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Beach-cast and drifting seaweed wrack is an important resource for marine and terrestrial macroinvertebrates in high latitudes

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ABSTRACT

Seaweeds are foundation species across near-subtidal and intertidal zones, including when detached and free-floating and then cast ashore as wrack. Wrack is sometimes removed by humans for aesthetics or to be used as fertilizer. The study of wrack as an important habitat and resource for macroinvertebrates in high latitudes has been limited. To determine which taxa might be impacted when wrack is removed, the composition and relative abundance of macroinvertebrates were quantified monthly and compared in areas with and without wrack in Kachemak Bay, Alaska. Relationships were assessed between macroinvertebrates and wrack line (tidal height, moisture content, seaweed biomass) and beach characteristics (wave exposure, beach slope, substrate types). Approximately 47,000 animals were counted and a total of 87 taxa were identified from beach-cast wrack, drifting wrack, and bare sediment habitats. Macroinvertebrate communities within beach-cast wrack and bare sediment habitats were significantly different. Beach-cast wrack generally had more terrestrially-derived animals, especially Coleoptera and Diptera. Bare beach sediment was predominantly occupied by Enchytraeida (annelids). Macroinvertebrate communities were most strongly influenced by seaweed biomass and tidal height of the wrack line. Beach-cast wrack and bare sediments were also compared to drifting wrack in shallow, nearshore waters. Drifting wrack was different and generally occupied by more marine-derived animals, especially Amphipoda, Gastropoda, Mytilida, and Polychaeta. Ecological succession in decaying beach-cast wrack was documented, with decomposers (e.g., Amphipoda and Diptera) being early colonizers, and predators (e.g., Coleoptera and Hymenoptera) arriving later. Understanding the importance of this unique and ecologically important habitat to macroinvertebrates is essential, as removals and reductions in wrack availability could influence macroinvertebrate community structure, higher trophic level consumers, and key ecological processes on beaches. This study is the first direct investigation into seaweed wrack-associated macroinvertebrate communities in a sub-Arctic system.

1. Introduction

The intertidal is a complex ecological system with various energy pathways that transition across its interface. This ecotone receives energy and nutrients from multiple donor systems, supporting unique macroinvertebrate communities that rely on the allochthonous input of organic subsidies (Jaramillo et al., 2006). Effects of these cross-boundary subsidies (Polis et al., 1997) are reflected in the productivity of intertidal food webs. Soft-sediment beaches, for example, are generally low in autochthonous primary production given the frequent disturbances of wave action, substrate instability, and tidal exchange (McLachlan et al., 1993). Macroinvertebrates at the fringe of the tide line on a beach are tolerant to these harsh conditions and increase productivity where organic marine and terrestrial subsidies accumulate to form patches of habitat (Jaramillo et al., 2006). Nearshore seaweed reefs and inland riparian donor systems are both sources of exported detritus that form habitat when deposited on beaches (Ulaski et al., 2023).

Collectively, the organic debris that accumulates onshore is known as beach-cast wrack and it supports intertidal macroinvertebrates and higher trophic level consumers. Ecologically, beach-cast wrack is key for maintaining diversity (Harris et al., 2014) and function (Defeo et al., 2009; Barreiro et al., 2011) on beaches by increasing macrofaunal biomass and species richness (Dugan et al., 2000; MacMillan and Quijón

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2012; Ruiz-Delgado et al., 2015; Vieira et al., 2016). The unique assemblages of macroinvertebrates that converge and persist in beach-cast wrack have the potential to feed higher trophic level consumers, including vertebrates (Dugan et al., 2003; Mellbrand et al., 2011; Fox et al., 2014; Ulaski 2022). Before detached seaweed and terrestrial debris wash ashore with tides, winds, and storms, they can drift hundreds of kilometers in the ocean (Krumhansl and Scheibling 2012). As a precursor to beach-cast wrack, drifting wrack creates habitat in the nearshore water column and benthos where macroinvertebrates and fish find refuge and forage among the loose debris (Duggins et al., 2016; Baring et al., 2018). Derived from the same sources, beach-cast and drifting wrack are spatial subsidies that create habitat in two very different systems.

Morphological differences among seaweeds that contribute to beach-cast wrack can determine the complexity and appeal of the habitat for intertidal inhabitants (MacMillan and Quijón, 2012). For example, some consumers prefer kelp wrack over seagrass or rockweed wrack due to more mucus secretion and lower concentrations of phenols in kelps (Mews et al., 2006; Michaud et al., 2019). Thus, biotic conditions of seaweed composition can influence the structure of associated macroinvertebrate communities, which in turn can affect the persistence of wrack on beaches. Variability in wrack supply can be explained by interactions of wave exposure, substrate type, and seasonality (Barreiro et al., 2011; Wickham et al., 2020; Ulaski et al., 2023). Seasonality of attached seaweed growth and community development (Ulaski et al., 2020) and general temporal oscillations of macroinvertebrate abundances (Ely et al., 2018) may be reflected in the communities that develop in wrack over time. Beach slope is another abiotic characteristic that is not only negatively correlated with the accumulation of beach-cast wrack (Harris et al., 2014; Wickham et al., 2020; Ulaski et al., 2023) but also with species richness of non-wrack associated benthic intertidal macroinvertebrates (McLachlan 1996).

As wrack decomposes, it releases nutrients into the surrounding area, acting as a fertilizer for nearby vegetation (Dugan and Hubbard, 2010; Dugan et al., 2011). In addition to wrack being applied to the soil as a mulch, it can be added to compost heaps as an activator. This recognition has led to increased interest by people to harvest wrack for use as garden fertilizer, and in some areas of the US (Alaska), Canada, Australia, and Ireland, wrack is harvested for personal and commercial uses (Kirkman and Kendrick 1997; McLaughlin et al., 2006; Holden et al., 2018). Removal of wrack from beaches is also common practice for aesthetic reasons in areas where recreation and tourism are high (Fairweather and Henry 2003; Noriega et al., 2012).

After wrack is deposited onto beaches, it either stays to begin desiccation and burial, goes back out to sea during a subsequent higher tide, or gets transported higher up the beach (Orr et al., 2005). Desiccation and decomposition of beach-cast wrack affect organism colonization and successional development of the wrack community (Olabarria et al., 2007). Succession of macroinvertebrate users of wrack is apparent throughout the stages of wrack decomposition (Colombini et al., 2000; Olabarria et al., 2007; Beeler 2009), and rates of decomposition vary among seaweed species (Mews et al., 2006). Aging wrack results in changes to the microclimate that it creates for consumers (Davis and Keppel 2021), and aged wrack is generally preferred over fresh wrack by consumers (Beeler 2009). Successional stages of wrack communities are important to understand, as wrack removal would impact these stages differently depending on the timing of deposition and removal.

1.1. Research questions

The aim of this study was to further our understanding of the importance of wrack habitat for macroinvertebrates in a glacially- and tidally-driven high latitude estuary. We developed the following three research questions to achieve this goal: 1) How do macroinvertebrate communities differ among beach-cast wrack, drifting wrack, and bare sediment habitats over time?; 2) How do macroinvertebrate communities in beach-cast wrack, drifting wrack, and bare sediment habitats correlate with biotic and abiotic environmental variables?; and 3) Does the beach-cast wrack of this system show predictable successional stages in its macroinvertebrate community? We tested the following three corresponding hypotheses: H1) The presence of beach-cast and drifting wrack increases macroinvertebrate community diversity; H2) Increased biomass of seaweed wrack supports higher macroinvertebrate abundance; and H3) Aging wrack is occupied by macroinvertebrate communities with different successional stages.

2. Materials & methods

2.1. Study area

This study was conducted in Kachemak Bay, a large high latitude fjord-type estuary in Lower Cook Inlet, Alaska (Fig. 1). The diverse array of macroalgae that populate the nearshore regions of the bay (Konar et al., 2010) are exposed to dynamic high latitude conditions including wind-induced stress, extreme tidal forcing (up to 9 m), and glacially-influenced freshwater flux, contributing to the accumulation of subtidal drifting organic material that washes ashore as wrack. This beach-cast wrack is historically harvested by the public (Glenn Hollowell, Alaska Department of Fish and Game, pers. comm.) for personal use as an additive to garden fertilizer, although harvest is highly regulated inside Kachemak Bay (Table 1).

For this study, twelve beaches were chosen throughout Kachemak Bay in areas easily accessible to the public along the Homer and Seldovia road systems or by small boat (Anchor Point, Bishop's Beach, Bluff Point, Camel Rock, Grewingk River, Halibut Cove, outer Jakolof Bay, inner Jakolof Bay, MacDonald Spit, Outside Beach, Tutka Bay, and Wosnesenski River; Fig. 1). Beaches were sampled monthly from April to August in 2021 but varied in the parameters that were examined (i.e.,

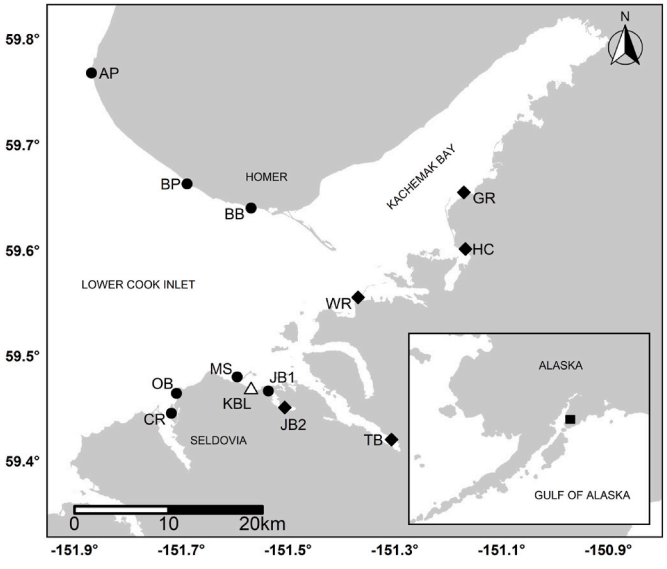

Fig. 1. Map showing study beaches located in Kachemak Bay, Alaska (black rectangle of inset map). Black circles denote study beaches from which beach-cast wrack and bare sediment samples were collected. Black diamonds denote study beaches from which beach-cast wrack and drifting wrack samples were collected. The white triangle refers to the location of the NOAA/University of Alaska Fairbanks (UAF) Kasitsna Bay Laboratory where macroinvertebrate community succession in aging wrack experiments were conducted. 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; MS = MacDonald Spit; OB = Outside Beach; TB = Tutka Bay; WR = Wosnesenski River; KBL = Kasitsna Bay Laboratory.

Table 1
Static site characteristics (seaweed fishery harvest limits, wave exposure, beach slope, and substrate type) used to assess spatial and temporal variability of wrack composition in Kachemak Bay, Alaska from April to August 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; MS = MacDonald Spit; 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	Wave Exposure	Slope (degrees)	Boulder (%)	Cobble (%)	Gravel (%)	Sand (%)
AP	Weight + Season	Semi-Exposed	1	0.0	11.2	16.8	72.0
BB	Weight + Season	Semi-Protected	1	0.0	80.9	19.1	0.0
BP	Weight + Season	Semi-Exposed	2	1.5	15.6	13.1	69.8
CR	Weight	Semi-Exposed	9	0.0	3.5	94.5	2.0
GR	Weight + Season	Semi-Exposed	8	0.0	17.0	39.5	43.5
HC	Weight + Season	Semi-Protected	10	0.0	0.0	95.0	5.0
JB1	Weight	Protected	6	0.0	30.0	70.0	0.0
JB2	Weight	Protected	19	90.0	10.0	0.0	0.0
MS	Weight	Semi-Exposed	7	0.0	0.0	28.6	71.4
OB	Weight	Semi-Exposed	7	0.0	0.4	99.6	0.0
TB	Weight + Season	Protected	2	0.0	25.2	74.8	0.0
WR	Weight + Season	Semi-Exposed	5	0.0	0.0	34.0	66.0

beach-cast wrack, drifting wrack, and bare sediment). Bare sediment samples were taken from areas that may receive wrack but were devoid of wrack during the time of collection. These months were examined given the results of a pilot study in which macroinvertebrates on beaches were rare during winter months, likely due to their intolerance to the icy conditions in which wrack was usually frozen and covered in snow.

2.2. Abiotic environmental variables

All sites were characterized for wave exposure, beach slope, and substrate type to examine relationships between static environmental conditions and macroinvertebrate communities found in beach-cast wrack, drifting wrack, and bare sediment habitats. Wave exposure and beach slope were determined from the National Oceanic and Atmospheric Administration's (NOAA) Alaska ShoreZone website (https://alaskafisheries.noaa.gov/mapping/sz_js/), under "Derived ShoreZone Attributes." Wave exposure was determined by the "Biological Wave Exposure" data from which exposure ranks are classified as exposed, semi-exposed, semi-protected, or protected. Beach slope was identified under "Intertidal Zone Slope," where calculated slopes (in degrees) are provided. Substrate type was characterized one time for each site within 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).

2.3. Wrack and macroinvertebrate collections

Biomass and composition of macroalgae along with biomass, composition, and abundance of macroinvertebrates that appeared in the beach-cast wrack and in the sand under the wrack were determined monthly from April to August 2021 at all twelve beaches (Fig. 1). Along a 50-m horizontal transect, a vertical transect was placed perpendicular every 5 m from the upper to the lower boundaries of the wrack line. 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. Randomly along each vertical transect, one 11-cm diameter steel corer was pushed down through the wrack and into the underlying sediment to a depth of approximately 10 cm to collect macroalgae and macroinvertebrates in the beach-cast wrack (n = 10 beach-cast wrack cores/site/month; Deidun et al., 2009; MacMillan and Quijón 2012; Heerhartz et al., 2014). Bare sediment cores were also taken above and below and at least 1 m away from the wrack line at seven of the beaches (Anchor Point, Bishop's Beach, Bluff Point, Camel Rock, outer Jakolof Bay, MacDonald Spit, and Outside Beach) to a depth of approximately 10 cm to quantify macroinvertebrate biomass, composition, and abundance in bare substrate (n = 10 bare sediment cores/beach/month).

Drifting wrack was collected at five of the beaches (Grewingk River, Halibut Cove, inner Jakolof Bay, Tutka Bay, and Wosnesenski River) by beach seining and was sampled from the nets using the same 11-cm diameter corer (pushed down through the wrack until contact with the net) used to collect beach-cast wrack and bare sediment samples. 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, the cores were placed at three fixed points along the net to collect any retained macroalgae and macroinvertebrates from the drifting wrack debris (n = 9 drifting wrack cores/beach/month).

All beach-cast wrack, drifting wrack, and bare sediment cores were immediately sieved separately through a 1-mm mesh bag in the swash zone (Dugan et al., 2003; McLachlan and Brown 2006; Schlacher et al., 2008; Deidun et al., 2009; MacMillan and Quijón 2012). All retained macroalgae and macroinvertebrates were immediately bagged by replicate and transported to a −20 °C freezer at the NOAA/University of Alaska Fairbanks (UAF) Kasitsna Bay Laboratory until subsequent processing. Frozen samples were thawed in trays filled with filtered seawater. Thawed samples were sorted, macroalgae were identified and weighed, and macroinvertebrates were identified to the lowest possible taxonomic level using keys (Lindroth 1969; Orth and Moore 1980; Gordon and Cartwright 1988; Arnett and Thomas 2000; Arnett et al., 2002; Lamb and Hanby 2005; Triplehorn and Johnson 2005; Lindeberg and Lindstrom 2010; Zanetti 2014; Suzumura et al., 2019; Klimaszewski et al., 2021) and reference specimens in the University of Alaska Museum, and counted and weighed. Representative voucher specimens were deposited in the UAM Insect Collection as Accession UAM-2022.09-Ulaski-Ento (non-marine arthropods) and in the UAM Marine Invertebrate Collection. Valid marine taxonomic genus and species names were obtained from WoRMS Editorial Board (2022).

During each monthly sampling event, tidal elevation of the beach-cast wrack line was measured using a site level and stadia rod. Ten haphazardly chosen seaweed samples of approximately 10 g each were collected from the wrack line for moisture content analysis using a loss-on-drying (LOD) technique (Olabarria et al., 2007; MacMillan and Quijón, 2012). Briefly, each seaweed wrack sample was weighed separately, dried in a drying oven at a constant temperature of 60 °C (for at least 24 h) until a constant weight was achieved (±0.01 g), and re-weighed to determine percent moisture content.

2.4. Succession experiments in beach-cast wrack

To determine if the beach-cast wrack of this system shows predictable successional stages in its macroinvertebrate community, 18 marked piles, each with 1- to 2-kg wet weight of freshly harvested macroalgae,

were homogenized by hand and deposited just above the highest predicted tide line of the cycle on a beach near the NOAA/UAF Kasitsna Bay Laboratory (Olabarria et al., 2007; MacMillan and Quijón 2012). The most common beach-cast wrack macroalgae, *Alaria marginata*, *Cymathaere triplicata*, *Fucus distichus*, *Palmaria* spp., *Saccharina latissima*, and *Ulva* spp., were collected to produce the artificial wrack piles and were consistent across months as these species were easily accessible for collection at low tides. Piles were 0.5 m in diameter and placed approximately 1–2 m apart and other naturally present accumulations of wrack were removed before placing the experimental plots. Experiments were conducted monthly from April to August 2021 ($n = 18$ experimental wrack piles/month). Surveyor's flags were placed next to each pile to mark their positions. Starting on Day 0, three of the piles were randomly sampled every three days (every six days in August) to quantify temporal changes in the macroinvertebrate communities ($n = 3$ experimental cores/sampling day). Each pile of wrack was sampled using one 11-cm diameter steel sediment corer pushed down through the wrack and into the underlying sediment to a depth of approximately 10 cm (Deidun et al., 2009; MacMillan and Quijón 2012; Heerhartz et al., 2014). Control cores were taken at the same tidal height from bare sediments to a depth of approximately 10 cm at least 1 m away from the experimental wrack piles during each sampling event ($n = 3$ control cores/sampling day). All experimental and control cores were immediately sieved separately through a 1-mm mesh bag (Dugan et al., 2003; McLachlan and Brown 2006; Schlacher et al., 2008; Deidun et al., 2009; MacMillan and Quijón 2012). Retained macroalgae and macroinvertebrates from the sieved cores were immediately bagged by replicate and placed into a −20 °C freezer at the NOAA/UAF Kasitsna Bay Laboratory until subsequent processing. Frozen samples were thawed in trays filled with a thin layer of filtered seawater. Thawed samples were sorted, macroalgae were weighed, and macroinvertebrates were identified to the lowest practical taxonomic level, counted, and weighed.

HOBO Pendant temperature loggers (Onset; Bourne, MA) were used to determine temperature microhabitats formed by the experimental wrack piles for the duration of each monthly experiment. Among the experimental wrack piles, a logger was attached to rebar and fixed above the sediment to record external ambient air temperatures over time. Loggers were also placed inside of a wrack pile and buried 5–10 cm in the sand underneath a wrack pile. Separate samples of macroalgae from each wrack pile were taken alongside each core for moisture content analysis using the LOD technique as described above ($n = 3$ moisture content samples/sampling day).

2.5. Statistical analyses

Statistical analyses were carried out in PRIMER v7 software with the PERMANOVA + package and the opensource R software (R Core Team 2021). Multivariate data were fourth root transformed following standardization so that measurements on relative community biomass and abundance were comparable given the slightly different methods of core collections among habitats (i.e., beach-cast wrack, drifting wrack, and bare sediment). Univariate data remained non-normal (Shapiro-Wilk test, biomass: $p < 0.001$; abundance: $p < 0.001$), but the robustness of analysis of variance (ANOVA) was considered appropriate for univariate analysis given the very large number of samples collected. Separate one-way ANOVA tests were used to determine variability in total macroinvertebrate biomass and abundance by site, month, and habitat (i.e., beach-cast wrack, drifting wrack, and bare sediment). When ANOVA tests suggested significance, Tukey honest significant difference (HSD) post-hoc tests were carried out to confirm pairwise differences. Separate resemblance matrixes were calculated using a Bray-Curtis similarity index for permutational analysis of multivariate macroinvertebrate community relative biomass and abundance data. A three-factor permutational multivariate analysis of variance (PERMANOVA) was used to test for responses of macroinvertebrate communities to grouping factors of site (random factor; 12 levels), month (random factor; 5 levels), and habitat (fixed factor nested in site; 3 levels). A cyclic resemblance model matrix was used in the RELATE routine to assess monthly shifts in macroinvertebrate communities. Non-metric multidimensional scaling (NMDS) ordinations were used to visually explore compositional dissimilarities among grouping factors. Similarity percentage (SIMPER) analyses were carried out to determine which macroinvertebrate taxa were most responsible for driving compositional differences among grouping factors. Pearson correlation coefficients were computed to assess relationships between beach-cast wrack, drifting wrack, and bare sediment macroinvertebrate communities (diversity, biomass, and abundance) and wrack line (tidal height, moisture content, and seaweed biomass) and beach characteristics (wave exposure, beach slope, and substrate types).

A separate Bray-Curtis similarity index was calculated to produce a resemblance matrix for permutational analysis of multivariate macroinvertebrate community data collected from the succession experiments. A three-factor PERMANOVA was used to determine macroinvertebrate community differences (species composition) between experimental and control groups (treatment as a fixed factor; 2 levels) and to test for succession in wrack-associated macroinvertebrate communities over months (random factor; 5 levels) and days (random factor nested in month; 8 levels). Separate one-way ANOVA tests were used to determine variability in total macroinvertebrate biomass and abundance and diversity (Shannon Index) by day of experiment and treatment (experimental and control). When ANOVA tests suggested significance, Tukey honest significant difference (HSD) post hoc tests were carried out to confirm pairwise differences. SIMPER analyses were carried out to determine which taxa were most responsible for driving compositional differences over time. Pearson correlation coefficients were calculated to determine if moisture content and/or wrack temperature correlated with variability in macroinvertebrate community composition.

3. Results

3.1. Abiotic environmental variables

Beach characteristics were variable among sites (Table 1). Most sites were semi-exposed, with some being more protected or semi-protected from wave action. Many of the sites had shallower slope angles under 10°, while inner Jakolof Bay had the steepest slope at 19°. Four sites had proportions of sand that were around 70% of the substrate, but most sites were predominantly characterized by gravel substrate.

3.2. Macroinvertebrate communities in beach-cast wrack, drifting wrack, and bare sediment

A total of 87 taxa were identified from approximately 47,000 individuals collected from beach-cast wrack, drifting wrack, and bare sediment habitats (Table 2). Removing effects of month and site by pooling the data, total macroinvertebrate biomass and abundance differed among the three habitats (ANOVA, biomass: $F_{2,1145} = 19.0$, $p < 0.001$; abundance: $F_{2,1145} = 14.0$, $p < 0.001$; Fig. 2). Total macroinvertebrate biomass and abundance in bare sediment were significantly lower than beach-cast wrack (Tukey, biomass: $p < 0.001$; abundance: $p < 0.001$) and drifting wrack (Tukey, biomass: $p < 0.001$; abundance: $p < 0.001$) habitats (Fig. 2). Total macroinvertebrate biomass in beach-cast wrack was significantly lower than in drifting wrack; however, total macroinvertebrate abundance was similar between beach-cast and drifting wrack habitats (Tukey, biomass: $p < 0.01$; abundance: $p = 0.28$). Differences in total macroinvertebrate biomass and abundance in beach-cast wrack were significant over time and among beaches (Table S1). Macroinvertebrate biomass in beach-cast wrack decreased after April (0.1 ± 0.03 kg m^{-2}) before increasing again in August (0.15 ± 0.03 kg m^{-2}), while abundance generally increased over time from April (829 ± 103 individuals m^{-2}) to August ($11{,}707 \pm 2518$ individuals m^{-2}). Spatially, beach-cast wrack in the northern-most site with a shallow

Table 2
Taxonomic list of macroinvertebrates identified from beach-cast wrack (BW), drifting wrack (DW), and bare sediments (BS) in Kachemak Bay, Alaska from April to August 2021. Habitat column indicates the habitats from which the taxa were collected. Feeding guilds are based on diet of primary feeding stage. The number of specimens collected for each taxon are binned into abundance codes (A = singletons and doubletons, B = 3–50 specimens, C = 51–500 specimens, D = >500 specimens, X = colonial organisms for which abundance was not determined).

Phylum	Class	Order	Family	Subfamily	Genus	Species	Habitat	Feeding Guild	Abundance
Annelida	Clitellata	Enchytraeida	Enchytraeidae (?)	(unidentified)			BW/DW/BS	Decomposer	D
	Polychaeta	Eunicida	Lumbrineridae		*Scoletoma*	(unidentified)	BW/DW	Predator	B
		Terebellida	Flabelligeridae		*Brada*	(unidentified)	BW	Omnivore	A
		(unidentified)					BW/DW/BS		D
Arthropoda	Arachnida	Acari	Bdellidae		*Neomolgus*	*N. littoralis*	BW/BS	Predator	B
			(unidentified)				BW/BS		C
		Araneae	Gnaphosidae	(unidentified)			DW	Predator	A
			(unidentified)				BW/DW	Predator	B
		Pseudoscorpiones	Neobisiidae	Microcreagrinae	*Halobisium*	*H. occidentale*	BW/DW/BS	Predator	B
	Chilopoda	Geophilomorpha	(unidentified)				BW/DW/BS	Predator	B
		Lithobiomorpha	(unidentified)				BW/DW	Predator	B
	Entognatha	Collembola	(unidentified)				BW/DW/BS	Detritivore	B
	Insecta	Coleoptera	Anthicidae	Anthicinae	*Anthicus*	(unidentified)	BW	Omnivore	A
			Cantharidae		*Malthacus*	(unidentified)	DW	Predator	A
			Carabidae	Harpalinae	*Amara*	*A. torrida*	BW	Predator	A
					Amara	(unidentified)	DW	Predator	A
					Dicheirotrichus	*D. cognatus*	DW	Predator	A
				Trechinae	*Bembidion*	(unidentified)	DW	Predator	B
			Curculionidae	Molytinae	*Sthereus*	*S. ptinoides*	BW	Herbivore	A
			Coccinellidae	Coccinellinae	*Hippodamia*	*H. quinquesignata*	DW	Predator	A
			Elateridae	Dendrometrinae	*Hypolithus*	*H. littoralis*	BW	Decomposer	A
				Negastriinae	*Neohypdonus*	(unidentified)	DW	Decomposer	A
			Heteroceridae		*Heterocerus*	(unidentified)	BW/DW	Microbivore	B
			Hydraenidae	Ochthebiinae	*Ochthebius*	(unidentified)	BW	Microbivore	A
			Hydrophilidae	Sphaeridiinae	*Cercyon*	*C. fimbriatus*	BW	Decomposer	C
			Lycidae		*Dictyoptera*	*D. simplicipes*	BW	Fungivore	A
			Pyrochroidae		*Dendroides*	*D. ephemeroides*	BW	Decomposer	A
			Scarabaeidae	Aegialiinae	*Aegialia*	*A. cylindrica*	DW	Decomposer	A
			Scraptiidae		*Anaspis*	(unidentified)	BW	Decomposer	A
			Staphylinidae	Aleocharinae	(unidentified)		BW/DW	Predator	B
				Aleocharinae	*Amblopusa*	*A. brevipes*	BW/BS	Predator	B
				Omaliinae	*Eusphalerum*	*E. pothos*	BW	Predator	A
				Staphylininae	(unidentified)		BW	Predator	B
					Cafius	*C. canescens*	BW	Predator	B
					Hadrotes	*H. crassus*	BW	Predator	B
				(unidentified)			BW/DW/BS	Predator	B
		Diptera	Bibionidae	(unidentified)			BW/DW	Decomposer	B
			Chironomidae	(unidentified)			BW/DW	Decomposer	C
			Culicidae	(unidentified)			BW	Microbivore	A
			Empididae	(unidentified)			BW	Predator	A
			Mycetophilidae	(unidentified)			BW	Fungivore	A
			Sciaridae	(unidentified)			BW	Decomposer	A
			Tipulidae	(unidentified)			BW/DW	Decomposer	B
			(unidentified)				BW/DW/BS		D
		Ephemeroptera	(unidentified)				DW	Decomposer	A
		Hemiptera	Aphididae	(unidentified)			BW/DW	Herbivore	B
			Cicadellidae	(unidentified)			BW/DW	Herbivore	C
			Psylloidea	(unidentified)			BW	Herbivore	A
			Saldidae	(unidentified)			BW	Predator	B
			(unidentified)				BW/DW		C
		Hymenoptera	Braconidae	Alysiinae	(unidentified)		BW/DW/BS	Predator	B
			Figitidae	Eucoilinae	(unidentified)		BW/DW	Predator	B

(*continued on next page*)

Table 2 (*continued*)

Phylum	Class	Order	Family	Subfamily	Genus	Species	Habitat	Feeding Guild	Abundance
			Formicidae	Formicinae	*Camponotus*	*C. herculeanus*	BW	Predator	A
					Formica	(unidentified)	BW	Predator	A
				Myrmicinae	*Leptothorax*	(unidentified)	BW	Predator	A
			Ichneumonidae	(unidentified)			BW/DW	Predator	B
			Vespidae	Vespinae	*Vespula*	*V. acadica*	BW	Predator	A
			(unidentified)				DW		B
		Lepidoptera	(unidentified)				BW/DW	Herbivore	A
		Neuroptera	Hemerobiidae	(unidentified)			DW	Predator	A
		Plecoptera	(unidentified)				BW/DW	Decomposer	A
		Trichoptera	(unidentified)				BW	Decomposer	A
	Malacostraca	Amphipoda	Ampithoidae		*Sunamphitoe*	*S. mea*	DW	Herbivore	D
			Caprellidae	(unidentified)			BW	Omnivore	A
			Talitridae		*Traskorchestia*	*T. traskiana*	BW/BS	Decomposer	D
		Cumacea	(unidentified)				BW/DW/BS	Detritivore	B
		Decapoda	Oregoniidae		*Hyas*	*H. lyratus*	DW	Omnivore	A
			Paguridae	(unidentified)			BW/DW	Omnivore	B
		Decapoda-Brachyura	(unidentified)				BS	Omnivore	A
		Decapoda-Caridea	(unidentified)				DW	Omnivore	B
		Isopoda	(unidentified)				BW/DW/BS	Omnivore	B
Bryozoa	Gymnolaemata	Ctenostomata	Flustrellidridae		*Flustrellidra*	*F. corniculata*	BW	Filter-feeder	X
	Stenolaemata	Cyclostomatida	Crisiidae		*Crisia*	(unidentified)	BW/DW	Filter-feeder	X
Echinodermata	Asteroidea	Forcipulatida	Asteriidae	(unidentified)			BW/DW	Predator	B
	Echinoidea	Echinoida	Strongylocentrotidae		*Strongylocentrotus*	(unidentified)	BW	Grazer	A
	Holothuroidea	(unidentified)					BW/DW	Scavenger	B
	Ophiuroidea	(unidentified)					DW	Scavenger	A
Mollusca	Bivalvia	Cardiida	Cardiidae		*Clinocardium*	(unidentified)	BW/DW	Filter-feeder	B
			Tellinidae		*Macoma*	(unidentified)	BW/DW	Filter-feeder	C
		Carditida	Astartidae		*Astarte*	(unidentified)	BW/DW	Filter-feeder	D
		Myida	Myidae		*Mya*	(unidentified)	BW/DW	Filter-feeder	B
		Mytilida	Mytilidae	(unidentified)			BW/DW/BS	Filter-feeder	D
		Venerida	Veneridae		*Saxidomus*	(unidentified)	BW	Filter-feeder	A
	Gastropoda		Lottiidae	(unidentified)			BW/DW	Grazer	C
		Cephalaspidea	Gastropteridae		*Gastropteron*	*G. pacificum*	DW	Planktivore	A
		(unidentified)					BW/DW/BS	Grazer	D
	Polyplacophora	Chitonida	Tonicellidae	Lepidochitoninae	*Tonicella*	(unidentified)	BW	Grazer	B

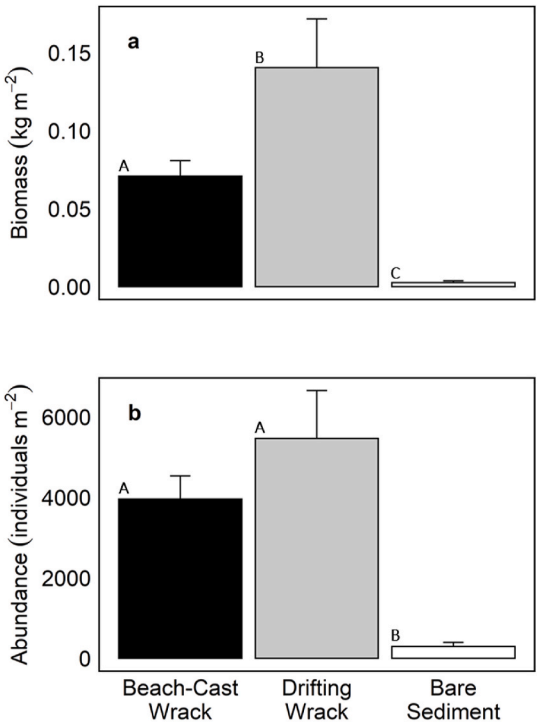

Fig. 2. Bar plots of mean total macroinvertebrate (a) biomass (kg m^{-2}) and (b) abundance (individuals m^{-2}) for beach-cast wrack, drifting wrack, and bare sediment habitats (bars represent standard error) from Kachemak Bay, Alaska in 2021. Significantly different means among habitats are denoted by different letters above each bar. If the letters above each bar are the same, then they are not significantly different ($\alpha = 0.05$).

beach slope and mostly sand substrate (Anchor Point) had the greatest biomass (0.26 ± 0.07 kg m^{-2}) and abundance (14,596 ± 4082 individuals m^{-2}) of macroinvertebrates relative to the other sites. Differences in total macroinvertebrate biomass in drifting wrack was not significant over time or among beaches; however, differences in abundance of drifting wrack were significant over time and among beaches (Table S1). Total macroinvertebrate abundance in drifting wrack peaked in June (10,002 ± 4576 individuals m^{-2}). Differences in total macroinvertebrate biomass and abundance found in bare sediment were not significant over time or among beaches (Table S1).

Though there were some similarities between beach-cast wrack and bare sediment macroinvertebrates, community composition based on biomass and abundance were significantly different among beach-cast wrack, drifting wrack, and bare sediment habitats when all beaches and months were combined (PERMANOVA, biomass: $F_{12,718} = 5.0$, $p = 0.001$; abundance: $F_{12,704} = 6.0$, $p = 0.001$; Fig. 3). SIMPER analyses revealed that differences in macroinvertebrate communities among habitats based on both relative biomass and abundance were mostly driven by Amphipoda, Enchytraeida, Coleoptera, Diptera, Gastropoda, Mytilida, and Polychaeta (Fig. 4). Beach-cast wrack generally had more Coleoptera and Diptera. Bare sediment communities were consistently composed mostly of Enchytraeida. Compared to beach-cast wrack and bare sediment, drifting wrack was occupied by more marine taxa and generally had more Amphipoda, Gastropoda, Mytilida, and Polychaeta. Differences in macroinvertebrate community composition were also significant among beaches and over time (Table S2). Though there were monthly differences in macroinvertebrate community composition, there were no significant seasonal trends across habitats (Table S3). SIMPER analyses revealed consistent site differences. In particular, the site adjacent to the largest watershed (Wosnesenski River) consistently had more Coleoptera contributing to community composition over all other sites, while a more protected site (Tutka Bay) consistently had more Geophilomorpha. The site with the most sand contributing to the substrate (Anchor Point) consistently had more Amphipoda contributing to community composition than all other sites. SIMPER analyses also revealed that monthly differences in macroinvertebrate communities among all habitats based on both relative biomass and abundance were mostly driven by Amphipoda, Enchytraeida, Coleoptera, Diptera, Gastropoda, Mytilida, and Polychaeta (Fig. 4). Proportions of Enchytraeida to relative biomass and abundance generally decreased across months in beach-cast wrack and bare sediment habitats, as proportions of Amphipoda, Diptera, and Coleoptera increased across months (Fig. 4). Gastropoda contributed to monthly differences in macroinvertebrate biomass and abundance proportions in drifting wrack (Fig. 4). Amphipoda alone accounted for approximately 28% and 33% of biomass and abundance, respectively, in beach-cast wrack. Dipteran flies (adults, pupae, and larvae combined) contributed proportions of 7% and 16% to biomass and abundance, respectively, to beach-cast wrack macroinvertebrate communities. The largest contribution to beach-cast wrack was Enchytraeida with 9% and 43% proportions of biomass and abundance, respectively.

3.3. *Response of macroinvertebrate communities to environmental characteristics*

Percent boulder substrate was removed from the analysis, because draftsman plots indicated collinearity of percent boulder substrate with beach slope (with a correlation cutoff of $|r| \geq 0.80$). Shannon Index, based on biomass calculated for macroinvertebrate communities in beach cast wrack, was positively correlated with tidal height of the

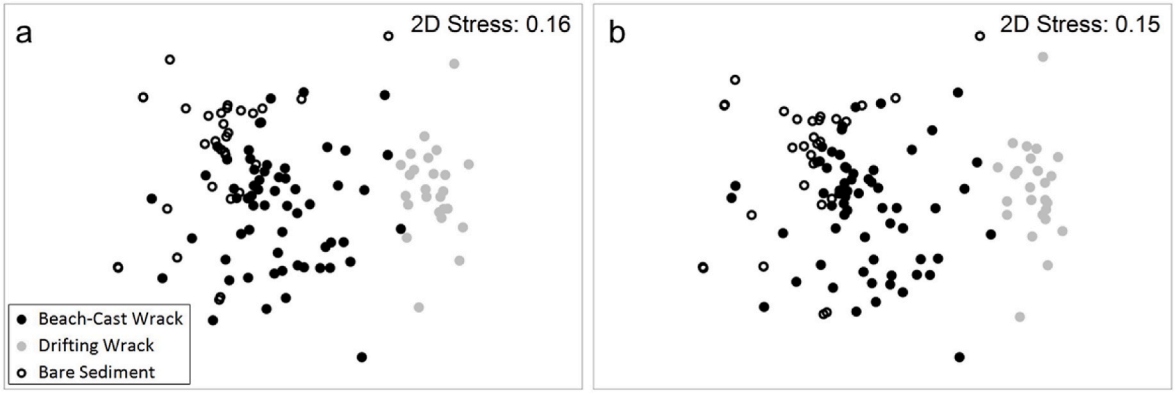

Fig. 3. Non-metric multidimensional scaling (nMDS) ordination plots based on relative macroinvertebrate community (a) biomass and (b) abundance in beach-cast wrack, drifting wrack, and bare sediment habitats from Kachemak Bay, Alaska in 2021. Each point represents the community at a monthly sampling event per site. Stress indicates how well the ordination summarizes the two-dimensional distances among the points.

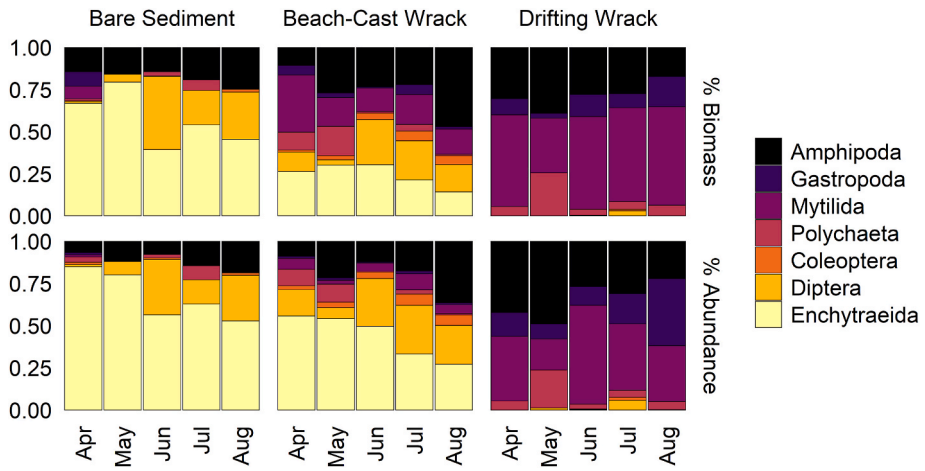

Fig. 4. Stacked bar plots of macroinvertebrate taxa that were most responsible (from SIMPER analysis) for driving compositional differences among bare sediment, beach-cast wrack, and drifting wrack habitats based on biomass (top panels) and abundance (bottom panels) in Kachemak Bay, Alaska in 2021.

wrack line and negatively correlated with percent sand substrate (Table 3). Shannon Index, based on biomass for macroinvertebrate communities in drifting wrack and bare sediment habitats, did not correlate with any of the tested environmental variables (Table 3). Shannon Index, based on abundance calculated for macroinvertebrate communities in beach cast wrack, was positively correlated with both tidal height of the wrack line and wrack biomass, but negatively correlated with wave exposure (Table 3). Shannon Index for macroinvertebrate communities, based on abundance in drifting wrack and bare sediment habitats, did not correlate with any of the tested environmental variables (Table 3). Total macroinvertebrate biomass and abundance in both beach-cast and drifting wrack was positively correlated with wrack biomass (Table 3), whereas total macroinvertebrate biomass and abundance in bare sediment did not correlate with any of the tested environmental variables (Table 3).

3.4. Succession in aging beach-cast wrack

Wrack piles created microclimates by retaining moisture and decreasing the temperature fluctuation range within the wrack relative to the surrounding ambient air temperatures; underlying sediments had the lowest temperature fluctuations (Fig. 5). Inside of the wrack piles, temperature changes lagged ambient air temperatures, and underlying sediment temperatures even more so. In general, the experimental wrack piles became occupied by a variety of decomposers, omnivores, and predators.

Total biomass and abundance of macroinvertebrate communities were significantly higher in experimental wrack piles than in bare sediment controls (ANOVA, biomass: $F_{1,126} = 13.03$, $p < 0.001$; abundance: $F_{1,126} = 18.4$, $p < 0.001$; Fig. 6). Macroinvertebrate communities generally increased in total biomass and abundance over the course of the experiments, with marginal differences across months (ANOVA, biomass: $F_{4,74} = 2.6$, $p = 0.05$; abundance: $F_{4,74} = 2.5$, $p = 0.05$; Fig. 6). Total biomass and abundance of macroinvertebrates peaked on Day 9 in June and July (Fig. 6). In April, May, June, and July, changes in total macroinvertebrate biomass (ANOVA, April: $F_{4,10} = 1.1$, $p = 0.41$; May: $F_{4,10} = 0.9$, $p = 0.52$; June: $F_{5,12} = 1.9$, $p = 0.17$; July: $F_{5,12} = 2.1$, $p = 0.14$) and abundance (ANOVA, April: $F_{4,10} = 1.2$, $p = 0.37$; May: $F_{4,9} = 3.4$, $p = 0.06$; June: $F_{5,12} = 1.7$, $p = 0.2$; July: $F_{5,12} = 1.9$, $p = 0.16$) were not significant over the 15–24 days of the experiment in each month. In the longer August experiment, total biomass and abundance of macroinvertebrates peaked on Day 18, when these parameters were significantly higher than the other days of the experiment for that month (ANOVA, biomass: $F_{4,9} = 4.8$, $p = 0.02$; abundance: $F_{4,9} = 17.8$, $p < 0.001$; Fig. 6). In addition, macroinvertebrate communities strongly increased in diversity (Shannon Index based on biomass and abundance; Fig. S1) after Day 0, but then fluctuated and often decreased towards the end of the monthly experiments.

The relationships between wrack moisture and macroinvertebrate diversity (Shannon Index based on abundance) were positive early in the season but became negative starting in June, although only the negative relationship in July was significant (Table 4). Wrack moisture content was negatively related to macroinvertebrate abundance in May and August (Table 4). The relationships between internal wrack temperature and macroinvertebrate diversity (Shannon Index based on biomass and abundance) were positive early in the season, with significant correlations in April, but were negative at the end of the season, with significant correlations in August (Table 4). Similarly, the relationships between internal wrack temperature and macroinvertebrate biomass and abundance were positive early in the season but negative at the end of the season (Table 4).

Macroinvertebrate communities that developed over time in the monthly wrack succession experiments were significantly different than bare sediment controls (PERMANOVA, biomass: $F_{1,70} = 140.7$, $p = 0.001$; abundance: $F_{1,70} = 111.6$, $p = 0.002$) and among days in each month (PERMANOVA, biomass: $F_{22,70} = 1.7$, $p = 0.03$; abundance: $F_{22,70} = 1.8$, $p = 0.03$). Removing the effect of day, community composition based on biomass was significantly different among months (PERMANOVA, $F_{4,70} = 2.4$, $p = 0.03$); however, community composition based on abundance did not change significantly among months (PERMANOVA, $F_{4,70} = 1.8$, $p = 0.09$). Few taxa were present on Day 0 of each experiment, but these included Enchytraeida, Araneae, Diptera, and Geophilomorpha. These taxa were also common in control samples from bare sediment. At least by Day 3 in every month except for April, both Amphipoda and Diptera appeared and, along with Enchytraeida, remained predominant for the remainder of the experiment (Fig. 7). Hydrophilidae (Coleoptera) were not present until Day 15 in May and Day 6 in June and July, but not until Day 12 in August (Fig. 7). Staphylinidae (Coleoptera) consistently were found on Day 9 in May, June, and July. Day 9 was not sampled in August, but Staphylinidae were present at least by Day 12 (Fig. 7). Isopoda only appeared in May on Day 15 (Fig. 7). Braconidae (Hymenoptera) only appeared in July and August, as early as Day 9, but usually occurred later in experiments on Days 12, 15, or 18.

The shift in proportions of different feeding guilds was variable over different months (PERMANOVA, biomass: $F_{4,87} = 3.0$, $p = 0.01$; abundance: $F_{4,87} = 2.8$, $p = 0.01$); however, some similarities were observed across months (Fig. 8). Decomposers were the predominant feeding

Table 3
Pearson correlations for macroinvertebrate communities (Shannon Index based on biomass and abundance, total macroinvertebrate biomass, and total macroinvertebrate abundance) versus environmental variables in beach-cast wrack, drifting wrack, and bare sediment habitats in Kachemak Bay, Alaska. Bold values indicate significance ($\alpha = 0.05$).

Habitat	Macroinvertebrate Data		Environmental Variable	Pearson's *R*	*p*-value
Beach-Cast Wrack	Shannon Index (Biomass)	vs.	**Tidal Height**	**0.7**	**<0.001**
			Moisture Content	0.003	1.0
			Wrack Biomass	**0.6**	**<0.001**
			Wave Exposure	−0.1	0.7
			Beach Slope	−0.07	0.7
			Percent Cobble	0.3	0.08
			Percent Gravel	0.1	0.7
			Percent Sand	−0.3	0.1
	Shannon Index (Abundance)	vs.	**Tidal Height**	**0.7**	**<0.001**
			Moisture Content	0.1	0.7
			Wrack Biomass	**0.6**	**0.001**
			Wave Exposure	−0.3	0.1
			Beach Slope	0.01	0.9
			Percent Cobble	0.3	0.1
			Percent Gravel	0.1	0.5
			Percent Sand	−0.3	0.1
	Total Biomass	vs.	Tidal Height	0.1	0.5
			Moisture Content	0.1	0.7
			Wrack Biomass	**0.6**	**<0.001**
			Wave Exposure	0.1	0.4
			Beach Slope	−0.3	0.1
			Percent Cobble	0.04	0.8
			Percent Gravel	−0.3	0.1
			Percent Sand	0.2	0.2
	Total Abundance	vs.	Tidal Height	0.1	0.6
			Moisture Content	0.2	0.4
			Wrack Biomass	**0.6**	**0.001**
			Wave Exposure	0.2	0.3
			Beach Slope	−0.1	0.5
			Percent Cobble	−0.1	0.7
			Percent Gravel	−0.1	0.8
			Percent Sand	0.1	0.6
Drifting Wrack	Shannon Index (Biomass)	vs.	Wrack Biomass	−0.1	0.5
			Wave Exposure	−0.1	0.5
			Beach Slope	0.001	1.0
			Percent Cobble	0.002	1.0
			Percent Gravel	0.2	0.5
			Percent Sand	−0.2	0.4
	Shannon Index (Abundance)	vs.	Wrack Biomass	−0.1	0.5
			Wave Exposure	−0.2	0.5
			Beach Slope	−0.1	0.8
			Percent Cobble	−0.1	0.8
			Percent Gravel	0.2	0.3
			Percent Sand	−0.2	0.4
	Total Biomass	vs.	**Wrack Biomass**	**0.4**	**0.04**
			Wave Exposure	0.04	0.8
			Beach Slope	−0.2	0.3
			Percent Cobble	0.4	0.1
			Percent Gravel	0.1	0.7
			Percent Sand	0.02	1.0
	Total Abundance	vs.	**Wrack Biomass**	**0.4**	**0.04**
			Wave Exposure	0.2	0.3
			Beach Slope	0.01	1.0
			Percent Cobble	0.2	0.4
			Percent Gravel	−0.1	0.7
			Percent Sand	0.1	0.5
Bare Sediment	Shannon Index (Biomass)	vs.	Tidal Height	0.4	0.04
			Wave Exposure	−0.2	0.3
			Beach Slope	−0.06	0.7
			Percent Cobble	0.2	0.2
			Percent Gravel	−0.01	1.0
			Percent Sand	−0.2	0.4
	Shannon Index (Abundance)	vs.	Tidal Height	0.4	0.05
			Wave Exposure	−0.1	0.5
			Beach Slope	0.02	0.9
			Percent Cobble	0.2	0.2
			Percent Gravel	0.1	0.5
			Percent Sand	−0.3	0.1
	Total Biomass	vs.	Tidal Height	0.04	0.9
			Wave Exposure	0.1	0.5
			Beach Slope	−0.2	0.3

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Table 3 (*continued*)

Habitat	Macroinvertebrate Data		Environmental Variable	Pearson's *R*	*p*-value
			Percent Cobble	−0.1	0.8
			Percent Gravel	−0.1	0.6
			Percent Sand	0.2	0.4
	Total Abundance	vs.	Tidal Height	0.03	0.9
			Wave Exposure	0.1	0.5
			Beach Slope	−0.1	0.5
			Percent Cobble	−0.1	0.7
			Percent Gravel	−0.04	0.8
			Percent Sand	0.1	0.6

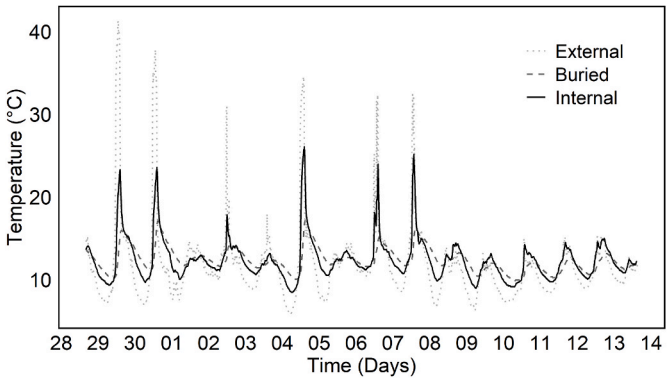

Fig. 5. Temporal variability in measured temperatures during a beach-cast wrack macroinvertebrate community succession experiment in Kachemak Bay, Alaska from 28 June to 14 July 2021. External temperature (ambient air outside of wrack piles) = dashed light gray lines; Buried temperature (buried 5–10 cm in sediment underneath of wrack piles) = dashed dark gray lines; Internal temperature (inside of wrack piles) = solid black lines.

guild for the duration of the experiments. In April, May, and July, predators (i.e., Araneae, Geophilomorpha, and Pseudoscorpiones) were present earlier than in June and August. Generally, predators and omnivores appeared in later successional stages (Fig. 8).

4. Discussion

Where beach-cast wrack is harvested mostly for fertilizer in high latitude regions, the resulting impact of this removal to coastal ecosystems has received little attention (except see Urban-Malinga and Burska 2009 for meiofaunal communities). As a precursor to beach-cast wrack, the association of macroinvertebrates to drifting wrack is also largely unknown. This study showed that seaweed wrack supports diverse communities of both marine and terrestrial macroinvertebrates in a glacially- and tidally-driven high latitude estuary. Additionally, macroinvertebrates with different taxonomic groupings and feeding guilds contributed to a classical order of succession within beach-cast wrack habitat. These findings of wrack community dynamics across seasons and habitats can be used in development of wrack resource management in Alaska and elsewhere.

4.1. Macroinvertebrate communities in beach-cast wrack, drifting wrack, and bare sediment

The present study determined that both beach-cast and drifting wrack improve habitat quality by supporting more diverse and greater numbers of macroinvertebrates compared to bare soft sediment beach habitats, supporting our hypothesis that the presence of beach-cast and drifting wrack increases macroinvertebrate community diversity. Bare sediments devoid of seaweed wrack were sometimes occupied by wrack-associated macroinvertebrates that may have appeared during previous wrack deposition events in those areas. Overall, beach-cast wrack

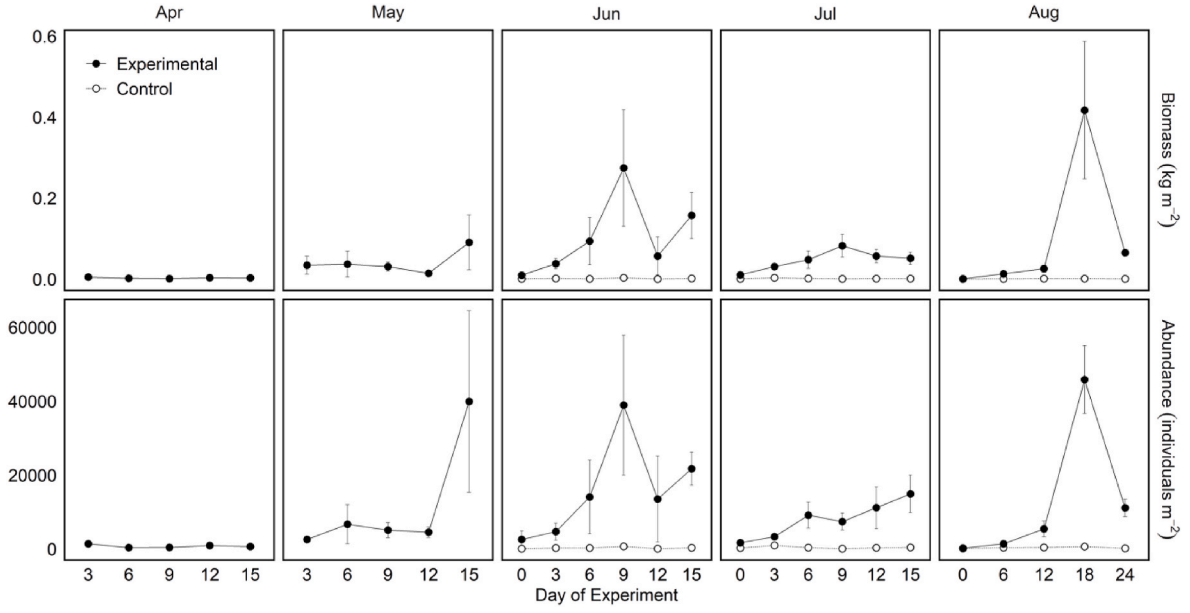

Fig. 6. Macroinvertebrate community means of total biomass (top panels) and abundance (bottom panels) over time (days) from monthly wrack succession experiments (bars represent standard error) in Kachemak Bay, Alaska in 2021. Experimental values represent macroinvertebrate communities collected from wrack piles. There were no controls (bare sediment) in April and May experiments.

Table 4
Pearson correlations for macroinvertebrate communities (Shannon Index based on biomass and abundance, total macroinvertebrate biomass, and total macroinvertebrate abundance) versus moisture content and internal wrack temperature of wrack piles from monthly succession experiments in Kachemak Bay, Alaska. Bold values indicate significance ($\alpha = 0.05$).

Month	Environmental Variable		Macroinvertebrate Data	Pearson's *R*	*p*-value
April	Moisture Content	vs.	Shannon Index (Biomass)	0.1	0.6
			Shannon Index (Abundance)	0.2	0.5
			Total Biomass	−0.1	0.8
			Total Abundance	0.1	0.7
	Internal Temperature	vs.	**Shannon Index (Biomass)**	**0.6**	**0.02**
			Shannon Index (Abundance)	**0.5**	**0.04**
			Total Biomass	−0.01	1.0
			Total Abundance	0.1	0.8
May	Moisture Content	vs.	Shannon Index (Biomass)	0.2	0.5
			Shannon Index (Abundance)	0.2	0.6
			Total Biomass	−0.4	0.1
			Total Abundance	**−0.7**	**0.004**
	Internal Temperature	vs.	Shannon Index (Biomass)	−0.2	0.5
			Shannon Index (Abundance)	−0.2	0.6
			Total Biomass	0.4	0.1
			Total Abundance	**0.7**	**0.003**
June	Moisture Content	vs.	Shannon Index (Biomass)	−0.2	0.4
			Shannon Index (Abundance)	−0.1	0.7
			Total Biomass	−0.2	0.5
			Total Abundance	−0.2	0.4
	Internal Temperature	vs.	Shannon Index (Biomass)	0.001	1.0
			Shannon Index (Abundance)	0.02	1.0
			Total Biomass	**0.5**	**0.05**
			Total Abundance	**0.5**	**0.03**
July	Moisture Content	vs.	Shannon Index (Biomass)	−0.4	0.1
			Shannon Index (Abundance)	**−0.5**	**0.03**
			Total Biomass	−0.4	0.1
			Total Abundance	0.1	0.7
	Internal Temperature	vs.	Shannon Index (Biomass)	−0.2	0.5
			Shannon Index (Abundance)	0.03	0.9
			Total Biomass	0.2	0.6
			Total Abundance	−0.2	0.4
August	Moisture Content	vs.	Shannon Index (Biomass)	−0.2	0.6
			Shannon Index (Abundance)	−0.3	0.4
			Total Biomass	−0.5	0.1
			Total Abundance	**−0.6**	**0.04**
	Internal Temperature	vs.	**Shannon Index (Biomass)**	**−0.6**	**0.02**
			Shannon Index (Abundance)	**−0.5**	**0.04**
			Total Biomass	−0.4	0.1
			Total Abundance	**−0.6**	**0.04**

supported more terrestrial taxa, while drifting wrack supported more marine taxa. Annelids were ubiquitous across beach habitats whether wrack was present or not, but the presence of wrack sometimes increased their abundance. Although a confident identification of the worms was not possible due to their poor state of preservation, their general shape, size, and abundance in decaying wrack is strongly suggestive of enchytraeid worms, which are known decomposers of wrack (O'Connor, 1967).

Drifting wrack that accumulates in surf zones can provide refuge for marine invertebrates and foraging grounds for fish (Clark 1997; Olds et al., 2018). In the present study, drifting wrack supported greater numbers of amphipods than did beach-cast wrack. Beach-cast amphipods may burrow beneath piles of wrack during the day to avoid warmer temperatures and predators and can be found actively feeding on and foraging in wrack at night (Dugan et al., 2003). Although some marine taxa, such as mussels and gastropods were common in drifting wrack, they were also present in beach-cast wrack, but were considered incidental based on their sessile life history and not actively using the beach-cast wrack habitat. However, when associated with drifting wrack, these species may rely on this habitat for assisted transport (Baring et al., 2018).

Beetles, such as those in the families Hydrophilidae and Staphylinidae, were also more common in wrack than in surrounding bare sediment and appeared rarely in drifting wrack. The hydrophilid, *Cercyon fimbriatus*, was the most abundant beetle species sampled and is a well-known specialist decomposer of wrack along North American Pacific shores (Suzumura et al., 2019). Terrestrial beetles such as these occurring in wrack have physiological adaptations that allow them to survive in the intertidal environment to broaden their access to food (Doyen 1976). For example, some staphylinids are adapted to the marine intertidal by reducing their metabolic rate and oxygen consumption when submerged in seawater (Topp and Ring 1988). Similarly, Heteroceridae were also found in both beach-cast and drifting wrack, probably due to their adaptation to reduce oxygen consumption when submerged in seawater during high tide (Doyen 1976). Other beetles, such as Hydraenidae, were also collected from beach-cast wrack and have been reported to inhabit saline shoreline environments in marine rockpools (Sabatelli et al., 2021). The largest-bodied predatory macroinvertebrate, present as both adults and larvae, was *Hadrotes crassus*, a staphylinid beetle, that feeds on crustaceans (primarily amphipods) and insects (Frank and Ahn 2011) followed by the smaller-bodied but more numerous staphylinid, *Cafius canescens*.

Some taxa collected from beach-cast wrack in the present study have rarely been collected in Alaska. Given that eucoiline wasps (Ashmead 1902) are parasitoids of dipteran larvae (Wu and Abe 2020), it is likely that the high concentrations of multiple dipteran life stages in decomposing wrack on beaches attracts such rarely collected parasitoid taxa. In Northern Europe and New Zealand, parasitoid Hymenoptera are known to associate with beach-cast wrack (Backlund 1945; Hodge and Early 2016). For example, in New Zealand, 20 species of Hymenoptera were identified in wrack, including common encounters of a parasitoid wasp species in the subfamily Eucoilinae (Hodge and Early 2016). Further investigations into wrack-associated macroinvertebrates could reveal more occurrences of habitat use by seldom collected taxa.

4.2. Response of macroinvertebrate communities to environmental characteristics

Macroinvertebrate communities in beach-cast and drifting wrack were often correlated with environmental characteristics, while bare beach sediment communities did not correlate with abiotic features. Macroinvertebrate community diversity in beach-cast wrack decreased with exposure to wave action in the present study. Though Dugan et al. (2003) found that swash climate and associated factors have little influence on wrack-associated macroinvertebrate communities, it is possible that higher levels of wave exposure directly affect wrack age. It may be that high exposure beaches do not allow wrack communities to fully mature. In the context of the intermediate disturbance hypothesis (England et al., 2008), high disturbance from exposed sites may be keeping the wrack community in an early successional state. Especially in areas with large tidal cycles (e.g., Kachemak Bay), waves during high

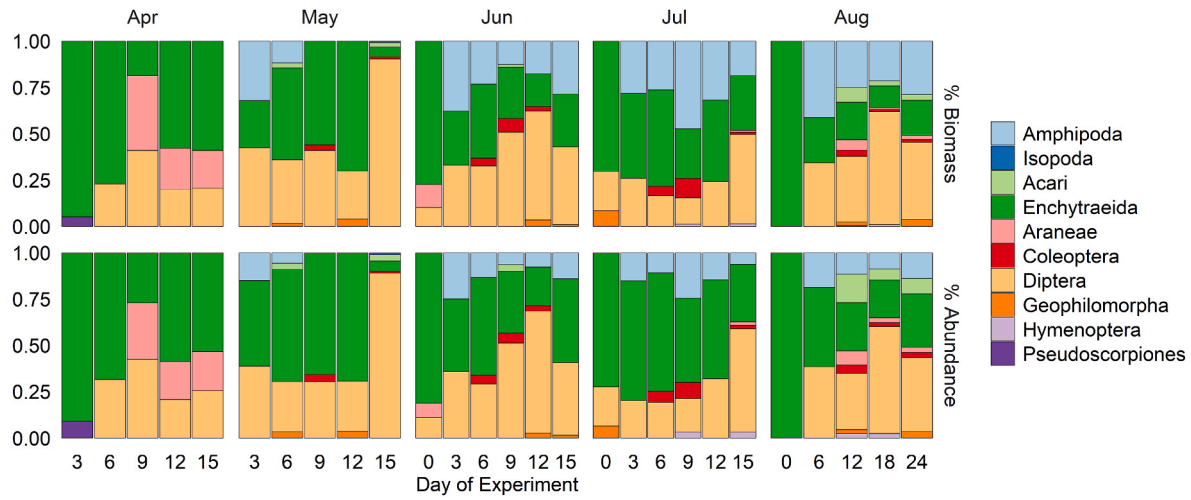

Fig. 7. Stacked bar plots of macroinvertebrate taxa that were most responsible (from SIMPER analysis) for driving compositional differences over time (days and months) during succession experiments in Kachemak Bay, Alaska, based on biomass (top panels) and abundance (bottom panels).

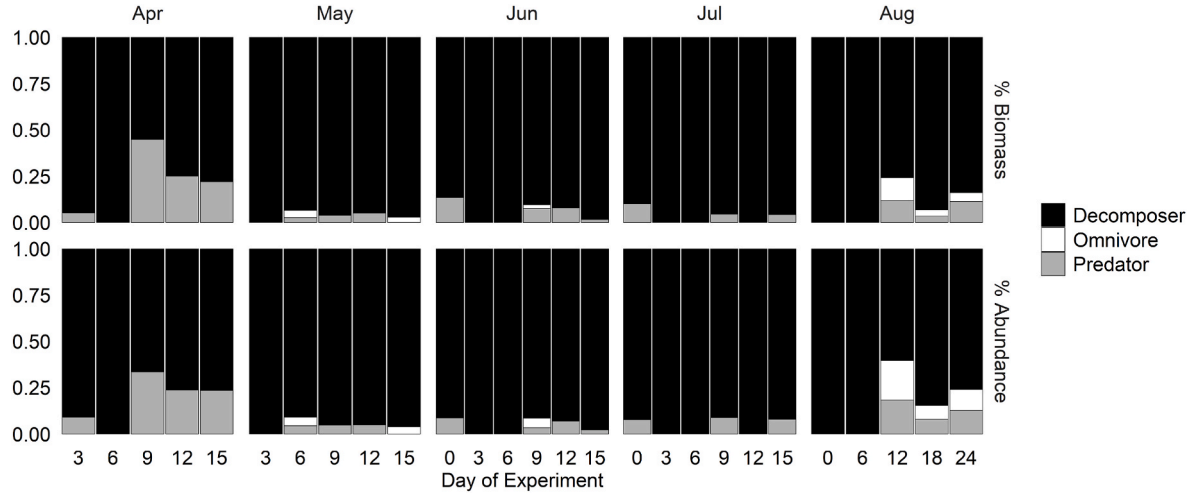

Fig. 8. Stacked bar plots of macroinvertebrate feeding guilds and their proportions of the communities based on the macroinvertebrate taxa most responsible (from SIMPER analysis) for driving compositional differences over time (days and months) during the succession experiments in Kachemak Bay, Alaska, based on biomass (top panels) and abundance (bottom panels). Feeding guilds are groupings of macroinvertebrates based on diet of the primary feeding stage.

tides may wash away wrack rather than transporting it higher on the beach. In the present study, wrack from the sites with the highest exposure to waves was inhabited by fewer taxa, including Amphipoda, Enchytraeida, or Diptera, with other taxa appearing more rarely. These taxa may be less sensitive to frequent disturbances by waves and associated effects due to their highly developed orientation behavior (Amphipoda; Scapini et al., 1995), increased mobility (Diptera), and ubiquity (Enchytraeida). Macroinvertebrate diversity, biomass, and abundance in drifting wrack and bare beach sediment did not change with level of exposure to waves. This may be because they do not rely on deposition of habitat, rather the persistence of drifting wrack is unaffected by exposure and bare beach sediment habitat is not reliant on deposition and removal of wrack subsidies.

Although total macroinvertebrate biomass and abundance in beach-cast wrack were not affected by substrate type, the present study determined that macroinvertebrate diversity decreased significantly with percent sand substrate. Where proportions of sand were greater than 70% of the substrate, beach-cast wrack was predominately occupied by Amphipoda and Enchytraeida. Amphipoda and Enchytraeida burrow in finer sediments with increased densities in wrack accumulations (Coupland and McDonald 2008; Malm 2016). Many studies that have characterized macroinvertebrate communities associated with wrack have been conducted on sandy beaches; however, some work has been done to characterize wrack degradation rates on coarser substrate (Heerhartz et al., 2016; Gilson et al., 2021). In the present study, proportions of cobble and gravel did not influence macroinvertebrate diversity, biomass, and abundance in any of the habitats (i.e., beach-cast wrack, drifting wrack, bare sediment). Though abiotic beach characteristics (e.g., substrate type, wave exposure) may influence wrack biomass accumulations on beaches seasonally (Ulaski et al., 2023), it is characteristics of the wrack itself that have more important roles in structuring macroinvertebrate communities.

Wrack biomass plays a more important role in wrack community development than the substrate on which wrack is deposited, supporting our hypothesis that increased biomass of seaweed wrack supports higher macroinvertebrate abundance. The present study found that macroinvertebrate diversity, biomass, and abundance increased with biomass of seaweed subsidies in beach-cast and drifting wrack. These findings are similar to other studies that found higher beach-cast wrack biomass increases macrofaunal biomass and species richness (Dugan et al., 2000; MacMillan and Quijón 2012; Ruiz-Delgado et al., 2015; Vieira et al., 2016). The increased biomass of wrack creates greater amounts of

complex habitat and food on beaches for different animals to exploit and partition, possibly decreasing competitive interactions (Colombini and Chelazzi 2003). For example, if wrack biomass is low, amphipods may leave wrack to find other feeding grounds to decrease intraspecific competition (Colombini and Chelazzi 2003). The increased biomass and abundance of macroinvertebrates with increased drifting wrack biomass is also likely due to the high densities of mussels and gastropods remaining attached and feeding on *Laminaria* spp. and *Ulva* spp. that get dislodged from the seafloor.

The tidal height at which the beach-cast wrack line was deposited positively correlated with diversity, biomass, and abundance of macroinvertebrate communities, possibly due to the higher wrack lines being older, giving the community time to reach more developed successional stages. This may also be explained by the accessibility of higher elevation wrack deposits to macroinvertebrates of upper intertidal or terrestrial origin, such as some beetles, ants, pseudoscorpions, spiders, and centipedes. Not only does higher elevation of wrack deposition attract more terrestrial arthropods, but the talitrid amphipods that feed on the wrack often inhabit the upper intertidal and supralittoral zones (Dugan et al., 2003). Similar to this present study, others have shown that macroinvertebrate communities are more strongly influenced by wrack biomass rather than beach morphodynamics (Dugan et al., 2003). Bare beach sediment macroinvertebrates did not change with tidal height, providing further evidence that wrack increases habitat quality across tidal elevations on beaches. Overall, the relative abundance of seaweed wrack and the elevation at which it is deposited on the beach are the most important and consistent drivers of macroinvertebrate diversity, biomass, and abundance. Wave exposure and substrate fostered differences only in diversity.

The present study found that macroinvertebrate diversity and abundance were sometimes negatively correlated with moisture content of the seaweed wrack itself. This negative correlation may reflect invertebrates tending to prefer aged wrack (Pelletier et al., 2011), which often lost moisture as the experiments progressed; however, a steady decline in moisture content of the wrack was not observable given the intermittent precipitation during each monthly experiment. Some intertidal macroinvertebrates (e.g., talitrid amphipods) can be positively influenced by temperature and moisture of the sands underneath the wrack (Olabarria et al., 2007). Although macroinvertebrate diversity, biomass, and abundance in the present study were positively correlated with internal wrack temperatures in the spring and early summer months, negative correlations were observed later in the summer. These opposing correlations may be an artefact of macroinvertebrate phenology and seasonal shifts from the beginning (April) to the end (August) of the experiments, and not directly related to wrack temperature. For example, in August, ambient air temperatures began to decrease over time, but macroinvertebrates still saw increases in diversity and abundance over time, thus depicting a negative correlation between the two variables.

4.3. Succession in aging beach-cast wrack

The present study documented taxonomic and feeding guild succession in aging wrack on high latitude beaches, supporting our hypothesis that aging wrack is occupied by macroinvertebrate communities with different successional stages. The order of colonization was representative of the facilitation model of ecological succession (Connell and Slatyer 1977). Under this model, ecological succession proceeds if the pioneer colonizers of the system modify the substrate to a point that is habitable for other organisms to settle and grow. Flies deposit their eggs onto moist piles of seaweed wrack, in which the fly larvae hatch and feed on the bacterial mats that are decomposing the wrack (Jędrzejczak 2002). This aged, decomposed wrack is generally preferred by herbivorous invertebrates that directly consume the seaweed (e.g., amphipods; Colombini and Chelazzi 2003; Pelletier et al., 2011). The richness and rapid reproduction of kelp flies and the developing larvae attract predators. Predatory Coleoptera and Araneae feed on arthropods, such as Acari and Diptera larvae that might also be foraging in the wrack (Colombini and Chelazzi 2003). The unexpected early appearance of predators in wrack during April and May was likely due to the presence of annelid prey already present in the sediment. The succession experiments corroborated likely biological interactions among taxa. For example, parasitoid hymenopterans (Alysiinae) were found in aging wrack only after dipterans, their prey, colonized and fly larvae began permeating the wrack. Centipedes (Geophilomorpha) are of terrestrial origin, but some species are tolerant of seawater and possibly use seaweed wrack as foraging grounds and means of passive dispersal (Barber 2011). Geophilomorpha are predators themselves but may also seek refuge in wrack (Barber 2011). This is likely, given that they disappeared early in the successional stages, but reappeared after biomass and abundance of wrack colonizers reached its peak. Predatory coleopterans were more abundant in wrack following surges in colonization by amphipods, likely due to the increased availability of prey. The most abundant of the coleopterans, the hydrophilid, *C. fimbriatus*, appeared earlier along with other decomposers. The flow of energy from these various scavengers and predators might then enter higher trophic levels (Dugan et al., 2003). In Alaska, birds such as crows and whimbrels have been found foraging in beach-cast wrack (Ulaski 2022).

5. Conclusions

Currently, there are few studies that have investigated the colonization of wrack in high latitude, tidally-driven glacial estuaries (e.g., Urban-Malinga and Burska 2009 for meiofanual communities). To our knowledge, this study is the first direct investigation into nearshore drifting and beach-cast seaweed wrack-associated macroinvertebrate communities in a sub-Arctic system and corroborates the general understanding that wrack is an important resource to ecological processes on beaches and in the near-subtidal at lower latitudes. Attached macroalgae growing on nearshore reefs are already in decline globally due to multiple stressors (Filbee-Dexter and Wernberg 2018), with direct harvesting as an ongoing and increasing threat to these systems (Krumhansl et al., 2016). Broader impact from human activity not only includes the direct loss of macroalgae, but also affects intertidal ecosystems. For example, climate change and associated heatwaves that have resulted in the decline of kelp forests globally (Krumhansl et al., 2016; Starko et al., 2022) may impact the valuable habitat provided by wrack both in the nearshore subtidal and intertidal beaches as the source of this subsidy is depleted. As source populations decline, so will the subsequent sink communities. Surveys demonstrated that beach-cast and drifting wrack are important habitats to many marine and terrestrial macroinvertebrates, with the most important environmental correlates to macroinvertebrate communities being the tidal elevation of the wrack line and the amount of wrack biomass that formed habitat. This reinforces the concern that declining kelp forests will have cross-ecosystem impacts. This research offers resource managers essential information on the importance of wrack to coastal systems and encourages attention be allocated toward wrack and shoreline habitats when crafting aquatic plant harvest regulations.

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Author contributions

Conceptualization, B.P Ulaski and B. Konar; Methodology, B.P. Ulaski and D.S. Sikes; Specimen Identification, B.P. Ulaski and D.S. Sikes; Formal Analysis, B.P. Ulaski; Investigation, B.P Ulaski and D.S. Sikes; Resources, B.P. Ulaski, B. Konar, and D.S. Sikes; Data Curation, B. P. Ulaski and D.S. Sikes; Writing – Original Draft Preparation, B.P. Ulaski; Writing – Review & Editing, B. Konar and D.S. Sikes; Visualization, B.P. Ulaski; Funding Acquisition, B.P. Ulaski and B. Konar.

Author statement

All material provided originate from the authors, and English is the primary language of all authors. The submission and publication of this manuscript has been approved by all authors: I (Brian P. Ulaski) was responsible for conceptualization, methodology, specimen identification, formal analysis, investigation, resources, data curation, writing of original drafts, visualization, and funding acquisition; Derek S. Sikes was responsible for methodology, specimen identification, investigation, resources, data curation, and review and editing of manuscript drafts; and Brenda Konar was responsible for conceptualization, resources, review and editing of manuscript drafts, and funding acquisition.

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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Appendix A. Supplementary data

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