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How landscape variables influence the relative abundance, composition, and reproductive viability of macroalgal wrack in a high latitude glacial estuary

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ABSTRACT

Beach-cast wrack is an important resource that is commonly harvested by humans, and its removal can have consequences for coastal ecosystems. To further our understanding of wrack dynamics within high latitude ecosystems, our study objectives were to: 1) quantify spatio-temporal differences in beach-cast wrack biomass and composition, 2) quantify and compare the composition of drifting and beach-cast wrack, 3) determine the reproductive status of beach-cast kelp and rockweed wrack, and 4) compare the efficacy of using drone and on-the-ground surveys to assess beach-cast wrack surface area at different spatial scales. This study was based in Kachemak Bay, Alaska, a high latitude estuarine system where wrack harvest is carefully regulated by the Alaska Department of Fish and Game. Wrack from eleven beaches was surveyed between March and September in 2018 and 2021. Coastline (substrate type, slope, and exposure) and adjacent watershed characteristics (percent glacial cover and range in seawater salinity) were determined for each site and found to correlate with diversity and compositional differences in drifting and beach-cast wrack throughout Kachemak Bay. Reproductive kelp and rockweed wrack were confirmed to be viable at all surveyed sites, which suggests that harvesting wrack has the potential to remove viable propagules from the reproductive pool. On-the-ground and drone-based surveys of beach-cast wrack both revealed similar seasonal patterns of patchy (spring) and continuous (summer) deposition onshore, confirming that aerial drone surveys are a useful and efficient tool for monitoring beach-cast wrack surface area. This study identified several factors that contribute to wrack relative abundance, distribution, composition, and reproductive viability, which can be used by resource managers to develop wrack stock assessment and sustainable harvest strategies.

1. Introduction

Wrack (dislodged accumulations of marine macroalgae and woody terrestrial debris) is a renewable natural resource that, when removed by humans, can disturb the ecological function of the beach ecosystem (Dugan et al., 2003; Kirkman and Kendrick, 1997). In some regions of the world, entire beaches are cleared of wrack for aesthetics (Dugan et al., 2003; Defeo et al., 2009), or the accumulation of wrack is inhibited by coastal armoring (Heerhartz et al., 2014). Wrack drifting in the nearshore is commonly harvested for animal feed in some areas of the world (Kirkman and Kendrick, 1997). The interplay between the ecological importance of wrack and society's desire to remove it has spurred research worldwide (Dugan et al., 2003; Vieira et al., 2016). However, the importance of this habitat and resource within higher latitude coastal ecosystems has not been extensively explored, especially in regions where there is a growing interest in wrack harvesting for use as a component to garden fertilizer (Glenn Hollowell, Alaska Department of Fish and Game, pers. comm.). The distinctiveness of harsh beach conditions (heat, desiccation, freezing, and snow) and seasonally limited light and growth periods are unique selective factors among high latitude coastal systems that shape particular species assemblages of wrack.

Habitat created by marine macroalgae, when dislodged, is transported from a marine ecosystem that supports fish and marine invertebrates to one that supports terrestrial invertebrates and their predators (Fox et al., 2014). Dislodged macroalgae provide subsidies of marine derived nutrients (MDN) to other nearshore (drifting wrack) and

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onshore (beach-cast wrack) ecosystems where *in situ* primary production may otherwise be limited (Kelly et al., 2012; Filbee-Dexter and Scheibling, 2016; Liebowitz et al., 2016). Foundational habitat formed by beach-cast macroalgal wrack may help facilitate early terrestrial nearshore successional processes of invertebrate communities and ecosystem assembly (Sikes and Slowik, 2010). Beach-cast wrack also helps maintain overall species diversity (Harris et al., 2014) and ecosystem function (Defeo et al., 2009; Barreiro et al., 2011), niche variation (Davidson et al., 2021), and facilitates trophic associations between marine and terrestrial systems (Roth, 2003; Obrist et al. 2020, 2022). Before being deposited onshore, drifting wrack often accumulates in surf zones, where near-subtidal and intertidal macroinvertebrates find refuge and fish find forage in the loose organic debris (Clark, 1997; Olds et al., 2018). Drifting wrack left on the beach by outgoing tides and storm surges increases onshore productivity (Dugan et al., 2003; Vieira et al., 2016). Further ecological effects of beach-cast wrack are evident through biogeochemical processing, where heaps of decomposing wrack directly increase MDN on beaches, fertilizing nearby vegetation (Lastra et al., 2018). Wrack deposits also enhance dune formation and the stability of the substrate (Hemminga and Nieuwenhuize, 1990, Innocenti et al., 2018).

Many factors contribute to the accumulation and composition of wrack on beaches. Climate and seasonality may shape the composition of wrack given differences in macroalgal life history strategies (Barreiro et al., 2011; Gomez et al., 2013). Annuals develop sporophytes seasonally, whereas perennials may contribute detrital material year-round. Changing oceanic conditions that threaten the persistence of anchored macroalgae with structural and nutritional value (Rugiu et al., 2018) may also affect the quality of macroalgae that wash ashore for intertidal and terrestrial consumers (Mews et al., 2006; Michaud et al., 2019). The seasonal and spatial variability of wrack abundance and composition may play a role in shaping wrack-associated macrofaunal communities (Olabarria et al., 2007; Pelletier et al., 2011). Longevity of wrack can depend on substrate type and the intensity of macroinvertebrate consumption, the latter of which can be reduced by the presence of rockweeds and seagrasses due to higher concentrations of phenolic compounds that deter consumers (Orr et al., 2005). Habitat use by invertebrates and rate of MDN release on a beach are likely dependent on which macroalgae and aquatic plants wash ashore.

Increased glacial outflow may negatively impact macroalgal reefs (Traiger and Konar, 2018), indirectly influencing wrack. Macroalgae require sufficient nutrients, light, temperature, and salinity for successful development (Ladah and Zertuche-Gonzalez, 2007). For high latitude ecosystems, these physical parameters in the near-subtidal and intertidal zones are substantially influenced by glacial outflow (Spurkland and Iken, 2011a; Larsen et al., 2015). Increased sediment scour from glacial silt can reduce the diversity of macroalgal assemblages (Balata et al., 2015). Suspended sediments increase turbidity, which reduces access to light and decreases the stability of reefs (Airoldi, 2003; Bonsell and Dunton, 2018). The introduction of freshwater to coastal systems lowers salinity below tolerable levels for many macroalgal species (Spurkland and Iken, 2011b; Rugiu et al., 2018). Given the known effects of freshwater and glacial input on nearshore macroalgal reefs, drifting and beach-cast wrack composition might look considerably different under variable physical parameters in a glacially influenced estuary.

Macroalgae can remain reproductively viable following detachment and deposition as wrack (McKenzie and Bellgrove, 2008; Ulaski and Konar, 2021). Kelps have robust independent early life-history stages (Ladah and Zertuche-Gonzalez, 2007) with typical spore dispersal ranging from 1 to 10 m from the adult sporophyte (Filbee-Dexter and Wernberg, 2018). Gametes are released by fucoids during non-turbulent conditions for successful settlement (Pearson and Brawley, 1996). However, kelps and fucoid propagules may also travel hundreds of kilometers depending on water column conditions during the time of release (Schiel and Foster, 2006). Reproductively viable fragments caught up in rafts of drifting wrack may be an important means of long-distance dispersal (McKenzie and Bellgrove, 2008). Resuspension of beach-cast wrack by tides (Orr et al., 2005) may also be a vector of gene flow between longshore populations (Kusumo and Druehl, 2000; Tatarenkov et al., 2007). Removal of beach-cast wrack through harvesting efforts may interfere with this mode of macroalgal propagule dispersal and genetic mixing.

There are many methodological approaches for estimating beach-cast wrack biomass and surface area (e.g., Dugan et al., 2003; Barreiro et al., 2011; Gomez et al., 2013; Wickham et al., 2020; Gilson et al., 2021). These methods can be labor-intensive, as beach length and topographical constraints add complexity to estimating wrack surface area on-the-ground (OTG). The use of unmanned aerial vehicles (drones) offers a labor-saving approach to coastal monitoring (Konar and Iken, 2018; Escobar-Sanchez et al., 2021; Pucino et al., 2021) and has been proven a feasible tool to map wrack on beaches (Pan et al., 2021). Routine implementation of aerial drone surveys offers an efficient, long-term, and reproducible monitoring practice available to coastal managers.

1.1. Objectives

The aim of this study was to further our understanding of wrack dynamics within high latitude ecosystems, in part, to aid resources managers in developing appropriate harvest regulations. To achieve that goal, we developed the following four objectives and corresponding hypotheses:

1. Quantify spatio-temporal differences in beach-cast wrack biomass and composition.

H1. Beach-cast wrack biomass and composition are similar over time and across beaches with different static environmental conditions.

2. Quantify and compare the composition of drifting and beach-cast wrack.

H2. Drifting and beach-cast wrack have similar macroalgal composition.

3. Determine the reproductive status of beach-cast kelp and rockweed wrack.

H3. Kelp and rockweed wrack can be reproductively viable after it is deposited on beaches.

4. Compare the efficacy of using drone and OTG surveys to assess beach-cast wrack surface area at different spatial scales.

H4. Measurements of beach-cast wrack surface area from drone and OTG surveys produce similar estimates.

2. Methods

2.1. Study area

This study was conducted in Kachemak Bay, a large fjord-type, glacially fed estuary in Lower Cook Inlet, Alaska (Fig. 1). Some incoming oceanic water diverging from the Alaska Coastal Current mixes with local waters and enters Kachemak Bay, joining the flow that generally circulates cyclonically (counterclockwise) along the coastline (Johnson, 2021). Tides also add inter-daily flow and circulation variation given the large changes between low and high tide in Kachemak

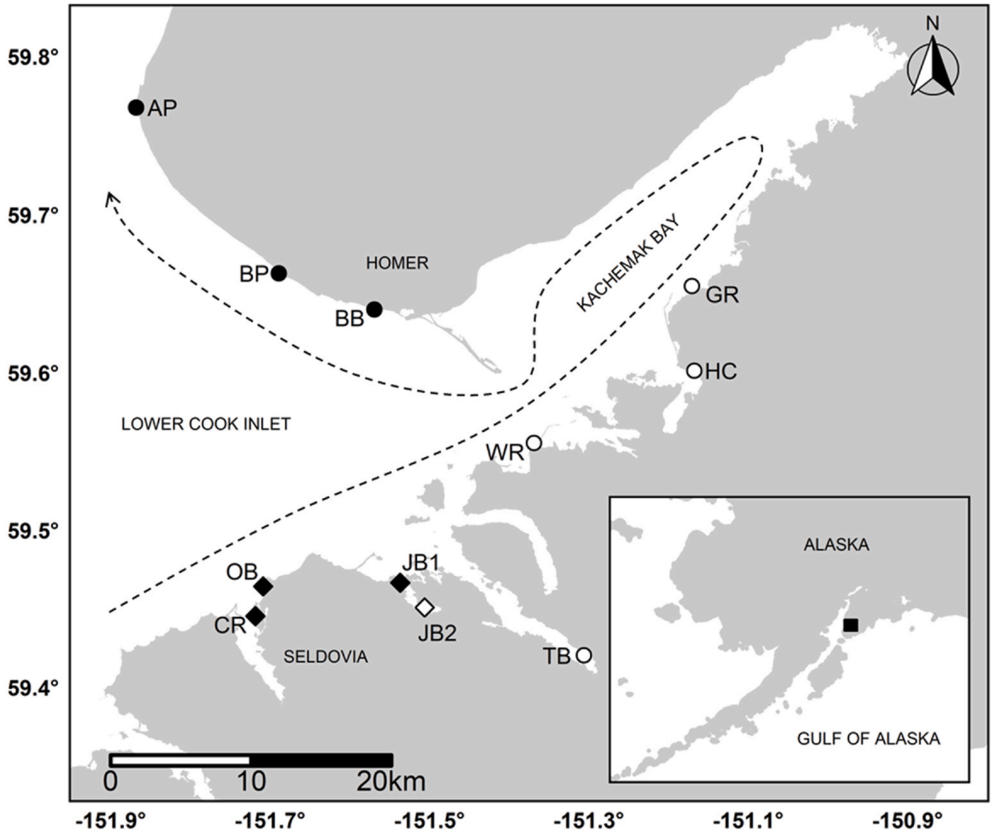

Fig. 1. Map of study beaches located in Kachemak Bay, Alaska (black rectangle of inset map) that were sampled in both 2018 and 2021 for spatio-temporal assessment of beach-cast wrack biomass and composition (black circles and diamonds), and the separate set of sites that were added in 2021 for assessment of drifting and beach-cast wrack compositional variability (white circles and diamonds). Circles denote sites located in a personal-use seaweed fishery and diamonds denote sites located in a subsistence-use seaweed fishery. Dashed line denotes generalized cyclonic water circulation along the perimeter of the bay (Johnson, 2021). AP = Anchor Point; BB = Bishop's Beach; BP = Bluff Point; CR = Camel Rock; GR = Grewingk River; HC = Halibut Cove; JB1 = outer Jakolof Bay; JB2 = inner Jakolof Bay; OB = Outside Beach; TB = Tutka Bay; WR = Wosnesenski River.

Bay, with tidal ranges reaching up to 8.5 m. The nearshore regions of the bay are populated by a diverse array of macroalgae (Konar et al., 2010). Extensive nearshore reef macroalgae wash up as beach-cast wrack, which has historically been harvested by the public most commonly for use as garden fertilizer (Glenn Hollowell, Alaska Department of Fish and Game, pers. comm.), and in most places it is highly regulated by the Alaska Department of Fish and Game. Currently, beach-cast wrack harvest is presumed to be relatively low but increasing, so precautionary restrictions are in place because stock status information for macroalgal populations in the area (including macroalgal wrack washed up on the beach) is too limited to develop an optimal harvest strategy and it is uncertain how increased harvest may alter the productivity and natural distribution of this resource. As such, six beaches were chosen as field sites in areas easily accessible to the public along the Homer and Seldovia road systems (Fig. 1).

Data were collected monthly from March to September in 2018 and 2021 to determine spatio-temporal variability in beach-cast wrack. Three sites were located on the north side of the bay (Anchor Point, Bishop's Beach, and Bluff Point; Fig. 1) in a personal-use seaweed fishery. In this region, there are added limitations to the harvesting of beach-cast wrack, i.e., commissioner's permits are required by the Alaska Department of Fish and Game for commercial activities (Alaska Administrative Code 5 AAC 37.420) and daily harvest limits for personal use are set (Alaska Administrative Code 5 AAC 77.532; Table 1). Three study sites were located on the south side (Camel Rock, outer Jakolof Bay, and Outside Beach; Fig. 1), situated west of Jakolof Point in an area where subsistence-use harvest is allowed (i.e., customary and traditional uses of wild resources). During 2021, five separate beaches on the south side of the bay (Grewingk River, Halibut Cove, inner Jakolof Bay, Tutka Bay, and Wosnesenski River; Fig. 1) were also sampled to investigate

Table 1
Static site characteristics (seaweed fishery harvest limits, region, coastline orientation, wave exposure, beach slope, and substrate type) used to assess spatial and temporal (i.e., monthly and between years) variability of wrack composition in Kachemak Bay, Alaska. AP = Anchor Point; BB = Bishop's Beach; BP = Bluff Point; CR = Camel Rock; GR = Grewingk River; HC = Halibut Cove; JB1 = outer Jakolof Bay; JB2 = inner Jakolof Bay; OB = Outside Beach; TB = Tutka Bay; WR = Wosnesenski River. Seaweed fishery harvest limits: Weight = 10 gal/person/day; Season = personal-use wrack harvests are allowed from January 1 to April 30 and September 1 to December 31 (Alaska Administrative Code 5 AAC 77.532).

Site	Seaweed Fishery Harvest Limits	Region	Orientation	Wave Exposure	Slope (degrees)	Boulder (%)	Cobble (%)	Gravel (%)	Sand (%)
AP	Weight + Season	North	Southwest	Semi-Exposed	1	0.0	11.2	16.8	72.0
BB	Weight + Season	North	South	Semi-Protected	1	0.0	80.9	19.1	0.0
BP	Weight + Season	North	Southwest	Semi-Exposed	2	1.5	15.6	13.1	69.8
CR	Weight	South	Northwest	Semi-Exposed	9	0.0	3.5	94.5	2.0
GR	Weight + Season	South	West	Semi-Exposed	8	0.0	17.0	39.5	43.5
HC	Weight + Season	South	Southwest	Semi-Protected	10	0.0	0.0	95.0	5.0
JB1	Weight	South	East	Protected	6	0.0	30.0	70.0	0.0
JB2	Weight	South	Southwest	Protected	19	90.0	10.0	0.0	0.0
OB	Weight	South	West	Semi-Exposed	7	0.0	0.4	99.6	0.0
TB	Weight + Season	South	Southwest	Protected	2	0.0	25.2	74.8	0.0
WR	Weight + Season	South	West	Semi-Exposed	5	0.0	0.0	34.0	66.0

relationships between detached wrack composition before (drifting) and after (beach-cast) deposition onshore relative to watershed characteristics.

2.2. Wrack collections

To quantify spatio-temporal differences in beach-cast wrack biomass and composition, in 2018, ten 0.25-m^2 quadrats were haphazardly placed along the wrack line at the six beaches (Fig. 1). The predominant wrack line from the recent high tide was sampled. Species composition, proportional biomass of each species, and total biomass of beach-cast wrack were estimated monthly from March to September. We defined biomass as a measure of mass per area (kg m^{-2}). All wrack within each of the quadrats was collected and bagged by replicate ($n = 10$ quadrats/beach/month) and wet weight of each macroalgal species was determined (see Dugan et al., 2011; Lastra et al., 2018; López et al., 2019). Wet weights were used as samples were collected primarily for compositional data, where each sample was standardized by the total biomass. Standardization of wet or dry biomass would not greatly affect the proportional contribution of each taxon to the total wrack biomass. Lindeberg and Lindstrom (2010) was used to identify macroalgae down to species level when possible given their decomposition state. During 2021, a modified sampling design was implemented at the same six beaches (modified from Barreiro et al., 2011 and Lastra et al., 2018) to include estimates of wrack surface area to accompany biomass and composition estimates. In 2021, a 50-m long horizontal transect was placed parallel to and centered on the wrack line. Along the horizontal transect, width of the wrack line was estimated by running a vertical transect every 5 m (perpendicular to the horizontal transect) out to the upper and lower boundaries of the wrack line ($n = 10$ vertical transects/beach/month). We defined the upper and lower end points where the boundaries of the wrack line started to lose definition and a gap of at least 1 m first occurred between scattered wrack material. To estimate surface area from OTG measurements, vertical wrack-width transects were averaged and multiplied by 50 m. Along each vertical wrack-width transect, one 0.25-m^2 quadrat was haphazardly placed and all wrack within each of the quadrats was collected and bagged by replicate ($n = 10$ quadrats/beach/month), and wet weight for each macroalgal species was determined.

Additional sampling was conducted in 2021 at a separate set of sites (Grewingk River, Halibut Cove, inner Jakolof Bay, Tutka Bay, and Wosnesenski River) to facilitate quantifying and comparing the composition of drifting and beach-cast wrack. Drifting wrack was collected by beach seining and was sampled from the nets using a semi-quantitative coring method. Monthly at each site, three nearshore beach seines were pulled by two people walking parallel to the shoreline for 4–5 min, one in ankle-deep water and one in approximately waist-deep water (net length = 15 m; mesh size = 1.2 cm). Once the net was brought ashore, 11-cm diameter cores were placed at three fixed points near the cod end to collect any retained drifting wrack for assessment of composition ($n = 9$ drifting wrack cores/site/month). Along the wrack line at the same beaches where drift was collected, beach-cast wrack was also sampled using the same 11-cm diameter corer pushed down through the wrack and into the underlying sediment to a depth of 10 cm ($n = 9$ beach-cast wrack cores/site/month; see Deidun et al., 2009; MacMillan and Quijón, 2012; Heerhartz et al., 2014). The contents of all cores were bagged by replicate. All drifting and beach-cast wrack samples were transported to the National Oceanic and Atmospheric Administration/University of Alaska Fairbanks Kasitsna Bay Laboratory and contents were sorted, identified to the lowest possible taxonomic level given their decomposition state, and weighed to determine relative biomass.

2.3. Environmental variables

To evaluate correlations between static environmental conditions and wrack composition among the sites, coastline orientation, wave exposure, beach slope, and percent substrate type (i.e., boulder, cobble, gravel, and sand) were characterized (Table 1). Physical watershed characteristics of total watershed area, percent glacier cover, percent forested area, and seawater temperature and salinity ranges were provided by Alaska EPSCoR (https://catalog.epscor.alaska.edu/) and used to assess compositional differences between drifting and beach-cast wrack at the separate sites added in 2021 (Table 2). For all sites, coastline orientation, wave exposure, and beach slope were determined from the National Oceanic and Atmospheric Administration's Alaska ShoreZone website (https://alaskafisheries.noaa.gov/mapping/sz_js/) under "Derived ShoreZone Attributes." Within these attributes, wave exposure was determined by the "Biological Wave Exposure" data to determine exposure classifications: protected, semi-protected, semi-exposed, or exposed. Beach slope was determined by the "Intertidal Zone Slope" data. Substrate type was classified for each beach with ten 1-m^2 quadrats haphazardly placed along the wrack line, from which percent cover of boulder, cobble, gravel, and sand was visually estimated (Wentworth, 1922).

2.4. Propagule release experiments

To determine if the reproductive tissues of the commonly harvested *Fucus distichus*, *Nereocystis luetkeana,* and *Saccharina latissima* found in the 2018 beach-cast wrack collections were viable, propagule release experiments (Siméon and Hervé, 2017; Traiger and Konar, 2017; Ulaski et al., 2020; Ulaski and Konar, 2021) were conducted at the Kasitsna Bay Laboratory. These species were chosen as representatives of the reproductive potential of wrack based on their visually distinguishable reproductive tissues in the field. To ensure that reproductive target species in the wrack were properly identified, only reproductive tissues with intact branches (*F. distichus*) and blades (*N. luetkeana* and *S. latissima*) were selected for propagule release experiments.

For *F. distichus*, reproductive tissue samples (receptacles bearing conceptacles) were rinsed with 0.2 μm-filtered seawater (filter-sterilized) and gently removed of sediment and macroscopic epiphytes. The receptacles were wrapped in a damp paper towel and placed in a 10 °C dark room for 1 h. Following the desiccation period, each receptacle was placed in individual plastic cups filled with 100 mL of 10 °C filter-sterilized seawater. Glass slides were placed at the bottom of each cup as a substrate for settling zygotes. The cups were then maintained at 10 °C with a photoperiod of 17 h of light (50 μmol photons m^{-2} s^{-1} fluorescent lighting) and 7 h of darkness (Ang, 1991; Siméon and Hervé, 2017) to mimic natural summer conditions. Cultivated *F. distichus* were then observed for developing zygotes under a compound microscope (observed under both 100X to 400× total magnifications) after 72 h. Individuals were scored as reproductively viable if settled zygotes began to cleave and show elongation in one hemisphere of the cell (Siméon and Hervé, 2017). Zygotes were not quantified.

For *N. luetkeana* and *S. latissima*, intact blades bearing sori were

Table 2
Watershed characteristics (total watershed area, percent glacier cover, percent forested area, overall seawater temperature range, and overall seawater salinity range) for the separate sites in Kachemak Bay, Alaska added in 2021 that were used to assess spatial variability of drifting and beach-cast wrack composition. GR = Grewingk River; HC = Halibut Cove; JB2 = inner Jakolof Bay; TB = Tutka Bay; WR = Wosnesenski River.

Site	Area (km^2)	Glacier (%)	Forest (%)	Seawater Temperature Range (°C)	Seawater Salinity Range
GR	111.5	60.0	2.3	−0.04–15.7	10.8–31.7
HC	55.6	16.1	6.5	1.2–15.3	13.6–31.4
JB2	18.9	0.0	64.3	−0.3–12.7	5.4–30.5
TB	65.7	8.0	17.9	−1.4–15.5	0.9–29.8
WR	256.6	27.3	17.5	0.5–14.1	5.7–31.6

rinsed with filter-sterilized seawater and gently removed of sediment and macroscopic epiphytes. A standardized 2.5 cm diameter disc of each ripe sorus was haphazardly removed and used for further analyses (Traiger and Konar, 2017; Ulaski et al., 2020; Ulaski and Konar, 2021). Sori discs were then wrapped in damp paper towel and gently desiccated for 1 h in a dark 10 °C cold room to stimulate a synchronous release of spores (Redmond et al., 2014). Each sorus disc was then placed in individual plastic cups filled with 100 mL of 10 °C filter-sterilized seawater and a glass slide. The cups were maintained at 10 °C with a photoperiod of 17 h of light (50 μmol photons m^{-2} s^{-1} fluorescent lighting) and 7 h of darkness to mimic summer conditions (Deiman et al., 2012). Microscope slides were observed under a compound microscope (400× total magnification) after 48 h, and viable spores were characterized by the presence of a germ tube. Spores were not quantified.

2.5. Aerial drone surveys

To determine if drone imaging could be used to scale-up OTG estimates of wrack surface area (m^2 km^{-1}), we used a DJI Mavic 2 Pro in 2021 at one of the beaches in the non-subsistence zone (Bluff Point) prior to each monthly OTG sampling event. We used wrack surface area, expressed as square meters of wrack per kilometer of beach, as a measure of relative abundance to facilitate comparing drone and OTG sampling methods. Monthly orthomosaics were created from drone imagery, providing a snapshot of beach-cast wrack surface area on a 20x larger scale (1-km transects) than what was achieved with OTG sampling (50-m transects). Opensource DJI Pilot PE mobile software was used to design a standardized monthly drone flight route using a gridded sampling approach for capturing aerial images. Flight altitude was set to 30 m above ground level (ground sampling distance = 0.71 cm $pixel^{-1}$) with a 1-km transect parallel to and centered on the wrack line resulting in approximately 30,000 m^2 of mapped coastline, repeated each month. Images were captured at a 90° camera angle (nadir) set to 80% and 70% front and side image overlap, respectively. Images were processed in Agisoft Metashape Pro (Agisoft LLC) to create the stitched orthomosaic maps that were analyzed for monthly beach-cast wrack surface area along the 1 km of coastline.

Each 50-m horizontal transect tape used for OTG sampling of beach-cast wrack was visible within each of the drone-derived orthomosaic maps and were used for ground-truthing and subsequent digital estimations of beach-cast wrack surface area. In Agisoft Metashape Pro, vertical measurements of wrack line width were taken every 5 m along the same 50-m transect that was surveyed OTG to directly compare drone and OTG methods. Vertical measurements along the 50-m transect were averaged and extrapolated to estimate beach-cast wrack surface area for 1 km of beach. Vertical measurements of wrack line width were also taken every 100 m along wrack lines observed on each 1-km long drone transect and were averaged to estimate wrack surface area to determine if the 50-m long transects were representative of the greater 1-km wrack line.

2.6. Statistical analyses

Statistical analyses were carried out in PRIMER v7 software with the PERMANOVA + package (Anderson et al., 2008) and opensource R software (R Core Team, 2021). Multivariate data were standardized to calculate relative biomass and then square root transformed to increase normality (Anderson et al., 2008; Clarke and Gorley, 2015). A Bray-Curtis similarity index was calculated to produce a resemblance matrix of multivariate data from the set of sites sampled in both 2018 and 2021 used to assess spatio-temporal variability in beach-cast wrack. To test our hypothesis that beach-cast wrack biomass and composition are similar over time and across beaches with different static environmental conditions, a four-factor permutational multivariate analysis of variance (PERMANOVA) was used to test for responses of beach-cast wrack composition to region (north and south shore; fixed factor), site (nested in region; random factor), year (random factor), and month (random factor). A separate Bray-Curtis similarity index was calculated to produce a resemblance matrix for permutational analysis of multivariate data from the separate set of sites sampled in 2021 used to assess compositional differences in drifting and beach-cast wrack. As such, to test our hypothesis that drifting and beach-cast wrack have similar macroalgal composition, a separate three-factor PERMANOVA was then used to test for responses of drifting and beach-cast wrack composition to habitat (drifting and beach-cast; fixed factor), site (random factor), and month (random factor). A cyclic resemblance model matrix was used in the RELATE routine to determine seasonal shifts of beach-cast wrack composition. Non-metric multidimensional scaling (nMDS) ordinations were used to visually explore spatial and temporal compositional dissimilarities among grouping factors. Similarity percentages (SIMPER) analyses were carried out to determine which taxa were most responsible for driving compositional differences among grouping factors (as in Terlizzi et al., 2005). The BEST-BIOENV procedure was carried out to determine if any environmental variables correlated with variability in wrack composition (Clarke and Warwick, 2001).

For univariate data, one-way analysis of variance (ANOVA) tests were used to determine variability in total beach-cast wrack biomass by region, site, year, and month. Separate ANOVA tests were used to determine variability in the Shannon Diversity Index between beach-cast wrack in the northern and southern regions of the bay and between drifting and beach-cast wrack habitats. To test our hypothesis that kelp and rockweed wrack can be reproductively viable after it is deposited on beaches, additional one-way ANOVA tests were used to determine temporal variability of individual and combined contributions of reproductive target species to total beach-cast wrack biomass. To test our hypothesis that measurements of beach-cast wrack surface area from drone and OTG surveys produce similar estimates, further one-way ANOVA tests were used to determine variability in surface area over time (months), between methods (drone and OTG), and between scales (meters and kilometers). When ANOVA tests suggested significance, Tukey honest significant difference (HSD) post hoc tests were carried out to confirm pairwise differences.

3. Results

3.1. Spatio-temporal variability in beach-cast wrack biomass and composition

We hypothesized that beach-cast wrack biomass and composition are similar over time and across beaches with different static environmental conditions. This hypothesis was mostly disproven, as beach-cast wrack was variably distributed on spatial and temporal scales. Total beach-cast wrack biomass was similar between years (ANOVA, $F_{1,826} = 0.02$, $p = 0.89$) with mean overall biomass of 1.03 ± 0.17 (SE) kg m^{-2} and 1.05 ± 0.35 kg m^{-2} in 2018 and 2021, respectively (Fig. 2). However, within each year, estimates of total beach-cast wrack biomass were significantly different across months (ANOVA, 2018: $F_{6,401} = 10.86$, $p < 0.001$, 2021: $F_{6,413} = 4.82$, $p < 0.001$; Fig. 2). Total beach-cast wrack biomass was greater in August than all other months in both years only on the north beaches. Total beach-cast wrack biomass was also significantly different among some sites (ANOVA, $F_{5,822} = 12.04$, $p < 0.001$) and between regions (ANOVA, $F_{1,826} = 33.37$, $p < 0.001$). A marked difference between total beach-cast wrack biomass in the northern and southern regions of the bay was a seasonal pattern that peaked in August in both 2018 (3.00 ± 1.36 kg m^{-2}) and 2021 (5.43 ± 4.20 kg m^{-2}) at the northern sites, whereas total biomass on the south side of the bay remained relatively steady over time in both years, ranging from only 0.16 ± 0.05 kg m^{-2} to 1.43 ± 0.97 kg m^{-2} (Fig. 2).

Species diversity of beach-cast wrack was similar between years (ANOVA, $F_{1,838} = 1.24$, $p = 0.27$). However, beach-cast wrack on the north side of the bay (Shannon Diversity Index H' = 1.10 ± 0.02) was significantly more diverse than those on the south side (Shannon

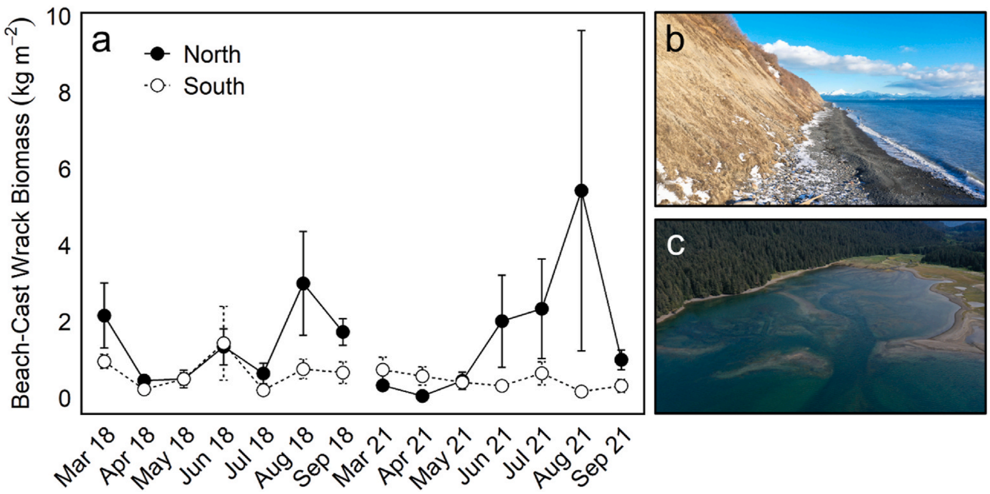

Fig. 2. (a) Total beach-cast wrack biomass (kg m^{-2}; bars represent standard error) showing differences between years and regions of Kachemak Bay, Alaska. Beach-cast wrack biomass peaks in August in both 2018 and 2021. Photographs showing general coastline differences between beaches sampled in the (b) north and (c) south regions.

Diversity Index H' = 0.88 ± 0.02; ANOVA, $F_{1,838} = 46.66$, $p < 0.001$; Fig. 3). In addition to these regional differences in overall diversity, compositional differences of beach-cast wrack were also significant between regions (PERMANOVA, $F_{1,748} = 2.99$, $p = 0.001$; Fig. 3a). Our hypothesis that beach-cast wrack biomass and composition are similar over time and across beaches with different static environmental conditions was further disproven as composition was variably distributed on spatial and temporal scales. Significant compositional differences were also seen between years in both regions (PERMANOVA, north: $F_{1,373} = 2.71, p = 0.01$; south: $F_{1,375} = 2.26, p = 0.04$) and across months in the northern region (PERMANOVA, $F_{6,373} = 1.97, p = 0.002$), but not in the southern region (PERMANOVA, $F_{6,375} = 1.15, p = 0.29$). SIMPER analyses indicated that differences between the regions were driven mostly by *Agarum*, *Alaria, Desmarestia*, dregs (unidentifiable algal remnants), *Fucus*, miscellaneous red algae, *Nereocystis,* and terrestrial matter, which cumulatively accounted for 72% of the dissimilarity (Fig. 3b). Temporally, changes in beach-cast wrack composition followed a seasonal pattern in the northern region in both years (cyclic RELATE, 2018: $\rho = 0.74, p = 0.002$, 2021: $\rho = 0.58, p = 0.002$). In the southern region, changes in beach-cast wrack composition did not follow a seasonal pattern in 2018 (cyclic RELATE, $\rho = 0.24$, $p = 0.13$), but did follow a seasonal pattern in 2021 (cyclic RELATE, $\rho = 0.78$, $p = 0.002$; Fig. 4). SIMPER analyses indicated that *Agarum*, *Fucus*, miscellaneous red algae, *Nereocystis*, terrestrial matter, and *Ulva*. were major contributors to the interannual and monthly differences in the northern region (Fig. 5). Whereas *Acrosiphonia*, *Agarum*, *Alaria*, *Cymathaere*, *Fucus*, miscellaneous red algae, *Nereocystis*, and terrestrial matter contributed to interannual and monthly variability in the southern region (Fig. 5). In both regions, seasonal changes in wrack composition were influenced by the seasonal growth and increased contributions of annuals later in the summer (e.g., *Alaria*, *Nereocystis*, and *Ulva*; Fig. 5).

Among all the static environmental variables assessed for the sites that were sampled in both 2018 and 2021 (i.e., wave exposure, beach slope, percent boulder substrate, percent cobble substrate, and percent sand substrate), spatial variability in beach-cast wrack composition were most highly correlated with wave exposure, beach slope, and percent boulder substrate (BEST-BIOENV, 0.419). Beaches in the northern region with greater percent cover of boulder and sand substrate and greater exposure to wave action accumulated more diverse wrack assemblages that contained more *A. clathratum* (Fig. 5). Whereas beaches in the southern region with steeper slopes accumulated less diverse wrack assemblages that were mostly comprised of *F. distichus*, *Laminaria* spp., and *N. luetkeana* (Fig. 5). Percent gravel and coastline orientation were not included in the analyses as draftsman plots indicated collinearity of these variables with others (correlation cutoff $|r| \geq 0.80$). However, steeper sloped beaches in the southern region were mostly gravel substrate.

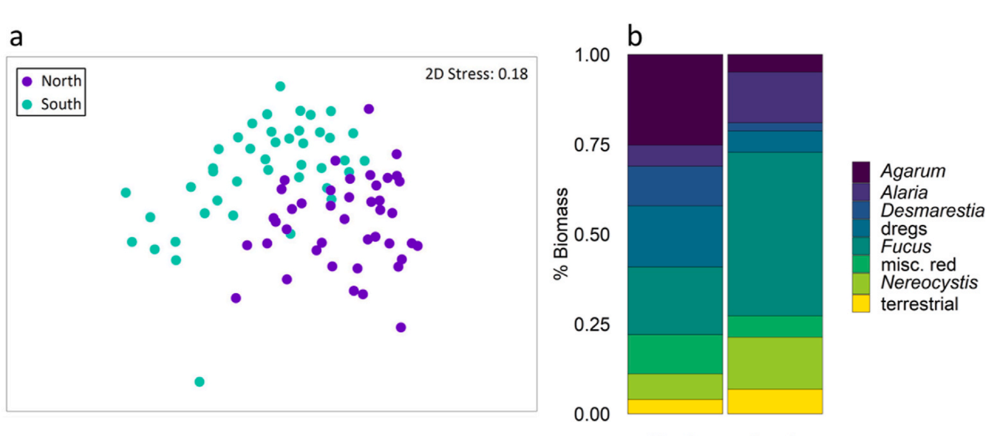

Fig. 3. (a) Non-metric multidimensional scaling (nMDS) ordination plot of beach-cast wrack composition in north (purple) and south (green) regions of Kachemak Bay, Alaska based on relative biomass (kg m^{-2}). (b) Stacked bar plot of seaweed taxa most responsible (from SIMPER analysis) for driving compositional differences in beach-cast wrack between the north and south regions based on biomass (kg m^{-2}). Stress indicates how well the ordination summarizes the two-dimensional distances among the points. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

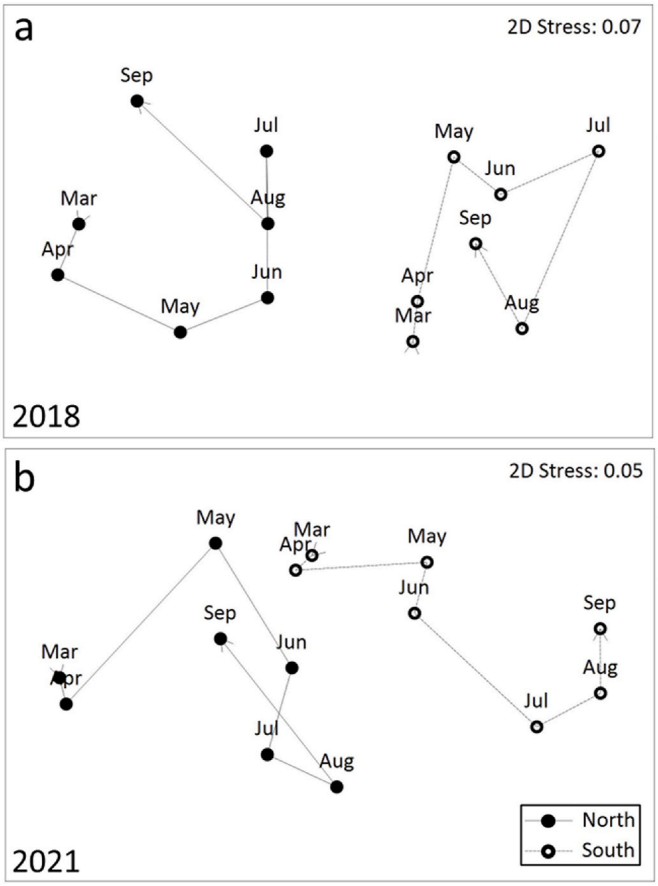

Fig. 4. Non-metric multidimensional scaling (nMDS) ordination plots of monthly beach-cast wrack composition in the north and south regions of Kachemak Bay, Alaska in (a) 2018 and (b) 2021 based on relative biomass (kg m^{-2}). Trajectories over time (months) are overlayed for each region in each year. Stress indicates how well the ordination summarizes the two-dimensional distances among the points.

3.2. Macroalgal composition of drifting and beach-cast wrack

Various red, green, and brown macroalgal species appeared in drifting and beach-cast wrack collections. Aquatic plants (e.g., seagrass), terrestrial matter, and diatom mats were also present in some of the samples. Drifting (Shannon Diversity Index H' = 0.73 ± 0.03) and beach-cast (Shannon Diversity Index H' = 0.76 ± 0.03) wrack were similar in overall diversity (ANOVA, $F_{1,527} = 0.54$, $p = 0.46$). Though overall diversity was similar between the two habitats, overall composition of macroalgal taxa in drifting and beach-cast wrack was significantly different (PERMANOVA, $F_{1,469} = 4.88$, $p = 0.003$; Fig. 6a), except for inner Jakolof Bay (PERMANOVA, $F_{1,93} = 1.52$, $p = 0.21$), disproving our hypothesis that drifting and beach-cast wrack have similar macroalgal composition. A SIMPER analysis removing the effects of site and month showed that compositional differences between the two habitats were driven mostly by *Acrosiphonia*, *F. distichus*, *Laminaria*, terrestrial matter, and *Ulva*, which cumulatively accounted for 74% of the dissimilarity between the habitats (Fig. 6b). Generally, more *Ulva* were present in drifting wrack, while more *F. distichus* and terrestrial matter were present in beach-cast wrack. Despite these habitat associations, site differences were significant (PERMANOVA, $F_{4,469} = 8.98$, $p = 0.001$) when the effect of habitat was removed, indicating that beach-cast wrack is likely highly influenced by the nearby drifting wrack and that there is significant variability in wrack composition along the coast. An interaction effect with site confirmed significant monthly differences in drifting and beach-cast wrack composition, with a SIMPER analysis indicating that compositional differences over time for all sites were driven mostly by *Acrosiphonia*, *Desmarestia*, *F. distichus*, *Laminaria*, terrestrial matter, and *Ulva* in both habitats (PERMANOVA, $F_{20,469} = 7.48$, $p = 0.001$; Fig. 7). The site adjacent to the largest watershed assessed (Wosnesenski River) saw the greatest increases in terrestrial matter to both drifting and beach-cast wrack later in the summer (Fig. 7).

Among all the environmental variables assessed for the separate sites on the south side of the bay that were added in 2021 (i.e., beach slope, percent cobble substrate, percent gravel substrate, total watershed area, percent glacier cover of watershed, percent forested area of watershed, seawater temperature range, and seawater salinity range), spatial differences in composition of drifting and beach-cast wrack were most highly correlated with percent glacier cover of watershed, beach slope, percent cobble substrate, percent gravel substrate, and seawater salinity range (BEST-BIOENV, 0.297). For this analysis, coastline orientation, wave exposure, percent boulder substrate, and percent sand substrate were not included in the analyses as draftsman plots indicated collinearity of these variables with others (correlation cutoff $|r| \geq 0.80$). The site with the steepest beach slope (inner Jakolof Bay) correlated with large contributions of *Laminaria* in both drifting and beach-cast wrack. Sites adjacent to watersheds with higher percent glacier cover (Grewingk River, Halibut Cove, and Wosnesenski River) also saw large contributions of *Laminaria* to both drifting and beach-cast wrack. The site that experienced larger salinity ranges and had the shallowest beach slope with the highest percent cobble substrate (Tutka Bay) correlated with greater contributions of *F. distichus* in drifting and beach-cast wrack consistently throughout the study period. The site with the smallest salinity range (Halibut Cove) also saw large contributions of *F. distichus* to beach-cast wrack, but not in drifting wrack. When gravel was 75% or more of substrate type there were large contributions of *F. distichus* to both habitats.

3.3. Reproductive viability of beach-cast kelp and rockweed wrack

Reproductive tissues of *F. distichus*, *N. luetkeana,* and *S. latissima* found in beach-cast wrack from April through September were confirmed to be viable from the propagule release experiments, supporting our hypothesis that kelp and rockweed wrack can be reproductively viable after it is deposited on beaches (Fig. 8). Combined contributions of all reproductive target species to total beach-cast wrack biomass varied significantly over time (ANOVA, $F_{6,413} = 6.38$, $p < 0.001$). The combined biomass of reproductive target species peaked in June (27% of total beach-cast wrack biomass), which was significantly higher than the other months. When proportions of total wrack biomass were analyzed individually for each target species, contributions of reproductive *F. distichus* varied significantly over time (ANOVA, $F_{6,413} = 8.44$, $p < 0.001$), whereas individual contributions of *N. luetkeana* (ANOVA, $F_{6,413} = 0.91$, $p = 0.49$) and *S. latissima* (ANOVA, $F_{6,413} = 0.97$, $p = 0.45$) were both similar over time. The predominant reproductive target species in wrack was . *distichus* and it appeared in wrack continuously starting in April, whereas contributions from *N. luetkeana* and *S. latissima* were intermittent throughout the study period. The greatest contribution of reproductive *F. distichus* to total wrack biomass occurred in June (23%), while the greatest contributions of reproductive *S. latissima* (4%) and *N. luetkeana* (6%) occurred later in the summer in July and August, respectively.

3.4. Aerial drone surveys of beach-cast wrack surface area

Estimates of beach-cast wrack surface area (m^2 km^{-1}) derived from digital measurements taken from drone imagery of the 50-m transect were consistently similar with OTG measurements of the same 50-m transect (ANOVA, $F_{1,128} = 0.07$, $p = 0.79$; Fig. 9), supporting our hypothesis that measurements of beach-cast wrack surface area from drone and OTG surveys produce similar estimates. Surface area estimates

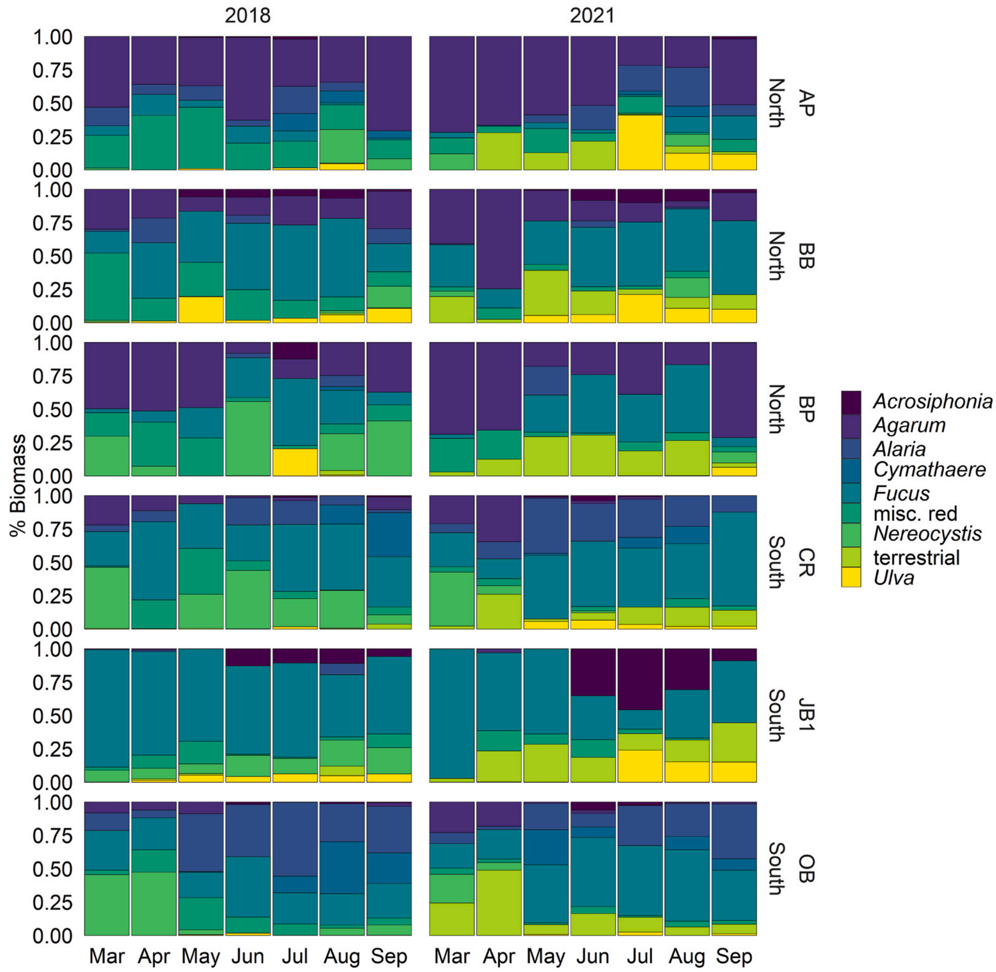

Fig. 5. Stacked bar plots of seaweed taxa most responsible (from SIMPER analysis) for driving compositional differences among sites over time (months) in north and south regions of Kachemak Bay in 2018 and 2021 based on biomass (kg m^{-2}). AP = Anchor Point; BB = Bishop's Beach; BP = Bluff Point; CR = Camel Rock; JB1 = outer Jakolof Bay; OB = Outside Beach.

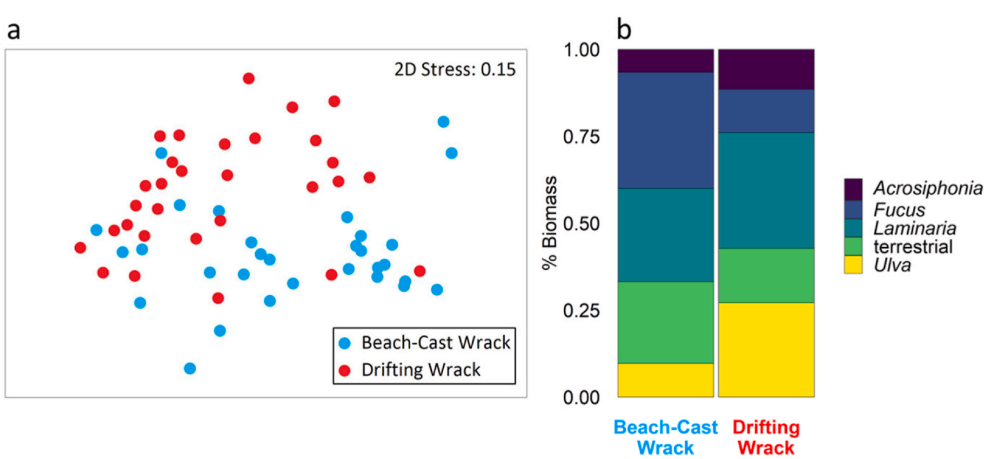

Fig. 6. (a) Non-metric multidimensional scaling (nMDS) ordination plot of drifting (red) and beach-cast (blue) wrack composition in Kachemak Bay, Alaska based on relative biomass (kg m 2). (b) Stacked bar plot of seaweed taxa most responsible (from SIMPER analysis) for driving compositional differences between drifting and beach-cast wrack based on biomass (kg m-2). Stress indicates how well the ordination summarizes the two-dimensional distances among the points. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

derived from the larger scale 1-km aerial drone transects were generally consistent with both smaller scale drone and OTG estimates from the 50-m transects once they had been extrapolated out to 1 km (ANOVA, $F_{2,187} = 0.82$, $p = 0.44$). However, during the March surveys, the 1-km aerial drone survey estimate was significantly larger (ANOVA, $F_{2,27} = 30.52$, $p < 0.001$) than the extrapolated surface area estimates derived from the 50-m scale aerial drone transect (Tukey, $p < 0.001$) and OTG transect (Tukey, $p < 0.001$; Fig. 9). Overall, beach-cast wrack surface area was significantly variable over time for all methods (ANOVA, $F_{6,183} = 125.6$, $p < 0.001$), with significantly more surface area in June according to 50-m scale drone (8705 ± 545 m^2 km^{-1}) and OTG (8370 ± 546 m^2 km^{-1}) transects, and the 1-km scale drone transect (9411 ± 546 m^2 km^{-1}). Generally, beach-cast wrack surface area slightly increased from March to May (except for the decrease from March to April according to the 1-

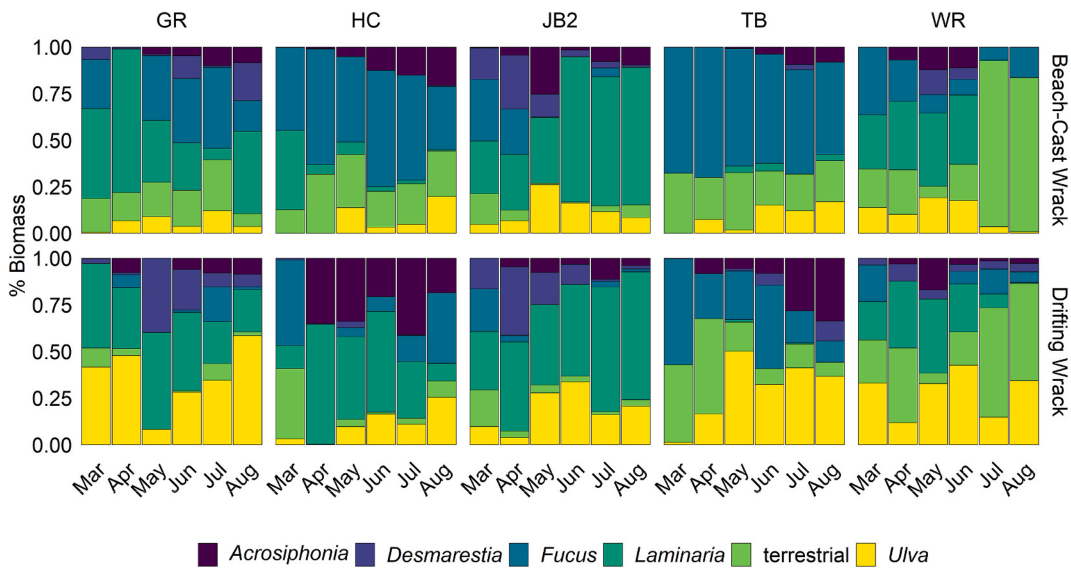

Fig. 7. Stacked bar plots of seaweed taxa most responsible (from SIMPER analysis) for driving compositional differences among sites in Kachemak Bay, Alaska in 2021 over time (months) in drifting and beach-cast wrack based on biomass (kg m^{-2}). GR = Grewingk River; HC = Halibut Cove; JB2 = inner Jakolof Bay; TB = Tutka Bay; WR = Wosnesenski River.

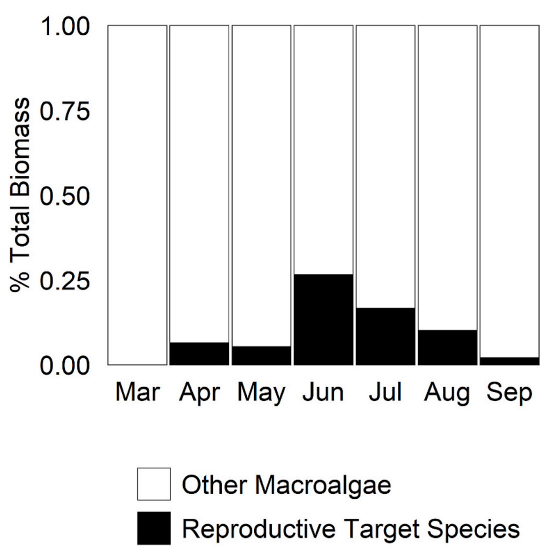

Fig. 8. Stacked bar plot of the cumulative proportions of reproductive target species (i.e., Fucus distichus, Nereocystis luetkeana, and Saccharina latissima) and all other macroalgae (including non-reproductive target species) to total beach-cast wrack biomass over time (months) in 2018 (all sites combined in Kachemak Bay, Alaska). In June, 27% of the total beach-cast wrack biomass was comprised of reproductively viable individuals of the three target species.

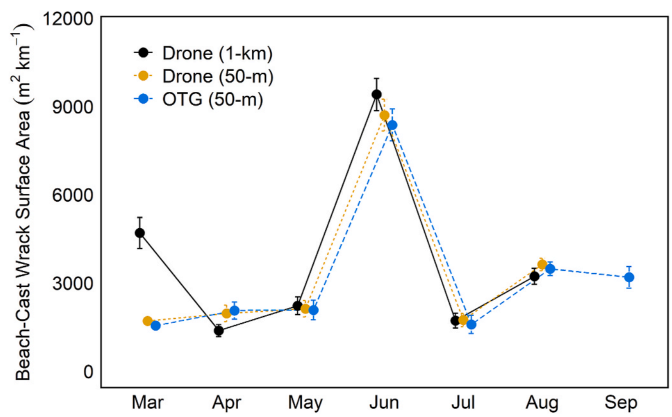

Fig. 9. Mean surface area (m^2 km^{-1}) of beach-cast wrack by month (bars represent standard error) estimated by three different methods at Bluff Point, Kachemak Bay, Alaska in 2021. Drone (1-km) = digital surface area estimates from 1-km drone transects (black); Drone (50-m) = digital surface area estimates from 50-m drone transects (orange); OTG (m) = surface area estimates from 50-m on-the-ground transects (blue). Beach-cast wrack surface area peaked in June according to estimates from all three methods. Drone surveys were not conducted in September. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

km drone transect) before peaking in June. After June, surface area decreased before increasing again into August and September.

4. Discussion

Precautionary restrictions on wrack harvesting in Alaska are in place because stock status information is currently too limited. Meanwhile, interest in macroalgal harvesting is growing, and it is uncertain how increased harvest may alter the productivity and natural distribution of this resource. The wide-ranging methodological assessment of macroalgal wrack dynamics in the present study has practical applications designed to help inform resource managers. This study identified the spatio-temporal variability in wrack distribution and composition, the viability of visually reproductive macroalgal wrack, and assessed the accuracy of drone imagery to monitor wrack distribution in a high latitude estuary. Altogether, these findings of wrack dynamics across seasons, years, and habitats can be used to aid development of wrack stock assessments and sustainable harvest strategies in Alaska and elsewhere.

4.1. Spatio-temporal variability in beach-cast wrack biomass and composition

Like other studies along the Pacific coast of North America (e.g., Wickham et al., 2020), this study found that beach-cast wrack is predominantly composed of *F. distichus* and various kelp species, though their biomass differed among sites and seasons, disproving our hypothesis that beach-cast wrack biomass and composition are similar over time and across beaches with different static environmental conditions. Wrack deposited in the southern study region was predominately composed of *F. distichus*, where its growth is ubiquitous on the rocky intertidal shores. Attached *F. distichus* stands are present but decrease in sandier areas on the north side of the bay (Ulaski et al., 2020), which is reflected in less *F. distichus* appearing in wrack in this region. This indicates that the transport of *F. distichus* onshore can be highly influenced by proximity of the beach to the source, similar to biogeographical patterns of macroalgal wrack in the US Pacific Northwest (Reimer et al., 2018). Furthermore, *Ulva* were also common, similar to wrack on the outer coast of Vancouver Island, British Columbia (Mews et al., 2006). Although *Ulva* do not have air bladders, they may have been common in wrack due to their intertidal location; when detached, their travel distance is likely short. However, the thin thalli of *Ulva* float very well and may disperse farther, as witnessed during green tides after bloom events that depend on them drifting (Yabe et al., 2009). *Ulva* are also short-lived annuals, which was represented by their increased contributions to wrack composition later in the summer. The seasonal growth of other annuals was also apparent in their appearance in wrack, including *A. marginata* and *N. luetkeana*. Though, overwintered *N. luetkeana* individuals did appear in wrack as early as March.

A noticeable difference in the present study compared to others from more temperate latitudes was the lack of eelgrass (*Zostera marina*) and other seagrasses that accumulated in beach-cast wrack (Orr et al., 2005; Mews et al., 2006; Wickham et al., 2020). Although eelgrass beds are found in the study area, eelgrass wrack was rare in this study. Eelgrass may have been rare in wrack due to the distance of isolated beds from the study beaches, or senescence timing followed the study period (Hansen and Reidenbach, 2013). The presence of *Z. marina* in wrack may release cadmium, which has carcinogenic properties (Franzen et al., 2019). Traces of cadmium appear in terrestrial plants that are fertilized with decomposing eelgrass wrack (Franzen et al., 2019). The presence or absence of eelgrass could influence where and when artisanal and commercial harvesting of wrack should be allowed (Franzen et al., 2019). Although the low presence of eelgrass in Alaskan wrack may have benefits to wrack harvesters, the harvesting community should be mindful of eelgrass presence in wrack.

Variability in spatio-temporal distribution of beach-cast wrack in Alaska is consistent with other studies that found greater accumulations on coastlines characterized by a variety of porous substrate types, such as boulder, cobble, pebble, gravel, or sand (Orr et al., 2005; Wickham et al., 2020). Gilson et al. (2021) found no significant difference in wrack accumulations between habitats defined by different substrate types but observed generally lower accumulations on sandy beaches compared to pebble beaches in Ireland. On the shores of British Columbia, Canada, substrate effects indicate there is a positive correlation between wrack biomass and grain size (Orr et al., 2005). The present study found that beaches characterized by the presence of boulders, in combination with high percentages of cobble and sand substrate, retained more diverse wrack among the heterogeneous substrates. However, beaches characterized by higher percent cover of gravel were also characterized by steeper slopes that generally accumulated less diverse beach-cast wrack, similar to other work that found negative correlations between shoreline slope and wrack accumulations (Wickham et al., 2020). Managers seeking to develop surveys to assess wrack distribution and abundance to determine appropriate harvest levels should consider incorporating substrate type and beach slope into their survey design.

Accumulation of wrack on beaches is largely influenced by localized environmental forcing (Orr et al., 2005; Gilson et al., 2021). Frequency and intensity of local storms along the coast of Chile contribute to the stranding of *Durvillaea antarctica* wrack on beaches, with higher inputs in austral summer and autumn (January to May) and lower inputs in austral spring (September to December; López et al., 2019). Proximity to reefs and topography of shorelines affect the distribution and composition of wrack (Gomez et al., 2013). As in the present study, regional differences in macroalgal species growing on nearby reefs can strongly influence local wrack composition (Gomez et al., 2013; Liebowitz et al., 2016). Detached macroalgae may also travel hundreds of kilometers to subsidize distant beaches (Hinojosa et al., 2010; Krumhansl and Scheibling, 2012), where dispersal is significantly affected by winds and tides (Barreiro et al., 2011; Hammann and Zimmer, 2014; Hawes et al., 2017). Coastlines with high tidal fluctuation and wave events increase wrack biomass (Suursaar et al., 2014).

Variability in wrack supply can be explained by interactions of wave exposure and seasonality (Barreiro et al., 2011). Some studies found that wave height is a significant explanatory variable in the distribution of wrack and its composition (Barreiro et al., 2011), while others found that wave height explains very little (Klosinski, 2015) or does not always correlate with surf zone force (Helmuth and Denny, 2003). In our study, though wave height was not assessed directly, seasonal peaks of beach-cast wrack biomass accumulated in the northern region that is more exposed to wave action. As oceanic waters circulate around the bay, it is possible that wrack accumulates along the way until reaching the outer northern extent where they are largely being deposited by wind-induced surface waves and extreme tidal exchanges over shallow beach slopes.

4.2. Macroalgal composition of drifting and beach-cast wrack

While beach-cast wrack has been well studied in many regions of the world, further efforts were made here to understand assemblage shifts across subtidal and onshore accumulations of wrack, as reports on drifting wrack are far less common (e.g., Hinojosa et al., 2011; Baring et al., 2018). As a precursor to beach-cast wrack, wrack drifting in the adjacent near-subtidal waters was expected to harbor many of the detached taxa that appeared on the beach. Our hypothesis, that drifting and beach-cast wrack have similar macroalgal composition, was mostly disproven as there were similarities in taxa found in each habitat, but their proportional contributions varied significantly. Differences in macroalgal thallus morphology and feeding preferences by intertidal consumers may explain why some taxa, including *Acrosiphonia* and *Ulva*, were more predominant in drifting than in beach-cast wrack. For instance, *Ulva* have thin sheet-like thalli that are often preferred by intertidal consumers (Watson and Norton, 1985). Likewise, filamentous *Acrosiphonia* are delicate and may disintegrate rapidly when cast ashore, while suspension in the water would help them maintain structural integrity. In Portugal, some taxa (e.g., *Sargassum muticum*) are more tolerant than others (e.g., *Laminaria ochroleuca*) of exposure to ultraviolet radiation and warmer temperatures out of the water (Rodil et al., 2015). In this current study, the robust structures of *A. clathratum*, *F. distichus*, and terrestrial matter were more predominant in beach-cast wrack than in drifting wrack. *Agarum* are generally less preferred as a source of nutrition over other algae (Dubois and Iken, 2012; Dethier et al., 2014) and terrestrial matter in the form of woody debris can also be significantly less preferred by intertidal consumers (Storry et al., 2006).

When drifting macroalgae wash ashore, they are exposed to air and accompanying physical and biological stresses. Individual tolerances to air exposure may contribute to the observed differences in composition between the drifting and beach-cast wrack habitats in the present study. Given the ambiguity of how long wrack was deposited on the beach prior to sampling, some species may have been further along in their decomposition due to exposure and consumption stresses, thus lowering their contributions to wrack. Tissue degradation rates after deposition onshore for *Macrocystis integrifolia*, *N. luetkeana*, and *Ulva* can take place over a single day, whereas *Fucus* spp. and *Phyllospadix* spp. can take a month to decompose (Mews et al., 2006). Differences in the rate of microbial colonization and subsequent decomposition also varies by macroalgal species (Dethier et al., 2014). For instance, aged *Agarum fimbriatum* detritus showed no increase in colonization of microbes over the course of five weeks, while *Saccharina subsimplex* showed significant microbial colonization that enhanced decomposition rates (Dethier et al., 2014).

Hydrodynamic settings (i.e., water motion influenced by winds, waves, and tides) can determine algal dislodgment and transportation (Biber, 2007). Given that drift algae can travel hundreds to thousands of kilometers (Olafsson et al., 2001), the composition found onshore may be the result of a combination of distant and local donor systems. Predominant species that washed ashore in the present study were local species that are common along Alaska's coast, but macroalgae that are not commonly local (e.g., *Macrocystis pyrifera*) also appeared in the wrack. The nearest documented beds of *M. pyrifera* are over 100 km away off the coast of the Kodiak Island archipelago (Susan Saupe, Cook Inlet Regional Citizens Advisory Council, pers. comm.), providing evidence that long-distance dispersal can influence wrack composition. Effects of hydrodynamics may also vary with species. For example, *F. distichus*, which occurs more in the intertidal than subtidal, contains positively buoyant air bladders when reproductive and can be easily pushed ashore by tides and wave action. Thallus morphology can determine how macroalgae move with currents after detachment (Gomez et al., 2013). In Spain, species with air bladders, including *Cystoseira*, *Fucus*, and *S. muticum*, dominate wrack piles in areas with high exposure to wave action (Barreiro et al., 2011). As such, morphological features of macroalgae and where they grow along the vertical intertidal gradient may influence their chances of being dislodged and washed ashore.

Beaches adjacent to larger watersheds with higher percent glaciation and more total forested area had higher contributions of *A. clathratum* and terrestrial matter. The appearance of *A. clathratum* in wrack under these conditions is consistent with its persistence and formation of subsurface reefs in regions with decreased salinity due to large freshwater input from substantial glacial melt (Filbee-Dexter et al., 2019). The smallest watershed assessed (Jakolof Bay), which also had no direct glacial discharge, accumulated drifting and beach-cast wrack that was mostly composed of *Laminaria* spp. This site is also the most protected site with unstable cobble interspersed among boulder, possibly explaining the expansive beds of *C. triplicata* and *S. latissima* kelps that grow in these conditions (Lindeberg and Lindstrom, 2010). Beaches exposed to seawater with the greatest ranges of temperature and salinity accumulated more *F. distichus*, which may be explained by the nearby growth of *F. distichus* and their tolerance to variable conditions in and out of the water (Smolina et al., 2016; McCabe and Konar, 2021). As such, the environmental effects of glacial inputs to nearshore macroalgal reefs and subsequently detached macroalgae may be species-specific. For instance, Traiger and Konar (2017) found that experimental glacial-induced sedimentation and order of settlement played a role in determining whether *N. luetkeana* or *S. latissima* outcompeted the other at the microscopic life stage. Intertidal species of the genus *Ulva* may be less impacted by increased glacial freshwater input given their tolerance to variations in salinity (Rybak, 2018). As mass glacial loss is accelerated by climate change (Hugonnet et al., 2021), continued effects of glacial discharge (e.g., increased sedimentation, decreased salinity) may shape nearshore and intertidal macroalgal communities and subsequent composition of drifting and beach-cast wrack (Spurkland and Iken, 2011b). Restructuring of macroalgal composition in wrack could affect rates of onshore nutrient cycling if it is predominantly composed of less palatable species for intertidal consumers, but further investigation into the implications of our results to the rate of transfer of MDN was outside the scope of this study. Slower decomposition at higher tidal elevations could also extend the longevity of wrack on a beach, extending the availability of wrack to harvesting.

4.3. Reproductive viability of beach-cast kelp and rockweed wrack

The viability of reproductive tissue from *F. distichus*, *N. luetkeana*, and *S. latissima* wrack confirmed our hypothesis, that kelp and rockweed wrack can be reproductively viable after it is deposited on beaches. This observation in a high latitude glacially influenced estuary expands the latitudinal range of observed viability of reproductive wrack. Reproductive kelp and rockweed wrack cumulatively accounted for over 25% of total wrack biomass in the June, with lower but still elevated proportions in July and August. Thus, removal of wrack through harvesting efforts may negatively impact the macroalgal reproductive pool depending on harvest timing. Management guidelines could support seasonal removal of wrack that avoid periods of high contributions of reproductive material. Further investigation into how significant the contribution reproductive beach-cast wrack has on standing populations (e.g., determining if these viable propagules ever make it back into the ocean) would help inform harvest regulations, but was beyond the scope of this study. Beach-cast wrack may get resuspended in the water by higher tides or storm-induced wave action (Orr et al., 2005; Pattiaratchi et al., 2011). Reproductive individuals deposited at the upper extent of the intertidal zone may be less likely to get resuspended and contribute to overall productivity, and therefore, may be more appropriate for harvesting. If wrack can remain reproductive, it may still be considered alive. Reproductive fronds of the intertidal Australasian fucoid, *Hormosira banksii*, released viable gametes up to eight weeks after detachment (McKenzie and Bellgrove, 2008). Furthermore, reproductive sporophytes of *M. pyrifera* remained viable after drifting for 21 days (Macaya et al., 2005), and up to 125 days (Hernández-Carmona et al., 2006).

Propagules generally only travel within meters of the anchored adult sporophyte (Filbee-Dexter and Wernberg, 2018), but the actual plants can travel for kilometers when adrift in the ocean. Hence, wrack persistence and distribution may play a role in species dispersal as wrack may offer some form of protection and transport for drifting reproductive material; however, this is likely to be species-dependent and mediated by local environmental conditions (Johansson et al., 2015). Population genetic structure is variable among species and spatial scales, and it is evident that drifting kelp and rockweed are a means of long-distance dispersal contributing to population connectivity (Amsler and Searles, 1980; Macaya et al., 2005; Saunders, 2014; Rothäusler et al., 2015). Contrastingly, dispersal of spores from drifting *M. pyrifera* likely was not the main source of recruitment to new sites and was not driving population genetic structure in southern California (Reed et al., 2004). Investigating connectivity of macroalgal populations and understanding how long reproductive tissue remains viable after deposition onshore, where it is susceptible to desiccation, would be relevant to managers seeking to craft harvest regulations for beach-cast wrack.

4.4. Aerial drone surveys of beach-cast wrack surface area

Previous drone work on mapping wrack or intertidal communities has revealed the feasibility of this technique in the field (Konar and Iken, 2018; Pan et al., 2021). We also found that drones are a useful tool for producing orthomosaic maps of beaches to facilitate estimates of wrack surface area and were just as accurate as OTG measurements. Both methods (drone and OTG) consistently resulted in very similar surface area estimates at the 50-m scale, supporting our hypothesis that measurements of beach-cast wrack surface area from drone and OTG surveys produce similar estimates. However, the 50-m transects were not always representative of the 1 km of beach surveyed by the drone, indicating patchy distribution of wrack along the beach, at least in some seasons. The 1-km drone transect captured more of the patchily distributed wrack piles in March, which were missed by the 50-m transects. The use of aerial drone surveys on large-scales (kilometers) is useful in achieving more representative wrack surface area estimates during winter and early spring months when transport onshore is pulsed and patchy (based on our early spring sampling), similar to observations of wrack supply in the Mediterranean Sea (Remy et al., 2021). Similar estimates between scales were made later in the growing season when macroalgal production was well underway and wrack supply was less patchy. This may be explained by the overwintered and low biomass of perennial and biennial species contributing to wrack at the end of winter and early spring. We would expect some winter wrack accumulation from storms (Balestri et al., 2006), but subtidal vegetation is limited, so wrack deposition is also limited. As the growing season progresses, annual macroalgal production starts to play a crucial role in supplying continuous, rather than pulsed, contributions of wrack to beaches. Continuous supply in summer may precede pulsed supply in fall (Remy et al., 2021). Hence, managers seeking to develop surveys to assess wrack abundance to determine appropriate harvest levels should consider wrack seasonal distribution in their survey design. More 1-km (or larger) transects are needed to accurately characterize surface area of patchily distributed wrack.

Drone surveys have their limitations. Depending on where study beaches are located (e.g., proximity to controlled airspace), permits may be required far in advance, and permit processing times may impede the flexibility that is often essential for field work. Good weather days are also required for safely operating a drone, further limiting scheduled survey efforts. Additionally, drone surveys conducted herein were only deployed at one beach for one season, so further research should expand these metrics both spatially and temporally. Furthermore, we want to emphasize that the nadir drone surveys conducted in this study provided only wrack surface area. The surface area estimates alone did not determine variability in composition or biomass available for harvesters. If species composition or biomass estimates are of interest, paired OTG surveys should be included in the survey design to sub-sample drone transects to scale-up estimations of biomass distribution.

5. Conclusions

The findings of this study expand our understanding of wrack distribution patterns within high latitude glacial estuaries and have important implications for management decisions regarding harvest timing and location given the identified patterns of deposition and reproductive viability of wrack throughout the summer. Beach-cast wrack composition varied with exposure to waves, beach slope, substrate type, and season, which has important implications for identifying appropriate areas and times for wrack harvest to mitigate impacts. Systematic large-scale drone surveys of beach-cast wrack would be a useful and accurate tool for managers interested in estimating wrack distribution and surface area to inform sustainable harvest practices, but they would need to be paired with OTG sampling to characterize wrack composition and biomass.

Shallow-sloped beaches characterized by heterogeneous sediments with higher percentages of boulder, cobble, and sand are areas where more diverse wrack with greater biomass might be available for harvest later in the season (August). Conversely, sites characterized by steep slopes and homogeneous gravel substrate do not accumulate as much wrack over time and might not offer suitable inputs of wrack to meet harvest demands. Additionally, harvesting attached reefs in protected areas might reduce the nearby accumulation of beach-cast wrack, since greater compositional similarity between drifting and beach-cast wrack in these areas suggests that protected beaches have less exchange with distant drifting macroalgal taxa. Late summer or early fall wrack harvests would also avoid the peak contribution of reproductive material to beach-cast wrack. However, research investigating diminishing viability and longevity of reproductive macroalgal tissue in beach-cast wrack will further help determine appropriate management strategies.

CRediT authorship contribution statement

Brian P. Ulaski: Writing – original draft, Funding acquisition, Formal analysis, Data curation, Investigation, Methodology. **Edward O. Otis:** Writing – review & editing, Methodology, Conceptualization. **Brenda Konar:** Writing – review & editing, Funding acquisition, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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