Flotsam and jetsam: a global review of the role of inputs of marine organic matter in sandy beach ecosystems

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ABSTRACT

Sandy beaches are iconic interfaces that functionally link the ocean with the land by the flow of marine organic matter. These cross-ecosystem fluxes often comprise uprooted seagrass and dislodged macroalgae that can form substantial accumulations of detritus, termed 'wrack', on sandy beaches. In addition, the tissue of the carcasses of marine animals that regularly wash up on beaches form a rich food source ('carrion') for a diversity of scavenging animals. Here, we provide a global review of how wrack and carrion provide spatial subsidies that shape the structure and functioning of sandy beach ecosystems (sandy beaches and adjacent surf zones), which typically have little in situ primary production. We also examime the spatial scaling of the influence of these processes across the broader seascape and landscape, and identify key gaps in our knowledge to guide future research directions and priorities. Globally, large quantities of detrital kelp and seagrass can flow into sandy beach ecosystems, where microbial decomposers and animals remineralise and consume the imported organic matter. The supply and retention of wrack are influenced by the oceanographic processes that transport it, the geomorphology and landscape context of the recipient beaches, and the condition, life history and morphological characteristics of the taxa that are the ultimate source of wrack. When retained in beach ecosystems, wrack often creates hotspots of microbial metabolism, secondary productivity, biodiversity, and nutrient remineralization. Nutrients are produced during wrack break-down, and these can return to coastal waters in surface flows (swash) and the aquifier discharging into the subtidal surf. Beach-cast kelp often plays a key trophic role, being an abundant and preferred food source for mobile, semi-aquatic invertebrates that channel imported algal matter to predatory invertebrates, fish, and birds. The role of beach-cast marine carrion is likely to be underestimated, as it can be consumed rapidly by highly mobile scavengers (e.g. foxes, coyotes, raptors, vultures). These consumers become important vectors in transferring marine productivity inland, thereby linking marine and terrestrial ecosystems. Whilst deposits of organic matter on sandy beach ecosystems underpin a range of ecosystem functions and services, these can be at variance with aesthetic perceptions resulting in widespread activities, such 'beach cleaning and grooming'. This practice diminishes the energetic base of food webs, intertidal fauna, and biodiversity. Global declines in seagrass beds and kelp forests (linked to global warming) are predicted to cause substantial reductions in the amounts of marine organic matter reaching many beach ecosystems, likely causing flow-on effects on food webs and biodiversity. Similarly, future sea-level rise and stormier seas are likely to profoundly alter the physical attributes of beaches, which in turn can change the rates at which beaches retain and process the influxes of wrack and animal carcasses. Conservation of the multi-faceted ecosystem services that sandy beaches provide will increasingly need to encompass a greater societal appreciation and the safeguarding of ecological functions reliant on beach-cast organic matter on innumerable ocean shores worldwide.

Keywords: Landscape ecology, Seascape, Spatial subsidy, Ecosystem functioning, Coastal ecosystems, Kelp forests, Seagrass beds, Detritus, Wrack, Carrion

CONTENTS

I. INTRODUCTION

Shorelines are formed by a diversity of coastal landforms, including sandy beaches, surf zones, various dune landscapes, subtidal and intertidal rocky reefs, and sea cliffs. Shorelines are also highly dynamic due to being the interfaces between the ocean and the land (Pilkey *et al.*, 2011). The world's coastlines have been widely transformed for human uses, providing valuable ecosystem services to society (Small & Nicholls, 2003; Bowen & Davis, 2006). Iconic sandy beaches cover 31% of the world's ice-free shoreline (Luijendijk *et al.*, 2018), and represent highly valued economic, ecological, recreational and cultural assets for societies around the world (Barbier *et al.*, 2011). Yet, beaches are also one of the most vulnerable coastal landforms due to the recurring action of waves, tides and wind on mobile sediments, are among the most heavily altered coastal features (Schlacher *et al.,* 2014) by coastal development, rising sea level, and increasingly frequent storms attributed to climate change (Dugan *et al*. 2010; Vousdoukas *et al*., 2020).

Beaches form an ecotone between the ocean and land, which is influenced by land and ocean inputs and processes. Beaches and adjacent surf zones along open coasts are often considered to have little *in situ* primary production, but their fauna can nevertheless be abundant and diverse (Brown & McLachlan, 1990). This paradox can be attributed, at least partly, to the flow of organic matter from productive to less productive ecosystems, i.e. 'spatial subsidies' (Polis *et al.*, 1997). Physically, sandy beaches are highly permeable systems due to the limited barriers and strong transport mechanisms through tides, waves and currents that allow vectors such as detached macrophytes (macroalgae and seagrass) and carrion (dead animals) to accumulate on land (Schlacher *et al*., 2013a; Hyndes *et al.*, 2014).

Inputs of organic matter in the form of detached macrophytes (wrack) and carrion (dead animals) from near- and off-shore ecosystems to surf zones and beaches (Figures 1A & 2) provide critical ecosystem functions (physical, chemical and biological processes within ecosystems) on many sandy beaches. These functions include: (1) providing a spatial subsidy to support high secondary production and biodiversity that underpin rich coastal food webs (e.g. Crawley *et al.*, 2009); (2) recycling nutrients (e.g. Dugan *et al*., 2011); (3) enhancing key habitats, such as fish nursery grounds and bird nesting sites (e.g. Crawley *et al.*, 2006; Schlacher *et al*., 2013a); and (4) trapping wind-blown sand facilitating beach accretion and dune formation (e.g. Dugan *et al*., 2005).

The organisms and functions linked to marine matter cast upon beaches were reviewed by Colombini and Chelazzi (2003). However, since then, significantly more research on these functions has been undertaken in more regions across the globe. Importantly, the effects of global warming on coastal systems that supply organic material to beaches, and on beaches themselves, are better understood (Vitousek *et al.,* 2017; Smale *et al.*, 2019). Indeed, marine heatwave events and subsequent poleward shifts in the distribution of tropical grazers have led to ecosystem shifts from kelp forests to barrens in parts of the world (Smale *et al.*, 2019), which has immense ramifications for ecosystems relying on kelp as subsidies. Changes to beach structure and habitat availability through erosion, sea-level rise, storms and coastal development (Lee *et al.*, 2018; Dugan *et al.,* 2008) strongly affect the ability of drift material to flow onto and be retained in these dynamic ecosystems. In addition, management activities, such as grooming, that actively remove wrack from beaches used for tourism, impact wrack-associated biota and processes (e.g. Schooler *et al*., 2019). Furthermore, introductions of invasive species through global warming or other human-induced mechanisms (e.g. Jiménez *et al.*, 2015) are likely to influence the supply and form of organic inputs to beach ecosystems.

Here, we review and synthesise the existing knowledge on the ecosystem functions of wrack and carrion in sandy-beach ecosystems. We also outline knowledge gaps and identify priorities for future research. We focus mainly on the dynamics and ecological pathways of marine matter becoming stranded on ocean shares, including the supply, retention, and processing of macrophytes and carrion, and how matter can be transferred inland and, conversely, back to sea. We reviewed the literature based on searches in Elsevier Scopus and Clarivate Web of Knowledge using the terms (“beach*” OR “shore” OR “surf zone”) AND (“wrack” OR “carrion” OR “allochthonous” OR “beach-cast”). Search results were supplemented with references cited in Colombini and Chelazzi (2003), and papers from the authors’ personal collections of papers on the topic. We first summarise the global distribution of the research effort and focus. Secondly, we provide an overview of the main forms and amount of wrack and carrion deposited on beaches and adjacent surf zones. We then examine several topics concerning the dynamics and influence of wrack and carrion subsidies to beaches, specifically: (1) factors influencing the availability, deposition and retention of these subsidies; (2) the role of subsidies in regulating faunal abundance and biodiversity; (3) the fate of wrack and carrion, particularly their roles in beach food-webs; (4) the spatial scaling of subsidy effects in sandy-beach ecosystems and across the broader seascape and landscape; and (5) the influence of anthropogenic changes and management interventions on wrack and carrion dynamics. Finally, we identify key knowledge gaps to guide future research.

II. THE CURRENT STATE OF KNOWLEDGE

(1) Thematic areas and the geography of the global research effort

We identified 305 papers that examined various aspects of wrack or carrion in sandy-beach ecosystems. Most (88%) focused on the beach, with fewer studies from the surf zone or waters adjacent to sandy beaches. Three thematic areas dominate the research effort (Table 1, Figure 3): (1) spatial or temporal patterns in the amount of wrack (“wrack dynamics”, 36%); (2) spatial or temporal patterns in the abundance of fauna (“fauna dynamics”, 32%); and (3) trophic ecology (30%). Themes with moderate research focus include population biology of fauna in wrack (16%), and chemical composition and processes or the nutrient dynamics of wrack (13%). Only 9% of studies have examined distribution patterns of carcasses or carrion on beaches (“carcass and carrion dynamics”). Similarly, only 9% of studies examined human use such as harvesting kelp for food products or biofuel and the human impact such as impacts of beach grooming on wrack-associated fauna. Few studies (8%) examined environmental processes and influences, including factors that affect the amount and composition of wrack on beach systems. Only 4% of the studies looked at decomposition or microbes in wrack, and a small number of studies examined topics such as invasion biology, human health, or genetics (Table 1).

Few studies (n=10) were published before the 1980s. The number of published studies almost doubled from 39 during the 1980s to 72 during the 2000s, and then doubled again to 157 articles during the 2010s, accounting for about 50% of the papers published so far on wrack or carrion in sandy-beach ecosystems. The majority of the research on wrack or carrion has been carried out in the United States (57 studies), Australia (46), Spain (32), Canada (21), United Kingdom (20) and New Zealand (18) (Figure 3). Other countries with moderate research effort (7-15) include Italy, South Africa, Chile, and Brazil. Notable areas with significant sandy-beach shorelines that have a paucity of studies on wrack and carrion inputs include most of the tropics, such as the Caribbean, central and north Africa, the Arabian Peninsula, south-east Asia, South America (except Chile and Brazil) and the polar regions (Figure 3).

(2) Global patterns in standing stock of wrack on beaches

Kelp and seagrass make up the bulk of wrack on sandy beaches (Figure 4). We found 53 papers that have quantified the amount, or composition, of wrack on sandy beaches or in adjacent surf zones. However, the metric used to report the amount of wrack is variable, including volume (L) or wet or dry weight (g or kg) of wrack within a linear metre or square metre of beach. These inconsistencies make comparisons challenging. To facilitate such comparisons, we reocommend that sufficient data should be presented (e.g.beach/surf zone width length, volume to biomass conversions) to allow standing stock (wet weight) per unit area to be calculated.

Because the most common unit has been kg wet weight (WW) per linear metre of beach, we use this measure to examine global patterns in standing stock. These estimates have been directly extracted from papers or by converting extracted dry weight estimates where conversion factors were available. Not surprisingly, the average biomass of wrack varies considerably across regions, from 0.1 to 325 kg WW m^{-1}, with the highest biomass in the Mediterranean Sea (Figure 4). High biomass of wrack (100-200 kg WW m^{-1}) has also been recorded along the beaches of south-western Australia, Argentina and western Canada.

The composition of wrack in sandy-beach ecosystems varies geographically, but often is dominated by macroalgae, particularly kelp species, and seagrasses (Figure 4). At a global scale, major factors that influence biomass and composition of wrack include the offshore benthic substrate type and the associated distribution, as well as rates of productivity and composition of coastal primary producers (seagrass, kelp, *etc*.) as potential sources of macrophytes. For instance, kelp forests span temperate to arctic regions, and kelp is, therefore, a major input of wrack along the coasts of with cooler waters, particularly the western USA, Chile, southern Africa, southern Australia and New Zealand (Figure 4). Dominant taxa include *Durvillea*, *Ecklonia*, *Lessonia*, *Macrocystis* or *Nereocystis*. In comparison, seagrasses span boreal to tropic regions, and form a major component of wrack along coastlines in the Mediterranean and Caribbean Seas, East Africa, and Australia (Figure 4), with *Posidonia*, *Zostera*, *Cymodocea*, *Halodule*, *Halophila* or *Thalassia* being the main genera. Indeed, seagrass is the only form of wrack on the beaches in the Mediterranean Sea where *Posidonia oceanica* can form major “banquettes” (wrack deposits). In the northern hemisphere (the Baltic Sea, Western Europe, Caribbean Sea and West coast of North America) and Argentina, other forms of macroalgae (red, green and non-kelp brown algae) also form major components of wrack (Figure 4).

Beside the inflow of macrophytes, carrion (dead invertebrates, fish, birds, and mammals as large as whales) can be numerous on beaches, where animals that die at sea wash ashore (Sikes & Slowik, 2010). However, few studies have focused on carrion or animal carcasses compared to beach-cast macrophytes (Table 1, Figure 3), possibly reflecting: (1) a lower proportion of carrion compared to wrack; (2) more episodic deposition and patchy distribution; (3) a more rapid consumption and removal by scavengers; or (4) a reluctance by researchers to work on decomposing carcasses.

(3) Factors influencing standing stocks of wrack

Standing stock of wrack in sandy-beach systems is highly dynamic, both in space and time. Wrack biomass can range over one to four orders of magnitude across locations within a region (Tarr & Tarr, 1987; Dugan *et al.*, 2003, 2011; Barreiro *et al.*, 2011; Liebowitz *et al.*, 2016; Holden *et al.*, 2018; Reimer *et al.*, 2018; Schooler *et al.*, 2019). Similarly, standing stock may show temporal variation from no visible accumulations to 10s or 1000s of grams dry weight per square metre, within hours to days (Ruiz-Delgado *et al.*, 2016; Vieira *et al.*, 2016), and across years (Barreiro *et al.*, 2011; Revell *et al.*, 2011; Jiménez *et al.*, 2015; Liebowitz *et al.*, 2016; Holden *et al.*, 2018). Wrack dynamics are influenced by the input, accumulation, and export of material, and are typically subject to three principal drivers: (1) the types and strength of physical forces that transport material; (2) the geomorphology of beaches; (3) the broader landscape context of beaches; and the characteristics or traits of the donor system (Table 2).

A variety of physical forces (e.g. tides, waves, currents, wind, etc.) transport material onshore. Thus, variation in physical forces results in variation in the deposition and resuspension of wrack on sandy beaches, operating at time scales from hours to weeks and over distances of 100s m to 100s km (Table 2, Figure 5). Rising tides tend to remove wrack from beaches while falling tides are more conducive to intertidal deposition of buoyant material (Figure 1A, Zobell, 1971, Orr *et al.*, 2005). Spring high tides also remove wrack (Zobell, 1971) or shift wrack deposits in an up-shore direction towards the base of dunes or bluffs backing the beach. Strong seasonal patterns of kelp deposition are often related to changes in wave climate (Zobell, 1971, Revell *et al.,* 2011)**.** For example, storms generated at monthly to annual time scales (Figure 5) uproot and transport large amounts of macrophytes to become, as drift material, deposited on beaches (Zobell, 1971; Revell *et al*., 2011; Liebowitz *et al.*, 2016). However, the effects of storms on the supply can be modified by changes in the life-history traits of potential wrack material in donor systems. For instance, early-season storms can dislodge and transport large amounts of macrophytes, resulting in less material being available when storms occur later in the growing season (e.g. Zobell, 1971). However, wrack supply is further complicated by differences in the overall life histories among primary producers in the donor systems. Some kelp species are annuals (e.g. *Nereocystis*), while others are perennials (e.g. *Macrocystis*), and some senesce as part of their life cycles (e.g. *Sargassum)*. Supply is also influenced by ocean-scale to global atmospheric and oceanic events, such as ENSO (Seymour, 2003) or heatwave events and broader ocean warming (Wernberg *et al.,* 2019), occurring over time scales of years to 1000s years and spatial scales of 10s to 10,000 km (Figure 5).

The geomorphology (e.g. slope, width) and aspect (orientation) of beaches influence standing stocks of wrack (Table 2), primarily by altering the capacity to retain drift material (Revell *et al.*, 2011; Liebowitz *et al.*, 2016). For example, Barreiro *et al.* (2011) showed that small, wave-sheltered beaches retain higher amounts of wrack than more exposed beaches in Spain, while deposition rates of buoyant material can be substantially different between windward and leeward shores (Lastra *et al.*, 2014). Wrack retention can also be influenced by the elevation, and the width and slope of the drier, upper part of beaches (Zobell, 1971; Revell *et al.*, 2011; Liebowitz *et al.*, 2016), while cobble beaches appear to retain more wrack than gravel or sandy beaches (Orr *et al.*, 2005). In addition, coastal armouring structures (seawalls, revetments) that reduce beach width and eliminate upper beach zones have been shown to have profound effects on the retention and standing stock of wrack (see Section III-1).

The proximity of beaches to donor ecosystems, and the form and condition of those systems, can strongly influence the supply of wrack to sandy shores. For example, in northern California, the deposition of macrophytes varies depending on the source of wrack to beaches: subtidal reefs, rocky intertidal shores and estuaries (Liebowitz *et al*., 2016). Moreover, beaches within 0.5 to 1 km of donor ecosystems were most strongly influenced by wrack from those sources, but the role of more distant (7 km) kelp beds was detectable during storm events (Liebowitz *et al*., 2016). Similarly, Reimer *et al.* (2018) showed that proximity of sources, ocean upwelling, estuarine outwelling, beach geomorphology and wave climate contributed to patterns of wrack on beaches in the US Pacific. Finally, wrack supply to beaches is influenced by the changing state of the donor systems. For example, excessive grazing by urchins can shift kelp forests to urchin barrens (Ling *et al.*, 2009), reducing the availability of wrack material over time scales of years to 10s of years and spatial scales <10s km (Figure 5).

(4) Links between wrack and fauna in beach ecosystems

(a) Invertebrates

Sandy-beach ecosystems have traditionally been viewed as 'harsh' environments, characterised by low diversity and abundance of intertidal invertebrates (Brown & McLachlan, 1990). This historical view does, however, largely ignore the pivotal role of wrack and carrion for the sandy beach fauna as well as associated biodiversity and productivity. The effect of wrack on overall intertidal biodiversity can be substantial, with wrack-associated invertebrates making up, on average, >45% of the species present on beaches that receive inputs of giant kelp in California (Dugan *et al*., 2003). In fact, intertidal species richness on Californian beaches is strongly and significantly correlated with kelp wrack abundance but not with beach morphodynamics (e.g. Dugan *et al.*, 2003; Schooler *et al*., 2017). Wrack supports invertebrate biodiversity (Figure 1A) by providing a food source for populations of specialized intertidal invertebrates and a refuge from environmentally stressful conditions, such as desiccation and predation (Dugan *et al.*, 2003; Crawley & Hyndes, 2007; Colombini *et al.*, 2009). However, in some cases, extensive deposits of wrack can have negative impacts on some invertebrates through physical disturbance or anoxia (e.g. meiofauna, McGwynne *et a*l., 1988; wedge clam, Soares *et al.*, 1997), but few studies have examined these disturbance processes.

Wrack contains specialized mobile intertidal invertebrates, highlighted by the greater species richness and density of invertebrates on beaches with wrack compared with those with little or no wrack both in south-western Australia (Ince *et al*., 2007) and the west coast of the USA (Dugan *et al.,* 2003). Similarly, the removal of wrack on beaches in USA, Brazil and Spain significantly reduced the diversity and density of these specialized arthropods (Dugan *et al.*, 2003; Schooler *et al.*, 2017; 2019; Vieira *et al.*, 2016). By contrast, the experimental addition of wrack to upper parts of beaches resulted in higher arthropod abundances, particularly amphipods, but also increased abundances of several beetle species in southern Australia (Schlacher *et al.*, 2017). Our analyses showed that beach-cast macrophytes positively influence invertebrate species richness and abundance (n = 15, Figure 6). The diverse suite of invertebrates that use wrack is composed of three main trophic guilds: (1) 'detritivores' that feed directly on the macrophytes; (2) bacterivores that feed mainly on bacteria attached to macrophytes; and (3) 'predators' and 'scavengers' feeding on live prey or animal carcasses of the detritivores and bacterivores.

Detritivores, represented almost exclusively by arthopods, form the most common and diverse trophic guild of invertebrates associated with beach-cast wrack. Amphipods dominate this guild (Figure 6), but other groups such as isopods and several beetle species (Tenebrionidae, Histeriidae and Curculionidae) are also common detritivores on stranded wrack in many areas (Griffiths & Stenton-Dozey, 1981; Dugan *et al*., 2003). Amphipods are almost ubiquitous in wrack deposits in temperate latitudes and are typically the most abundant taxon in fresh wrack deposits around the globe (Figure 7). Amphipods in beach-cast wrack mostly belong to the family Talitridae, including the genera *Talitrus*, *Megalorchestia,* and *Orchestoidea*. Importantly, although highly mobile and building a new burrow every day, amphipods and several other beach crustaceans brood their young, possess no planktonic life stages, and have limited dispersal as adults. This combination of traits makes these populations dependent on local reproduction and survival (Dugan *et al*., 2013; Hubbard *et al.*, 2014). Overall, wrack biomass strongly influences the density and biomass of amphipods, revealing a unimodal response where peak densities of amphipods occur at moderate levels of wrack biomass, dropping at very high levels of wrack biomass (Figure 6). At very high levels of wrack standing stock, The reduced abundances of amphipods very high levels of wrack standing stock likely reflects compaction, anoxia, and other unfavourable environmental conditions created by large amounts of decomposing organic matter (e.g. McGwynne *et al*., 1988). Combining their high consumer densities, which can exceed 10,000 to 100,000 individuals per m beach (e.g. Lastra *et al.*, 2008, Lowman *et al*., 2019), and their high feeding rates on wrack (see below), they play a crucial role in linking the wrack subsidies from donor ecosystems to higher trophic levels in sandy-beach ecosystems (see Section II-6).

Dipteran flies form one of the most abundant bacterivore groups in wrack deposits, and are almost ubiquitous in wrack across the globe (Figure 7). Even though diets show large variation between dipteran families, bacteria are likely the most common food source for Diptera in beach-cast wrack, as shown for *Coelopa frigida* (Cullen *et al.*, 1987). Seaweed or kelp flies, belonging to several families within Sciomyzoidae, are the most common dipteran group in wrack (e.g. Egglishaw, 1960; Dobson, 1974), but dipterans from taxa such as *Fucellia* spp. (Anthomyiidae), Ephydridae, and Sphaeroceridae are also common in wrack and are typically important bacterivores (Cole, 1969; Griffiths & Stenton-Dozey, 1981; Oosterbroek, 2006). The larvae of these flies feed on kelp and bacteria (Cullen *et al.*, 1987), forming an important bacterivore compartment in the food web of beach-cast wrack. Similar to amphipods, the abundance of kelp and seaweed flies is also strongly correlated with wrack biomass on for beaches in Calfornia (Dugan *et al*., 2003). However, several much smaller fly species from several families are often overlooked in standard surveys (Cole, 1969) and would be worthy of future investigation.

The main groups of invertebrates feeding on detritivores and bacterivores in beach-cast wrack deposits are beetles (particularly Staphylinidae, Carabidae and Histeriidae) and spiders (Moore & Legner, 1976; Griffiths & Griffiths, 1983; Mellbrand *et al*., 2011). Wrack-associated beetles include endemic species, some of which are flightless species completing their entire lifecycle in the intertidal zones of beaches. For example, the staphylinid species *T. pictus* in North America have a specialized diet, completing their entire life-cycle feeding on amphipods (Orchestoidea) in the intertidal zones of beaches (Craig, 1970; Richards, 1982), while *Aleochara* spp. parasitize seaweed fly larvae (Yamazaki, 2012). In general, few invertebrates have been reported as predators on amphipods (except for *T. pictus*), but more species have been reported to prey on the abundant dipteran larvae (Yamazaki, 2012). However, many species have a fairly broad diet, such as most spiders (Verschut *et al*., 2019).

Since wrack deposition on beaches is generally highly dynamic over time, invertebrate species utilizing this resource need high mobility and rapid development to make the best use of an essentially ephemeral resource. Mobility is also critical to avoid being washed out to sea with the wrack during high tides, but some species are also reported to have very low mobility (Schooler et al. 2017). Not surprisingly, stranded macroalgal deposits are often colonized by mobile macroinvertebrates (particularly amphipods and dipterans) within a few hours of deposition, followed by predatory staphylinid beetles (Pelletier et al 2011, Yanenik, 1980). The subsequent rates of larval development can be enhanced by elevated temperatures within the masses of stranded wrack. Studies from Britain suggest that the life cycle of kelp flies (*Coelopa* sp.) is completed within a month, depending on temperature (Dobson, 1974). Fast larval development is supported by the elevated temperatures within the masses of stranded wrack, particularly in the larger, deeper wrack beds, where temperature may be >10°C above ambient levels (Crafford & Scholtz, 1987) and moisture is maintained (Kompfner, 1974), but not in smaller clumps where the temperature is more similar to air temperature (Dobson, 1974). Development that is coordinated to wrack deposition has also been suggested for some *Coelopa* spp, where larvae develop in spring high tide deposits of wrack and emerge from pupae by the next spring tide (Kompfner, 1974). Development times for different kelp fly species may be linked to tidal elevation with species at lower elevations developing faster (Kompfner, 1974). The initial burst in the colonisation of freshly-stranded wrack by selected macroinvertebrates is followed by a succession of other species (Yaninek, 1980), and a gradual increase in meiofauna, such as nematodes, oligochaetes and mites (Jedrzejczak, 2002a), followed by coleopteran species that arrive late in the succession of fauna in wrack beds (Griffiths & Stenton-Dozey, 1981; Colombini *et al.*, 2000).

In addition to quantity, the composition of the wrack input can influence invertebrate assemblages, but this effect seems to vary among consumer species (Mews *et al.*, 2006; Olabarria *et* *al.*, 2010). For example, in south-western Australia, densities of invertebrates were greater in experimental plots of seagrass compared to *Sargassum* on the beach (Mellbrand *et al.*, 2011), while the amphipod *Allorchestes compressa* showed a preference for macroalgae over seagrass in the surf zone (Crawley & Hyndes, 2007). Similarly, in southern California, amphipods (*Megalorchestia spp.*) preferred experimental wrack patches comprising kelp rather than seagrass, and different *Megalorchestia* species varied in their colonization rates of wrack patches, perhaps to avoid competition with congeners (Michaud *et al.,* 2019). The causes of these different affinities are likely to be complex when the macrophytes making up wrack vary in age, and therefore levels of decomposition, and also in terms of physical structure, nutrient content, palatability and bacterial community (see Section II-5a).

(b) Fishes

Wrack in the surf zones of ocean beaches provides important feeding, sheltering, and nursery habitats for a diversity of fishes (Figure 1A; Crawley *et al.*, 2006; McLachlan & Defeo, 2017; Ortodossi *et al.*, 2019). Drifting macrophytes are widely reported to influence the abundance, diversity, and species composition of surf fishes (e.g. Robertson & Lenanton, 1984; van der Merwe & McLachlan, 1987; Marin Jarrin & Shanks, 2011; Andrades *et al.*, 2014), but the ecological function of wrack as fish habitat remains poorly understood, largely because few studies (n = 20) have examined how macrophyte accumulations affect fish populations, assemblages, or food-webs (Olds *et al.*, 2018). Studies that examine the links between wrack and surf fishes come mainly from Australia (n = 12), limiting the broader generality and highlighting the need to gain a more global understanding of the role of drifting macrophytes for fish in surf zones. Nevertheless, the biomass of drifting macrophytes in surf zones can shape the composition of fish assemblages, modify patterns in fish diversity, abundance, and biomass, and alter the structure of coastal food-webs (Crawley *et al.*, 2006; Clark *et al.*, 1996a; Baring *et al.*, 2014; Vargas-Fonseca *et al.*, 2016). Fish abundance (n = 15 studies) and biomass (n = 2 studies) are mostly positively correlated with standing stock of wrack, whereas fish diversity is greatest at moderate levels of wrack biomass (n = 9 studies) (Figure 8).

Most research on the role of surf-zone wrack has focused on fish assemblages, whereas data on its significance for individual taxa are sparse (Clark *et al.*, 1996b; Lacerda *et al.*, 2014; Baring *et al.*, 2016). Greater biomass of drift macrophytes has been reported to have positive effects on the abundance and diet of several fish species (Robertson & Lenanton, 1984; Andrades *et al.*, 2014; Baring *et al.*, 2019). However, some species show either a neutral (Robertson & Lenanton, 1984) or negative (Crawley *et al.*, 2006) response to increasing wrack biomass in surf zones, presumably due to high densities of wrack impeding the movement and foraging of fish with particular morphological and feeding traits. Wrack in surf zones is likely to have positive effects on fish by providing enhanced feeding opportunities (n = 9 studies) (Figure 8). Numerous fish species have been reported to prey on epifaunal amphipods that accompany drifting macrophytes (Crawley *et al.*, 2006; Baring *et al.*, 2018). Variation in the type of drifting macrophytes can also affect fish abundance, which is likely to primarily reflect the different affinities of their prey to different macrophytes as habitat and food. For example, the amphipod *A. compressa* displays a strong preference for brown algae as food and habitat (Crawley & Hyndes, 2007) and forms the main diet of juvenile fish that have a strong affinity to drifting wrack (Crawley *et al.*, 2006). The types of drifting macrophyte in surf zones are therefore likely to influence the bottom-up control of food webs in this ecosystem.

(c) *Birds, Mammals and Reptiles*

Due to their high mobility, birds, mammals, and reptiles can use a range of resources across the landscape, but many have been linked to wrack or carrion on sandy beaches either directy or indirectly as a food resources. Birds are often the most abundant vertebrate on sandy beaches, often responding to prey resources. Birds foraging on beaches include shorebirds or waders, gulls, and wide variety of terrestrial birds (vultures to flycatchers) (Dugan *et al.*, 2003). Waders and passerines feed on wrack-associated prey (Lopez-Uriarte *et al*., 1997; Dugan *et al*., 2003) as well as other invertebrates, while gulls, raptors ravens, crows and vultures feed on carrion (Table 5). Abundance and diversity of birds, particularly wintering waders or shorebirds that can reach high abundance (>100 km^{-1}), can be strongly and positively correlated with the abundance of stranded wrack and wrack-feeding invertebrates (Tarr & Tarr, 1987; Dugan *et al.*, 2003), reflecting the provision of wrack-associated invertebrates as prey (Griffiths *et al*., 1983; Dugan *et al*., 2003; Schlacher *et al*., 2017). Relationships between bird abundance and wrack can be stronger for the plovers, which are visual surface feeders and include IUCN listed species in many parts of the world (e.g. Western snowy plover on the California coast; Dugan *et al*., 2003).

For mammals, many terrestrial species occasionally forage on living macrophytes or invertebrates in the lower intertidal zone at low tide (Carlton & Hodder, 2003). Populations of the coyote (Rose & Polis, 1998) and foxes (Cypher *et al.,* 2014; Bingham et al., 2018; Schlacher et al., 2020) have been linked directly to either marine-derived carrion or wrack-associated invertebrates as food sources (Table 5). In comparison, deer species have been observed foraging directly on beach-cast macroalgae (Conradt, 2000; Hansen *et al.*, 2019). In terms of lizards, the side-blotched lizard (*Uta stansburiana*) consumes marine algae (Barrett *et al.*, 2005), while the brown tree lizard (*Anolis sagrei*) is strongly attracted to wrack (Spiller, 2010).

Far less is known about the use of wrack by birds, marine mammals and reptiles in the surf zone. We do know that many species (e.g. ducks; Neff *et al.*, 2011; otters and sea lions; Somers, 2000; Osterrieder *et al.*, 2017; sea turtles, penguins and sea lions; Tershy *et al.*, 1997; Witherington *et al.*, 2011; Colombelli-Négrel, 2019) occur regularly in the waters adjacent to beaches. Some birds, such as geese and swans (Percival & Evans, 1997; Choney *et al.*, 2014), are known to feed on subtidal or intertidal seagrass in meadows along the shoreline of sheltered coastal systems. However, there is a paucity of studies linking birds, mammals and reptiles to surf-zone wrack as a food source or habitat, with the exception of the cormorant *Phalacrocorax varius*, which has been observed to actively forage for fish in surf-zone wrack in Australia (Robertson & Lenanton, 1984). Clearly, there is a need to gain knowledge in this area to better understand the influence of wrack on higher-order consumers.

(5) Biological processing and fate of wrack

(a) Decomposition processes

Wrack on sandy beaches represents a rich source of organic matter, which is evidenced by the rich macroinvertebrate fauna. The principal mechanisms breaking down this organic matter pool on sandy beaches are microbial decomposition, physical processing and consumption by intertidal invertebrates (Figure 9A; Jedrzejczak, 2002b; Lomstein *et al*., 2006; Lastra *et al*., 2008; 2015; Rodil *et al.*, 2015b). Once macrophytes are stranded, bacterial concentrations increase drastically (Koop *et al.*, 1982a; Cullen *et al.*, 1987; Urban-Malinga & Burska, 2009). For example, bacterial biomass increased 12-fold on kelp (*Ecklonia maxima*) that was stranded for eight days (Koop *et al.,* 1982a). The microbial communities associated with wrack likely develop from the biofilm of the macrophytes transported into the beaches rather than from the microbial community in the surrounding water. Macroalgae and seagrasses are covered in diverse microbial communities that include bacteria, microalgae, fungi, and protists, and are highly specific and distinct from the seawater microbiome (Wahl *et al*., 2012; Tarquinio *et al*., 2019). For instance, Bacteriodetes and Proteobacteria are dominant phyla in the biofilm of macroalgae and seagrasses (Wahl *et al*., 2012; Tarquinio *et al*., 2019, Bacteriodetes: 25%-50%, Berdan, unpubl. data), while making up only a small portion of seawater microbiome (Sunagawa *et al*., 2015). However, bacterial assemblages vary somewhat between species of algae in wrack (Rodil *et al.*, 2015a), similar to biofilms across species on living macroalgae (e.g. Staufenberger *et al.*, 2008; Trias *et al.*, 2012). The analysis of these microbial communities is still in its infancy, and there is a clear gap that needs filling with regard to the microbial communities and their role in wrack and sandy-beach ecosystems.

As heterotrophic bacteria digest macrophytes, they convert organic carbon and nitrogen into simpler forms of dissolved organic and inorganic nutrients, which are released into the water column, or incorporated into bacterial biomass (Säwström *et al.*, 2016). While this role is better known for other marine ecosystems, Rodil *et al.* (2019) is one of a few studies demonstrating a strong positive relationship between bacterial diversity and dissolved inorganic nitrogen in wrack deposits. The assimilation of nutrients by bacteria would allow them to flow into higher trophic levels in wrack accumulations (Figure 9A.

(b) Consumption by detrivores

Invertebrate detritivores can rapidly process large quantities of wrack in sandy-beach ecosystems. For instance, talitrid amphipods can eat >50% of macroalgal wrack standing stock, thus playing a pivotal role in wrack turnover (Colombini *et al.*, 2000; Dugan *et al.*, 2003; Lastra *et al.*, 2008). However, feeding preferences caused by differences in palatability influence consumption rates in wrack accumulations (e.g. Michaud *et al*., 2019). Kelp and other species of brown algae are generally the preferred food source for talitrid amphipods whereas seagrass species (e.g. *Phyllospadix*) and green algae (e.g. *Ulva* spp.) are generally the least preferred food resource (Table 3, Figure 10). Differences in preference can vary among regions and among life stages of wrack detritivores. For example, Duarte *et al*. (2008, 2010) showed that adults of the amphipod *Orchestoidea tuberculata* preferred *D. antarctica* over the algae *M. pyrifera* and *L. nigrescens*, whereas the juveniles preferred *L. nigrescens* (Duarte *et al*., 2010). Interestingly, the stark contrast in consumption rates between *Durvillaea* and *Macrocystis* reported from Chile is not found for *Bellorchestia quoyana* in New Zealand, where both kelp species were consumed at similar rates (Suárez-Jiménez *et al.*, 2017a). These differences may reflect varying feeding preferences among amphipod species or differences in nutritional quality of food sources between sites, making it difficult to generalize about consumption and resultant turnover rates of beach wrack, at least within brown algae. However, the far lower consumption rates of seagrass (Crawley & Hyndes, 2007) indicate that this type of wrack has much lower dietary benefits despite its high biomass in wrack in sandy-beach systems in many regions (Figure 4).

The nutritional quality of wrack obviously plays a critical role in determining feeding choices in invertebrate detritivores on beaches (Lastra *et al.*, 2008; Duarte *et al.*, 2010, 2011, 2016), similar to mesograzers on living macrophytes in subtidal ecosystems (Duffy & Hay, 1991; Poore & Steinberg, 1999). Protein content of algae is considered a key trait in determining the nutritional quality of food sources (Cruz-Rivera & Hay, 2000), similar to the case for plant consumers in other systems (White 1993), and appears to selectively influence feeding by detritivores on sandy beaches (e.g. Duarte *et al.*, 2011, 2016; Benítez *et al.*, 2016). Physical structure (shape and toughness) and the presence of chemical defenses (secondary metabolites) have also been shown to influence food selection in these taxa (e.g. Pennings *et al.*, 2000; Cruz-Rivera & Hay, 2003). However, the age of the detritus (related to the level of decomposition) and algal structure seem more important than chemical defenses for food choice by detritivores in these systems (Pennings *et al*., 2000; Duarte *et al*., 2010, 2011, 2016; Lastra *et al.,* 2015). Furthermore, environmental factors such as moisture and solar radiation influence the nutritional quality and palatability of wrack (Lastra *et al.*, 2015; Rodil *et al.*, 2015b). Even small changes in ambient UV radiation may modify the structural and nutritional status of wrack (Rodil *et al.*, 2015b), while ocean acidification induces changes in algal palatability and protein concentration of macrophytes (Benitez *et al.*, 2016; Duarte *et al.*, 2016). As expected, growth rates and survival of detritivores are strongly linked to food preference and the nutritional quality of their preferred food (Table 3). For example, Lastra *et al*. (2008) showed that the preferred macroalgae species sustained the highest growth rates in *M. corniculate*, and this pattern was observed also for other amphipods (Duarte *et al*., 2010, 2011).

(c) Interactions between detritus, microbes and detritivores

The interactions between detritus, microbes and detritivores are likely to play critical roles in detrital food webs, and we know that microbes often improve the quality and appeal of detritus as a food source (Zimmer & Topp, 1997), or are consumed directly by detritivores (Thompson *et al*., 1999) in terrestrial systems. Yet, the role of invertebrates in the decomposition of detrital macrophytes in sandy-beach ecosystems is unclear. While some studies suggest that macroinvertebrates can enhance decomposition of wrack by fragmentation, others suggest that they have fairly small effects on decomposition rates (Jedrzejczak, 2002b; Catenazzi & Donnelly, 2007). In contrast, Urban-Malinga *et al.* (2008) and Urban-Malinga and Busrka (2009) suggest that meiofauna species, particularly bacterivorous nematodes, have much stronger effects on algal decomposition rates.

In beach systems, stranded macrophytes may have undergone decomposition for hours to days (e.g. Griffiths & Stenton-Dozey, 1981; Colombini *et al.*, 2000; Jaramillo *et al.*, 2006), which affects the chemical condition (e.g. nutritional quality) (Rothäusler *et al.*, 2005; Rothäusler & Thiel, 2006), and its palatability to consumers. As suggested above, the level of decomposition is important for detritivore food preferences, but this is variable across amphipod species (Lastra *et al.*, 2014). However, some detritivores (amphipods and nematodes) may feed directly on bacteria (Porri *et al*., 2011; Urban-Malinga & Burska, 2009). Similarly, many dipteran larvae feed primarily on the wrack-associated bacteria rather than the wrack itself (Cullen *et al.*, 1987), producing a pathway that can lead to the decomposition/consumption of >30% of stranded kelp (Crafford & Scholtz, 1987). Bacteria would provide a more nutritious food source than the macrophytes themselves, by having a lower C:N ratio (Fukuda *et al.*, 1998), and higher levels of lipids and poly-unsaturated fatty acids (de Carvalho & Caramujo, 2012). Again, more on the role of microbes in the fate of wrack in sandy beach ecosystems is needed.

Differences in wrack decomposition rates can reflect not only chemical qualities but also differences in morphological traits of the macrophytes forming the wrack (Duggins & Eckman, 1997; Bucholc *et al.*, 2014). For example, the kelps *M. pyrifera*, *Saccorhyza polyschides* and *Undaria pinnatifida* are morphologically simple algae with soft, long and strap-like blades that stack in layers on the sand (Lastra *et al*., 2008; Rodil *et al.*, 2019). These algae can decompose rapidly through the joint action of detritivores and microbes (Rodil *et al.*, 2019). By contrast, *Sargassum muticum* and *Cystoseira baccata* are morphologically more complex, having tough thalli bearing secondary and tertiary branches, and decompose much more slowly (e.g. Olebarria *et al*. 2010). In comparison, the structural molecules in seagrasses, which are vascular marine plants, are refractory and slow to break down (Trevathan-Tackett *et al.*, 2017). This reduceboth decomposition and consumption (see above) and allow large banquettes of seagrass to accumulate in some regions, such as the Mediterranean Sea (see Figures 2 & 4).

(d) Nutrient fluxes and chemical transformation

Sandy beaches have long been considered ‘biogeochemical hotspots’, ‘reactors’, or ‘digestors’, reflecting high levels of nutrient fluxes and transformations (e.g. Pearse *et al*. 1942). Wrack accumulations represent peak hotspots for biogeochemical processes as indicated by high metabolic rates that release high levels of CO_2 (Coupland *et al.*, 2007; Gómez *et al.*, 2018). Indeed, CO_2 production by wrack accumulations on beaches can surpass the most active soils on Earth (Gómez *et* *al*., 2018). Similarly, wrack on beaches can be three times more metabolically active than subtidal seagrass or macroalgal beds (e.g. Coupland *et al*., 2007; Lastra *et al*., 2018; Liu *et al*., 2019). In contrast, methane emissions from wrack appear to be negligible (Liu *et al*., 2019), despite wrack having a demonstrated potential for biogas production (Kaspersen *et al*., 2016; Misson *et al*., 2020).

During consumption and decomposition of wrack in sandy-beach, complex biomolecules are transformed to simpler organic forms and mineralised to inorganic nutrients (e.g. NH_4, NO_3 and PO_4) (Coupland *et al*., 2007; Dugan *et al*., 2011; Lowman *et al*., 2019). Since nitrogen (N) is often the limiting nutrient in coastal marine ecosystems (Howarth & Marino, 2006), much of the focus of nutrient processes in beach ecosystems has been on N cycling, including standing stocks and fluxes (Goodridge & Melack, 2014). Nitrogen produced during mineralisation of wrack can enter a number of pathways: (1) incorporated into the food web, primarily via uptake by surf-zone phytoplankton and possibly by benthic microalgae; (2) flushed back to the sea; (3) lost to the atmosphere via denitrification; (4) incorporated into dune vegetation; and (5) immobilised in recalcitrant pools after burial in the long-term sedimentary sink (Figure 9A) (McLachlan & McGwynne, 1986; McLachlan & Romer, 1990). Nitrogen fixation in bare sands, decaying wrack, or surf zones is probably a negligible component of the N cycle of these systems, while denitrification rates on exposed beaches are low and restricted to the few top cm of the sand (McLachlan & Romer, 1990). Denitrification only accounted for 2% of the N supplied by kelp or 5-10% of the overall N inputs to the beach (McLachlan & McGwynne, 1986). Both nitrification (oxidation of ammonia to nitrate to nitrite) and denitrification (reduction of nitrate to nitrogen gas) are processes mainly associated with the groundwater, likely reflecting N inputs from the land rather than from the wrack itself (e.g. Santoro *et al*., 2006).

While the role of sandy beaches in the processing of organic matter and nutrient cycling has been repeatedly demonstrated, the question of whether beaches function as sources or sinks of nutrients remains largely unanswered, and there are differences among nutrient species and locations (e.g. Cockcroft & McLachlan, 1993; Goodridge & Melack, 2014; Prasad *et al*., 2019). Supporting the “sink” hypothesis, buried beach-cast kelp (*Fucus*) has been shown to enhance the growth of pioneer dune vegetation in the Netherlands (van Egmond *et al*., 2019), while the seagrass *Posidonia oceanica* provides an important nutrient source for adjacent dune vegetation in the Mediterranean Sea (Cardona & García, 2008; Jiménez *et al*., 2017), where wrack is dominated by seagrass (Figure 4). However, supporting the “source” hypothesis, field studies show that kelp decaying on the beach can rapidly leach high concentrations of dissolved nutrients (DIN, DON, DOC, TDN and TDP, for definitions see Figure 9) for plant uptake and export (Koop & Lucas 1983; McGwynne *et al.* 1988; Dugan *et al*., 2011). The concept of wrack-covered beaches functioning as nutrient sources is supported by the correlation between wrack biomass and DIN concentration in surf zone water reported in California (Dugan *et al*., 2011) and by the increased productivity of local or invasive macroalgal species and phytoplankton blooms in waters adjacent to shorelines with increased wrack biomass load (Cockcroft & McLachlan, 1993). The source and sink role may vary over time and leaching is likely to be greater in late summer to autumn when TDN fluxes from the beach are greater (Dugan *et al*., 2011), or during beach erosion episodes that release stored N in intertidal porewater to the ocean.

Our capacity to reject either hypothesis is limited by the paucity of comprehensive studies examining nutrient dynamics in sandy-beach ecosystems characterised by wrack input, and their ability to return nutrients to adjacent coastal ecosystems. For example, outflow of DON may contribute to production in adjacent coastal systems as decomposing kelp is known to leach large amounts of DON (Hyndes *et al*., 2012). Exported DON is likely to be remineralised by highly abundant heterotrophic bacteria in the biofilm of living macrophytes (Egan *et al*., 2013; Tarquinio *et al*., 2019) in adjacent ecosystems (e.g. kelp forests or seagrass beds) and provide DIN to their hosts (e.g. Tarquinio *et al*., 2018). In addition, nutrient budgets need to consider all sources of nutrients, including groundwater. In some regions, the discharge of groundwater derived from further inland can contribute 50-99% of the total submarine groundwater discharge (Urish & McKenna, 2004; Li *et al.*, 2011) and supply nutrients to beach ecosystems (Santoro *et al.*, 2006; Loveless & Oldham, 2010).

(e) Scavenging

Carrion tissue forms a highly nutritious and widespread food resource that is exploited by a rich diversity of scavengers (Table 5; Wilson & Wolkovich, 2011). Like detrital macrophytes, carrion supply is often highly variable in time and space, and is likely to be a nutritional and energetically important resource in many beach food webs. There is generally no physical barrier to prevent animal carcasses from becoming stranded on beaches, or for scavengers to reach those carcasses, making animal carcasses an accessible and favourable food source for consumers on ocean-exposed sandy shores (Schlacher *et al.*, 2013a). This food source is consumed by scavengers, which can be categorised into two functional groups: (1) facultative scavengers, which feed on live prey as predators and on dead animals as scavengers (e.g. foxes, birds of prey), and (2) obligate scavengers that rely exclusively on carrion as their sole nutrition (e.g. vultures; Ruxton & Houston, 2004). It is, however, increasingly recognized that most 'predators' will readily scavenge and many marine carnivores will also consume dead animal matter (Britton & Morton, 1994).

A wide variety of scavenging species is found on sandy beaches worldwide, encompassing both invertebrates (e.g. whelks, isopods, polychaetes, beetles, ghost crabs, dipterans, etc.), and vertebrates (e.g. reptiles, raptors, and carnivorous mammals) (Table 5). Some of the best-studied invertebrate scavengers on sandy beaches are gastropods, particularly the genus *Bullia* in South Africa (Brown, 1961), which rapidly detect and consume a wide range of carrion (Brown & McLachlan, 1990). Crustaceans (e.g. isopods, amphipods, decapods) contain many taxa that consume carrion (Brown & McLachlan, 1990). For example, a species of *Tylos* shifts its diet ontogenetically, with juveniles preferring carrion, whereas adults prefer seaweed (Kensley, 1974; Brown & McLachlan, 1990). Hippid crabs (*Hippa* spp.) are important scavengers on tropical island beaches, catching and consuming Portuguese man of war as they wash on to the beach (e.g. Lastra *et al.*, 2016). Ghost crabs (*Ocypode* spp.) are the largest invertebrate on many sandy beaches, occupying a range of trophic levels formed by a diverse diet that regularly includes dead animal flesh (Lucrezi & Schlacher, 2014). In fact, when given a choice, ghost crabs strongly prefer carrion over algae and plants (Rae *et al.*, 2019). The strandline of beaches also harbour a rich fauna of insect carrion feeders, including a high diversity of Coleoptera (beetles) (Rozen *et al.*, 2008; Irmler, 2012). However, despite insects being considered as important scavengers of animal carcasses in other terrestrial systems (Quilter, 1987; Morritt, 2001), little is known about their role as scavengers on sandy beaches (Blandford *et al.*, 2019).

Reptiles, birds and mammals are functionally important scavengers in many ecosystems, and their role in sandy beach ecosystems is becoming more apparent. In Australia, lace monitors (*Varanus* spp.) are widespread consumers of birds, fish, mammals, amphibians, eggs, and insects, and carrion can at times dominate their diet (Guarino, 2001). Indeed, lace monitors regularly consume fish carcasses (Schlacher *et al.*, 2013b; Bingham *et al.*, 2018). Similarly, in the USA, cottonmouth snakes (*Agkistrodon piscivorus conanti*) traverse areas of vegetation at the beach's edge and feed on fish that have been discarded, or regurgitated, by colonial waterbirds (Lillywhite *et al.*, 2008). Also, birds such as raptors can dominate carrion consumption in landscapes not strongly altered by urbanization, followed by corvids and gulls (e.g. Huijbers *et al.*, 2016). Similarly, many mammals are attracted to, and feed on, stranded dead animals on sandy beaches, including hyenas, black-backed jackals, coyotes, dingos, foxes, feral pigs, and even lions (Table 5). Strandings of cetaceans and dead seals are prominent examples of carrion providing intermittent bounties for carnivores (Behrendorff *et al.*, 2018).

(6) Connectivity with adjacent ecosystems

The transfer of drift macrophytes and carrion from the sea to the beach can provide a significant energy subsidy to beach food webs. Such spatial subsidies (i.e. organic matter and nutrients crossing ecosystem boundaries) increase secondary productivity and biodiversity in sandy-beach ecosystems which ar echaracterised as having low *in situ* primary productivity. This cross-ecosystem exchange is facilitated by the high porosity of the beach/ocean ecotone, allowing the free flow of drift macrophytes and carrion into beach and surf-zone systems. In the preceding sections, we have highlighted that seagrasses and particularly brown algae (mainly kelp) provide the main vectors for this subsidy by supporting food webs as well as creating habitat for a diversity of microbes, invertebrates, fish, birds, reptiles and mammals in beach ecosystems (Figure 9). Biological and physical processes recycle this imported material through consumption, fragmentation and decomposition, releasing dissolved nutrients back into the water or transferring nutrients through the food web and ultimately exporting those nutrients beyond its borders into other coastal ecosystems on land or in the sea (Figure 9). However, the spatial extent and magnitude of this transfer of nutrients into other ecosystems is generally not well quantified for most settings.

Wrack deposits on the beach are often concentrated close to the waterline but regularly extend higher on the shore through the action of high tides, storm surges, and wind-driven transport. Further inland transport of wrack- or carrion-derived material depends on its direct or indirect consumption or transport by more mobile animals and their subsequent inland movement. For instance, Mellbrand *et al*. (2011) showed that seaweed flies feeding on wrack, and predators, such as spiders feeding on detritivores in wrack, may move marine carbon many metres inland. However, this movement was not detectable beyond the primary dune, most likely due to the dilution of marine-derived material as other land-based food sources become more available, or the limited movement of those invertebrates feeding directly or indirectly on marine-derived material, or a combination of both.

Larger and more mobile consumers are likely to provide a greater role as vectors for the inland transport of marine-derived material. Since invertebrates associated with beach-cast wrack provide an important food source for a variety of birds, such as plovers, swallows, and flycatchers (e.g. Dugan *et al.*, 2003; Schlacher *et al.*, 2017), it logically follows that this marine-derived material may enhance the breeding success and productivity of these birds. Such bottom-up control of populations is also likely for other mobile animals that assimilate nutrients from invertebrates associated with beach-cast wrack, such as lizards (Barrett *et al.*, 2005; Spiller *et al.*, 2010), rodents, foxes, and bears (Ricci *et al.*, 1998; Stapp & Polis, 2003; Fox *et al.*, 2014) as well as feral pigs (Dugan, pers. obs.). Also, deer can forage directly on wrack (Conradt, 2000), while domestic livestock, such as cattle and sheep, can be common on beaches in some regions (Dugan, pers. obs), and may also graze on wrack. However, this mechanism has not been tested, and the magnitude of the subsidy for these mobile consumers will depend on: (1) the proportion of their food derived from the wrack; (2) the inland extent of their movement; and (3) the extent to which they contribute to higher trophic levels or the release of nutrients in inland areas through their faeces or carcasses.

Feeding of carrion by scavengers on sandy beaches illustrates a broader functional role of the transfer of nutrients and organic matter across ecosystem boundaries, linking food webs at the landscape scale and creating meta-population dynamics in the consumers. The mobility of birds makes them pivotal vectors for transferring nutrients and energy across ecotones, including consumption and transfer of carrion-derived matter across surf-beach-dune landscapes (Figure 9C; Whelan, *et al.*, 2008). Flying enables birds to search over large areas and detect patchy resources (i.e. carcases) in ways generally not possible for other consumers. The spatial extent of other mobile scavengers, such as rodents and foxes, is also likely to be large. One of the most seminal contributions to understanding the pivotal role of carrion subsidies on sandy shores comes from Rose and Polis (1998), who showed that coyote (*Canis latrans*) populations were 2-14 times higher on the coast compared to upland areas. In their study system, food supply that included carcasses washed ashore, was greater on the coast (Rose & Polis, 1998).

Wrack stranded high on the shore may also influence both vegetation and the landscape structure of this dynamic zone. For example, seasonal pulses of wrack, primarily *Sargassum*, deposited by storms have been shown to enhance native shrubs and trees (Spiller *et al*., 2010). Such wrack deposits may provide nutrients, propagules and a favourable microhabitat for terrestrial plants, particularly the salt-tolerant pioneering species typical of coastal strand and foredune habitats (Dugan & Hubbard, 2010). The propagules of many dune plants can be transported and delivered with wrack and other drift material (e.g. Hesp, 2002). Similar to pioneering dune plant species, wrack deposits can act as ecosystem engineers that influence the geomorphology of shorelines by trapping wind-blown sand to form hummocks and embryo dunes, at least in the short term (Nordstrom *et al*., 2011). These features can then buffer beaches and dunes from erosion during storms.

The return of wrack-derived nutrients back into coastal waters is likely to occur through two main processes. Firstly, the breakdown and decomposition of wrack release large quantities of dissolved nutrients (e.g. Dugan *et al*., 2011) and fine particulates (Soares *et al*., 1997) that provide vectors for the return of nutrients back to the sea. However, the spatial extent of this return of nutrients is largely not quantified. It is likely that dissolved nutrients are rapidly diluted, but they may be utilized by intertidal and shallow subtidal primary producers, such as surfgrasses and kelps (Dugan *et al*., 2011). However, it does appear that organic matter derived from detrital kelp along the beach of South Africa supports populations of the subtidal filter-feeding bivalve *Donax serra* (Soares *et al.*, 1997). Furthermore, while some studies have concluded that fine particulate kelp supports filter and suspension feeders in other coastal systems (e.g. Stuart *et al.*, 1982; Duggins *et al.*, 1989), the evidence is equivocal (Miller & Page, 2012; Yorke *et al*., 2013). Thus, the supply rate of particulate kelp from beaches may be important for suspension feeders in coasts across the globe, a predictive hypothesis that requires testing. Secondly, surf-zone wrack can provide an important feeding and sheltering habitat for fish, particularly for juveniles. For example, some fish feed almost exclusively on wrack-associated amphipods in the surf zones of south-western Australia (Crawley *et al*., 2006). Through the ontogenetic movement of those juveniles towards their more offshore spawning grounds, they form vectors for the return of wrack-derived nutrients into other marine ecosystems across coastal seascapes. The spatial extent and magnitude of this mechanism remain, however, unknown. The extent to which the return of nutrients from beach and surf-zone wrack to adjacent coastal systems, regardless of the vector, occurs is likely to differ: (1) under different types, and periodicities of subsidies (e.g. kelp, seagrass, carrion) supplied to sandy beach ecosystems; (2) the residence time and dominant processes (e.g. decomposition, grazing, transport) acting on the wrack in those systems; (3) the type of vectors (e.g. fish, bird, reptile, mammal, invertebrate); (4) physical processes (e.g. tide and storm surges) that erode beaches and export nutrients and wrack; and (5) the seascape and landscape contexts.

III. HUMAN USE, IMPACTS AND MANAGEMENT

(1) Beach grooming and harvesting

Once stranded on beaches, wrack deposits can be impacted by humans, such as beach grooming and harvesting (Figure 1B). Beach grooming intentionally removes macrophyte wrack, litter and other debris from beaches, usually through raking and sieving the sand using specialized heavy equipment often on beaches in populated or urban areas (Figure 2G,H; Dugan *et al.*, 2003; Fanini *et al.*, 2005; Dugan & Hubbard, 2010). Grooming can be intensive and frequent (daily to weekly) and can have strong effects on the habitat quality, biodiversity, geomorphology, and functioning of beach ecosystems. In addition to the physical disturbance that can impact dune formation and plant colonisation (Dugan & Hubbard, 2010), beach grooming has been shown to reduce the species richness, abundance, and biomass of wrack-associated fauna, such as amphipods, isopods, beetles and flies (Dugan *et al.*, 2003; Gilburn, 2012; Schooler *et al.*, 2019). In southern California, impacts of widespread grooming have contributed to local and regional losses of populations of vulnerable wrack dependent taxa, such as isopod species occurring only on beaches (Hubbard *et al*., 2014). Although meiofaunal communities can recover quickly (24 h) from a single, short-term grooming event (Gheskiere *et al*., 2006), the consequences of repeated, regular beach cleaning may be significant for these intertidal communities. These direct impacts are likely to extend through the food web and affect mobile predators, such as shorebirds that are reliant on wrack-associated prey as food.

The practice of beach grooming or raking is widespread globally and is often a component of well-established management regimes for beaches used for tourism and recreation (Davenport & Davenport, 2006). For example, ~45% (>150 km) of sandy beaches are groomed at least seasonally in densely populated southern California (Dugan *et al*., 2003), while >106,000 m^3 of *Posidonia* wrack are estimated to be removed in one year from 44 beaches on the island of Sardinia (de Falco *et al*., 2008). Beach rating systems and 'ecolabels' often contain criteria that encourage the removal of wrack as part of their rating scores (Zielinski *et al.*, 2019). The Blue Flag Program is the largest of these ecolabels and includes over 4,000 beaches in 47 countries (Boevers, 2008). Klein and Dodds (2018) suggest that this program emphasizes tourism promotion over environmental protection and conservation of beach ecosystems. Indeed, many Blue Flag rated beaches are very likely to have management regimes that remove wrack and thereby cause reductions in ecological and environmental quality (Spain; Mir-Gual *et al.*, 2015) and in biodiversity (Scotland; Gilburn, 2012) compared with the beaches where wracks remains. Thus, the concept of 'cleaning' the beach ignores the ecological and conservation value of wrack to the beach ecosystems and broader seascapes/landscapes.

Macroalgal wrack is regularly harvested in some regions of the world, including Chile, North America, Ireland and Australia (Kirkman & Kendrick, 1997; Holden *et al.*, 2018). Native macroalgal species are harvested for a variety of uses including alginate and agar, cattle feed, soil fertilizers and conditioners, and feed for abalone hatcheries, while seagrasses are harvested for insulation and soil fertilizer (Kirkman & Kendrick, 1997). Methods and equipment used in harvesting macrophytes from beaches vary from artisanal hand picking (a few tonnes y^{-1}) to commercial harvesting using heavy equipment, such as bulldozers (100s to 1,000s of tonnes y^{-1}, Holden *et al*., 2018). Harvesting can remove large proportions of beach wrack. For example, harvests of drift bull kelp (*D. potatorum*) on Australia's King Island (average harvests of 2,500 tonnes y^{-1}, Holden *et al*. 2018) account for ~50% of the kelp deposited annually on beaches (Kirkman & Kendrick, 1997). Non-native species may also be harvested. For example, quotas of 900-1,500 tonnes y^{-1} for the invasive red alga (*Mazzaella japonica*) accounts for <16% of the available biomass along a shoreline section of Canada's Vancouver Island (Holden *et al*., 2018). Overall, the harvest methods and their associated impacts, and the relative magnitude of wrack harvest are not well documented (see Kirkman & Kendrick, 1997; Holden *et al*., 2018), suggesting this is a significant gap in the information needed to manage wrack harvest on sandy beaches. A report on impacts of wrack harvest in Ireland recommended using non-mechanical harvest methods, prohibiting removal of sediment or substrate and minimizing disturbance to surrounding environments for commercial wrack harvest (McLaughlin *et al*., 2006 as cited in Holden *et al*., 2018).

(2) Shoreline armouring and coastal development

Many shorelines, including those formed by sandy beaches, have been profoundly altered through the construction of coastal armouring structures and extensive shoreline development (Charlier *et al*., 2005) (Figure 1B). Coastal developments, like ports and marinas, that cover or remove sandy beaches profoundly impact beach ecosystem habitat and function on at least the scale of the development (see Dugan *et al*., 2012; Hubbard *et al*., 2014). Shoreline armouring, such as seawalls and revetments, is a common practice used around the world to protect coastal development and infrastructure from erosion and coastal hazards (Airoldi *et al*., 2005; Dugan *et al*., 2012), and have received the most attention with regards to their environmental impacts (Dugan *et al*., 2012, 2017). This form of armouring has been shown to reduce the overall width of sandy beaches, with the greatest impacts in the upper part of the intertidal zone (Dugan *et al.*, 2008; Jaramillo *et al*., 2021). The resulting losses in upper beach zone, suitable for the retention of wrack, disrupt the trophic subsidy provided by donor ecosystems and significantly reduce the diversity and abundance of wrack associated invertebrates (e.g. Dugan & Hubbard, 2006; Dugan *et al*., 2008; Jaramillo *et al.,* 2012, 2021; Dethier *et al*., 2016). Importantly, these impacts extend up the food web, where armouring can significantly reduce the use of beaches by shorebirds and seabirds (Dugan & Hubbard, 2006; Dugan *et al.*, 2008). Similar impacts may also extend to surf zone fish, but more research is needed to evaluate this. Other forms of armouring, such as groynes and detached breakwaters, may increase or decrease the standing stock of wrack on beaches and in surf zones, depending on the scale, orientation and design of those structures (e.g. Airoldi *et al*., 2005, Dugan *et al*., 2012; Martin *et al.,* 2005).

Although small-scale beach restoration efforts suggest that biodiversity and ecosystem functions of beaches can be restored through the removal of armouring structures (Lee *et al.*, 2018), increased armouring of shorelines is the expected global trend as coastal hazards increase with climate change. As sea level rises, the effects of coastal squeeze exerted by existing armouring structures on beaches are also expected to increase as structures interact more frequently with waves and tides (Dugan *et al.,* 2017). Robust evaluations of the ecosystem services provided by intact dune-beach-surf zone systems, and the protocols for quantifying the often dynamic indicators of those services, are generally not available for proposed armouring projects (King *et al*., 2018). As a result, other than recreation and storm buffering, values of the ecological functions and services of beaches are rarely applied to assess the impacts of these projects. New approaches to evaluating beaches as ecosystems, based on restoration or replacement costs, are urgently needed for mitigating the impacts of shoreline armouring, especially as pressures from sea level rise and coastal squeeze intensify (e.g. King *et al*., 2018).

(3) Invasive Species

Numerous species of non-native algae have been introduced to coastal waters, either via human activities (e.g. shipping) or as a result of species range shifts due to ocean warming (Hurd *et al.*, 2014). For example, the green alga *Codium fragile* and the kelp *Undaria pinnatifida*, both originally from the north Pacific Ocean, now have near-global distributions (Hurd *et al*., 2014). The ecological impacts of invasive species on subtidal habitats are equivocal (Suárez-Jiménez *et al.*, 2017b and references within), but we know far less about the impacts of these invasive species as beach-cast wrack (see Quijon *et al*., 2017) even though they can be commonly cast ashore (e.g. Pirize *et al.*, 2003; Rodil *et al.*, 2008). Certainly, the composition, quality and perhaps the biomass, of the beach-cast material could be affected by the displacement of native reef algae with invasive species, thereby altering the inputs and food value. However, this effect will depend on the life cycle patterns and buoyancy of the invasive species, which alter the ability of the invasive algae to be transported to the beach and the timing of the detrital input. For example, *U. pinnatifida* is now a major component of subtidal reefs in New Zealand, but contributes little to beach wrack, which likely reflects the lack of buoyant structures (e.g. pneumatocysts or buoyant blades) present in the native *M. pyrifera* and *D. antarctica* that are common in beach wrack in the region (Suarez-Jimenez *et al*., 2017a). However, the invasive brown alga *Sargassum horneri* is an annual species that can outcompete native kelp species and can seasonally dominate the wrack deposited on some

California beaches (Marks *et al.*, 2020). Beach-cast of its congeneric *S. muticum* appears to either alter or have no effect on the invertebrate composition and densities compared to native macroalgal species (Rodil *et al.*, 2008; Cacabelos *et al.*, 2010). While *S. muticum* appears to contribute to the food web on some beaches (Olabarria *et al.*, 2009), the magnitude of an invasive species' influence on beach food webs will be dependent on the ability of native consumers to utilise the new resource and the nutritional quality and palatability of the food source. For example, while the invasive *U. pinnatifida* has similar nutrient characteristics to native species in New Zealand, the consumption of this invasive species by the amphipod *B. quoyana* appears to be hindered by its physical properties such as toughness (Suarez-Jimenez *et al*., 2017b). With few studies focusing on the impacts of invasive species on food webs and ecosystem structure of beach systems, it is presently not possible to make generalisations of this potential impact.

(4) Climate change impacts to recipient and donor ecosystems

Arguably, the greatest threat to sandy-beach ecosystems is the effect of climate change, especially sea-level rise, more intense and frequent storms, and ocean warming (Figure 1C). Sea level rise and storm frequency are projected to intensify beach loss, through increased erosion rates, inundation, and coastal squeeze (Vitousek *et al*., 2017). These processes will significantly impact beach ecosystems and their functioning, including the loss of habitat available for wrack deposition and retention, and the survival of associated endemic biota (see Schlacher *et al.,* 2008; Myers *et al*., 2019). Impacts of sea level rise to beaches are projected to manifest earliest in the upper zones of beaches where wrack deposits support biodiversity and coastal food webs (Dugan *et al*., 2012, 2013). These vulnerable zones have already been widely impacted by coastal armouring and development, sediment starvation, and beach management practices (Dugan *et al*., 2008; 2013; Myers *et al.*, 2019). A case study of several Californian beaches projected that a 0.5m increase in sea level would result in a 75% loss of the upper beach zone where wrack accumulates and is processed, eliminating ~50% of intertidal biodiversity and numerous vital ecosystem functions (Myers *et al*., 2019). Furthermore, recent El Nino Southern Oscillation events that cause a combination of warming, storms and sea-level rise (i.e. proxy for climate change), combined with a multi-year drought, have caused historically high levels of beach erosion and loss, with beaches retreating beyond previous extremes along the southern portion of the northeastern Pacific coast (Barnard *et al*., 2017).

Ocean warming, and related marine heatwave events, will also strongly affect key donor ecosystems that supply organic material in the form of drift macrophytes to beaches and surf zones (Figure 1C). Important donor ecosystems, such as kelp forests, are already being affected by ocean warming worldwide (Wernberg *et al*., 2109). For example, heatwave events have led to local extinctions of the kelp *E. radiata* (Wernberg *et al.*, 2016) and severe reductions in the biomass of seagrass meadows (Arias-Ortiz *et al.*, 2018) along the west coast of Australia. Furthermore, increasing sea temperatures have either led to, or are predicted to, extend the ranges of tropical macrophytes and consumers into higher latitudes (temperate regions) (Vergés *et al.*, 2014; Hyndes *et al.*, 2016). Ultimately, these climate-driven effects will limit the supply, or alter the form, of macrophytes and alter the ecosystem functioning of sandy-beach ecosystems in those regions. Additionally, ocean warming is likely to alter the rates of wrack processing by detritivores on beaches, since it is projected to reduce the body size and fecundity of intertidal biota, including talitrid amphipods that are key consumers of wrack (Jaramillo *et al*., 2017). Furthermore, Ocean Acidification will affect the donor ecosystems. This global stressor is being shown to change the nutritional quality of algae which will affect the trophic behaviour of detritivores in sandy-beach ecosystems (Benitez et al., 2016; Duarte et al., 2016).

To understand these processes, we argue for the need for studies at larger spatial and temporal scales, involving the dynamics of wrack inputs and connectivity of beaches to source ecosystems, presumably using data from remote sensing and other synoptic resources. For example, wrack on tropical beaches have essentially been ignored, yet they are experiencing increased deposition of *Sargassum* (Maurer *et al.*, 2015; Schell *et al.*, 2015), and other macroalgal inputs as coral reefs transition to turf macroalgae (Sura *et al.*, 2019). Quantifying the biomass and composition of wrack will play a critical role in determining the shifts in supply over these time scales, and particularly in relation to the impact of the shifting state of donor systems due to climate change and invasive species.

IV. CONCLUSIONS AND FUTURE DIRECTIONS

Sandy beaches are iconic features of coastlines, globally prized for providing valuable ecosystem services such as coastal protection, support of wildlife, fisheries, unique biodiversity, and the creation of tourism and recreation opportunities (Barbier *et al*., 2011). Here, we show that large quantities of detrital macrophytes can flow into and be processed in this shoreline ecotone worldwide. Supply and retention of wrack are influenced by the oceanographic processes that transport it, the geomorphology, orientation and landscape context of beaches, and the condition, life history and morphological characteristics of species that produce the wrack in marine donor ecosystems. When retained in beach ecosystems, wrack often creates hotspots of microbial metabolism, secondary productivity, biodiversity and nutrient remineralization. Decomposition of wrack results in the release of dissolved organic and inorganic nutrients that can return to coastal waters. Beach-cast kelps particularly play a key trophic role, as an often abundant and preferred food source for mobile intertidal invertebrates (mainly amphipods) that channel imported algal productivity to predatory invertebrates, fish, birds and other higher order consumers. These predators are likely to form important vectors for the return of wrack-derived nutrients across coastal seascapes and landscapes. The role of beach-cast marine carrion is likely to be underestimated, as it can be consumed rapidly by highly mobile scavengers (e.g. foxes, coyotes, raptors, vultures). These scavengers are likely to be important vectors in transferring marine productivity inland, linking marine and terrestrial ecosystems.

We show that influxes of marine-derived material can substantially enhance ecosystem services in sandy beach ecosystems through augmenting biodiversity and fisheries, and by supporting specialized predators and scavengers. Despite this, the perceived loss of aesthetics and amenity due to the accumulations of wrack on beaches appears to overshadow those ecological values. This is exemplified by widespread beach grooming or raking that removes beach-cast wrack as a management practice to improve beach aesthetics and amenity for tourism and recreation. Since this practice can have strong effects on the habitat quality, biodiversity, and functioning of beach ecosystems, as well as ecosystems beyond its borders, the benefits related to tourism and recreation need to be balanced against the other ecosystem services beaches provide. Similarly, the construction of structures such as seawalls, marinas and groynes alter oceanographic conditions and beach morphology, and therefore the supply and retention of subsidies of organic material to beaches ecosystems. Consequently, conservation efforts should consider creating societal awareness on the ecological importance of stranded organic matter, which is mainly seen just like garbage.

Based on our assessment, the transfer and deposition of organic matter across open coastal seascapes is at risk from habitat loss and climate change (Hyndes *et al.*, 2014, Myers *et al.*, 2019). Rising sea level will lead to the loss of habitat available for wrack deposition and retention, significantly impacting the functioning of beach ecosystems (Myers *et al*., 2019). Also, while not consistent across regions, seagrasses and kelp have been in general decline, with declines of 7% and 2% yr^{-1} in recent years for the respective systems (Waycott *et al.*, 2009; Krumhansl *et al.*, 2016). Further losses are occurring through ocean warming and heatwave events (Arias-Ortiz *et al.*, 2018; Wernberg *et al.*, 2019), thereby reducing the supply of organic material from donor to recipient coastal ecosystems in some regions. Such losses of donor material and the ability for beaches to retain material provide the greatest and most widespread threat to the ecosystem function and services provided by subsidies of wrack and carrion in sandy-beach ecosystems. This impact will be more pronounced in temperate regions around the globe where kelp subsidies are a prominent component of wrack, since kelp plays a disproportionately important role in their food webs of these beaches. To evaluate the overall impact that climate change, coastal management practices, and development will exert on sandy beaches and the ecosystem services supported by subsidies wrack, far greater research effort is clearly needed to quantify the range of ecosystem functions and services that wrack provides. We recommend that this research effort should focus particularly on the: (1) nutrient cycling and comprehensive budgets in beach ecosystems; (2) input and processing of carrion on sandy beaches; (3) role of microbes and invertebrtaes in processing wrack and carrion, and their influence on food webs in the beach ecotone; and (4) spatial extent and magnitude of the flow of wrack- and carrion-derived nutrients into coastal seascapes and landscapes, including the scale of the movement of predators and wildlife (e.g. fish, birds, mammals) and scavengers (e.g. birds, mammals) linked to these marine subsidies.

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Table 1. Themes addressed by the peer-reviewed literature on beach-cast organic matter (plant wrack and animal carrion). The total number of studies identified was 305, but many papers straddled, or covered, more than one theme.

Theme	# studies	Percentage
Wrack dynamics (temporal & spatial variability)	111	36.4
Faunal dynamics (temporal & spatial variability)	96	31.5
Trophic ecology	92	30.2
Population biology	49	16.1
Chemical composition and processes	41	13.4
Carrion & carcass dynamics	28	9.2
Human use and impacts	27	8.9
Environmental processes & influences	23	7.5
Decomposition & microbes	11	3.6
Dispersion of sources	7	2.3
Human health	6	2.0
Invasive biology	5	1.6
Hydrodynamics	4	1.3
Influence on dunes	4	1.3
Genetics	3	1.0
Inventory of taxa	3	1.0
Methods	3	1.0
Restoration	3	1.0
Taxonomy	2	0.7
Fauna physiology	1	0.3
Movement of fauna	1	0.3
Sediment transport	1	0.3

Table 2. Factors that either positively or negatively affect the deposition and retention of wrack on beaches. References listed in SOM1.

Factor	Description	References
State of Donor Ecosystem		
Standing stock	Biomass of subsidy & availability for export	Cavanaugh *et al*. (2011)
Senescence/growth	Primary productivity, Biomass availability/ turnover/nutritional condition & availability for export	Rodriguez *et al*. (2013, 2016)
Macrophyte phenology	Annual vs perennial, seasonal cycles of export	Hamilton *et al*. (2020)
Management	Direct harvest, grooming, fisheries, marine protected areas, biomass available for export	Dugan & Hubbard (2010)
Characteristic of beach		
Proximity to Donor Ecosystems	Rocky reef, kelp forest, seagrass bed, estuary, rocky intertidal	Orr *et al.* (2005), Reimer *et al.* (2018), Liebowitz *et al*. (2016)
Beach Morphology	Width of zones and slopes affect delivery and retention	Orr *et al.* (2005), Revell *et al*. (2011), Barreiro *et al.* (2011), Wickham *et al.* (2020)
Beach Orientation	Shore orientation relative to prevailing swell and currents affects delivery and retention	Orr *et al.* (2005), Gomez *et al*. (2013)
Back Beach Type	Retention and fate of wrack varies among Dune-, cliff- and seawall-backed shores	Dugan *et al*. (2008), Heerhartz *et al.* (2014)
Beach Management	Grooming and armouring alter retention and fate	Dugan & Hubbard (2010), Schooler *et al.* (2019)
Sediment supply/budget	Availability and resilience of beach habitat affects retention	Zoulas & Orme (2007), Orme *et al.* (2011), Griggs & Patsch (2018)
Disturbances		
Storm Events	Changes in wave height affects donor and recipient ecosystems through removal & erosion	Barreiro *et al.* (2011), Reed *et al*. (2011)
Storm Season	Wave-driven removal of substrate and subsidies	Cavanaugh *et al*. (2011), Reed *et al.* (2011)

Climate Events	El Nino, NPGO, marine heatwaves, etc. change primary production, supply and dynamics of recipient ecosystem	Cavanaugh *et al*. (2011), Revell *et al*. (2011), Thomsen *et al.* (2019), Strydom *et al*. (2020)
Climate Change	Increased ocean temperature and SLR: warming impacts kelp forests/seagrass beds and SLR causes loss of beach habitat	Jordà *et al*. (2012), Krumhansl *et al.* (2016), Bell *et al.* (2018), Cavanaugh *et al.* (2019)
Overgrazing	Effect on standing stock & resilience, urchins and urchin barrens, biomass available for export	Rose *et al.* (1999), Ling *et al*. (2015), Ling *et al*. (2019), Rogers-Bennett & Catton (2019)
Invasive Species	Outcompete natives, altered life cycles and biomass production/export and food quality	Marks *et al*. (2018), Schiel *et al*. (2018)
Ocean Processes	**Drivers of Exchanges**	
Tides	Daily and semi-lunar tides affect delivery and retention on beaches	Zobell (1971), Revell *et al*. (2011), Orr *et al*. (2005)
Wave Climate	Event, season and climate driven wave dynamics affect donor (loss of biomass, whole plants) and recipient (wrack biomass dynamics and beach erosion/rotation/retention) ecosystems	Zobell (1971), Revell *et al*. (2011), Liebowitz *et al*. (2016)
Currents	Transport and delivery of macrophytes to beaches. Can move wrack along and on and off the beach	Orr *et al.* (2005), Gomez *et al.* (2013), Liebowitz *et al.* (2016)
Sea level rise	Erosion and long term loss of recipient beach habitat zones affects retention of wrack	Myers *et al*. (2019)
Wind	Surface currents and erosion processes affect both donor and recipient ecosystems, wrack burial and transport inland	Rossi & Underwood (2002), Hammann & Zimmer (2014), Liebowitz *et al*. (2016), Del Vecchio *et al*. (2017)

Table 3. Food preference and comparison of different food types on growth and survival rates of amphipods and ghost crabs. Food sources that a consumer species preferred equally are given the same rank (+ = dune vegetation; * = fine particles).

Variable	Taxa	Consumer species	Food source							Reference
			Kelp	Other brown	Red	Green	Seagrass	Other	Carrion	
Food preference	Amphipod	*Allorchestes compressa*	1	1	2	2	4			Crawley & Hyndes (2007)
	Amphipod	*Allorchestes compressa*	1	2	3	3	3			Robertson & Lucas (1983)
	Amphipod	*Bellorchestia quoyana*	1			2				Suarez-Jiminez *et al*. (2017)
	Amphipod	*Orchestoidea tuberculata*	1				2			Lastra *et al*. (2008)
	Ghost crab	*Ocypode convexa*	2				2	2^{+}	1	Rae *et al.* (2019)
Growth	Amphipod	*Allorchestes compressa*	1		3		4	2^{*}		Robertson & Lucas (1983)
	Amphipod	*Megalorchestia corniculate*	1				2			Lastra *et al*. (2008)
Survival	Amphipod	*Allorchestes compressa*	1		3		4	2^{*}		Robertson & Lucas (1983)
	Amphipod	*Notorchestia* sp.		1		2	3			Poore *et al*. (1980)

Table 4. Median percentage contribution of different types of food sources to the diets of consumers in wrack based on mixing model outputs of stable isotopes for consumers (mix) and potential food (sources) extracted from peer-reviewed literature. POM = fine particulate organic matter in sediment or water column.

Taxa	**Consumer species**	**Food source**							**Region**	**Reference**
		Brown algae	**Red algae**	**Green algae**	**Seagrass**	**Dune plants**	**POM**	**Carrion**		
Beach										
Amphipod	*Talitrus saltator*	16	-	5	-	32	29	16	Atlantic (East)	Bessa *et al*. (2014)
Amphipod	*Talorchestia brito*	31	-	12	-	17	22	19	Atlantic (East)	Bessa *et al*. (2014)
Amphipod	*Tylos europaeus*	22	-	18	-	13	31	13	Atlantic (East)	Bessa *et al*. (2014)
Amphipod		5	12	-	25	21	-	-	Eastern Indian Ocean	Ince *et al.* (2007)
Amphipod	*Talorchestia capensis*	8	9	8	-	-	9	-	Southern Arica	Porri *et al*. (2011)
Ghost crab	*Ocypode convexa*	17	9	-	9	15	-	10	Eastern Indian Ocean	Rae *et al.* (2019)
Surf zone										
Amphipod	*Allorchestes compressa*	32	14	-	54	-	-	-	Eastern Indian Ocean	Crawley *et al*. (2009)

Table 5. Examples of scavengers and the carrion they consumer on ocean-exposed sandy beaches reported in the peer-reviewed literature. References listed in SOM2.

Scavenger(s)	Carrion type	Location	Reference
Invertebrates			
Whelks *(Bullia rhodostoma, B. digitalis)*	jellyfish	South Africa	Brown (1961, 1971)
Nassarius festivus	fish	Hong Kong	Morton & Yuen (2000)
Isopods (Cirolanids)	various drift organisms	USA (California)	Dugan *et al.* (2003)
Polychaetes	various drift organisms	USA (California)	Dugan *et al.* (2003)
Beetles	various drift organisms	USA (California)	Dugan *et al.* (2003)
Ghost Crabs (Ocypode spp.)	diverse / mixed carrion	multiple countries and locations	Wolcott (1978), Lucrezi & Schlacher (2014), Rae *et al.* (2019)
Reptiles			
Lace Monitor (*Varanus varius)*	fish	Australia (East Coast)	Schlacher *et al.* (2013a), Schlacher *et al.* (2013b) Bingham *et al.* (2018)
Cottonmouth Snake (*Agkistrodon piscivorus conanti*)	fish	USA (Florida, Gulf Coast Islands)	Lillywhite *et al.* (2008)
Birds			
Corvidae (crows & ravens)	fish	Australia (East & South Coast)	Huijbers *et al.* (2013), Schlacher *et al.* (2013a), Schlacher *et al.* (2013b), Brown *et al.* (2015) Huijbers *et al.* (2016b), Huijbers *et al.* (2016a), Bingham *et al.* (2018)
Sea Gulls (several spp.)	fish	Australia (East & South Coast)	Huijbers *et al.* (2013), Schlacher *et al.* (2013a), Huijbers, 2016), Schlacher *et al.* (2013b), Huijbers *et al.* (2016a), Bingham *et al.* (2018), Brown *et al.* (2015)
White-Bellied Sea Eagle (*Haliaeetus leucogaster)*	Various mammals, other birds, fish, and crabs	Australia (various coastal areas)	Smith (1985), Huijbers *et al.* (2013), Schlacher *et al.* (2013a), Schlacher *et al.* (2013b) Brown *et al.* (2015), Huijbers *et al.* (2016b), Huijbers *et al.* (2016a), Bingham *et al.* (2018)
Whistling Kite (*Haliastur sphenurus)*	Various terrestrial and marine animals (rodents, reptiles, fish)	Australia (woodland and coastal areas)	Gosper (1983), Huijbers *et al.* (2013) Schlacher *et al.* (2013a) Schlacher *et al.* (2013b), Brown *et al.* (2015) Huijbers *et al.* (2016b), Huijbers *et al.* (2016a) Bingham *et al.* (2018)
Brahminy Kite (*Haliastur indus*)	Marine carrion such as fish and crabs	Australia (various coastal areas)	(Smith *et al.*, 1978; Lutter H, 2006) (Lutter *et al.*, 2006) (Huijbers *et al.*, 2013; Schlacher *et al.*, 2013a; Schlacher *et al.*, 2013b; Brown *et al.*, 2015; Huijbers *et al.*, 2016b; Huijbers *et al.*, 2016a; Bingham *et al.*, 2018)
Mammals			
Coyote (*Canis latrans*)	Seals, birds, sea turtles, fish, marine arthropods	CA, USA	Rose & Polis (1998)
Tasmanian Devil (*Sarcophilus harrisii)*	fish	Australia, (Tasmania)	Moore (2002), Schlacher pers. obs.
Brown Hyena (*Parahyaena brunnea*)	Cape fur seals carcasses	Namibia (Skeleton Coast)	Skinner *et al.* (1995), Kuhn *et al.* (2008)

Black-backed Jackal (*Canus mesomelas*)	Mammals (seal pups), birds, and fish	Namibia (Skeleton Coast)	Oosthuizen *et al.* (1997), Avery *et al.* (1987)
Dingo (*Canis lupus dingo*)	Broad range of stranded material including dugong and whale carcasses	Australia (East Coast, Fraser Island)	Moore (2002), Behrendorff *et al.* (2016), Behrendorff *et al.* (2018)
Red fox (*Vulpes vulpes*)	fish	Australia (East & South)	Huijbers et al. (2013), Brown *et al*. (2015), Huijbers *et al*. (2016b), Huijbers *et al*. (2016a), Bingham *et al*. (2018)
Dogs & Cats (feral and domestic)	fish	Australia (East & South)	Huijbers *et al.* (2013)

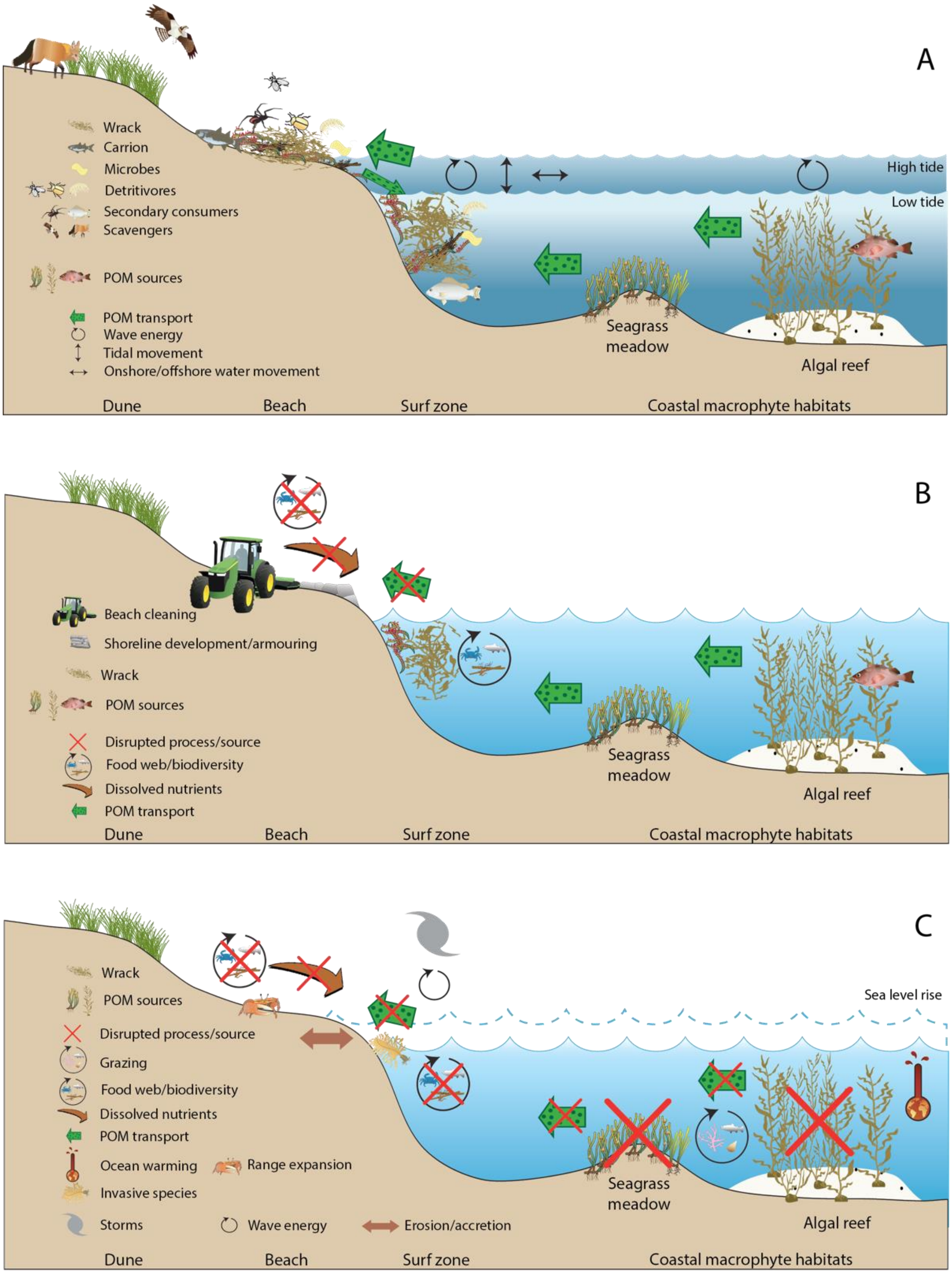

Figure 1. Conceptual diagrams of wrack dynamics in beach ecosystems. (A) the principal sources, transport routes, and biological fates of marine organic material cast upon sandy beaches; (B) disruption of natural processes caused by beach grooming and coastal armouring; and (C) predicted consequence of climate change for the supply, type and biological fates of marine organic matter in sandy beach ecosystems. Diagrams created using IAN Image Library (http://ian.umces.edu).

Figure 2. Wrack, scavengers and human disturbance on sandy beaches. Wrack on beaches in (A) Cape Town, South Africa [photo L. Harris]; (B) Santa Barbara County, USA [photo J. Dugan]; (C) Salina Bay, Malta [photo M. Mateo]; and (D) Perth, Australia [photo G. Hyndes]. Dingo (E) and white-bellied sea eagle (F) scavenging on carrion on beaches near Brisbane, Australia [photos A. Olds], and beach cleaning on beaches in (G) Brisbane, Australia [photos A. Olds] and (H) Carpinteria, USA [photo J. Dugan].

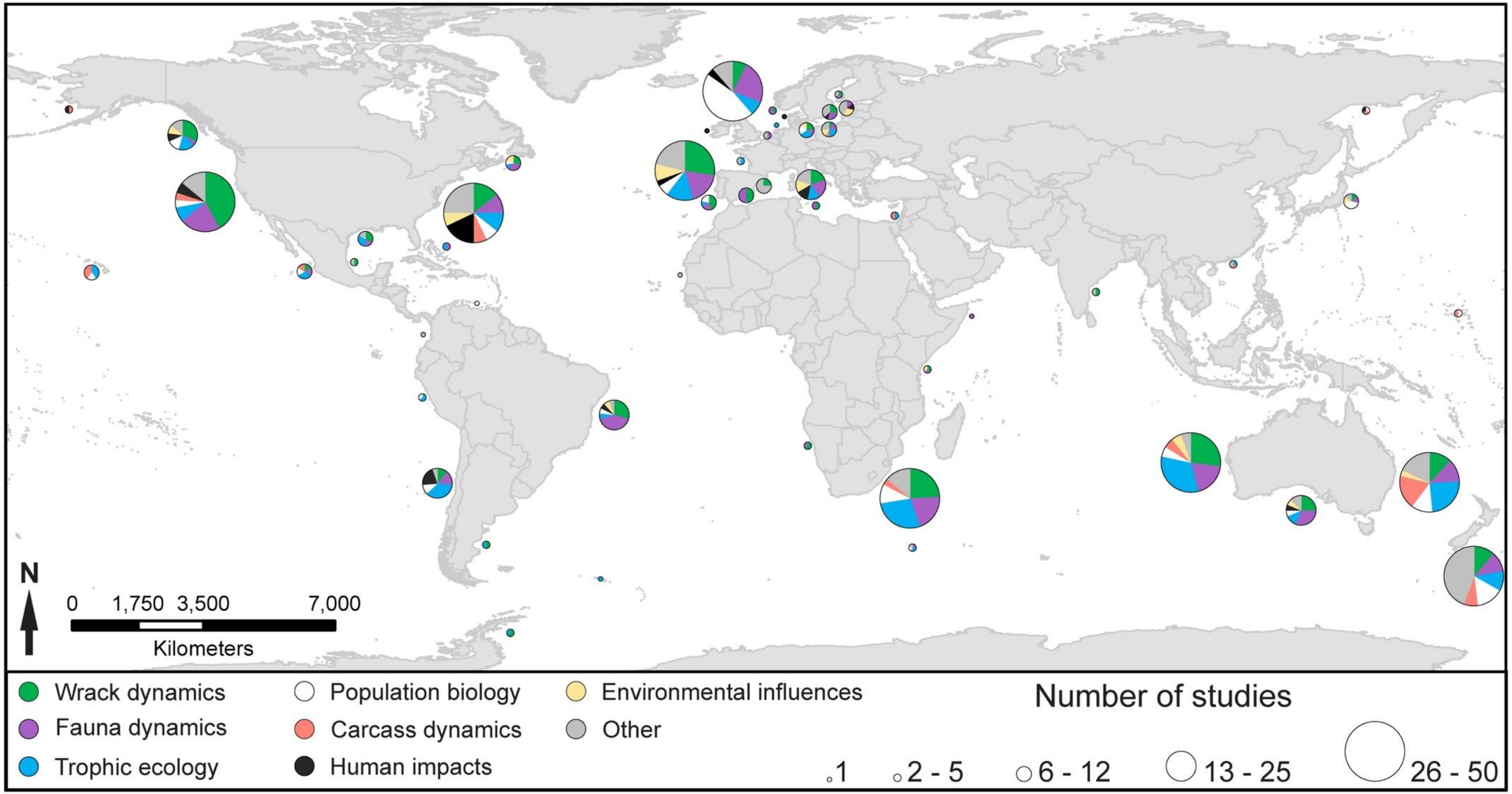

Figure 3. Global distribution of studies (n=305) classified by the main theme with respect to wrack and carrion on sandy beaches and in surf zones. Pie charts illustrate the different themes of published studies, with the size indicating the total number of studies for a region. Note that more than one theme could be covered by each paper, but the number of studies in each region reflects the total number of papers regardless of theme.

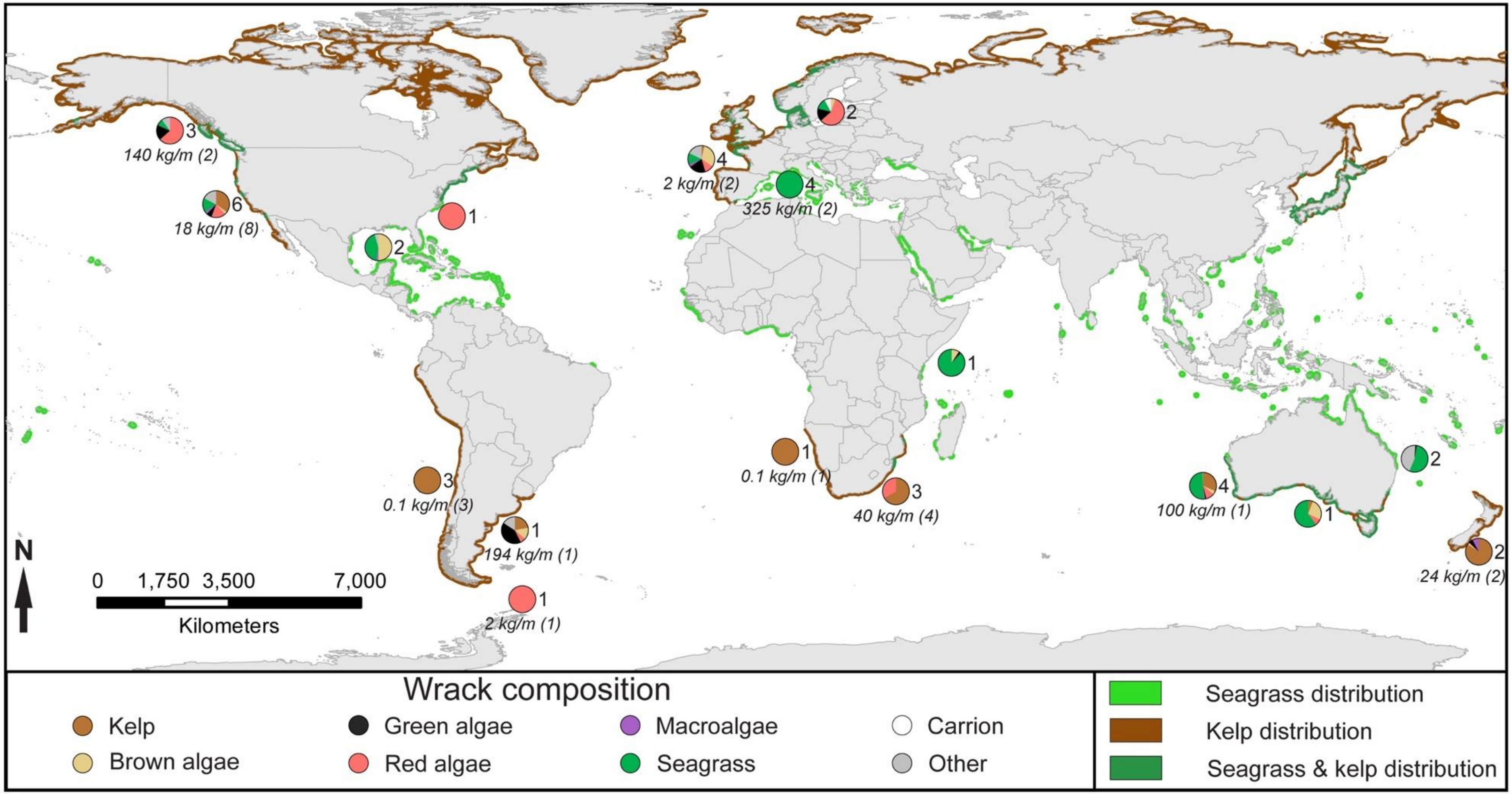

Figure 4. Global patterns in wrack composition (n=41) and wet weight (n=27) of wrack (kg WW wrack m^{-1} of coastline) on beaches and in surf zones based on published papers. Numbers in plain text to the right of each pie chart indicate the number of studies, whereas the text in italics below the pie charts indicates the average biomass in each region. Wrack composition was based on wet and dry weight and volume data, while weight data were based on those studies where weight was either provided or could be converted to wet weight per linear metre of coastline. Distribution of seagrass from UNEP-WCMC seagrass maps based on Green & Short (2003), while kelp distributions are based on those shown in Filbee-Dexter & Wernberg (2018).

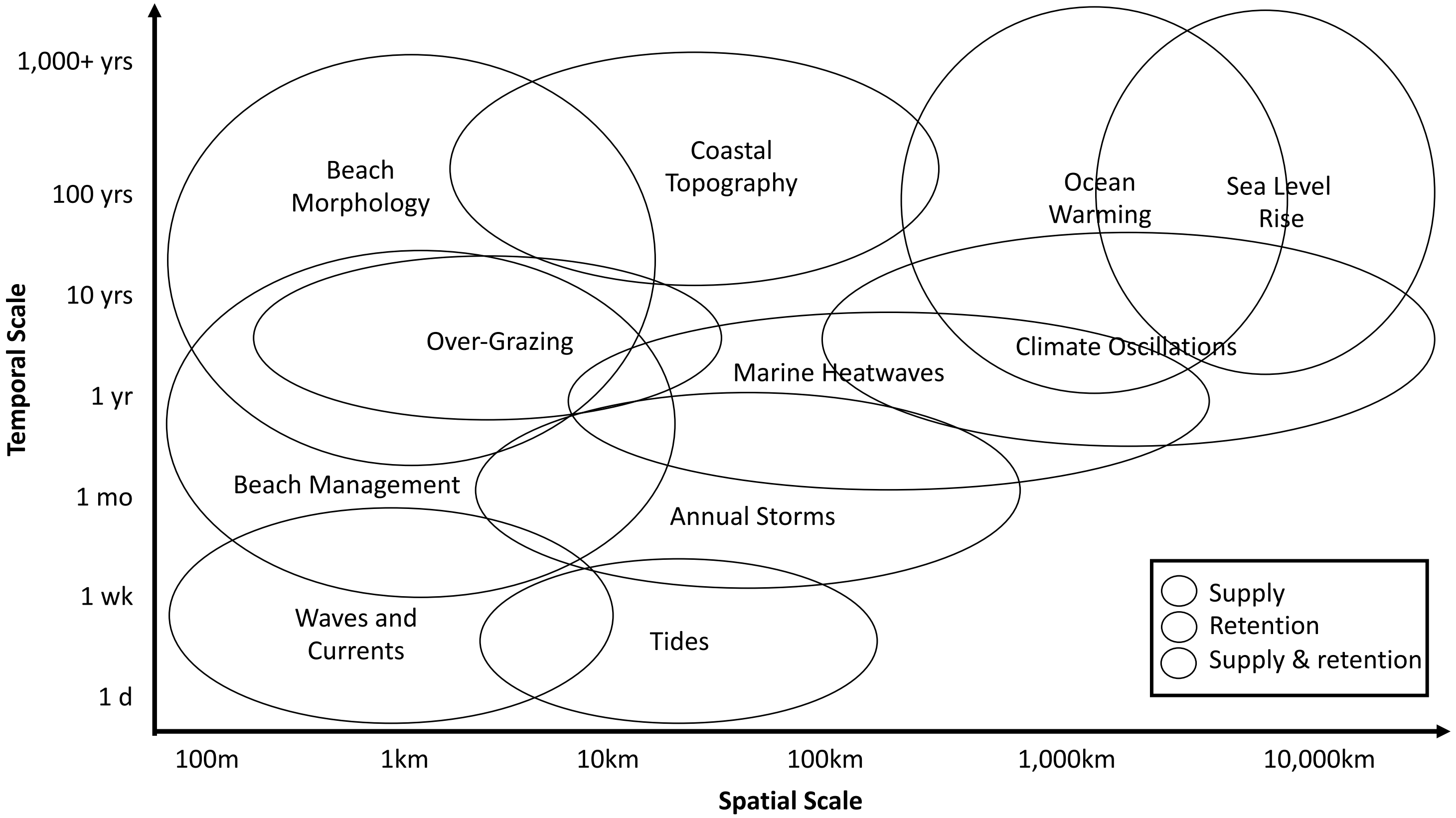

Figure 5. Coastal, oceanographic and atmospheric factors that influence wrack supply and retention on sandy beaches, and the spatial and temporal scales at which they operate. Sources of information provided in Table 2. Supply = the processes that influence the input of wrack in beach ecosystems; retention = the processes that influence the ability for wrack to remain in beach ecosystems. Beach management refers to management practices such as beach grooming and armouring that influence supply and retention of wrack, while over-grazing refers to impacts on donor systems such as kelp forests due to grazing pressure.

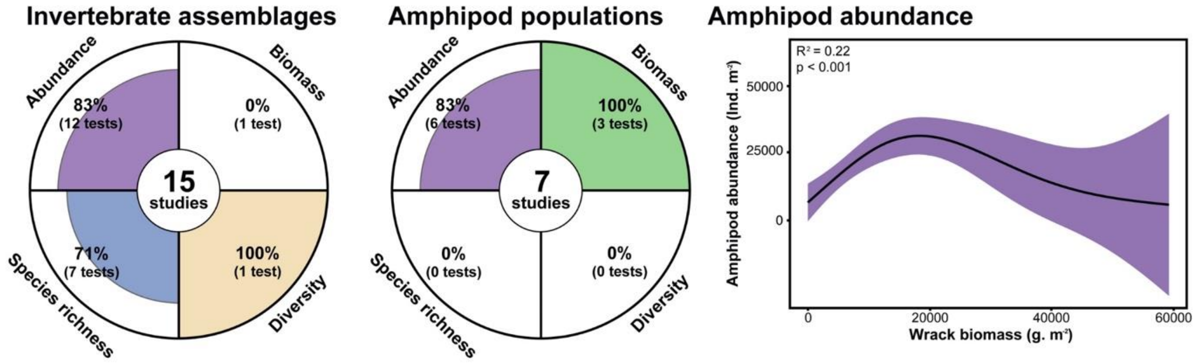

Figure 6. The numbers and proportions of papers with a focus on different aspects of total invertebrate assemblages and amphipod populations in wrack on beaches and in surf zones, and the relationship between amphipod abundance and wrack biomass (g wet weight per m^2) based on data extracted from peer-reviewed literature. Circle quarters represent summaries of correlations with invertebrate assemblages and amphipod populations (i.e. abundance, biomass, species richness, diversity). In each quadrant, the number of studies are displayed in parentheses, and the percentage of studies reporting a significant effect for each variable is illustrated by each quadrant's size and as text (e.g. 83% of invertebrate studies report positive effects on invertebrate abundance).

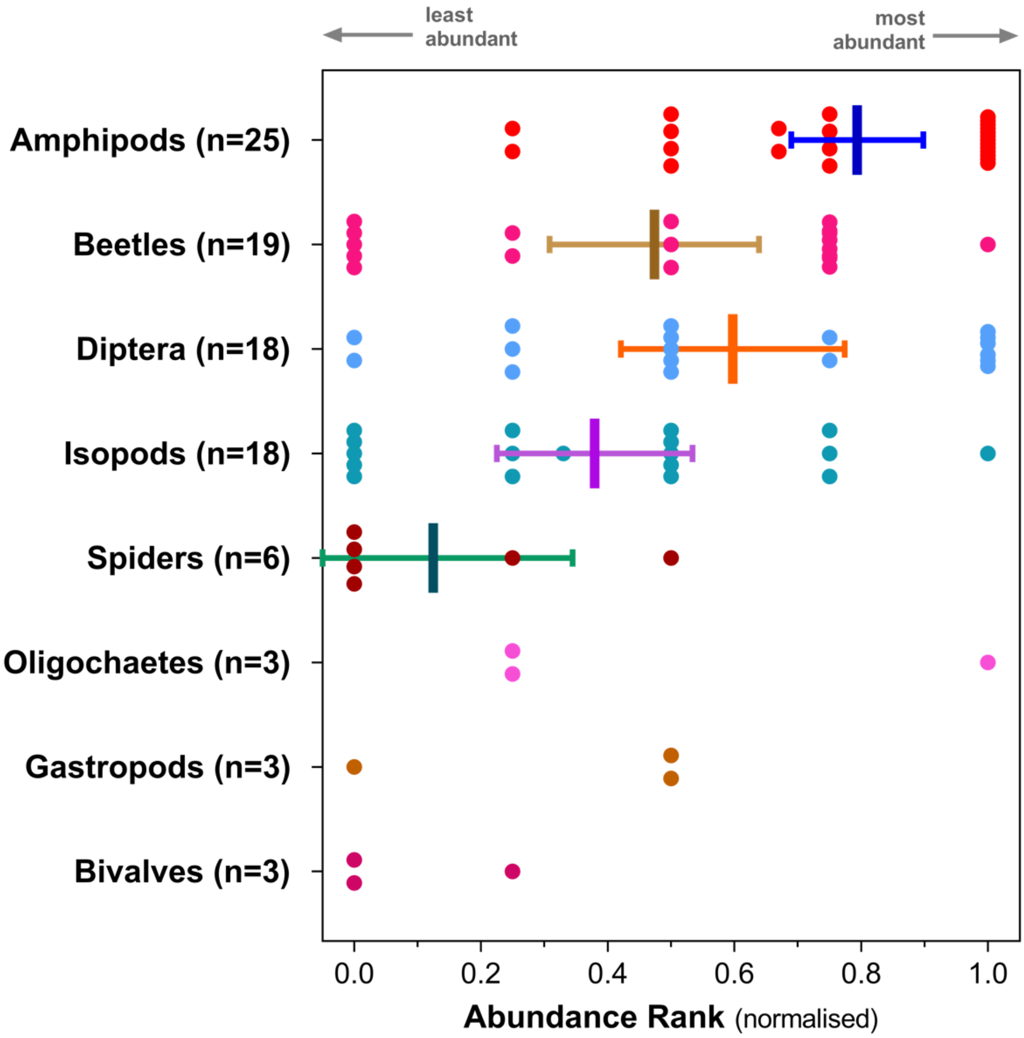

Figure 7. Rank abundance (normalised) of the main invertebrate taxa found on the beach and in the surf zone based on extracted data from the peer-reviewed literature. Dots indicate the ranks of taxa in individual studies, while the vertical lines denote the mean rank and horizontal lines the 95%CI.

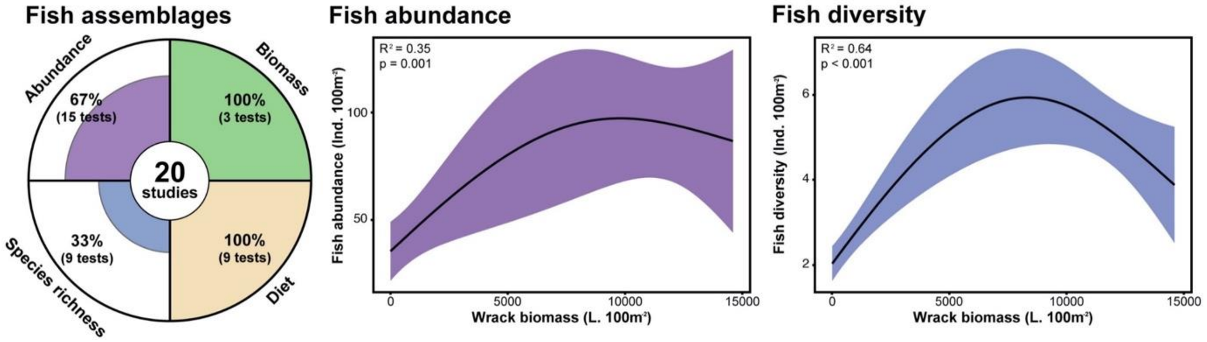

Figure 8. The numbers and proportions of papers with a focus on different aspects of fish assemblages in the wrack in surf zones, and the relationship between fish abundance and diversity with wrack volume (litres per 100 m^2) based on data extracted from peer-reviewed literature. Circle quarters represent summaries of correlations with fish assemblages (i.e. abundance, biomass, species richness, diet). In each quadrant, the number of studies are displayed in parentheses, and percentage of studies reporting a significant effect for each variable is illustrated by each quadrant's size and as text (e.g. 67% of studies on surf fish assemblages report positive effects on wrack on fish abundance).

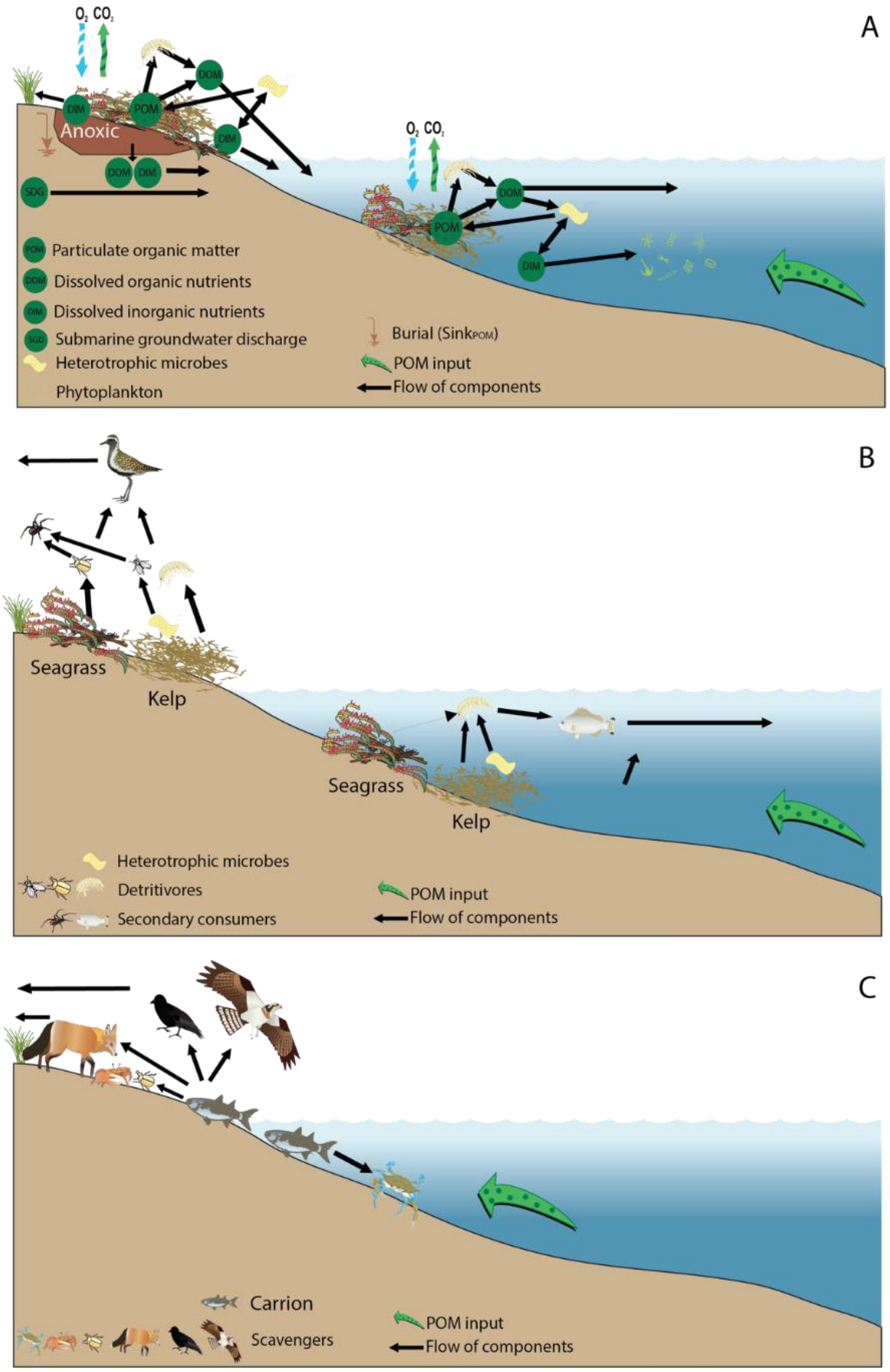

Figure 9. Conceptual diagram of: (A) decomposition and nutrient cycling; (B) grazer/detritivore food web; and (C) scavenging pathways as key processes for the fate of stranded organic material in beach ecosystems. Diagrams created using IAN Image Library (http://ian.umces.edu).

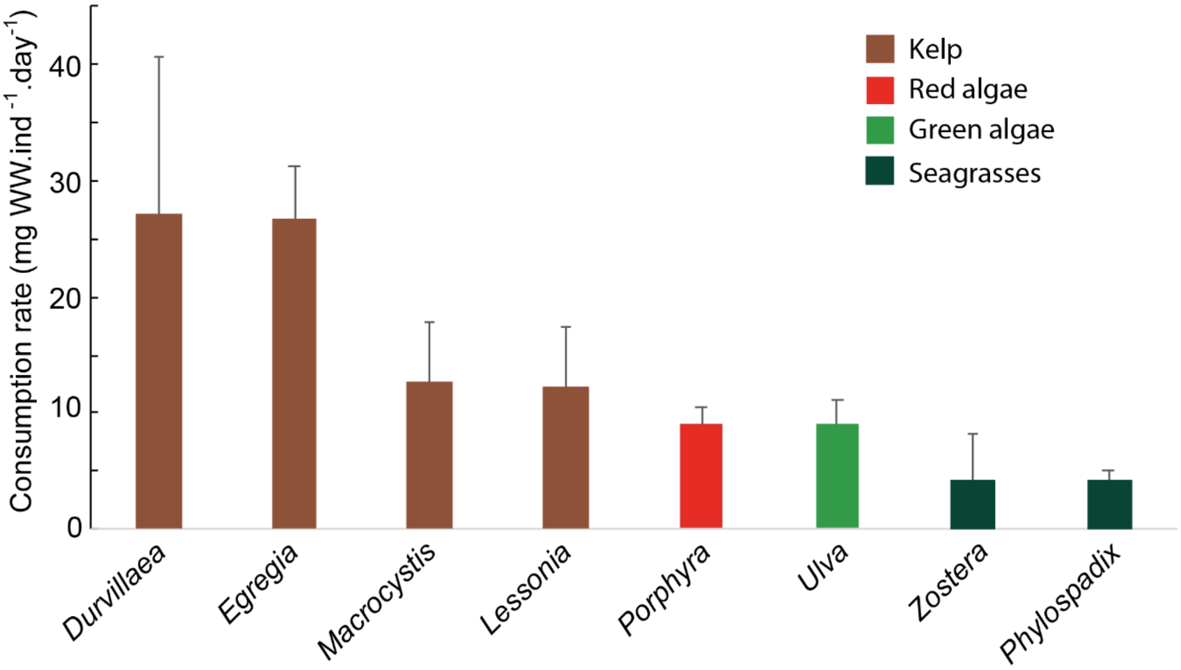

Figure 10. Consumption rates (mean + se, mg WW macrophyte.ind^{-1}.day^{-1}) by amphipods fed on different sources of wrack in beach and surf zone habitats. Error bars = 1SE.