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INFLUENCE OF MARINE ALLOCHTHONOUS INPUT ON SANDY BEACH COMMUNITIES

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Abstract This review provides an overview of the importance of beach accumulations of macrophytes and other organic beach-cast material on the ecology of sandy beach ecosystems. It describes the composition of these allochthonous subsidies, their abundance on beaches in relation to seasonal, lunar, tidal and spatial trends, their decomposition and utilisation by bacterial, meio- and macrofaunal communities. The paper then analyses the community structure and the species succession in both macrophyte wrack and carrion and reports the most important findings on individual wrack-inhabiting species (amphipods, isopods, dipterans). Other aspects, such as feeding and microclimatic preferences of certain species and their interactions in wracks, are also discussed. Links to vertebrate species and other secondary consumers that exploit beach-cast macrophytes and carrion as trophic resource are considered, and the importance of wrack in recycling nutrients to nearshore coastal ecosystems is stressed. The beneficial and detrimental effects of organic beach-cast material on both plants and animals of beach and nearshore communities and on the geomorphology of coastal beach-dune systems are pointed out. Another section is dedicated to human use of beach-cast macrophytes through harvesting of economically important species and of other stranded material through its exploitation for traditional reasons. The effects of harvesting on local faunal communities and on the stability of the dunes is discussed. A final section of the paper includes the positive and negative effects of man-made debris on sandy-beach ecosystems and briefly reviews the major findings.

Introduction

The ocean/land interface occupies about 8% of the earth's surface (Ray & Hayden 1992) along 594 000 km of coastline (Hammond 1990). In this ecotone terrestrial and aquatic habitats interact intensively altering salinity, turbidity, nutrients and climatic regimens in coastal waters through freshwater runoffs on the one hand and affecting productivity of coastal areas through a large input of material from the adjacent aquatic systems on the other. The spatial boundaries are continuously crossed by the basic components of food webs. Ecologists are now more aware of how ecosystems are closely bound to one another and how factors outside a system may significantly affect or even dominate local patterns and dynamics. Polis et al. (1997) defined this exchange of organic matter between habitats “a spatial subsidy”, as

a donor-controlled resource (prey, detritus, nutrient) from one habitat to a recipient (plant or consumer) from a second habitat which increases population productivity of the recipient, potentially altering consumer resource dynamics in the recipient system.

Physical (wind and water) and biotic (mobile consumers) vectors are mainly responsible for cross-boundary transportation of nutrients both towards sea and land.

Compared with rocky and estuarine mud-flats, sandy beaches have very little *in situ* primary production (Inglis 1989, Brown & McLachlan 1990). The resident primary producers are represented by epi-psammic diatoms. On flats of fine sand found on sheltered beaches these may contribute to some primary productivity but never with high values (from $0 \text{ gC m}^{-2} \text{ yr}^{-1}$ to $50 \text{ gC m}^{-2} \text{ yr}^{-1}$ according to beach exposure, Leach 1970, Hartwig 1978). Thus macrofaunal communities rely almost entirely on organic inputs that arrive from the surf zone (surf diatoms, flagellates) or from the sea (stranded macrophytes, carrion, dissolved organics, particulates) through oceanic processes, such as upwelling, currents, waves and tides. Primary consumers, such as suspension feeders (crabs, bivalves) and herbivores (crustaceans, insects) consuming phytoplankton, particulate organic material, kelp, and seagrass, then become prey of secondary consumers (crabs, beetles). In turn, vertebrate predators (fishes, lizards, shorebirds, foxes and other scavenger species) prey upon both primary and secondary consumers and are largely responsible for the consumption of drift carrion. Hence allochthonous resources, which in many cases are ephemeral and present seasonal and spatial fluctuations, are likely to affect all levels of the food web of a sandy beach.

Marine inputs on beaches all over the world, however, include both organic and inorganic material. The latter, mainly composed of man-made debris of different origin, recently has become a growing concern in many countries. Floating, submerged and stranded beach litter is more than an aesthetic issue, causing a significant threat to marine mammals, seabirds, turtles and fishes either through entanglement or ingestion (Laist 1987). From a recreational standpoint the economic value of tourist resorts may be reduced by these factors (Ryan & Moloney 1990) and, in some cases, the debris may become hazardous to human health (Philipp et al. 1993, 1994). Unfortunately, management strategies induced by stranded litter on beaches frequently have a negative impact on beach communities.

The aim of this paper is to review the most recent and major findings upon organic and inorganic beach-cast material. Organic allochthonous input is analysed from several aspects, starting from its composition, abundance on beaches, processes of decomposition and exploitation by meio- and macrofaunal communities. Species succession is discussed for both macrophyte beach cast and carrion and the most important findings on individual wrack-inhabiting species are reported. Attention is given to intra- and interspecific interactions in wracks and to feeding preferences of arthropod species. The term "wrack" in this review refers not only to plants or stranded seaweed but is applied generally to any organic beach-cast material. The influence of organic beach-cast material on both terrestrial vertebrate species (shorebirds and other land species) and offshore consumers (filter-feeders, grazers, fishes) is also considered. The paper then analyses the beneficial and detrimental effects of wrack availability on animals and on the geomorphology of beaches, the exploitation of organic beach casts and their use by humans. The effects of removal of this material from beaches on invertebrate populations is also discussed.

A final section is dedicated to inorganic beach-cast material. Because of its impact on beaches it has attracted the attention of scientists worldwide. The major studies are

reviewed, and the positive and negative effects of man-made debris on sandy-beach ecosystems are briefly discussed.

Organic components of beach-cast material

Macrophytes

Algae

In many coastal areas the production of marine macrophytes in offshore beds is extremely high. This production consists mainly of large brown algae, commonly referred to as kelps, and seagrasses. The dominant orders of the algae belong to the Laminariales (technically kelps) and Fucales. While the intertidal zone is inhabited primarily by the fucoids, the subtidal is dominated by laminarians. Because of their high productivity and complicated biological structure kelps have received much attention (Mann 1972, 1973, 1982, Field et al. 1977, 1980a,b, Velimirov et al. 1977, Chapman & Craigie 1978, Newell et al. 1982, Kirkman 1984, Dayton 1985, Kirkman & Kendrick 1997). Species of *Laminaria* occur worldwide and dominate both sides of the Atlantic and the coasts of China and Japan. In New Zealand, Australia and South Africa many kelp forests are dominated by *Ecklonia* species whereas the giant kelp, *Macrocystis pyrifera* is found in the northeast Pacific, southern Australia, New Zealand, South Africa, Peru, Chile, and Argentina where it forms dense forests (Dayton 1985, Kirkman & Kendrick 1997). Environmental factors influencing kelp communities, such as light, substrata and sediment, nutrients, water motion, salinity and temperature together with population dynamics, life-history studies, patch dynamics, dispersal and grazers have been reviewed by Dayton (1985). An estimate of 12% of kelp biomass or 6% of kelp production has been reported to break free during storms (Griffiths & Stenton-Dozey 1981, Jarman & Carter 1981) much of which (2.5%) is deposited annually on beaches (Koop et al. 1982b). The significance of kelp-derived organic carbon to the nearshore secondary production has also been assessed (Duggins et al. 1989). Kelp biomass enters the nearshore food web by releasing particulate and dissolved organic matter during growth and senescence and provides a significant resource of carbon and nitrogen for the assemblages of both pelagic and benthic suspension feeders (Stuart et al. 1982, Seiderer & Newell 1985, Mann 1988, Fielding & Davis 1989, Bustamante et al. 1995, Bustamante & Branch 1996). Also, the considerable quantity of stranded kelp on beaches may re-enter the nearshore food web as particulate and dissolved organic matter after decomposition (Robertson & Hansen 1982, Walker et al. 1988, Duggins et al. 1989).

Seagrasses

Another consistent part of the organic beach cast is represented by freshly-detached seagrasses. Seagrasses are the sole marine representatives of the Angiospermae that by the Eocene had widely disappeared in the Asian-Pacific and the neo-tropics. Three families (Cymodoceaceae, Posidoniaceae, Zosteraceae), belonging to the Order Potamogetonales

contain several widespread genera (*Amphibolis*, *Cymodocea*, *Halodule*, *Syringodium*, *Thalassodendron*, *Posidonia*, *Zostera*, *Heterozostera*) (classification according to den Hartog 1970, Tomlinson 1982, Kuo & McComb 1989). *Posidonia* grows on sandy or silty substrata from the intertidal zone to a depth of 40 m according to the amount of photosynthetic light that it receives. It is considered a poor coloniser as it colonises only a few square metres over 10 yr to 50 yr (Kirkman 1985, Kirkman & Kuo 1990). Nine species of *Posidonia* are currently recognised. *P. oceanica* occurs throughout the Mediterranean and Atlantic Ocean and eight other species are found in western Australia, two of which (*P. sinuosa* and *P. angustifolia*) form the largest meadows (Kirkman & Kendrick 1997). Meadows of Zosteraceae are not extensive where *Posidonia* is the main meadow-forming species. In sheltered estuaries and intertidal mudflats, however, considerable areas can be taken up by zosteraceans (Hemminga & Nieuwenhuize 1991, Kirkman & Kendrick 1997). Species belonging to the genera *Thalassodendron* and *Syringodium*, commonly found along the coasts of the Indian Ocean, made up an average of $88 \pm 18\%$ of the beach cast along the Kenyan coast with *Thalassodendron ciliatum* as the dominant species (Hemminga et al. 1995, Ochieng & Erftemeijer 1999, Obura 2001). This species, which attaches to both hard and soft substrata, provides an important habitat for many coral reef species. An extensive description of the composition of the seagrass beds in the Seychelles reported *Thalassia hemprichii* as the dominant species (Taylor & Lewis 1970). Direct grazing on seagrasses is generally limited (Thayer et al. 1984). The major part of the biomass ages and dies and forms the basis for the detrital food chain. A part of the organic material is retained *in situ* and recycled within the seagrass beds. Several workers (Kikuchi 1974, Adams 1976, Lenanton et al. 1982, Robertson & Lenanton 1984) have demonstrated that the associated invertebrate community provides sustenance for fishes that use seagrasses as important nursery grounds. Another part of the seagrass biomass is exported from the meadows as dissolved organic matter or partially fragmented leaves. In this form it is transferred to submerged depressions on bare sand throughout the intertidal and subtidal areas or further offshore to the deep ocean floor where it contributes to the carbon and nutrient cycles (Josselyn et al. 1983, Fry & Virnstein 1988). Furthermore, storms, associated wave action and heavy swells remove huge amounts of seagrass material and accumulate them along shores forming large wrack banks (Lenanton et al. 1982, Brown & McLachlan 1990). Thus the accumulation of beach-cast material is a result of the interactions between dense nearshore seagrass meadows and physical factors such as winds, currents, waves and tides that determine their exposure to water motion (Ochieng & Erftemeijer 1999).

Abundance of stranded macrophytes

The abundance of stranded macrophytes on beaches is extremely variable and depends on the vicinity to rocky shores and reefs or to seagrass meadows. Marsden (1991a) working on a sandy beach in New Zealand calculated an average monthly wet weight of organic material of $11.25 \text{ kg } 5 \text{ m}^{-1}$ (SE mean = 3.78 kg) indicating a low organic input. On other occasions inputs can be very high. An estimate of $2179 \text{ kg } \text{m}^{-1} \text{ yr}^{-1}$ of kelp wrack was calculated for a beach on the western coast of South Africa (Stenton-Dozey & Griffiths 1983) a value very similar to that established for a nearby rocky shore, namely $1200\text{--}1800 \text{ kg } \text{m}^{-1} \text{ yr}^{-1}$ (Koop & Field 1980). On another South African beach near Port Elisabeth the total wrack input estimated was $2920 \text{ kg } \text{m}^{-1} \text{ yr}^{-1}$ (McLachlan & McGwynne 1986) whereas on beaches near Perth, western Australia $240 \text{ t dw km}^{-1} \text{ coastline yr}^{-1}$ of detached plants were processed

through the sandy beach system (Hansen 1983). In southern California an input of $473 \text{ kg ww m}^{-1} \text{ yr}^{-1}$ of macrophyte wrack was estimated for a beach by Hayes (1974) and on 15 midriff islands of the Gulf of California values of algal wrack deposited ranged between $1000\text{--}2000 \text{ kg m}^{-1} \text{ yr}^{-1}$ (Polis et al. 1997). Recently, Hobday (2000) in the Southern California Bight showed that there was an instantaneous abundance of 39 000 to 348 000 drifting rafts of kelp (*Macrocystis pyrifera*), which potentially could be stranded on beaches between late winter and early spring.

Seasonal, lunar, tidal and spatial fluctuations in beach wrack accumulations have been recorded by many authors (Messana et al. 1977, Koop & Field 1980, Behbehani & Croker 1982, Stenton-Dozey & Griffiths 1983, Hansen 1984, Moggi 1987, Chelazzi et al. 1990, Marsden 1991a, Ochieng & Erftemeijer 1999, Colombini et al. 2000). Studies carried out on South African beaches showed that input of kelp debris had a clear cyclical pattern of deposition with a higher standing stock during winter but a lower standing stock during summer periods (Koop & Field 1980, Stenton-Dozey & Griffiths 1983). Along the beaches of the Mombasa Marine National Park and Reserve in Kenya, Ochieng & Erftemeijer (1999) showed that accumulation of beach cast was markedly seasonal with largest amounts observed during the SE monsoon (March to October) and minimal amounts during the NE monsoon (November to March). Moggi (1987), on a Somalian beach, showed that the composition of the beach cast varied according to the season with a dominance of *Thalassodendron ciliatum* during October–November and a more or less equal quantity of *Syringodium isoetifolium*, *Thalassodendron ciliatum* and *Sargassum* sp. during July–August. The different wrack compositions in the two periods of study were again explained by the opposite prevailing winds (NE and SW monsoons in the two periods, respectively) and by the presence of seagrass meadows of *Thalassodendron ciliatum* to the north of the study area (Colombini et al. 2000). Beach debris accumulation may also be regulated by lunar and tidal phases. Wrack mounds can be moved up and down the beach from neap to spring tides and in some cases can be entirely replaced in a semi-lunar period (Messana et al. 1977, Stenton-Dozey & Griffiths 1983, Colombini et al. 2000). During this period the wrack beds are subjected to dehydration, ageing, sand covering, fragmentation and decomposition. On a beach on the west coast of Cape Peninsula, South Africa, Griffiths & Stenton-Dozey (1981) showed that rates of dehydration were higher for individual kelp fronds than those of artificially prepared banks. The moisture content of a single plant fell to 25% on day 6 (neap tide) while that of the bank was still 55% after the same period of time. However, both kinds of deposits lost water rapidly at first and then more gradually as the outer surface hardened. Furthermore, there was a very rapid decline in dry mass with kelp banks declining to 50% of their initial mass by day 2 and to 20% by day 14 (spring tide), whereas individual plants lost 65% of their initial dry mass over a fortnight. A marked tidal influence was also shown on the quantity of beach-cast material with greater accumulations during spring tide periods compared with neap tide periods (Ochieng & Erftemeijer 1999). Studies on the longshore distribution of beach-cast material showed that beach wrack was not uniformly distributed but often accumulated in specific sectors of the beach (Koop & Field 1980, Hansen 1984) or adjacent to rocky protrusions (Ochieng & Erftemeijer 1999). Over the width of the beach, following periods of high wave exposure, wracks can be fairly evenly distributed or can be deposited along one or more drift lines, usually at high water springs and in bands or in a band down to the level of the most recent high tide (Marsden 1991a, Ochieng & Erftemeijer 1999). On other occasions drift material can accumulate into patches from the extreme high water of spring tide to mean tidal levels (Marsden 1991a, Colombini et al. 2000).

Stranding of other organic material

Besides algae and seagrasses, the organic material of beach cast can be composed of a heterogeneous quantity of wood fragments, fruits, seeds and carrion. This kind of material is highly erratic and its stranding on beaches depends mainly on currents, winds and wave action.

Driftwood

Stranding of large logs is generally common on beaches close to fluvial systems or to areas where beach dune erosion is high. This phenomenon is quite common over the Mediterranean, where beach dune systems, with their associated Mediterranean maquis, and historically important reforested areas (pinewood plantations) have been entirely devastated by processes of erosion due to the construction of ports, jetties, breakwaters and other coastal structures. Most of the wood material is taken offshore and then cast ashore where it tends to concentrate in specific areas of the coast. Large stranded driftwood becomes an important habitat to many beach arthropods (amphipods, isopods, chilopods, coleopteran insects) and vertebrates (toads, lizards, snakes, mice) that use it as temporary or permanent shelter (Caussanel 1970, Colombini & Chelazzi 1991) or as food source as in certain xylophagous insects. In Europe the curculionid, *Mesites aquitanus*, for example, feeds and carries out its entire life cycle exclusively in pinewood which previously drifted in the sea, whereas the amphipod *Macarorchestia remyi* and larvae of the scarabaeid, *Callicnemis latreillei*, are directly confined to the sand underlying large beached logs. Here they find suitable microclimatic conditions to grow and develop into the adult phase (Caussanel 1965, 1970). In other cases, scavenger species, such as *Phytosus nigriventris*, can be indirectly tied to driftwood as it feeds on fungus colonies associated with decomposing wood debris (Caussanel 1965, Moore & Legner 1976, Colombini et al. 2002). In South Africa, Callan (1964) reported that driftwood communities were mainly composed of beetles (Carabidae and Staphylinidae). Occasionally, however, the oedemerid beetle *Apterosessinia peringueyi* dominated. The larvae tunnelled directly into the wood, whereas the adults were found associated with the sand underneath.

Fruits and seeds

Stranding of fruits and seeds together with macrophytes in beach-cast material is a common phenomenon in the tropics. At times these can be found mixed within the wracks or scattered along the beach. On a Somali beach, Moggi (1987) reported consistent quantities of fruits belonging to the Sterculiaceae, Pandanaceae, Palmae families, seeds of Mimosaceae family and more rarely mangrove fruits, seeds and hypocotyls in the wrack beds of the beach. Most seeds belonged to species not found among the flora of Somalia and probably originated along the coasts of Tanzania and Kenya arriving on the beach by means of ocean currents.

Seeds provide the vital genetic link and primary dispersal agent between successive generations of plants (Gunn & Dennis 1973). An array of plant species have propagules that are adapted for dispersal by sea and, especially on many oceanic islands, sea-dispersed species account for a disproportionate number of the total number of plant species. These propag-

ules are very buoyant with thick protective shells that are impervious to salt water. Tropical drift seeds and fruits are remarkable because they can survive months or even years at sea. Strandings of disseminules on beaches, originating from distant sources, are highly discontinuous and the rate of deposition of floating seeds can depend on surface winds and currents (Green 1999). The best known plant drifter is the coconut (*Cocos nucifera*). According to Dennis & Gunn (1971) this species is indigenous to the Indo–Malaysian region and has been spread to many Pacific Island groups by sea currents. It was calculated that 3000 miles is the average maximum distance that a coconut can remain afloat and still be viable. Coconuts establish on well-drained coral sand beaches of tropical islands and atolls with adequate rainfall and temperatures more than on shores of continents. Rosengarten (1986) assessed that naturally dispersed coconuts can withstand occasional brief saltwater flooding when developing and that coconut palms obtain freshwater and mineral nutrients from a lens of freshwater that literally floats above the denser salt water beneath the beach sand. Generally both fruits and seeds represent a highly nutritional resource for the macrofauna of beach communities. On the beach of Sar Uanle, Somalia, stranded coconuts were exploited by several tenebrionid species both as refuge and food source. When the internal seed was accessible to the beetles, this constituted a precious food source, even on a highly subsidised beach like Sar Uanle (I. Colombini & L. Chelaizzi, pers. obs.).

Carriion

Carriion represents another important component of beach-cast material. Drift carrion is common on most beaches, where it is mainly represented by jellyfishes, siphonophores, chondrophores, bivalve mussels, tunicates, fishes, turtles, seabirds, cetaceans and other animals (Brown & McLachlan 1990). Polis & Hurd (1996a) estimated that beached carrion converts to more secondary productivity than an equal mass of algal detritus. In fact, the production efficiency (mass gained by consumers/mass of food) of terrestrial poikilothermic consumers of flesh is about twice that of herbivores and five times that of detritivores (Brafield & Llewellyn 1982). Compared with macrophyte and land productivity, carrion represents a minor food source. However, this material becomes extremely important on beaches where allochthonous input is low or on beaches near colonies of pinnipeds and seabirds (Lord & Burger 1984a,b). Attempts to measure carrion input have been made in only a few studies where calculated values of dry mass of animal carcass were $110\text{ g m}^{-1}\text{ yr}^{-1}$, $340\text{ g m}^{-1}\text{ yr}^{-1}$ and $530\text{ g m}^{-1}\text{ yr}^{-1}$ in three islands of the Gulf of California and $120\text{ g C m}^{-1}\text{ yr}^{-1}$ on a beach in the eastern Cape (McGwynne 1980, Polis & Hurd 1996a). On islands, the enormous amount of allochthonous input far exceeds the autochthonous terrestrial productivity on a per-square-metre basis (i.e. many islands worldwide receive more energy from the sea than from land plants) (Lord & Burger 1984a, Burger 1985, Polis & Hurd 1996a, Polis et al. 1997). Furthermore, seabirds transport a tremendous quantity of nutrients to land via guano, eggs, feathers, bodies of dead chicks and food scraps.

Marine input of carrion supports many land detritivore, scavenger and predator populations, and this subsidy allows secondary consumers to maintain relatively larger coastal population densities. However, consumer dynamics cannot be solely explained by local productivity and more than one conduit of energy flow must be considered. Morritt (2001) reported greater populations of the amphipod *Orchomene nanus*, a crab carrion specialist, in the South Basin of Lough Hyne (Ireland) and correlated its distribution with that of the

different crab species likely to provide a predictable source of carrion. The hydrographical conditions of the site (greater water movements) may also have been partly responsible for the higher population densities of the amphipod, as they helped the transport of organic molecules released from carrion, which attracted more *O. nanus*. In Baja California del Norte (Mexico), carrion and marine prey made up about 50% of the trophic needs of coastal coyotes and the coastal population densities were higher than those of inland areas (Rose & Polis 1998). Furthermore, the study showed that the allochthonous input depressed *in situ* prey. In fact, the increase of these marine-subsidised coyotes (*Canis latrans*) depressed local rodent populations whereas in other areas (islands), lacking large predators, higher populations of rodents were supported. In the Bering Sea, scavenging on walrus (*Odobenus rosmarus*) carcasses allowed red fox (*Vulpes vulpes*) populations to reach densities 10 times greater on islands compared with mainland populations (Hersteinsson & MacDonald 1982, Zabel & Taggart 1989). More examples of marine subsidised consumers include Arctic foxes (*Alopex lagopus*), which exploited littoral animals such as crabs, molluscs and sea urchins (Andriashek et al. 1985) and scavenged the remains of polar bear (*Ursus maritimus*) kills (Sheldon 1991). The same was true for black-back jackals (*Canis mesomelas*), lions (*Panthera leo*) and brown hyenas (*Hyaena brunnea*) which foraged on marine-based carrion along the African coastline and reached higher population densities compared with inland areas (Bridgeford 1985, Avery et al. 1987, Hiscocks & Perrin 1987; see also Moore 2002).

In other cases, the behavioural responses of subsidised vertebrates change in relation to carrion. For example, on Round Island (Alaska) Zabel & Taggart (1989) found a direct relationship between polygyny of red foxes and abundance of food resources. They showed that foxes depended on nesting adult birds and chicks, and these were both preyed upon or scavenged on the beaches. When the nesting failure of seabirds occurred in relation to the occurrence of El Niño in the Bering Sea, there was a shift from facultative polygyny to monogamy in the red fox population. In another study on a Mediterranean coastal population of the red fox, an analysis of scats showed that beach carrion was deliberately included in the diet but other items, such as arthropods (amphipods, isopods, tenebrionids, dipterans and dermapterans), might have been accidentally ingested with this diet and not actively searched for by the foxes (Ricci et al. 1998). In a study of a massive wreck of guillemots (*Uria aalge*) on two beaches in Resurrection Bay, Alaska, scavenger species such as bald eagles (*Haliaeetus leucocephalus*), northern ravens (*Corvus corax*), glaucous-winged gulls (*Larus glaucescens*), river otters (*Lutra canadensis*), wolverine (*Gulo gulo*) and American black bears (*Ursus americanus*), were the main agents responsible for carcass removal, whereas beach to beach transport appeared to be of minimal importance (van Pelt & Piatt 1995). An inverse relationship between the persistence of beach-cast guillemots and their degree of freshness was also shown with fresh carcasses being searched for and actively removed within a few days after deposition. For invertebrate species there are quite a few behavioural studies that analyse feeding behaviour and competition for carrion on sandy shores of Hong Kong (Morton 1990, Britton & Morton 1992, 1993, 1994, Cheung 1994, Morton & Yuen 2000). These works have mainly considered the gastropod, *Nassarius festivus*, which feeds on moribund bivalves, fishes and decapods washed ashore, and report the opportunistic behaviour of this species, including long-distance detection, fast locomotion towards the food source and rapid ingestion of large amounts relative to its body weight. Intra- and interspecific competition for carrion also occurs in many species (Britton & Morton 1993, 1994), and recently, through field and laboratory experiments (Morton &

Yuen 2000), these interactions have been demonstrated between two sympatric scavenger species, *N. festivus* and the hermit crab *Diogenes edwardsii*.

In another study it was stressed that carrion could serve as a “bank” for species. Pugh & MacAlister (1994) found that whalebone debris, a semi-artificial permanent substratum that had a humid temperature-buffered microclimate, formed a reservoir from which several species of mites could colonise adjacent supralittoral, littoral and nearshore habitats.

Another important allochthonous input, which is not truly carrion but needs to be mentioned, is the spawning of certain species in the intertidal zone of sandy beaches. In the Delaware Bay, shorebirds such as red knot (*Calidris canutus*), ruddy turnstone (*Arenaria interpres*), sanderling (*Calidris alba*) and semipalmated sandpiper (*Calidris pusilla*) stop over and feed on horseshoe crab (*Limulus polyphemus*) eggs, as well as infaunal benthic invertebrates, and store enough fuel in the form of fat and muscle protein to complete spring migration towards breeding grounds in the Arctic (Castro & Myers 1993, Botton et al. 1994, Tsipoura & Burger 1999). The study of the distribution and abundance of migrant shorebirds in Delaware Bay (Clark et al. 1993) indicated that annual variations could be related to nutrient fluctuations and these fluctuations could influence stopover patterns of migrants.

Breakdown of beach-cast material

Leaching and microbial processes, meiofauna

Once macrophytes are cast ashore they undergo physical processes of fragmentation, decomposition and remineralisation by bacteria, meiofauna and grazers. The fragments and mineralised components are then transported to the nearshore marine environment or to the atmosphere or stored *in situ* within the beach. Valiela et al. (1985), in describing the decomposition of saltmarsh grasses using the litter bag technique, identified three distinct phases. Initially, the organic material is lost at a fast rate and leaching of hydrolysed compounds from the plant material is the major mechanism. Microbial degradation of the organic matter is said to be the major source of weight loss in the second stage, while the third stage is characterised by a slower decay of refractory material. However, this pattern was not so obvious in Inglis' (1989) work where the loss of algal dry weight was essentially linear and this difference was explained by the presence of a decay-resistant fraction in the algal detritus.

The importance of microbial regeneration of nutrients from the decomposition of stranded macrophytes has been assessed by several authors (McLachlan et al. 1981, Koop et al. 1982a,b, Koop & Griffiths 1982, Newell et al. 1982, Stenton-Dozey & Griffiths 1983, McLachlan 1985). Bacteria assume paramount importance in the energetics of the sandy beach and from standing stock estimates and annual turnover of the different components of the biota it was calculated that bacteria account for as much as 87% of annual beach production (Koop & Griffiths 1982). Koop et al. (1982b) showed that 90% of leachates derived from the stranded kelp *Ecklonia maxima* was utilised by bacteria. Calculations on carbon flow indicated that 23–27% of the carbon in kelp was converted to bacterial carbon and the residual, which was not incorporated into bacteria, was mineralised by the sandy beach microbes within 8 days. These authors stressed that the microbial community occupied a

central role in the rapid regeneration of inorganic material. Bacteria are also important as they colonise faeces produced by primary consumers and convert them to a suitable food source for filter feeders (Newell et al. 1982). Subsequently all this material is returned to the sea and supports detrital-based nearshore foodwebs (McLachlan et al. 1981, Duggins et al. 1989). However, on a South African beach, Koop et al. (1982a) estimated that only $0.4 \text{ g m}^{-1} \text{ d}^{-1}$ of carbon and $0.2 \text{ g m}^{-1} \text{ d}^{-1}$ of nitrogen is returned to the sea. They suggested that primary production in the adjacent subtidal communities was more dependent on *in situ* remineralisation of nutrients and on local upwelling than on nutrients originating from beach-cast materials. Also in question was whether sandy beaches accumulated nitrogen by incorporation into microbial or faunal biomass or in inorganic form in the groundwater. This controversial issue was addressed by McLachlan & McGwynne (1986) who concluded that beaches can act as nitrogen sinks or sources for nutrients depending on their state. Eroding and stable beaches are unlikely to be nitrogen sinks, while prograding beaches, where ground water flow is not high enough to flush nutrients from the system faster than the sand accumulates them, probably act as sinks. High levels of interstitial nutrients associated with the remineralisation of beach-cast materials have also been reported at other beaches of western Australia (McLachlan 1985). Comparing two modally reflective beaches, with and without large amounts of wrack deposits, higher values of the dry biomass of the macro- and interstitial fauna were found when beach cast was present. This difference was due to the less dynamic conditions of the beach and to the enrichment of the interstitial system by wrack leachates. Furthermore, there was an inverse correlation between both bacterial and protozoan numbers and meiofauna numbers suggesting that grazing by the latter kept down bacteria densities.

Studies on the meiofauna (McIntyre 1968, McLachlan 1977, 1985, Koop & Griffiths 1982, Brown & McLachlan 1990) and of its zonation (McLachlan 1980) indicate nematodes and oligochaetes as dominant taxa, and that their distribution patterns are directly related to the distribution of the wrack, below which concentrations of dissolved organic material (DOM) were exceedingly high (Koop & Griffiths 1982). This distribution suggests that the meiofauna used the leachates as a food source directly, but the possibility that the DOM is used initially by the bacteria, which in turn are used as a food source by the meiofauna cannot be precluded (McLachlan 1985). However, beach-wrack accumulation can also affect infauna adversely by restricting oxygen exchange and according to McLachlan (1985), meiofauna did not occur in areas of dense wrack accumulations. McGwynne et al. (1988) concluded that interstitial meiofauna can be affected by the toxic effects of hydrogen sulphide, low pH and low oxygen concentrations in the porewater under the wracks. Alkemade & van Rijswijk (1993), studying the decomposition of stranded seaweed along the Antarctic coast, found an interesting correlation of the number of nematodes with the height of the location (relative to water), the carbon:nitrogen ratio and the salinity of the sample. Larger nematode populations occurred as the nitrogen content increased relative to carbon content, and for material stranded at higher locations on the beach. The negative correlation between salinity and nematode numbers was presumed from the limited population growth in situations with high tidal influences. Nematode numbers were also indirectly dependent on sediment composition and water content with higher numbers found in situations with melt water runoff.

Although numerically the meiofauna exceed the macrofauna, with an average ratio of $10^5:1$, the former never attains the high biomass of the latter due to their small size. Estimates of mean biomass ratios therefore approximate to 1:5 (McLachlan 1985). Based on

production estimates, the meiofauna and macrofauna were of approximately equal importance on four exposed sandy beaches in South Africa, where meiofauna were dominant on two beaches and macrofauna on the other two (McLachlan 1977). Although beaches supporting high concentrations of macrofauna are generally associated with a sparser meiofauna (McIntyre 1968), McLachlan (1977) concluded that the meiofauna and the macrofauna were quite distinct components of the beach fauna and suggested that the meiofauna, even if not part of the macrofauna food chain, was of great quantitative importance in the energy flow. The interstitial system thus has the prime function of processing the organic materials having heterotrophic bacteria at the base and predatory meiofauna at the apex of the food chain. Within this process, nutrients are then returned to the sea (Brown & McLachlan 1990).

Rates of litter decomposition are highly variable and are influenced by both site- and time-specific environmental conditions and in most cases depend on the composition of the wracks themselves. Smith & Foreman (1984) individually tested ten of the most important seaweeds within a seaweed community in the southern Strait of Georgia (British Columbia, Canada) using the litter bag technique. They showed that rates of decomposition of submerged samples varied among species with the time required for litter to disappear from bags ranging from 6 days to 70 days. This rate depended mainly on the contents of crude fibre and detritus particle size. More rapid decomposition occurred in those species with lower crude fibre content and decreasing particle size, probably due to a greater surface area of particulate material exposed to microbial attack. Similar findings were recorded for seagrass leaves where rates of decomposition increased in relation to an increase of the rates of leaching and microbial degradation as particle size of the detritus decreased (Harrison & Mann 1975, Robertson & Mann 1980). On an East African coast, leaves of the seagrass *Thalassodendron ciliatum* took 42 days to lose 50% of their initial ash-free dry weight in litter bag experiments (Ochienga & Erftemeijer 1999). A slight reduction in the decomposition rate of seagrass material was obtained when litter bags were buried and the reduction was attributed to a reduced exposure to wave action at high tide and to reduced drying by the sun, oxygen availability and grazing by the fauna. In a mudflat area in Mauritania, Hemminga & Nieuwenhuize (1991), with this same technique, showed that the time required for 50% weight loss of *Zostera* and *Cymodocea* leaf litter was 158 days and 50 days, respectively, in the intertidal zone, whereas these figures were reduced to 49 days and 37 days in the subtidal zone. In another study on the decomposition of stranded seaweed along the Antarctic coast (Alkemade & van Rijswijk 1993), it was demonstrated that abiotic location-related characteristics, such as the water content of the stranded seaweed and sediment composition, strongly influenced the decomposition rates. These rates were high when water content of the deposits was high. Furthermore, tidal inundation and melt-water flows increased weight losses of seaweed by carrying away small fragments into the sea. With lower water content, the debris dried out and there was a decrease in bacterial respiration, leading to a lower rate of breakdown of the decaying material (Newell et al. 1985). In stranded algal deposits found on a sandy beach of South Africa, Koop et al. (1982b) estimated that kelp decomposed and was replaced over an 8-day cycle. Only a small amount of this organic material was consumed by the macrofauna, whereas 94.2% of nitrogen from the kelp debris was incorporated into the bacteria and this incorporation was accompanied by a mineralisation of approximately 70% of the carbon (Koop et al. 1982a). In a similar experiment on the giant kelp *Macrocystis pyrifera*, Inglis (1989) calculated that within 18 days the algae in the litter bags had lost 41–64% of their initial dry weight and that the involvement

of the macrofauna was insignificant. This result contrasts with the findings of Griffiths & Stenton-Dozey (1981) who estimated that grazers removed 60–80% of the organic input from their study site in 20 days.

Even if the above findings are controversial, the importance of detrital grazers on decomposition rate of macrophytes is generally accepted. Macrofaunal consumers such as isopods, amphipods and dipteran larvae fragmentise the detritus, accelerate decomposition through the spread of bacteria and make the material more available to decomposition through their burrowing-activities (Robertson & Mann 1980, Stenton-Dozey & Griffiths 1980, Harrison 1982, Bedford & Moore 1984, Inglis 1989). Also, nematodes and other meiofauna can be of considerable importance in re-elaborating the debris and their activity can stimulate bacterial metabolism and lead to a rapid decay of beach-cast material (Heip et al. 1985). However, leaching of compounds as polyphenols and tannins from seagrass leaves, which have been implicated as grazing inhibitors (Harrison 1982), may be needed before detritivores will begin to fragment the deposits. Harrison (1982) has demonstrated how minor constituents of *Zostera marina* leaves control rates of fragmentation and microbial decay by limiting the growth of algae and bacteria and the activity of amphipod grazers. On the other hand, grazers such as the amphipod *Gammarus locusta* can slow down or even inhibit algal decomposition by selectively removing rotting weeds (Bedford & Moore 1984).

Macrofaunal beach-wrack communities and species succession

Herbivores, detritivores and predators of stranded macrophytes

Numerous studies report on the macrofaunal community of macrophyte wracks from different parts of the world (Bigot 1970, Moore & Legner 1973, Griffiths & Stenton-Dozey 1981, Behbehani & Croker 1982, Griffiths et al. 1983, Stenton-Dozey & Griffiths 1983, Lavoie 1985, McLachlan 1985, Inglis 1989, Chevin 1998, Ochieng & Erftemeijer 1999, Colombini et al. 2000, de Rougemont 2000, Dugan & Hubbard in press). The fauna of beach-cast wrack is generally diverse due to location, beach morphology, season, climate and vegetation cover. In Madagascar, Bigot (1970) found a richer and more abundant fauna in wrack deposits higher up on the beach with tenebrionids and spider species dominant. On a South African beach a total of 22 species of Coleoptera, three Diptera and two Amphipoda were identified in the kelp wrack (Griffiths & Stenton-Dozey 1981). In New Zealand, Inglis (1989) distinguished 22 macrofaunal species of which six species (an amphipod, a dipteran, a centipede and three beetles) made up 93% of the individuals of the wrack-bed community. In northern New England, the beach wrack community was dominated by an amphipod species (*Orchestia platensis*) and oligochaetes that made up 86% of the total numbers (Behbehani & Croker 1982). These were followed by Collembola species, while predatory species constituted only 2% of the total. De Rougemont (2000), studying the beetle community associated with seaweed jetsam in Hong Kong, found that the fauna was less diverse in tropical and subtropical areas compared with temperate regions (e.g. 11 kelp fly predators and five marine staphylinids in Hong Kong compared with 22 and 11, respectively, in Japan, Shibata (1993)) and that other families (Carabidae, Scarabaeidae, Tenebrionidae), abundant in Europe, appeared to be absent in the tropics. On a reflective beach of

western Australia wracks were generally poor in species and the only important macrofaunal species living in the wracks was the amphipod *Allorchestes compressa* (McLachlan 1985), also found in abundance in the drifting wracks of the surf zone (Robertson & Lucas 1983). Colombini et al. (2000), analysing the community structure of wrack beds along a Somalian beach, found that species composition and abundance varied according to the season with a dominant (90%) amphipod species (*Talorchestia martensii*) in October–November and a more diverse fauna, composed of amphipods, isopods, gastropods and coleopteran staphylinid species in July–August. In contrast to other works, where dipteran species were the major components of the beach-cast material (Stenton-Dozey & Griffiths 1980, Inglis 1989, Phillips & Arthur 1994, Phillips et al. 1995a,b, Hodge & Arthur 1997), in the wracks of the Somalian beach dipteran larvae were completely absent. This absence was related to the short residence time of the beach wrack (10 day cycle) that would not permit successful dipteran breeding (Dobson 1974a,b, Stenton-Dozey & Griffiths 1980). In a survey of 15 beaches of Southern California, Dugan & Hubbard (in press) calculated that the biomass of talitrid amphipods, *Megalorchestia* spp. ranged from 1 g m^{-1} to 378 g m^{-1} and composed most of the wrack-associated macrofaunal biomass at all but two sites. On the latter beaches, the isopod *Tylos punctatus* was the major component. These authors found a positive correlation between the number of wrack-associated species (especially Coleoptera species) and the total cover and the % cover of macrophyte wrack on ungroomed beaches. Furthermore, species richness of wrack-associated macrofauna varied significantly between groomed and ungroomed beaches with very low values on mechanically cleaned beaches. Also, mean abundance of wrack-associated macrofauna was nine times greater on ungroomed beaches with low wrack cover than on groomed beaches. The authors showed the importance of wrack subsidies because they increased the total macrofaunal abundance on beaches by supporting an increased abundance of wrack-associated macrofauna and major consumers, such as amphipods.

Species succession in macrophyte wracks

Ephemeral resource units, such as wrack-bed communities and carrion, are generally characterised by a successional change of species with different groups associated with different qualitative stages of decomposition and ageing of the wrack. Lavoie (1985) suggested that the major invertebrate groups could be subdivided into “early”, “mid” and “late” in relation to their appearance in the wrack. A temporal separation of arrival at a specific food source may have a number of important consequences with regard to subsequent species interaction and community development (Hodge et al. 1996, Hodge & Arthur 1997). In some cases, early arrival can confer a competitive advantage, with late species encountering severe inhibition and early species being unaffected by the subsequent presence of the later species. Another process consists of an interspecific facilitation, with late species benefiting from the presence of the earlier arrival of primary colonists. These early arrivals modify the resource qualitatively and make it more suitable for the later species (Connell & Slatyer 1977, Schoenly & Reid 1987, Heard 1994). Finally, a temporal separation may simply result in a reciprocal avoidance, reducing levels of interspecific interference at the food source.

Amphipods are considered to be the primary colonisers of newly deposited wracks because they have a tendency to forage on freshly stranded material where high densities are reached (Moore & Legner 1973, Griffiths & Stenton-Dozey 1981, Behbehani & Croker

1982, Inglis 1989, Marsden 1991b, Colombini et al. 2000). A comparative study of the mean zonations of different wrack-inhabiting species showed that amphipods were the group closest to the sea and gradually changed their zonation according to the semi-lunar cycle (Colombini et al. 2000).

Other early wrack colonisers are isopod species, such as *Littorophiloscia tropicalis* (Chelazzi & Ferrara 1978, Colombini et al. 2000). This species uses wracks as a refuge and a food source and during the nocturnal low tides leaves the wrack mounds and moves around like other terrestrial intertidal isopods (Kensley 1974).

In New Zealand, adult Diptera colonised wrack beds within the first 24 h (Inglis 1989) whereas Lavoie (1985) suggested that all the dipterans found on Californian wrack beds occurred within the first 4 days. Similar results were obtained for species of British seaweed fly (Dobson 1974a, Hodge & Arthur 1997). Generally, adults of sandy-beach kelp flies are insignificant consumers of kelp because their activity is mainly limited to eating exuded substances and laying eggs (Griffiths & Stenton-Dozey 1981). However, the larvae, generally found associated with decaying seaweed, contribute greatly to the breakdown of kelp tissue as a result of their feeding and tunnelling activity (Stenton-Dozey & Griffiths 1980, Inglis 1989, Chown 1996). Using the consumption rates and larval densities of two dipteran species (*Paractora trichosterna* and *Antrops truncipennis*) Chown (1996) estimated kelp consumption to be 714–870 g dry mass kelp m⁻² over his 7-wk period of study. For another dipteran species, *Fucellia capensis*, a value of 0.25 mg dry kelp mg⁻¹ wet larva day⁻¹ was calculated (Stenton-Dozey & Griffiths 1980). The bacterial populations of seaweed may be consumed by *Coelopa* larvae. It has been suggested that either some constituent of bacterial cells is required or that there is a need for a chemical of algal origin which is released only through bacterial action. Experimental work indicated that *Coelopa* larvae were able to grow on bacteria not associated with marine algae, supporting the hypothesis that the bacteria themselves were being used as a supply of nutritive energy (Cullen et al. 1987).

Early invaders of wracks are followed by other insect species, mainly Coleoptera, that colonise the beds as these dry out (Moore & Legner 1973, Griffiths & Stenton-Dozey 1981, Colombini et al. 2000). However, as for isopod species, beetles contribute only about 10% of the total number of animals (Stenton-Dozey & Griffiths 1983). Herbivorous coleopterans, such as Tenebrionidae, Hydrophilidae, Curculionidae and Scarabaeidae, can be found feeding on individual kelp fronds but are considered to be of minor significance as consumers of kelp. In fact, only 3.5% of the kelp deposited on the beach is consumed by herbivorous Coleoptera, whereas amphipods and kelp-fly larvae consume 52.7% and 14.7%, respectively (Griffiths et al. 1983). Carnivorous beetles, belonging to the Staphylinidae, Histeridae and Carabidae families, form a large component of the wrack-bed fauna and tend to prey on larvae of dipterans and other insects. Chevin (1998) has listed a number of predatory species that occurred in wracks along the French Atlantic coast. Colombini et al. (2000) reported that the histerid, *Halacritus algarum*, is a “late” coloniser of wrack because of its tendency to prey on insects in decaying plant material. On the other hand the staphylinid *Cafius ragazii*, a fairly “early” wrack invader, strictly followed the changes in zonation of the wracks in relation to the semi-lunar phase, indicating a strict predator–prey relationship. Other species, such as the ptilid, *Actinopteryx fucicola*, remained in the wracks only until the moisture conditions became unsuitable for saprophytic fungi, the spores of which constitute its principal food. The authors concluded that the successional colonisation of wracks was strongly influenced by the species’ physiological and trophic needs and their appearance or

disappearance in the wracks was due to the progressive microclimatic changes of the deposits in relation to their varying position on the beach.

Species succession in carrion

Another discrete and ephemeral system is represented by carrion stranded on the shore. This, like macrophyte wracks and other resources limited in time (e.g. dung, Valiela 1974, Koskela & Hanski 1977), is good material for the study of arthropod invasion, utilisation and succession. Carrion communities are also excellent for elucidating time-dependent patterns. Carcass microhabitat is small, has clear boundaries and frequently less than 30 necrophilous species are found on small carcasses. The carrion arthropod community develops primarily as a continuum of gradual change (Schoenly & Reid 1987). The major temporal features of carrion arthropod development include: a rapid invasion by feeding dipterans and ants, a period of maximum arthropod diversity achieved when carcass tissues are most attractive to consumers and a period of monotonic decline in arthropod richness as the carcass resource becomes depleted (Schoenly 1983, Schoenly & Reid 1983, 1987). These findings are based on studies of carcass of other environments (namely deserts) but many similarities can be found with beach-cast carrion.

In xeric habitats carcasses are subjected to rapid microhabitat changes (desiccation) and sand covering. Thus the utilisation of the resource by each species is limited in time. Furthermore, persistence of carcasses on beaches may vary widely from beach to beach and from season to season depending on beach aspect, orientation, exposure and substratum, nearshore currents, wave intensity, tidal ranges, weather and on the density and activity of scavengers (Bodkin & Jameson 1991). A facilitation mechanism on behalf of the early invaders (flies, ants) has been suggested by Connell & Slatyer (1977) and appears to fit well to species succession in carrion. Dipterans and ants are viewed as the most efficient colonists because of their good dispersal abilities and high densities (McKinnerney 1978). Through their combined tunnelling and feeding actions they facilitate the access of necrophagous taxa, such as trogid and dermestid beetles, to internal tissues. Other taxa, such as burying beetles (Silphidae: *Nicrophorus* spp.), arrive later on larger carcasses for feeding but use smaller and secure carcasses for interment and reproduction (Wilson & Knollenberg 1984).

In a study of arthropod succession on a leatherback turtle (*Dermochelys coriacea*) stranded along a beach of French Guiana (Fretey & Babin 1998) a facilitation mechanism was achieved by vertebrate scavengers (black vultures, *Coragyps atratus*) that fed on the fresh carcass some hours after stranding. Torn flesh attracted dipterans (calliphorids) that soon started oviposition. On the following day, coleopteran species (Scarabaeidae, Carabidae) were observed, while during the night Blattodea and other nocturnal coleopterans, mainly tenebrionids, exploited the carcass. By the third day dipteran larvae emerged from the holes and attracted staphylinids and histerids. Species richness peaked on the fifth day, with all the above orders contemporaneously present on the turtle. By the seventh day the carcass was picked clean, although Diptera and Coleoptera were still the main groups represented on the carcass. Carabids, staphylinids and histerids were mainly predator species, hence their arrival occurred after development of their prey (fly larvae). Scarabaeids were coprophagous or detritivorous and contributed to the decomposition of the carcass, while tenebrionids were sometimes saprophagous, mycetophagous or predators according to the species. Necrophagous arthropods were selectively attracted by the odour released

during the process of decay and, when the changing conditions in the substratum became unfavourable, the earlier colonists were replaced by other species. Each member of the insect family had a specific role in the decomposition of carrion, intervening according to its feeding and reproductive requirements and contributing to nutrient recycling. In a similar study on species succession on red-eared turtle (*Pseudemys scripta elegans*) carrion in a wooded area in Massachusetts (Abell et al. 1982), an accelerated process of breakdown and decay in the presence of saprophagous arthropods was observed when this was compared with arthropod-free carrion. Calliphorid flies were again the dominant species of the carrion community whereas the lack of large numbers of Formicidae and Scarabaeidae was related to the presence of the shell, which induced higher water retention levels and temperature. There was also a clear succession between sarcophagid, calliphorid, syrphid, drosophilid and muscid larvae while the Coleoptera species showed a greater degree of coexistence and temporal overlap.

The importance of insects as decomposers was clearly pointed out in other studies on beach carrion (Lord & Burger 1984a,b). Studying the decomposition of gull (*Larus argentatus* and *L. marinus*) and harbour seal carcasses (*Phoca vitulina*) the workers emphasised that marine invertebrates (e.g. crabs, amphipods) and scavenging birds had a negligible impact upon decay and that few arthropod species dominated the process. On harbour seal carcasses (Lord & Burger 1984b) blow-fly larvae and dermestid beetles were the primary carrion consumers. The former consumed the internal viscera and the soft tissues within approximately 14 days, whereas the latter ate the remaining tissues within 20 days. The importance of dermestids in the decomposition process was also reported for other carcass types in different environments (McKinnerney 1978). Spiders, staphylinid and histerid beetles were the major predators of the necrophagous species. However, several beetle taxa, such as Silphidae, which often occur as carrion inhabitants, were not found on seal carcasses and their absence was related to the harsh marine conditions encountered in the rocky supratidal zone. In less extreme environmental conditions a greater number of predatory insects can be supported, as was reported for gull carcasses in vegetated habitats (Lord & Burger 1984a). In this case, moderate climatic conditions increased arthropod colonisation and survival, resulting in an increase of the arthropod community. In particular, consumption and decomposition rates were reduced because there were more predator species and fewer carrion consumers in this habitat.

Observations on a dolphin (*Stenella* sp.) carcass stranded on a beach of Southern Italy again indicated the importance of insect species in the consumption of the animal (pers. obs.). The dolphin had been stranded about 20 days before the arthropods were analysed and half of its body, with all internal soft parts, had already been consumed (i.e. the bones were half picked clean). Dipteran larvae were most abundant and represented the dominant taxa. These larvae attracted coleopteran predators, mainly staphylinids and histerids, which constituted 49% of the total taxa present on the carcass (excluding dipterans from counts). Fewer amphipod and isopod species were present (3% and 16%, respectively) as would be expected from the advanced state of decay. The remaining 32% of the taxa was represented by scavenging tenebrionids (*Phaleria* spp.).

Not only predatory beetles but also shorebirds are opportunistic feeders on flies, larvae and other insects associated with carrion. Sanderlings (*Calidris alba*) were reported to forage on fly species associated with carcasses of laughing gull (*Larus atricilla*), northern gannet (*Morus bassanus*), common loon (*Gavia immer*) and striped burrfish (*Chilomycterus*

schoepfi) and on one occasion birds were seen protecting a carcass from other avian predators such as the black-bellied plover (*Pluvialis squatarola*) (Grant 1997).

Both macrophyte wracks and carrion must be considered as a “processing chain”, that is, as units of a resource passing through a sequence of condition changes over time, with consumers specialising in a specific resource in each condition and influencing the rate at which the resource is transformed (Heard 1994). In this process, a range of interspecific interactions can be found and can vary from amensal to commensal depending on a number of factors. These factors include temporal scale, species composition and relative processing rates and efficiencies (Heard 1994, Hodge & Arthur 1996).

Intra- and interspecific interactions in wracks and feeding preferences

Macrofaunal species (amphipods, isopods and dipteran larvae) are the major primary consumers of beach-wrack macrophytes and there are many studies on individual species within the macrophyte community, and their interactions in the wracks (Craig 1970, 1973, Dobson 1974a,b, Hayes 1974, Kensley 1974, Koop & Field 1980, 1981, Robertson & Mann 1980, Stenton-Dozey & Griffiths 1980, Venables 1981, Behbehani & Croker 1982, Agnew & Moore 1986, Marsden 1991a,b, Phillips & Arthur 1994, Phillips et al. 1995a,b, Chown 1996, Hodge & Arthur 1997, Persson 1999, Pennings et al. 2000). Amphipod species are usually numerically dominant in wracks. Much attention has been given to the biological cycles, population densities, daily production and respiration estimates of *Orchestia* and *Talorchestia*, species commonly found associated with macrophyte deposits (Venables 1981, Behbehani & Croker 1982, Marsden 1991a,b). Persson (1999), in studying the growth and reproduction of *Orchestia gammarellus* in wrack beds of beaches along the Baltic Sea, showed the influence of wrack type on the growth rates and reproductive patterns of the amphipods. Growth rate of the summer generation was significantly higher in beds dominated by the eel-grass, *Zostera marina*, and this increased growth was probably due to the higher temperatures that were reached, because this type of wrack was generally drier than the algal beds. Higher temperature increased molting frequency and induced higher growth rates. In wrack beds of the alga *Fucus vesiculosus*, overwintering individuals had a significantly greater mean length compared with those overwintering in eel-grass, indicating that some benefits were obtained by animals living in the algae. Studies on feeding preferences indicated that *Orchestia gammarellus* preferred to ingest algal material rather than angiosperms (Moore & Francis 1985) perhaps because it was softer and easier to handle (Bedford & Moore 1984) or because it attained a higher density of microorganisms. In fact, it was demonstrated that neither seagrass litter nor algal material were digested by the amphipods (Lopez et al. 1977, Bedford & Moore 1984) but that the beach-hoppers used the attached micro-organisms as a source of nutrient instead. Colombini et al. (2002) showed that the differences found in the non-uniform spatial distribution of two amphipod species (*Talorchestia brito* and *Talitrus saltator*) living along a Tunisian beach were due to the patch distributions of stranded food items.

Another study on the feeding preferences of three North American supralittoral crustacean species (the isopod *Ligia pallasii*, and the two amphipods *Megalorchestia californiana* and *Traskorchestia traskiana*) showed that the three species had similar feeding preferences and suggested that these were based on general algal traits rather than on particular adaptations of specific herbivores (Pennings et al. 2000). Furthermore, the three

species showed a tendency to prefer aged over fresh seaweeds. Preference for older wrack was basically explained by its reduced water content. Because rate of food intake is limited by its volume, a given volume of aged seaweed will have several times the organic and mineral content of the same volume of fresh material. This concentration of organics was strongly preferred by the talitrids, especially, when time for feeding was limited (Carefoot et al. 1998). Also, the reduced quantity of defensive compounds, such as phenolics and terpenes, which leach and break down once the seaweeds begin to desiccate, probably render older wracks more palatable than fresher ones, as was demonstrated for senescent angiosperm leaves (Harrison 1982, Valiela et al. 1979). On the contrary, two other amphipod species *Echinogammarus pirloti* and *E. obtusatus* showed neither a preference for old versus fresh seaweed nor for substrata containing high or low loadings of bacteria. However, both preferred the "softest" food material, usually decaying *Laminaria digitata*, and Agnew & Moore (1986) suggested that the role of micro-epiphytes (bacteria, diatoms) in the diets of these amphipods may be of minor importance. Instead, the deficit of nitrogen may be supplemented by feeding on meiofaunal crustaceans, dead conspecifics, moulted exoskeletons or by coprophagy. In *Orchestia scutigerula*, Moore et al. (1995) noticed that this beach-hopper fed on a large spectrum of materials, although items like diatoms crustacean and mite fragments were in the minority. Tussock grass and green algal debris were highly consumed, although there was evidence that their attractiveness changed over time in favour of algae. This change was related to the conditions of the deposits, where different materials were available in different proportions, depending on their location on the beach and on their time of stranding. In fact, there was a decline of algal-derived fragments in the gut contents of *O. scutigerula* with landward shifts of the debris. Preference experiments indicated that these talitrids preferred brown algae to certain red and green algae, which are known to be protected chemically (Paul et al. 1987, Hay & Fenical 1988). It was also evident that *O. scutigerula* fed on vegetable material of the softest texture, avoiding harder materials like the vascular tissue of tussock grass. Observations on the feeding behaviour of the surf-zone inhabiting amphipod *Allorchestes compressa* also indicated that these amphipods fed on small particles of both seaweeds and seagrass but deliberately avoided red algae and preferred the decomposing tissues of the laminarian *Ecklonia radiata* taken from beached stacks of macrophytes (Robertson & Lucas 1983).

Studies on individual isopod species in relation to macrophyte wrack deposits have been carried out by a number of workers (Hayes 1974, Kensley 1974, Koop & Field 1980, 1981, Robertson & Mann 1980). Koop & Field (1980) came to the important conclusion that the life histories of species inhabiting this protected microhabitat were governed by biological factors such as food availability more than by physical ones, as might be expected in supralittoral species. They showed an increased growth and reproductive development of *Ligia dilatata* during winter and related it to the clear seasonal pattern of kelp debris availability. Following periods of high food availability, in early spring ovigerous females and new cohorts appeared, showing that the surplus of assimilated energy was used for reproduction. Furthermore, field observations indicated that *L. dilatata* ate only debris of the kelp *Ecklonia maxima* and thus depended almost entirely on cast material as a food source. In another study on the energy flow through a population of the same isopod species, fast consumption and egestion rates, coupled with low assimilation and growth efficiencies suggested *Ligia dilatata* may be a major energy transformer (Koop & Field 1981). Of its total energy consumed, only 1.3% was channelled into production whereas 72% was extruded as faecal pellets. These, together with kelp fragments and dissolved organic matter released

mechanically by trituration, are then suspended and returned to adjacent aquatic ecosystems. Beach-cast material can also influence the spatial distribution patterns of isopod species on beaches. Hayes (1977), studying a Californian population of *Tylos punctatus*, found more isopods burrowed beneath or near piles of stranded kelp than in regions where kelp mounds were absent. On a Mexican beach, Simmons (in Brown & Odendaal 1994) found that the distribution of active *T. punctatus* could be related to the distribution of its primary food source *Zostera marina* and that the degree of wrack moisture was an important element in attracting the isopods. Kensley (1974) came to a similar conclusion for South African populations of *Tylos granulatus* and *T. capensis*, in which the distribution patterns of both burrowing and foraging individuals were studied in relation to the distribution of kelp deposition on the beach. Food preference experiments have shown that isopods were attracted to the food source by olfactory means, and food items with stronger odours were preferred. Generally, high isopod numbers corresponded with the presence of food deposits. As in other isopod species, juveniles and adults, preferred drier brown algae to fresh, and both age groups preferred animal matter when given the choice between animal and macrophyte debris (Pennings et al. 2000).

In two sympatric scavenger tenebrionid species of the genus *Phaleria* (*P. provincialis* and *P. bimaculata*) the bacteria isolated from the gut contents were studied by physiological and molecular analysis (Barberio et al. 2001). The study showed a higher biodiversity of bacteria in *P. bimaculata* than in *P. provincialis* indicating a difference in foraging areas and, indirectly, in food preferences.

Studies on dipteran species associated with kelp material washed ashore are abundant in the literature and can be reviewed according to the geographical location of the species. In the sub-Antarctic, Marion Island and South Georgia have been studied. At Marion Island (Crafford 1984, Crafford & Scholtz 1987, Klok & Chown 2001), attention has been focused on *Paractora dreuxi*. This species contributed to the degradation of stranded kelp, mainly *Durvillaea antarctica*, by consuming the stranded material directly or by tunnelling through the decaying fronds and thus increasing microbial decomposition. Recently, distinct ontogenetic differences in thermal tolerance and water balance have been elucidated for this species and related to the effects of global climatic change, which consequently produced pronounced microclimatic changes in the wracks (Klok & Chown 2001). Crafford & Scholtz (1987) estimated that the larvae of *Paractora dreuxi* were responsible for 35% loss of kelp dry mass during kelp degradation and that this species was important in the recycling of nutrients in the terrestrial ecosystem of the island. At Husvik Harbour, South Georgia, Pugh & MacAlister (1994) found that two kelp flies, *P. trichosterna* and *Antrops truncipennis*, were obligate feeders of stranded seaweeds. Chown (1996) showed that these two flies contributed significantly to kelp degradation, with *Paractora trichosterna* responsible for 12% of kelp dry biomass in beds protected from vertebrate trampling and 20% in the exposed ones. In comparison, *Antrops truncipennis* was responsible for an additional 3% loss in the exposed and 8% in the protected beds. *Paractora trichosterna* was macropterous and not brachypterous like *P. dreuxi* at Marion Island and this difference in wing development was related to the different strategies adopted by the two species for the utilisation of stranded seaweeds. At Husvik, seaweeds were deposited as strings or small patches and thus favoured the retention of a flight capacity. At Marion Island, where there was the tendency of seaweeds to form large stranded beds, brachyptery was favoured. The differences found in the biomass of the two species indicated that they were utilising kelp in different ways, with *Antrops truncipennis* favouring more sheltered

areas where it deposits its eggs. The author concluded that the dipteran assemblage associated with wrack was important in wrack decomposition and contributed significantly to nutrient recycling.

In the British Isles, much work has been carried out on the seaweed flies of the genus *Coelopa*, which are considered to be a major component of the wrack beds (Day et al. 1980, 1982, 1983, 1987, Butlin et al. 1982, 1984, Butlin & Day 1985, 1989, Cullen et al. 1987, Phillips & Arthur 1994, Phillips et al. 1995a,b, Leggett et al. 1996, Hodge & Arthur 1997). Earlier works on shore-flies were mainly based on systematic and life-history studies, particularly on two closely related species, *Coelopa frigida* and *C. pilipes* (Egglishaw 1960, Dobson 1974a,b, 1976, Simpson 1976). Dobson (1974a,b) analysed the breeding cycles of the two species in relation to the duration and type of wrack and studied the variations in population size, in species composition and the effects of the destruction of the wrack-beds on the two *Coelopa* species. In a study of the larvae of some dipteran species associated with wrack on Californian beaches, Kompfner (1974) emphasised the different strategies adopted by the flies in the exploitation of the available food and habitat resource. One species (*C. vanduzeei*) found exclusively in the lower, wetted beach wracks, developed quickly, whereas others (*Fucellia costalis*, *F. rufitibia*), occurring in the mid- and upper-beach levels, were able to use the wrack for longer periods of time and consequently had a longer pupal stage.

The genetics of seaweed flies have also been studied in some detail. It has been demonstrated that all northern European populations of *Coelopa frigida* are polymorphic for a large inversion on chromosome I (Butlin et al. 1982, Day et al. 1982, 1983) and that polymorphism is maintained by selection. Laboratory experiments have indicated that at least three types of selection may occur: heterokaryotypic advantage in egg-to-adult viability (Butlin et al. 1984), variation in development time (Day et al. 1980) and sexual selection (Butlin et al. 1982, Day et al. 1987). Butlin & Day (1989) studied the connections between environmental variables (i.e. composition, surface area, depth, extent of decomposition, temperature, degree of moisture of seaweed beds) and inversion frequencies, while Leggett et al. (1996) assessed the genetic effects of competition in *C. frigida* and *C. pilipes*. Leggett et al. concluded that both intra- and interspecific competition can be fierce and appear to be the force maintaining, rather than eliminating, genetic variation.

In a more ecological study, Phillips et al. (1995b) showed that these two *Coelopa* species frequently coexisted, despite competition and that the temperature of the wrack had an important role in the distributions of the larvae. *C. frigida* larvae preferred cooler parts of the bed whereas *C. pilipes* larvae preferred the warmer ones. These distributions were shown to be caused by the behaviour of the larvae themselves rather than a selection made by ovipositing females. The different micro-distributions within beds caused competitive abilities to be frequency-dependent and thus permitted coexistence. In another study (Phillips et al. 1995a) it was shown that the different egg distribution of the two fly species depended on a different preference for seaweed species, rather than on microhabitat factors such as temperature and humidity, with *C. pilipes* showing stronger preferences for *Fucus* than did *Coelopa frigida*. Once established in the wrack, larvae were able to move around according to their microhabitat preferences. The distributions and interspecific interactions of the *Coelopa* species and of the other fauna found within the wrack beds were analysed by Phillips & Arthur (1994). They found that all of the animals were non-randomly distributed in the wracks. *Coelopa* larvae aggregate in warmer and deeper areas, in agreement with the fact that breeding sites occurred in parts of decaying weed where temperature was raised by

anaerobic decay (Egglshaw 1960, Dobson 1974a). This contrasts with amphipod species, which presented a negative correlation with temperature and dominated the community in cool wrack beds but were not significantly influenced by depth within the bed. Enchytraeids were different again and were dependent on depth of the wrack but not on the temperature. Finally, the distribution of the commonest predator species (the staphylinid *Cafius xantholoma*) was correlated with the distribution of its prey (dipteran larvae, enchytraeids) more strongly than with the abiotic factors. It was concluded that the different specialisations would tend to reduce the intensity of any competitive interactions between the *Coelopa* species and the other groups. In a more detailed study on the interactions between the three commonest seaweed species, *C. frigida*, *C. pilipes* and *Thoracochaeta zostera* (Hodge & Arthur 1997) it was shown that there were no systematic differences in the colonisation patterns of the wrack with all three species arriving soon after wrack deposition. However, a form of priority effect might have been produced through the oviposition behaviour of females, which differed among species. *C. frigida* tended to lay eggs in batches while the other two species laid eggs singly. In this case the competitive stage of the larvae of *C. frigida* could occur earlier and at higher densities on the wracks compared with those of other flies. The other two species would then be at a disadvantage and would suffer because of their interactions with the larger and more competitive *C. frigida* larvae. The authors found that all pairwise interactions were extremely asymmetric with *C. frigida* being the strongest competitor species and *Thoracochaeta zostera* the weakest. Furthermore, a strong facilitatory effect of *Coelopa pilipes* on *C. frigida* was observed on the latter's emergent population size, which was more than double when reared on chopped seaweed. The minced seaweed was used to simulate the fragmentation of seaweed by the fly larvae in the field. This facilitatory effect was explained by the resource modification theory, according to which the larvae of *C. pilipes* changed the nature of the resource, perhaps physically, chemically or microbially, to favour feeding of *C. frigida* larvae. This facilitation, combined with the inhibition of *C. pilipes* by *C. frigida*, produced a contramensal interaction common in other interspecific interactions (Hodge & Arthur 1996).

Shorebirds and other terrestrial animals linked to wracks

Beach-cast macrophytes supporting prey resources are commonly exploited by a number of shorebirds. In Australia, the ruddy turnstone (*Arenaria interpres*), the hooded plover (*Charadrius rubicollis*) and the silver gull (*Larus novaehollandiae*) were all found closely associated with beach-wrack accumulations (Kirkman & Kendrick 1997). The hooded plover was most abundant where there were large amounts of macroalgae. Plovers nested close to macroalgae, making small depressions in the sand, and fed on crustaceans, molluscs, insects, and polychaetes associated with the wracks (Schulz & Bamford 1987). In a few other studies, the distribution and abundance of shorebirds and other avian predators were related to densities of standing stocks of stranded algae. On beaches of the Skeleton Coast, Namibia, Tarr & Tarr (1987) reported higher shorebird densities in areas with higher densities of kelp stranded on the shores, and it has been shown that beaches with high kelp inputs supported 75% higher biomass of potential prey organisms than did beaches lacking stranded kelp (Tarr et al. 1985). The potential importance of prey associated with macrophyte wracks was also stressed by Griffiths et al. (1983) for beaches in the western Cape of

South Africa. Polis & Hurd (1996b) estimated that the overall arthropod abundance in areas receiving input from the ocean was 2.5 to >550 times greater than mainland sites away from such input. Bradley & Bradley (1993), comparing censuses of over-wintering shorebirds in southern California before (1969–73) and after kelp recovery (1984–6), found that five shorebird species (spotted sandpiper, *Actitis macularia*, wandering tattler, *Heteroscelus incanus*, whimbrel, *Numenius phaeopus*, black turnstone, *Arenaria melanocephala* and ruddy turnstone, *Arenaria interpres*) out of nine increased dramatically in abundance during the second census period. The authors suggested that the increase was caused by the recovery of kelp beds off the coast, which in turn increased prey availability to foraging shorebirds. This was indirectly confirmed by the insignificant increases found for other species (black-bellied plovers, *Pluvialis squatarola*) which did not utilise algal windthrow. On two beaches in Baja California, Lopez-Uriate et al. (1997) suggested a relationship between migrating shorebirds and wrack-associated prey. In particular, at Punta Cabra, the semipalmated plover (*Charadrius semipalmatus*), which generally preferred amphipods over other food items, benefited from the extremely abundant kelp wrack washed ashore. In this locality, a similar relationship was also found for the spotted sandpiper (*Actitis macularia*). The high abundance of snowy plovers (*Charadrius alexandrinus*), which generally prefer dune-backed beaches, was attributed to the distribution of the staphylinid *Bledius* sp. found in abundance on this beach (Grover & Knopf 1982). In a recent study on southern Californian shores, Dugan & Hubbard (in press) found positive correlations between the wintering abundance of two plover species (black-bellied plovers, snowy plovers) and the standing crop of wrack. The positive correlations found between the abundance of the two species and the abundance and species richness of the wrack-associated invertebrates suggested that this relationship was due to the increase of prey availability in the wrack subsidies. The authors stressed that human disturbance, such as beach grooming, has a heavy impact on the composition and trophic structure of the macrofauna community. This grooming may significantly reduce the prey resources available to shorebirds and seriously threaten endangered species.

Not only beach-cast material but also macrophytes present in the intertidal zone were shown to be important for some migratory birds (Percival & Evans 1997). A direct relationship between biomass density of macrophyte food supplies, such as eel-grass species (*Zostera noltii* and *Z. angustifolia*) and green algae (*Enteromorpha* spp.), and the distribution of brent geese (*Branta bernicla*) was assessed. It was demonstrated that food intake rate rapidly declined as food biomass density decreased through the season. Consequently, the birds responded by additional foraging during the night, and when this was no longer possible the birds moved out of the site. The lower threshold of vegetation biomass densities was about 5 g m⁻² and was determined by the birds' energy requirements.

Apart from shorebirds, other secondary consumers connected to macrophyte subsidies are represented by spiders, scorpions, lizards, rodents and coyotes. In the states of Baja California Norte and Sonora (Mexico) these consumers were from 3 to 24 times more abundant on the coast and on small islands compared with inland areas and larger islands (Polis & Hurd 1995, 1996a,b, Rose & Polis 1998). In particular, in the Baja system, terrestrial consumers (spiders, scorpions, and lizards) ate prey, primarily arthropod species derived from the marine food web, which made up 95–99% of their diet. These conduits of marine productivity made the abundance of potential prey significantly higher in the supralittoral. Consequently, the population of spiders found along the coast was six times more abundant than that of inland areas (Polis & Hurd 1995). This relationship was also confirmed by stable

carbon and nitrogen isotope analysis, which showed that the spiders' diets were significantly more marine based than those of the inland populations (Anderson & Polis 1998). Scorpions likewise benefited from allochthonous flow from the sea. Along the shores of the Gulf of California, the supralittoral scorpion *Vaejovis littoralis* reached densities of 8–12 ind. m⁻², whereas in inland areas the density of all species combined reached a value of only 0.2–1.0 ind. m⁻² (Due & Polis 1985). For lizard populations, estimates were four times more abundant in the supralittoral zone than inland areas (Polis & Hurd 1996b). Further up the food chain coastal coyote populations, subsidised by the flow of abundant and diverse resources from the sea, also showed an increase in density, with populations 2.4–13.7 times more dense than in adjacent inland areas (Rose & Polis 1998). The coastal coyotes ate not only many living marine species (arthropods such as crustaceans and larvae of insects that eat algal drift, algae and molluscs) but also many terrestrial creatures that exploited marine input (arthropods, lizards, land birds and coastal rodents). This diverse and conspicuous marine input, together with the *in situ* terrestrial food supply had the effect of increasing the dietary spectrum and food intake of coastal coyotes compared with those of inland populations.

Offshore consumers of wracks

Filter feeders, grazing gastropods and fishes

Once deposited on shores, macrophyte wracks are fragmentised and decomposed. These wracks form an important food resource consisting of fragments of seagrasses and algae, bacteria, meiofauna and beach macrofauna which, during storms, can be washed back to the sea and form the basis for primary production and food chains in nutrient-poor coastal waters (Robertson & Hansen 1982). Filter-feeders, grazing gastropods and fishes are the major consumers of this food resource. It has been emphasised that particulate organic material from kelp detritus greatly increased the growth rates of offshore benthic and pelagic filter feeders (Duggins et al. 1989). The use of macrophyte-derived detritus by higher trophic levels, and its role in the secondary production has also been stressed by a number of other workers (Mann 1988, Duggins et al. 1989, Bustamante et al. 1995). Bustamante & Branch (1996) related the high biomass of filter-feeders on exposed shores to a higher concentration of particulate food and a more rapid replenishment than occurs on sheltered shores. Soares et al. (1997), studying populations of *Donax serra*, estimated the degree to which annual carbon requirements of this species were met by food originating from kelp. Pathways of this food resource were considered in both nearshore waters and after kelp stranding on the shore. In these habitats food became available to *D. serra* as particulate organic matter from frond erosion, drifting and stranded fragmentised kelp, pelagic bacteria in nearshore waters and intertidal bacteria and faeces from primary and secondary consumers (Newell et al. 1982, Griffiths et al. 1983). It was estimated that kelp detritus, bacteria and kelp consumers' faeces available in the water column surpassed several times the carbon and nitrogen requirements for both intertidal and subtidal clam populations and suggested that beach clams may have benefited from these energy subsidies (Soares et al. 1997). Other works in

Western Australia (Wells & Keesing 1989, Schiebling 1994) report that species such as Roe's abalone (*Haliotis roei*) feed exclusively on drifting fragments of macroalgae.

Lenanton et al. (1982) studied the diversity and abundance of the mobile epifauna associated with nearshore, detached macrophyte accumulations in Western Australia. The amphipod *Allorchestes compressa*, inhabiting wrack deposits and feeding on *Ecklonia radiata* (Robertson & Lucas 1983), could be returned to the surf zone during rough weather and constituted the major prey item of the juveniles of four fish species (the yellow-eyed mullet *Aldrichetta forsteri*, the cobbler *Cnidogobius macrocephalus*, the school whiting *Sillago bassensis* and the Australian herring *Arripis georgianus*). The data showed that the arrival of juvenile fishes on the open coast in late winter corresponded with the period of greatest deposition of detached macrophytes in the surf zone. The volumes of detached vegetation and associated amphipods were sufficient to support the fishes during summer months. Nearshore accumulations of detached macrophytes could provide an alternative feeding habitat for these benthic feeders, of which one, *Aldrichetta forsteri*, is normally restricted to shallow estuaries or sheltered embayments (Robertson 1980). The abundance and species composition of the surf-zone fish community also correlated positively with the quantity of detached macrophytes and with the prey densities (Robertson & Lucas 1983, Robertson & Lenanton 1984).

Effects of physical presence of stranded wrack on plants and animals

Beneficial effects

The previous paragraphs have reviewed the effects of the presence of organic beach-cast material on both invertebrates and vertebrates of beach and nearshore communities. It has been shown that, generally, these allochthonous subsidies have beneficial effects on the different communities, increasing species richness and population densities. Apart from providing food, the most obvious physical effect of wrack deposits is to provide shelter, and a suitable microhabitat for a number of different taxonomic groups of animals (Lavoie 1985, Colombini et al. 2000) and to act as important links between habitats. In fact, organic material stranded on beaches forms the basic element of food webs through which energy is transformed from one component to the other (Brown & McLachlan 1990, Polis & Hurd 1996a,b, Polis et al. 1997).

Another beneficial effect consists of species dispersion through floating beds, a phenomenon particularly common for coleopteran insects that can survive for several days at sea (Chevin 1998). Also, the widespread distribution of the coconut crab (*Birgus latro*) throughout the western tropical Pacific region up to the islands of the Indian Ocean can be explained by taking into account the dispersal of tropical seeds. In fact, Harries (1983) postulated that the tiny post-larval stage (glaucothoe) was spent in the moist husk of floating coconuts and that the ancestors of today's coconut crabs may have migrated on floating coconuts to remote islands and atolls of the South Pacific. Vertebrate species may also have used drift material to reach distant islands. This seems to be the case for some reptiles of the Galapagos Islands, such as the marine iguanas (*Amblyrhynchus cristatus*) which many thousands of

years ago may have ridden large rafts of tangled vegetation broken loose from riverbeds of Ecuador's Guayas River and drifted by the swift currents to the sea (De Roy Moore 1980). This theory is supported by the fact that only certain animals (reptiles and not amphibians) are present in the Galapagos, reflecting their ability to accomplish and survive such travels. Recently, however, phylogenetic analyses and age estimations have suggested an alternative hypothesis based on *in situ* speciation. According to this hypothesis the land and marine iguana inhabited the former, now sunken, islands of the Galapagos but became separated within the archipelago (Rassmann 1997).

Plants also can benefit from the presence of stranded seaweeds on shores through the amelioration of soil characteristics (Hesp 1991, Haslam & Hopkins 1996). Foredune plants can receive nutrients, including seaweeds and carrion, from sand movements and swash deposition or through algal foam blown onshore. These species adapt to the different input of nutrients using different strategies for the absorption of mineral nutrients, i.e. via salt spray or soil (Hesp 1991). Haslam & Hopkins (1996) investigated the effects of the brown seaweed *Laminaria digitata* on the pore volume and size distribution, aggregate stability, soil microbial biomass and biological activity (respiration and N mineralisation) of sandy soil. Pore volume and total water holding capacity was increased by kelp addition. Aggregate stability, together with soil microbial biomass content and soil respiration rate were also significantly greater. The rate of potential N mineralisation also increased by kelp amendment. In another coastal environment (salt marsh) a similar beneficial effect of wrack deposition to plants was reported by Pennings & Richards (1998). In a southwestern Atlantic salt marsh the plant biomass of *Batis maritima* was several times higher in elevated zones compared with lower ones. This increase was associated with the presence of wrack in the elevated zones, which ameliorated the soil characteristics by lowering salinities and organic content and producing better percolation rates. Thus wrack deposition had an important role in reinforcing pre-existing flood and salinity gradients caused by terrestrial runoff and elevation.

Detrimental effects

There are a few cases in which kelp stranded on shores has a detrimental effect on invertebrates. McLachlan (1985), for example, stated that large accumulations of beach macrophytes could limit oxygen exchange and the presence of the meiofauna could be seriously affected. Another case was reported by Soares et al. (1996) for clam communities. These authors, surveying 12 beaches in South Africa, indicated that biomass and density of adults of the wedge clam, *Donax serra*, were significantly higher on beaches with lower stranded kelp cover. Adults were centred in different zones according to different kelp cover. They were found in the low intertidal to subtidal where kelp cover was high and also in the mid-intertidal where no kelp was found. It was supposed that stranding of kelp produced a physical disturbance of the clams and this may have affected both feeding and burrowing activities. Feeding time could be decreased by the siphons making contact with the kelp and withdrawing into the shell and by the presence of a shadow that could stimulate this same reaction in response to presumed predators. Stranding of kelp also disrupts the swash and decreases water flow through the sand (McLachlan et al. 1985) and thereby affects food intake. Similarly, the surging back and forth of kelp would mechanically disturb slow burrowing adult clams and their reburrowing times would be increased. Consequently, they

would be dislodged downshore while smaller juveniles, which burrow faster, would be found in the uppershore, which explains the differences in the spatial distribution found for adults and juveniles (Donn 1990, Soares et al. 1996). The disturbance would be magnified when coupled with other physical factors such as low temperatures and small waves on pocket beaches with steep slopes and coarse sands. Predation of dislodged animals by gulls could explain the clam-free 14–20 m above the swash observed in two of the 12 beaches studied by Soares et al. (1996).

In other coastal environments disturbance of plant communities by wrack deposition has been reported (Valiela & Reitsma 1995, Brewer et al. 1998, Fischer et al. 2000). Burial by floating plant debris is one of the main factors affecting saltmarsh plant communities because it can kill underlying vegetation and create mosaic patches of different stages of secondary succession (Bertness & Ellison 1987, Valiela & Reitsma 1995). Removal of the deposited mats by the tides leaves hypersaline bare patches and creates opportunities for the establishment of other salt-tolerant species and determines different community patterns (Bertness & Ellison 1987, Brewer et al. 1998).

Geomorphological importance of wrack

Together with other factors (Hellemaa 1998), accumulations of stranded macrophytes along beaches have the important role of inducing dune formation. Wracks are particularly important on exposed beaches where they stabilise the foreshore by enhancing the organic and moisture contents, allowing pioneer plants to establish (Llewellyn & Shackley 1996). In Mauritania, Hemminga & Nieuwenhuize (1990) reported massive accumulations of seagrass litter on the shores between Iouik and Ten Alloul of the Banc d'Arguin and associated it with local dune formation. The profiles of the beach on the seaward side showed a stepwise formation with alternating layers of sand and seagrass litter. These were covered by sand originating from the Sahara during strong winds. It was proposed that the interacting process of massive stranding of seagrass litter and the seaward transport of desert sediment particles resulted in a dynamic process of dune formation, with the tendency of this process to shift in a seaward direction. The higher parts of the dune are then stabilised by the colonisation of halophyte pioneer plants (e.g. beach vines). A similar process has been suggested for the stable dunes of Cervantes in western Australia (Hesp 1984). In this case the *in situ* porous sand that quickly dried out and the winds that carried the sand towards land were the factors implicated in the process. The aeolian capacity for sand transport weakened as it encountered an obstacle so that sand accumulated behind and around it, forming an embryo dune. In Kingston, South Australia, Kirkman & Kendrick (1997) indicated that *Posidonia* remains at the base of the coastal dunes could be implicated in dune formation through trapping and binding of the drifting sand. Prince et al. (1968), investigating the effect of artificial seaweed on beach erosion, concluded that artificial seaweed can build-up beaches by promoting an onshore transport of material.

In the past decade the effect of kelp harvesting on dune erosion has been investigated along the Norwegian coast (Berg & Munkejord 1991, Løvås & Tørum 2001). Along the Jæren coastline, increased dune erosion was observed following an increase of kelp harvesting. It was shown that forests of *Laminaria hyperborea* had a damping effect on wave action. This attenuation was reduced when kelp was harvested and dune erosion ensued.

Furthermore, it was demonstrated that kelp modified the water velocity profile. In a region above the canopy layer, the time-averaged water velocity was in a shoreward direction whereas the undertow was confined to a region higher up in the water column. Hence it was concluded that sea vegetation, and especially *L. hyperborea*, dampen the waves significantly depending on the wave length: water depth ratio and that intense harvesting may severely affect coastal erosion. Such vegetation may also contribute to the maintenance of the shoreline through root mats that stabilise the bottom and protect the sediment surface from erosion (Fonseca & Fisher 1986).

Human use of beach-cast material

Harvesting of seaweeds and seagrasses

In many parts of the world beach-cast wrack and subtidal macroalgae are harvested because they are considered economically important resources (Berg & Munkejord 1991, Pacheco-Ruíz & Zertuche-González 1996, Kirkman & Kendrick 1997). In areas where wrack has accumulated in large quantities, its decomposition, production of hydrogen sulphide gas and fly plagues have a negative impact on human use of beaches and are considered a serious problem for beach management (Blanche 1992). Thus, harvesting of stranded macrophytes is seen as a positive means of cleaning beaches that are important for recreational use and tourism, and for producing a variety of valuable products. Beach-cast and subtidal macrophytes are used as house insulation, garden fertiliser and soil improvers, stock and mariculture feeds, and alginates and agar are employed as additives to human food, medical, cosmetic and pharmacological products (Jolivet et al. 1991, Haslam & Hopkins 1996, Kirkman & Kendrick 1997).

Kirkman & Kendrick (1997) reviewed harvesting activities in Australia and examined their impact on littoral and nearshore marine communities. They reported that only a few places in temperate Australia were harvested and that the major industry, based on collecting stranded bull kelp (*Durvillaea potatorum*), was on King Island in Bass Strait. The local population collected bull kelp from the swash zone as it washed up and air-dried it for 2 wk on racks supplied by the industry. Once dried, the kelp was processed by the factory by crushing into fingernail and sand grain size pieces before shipment to Kelp Industries (KELCO) in Scotland. Here it was further dried and chipped before being sent to Alginate Industries, UK for making into alginates. It is believed that harvesting has had little impact on the populations of bull kelp but other factors, such as warm sea temperature and decreased frequency of storms, might have caused resource shifts. Other by-products of the King Island industry were smaller grains and dust sold for stock feeds and as soil improvers, respectively. In Australia, abalone mariculture and aquaculture industries are other important users of stranded and drifting macroalgae (Kirkman & Kendrick 1997). However, total reliance on wild stocks is not sustainable and artificial feeds and mixtures of artificial feeds and dried macroalgae are now being developed. Beach-cast seagrass leaves of the genus *Posidonia* were also harvested at Kingston, South Australia and used as soil improvers by locals or sold to the Japanese market. No quantitative estimates have been made of the harvest and therefore little is known of how beach removal can affect nutrient return to nearshore communities.

In the Gulf of California, Pacheco-Ruíz & Zertuche-González (1996) listed 55 potentially commercial seaweed species and found that the most abundant were the phaeophytes, *Sargassum johnstonii*, and *S. sinicola*, which were used as a source for alginates and fertilisers; the rhodophytes, *Eucheuma uncinatum* and *Gigartina pectinata* used as source of carageenan, and the chlorophytes *Ulva lactuca* and *Enteromorpha* spp. used in medicine as well as for human consumption. These species are annual, and the necessity for further studies to determine the sustainable harvest capacity and/or culture practices necessary for commercial exploitation has been stressed (Barilotti & Zertuche-González 1990).

In reviewing the effects of marine algal extracts on the productivity of agricultural plants, Jolivet et al. (1991) listed several beneficial effects when these extracts were added to the soil, notably an increased resistance of the plants to parasites, fungal attacks and to lower temperatures and humidities. Moreover, when sprayed on leaves the extracts improved germination of seeds, growth and development, enhanced mineral absorption from soil and increased quality of certain plant crops.

Marine macroalgae and seagrasses have been used as soil fertiliser by coastal populations for many centuries. On the Tyrrhenian coast of Italy, particularly in the Maremma region at the beginning of the twentieth century, seagrasses of the genus *Posidonia* and *Cymodocea* were commonly collected by local farmers, dried and used as fertilisers or as cattle bedding. In Italy this practice has long been abandoned in favour of more practical commercial products. However, elsewhere in the Mediterranean beach-cast macrophytes are still exploited by local populations. Along the coast of Tunisia, (Gulf of Gabès) the collection of stranded *Zostera* sp. by individual farmers is still a common practice and is used as an additive to the soil of olive tree plantations (I. Colombini & L. Chelazzi, pers. obs.).

Along the coast of the Indian Ocean, beach-cast macrophytes have been exploited by local populations for other uses. For example, at Danane, a beach locality to the south of Mogadishu, Somalia, local women bake their pottery using large heaps of burning seagrass *Thalassodendron ciliatum*. This technique is typical of the area and has been a tradition of these coastal tribes for a long time, as testified by the pottery found in many Palaeolithic sites along the coast of East Africa (pers. obs.).

Use of other stranded material

The exploitation of other material of organic origin stranded on beaches by coastal populations is a worldwide practice. In Africa, large stranded logs have always been of value to coastal populations for their use in the construction of “sanbûqs” and of smaller “dahws”, typical fisherman boats found along the Indian Ocean (Grottanelli 1955).

In the past, ambergris represented an important resource and was actively sought along shores because it was more valuable than gold. Along the oriental coast of Africa, from the Bagiuni Islands to Madagascar, this material has been traded with Giava, Sumatra and China since AD945 (Grottanelli 1955). At the beginning of the twentieth century ambergris was sold in northern Somalia at 10 times its weight in silver (Robecchi Bricchetti 1903). In the 1930s ambergris was sold by auction and half of the proceeds of the sale was property of the state (Zoli 1927). This material, produced in the alimentary tract of sperm whales (*Physeter macrocephalus*), consists of a greasy waxy secretion found around squid beaks, squids being the preferred food item of sperm whales (Tinker 1988). Ambergris produces a highly fragrant and spicy smell and was an important fixative in the perfume industry, where it has

now been replaced by the synthetic molecule ambreina. However, searches for stranded ambergris are still carried out in many countries such as Mauritania, Somalia and India. Because stranding occurs in certain areas of the coast more than others the local toponymy has been influenced. For example, there are placenames along the coast of Somalia that reflect the stranding of this material (Ambershiek). Besides its use in perfumery, ambergris was also burnt as incense or eaten for medicinal purposes, where its effect was comparable to a modern estrogen cure. In the city of Mecca ambergris is still sold, and men and women in Iran eat it to cure infertility. In Morocco it is traditionally used to add aroma to tea.

Stranded carrion represents another important organic material that can be exploited by coastal populations of the Indian Ocean. In Somalia, when turtles were washed ashore, it was common to extract their fat. Traditionally this was used by locals as body cream as there was the belief that it had regenerative properties and stimulated male sexual faculties. Also, carrion of the crab *Ocypode ryderi* was used by coastal tribes to attract the so-called “imbe”, a small gastropod (*Marginella monilis*) with a white porcelain shell, employed to make necklaces that were sold in the local market (Grottanelli 1955).

Stranded shells of the Cypraeidae family (Mollusca Gasteropoda) acquired a historical, cultural and economical importance in past centuries, and were actively sought by coast-dwelling peoples. Along the Somalian coast these were collected by women and children and sold for 20–22 shillings per hundred kg (Grottanelli 1955). Used as money by many populations until recently and as ornament for both living and dead since ancient Egyptian times, these shells are now employed in the tourism industry or sold for collections.

Effects of human removal of wracks on invertebrate populations

Mechanical beach-cleaning of organic beach-cast material

Recently, the increasing use of beaches as recreational areas has pressed regional authorities of many countries to remove all natural flotsam, such as detached macrophytes, driftwood and carrion, together with sanitary refuse and other litter of human origin such as glass, metal, plastic and their derivatives (Ryan & Swanepoel 1996). Mechanical removal has been seen as a cost-effective way of removing unwanted debris and has been employed by many coastal authorities without considering the long-term detrimental consequences on coastal environments. There is growing concern with the issue and some studies have been carried out to evaluate the impact of mechanical beach-cleaning on shores. Davidson et al. (1991) concluded that beach-cleaning machines had a damaging impact on invertebrate populations and that in areas of high recreational pressure the stability of the dunes would also be affected. Kirby (1992) reinforced this concern, stating that the removal of driftwood and especially large jetsam could have a damaging effect on certain isopods and ground beetles that use this debris as shelters. Llewellyn & Shackley (1996) compared four mechanically cleaned sections of Swansea Bay, UK, with a control area with no mechanical cleaning or hand-picking. The survey indicated that mechanical beach-cleaning had a serious deleterious effect on the overall strandline-related species diversity and abundance. Recently, Dugan & Hubbard (in press) came to the same conclusions when comparing groomed with ungroomed beaches during a survey of 15 southern Californian beaches. Both the removal

of strandline debris by raking machines that scour the sand to a depth of 5 cm, and the compression of sand by heavy equipment such as tractors and trucks may have an adverse effect on the invertebrate communities buried in the sand and on sediment transport (Llewellyn & Shackley 1996). It is interesting to note that in those sections of mechanically cleaned beaches where cleaners were unable to operate, a small remnant population of strandline invertebrates could still be found. It was suggested that management strategies should compromise and clean mechanically only those sections of the beach designed for recreational use, whereas hand-picking methods should be employed to collect tourist and shipping-related litter, leaving most of the organic debris. This would permit invertebrates to recolonise mechanically cleaned areas and would reduce impact on species. In a recent study of the Polish coastline, Weslawski et al. (2000) showed a marked decline in the localities inhabited by the sandhopper *Talitrus saltator* and of its average density when these were compared with previous recordings. Several reasons such as pollution, climatic changes in storm frequency, severity of winters, the rise in sea level, changes in trophic conditions and increase in recreational use of beaches were all proposed to have caused the decline in the species. Again, mechanical cleaning was regarded as an important limiting factor for sandhoppers and it was stressed that amphipods could still recover if several kilometres of less frequently visited beaches between crowded areas were left untouched.

Inorganic beach-cast material

Man-made marine debris

Allochthonous input from the sea to shores all over the world includes inorganic debris usually associated with human activities. This material has increased significantly in the twentieth century, and the material quality has also changed in line with socio-economic progress. Thus man-made debris has become an important component of beach-cast material. In many cases, according to its nature, it is practically inseparable from macrophyte deposits and thus its presence on beaches definitely has an influence on local faunal communities.

Beach litter originates from many sources: marine, riverine and the beach itself. Industry, domestic sewage, illegal dumping at sea from ships and public negligence are all factors implicated in the phenomenon. Litter has a detrimental effect on beaches and the marine environment in many ways. Floating and submerged debris can threaten marine mammals, seabirds, turtles, fishes and crustaceans through ingestion and entanglement (Fowler 1987, Laist 1987, Ryan 1987, Bugoni et al. 2001, Tomás et al. 2002). Litter washed ashore by tides or discarded by tourists also has an economic impact. This includes loss of aesthetic value of recreational areas relevant to tourism-generated income (Ryan & Moloney 1990), and loss of fish catches caused by loss of fishing gear (Dixon & Dixon 1981). Additionally, it may be dangerous to human health, especially in the case of medical, military and some industrial wastes (Dixon & Dixon 1981). Marine debris is now considered a problem worldwide and much work has been accomplished in this context.

Several recent studies on beach litter have been undertaken to determine the quality and quantity of man-made debris on a beach at a specific time, and how it varies in space and

time (e.g. Frost & Cullen 1997, Haynes 1997, Madzena & Lasiak 1997, Walker et al. 1997, Thornton & Jackson 1998, Velander & Mocogni 1998, Moore et al. 2001, Williams & Tudor 2001a,b). In a study on Israeli beaches in the Mediterranean the importance of beach geomorphology on coastal pollution was shown, and beach width, ridge, and runnel morphology and beach porosity were pointed out as dominant factors that may influence the deposition of litter (Bowman et al. 1998). Because the composition of litter and its location on beaches is very variable and depends on many physical processes there have been a variety of methods to describe and monitor beach litter. Data collected in different ways make comparisons very difficult and standardisation impossible. Velander & Mocogni (1999) compared 10 methods for sampling beach litter on 16 beaches in Scotland to ascertain the effectiveness of the various methods. It was concluded that different methods did produce significantly different results and each method had advantages and disadvantages. Thus selection of a collection method will depend on the information required. In other studies an evaluation of the status of debris was made using a set of indicator items to identify trends over time (Rees & Pond 1995, Ribic 1998). However, it was concluded that caution should be used when collecting data by this method because selected indicator items do not always reflect general trends of the remaining litter on the beach (Ribic 1998).

Litter clearance on beaches is a main issue of coastal management. It can be seen as an instructive exercise when members of local communities are involved but it has been demonstrated that it is only a temporary management strategy (Williams & Tudor 2001a,b). In fact, depending on the sites, beaches become littered very rapidly again and on some occasions buried litter can re-emerge at the sand surface (Williams & Tudor 2001b). Costs of litter picking have greatly increased so beach managers are looking for alternative management options. Moreover, beach cleaning does not solve the problem, which should be tackled at the source (Velandar & Mocogni 1998, Williams & Tudor 2001a,b). In some cases sources are easy to identify because they are local (Uneputty & Evans 1997, Willoughby et al. 1997) but in coastal situations sources can be international, with litter originating from other countries. For example, American litter may be deposited on western European shores (Olin et al. 1995). Management strategies therefore need to overcome international barriers and solve political and practical problems. In the past, source location has focused on the minutiae of identifying items of the litter, whereas now it has been understood that a combination of both a good taxonomy and methodologies that look at the mixtures of litter is required. Earll et al. (2000) stressed that prevention at the source will become a reality only when stronger links are established between measurement and management. Only by providing measured profiles of the quality of litter types, can the trends in the input of items be assessed and prevention programmes be applied directly to sources.

Influence of man-made debris on beach ecosystems

The presence of anthropogenic debris on beaches is generally viewed as an aesthetic degradation of wilderness values. In developing countries, the presence of litter on beaches is seen as an important source of materials (plastic containers, nets, ropes) actively sought and re-used by local coastal populations. However, in most developed countries beach litter is an economically important issue and each year management measures are taken to remove tons of litter stranded ashore. Apart from having a public service and educational value, this practice is extremely costly, does not solve the problem and, according to the methods

employed, it can cause great damage to beach communities resulting in a decrease in species richness and abundance. The use of large mechanical beach cleaners, trucks to collect litter and tractors to remove large debris (refrigerators, television sets, tyres, plastic and fibre-glass car and boat pieces, vessel ropes) all have detrimental effects on plants and animals. However, some invertebrate and vertebrate species may exploit man-made objects as shelters, which provide the microclimatic characteristics necessary for the survival of specific species. Some forms of beach litter may collect rainfall and thus offer a precious source of freshwater. Others can act as lure traps, as in the case of plastic drinking bottles, which attract invertebrates with their sugar contents and become mortal traps as these dry out or when removed by cleaners (I. Colombini & L. Chelazzi, pers. obs.). Large items of debris also attract scototactic animals from great distances and result in a massive concentration of species (Colombini & Chelazzi 1991, Colombini et al. 1994). When this debris is collected, enormous quantities of invertebrates are trapped and removed from beaches with a consequent decrease in biodiversity (I. Colombini & L. Chelazzi, pers. obs.). Furthermore, trampling on beaches and foredunes with mechanical beach cleaners physically affects buried species and pioneer vegetation of foredunes. The destruction of foredune plants, and in particular of those that have a binding function, has a destabilising effect on the sand sediment and results in the subsequent erosion of the dune (Brown & McLachlan 1990). Sometimes litter is collected and piled up by bulldozers and burned or buried directly on the beach. This also is a very destructive method and has a heavy impact on the faunal communities and on the stability of the beach itself (I. Colombini & L. Chelazzi, pers. obs.).

Conclusions

This review has emphasised the importance of allochthonous input from the sea to beach and nearshore communities. Invertebrates and vertebrate species (including man), in some way or another, have always taken advantage of these subsidies. In some cases, species have become totally dependent upon their presence on beaches and have evolved biological cycles entirely linked to beach casts. In other cases, species have adapted their abundance, their spatial distribution and their feeding ecology in relation to the spatial and temporal patterns of wrack deposition. Studies on species succession in macrophyte wracks have indicated that these subsidies stand at the base of the beach food chains and that many species need an interspecific facilitation process before they can exploit the resource. All levels of the food chain are intimately linked to one another and sometimes there are great advantages for secondary consumers that, when subsidised, can reach higher population densities. The exploitation of man-made debris by certain beach species has been made possible through behavioural plasticity, an important key factor that has been rigorously selected for in the evolution of the sandy beach macrofauna living in such a harsh environment. Also, humans have benefited from beach-cast material over the centuries and still make use of important macrophyte deposits for economic reasons.

Beach ecotones are naturally unpredictable environments, continuously evolving and heavily influenced by both sea and land. Being restricted in width these environments can be directly affected by human encroachment from land or indirectly by marine and riverine input. Impacts on beaches can vary according to a number of factors, which include human population densities along coastlines, vicinity to river mouths and delta, economy of coun-

tries, presence of tourism, and geographical position. Beaches along seas (Red Sea, Black Sea, Mediterranean Sea, Baltic Sea) suffer more anthropogenic impacts compared with those of oceans because of higher human concentration. For example, in the Mediterranean, beaches have been under the influence of man and of his activities for more than 2000 yr and have been gradually modified through time. However, in the past 50 yr, changes have been extremely rapid and disruptive and consequently have seriously jeopardised the equilibrium of most Mediterranean beach ecosystems. Rapid social changes associated with the need to exploit beaches for tourism revenue or through harvesting of beach casts have produced environmental changes of beaches all over the world. An increasing awareness of the seriousness and urgency of the problem has induced many modern scientists to concentrate much of their effort on understanding how beach ecosystems operate and of the main forcing factors implicated in the system. Linkages between marine and terrestrial food webs are now becoming clearer although much work still needs to be done on the dynamics of the system and on how river plumes influence beach and nearshore communities (see Gillanders & Kingsford 2002 for review). With an increase in the knowledge of ecosystem functioning there might be a chance for future sustainable management of beach ecosystems and managers, decision makers and local authorities might become aware of the long-term consequences of their actions. There is the hope that different policies will be adopted in the removal of organic and man-made debris from beaches or in prevention at the source. An alternative could be the protection of certain areas at regular intervals along the coast that could serve as buffer areas where reasonable levels of biodiversity could be maintained. More communication needs to be achieved between coastal managers and scientists and this may represent a challenging task for the future.

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