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NOTE

Macrophyte wrack on sandy beaches of the US Pacific Northwest is linked to proximity of source habitat, ocean upwelling, and beach morphology

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ABSTRACT: Marine macrophyte wrack (macroalgae and seagrasses) frequently washes onto beaches but little is known about the factors controlling its biogeographic variability. We report on a large-scale study of macrophyte wrack deposition patterns on the US Pacific Northwest coast. We measured macrophyte wrack on 12 sandy beach sites from southern Washington to northern California. We found the highest wrack biomass (g m^{-2}) occurred on southern beaches but the greatest wrack patch density (number m^{-2}) occurred on northern beaches, resulting in some northern sites having orders of magnitude more wrack than other sites. Eelgrass (*Zostera marina* and *Z. japonica*) was present in wrack in the greatest proportions at northern sites, and kelp (e.g. *Nereocystis luetkeana* and *Macrocystis integrifolia*) was present in the greatest proportions at central and southern sites. Further analyses showed that the proximity of estuary and rocky reef habitats, ocean upwelling, and beach geomorphology and wave climate all contributed to the biogeographic patterns of beach wrack. We also found new evidence that estuarine outwelling combined with ocean upwelling can significantly contribute to these patterns.

KEY WORDS: Macrophyte wrack · Nutrient subsidies · Beach and dune ecosystems · Estuarine outwelling · Ocean upwelling · Beach morphodynamics · Eelgrass · Kelp

INTRODUCTION

Coastal habitats are connected through the movement of ecological subsidies (nutrients and organic matter) in complex and often unpredictable ways. The addition of subsidies can affect local primary and secondary production, influencing food webs and ecosystem functions (Polis & Hurd 1996, Spiller et al. 2010). Although these effects have been observed at local scales, few studies have examined the contribution of subsidies at large, regional spatial scales, or whether inherent biophysical variability may affect how ecosystems receive subsidies (but see Orr et al. 2005, Liebowitz et al. 2016).

Macrophyte wrack, comprising dislodged macroalgae, seagrasses, and other estuarine plants, is an important coastal subsidy (Colombini & Chelazzi 2003). Research in California and Washington (USA), where marine systems are highly productive, shows that macrophyte wrack is an important driver of beach food web structure and diversity (Dugan et al. 2003, Heerhartz et al. 2016). Marine wrack also contributes nutrients to vegetation on dunes (Del Vecchio et al. 2013), potentially affecting the production of plants, their sand capture abilities, and coastal protection.

Here, we report on a large, regional-scale study of macrophyte wrack deposition patterns on sandy beaches of the Pacific Northwest, USA. Our goal was

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to determine the contributing factors to macrophyte wrack distribution and abundance patterns across a 900 km extent from central Washington to northern California. We investigated the relationships between macrophyte wrack deposition on beaches and 3 factors that vary regionally along this coast: the spatial distribution of estuary and rocky reef source habitats, ocean upwelling and its effect on macrophyte production, and the geomorphology and wave climate of sandy beaches.

Within the California Current System (CCS) of the Pacific coast (USA), ocean upwelling is an important process that underlies macrophyte primary production (Menge et al. 2015) and thus potentially influences the amount and type of wrack that washes onshore at regional scales. Upwelling brings cold, nutrient-rich water to the surface when strong northerly summer winds blow across nearshore surface waters, creating spatial and temporal productivity differences along the coast. For example, the northern California coast experiences stronger and more persistent upwelling than the Oregon coast, resulting in nitrogen-enriched coastal waters in the southern reaches of the CCS.

Ocean upwelling strength has different consequences for primary producers living in rocky shore compared to estuarine habitats. Rocky shores that experience persistent upwelling conditions are dominated by macroalgae (Menge et al. 2015). Likewise, estuaries exposed to more persistent upwelled waters have greater macroalgal production but, conversely, much lower eelgrass *Zostera marina* production (Hessing-Lewis & Hacker 2013). As a consequence of its contrasting effects on macroalgae versus eelgrass production, we hypothesize that variability in upwelling intensity, coupled with the spatial distribution of rocky reefs and estuaries, primarily determine the amount and type of wrack delivered to sandy beaches.

Once wrack makes it to the shoreline, we further hypothesize that beach geomorphology and nearshore hydrodynamics ('beach morphodynamics'; Wright & Short 1984) affect wrack deposition patterns. Beach attributes vary along the Pacific coast due to differences in the geology of the shoreline, sand grain size, and the incident wave climate (Di Leonardo & Ruggiero 2015). Beaches classified as dissipative are typically shallow sloping and made up of fine sand (Wright & Short 1984). On these beaches, waves tend to break farther out in nearshore waters and dissipate over wider surf and swash zones dominated by low frequency motions, potentially creating conditions favorable for wrack deposition. Beaches classified as intermediate to reflective are steeper and contain coarser sand. On these beaches, plunging breakers dissipate wave energy over narrower surf zones, creating conditions potentially less conducive to wrack deposition.

In this study, we surveyed 12 dune-backed sandy beach sites to test 3 interrelated hypotheses important to macrophyte wrack distribution and abundance — (1) distance to nearest source habitat: beaches near estuaries will have more eelgrass compared to beaches near rocky reefs, which will have more kelp, (2) ocean upwelling: eelgrass wrack will be more abundant in regions of weaker, intermittent upwelling and kelp wrack will be more abundant in regions of stronger, more persistent upwelling, and (3) beach morphodynamics: dissipative beaches will have greater amounts of wrack than intermediate beaches because the shallow slope of the beach and low frequency swash will strand more wrack on the shoreline.

MATERIALS AND METHODS

Study sites

Our study spanned 900 km along the coast at 12 sites used in previous dune research (Hacker et al. 2012; see Fig. 1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m594p263_supp.pdf). Using Google Earth (version 7.1.2.2041), we measured the distances between each of our study sites and the nearest estuary and rocky reef headland. Daily values of the Bakun upwelling index (cross-shore transport in units of m^{-3} s^{-1} per 100 m of coastline) were obtained for each of our sites (within 1° latitude or less) from the NOAA Pacific Fisheries Environmental Laboratory database (http://coastwatch.pfeg.noaa.gov/erddap/griddap/erdlasFnTran6.html). We calculated the average values for each site over the summer (May to October 2013), as an integrated measure of the influence of upwelling on macrophyte wrack production.

We obtained a non-dimensional surf similarity parameter, the Iribarren number, for each site from data analyzed by Di Leonardo & Ruggiero (2015) for US Pacific Northwest beaches (exceptions were Sites FL and CME, where data were lacking; see Fig. 1 and Table S1 for site names and locations). The Iribarren number,

$$\xi b = \frac{S}{\left(\frac{H_b}{L_0}\right)^{\frac{1}{2}}}$$

combines beach geomorphology and wave climate parameters, where S is the foreshore beach slope, H_b

is the breaking wave height, and L_0 is the deep water wavelength. See Di Leonardo & Ruggiero (2015) for methodological details.

Wrack distribution surveys

Wrack surveys were conducted on beaches from September to October 2013, the time of year when wrack abundance is greatest (Reimer 2014). At each beach site, we established 3 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 highest intertidal level most recently wetted by waves. We used this level to delineate the lower boundary of the block because wrack is deposited at or above this elevation. Within each block, we established one primary transect parallel to the shore that ran through the zone with the most dense wrack. We then delineated 5 secondary transects, perpendicular to the shore along the primary transect at 0, 25, 50, 75, and 100 m. For most of the sites and blocks, the 50 m transect location corresponded to the transect locations of Hacker et al. (2012) (see Table S1).

We placed a 1 m^2 quadrat at the intersection of the primary and secondary transects (every 25 m or 5 quadrats per block) and counted and collected the macrophyte wrack patches (i.e. macroalgae, seagrasses, and other estuarine vegetation) within those quadrats. Patches were visually identified as discrete piles of macrophytes that were not in contact with one another. In addition, along a 10 m swath around each of the secondary transects, we counted macrophyte wrack patches. Samples were returned to the lab and stored at −20°C until processing. Processing involved sorting the material to the lowest taxonomic classification possible, drying at 60°C to constant mass, and then weighing.

Statistical analyses

All analyses were conducted using the R platform, version 3.0.2 (R Development Core Team 2016). Wrack distribution and abundance patterns were expressed using 4 response variables for each block within a site: wrack patch density (patches m^{-2}), total wrack patch density (patches per block), wrack biomass (g m^{-2}), and total wrack biomass (kg $block^{-1}$). Wrack patch density was calculated by dividing the total patch count along the five 10 m wide secondary transects within each block by the area over which they were counted. Total wrack patch density was calculated by multiplying the patch density by the total area of the block. Wrack biomass was determined directly from the five 1 m^2 quadrats within each block. Total wrack biomass was calculated by multiplying the wrack biomass by the total area of the block. All 4 response variables were tested for differences among sites and blocks using single factor ANOVAs. Bonferroni-Dunn post hoc tests were conducted on significant factors. All response variables were log transformed before analyses to normalize the data.

We examined the composition of wrack by placing each species into 1 of 7 functional groups: kelp, other brown algae (excluding kelp), green algae, red algae, surfgrass, eelgrass, and other estuarine plants (excluding eelgrass) (see Table S2). We determined 3 response variables including the proportion of wrack biomass (g m^{-2} divided by the total g m^{-2}), wrack biomass (g m^{-2}), and total wrack biomass (kg m^{-2}) for each functional group separately. We used multiple regression analyses to test whether the 3 response variables for either kelp or eelgrass were correlated with the distance to the nearest rocky reef (for kelp) or estuary (for eelgrass) and ocean upwelling, and whether there was a distance by upwelling interaction. All response variables were square-root transformed before analyses to normalize the data.

We used regression analysis to determine the relationship between beach morphodynamics (Iribarren number) and 2 wrack response variables (total wrack patches and wrack biomass) given above at a subset of sites where kelp and/or eelgrass was abundant (defined as at least 25% of wrack biomass) and Iribarren numbers were available. Included were Sites SL, SB, SSJ, UD, NS, and BAN for kelp and Sites GH, LB, FS, CL, and NS for eelgrass. Note that Site SL had very little kelp or eelgrass but abundant other brown algae (32%) and was classified as a kelp site. In addition, Site NS was classified both as a kelp and eelgrass site given the co-dominance of both groups (25 and 50%, respectively).

RESULTS

Beach site characteristics

Distances between our sites and estuaries and rocky reefs, ocean upwelling, and beach morphodynamics all varied substantially across the study region (Fig. 1). Most sites in the north were near estuaries compared to those in the south, which were near rocky reefs, but some sites (i.e. Sites CL, SL, SB,

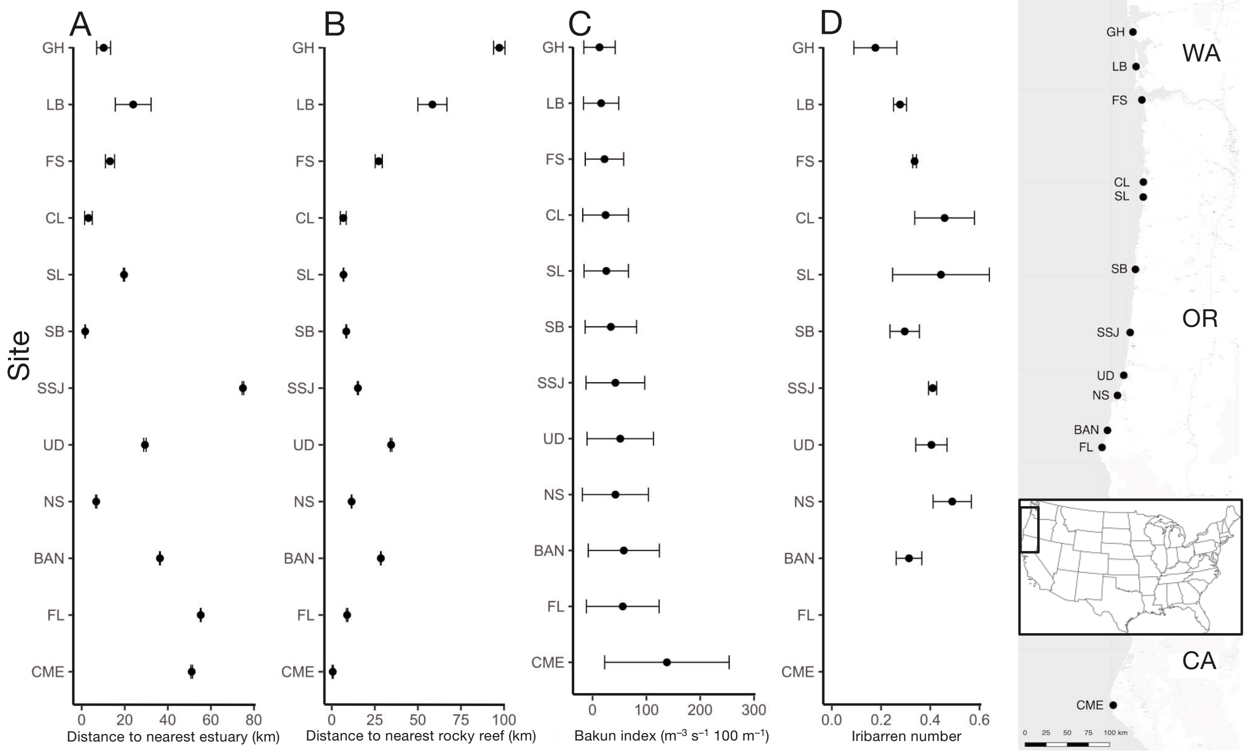

Fig. 1. Sandy beach sites and important physical characteristics along the US Pacific Northwest coast (inset). Mean (±SE) (A,B) distance to the closest estuary or rocky reef; (C) mean (±SE) daily Bakun upwelling index (m^{-3} s^{-1} 100 m^{-1} of coastline); and (D) Iribarren number, a parameter used to characterize beach geomorphology and wave climate. See Table S1 in the Supplement at www.int-res.com/articles/suppl/m594p263_supp.pdf for site abbreviations and locations

and NS) were close to both estuaries and rocky reefs (Fig. 1A,B). Upwelling intensity also varied across our sites, with weaker and more intermittent upwelling conditions present at higher latitudes and stronger and more persistent upwelling present at lower latitudes (Fig. 1C). Beach morphodynamics varied across our study region. Beaches in the north coast tended to be highly dissipative (Iribarren numbers less than 0.4) compared to central and southern sites, where beaches were slightly steeper, in the low intermediate range (Iribarren numbers between 0.4 and 0.6) (Fig. 1D). Finally, block area differed depending on beach width but there was no pattern with latitude (see Table S1).

Wrack distribution, abundance, and composition

We found that wrack patch density ($F_{11,24}$ = 33.11, $p < 0.001$, n = 36), total wrack density ($F_{11,24}$ = 7.63, $p < 0.001$, n = 36), wrack biomass ($F_{11,24}$ = 4.04, p = 0.002, n = 36), and total wrack biomass ($F_{11,24}$ = 11.68, p = 0.0001, n = 36) varied across beach sites (Fig. 2). Wrack patch densities (m^{-2} and block^{-1}) were greatest at northern beaches compared to central and southern sites (Fig. 2A,B). Wrack biomass m^{-2} was greatest at the 3 most southern sites (Sites BAN, FL, CME) and lowest at 2 northern sites (Sites LB, FS) (Fig. 2C). Total wrack biomass per block showed variability among sites with high total biomass at 3 sites in the north (Sites GH, LB, CL) and south (Sites NS, BAN, CME) (Fig. 2D). All central sites (Sites SL, SB, SSJ, UD) had very low total biomass (Fig. 2D).

The composition of macrophyte wrack varied among sites, with a high proportion of eelgrass at the northern sites and of kelp at central and southern sites (Fig. 3). Most central sites had a high diversity of wrack that included most, if not all, functional groups. Three of the sites (Sites SL, UD, and NS) had kelp and eelgrass in relatively equal proportions with abundant surfgrass and other brown algae as well.

Factors important to wrack distribution and abundance

We found that the proportion, biomass, and total biomass of kelp wrack increased on beaches both close to rocky reefs and exposed to more persistent ocean upwelling conditions (Fig. 4, Table S3), and

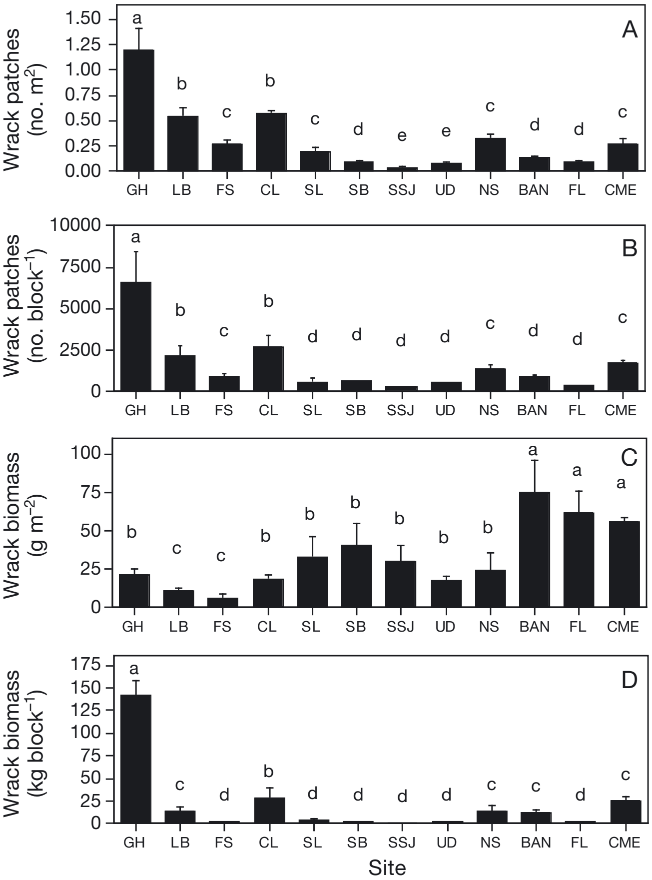

Fig. 2. Mean (±SE) (A) wrack patch density, (B) total wrack patch density, (C) wrack biomass, and (D) total wrack biomass. Sites are listed from north to south (see Table S1 for site abbreviations and locations). Bars with different letters represent significant differences at $p < 0.05$

there was an interaction between distance and upwelling for all response variables except total kelp biomass (Table S3). Moreover, the proportion, biomass, and total biomass of eelgrass wrack increased on beaches close to estuaries and those exposed to less persistent ocean upwelling conditions (Fig. 4, Table S3), and there was an interaction between distance and upwelling for all response variables except eelgrass wrack biomass (Table S3).

Finally, we found macrophyte wrack abundance increased on dissipative beaches (Iribarren number < 0.4) compared to intermediate beaches (Iribarren number ≥ 0.4) (Fig. 5). For beaches dominated by eelgrass, wrack patch number increased on more dissipative beaches (Fig. 5A) but there was no such variation in eelgrass wrack biomass (Fig. 5B). For beaches dominated by kelp, wrack patch number did not vary across beach types (Fig. 5A) but kelp wrack biomass did increase on more dissipative beaches (Fig. 5B).

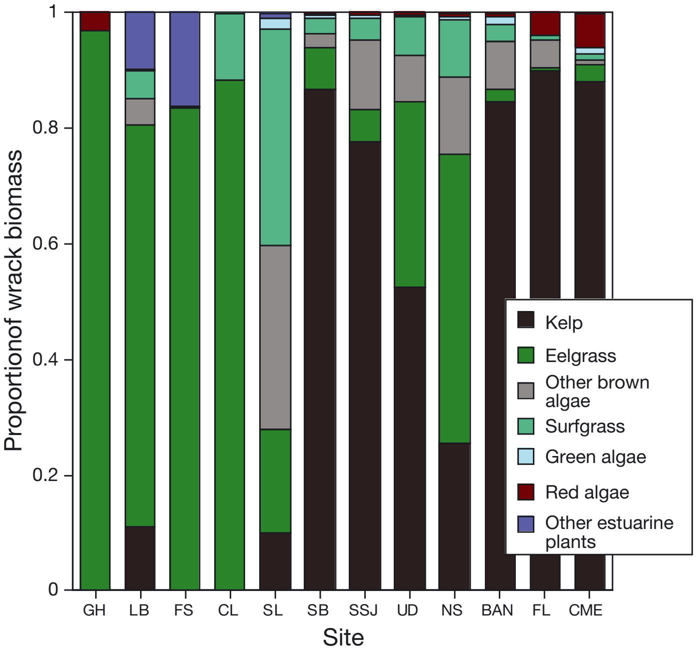

Fig. 3. Proportion of biomass of macrophyte wrack functional groups at each site. Species within each functional group are listed in Table S2. Sites are listed from north to south (see Table S1 for site abbreviations and locations)

DISCUSSION

Our study provides strong evidence that, at a regional scale, wrack deposition on sandy beaches varies in magnitude, by functional group, and largely depends on the co-varying factors of proximity to source, ocean upwelling, and beach morphodynamics. Our results corroborate those of Liebowitz et al. (2016), who concluded that wrack subsidies are largely determined by the donor ecosystem and that aspects of transport and beach morphology explain some additional spatial variation. A unique aspect of our work is evidence that estuarine outwelling combined with ocean upwelling can significantly contribute to the patterns of macrophyte deposition in coastal ecosystems.

We found a strong latitudinal pattern in macrophyte wrack deposition that was correlated with the location of estuaries and rocky reefs as source habitats as well as the influence of ocean conditions on the dominant source of macrophytes in those habitats (Fig. 4, Table S3). For example, in the north, where estuaries are common and upwelling is weaker and intermittent (Sites GH to CL), wrack patches were numerous but small, and primarily composed of eelgrass (Figs. 1–3). In the south, where rocky reefs are common and upwelling is strong and persistent (Sites BAN to CME), beach sites had fewer wrack patches

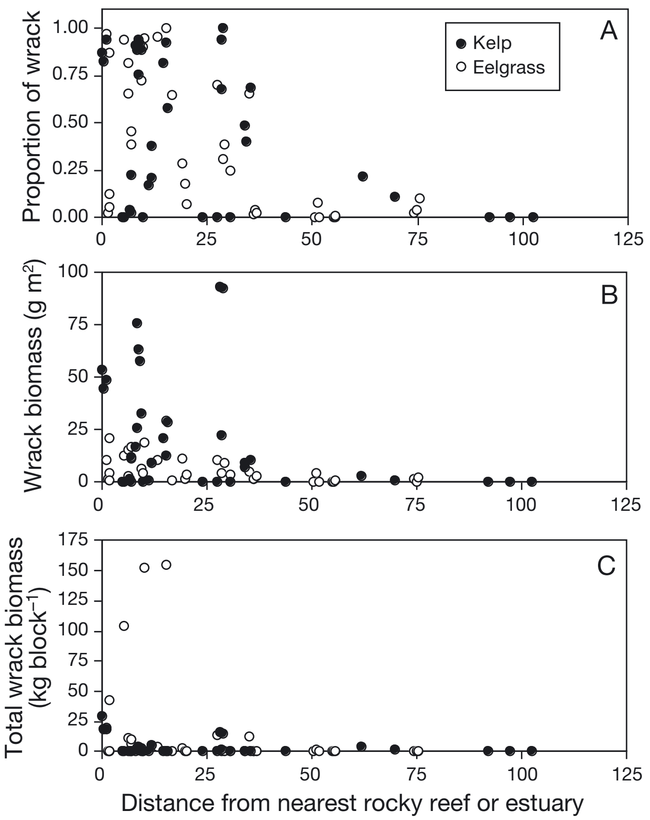

Fig. 4. Relationships between the (A) proportion, (B) biomass, and (C) total biomass of kelp and eelgrass wrack as a function of the distance from the nearest rocky reef (kelp) or estuary (eelgrass). See Table S3 for the statistical results

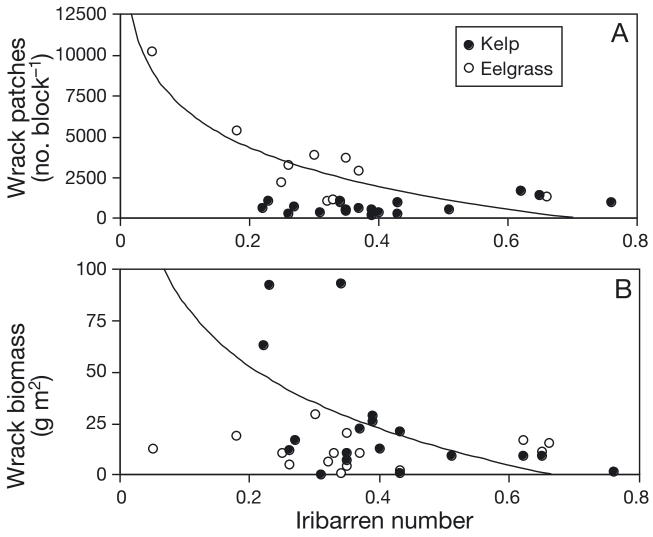

Fig. 5. Relationships between the (A) total number of wrack patches and (B) wrack biomass of kelp or eelgrass and beach morphodynamics (Iribarren number). Lines represent significant logarithm regression curves: (A) eelgrass, $y = -7958 \log x - 1218$, $r^2 = 0.75$, $F = 10.97$, p = 0.0056) and (B) kelp, $y = -100.9 \log x - 17.8$, $r^2 = 0.27$, $F = 4.60$, p = 0.0400

but they were higher in biomass and primarily composed of kelp (Figs. 1–3). In the central region, where both estuaries and rocky shore source habitats are common and upwelling is stronger but intermittent (Sites SL to NS), beach sites had relatively small amounts of wrack and they were composed of a diversity of macrophyte groups (Figs. 1–3).

We also found support for the role of beach morphodynamics on wrack deposition patterns, with dissipative beaches having more macrophyte wrack than intermediate beaches (Fig. 5). This pattern was similar to that in Barreiro et al. (2011), who found that macrophyte wrack was most abundant on beaches with lower wave energy. Previous research has also shown that buoyant kelps strand on high wave energy beaches, and as a result, make up a larger portion of the wrack found there (Orr et al. 2005, Barreiro et al. 2011). Although we did not see this pattern for kelp versus eelgrass, our beaches were mostly dissipative, and thus may not have provided enough variability to detect such functional group-specific depositional patterns.

Estuarine outwelling and its implications for beach and dune ecosystems

Even though proximity to source habitat is an obvious factor that affects the distribution and abundance of wrack along shorelines worldwide, one surprising result from our study was the role of estuaries in providing substantial wrack subsidies to open coast beaches. We did not investigate the mechanisms of eelgrass transport, but there is evidence that upwelling-influenced estuaries have higher flushing rates (Duxbury 1979), and coupled with tidal flows and high eelgrass production, could serve to export significant amounts of wrack to nearshore waters and the coastline.

The transport and use of carbon and nutrients from estuaries to outer coast ecosystems, known as outwelling, was proposed by Odum (1980) for salt marshes. Estuarine outwelling has been debated (e.g. Dame & Allen 1996), and studies have shown that subsidies from estuaries vary in their importance to coastal ecosystem productivity (e.g. Winter et al. 1996, Duarte et al. 2017). Given that eelgrass was present at every site we sampled, and in very large amounts at some sites, an important next question is whether eelgrass wrack differs from macroalgae wrack in its influence on beach and dune functions.

Wrack provides organic matter and nutrients, particularly nitrogen and phosphorus, to beaches (e.g.

Dugan et al. 2011), and thus can serve as a source of nutrients for dune plants. In our system, foredunes — linear ridges of sand behind the beach — were formed by the introduction of *Ammophila arenaria* and *A. breviligulata*, 2 non-native beach grasses efficient at accreting sand (Hacker et al. 2012, Zarnetske et al. 2012). These introductions facilitated a shift to tall, stable foredunes that now provide important coastal protection services by decreasing erosion and flooding (Biel et al. 2017). Thus, if wrack facilitates dune plant growth in our system, we predict that some regions with more wrack, or with particular kinds of wrack, may have better beach grass growth, sand accretion, and ultimately coastal protection. This work represents a foundation upon which future studies can explore the effects of wrack subsidies on beach and dune ecosystems in ocean upwelling-dominated regions. With climate change and coastal development occurring in tandem, understanding the links between coastal oceans and beach and dune ecosystems is an increasingly important challenge.

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