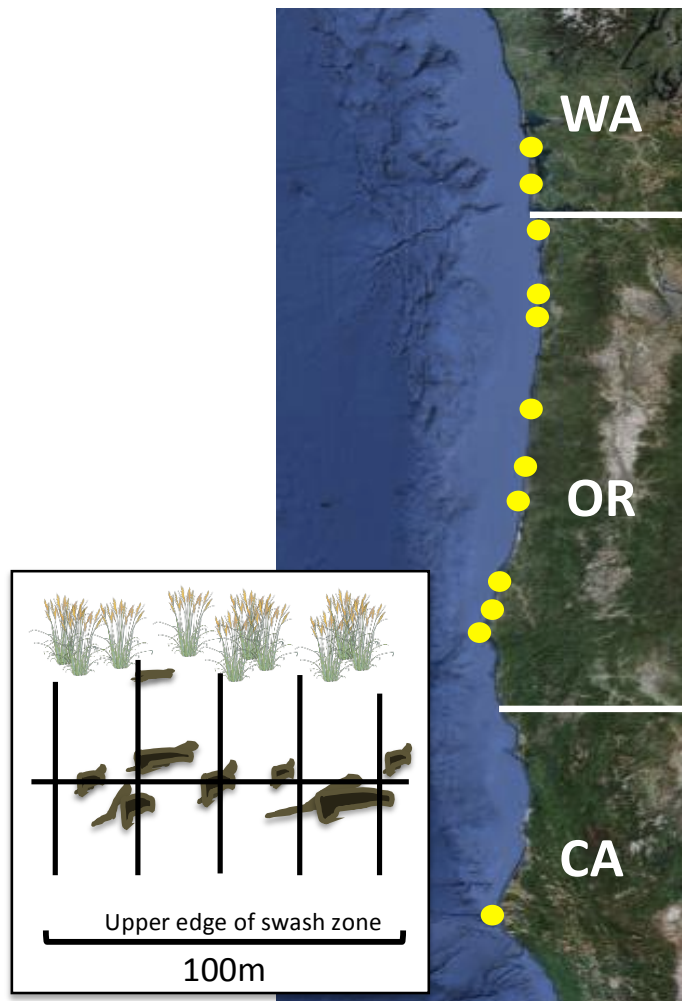


Figure 1. Location of survey sites and experimental design. Sites, from north to south, are Greys Harbor (GH), Long Beach (LB), Fort Stevens (FS), Cape Lookout (CL), Sand Lake (SL), South Beach (SB), Siuslaw South Jetty (SSJ), Umpqua Dunes (UD), North Spit (NS), Bandon (BAN), Flora's Lake (FL) and Cape Mendocino (CME). Inset: Diagram of block sampling design. Along the 100m primary transect parallel to the shore, five secondary belt transects were established every 25m within a block. Patches were collected within 1-m² quadrats placed at the intersection of the primary and secondary transect lines.

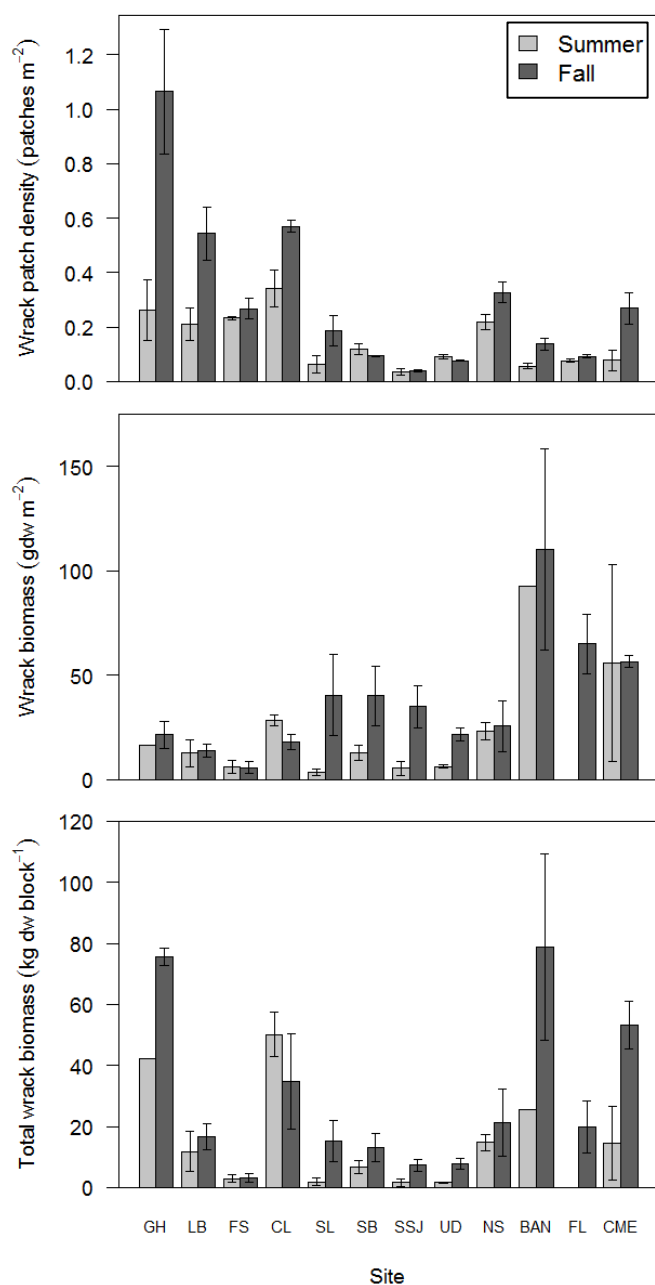


Figure 2. Site means (\pm SE) of wrack patch density (patch m^{-2}), wrack biomass (grams dry weight m^{-2}) and total wrack biomass (kilograms dry weight block $^{-1}$). Sites listed from north (GH) to south (CME). GH=Grays Harbor, LB=Long Beach, FS=Fort Stevens, CL= Cape Lookout, SL=Sand Lake, SB=South Beach, SSJ=Siuslaw South Jetty, UD=Umpqua Dunes, NS=North Spit, BAN=Bandon, FL=Flora's Lake, CME=Cape Mendocino. n=3 blocks per site for all sites within each season, except for the summer biomass survey of GH and BAN (n=1).

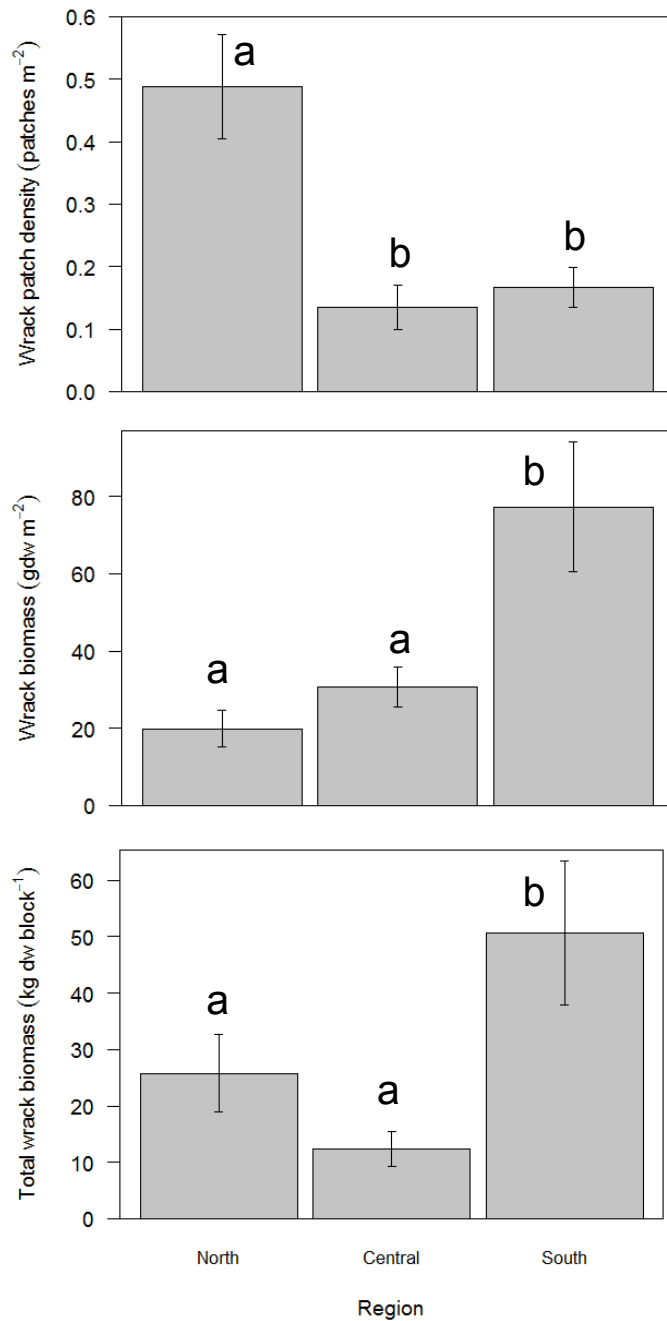


Figure 3. Means (\pm SE) by region of wrack patch density, wrack biomass m⁻² and total wrack biomass for the fall survey. Letters indicate statistical significance, determined using linear mixed-model with Tukey's contrasts. North region n=15, Central region: n=12, South region: n=9. See Table 1 for sites contained within region.

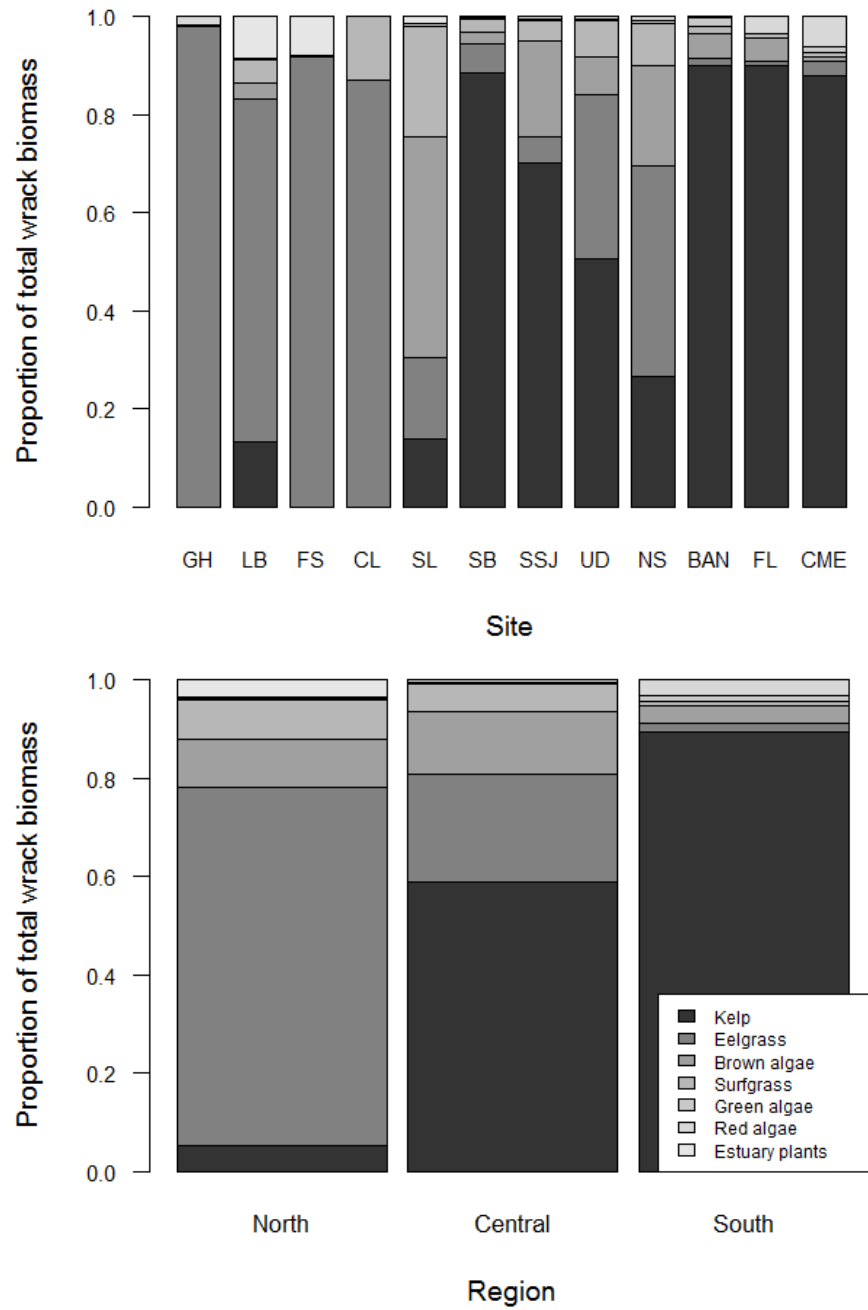


Figure 4. Mean proportion of each functional group within a) sites and b) regions during the fall survey. Proportions were calculated from the biomass of each functional group (grams dry weight) found in the wrack samples collected at each site.

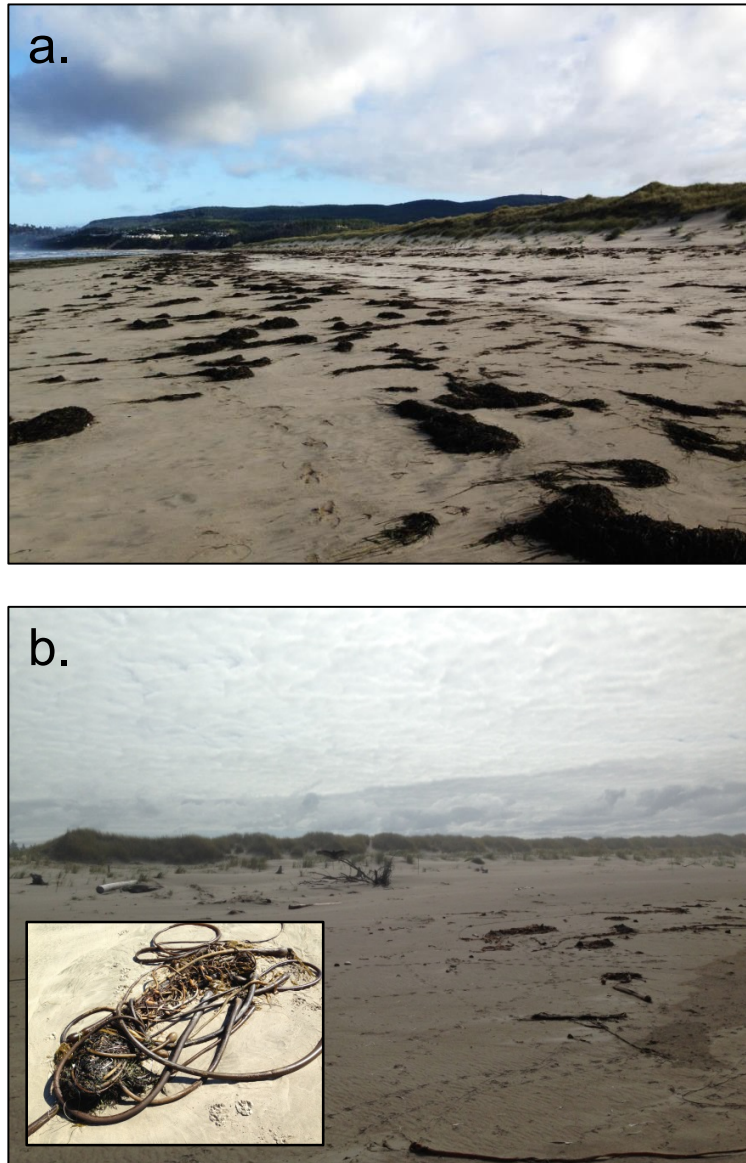


Figure 5. Photographs of sites with wrack primarily composed of a) eelgrass (Cape Lookout) and b) kelp (Bandon). Inset shows close-up of large kelp patch composed mostly of *Nereocystis luetkeana*, which were frequently found at sites in the central and south regions in fall of 2013.

Table 1. Environmental and physical characteristics of each site. Numbers reported are means (+/- standard errors) of the three blocks sampled at each site. Site are Greys Harbor (GH), Long Beach (LB), Fort Stevens (FS), Cape Lookout (CL), Sand Lake (SL), South Beach (SB), Siuslaw South Jetty (SSJ), Umpqua Dunes (UD), North Spit (NS), Bandon (BAN), Flora's Lake (FL) and Cape Mendocino (CME) (Appendix A).

Region	Site	Lat / Lon	Shoreline change rate (m yr ⁻¹)	Rocky reef distance (km)	Estuary distance (km)	Cross-shore upwelling (m ³ s ⁻¹ 100 m ⁻¹)	Alongshore upwelling (m ³ s ⁻¹ 100 m ⁻¹)
North	GH	46.80 / -124.10	13.37 (13.32)	55.42 (4.83)	8.04 (2.58)	12.88 (29.16)	7.28 (22.52)
	LB	46.48 / -124.06	2.69 (2.11)	58.57 (12.94)	15.04 (6.19)	15.91 (32.70)	11.25 (23.47)
	FS	46.18 / -123.98	0.35 (0.36)	27.95 (2.59)	13.13 (3.36)	22.14 (35.67)	-0.02 (27.57)
	CL	45.42 / -123.96	-1.17 (0.59)	6.68 (2.71)	3.12 (2.82)	24.21 (42.44)	10.98 (26.00)
	SL	45.28 / -123.96	-0.97 (0.04)	6.82 (0.29)	0.54 (0.26)	25.46 (41.25)	5.44 (25.74)
Central	SB	44.60 / -124.07	-0.11 (1.42)	13.42 (0.23)	1.61 (0.24)	33.94 (47.79)	-4.55 (31.81)
	SSJ	44.01 / -124.14	1.51 (1.02)	28.26 (0.60)	1.78 (0.51)	42.40 (54.52)	-3.39 (29.10)
	UD	43.60 / -124.22	-0.68 (0.32)	34.48 (0.73)	8.19 (0.98)	51.48 (61.71)	1.96 (31.86)
	NS	43.40 / -124.31	-0.62 (0.42)	11.52 (0.30)	6.72 (0.46)	42.43 (61.33)	14.56 (23.57)
South	BAN	43.07 / -124.44	0.66 (0.69)	8.19 (0.08)	7.73 (0.30)	58.05 (66.07)	2.83 (24.99)
	FL	42.90 / -124.51	-0.35 (0.43)	8.91 (0.67)	26.64 (0.32)	56.14 (67.61)	19.60 (26.38)
	CME	40.35 / -124.36	-0.81 (0.24)	0.58 (0.53)	6.79 (0.68)	138.11 (115.65)	12.54 (31.00)

Table 2. Summary of linear mixed-effects model output for wrack patch density (patches m⁻²), wrack biomass (gdw m⁻²) and wrack total biomass (kg block⁻¹) by a) site and b) region. Sample size differences between patch density and the two biomass measures are due to issues that occurred during wrack sample processing. The random effect term accounts for the within-site and within-region variability between blocks. Significance of the fixed effects were analyzed using a Type II Wald χ^2 test (reported).

a. SITE LEVEL							
Response	Sample size (N)	Fixed effect	df fixed effect	χ^2 (p)	Random effect	Variance random effect	Standard deviation random effect
Wrack patch density	70	Site	11	326.38***	(block site)	0.01	0.10
		Season	1	63.55***			
		Site:Season	11	68.23***			
Wrack biomass	61	Site	10	52.12***	(block site)	0.16	0.41
		Season	1	24.08***			
		Site:Season	10	39.57***			
Wrack total biomass	61	Site	10	98.71***	(block site)	0.15	0.39
		Season	1	19.08***			
		Site:Season	10	31.15***			

*p<0.05, **p<0.001, ***p<0.0001

Table 2. (Continued)

b. REGION LEVEL							
Response	Sample size (N)	Fixed effect	df fixed effect	χ^2 (p)	Random effect	Variance random effect	Standard deviation random effect
Wrack patch density	North=14 Central=12 South=9	Region	2	29.83***	(block region)	2.05×10^{-11}	1.05×10^{-5}
Wrack biomass	North=14 Central=12 South=9	Region	2	23.84***	(block region)	1.57×10^{-11}	3.96×10^{-6}
Wrack total biomass	North=14 Central=12 South=9	Region	2	13.43**	(block region)	1.75×10^{-11}	4.18×10^{-6}

*p<0.05, **p<0.001, ***p<0.0001

Table 3. Log-transformed parameter estimates for contrasts between regions. Responses are wrack patch density (patches m⁻²), wrack biomass (gdw m⁻²) and total wrack biomass (kg block⁻¹). Estimates obtained using Tukey's contrasts for simultaneous tests of general linear hypotheses (H₀ contrast = 0). Percent change between regions was calculated by multiplying the estimate by 100, and only reported for contrasts that rejected H₀.

Response	Fixed effect	Contrast	Estimate	Standard error	z-value (p)	Percent change between regions
Wrack patch density	Region	north - central	1.07	0.20	5.21***	107%
		south - central	0.25	0.23	1.08	-
		south - north	-0.82	0.22	-3.67***	-82%
Wrack biomass	Region	north - central	-0.61	0.31	-1.97	-
		south - central	0.97	0.33	2.90*	97%
		south - north	1.58	0.32	4.88***	158%
Wrack total biomass	Region	north - central	0.40	0.40	1.00	-
		south - central	1.38	0.45	3.08**	138%
		south - north	0.98	0.43	2.25*	98%

*p<0.05, **p<0.001, ***p<0.0001

Table 4. Summary of linear mixed-effects model testing for the effects of environmental parameters on wrack patch density (patches m⁻²), wrack biomass (g dw m⁻²) and total wrack biomass (kg block⁻¹). Predictor importance was tested using a χ^2 drop-in-deviance test comparing nested models. Only variables that appeared in the final model are listed. Significance of predictors was analyzed using a Type II Wald χ^2 test (reported).

Response	Sample size (N)	Fixed effect	df fixed effect	χ^2 (p)	Estimate	Standard Error
Wrack patch density	70	(Intercept)	-	-	-1.41	0.26
		Cross-shore upwelling	1	7.77**	-0.01	0.003
		Alongshore upwelling	1	5.16*	0.04	0.02
Wrack biomass	64	(Intercept)	-	-	2.33	0.42
		Cross-shore upwelling	1	3.99*	0.01	0.005
Wrack total biomass	64	(Intercept)	-	-	1.41	0.64
		Cross-shore upwelling	1	0.18 ns	0.003	0.009
		Alongshore upwelling	1	3.95*	0.08	0.04
		SCR	1	2.23 ns	0.42	0.28

***p<0.001, **p<0.01, *p<0.05

Table 5. Effect of environmental predictors on the biomass of a) kelp and b) eelgrass. Results obtained from general linear regression, with all predictors included in the model. Environmental parameters are abbreviated as follows: *avg_cross*=average cross-shore upwelling; *avg_along*=average alongshore upwelling; *log_scr*=log-transformed shoreline change rate; *reef_dist*=distance to rocky reef; *est_dist*=distance to estuary.

a. KELP			
Environmental Parameter	Wrack Estimate (p)	Standard error	t-value
Intercept	60.22 ns	54.96	0.28
avg_cross	1.33 ns	0.73	0.07
avg_along	-2.74 ns	3.58	0.45
log_scr	139.02***	39.48	8×10^{-4}
reef_dist	-6.98***	1.77	2×10^{-4}
est_dist	7.52 ns	3.97	0.06
b. EELGRASS			
Environmental Parameter	Wrack Estimate (p)	Standard error	t-value
Intercept	42.51***	9.97	7.4×10^{-5}
avg_cross	-0.48***	0.13	6.1×10^{-4}
avg_along	2.84***	0.65	5.0×10^{-5}
log_scr	-3.51 ns	7.19	0.63
reef_dist	0.40 ns	0.32	0.22
est_dist	-2.05**	0.72	0.01

* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

APPENDICES

Appendix A

Table A1. Latitude and longitude for each block sampled at each site, and how they correspond with sites and transects sampled in Hacker et al. 2012. Hacker and colleagues previously established these transects during studies of dune geomorphology and vegetation. We centered the blocks in the current study along the same transects, when possible, so that future efforts could be related to prior data. NA = no corresponding transect.

Site name	Hacker et al. 2012 transect name	Latitude	Longitude
Grays Harbor	GH18	46° 51' 3.3228"	-124° 6' 47.2674"
	GH05	46° 47' 57.3714"	-124° 5' 57.822"
	GH11	46° 45' 33.2814"	-124° 6' 9"
Long Beach	LB1020	46° 33' 10.5696"	-124° 3' 42.9186"
	LB05	46° 29' 5.049"	-124° 3' 33.3396"
	LB36	46° 19' 18.2454"	-124° 4' 6.5238"
Fort Stevens	FS02	46° 12' 21.2214"	-123° 59' 53.5014"
	FS03	46° 10' 49.134"	-123° 58' 52.4424"
	FS01	46° 8' 56.5512"	-123° 57' 51.3036"
Cape Lookout	CL03	45° 25' 38.661"	-123° 57' 37.3644"
	CL02	45° 25' 18.354"	-123° 57' 39.69"
	CL01	45° 22' 53.2554"	-123° 57' 59.13"
Sand Lake	SL02	45° 17' 8.952"	-123° 57' 48.8736"
	SL01	45° 16' 55.7076"	-123° 57' 46.7208"
	SL03	45° 16' 52.0062"	-123° 57' 43.7112"
South Beach	SB03	44° 36' 28.2486"	-124° 4' 6.3582"
	SB02	44° 36' 15.2964"	-124° 4' 1.6068"

	SB01	44° 35' 56.3958"	-124° 4' 2.1462"
Siuslaw South Jetty	NA	44° 0' 41.112"	-124° 8' 12.2064"
	NA	44° 0' 22.2006"	-124° 8' 12.7536"
	NA	44° 0' 2.4222"	-124° 8' 14.0994"
Umpqua Dunes	UD02	43° 36' 30.8196"	-124° 13' 6.888"
	UD01	43° 35' 48.5658"	-124° 13' 17.5758"
	UD03	43° 35' 35.6994"	-124° 13' 21.5364"
North Spit	NA	43° 24' 13.9968"	-124° 18' 17.7012"
	NA	43° 24' 7.8696"	-124° 18' 20.1888"
	NA	43° 23' 51.7056"	-124° 18' 31.971"
Bandon	BAN-NR3	43° 4' 3.6804"	-124° 26' 17.397"
	BAN-NR2	43° 3' 57.5208"	-124° 26' 16.8576"
	BAN-NR1	43° 3' 42.681"	-124° 26' 21.2136"
Flora's Lake	NA	42° 54' 12.1386"	-124° 30' 31.269"
	NA	42° 54' 2.2674"	-124° 30' 38.0982"
	NA	42° 53' 54.6252"	124° 30' 44.0598"
Cape Mendocino	NA	40° 21' 25.0698"	-124° 21' 46.6626"
	NA	40° 21' 1.5408"	-124° 21' 44.3766"
	NA	40° 20' 42.018"	-124° 21' 45.558"

Appendix B.

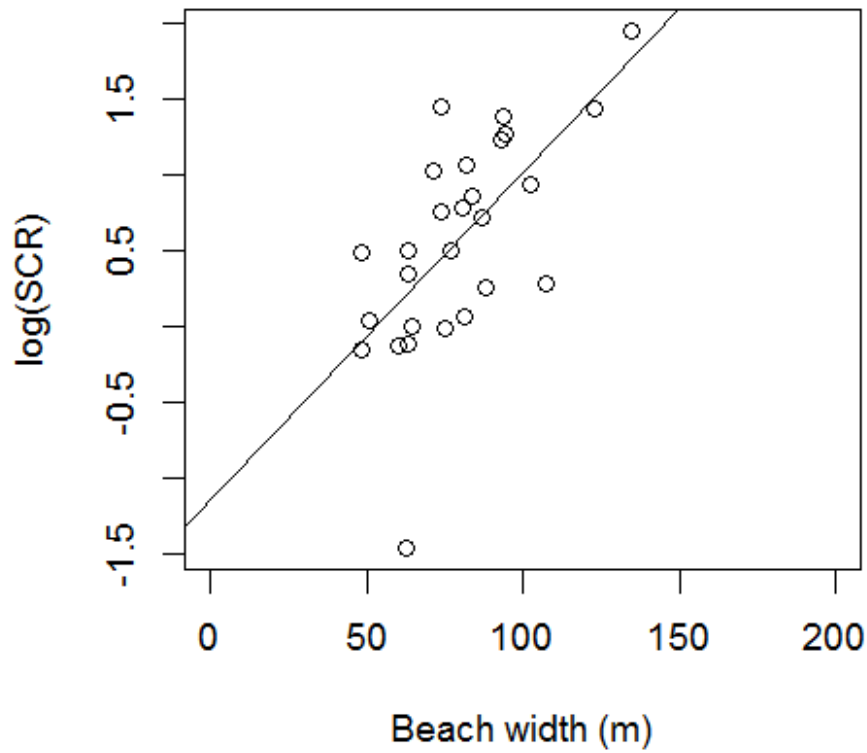


Figure B1. Relationship between beach width (meters) and log-transformed shoreline change rate (meters per year) across study sites ($F_{1,52}=37.94$, $p<0.001$, $\text{adj. } R^2=0.41$). Pearson's product-moment correlation = 0.65 ($t_{52}=6.16$, $p<0.001$). Data from Ruggiero et al. (2013) and Hapke et al. (2010).

Appendix C.

Table C1. Comprehensive list of macrophyte species found in wrack samples collected at all sites.

FUNCTIONAL GROUP	SPECIES
Brown algae	<i>Ahnfeltiopsis gigartinoides</i>
	<i>Analipus japonica</i>
	<i>Coilodesme californica</i>
	<i>Desmarestia</i> sp.
	<i>Dictyoneuropsis reticulata</i>
	<i>Fucus distichus</i>
	<i>Pelvetiopsis limitata</i>
	<i>Postelsia palmaeformis</i>
	<i>Sargassum muticum</i>
	<i>Scytosiphon</i> sp.
<i>Soranothera ulvoidea</i>	
Eelgrass	<i>Zostera japonica</i>
	<i>Zostera marina</i>
Green	<i>Acrosiphonia</i> sp.
	<i>Chaetomorpha</i> sp.
	<i>Cladophora</i> sp.
	<i>Codium fragile</i>
	<i>Ulva</i> spp.
Kelp	<i>Alaria marginata</i>
	<i>Cystoseira osmundacea</i>

	<i>Egregia menziesii</i>
	<i>Laminaria</i> spp.
	<i>Lessoniopsis littoralis</i>
	<i>Macrocystis integrifolia</i>
	<i>Nereocystis luetkeana</i>
	<i>Saccharina sessilis</i>
Other estuary plants	<i>Potamogeton richardsonii</i>
	<i>Myriophyllum spicatum</i>
Red	<i>Botryoglossum farlowianum</i>
	<i>Callophyllis</i> sp.
	<i>Ceramium</i> spp.
	<i>Chondracanthus canaliculatus</i>
	<i>Corallina</i> sp.
	<i>Cryptopleura</i> sp.
	<i>Cumagloia andersonii</i>
	<i>Endocladia muricata</i>
	<i>Gelidium</i> sp.
	<i>Halosaccion glandiforme</i>
	<i>Hymenena</i> sp.
	<i>Mastocarpus</i> spp.
	<i>Mazzaella</i> spp.
	<i>Microcladia</i> spp.
	<i>Neorhodomela</i> spp.
	<i>Odonthalia</i> spp.

Osmundea spectabilis

Pikea pinnata

Plocamium spp.

Porphyra spp.

Prionitis spp.

Pterochondria woodii

Ptilota sp.

Smithora naiadum

Surfgrass

Phyllospadix spp.

Appendix D.

Table D1. Post-hoc site contrasts (Tukey's contrasts for linear mixed-effect models) for a) wrack patch density (patches m^{-2}), b) wrack biomass (grams dry weight m^{-2}) and c) total wrack biomass (kilograms block $^{-1}$). Each contrast tests the linear hypothesis $H_0=0$ between sites. *** $p<0.0001$, ** $p<0.001$, * $p<0.05$.

A. PATCH DENSITY:

	Estimate	Std. Error	z value	Pr(> z)
CL - BAN == 0	1.26082	0.21477	5.871	<0.01 ***
CME - BAN == 0	0.09878	0.21477	0.460	1.0000
FL - BAN == 0	0.16619	0.21477	0.774	0.9999
FS - BAN == 0	0.96548	0.21477	4.495	<0.01 ***
GH - BAN == 0	0.93334	0.21477	4.346	<0.01 ***
LB - BAN == 0	0.83470	0.21477	3.886	<0.01 **
NS - BAN == 0	0.90344	0.21477	4.207	<0.01 **
SB - BAN == 0	0.44502	0.21477	2.072	0.6490
SL - BAN == 0	-0.03848	0.21477	-0.179	1.0000
SSJ - BAN == 0	-0.23891	0.21477	-1.112	0.9951
UD - BAN == 0	0.27833	0.21477	1.296	0.9818
CME - CL == 0	-1.16204	0.19243	-6.039	<0.01 ***
FL - CL == 0	-1.09463	0.19243	-5.689	<0.01 ***
FS - CL == 0	-0.29534	0.19243	-1.535	0.9350
GH - CL == 0	-0.32748	0.19243	-1.702	0.8730
LB - CL == 0	-0.42612	0.19243	-2.214	0.5434
NS - CL == 0	-0.35738	0.19243	-1.857	0.7916
SB - CL == 0	-0.81580	0.19243	-4.240	<0.01 **
SL - CL == 0	-1.29929	0.19243	-6.752	<0.01 ***
SSJ - CL == 0	-1.49973	0.19243	-7.794	<0.01 ***
UD - CL == 0	-0.98248	0.19243	-5.106	<0.01 ***
FL - CME == 0	0.06741	0.19243	0.350	1.0000
FS - CME == 0	0.86670	0.19243	4.504	<0.01 ***
GH - CME == 0	0.83456	0.19243	4.337	<0.01 ***
LB - CME == 0	0.73592	0.19243	3.824	<0.01 **
NS - CME == 0	0.80466	0.19243	4.182	<0.01 **
SB - CME == 0	0.34624	0.19243	1.799	0.8242
SL - CME == 0	-0.13725	0.19243	-0.713	0.9999
SSJ - CME == 0	-0.33769	0.19243	-1.755	0.8480
UD - CME == 0	0.17956	0.19243	0.933	0.9990
FS - FL == 0	0.79930	0.19243	4.154	<0.01 **
GH - FL == 0	0.76715	0.19243	3.987	<0.01 **
LB - FL == 0	0.66851	0.19243	3.474	0.0262 *
NS - FL == 0	0.73726	0.19243	3.831	<0.01 **
SB - FL == 0	0.27883	0.19243	1.449	0.9567

SL - FL == 0	-0.20466	0.19243	-1.064	0.9967
SSJ - FL == 0	-0.40509	0.19243	-2.105	0.6253
UD - FL == 0	0.11215	0.19243	0.583	1.0000
GH - FS == 0	-0.03214	0.19243	-0.167	1.0000
LB - FS == 0	-0.13079	0.19243	-0.680	1.0000
NS - FS == 0	-0.06204	0.19243	-0.322	1.0000
SB - FS == 0	-0.52046	0.19243	-2.705	0.2269
SL - FS == 0	-1.00396	0.19243	-5.217	<0.01 ***
SSJ - FS == 0	-1.20439	0.19243	-6.259	<0.01 ***
UD - FS == 0	-0.68715	0.19243	-3.571	0.0185 *
LB - GH == 0	-0.09864	0.19243	-0.513	1.0000
NS - GH == 0	-0.02990	0.19243	-0.155	1.0000
SB - GH == 0	-0.48832	0.19243	-2.538	0.3194
SL - GH == 0	-0.97181	0.19243	-5.050	<0.01 ***
SSJ - GH == 0	-1.17225	0.19243	-6.092	<0.01 ***
UD - GH == 0	-0.65500	0.19243	-3.404	0.0335 *
NS - LB == 0	0.06875	0.19243	0.357	1.0000
SB - LB == 0	-0.38968	0.19243	-2.025	0.6822
SL - LB == 0	-0.87317	0.19243	-4.538	<0.01 ***
SSJ - LB == 0	-1.07360	0.19243	-5.579	<0.01 ***
UD - LB == 0	-0.55636	0.19243	-2.891	0.1453
SB - NS == 0	-0.45842	0.19243	-2.382	0.4229
SL - NS == 0	-0.94192	0.19243	-4.895	<0.01 ***
SSJ - NS == 0	-1.14235	0.19243	-5.937	<0.01 ***
UD - NS == 0	-0.62511	0.19243	-3.249	0.0536 .
SL - SB == 0	-0.48350	0.19243	-2.513	0.3338
SSJ - SB == 0	-0.68393	0.19243	-3.554	0.0196 *
UD - SB == 0	-0.16669	0.19243	-0.866	0.9995
SSJ - SL == 0	-0.20043	0.19243	-1.042	0.9973
UD - SL == 0	0.31681	0.19243	1.646	0.8968
UD - SSJ == 0	0.51724	0.19243	2.688	0.2342

B. BIOMASS m⁻²

	Estimate	Std. Error	z value	Pr(> z)
CL - BAN == 0	-1.0079	0.7646	-1.318	0.9667
CME - BAN == 0	-1.2724	0.7646	-1.664	0.8530
FS - BAN == 0	-2.7886	0.7646	-3.647	0.0114 *
GH - BAN == 0	-1.4632	0.9345	-1.566	0.8963
LB - BAN == 0	-2.0290	0.7646	-2.654	0.2153
NS - BAN == 0	-1.2432	0.7646	-1.626	0.8711
SB - BAN == 0	-1.8858	0.7646	-2.466	0.3191
SL - BAN == 0	-3.3801	0.7646	-4.421	<0.01 ***
SSJ - BAN == 0	-3.1564	0.7646	-4.128	<0.01 **
UD - BAN == 0	-2.4976	0.7646	-3.267	0.0421 *
CME - CL == 0	-0.2645	0.5474	-0.483	1.0000

FS - CL == 0	-1.7807	0.5474	-3.253	0.0429 *
GH - CL == 0	-0.4553	0.7670	-0.594	1.0000
LB - CL == 0	-1.0211	0.5474	-1.865	0.7367
NS - CL == 0	-0.2353	0.5474	-0.430	1.0000
SB - CL == 0	-0.8779	0.5474	-1.604	0.8808
SL - CL == 0	-2.3722	0.5474	-4.334	<0.01 ***
SSJ - CL == 0	-2.1484	0.5474	-3.925	<0.01 **
UD - CL == 0	-1.4897	0.5474	-2.721	0.1850
FS - CME == 0	-1.5162	0.5474	-2.770	0.1654
GH - CME == 0	-0.1908	0.7670	-0.249	1.0000
LB - CME == 0	-0.7566	0.5474	-1.382	0.9535
NS - CME == 0	0.0292	0.5474	0.053	1.0000
SB - CME == 0	-0.6134	0.5474	-1.121	0.9902
SL - CME == 0	-2.1077	0.5474	-3.850	<0.01 **
SSJ - CME == 0	-1.8840	0.5474	-3.442	0.0235 *
UD - CME == 0	-1.2252	0.5474	-2.238	0.4717
GH - FS == 0	1.3254	0.7670	1.728	0.8198
LB - FS == 0	0.7596	0.5474	1.388	0.9520
NS - FS == 0	1.5454	0.5474	2.823	0.1445
SB - FS == 0	0.9028	0.5474	1.649	0.8603
SL - FS == 0	-0.5915	0.5474	-1.081	0.9927
SSJ - FS == 0	-0.3678	0.5474	-0.672	0.9999
UD - FS == 0	0.2910	0.5474	0.532	1.0000
LB - GH == 0	-0.5658	0.7670	-0.738	0.9997
NS - GH == 0	0.2200	0.7670	0.287	1.0000
SB - GH == 0	-0.4226	0.7670	-0.551	1.0000
SL - GH == 0	-1.9169	0.7670	-2.499	0.2990
SSJ - GH == 0	-1.6931	0.7670	-2.208	0.4944
UD - GH == 0	-1.0344	0.7670	-1.349	0.9607
NS - LB == 0	0.7858	0.5474	1.436	0.9399
SB - LB == 0	0.1432	0.5474	0.262	1.0000
SL - LB == 0	-1.3511	0.5474	-2.468	0.3167
SSJ - LB == 0	-1.1274	0.5474	-2.060	0.6022
UD - LB == 0	-0.4686	0.5474	-0.856	0.9990
SB - NS == 0	-0.6426	0.5474	-1.174	0.9859
SL - NS == 0	-2.1369	0.5474	-3.904	<0.01 **
SSJ - NS == 0	-1.9132	0.5474	-3.495	0.0199 *
UD - NS == 0	-1.2544	0.5474	-2.292	0.4328
SL - SB == 0	-1.4943	0.5474	-2.730	0.1824
SSJ - SB == 0	-1.2706	0.5474	-2.321	0.4128
UD - SB == 0	-0.6118	0.5474	-1.118	0.9904
SSJ - SL == 0	0.2237	0.5474	0.409	1.0000
UD - SL == 0	0.8825	0.5474	1.612	0.8775
UD - SSJ == 0	0.6587	0.5474	1.203	0.9829

C. TOTAL BIOMASS:

	Estimate	Std. Error	z value	Pr(> z)
CL - BAN == 0	0.76953	0.85718	0.898	0.9985
CME - BAN == 0	-1.01241	0.85718	-1.181	0.9852
FS - BAN == 0	-2.16054	0.85718	-2.521	0.2854
GH - BAN == 0	1.16753	1.04672	1.115	0.9906
LB - BAN == 0	-0.91527	0.85718	-1.068	0.9934
NS - BAN == 0	-0.62783	0.85718	-0.732	0.9998
SB - BAN == 0	-1.54668	0.85718	-1.804	0.7758
SL - BAN == 0	-3.23389	0.85718	-3.773	<0.01 **
SSJ - BAN == 0	-3.07825	0.85718	-3.591	0.0140 *
UD - BAN == 0	-2.58338	0.85718	-3.014	0.0871 .
CME - CL == 0	-1.78194	0.61678	-2.889	0.1237
FS - CL == 0	-2.93007	0.61678	-4.751	<0.01 ***
GH - CL == 0	0.39800	0.86098	0.462	1.0000
LB - CL == 0	-1.68480	0.61678	-2.732	0.1807
NS - CL == 0	-1.39735	0.61678	-2.266	0.4527
SB - CL == 0	-2.31620	0.61678	-3.755	<0.01 **
SL - CL == 0	-4.00342	0.61678	-6.491	<0.01 ***
SSJ - CL == 0	-3.84778	0.61678	-6.238	<0.01 ***
UD - CL == 0	-3.35290	0.61678	-5.436	<0.01 ***
FS - CME == 0	-1.14814	0.61678	-1.861	0.7404
GH - CME == 0	2.17994	0.86098	2.532	0.2800
LB - CME == 0	0.09713	0.61678	0.157	1.0000
NS - CME == 0	0.38458	0.61678	0.624	1.0000
SB - CME == 0	-0.53427	0.61678	-0.866	0.9989
SL - CME == 0	-2.22148	0.61678	-3.602	0.0134 *
SSJ - CME == 0	-2.06584	0.61678	-3.349	0.0327 *
UD - CME == 0	-1.57097	0.61678	-2.547	0.2721
GH - FS == 0	3.32808	0.86098	3.865	<0.01 **
LB - FS == 0	1.24527	0.61678	2.019	0.6314
NS - FS == 0	1.53272	0.61678	2.485	0.3070
SB - FS == 0	0.61387	0.61678	0.995	0.9963
SL - FS == 0	-1.07334	0.61678	-1.740	0.8132
SSJ - FS == 0	-0.91771	0.61678	-1.488	0.9246
UD - FS == 0	-0.42283	0.61678	-0.686	0.9999
LB - GH == 0	-2.08280	0.86098	-2.419	0.3488
NS - GH == 0	-1.79536	0.86098	-2.085	0.5833
SB - GH == 0	-2.71421	0.86098	-3.152	0.0593 .
SL - GH == 0	-4.40142	0.86098	-5.112	<0.01 ***
SSJ - GH == 0	-4.24578	0.86098	-4.931	<0.01 ***
UD - GH == 0	-3.75091	0.86098	-4.357	<0.01 ***
NS - LB == 0	0.28745	0.61678	0.466	1.0000
SB - LB == 0	-0.63140	0.61678	-1.024	0.9953
SL - LB == 0	-2.31862	0.61678	-3.759	<0.01 **
SSJ - LB == 0	-2.16298	0.61678	-3.507	0.0186 *
UD - LB == 0	-1.66810	0.61678	-2.705	0.1934
SB - NS == 0	-0.91885	0.61678	-1.490	0.9239
SL - NS == 0	-2.60606	0.61678	-4.225	<0.01 **

SSJ - NS == 0	-2.45043	0.61678	-3.973	<0.01 **
UD - NS == 0	-1.95555	0.61678	-3.171	0.0557 .
SL - SB == 0	-1.68721	0.61678	-2.736	0.1793
SSJ - SB == 0	-1.53158	0.61678	-2.483	0.3089
UD - SB == 0	-1.03670	0.61678	-1.681	0.8452
SSJ - SL == 0	0.15564	0.61678	0.252	1.0000
UD - SL == 0	0.65051	0.61678	1.055	0.9940
UD - SSJ == 0	0.49488	0.61678	0.802	0.9995

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