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The Belgian sandy beach ecosystem: a review

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Conflict of interest
The authors declare no conflict of interests.

Abstract

This paper reviews the available knowledge on sedimentology, hydrodynamics and five major ecosystem components (microphytobenthos, vascular plants, terrestrial arthropods, zoobenthos, and avifauna) of Belgian sandy beaches. It covers the area from the foredunes to the lower foreshore, takes an ecosystem approach to beaches of this specific geographic area. Morphodynamically, Belgian beaches are (ultra-)dissipative, macrotidal, and wide. Characteristic grain sizes are 160–380 μm. The sand becomes coarser, beach slopes steeper and tidal range smaller towards the south-west, where beaches have also been frequently reshaped by human interference such as nourishment. Beach organisms are highly adapted to this unique environment and can reach high numbers. We show that even on a heavily populated coastline subjected to intense recreational and development pressure, beaches provide critical, yet threatened, habitats. Vascular plants growing near the drift line, on the dry beach and in the embryonic dunes are mostly short-lived and thalassochorous; the most common species include sea rocket (*Cakile maritima*), prickly saltwort (*Salsola kali* subsp. *kali*), and sea sandwort (*Honckenya peploides*). These zones are habitat to a highly diverse suite of terrestrial arthropods of halobiontic, halophilous and haloxene species; prominent members are sandhoppers (*Talitrus saltator*) and dipterans (flies). Microphytobenthos, mainly diatoms, is an important primary producer on Belgian beaches but is not well known. The meio- and macrobenthos of Belgian beaches contains specific assemblages such as the *Scolelepis squamata–Eurydice pulchra* community of the upper intertidal zone. Birds no longer nest on the beaches itself, but Belgian sandy shores continue to function as important resting and foraging areas for birds such as the sanderling *Calidris alba*. We identify several human pressures on the beach ecosystems arising from recreation, beach management and fisheries.

Problem

Belgian beaches have been strongly modified by humans. They are highly developed for recreational purposes, and most have concrete dykes that separate the littoral part of the beach from the dunes. They may appear biologically poor and resilient to human interference, but in fact are ecologically rich and threatened ecosystems. Beach nourishment is a prominent form of human impact (Speybroeck *et al.* 2006), as are beach cleaning (removal of strandline material), profiling of the dry beach, implants of brushwood hedges, and trampling. In this review, we present an ecosystem perspective of beaches, emphasizing their biological values, reviewing their biodiversity, and identifying the anthropogenic pressures acting on Belgian beach ecosystems.

Throughout the review, we use a zonation scheme that comprises: (i) the supralittoral zone above the high water line but influenced by sea water, including embryonic dunes, the dry beach and the strand line; (ii) the littoral (intertidal) zone between high- and low water; and (iii) the infralittoral zone, defined as the seaward continuation of the beach to a depth of 4 m below MLWS. Five major ecosystem components will be reviewed, encompassing: (i) microphytobenthos (*i.e.* photosynthetic micro-organisms, eukaryotic algae); (ii) terrestrial arthropods of the strandline, the dry beach and the embryonic dunes; (iii) vascular plants; (iv) zoobenthos (macrobenthos, meiobenthos, hyperbenthos and epibenthos); and (v) birds. Because the beach biota are strongly influenced by the physical environment, hydrodynamic and sediment properties of beaches will be summarized.

The Physical Environment

The Belgian coast is a 65-km long, southwest to northeast directed, rectilinear sandy shoreline, which in the east abuts the Westerschelde estuary in the Netherlands (Fig. 1). Belgian beaches display a macrotidal, semi-diurnal tidal regime. The average amplitude at spring tide varies from about 5 m at the French border and descends until 4.3 m towards the east (Fremout 2002). Winds and waves are mostly from the southwest to northwest, and the southwest/northeast directed flood current (>1 $m \cdot s^{-1}$) gives rise to a residual drift towards the northeast. The dominant southwesterly winds also induce a north-eastern aeolian drift. Storm winds coming from the northwest to north cause most coastal erosion (Anonymous, 1993). Average significant wave height in the nearshore zone ranges between 0.5 and 1 m at a period of 3.5–4.5 s (Anonymous, 1993).

The slope of the intertidal zone varies between 0.8% and 2.5% and increases towards the east. The width of the intertidal zone varies between 200 and 500 m, and decreases towards the east. The broad, intertidal zone along the western coast has a slope between 1% and 1.3% and is characterized by runnels and ridges, breached by outlets, which drain the water during ebb tides. Beaches further to the east have a steeper slope (>1.4%) and their profile shows less relief. From Bredene-Hippodroom towards the east, the beach profile becomes more irregular. In the past, these beaches were subjected to the highest coastal erosion and have therefore been frequently nourished.

Belgian beach sand consists mainly of quartz, supplemented by calcareous particles (*i.e.* shell hash) that can be locally abundant (De Moor & De Decker 1981). Most beach sediments do not contain significant amounts of fines, except for local enrichments in runnels (Degraer *et al.* 2003a). Sand on Belgian beaches has an average median grain size of 200–220 μm, with a cross-shore variation in median grain size of 160–380 μm. The sediment

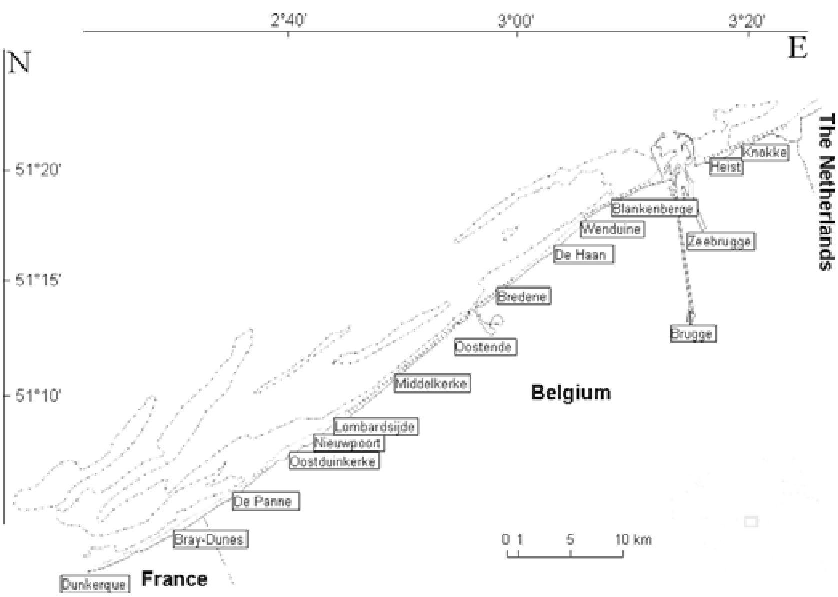

Fig. 1. The Belgian coast with indication of municipalities.

becomes coarser from the west to the east. From the French-Belgian border to Raversijde-West, this trend of coarser sediment is broadly uniform, while further to the east, this trend is more irregular. The largest fluctuations in particle size occur east of Heist, which is partially attributable to a long history of beach nourishment in this area (De Moor 2006).

On the basis of sequential beach profiling, De Moor (1979, 1988, 1993, 2006) argued that a natural cycle of beach erosion and accretion occurs on Belgian beaches. It remains, however, unresolved whether long term changes are because of slow moving waves of sand (Verhagen 1989) or to changes in wave energy. Beaches of the western coast are mostly stable and accreting. Eastern beaches are more variable and impacted by human interventions such as nourishment and reprofiling. The foot of the coastal dunes is accreting along most of the Belgian coast, because of the frequent and widespread placement of brushwood hedges (De Wolf 2002). De Wolf (2002) reports that the beaches of Bredene-Hippodroom to Wenduine, the beach immediately in the lee of the eastern harbour wall of Zeebrugge, and the beaches in front of dykes (*e.g.* Duinbergen, Knokke-Zoute and Lekkerbek) are usually erosive. Beaches further to the east (towards the Dutch border) are generally stable, except for erosion at the mouth of the Zwin.

Based on tidal amplitude, modal breaker height, wave period, and sediment parameters, Belgian sandy beaches are classified as dissipative to ultradissipative (*sensu* Short 1996, 1999) (Fig. 2). This indicates that processes of the swash and surf zone are important in structuring the morphology of the upper intertidal, whereas the middle and lower intertidal zones are more strongly influenced by surf zone processes and dissipating waves. Swash processes can be locally significant and may cause the formation of ridges. Tidal currents are important in the infralittoral zone.

The Biological Environment

Vascular plants

Vascular plants are limited to the supralittoral near the drift line, the upper dry beach, and the embryonic dunes. Most species are short-lived and adapted to the dynamic nature of these habitats. In stable, supralittoral areas perennial plant species can also become established (Provoost *et al.* 2004; Van Landuyt *et al.*, 2000). Most species disperse via floating seeds that can resist seawater for a long time (*i.e.* thalassochory), enabling them to colonize strand lines (Rappé 1996, 1997). A number of species also grow on man-made structures, such as the population of the sea beet (*Beta vulgaris* ssp. *maritima*) on a dyke at Nieuwpoort. All of these taxa can be considered as tolerant to salty soils.

The most common species along Belgian beaches is the sea rocket (*Cakile maritima*), often accompanied by prickly saltwort (*Salsola kali* subsp. *kali*) and sea sandwort (*Honckenya peploides*). Rarer species are grassleaf orache (*Atriplex littoralis*), sea beet (*Beta vulgaris* subsp. *maritima*), frosted orache (*Atriplex laciniata*), yellow horned-poppy (*Glaucium flavum*) and Ray's knotgrass (*Polygonum oxyspermum* subsp. *raii*); the latter has a very limited distribution range in northwest Europe (Jalas & Suominen, 1979). Fairly recently (Rappé 1984), Babington's orache (*Atriplex glabriuscula)* was recorded on Belgian beaches and is not uncommon. Sea-kale (*Crambe maritima*) and Rock Samphire (*Crithmum maritimum*) are much rarer (Rappé & Goetghebeur 1975; Rappé 1989a,b, 1996; Van Landuyt *et al.* 2006). Sea couch (*Elymus farctus* subsp. *boreoatlanticus*), often within stands of *Cakile*, initiates the development of primary dunes. When the input of sand is sufficient, the embryonic dunes will grow and the soil salinity will gradually decrease to brackish or fresh. At this stage, marram (*Ammophila arenaria*) starts dominating and becomes the dune-forming species. Locally, foredune

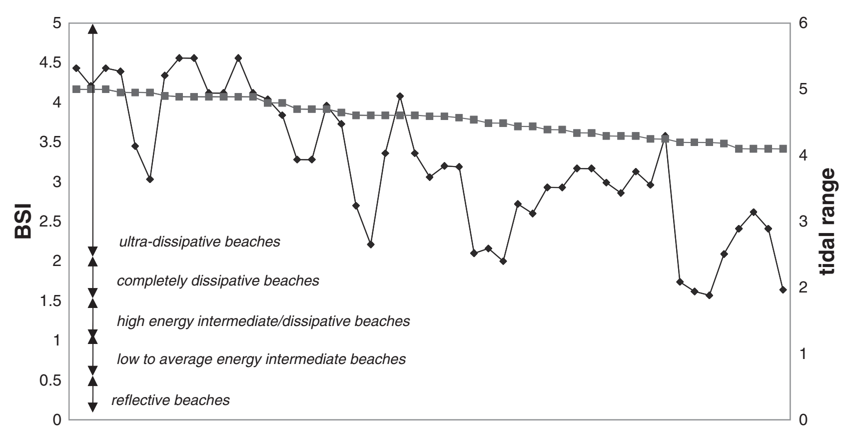

Fig. 2. Beach state index (BSI – McLachlan *et al.* 1983) and mean amplitude of spring tidal range (m). Westernmost localities are at the left, easternmost ones at the right of the graph.

species, such as sea holly (*Eryngium maritimum*), sea bindweed (*Calystegia soldanella*) and sea spurge (*Euphorbia paralias*), can be found in these embryonic dunes (Rappé *et al.* 1996; Provoost *et al.* 2004). On sheltered, gently-sloping beaches where silt accumulates (green beach), the flora is complemented by saltmarsh species such as the sea-blite (*Suaeda maritima*), glasswort (*Salicornia* spp.), and sea-milkwort (*Glaux maritima*); this only occurs at the 'Baai van Heist', which harbours the richest beach vegetation in Belgium (Devos *et al.* 1995; Cosyns *et al.* 1999; Van Landuyt *et al.* 2000). All of the typical species of the supralittoral zone are classified on the Red List as rare to (highly) endangered (Van Landuyt *et al.* 2006). Apart from the impact of beach nourishment, supralittoral vascular plants are affected by a number of other human impacts. Recreation and mechanical beach cleaning can be considered as the most significant threats to supralittoral vegetation and embryonic dunes (Provoost *et al.*, 1996, Provoost *et al.* 2004). Brushwood hedges, planted for coastal defence reasons, offer some protection against such disturbances, and therefore constitute an important habitat.

Terrestrial arthropods

The arthropod fauna of the strand line, the dry beach, and the embryonic dunes comprises a diverse range of species adapted to varying degrees to salty environments. Species can be classified into: (i) halobiontic species that are restricted to salty environments; (ii) halophilous species, living in both salt- and freshwater environments; and (iii) haloxene species that are incidental visitors to beaches. Many species depend on stranded material for food and habitat.

There is a considerable body of information on European arthropods associated with wrack deposits on beaches (Backlund 1945; Ardö 1957; Tsacas 1959; Remmert 1964; Egglishaw, 1959; Caussanel 1970; Cheng 1976; Dobson 1976; Doyen 1976; Moore & Legner 1976; Louis 1977; Bergerard 1989). Wrack consists mostly of kelps and other brown algae that support detritivores (mainly flies) and their predators and parasites. Common dune species (isopods, spiders and carabids) are often encountered in the wrack, especially if a connection between the dunes and the beach remains (J.-P., Maelfait, unpublished data). The sandhopper *Talitrus saltator* (Amphipoda, Talitridae) is a dominant species of the strand line (Lincoln 1979), and plays an important role as a primary consumer of wrack material (Robertson & Mann 1980; Griffiths *et al.* 1983; Stenton-Dozey & Griffiths 1983; Adin & Riera 2003). During spring tides, the amphipods migrate from the high-water line to the frontal row of the dunes, where they can reach high numbers (J.-P. Maelfait, unpublished data).

Carnivorous mites (Gamasina) feed on springtails and other invertebrates (Koehler *et al.* 1995; Salmane 2000). Some mite species are restricted to the strand line (*e.g. Thinoseius* spp.; Egglishaw, 1959; Remmert 1964) and the dry beach or embryonic dunes; these species become locally extinct if wrack material is removed. There are no records of spiders (Aranea) being restricted to beaches in Belgium, but occasionally some species on the Red List can be found on beaches (Maelfait *et al.* 1998). Spiders can be found in the wrack because of anemo-hydrochory, a process where in which winds dislocate them to coastal waters and waves and currents strand them on the beach (Palmen 1944); the importance of this dispersal mechanism for spiders remains, however, unknown.

On the dry beach, springtails (Collembola) are trophically closely associated with the mycorrhiza of several plant species such as the creeping willow *Salix repens* (Read 1989). Because of the positive effect these mycorrhiza have on sediment stability, dispersal of mycorrhiza by springtails can affect sediment stability (Koehler *et al.* 1995). Two species (*Folsomia sexoculata* and *Isotoma maritima*) only feed on rotting seaweeds (Janssens 2002).

Fourteen families of beetles (Coleoptera) have been recorded on Belgian beaches (Haghebaert 1989). The most species-rich families are Staphylinidae (13 spp) and Carabidae (20 spp; Haghebaert 1989). Desender (2004) provides an overview of the beach and dune carabid and cicinelid beetles of the Belgian coast. At least 46 species have been recorded from the strand line, of which 34 are true halobiontic and 12 are halophilous or haloxene species. Most species are predators (Bergerard 1989), but grazers (*e.g. Bledius arenarius, Bledius subniger*) and parasites (*e.g. Aleochara* spp.) also occur. Species of the genus *Blebius* play a key role in the food web of the strand line (Den Hollander & Van Etten 1974; Steidle *et al.* 1995). *Cafius xantholoma* is the most common rove beetle of Belgian beaches (Haghebaert 1989), and predatory ground beetles and tiger beetles (Carabidae and Cicindelidae) are adapted to life on sandy substrates (Turin 2000) by having digging legs or long legs to counter overheating. *Cicindela maritima* and *Bradycellus distinctus* are halophilous species that are mainly found on the dry beach and in the foredunes (Turin 2000). *Amara convexiuscula* and *Bembidion normannum* can be abundant under wrack deposits (Turin 2000).

Diptera (flies and mosquitoes) are restricted to the supralittoral zone and are the most abundant group of beach insects, their larvae feeding on the organic matter of the strand line (Ardö 1957; Tsacas 1959). There is a considerable body of information on Belgian beach Diptera, that includes both faunal inventories (Meunier 1898; Villeneuve 1903; Bequaert 1913; Bequaert & Goetghebuer 1913; Goetghebuer 1928, 1934, 1942; Grootaert & Pollet

1988, 1989; Grootaert 1989), as well as more ecologically oriented studies (Pollet & Grootaert 1994, 1995, 1996); a summary can be found in Grootaert & Pollet (2004). *Chersodromia* spp. (Hybotidae) are tiny flies whose larvae live in the burrows of sandhoppers (Tsacas 1959). Prior to 1980, *Chersodromia hirta* was rather common, but today, the species is threatened (P. Grootaert, unpublished data). *Aphrosylus* species (Dolichopodidae) are typically encountered on hard substrates, while foraging individuals can also be found on beaches. Kelp flies (Coelopidae), their larvae feeding on seaweeds, occur almost exclusively on stranded brown algae (Egglishaw, 1959, 1961; Dobson 1974), possibly constituting an important food source for wading birds (Smit & Wolff 1981). No diptera are restricted to the dry beach, although species typical of the foredunes are occasionally encountered there (Pollet 2000; Pollet *et al.* 2004).

The arthropods of Belgian beaches are threatened mainly by recreation and removal of wrack (beach cleaning) that disrupts and impedes the formation of embryonic dunes. Examples are a negative correlation between trampling and the abundance of *Talitrus saltator* (Weslawski *et al.* 2000), and fewer kelp flies on cleaned beaches (P. Grootaert, unpublished data).

Microphytobenthos

The microphytobenthos of intertidal sediments is usually dominated by diatoms, but dense populations of Cyanobacteria, Dinoflagellates, Euglenoids, Crypto- and Chrysophyta may also occur (Macintyre *et al.* 1996; Barranguet *et al.* 1997; Noffke & Krumbein 1999). Microphytobenthos are important primary producers in intertidal environments and contribute substantially to benthic biomass (De Jonge & Van Beusekom 1995; Macintyre *et al.* 1996), but information on sandy beach is more limited (Meadows & Anderson 1968; Steele & Baird 1968; Amspoker 1977; Asmus & Bauerfeind 1994; Fernandez-Leborans & Fernandez-Fernandez 2002). Sandy sediments are mostly dominated by attached forms (epipsammon), whereas free-living forms (epipelon and tychoplankton) prevail in muds. Sediment characteristics (*e.g.* stability, porosity, permeability, light penetration, concentration of dissolved gasses, water content, *etc.*) are important drivers for the biological activity and species composition of the microphytobenthos, and sediment type therefore largely determines the distribution and community structure of the microphytobenthos (Sabbe 1997; Paterson & Hagerthey 2001).

A total of 120 species of microphytobenthos have been reported for Belgian beaches (van der Ben 1973; Blondeel 1996), and 200 benthic diatom species are reported for tidal flats in the Westerschelde estuary (Sabbe 1997). Microphytobenthos is likely to be an important food source for micro-, meio- and macrobenthos (*e.g.* Sundbäck & Persson 1981; Middelburg *et al.* 2000; Graneli & Turner 2002; Moens *et al.* 2002), but their energetic importance remains poorly quantified for food webs on sandy beaches.

Specialized surf zone diatoms are mainly known from the Southern Hemisphere (Campbell 1996). The same species occur in Europe (Blondeel 1996), but nothing is known about their trophic role and ecology. Because of the high levels of turbidity in the infralittoral zone, little *in situ* primary production is predicted in the sediments; tychoplankton, plankton and re-suspended microphytobenthos are more likely to be important in these environment.

Zoobenthos

Knowledge of the intertidal meiofauna on Belgian beaches is limited (Gheskiere *et al.* 2002, 2004; Gheskiere *et al.* 2006; Kotwicki *et al.*, 2005). Fifteen meiofauna taxa have been recorded, with Nematoda, Harpacticoida and Turbellaria being dominant. On the beach of De Panne, meiofaunal densities increase from the upper littoral (56 ± 13 ind. per $10\ cm^2$) towards the lower littoral zone (3518 ± 540 ind. per $10\ cm^2$; Gheskiere *et al.* 2002). Nematode species richness increases from the upper littoral (eight species), reaching a maximum around the mid-tide level (34 species). Three species associations were classified: (i) dry beach – supralittoral, including typically marine, brackish, and terrestrial free-living nematodes such as *Rhabditis* sp. and *Axonolaimus helgolandicus*; (ii) upper intertidal (*Trissonchulus* sp., *Dichromadora hyalocheile* and *Theristus otoplanobius*); and (iii) lower intertidal (*e.g. Odontophora phalarata, Odontophora rectangula, Cyartonema elegans* and *Chaetonema riemanni*; Gheskiere *et al.* 2004).

Of the marine zoobenthos, the macrobenthos is the best investigated group. Similar to many beaches worldwide (McLachlan & Jaramillo 1995), polychaetes (bristle worms) and crustaceans dominate the macrobenthic fauna of Belgian beaches (Degraer *et al.* 1999a, 2003a). Highest macrobenthos abundance and diversity ocurr on gently-sloping, broad, and fine-grained beaches (Degraer *et al.* 2003a). Conversely, reflective beaches (east of Oostende) have fewer species at lower densities, but they harbour a number of rare species such as the polychaetes *Hesionides arenaria* and *Ophelia rathkei,* and the amphipod *Haustorius arenarius* (Degraer *et al.* 2003a).

The fauna shows a cross-shore gradient in species composition. The upper littoral zone is species-poor but high in density. This community is dominated by the polychaete *Scolelepis squamata*, the isopod *Eurydice pulchra,* and two amphipods *Bathyporeia pilosa* and *Bathyporeia sarsi* (Degraer *et al.* 2003a; Van Hoey *et al.* 2004). More species ocurr in the lower intertidal, but are lower

(Degraer *et al.* 2003a). Species typical of the lower littoral zone include *Nephtys cirrosa, Donax vittatus* and several polychaete species such as *Spio* spp. and *Spiophanes bombyx*. Species of this zone can withstand short exposure to the air, but they reach highest numbers in the infralittoral (Degraer *et al.* 1999a). Zonation patterns of several species change seasonally, occurring lower on the beach in winter (*e.g.* Degraer *et al.* 1999a). Biomass values for macrobenthos on Belgian beaches range between 40 and 800 mg AFDW m^{-2} (Elliott *et al.* 1997).

Macrobenthic organisms are a major food source for birds, epibenthic fishes (*e.g.* Plaice *Pleuronectes platessa*), and larger crustaceans (*e.g.* Brown shrimp *Crangon crangon;* Beyst *et al.* 1999). Several flatfish species depend on intertidal infauna during their juvenile stages, and the littoral zone acts as a nursery for them. Juvenile flatfish migrate inshore and upshore on rising tides to escape predators and access intertidal feeding areas (Beyst *et al.* 1999). This is also the case for hyperbenthic organisms like mysids (Beyst *et al.* 2001a). The surf zone also serves as a migration route between nursery grounds and between nursery grounds and the deeper nearshore habitats (Beyst *et al.* 2001a,b). Both flat, ultradissipative beaches and intermediate beaches are inhabited by high numbers of flatfishes, with highest species richness values on intermediate shores (Beyst *et al.* 2002a,b). Lower species richness on the more reflective beaches along the eastern coast might be because of the influence of the nearby Westerschelde estuary. Several Belgian beaches, especially along the western coast, have runnels and ridges. The runnels remain submerged over a longer period of time and accumulate organic matter. They contain a benthic fauna, which resembles that of the infralittoral (Boulez 2002), and support more macrobenthic species at higher density than adjacent sand banks.

In contrast to the littoral zone, with only one typical macrobenthic community, several communities can be found on the foreshore. Four subtidal macrobenthic communities (*Abra alba–Mysella bidentata*, *Nephtys cirrosa, Ophelia limacina–Glycera lapidum, Macoma balthica*) are associated with different sediment types (Degraer *et al.* 2003b; Van Hoey *et al.* 2004). These communities are, however, not homogeneously distributed on the Belgian foreshore. East of Oostende, the species-poor, but highly abundant *M. balthica* community (87% of sample stations) dominates, while it is uncommon west of Oostende (7% of sample stations; Degraer *et al.* 2003b). West of Oostende, three subtidal community types are found at roughly comparable spatial coverage. The most speciose assemblage with the highest abundance (*A. alba – M. bidentata)* dominates the Western Coastal Banks, and contains many bivalves. Because of their importance as food for species such as the common scoter *Melanitta nigra* and the Atlantic cod *Gadus morhua* (Degraer *et al.* 1999b), and because of the high species richness and abundance of the macrofauna (Van Hoey *et al.* 2004), this community is considered amongst the ecologically most valuable on the Belgian Continental Shelf (Degraer & Vincx 2003).

The dry beach and the strand line are most heavily impacted by tourism. Hence, the interstitial fauna of the dry section on tourist beaches is characterized by only one or few hardy forms that are taxonomically closely related (Gheskiere *et al.* 2005a,b). The benthic fauna of the littoral zone is mostly impacted by coastal defence and tourism. On the Belgian foreshore, human activities are common and widespread (Maes *et al.* 2000). Kerckhof & Houziaux (2003) give an overview of the major threats to the subtidal marine fauna on the Belgian Continental Shelf that include: (i) beam trawl fisheries; (ii) dredging and dumping of dredged materials; (iii) introduction of invasive species; (iv) coastal defence; (v) eutrophication; and (vi) pollution. While less intense and less frequent in the intertidal zone compared to nearshore waters, beam trawling can have severe impacts on benthic systems. Several reef-building species [*e.g.* oysters (oyster banks), sand mason worm *Lanice conchilega* (*Lanice* reefs), sponges] are highly vulnerable to bottom-contact fishing activities. By creating new habitats (hard substrates) and altering the original habitats, coastal defence has had a drastic impact on the Belgian foreshore, but impacts on the fauna are poorly known.

Avifauna

The supralittoral zone is important as a nesting area for birds, but during the twentieth century, most Belgian beaches became unsuitable for nesting of coastal birds because of anthropogenic pressures that destroyed nesting habitat and caused disturbance (Stienen & Van Waeyenberge 2004). The Kentish plover *Charadrius alexandrinus* and little tern *Sterna albifrons* can be expected to breed here, both species being included in the Red Data List as breeding birds threatened with extinction (Vermeersch *et al.* 2004). In 1954, 45 breeding pairs of Kentish plover were observed on Belgian beaches (Raes 1989). During the onset of the 21st century, breeding numbers in coastal environments dropped to less than three pairs (Vermeersch *et al.* 2004, 2006). During the last century, upto 75 pairs of little terns were nesting on Belgian beaches, but halfway through the century, the numbers heavily dropped and the last nesting in a natural habitat dates back to 1973 (Van Den Bossche *et al.* 1995; Devos & Anselin 1996; Anselin *et al.* 1998; Seys 2001).

However, with the development of the port of Zeebrugge in the 1980s, vast areas of sandy, sparsely vegetated and relatively undisturbed land were created.

These mimicked natural processes in coastal areas and attracted large numbers of coastal breeders (Stienen & Van Waeyenberge 2002, 2004; Stienen *et al.* 2005). The distribution of both Kentish plover and little tern is now limited to the Zeebrugge port and the adjacent reserve 'Baai van Heist' (Courtens & Stienen 2004; Stienen *et al.* 2005). In Zeebrugge-Heist, numbers reached 108 and 425 pairs for Kentish plover and little tern, respectively.

The supralittoral on Belgian beaches also functions as a resting and foraging area, mainly in winter and during migration. At high tide, most gulls and waders use the supralittoral to rest or as a place to gather before moving to high water roosts. The most important high-water roosts are located near larger tidal flats and on groins. Tidal flats are, apart from being used by gulls, also used by foraging wading birds (oystercatcher *Haematopus ostralegus* and dunlin *Calidris alpina*, smaller numbers of grey plover *Pluvialis squatarola*, ringed plover *Charadrius hiaticula* and common redshank *Tringa tetanus* – Speybroeck *et al.* 2005). High tide roosts of turnstone *Arenaria interpres*, purple sandpiper *Calidris maritima* and sanderling *Calidris alba* are mainly on groins along the midcoast (Engledow *et al.* 2001, Becuwe *et al.*, 2006). Numbers of turnstone and purple sandpiper strongly increased after 1975 along with the increased use of hard substrates for coastal defence (Becuwe *et al.*, 2006). Turnstones feed in the supralittoral zone on strand line material (Smit & Wolff 1981; Becuwe *et al.*, 2006).

In the intertidal area, standardized counts of wading birds at low tide were carried out in four recent studies (Engledow *et al.* 2001; Stuer 2002; De Groote 2003; Speybroeck *et al.* 2005). Many bird species feed on intertidal macrofauna. On Belgian sandy beaches, this applies primarily to gulls and wading birds, the latter being mainly oystercatcher, dunlin and sanderling (Engledow *et al.* 2001; Stuer 2002; Speybroeck *et al.* 2005). During the winter of 2000–2001, approximately 1450 oystercatchers and up to 350 sanderlings were present along the Belgian coast (Engledow *et al.* 2001). On average, respectively for both species, more than 50% and 70%, were counted on the beach.

During winter, oystercatchers feed nearly exclusively on shellfish (Camphuysen *et al.* 1996; Hulscher 1996; Zwarts *et al.* 1996), whereas dunlin typically feed on oligochaetes and polychaetes (Kelsey & Hassall 1989; Mouritsen & Jensen 1992; Nehls & Tiedemann 1993). They preferably feed on easily penetrable, wet substrates along the edges of gullies and along the low water line (Stuer 2002). Sanderling feeds in the swash zone and are partly depending on the presence of the polychaete *Scolelepis squamata* as prey, but also various other prey washed ashore (Smit & Wolff 1981; Mooij 1982; Dankers *et al.* 1983; McLachlan 1983; Glutz von Blotzheim *et al.* 1984; De Meulenaer 2006).

Common gull *Larus canus* and black-headed gull *Larus ridibundus* frequently forage on worms and shrimps in the littoral zone, around the high tide mark and in puddles and pools of stagnant water; other species of gulls (like great black-backed gull *Larus marinus*) depend much more on infralittoral food (Spanoghe 1999; Engledow *et al.* 2001; Stuer 2002). Gulls also feed on stranded dead animals and on food left behind by man (Engledow *et al.* 2001; Stuer 2002). The total number of gulls varied from about 7000 to 32,000 individuals; summer numbers are much lower at about 6000 individuals (Spanoghe & Devos 2002). Speybroeck *et al.* (2005) found peak numbers of gulls during autumn migration and a low during the breeding season. The herring gull *Larus argentatus* is the most common species (40–70%); black-headed gull *L. ridibundus* is second (13–42%). The common gull, lesser black-backed gull *Larus fuscus* and great black-backed gull mostly make up <10% of the total number of gulls (Spanoghe 1999; Spanoghe & Devos 2002). Common tern *Sterna hirundo* and sandwich tern *Sterna sandvicensis* make use of both supralittoral and littoral zones in and around the harbours of Zeebrugge, Oostende and Nieuwpoort to roost but also to gather before and after the nesting season (Speybroeck *et al.* 2005).

The shallow waters of the Belgian coast are of international importance for a number of seabirds (Seys 2001; Van Waeyenberge *et al.* 2001; Stienen *et al.* 2002; Haelters *et al.* 2004), of which most species can be considered coast-dependent, at least in a specific season (common scoter *Melanitta nigra*, crested grebe *Podiceps cristatus*, little gull *Larus minutus*, little tern, common tern and Sandwich tern).

All these species are dependent on shallow waters and the associated food resources, which are within the first 10 km from the shore. Only few species strongly depend on the actual foreshore. For the common scoter, the western coast is of primary importance. Peak numbers occurred in 1994 with 15475 indivuduals residing in Belgian waters.

Common scoters depend on the presence of small bivalves (*Spisula* spp., nowadays probably *Ensis* spp.) at shallow depths. They are extremely sensitive to disturbance (*e.g.* by shipping and air traffic) and oil pollution (Camphuysen 1998). Shell fisheries (beam trawls) pose a threat to the species (Degraer *et al.* 1999b).

Great crested grebes are winter visitors (mainly December-February) and they are generally limited to 15 km offshore. From 2000 onwards, numbers residing in Belgian coastal waters have increased, with peak numbers of 12,700 individuals counted in January 2003. This species is strictly piscivorous. Grebes are not very sensitive to disturbance, but because of their swimming lifestyle they are sensitive to oil pollution, although remarkably low numbers stranded along the Belgian coast during the Tricolor oil spill (Stienen *et al.* 2004).

Little gulls reach the highest numbers during migration (March–April and September–October). In autumn, they are most closely associated with coastal areas. At maximum, 3670 individuals were counted in Belgian waters, and Haelters *et al.* (2004) estimated that a very large proportion of the global population (almost 100%) may use the Belgian coast as a migration corridor. Little gulls are not very sensitive to disturbance, but because they rest at sea during night, they may be sensitive to oil pollution.

The Sandwich tern is both a summer visitor (nesting bird at Zeebrugge) and a passage migrant. The species is present in Belgian marine waters from April to November. The species mainly feeds in coastal waters (Haelters *et al.* 2004; Del Villar d'Onofrio 2005). Sandwich terns are visual predators, which feed on a limited number of fish species (Stienen *et al.* 2000). Thus, they are sensitive to water pollution with accumulating toxic substances and possibly also to elevated turbidity (Brenninkmeijer *et al.* 2002). Breeding numbers peaked in 2005, when 4067 pairs (7.2% of the biogeographical population) nested in the port of Zeebrugge (Stienen *et al.* 2004, Everaert & Stienen, 2007). An estimated 67% of the biogeographical population uses the Belgian coastal waters as a migration corridor (Stienen *et al.* 2007).

The common tern is both a summer visitor (nesting at Zeebrugge) and a migrant, present from April until November. Highest numbers are reached at Zeebrugge port, but foraging areas are situated upto 5 km offshore (Haelters *et al.* 2004; Del Villar d'Onofrio 2005; Courtens *et al.* 2006). In Zeebrugge port, breeding numbers peaked at 3052 pairs in 2003 (4.8% of biogeographical population), but numbers of migrants passing along the Belgian coast may very well exceed 50%. Common terns are sensitive to the presence of accumulating toxic substances and collisions with wind turbines (Becker *et al.* 1998; Thyen *et al.* 2000; Everaert & Stienen 2007). Unlike Sandwich terns, they are often found foraging in turbid waters and are probably less sensitive to elevated water turbidity.

For little terns, it is mainly the Zeebrugge harbour and the surrounding area within a 2-km radius which are important. Like the other two tern species, they are top predators that are sensitive to pollution of accumulating substances. A lower transparency of the seawater may have a negative effect on the feeding success of this visual hunter. All of the mentioned tern species are sensitive to changes in the abundance of their prey fish. This may lead to large fluctuations in breeding success and to changes in the size of their populations (Stienen 2006).

An overview of the threats that coastal nesting birds face in northwestern Europe, is given by Meininger & Graveland (2002). Important causes for loss of nesting grounds on beaches for terns and plovers in Belgium are disappearance of the grounds themselves, in part as a consequence of industrial development and the construction of bungalow parks (Arts 2000; Stienen *et al.* 2005) and the loss of natural dynamics in these areas. Recreation also poses a serious threat to nesting areas, leading to decreased breeding success, lowered densities and shrinking global distribution (Pienkowski 1993; Schulz & Stock 1993). Seabird populations are often limited in size by the availability of their food (Birkhead & Furness 1985; Croxall & Rothery 1991). Changes in tern population have been linked to fluctuations in food resources, mainly fish of the families of Clupeidae and Ammodytidae (Monaghan *et al.* 1989; Vader *et al.* 1990; Brenninkmeijer & Stienen 1994; Meininger *et al.* 2000; Stienen 2006). Thus, excessive fisheries of prey species can pose a serious threat (Furness & Tasker 2000). Other threats are predation by mammals and gulls as well as competition for breeding space between gulls and terns (Thyen *et al.* 1998; Quintana & Yorio, 1998; Meininger & Graveland 2002; Becker & Ludwigs 2004). Toxins entering the food web and being accumulated in eggs may affect coastal breeding birds (Becker *et al.* 1998; Thyen *et al.* 2000).

Discussion

Figure 3 provides a schematic representation of the spatial distribution and trophic role of key taxa on Belgian beaches. The strand line presents a distinct boundary between the marine and terrestrial environment, with little biological interaction across it. Stranded wrack is an indispensable input of organic matter for beach animals and plants, but may be a semi-closed system with relatively weak connections to the intertidal biota. However, nematodes, birds and some arthropods (at low tide) use more than one part of the beach. The boundary between the littoral and infralittoral parts is less distinct. For example, there is a gradual transition in macrobenthic assemblages from the lower intertidal to the foreshore, and flatfish undertake tidal migrations.

Vascular plants are important primary production of the supralittoral zone, whereas microphytobenthos fix carbon in the littoral zone and possibly further downshore. The importance of the latter for the zoobenthos is not known, although *Bathyporeia* species may feed on epipsammic diatoms. Detritivory is widespread: *Talitrus saltator* is a key decomposer of wrack in the supralittoral zone, and most macrobenthic fauna in the littoral zone are consume detritus. Very little is known about biological interactions on Belgian sandy beaches, providing opportunities for future research.

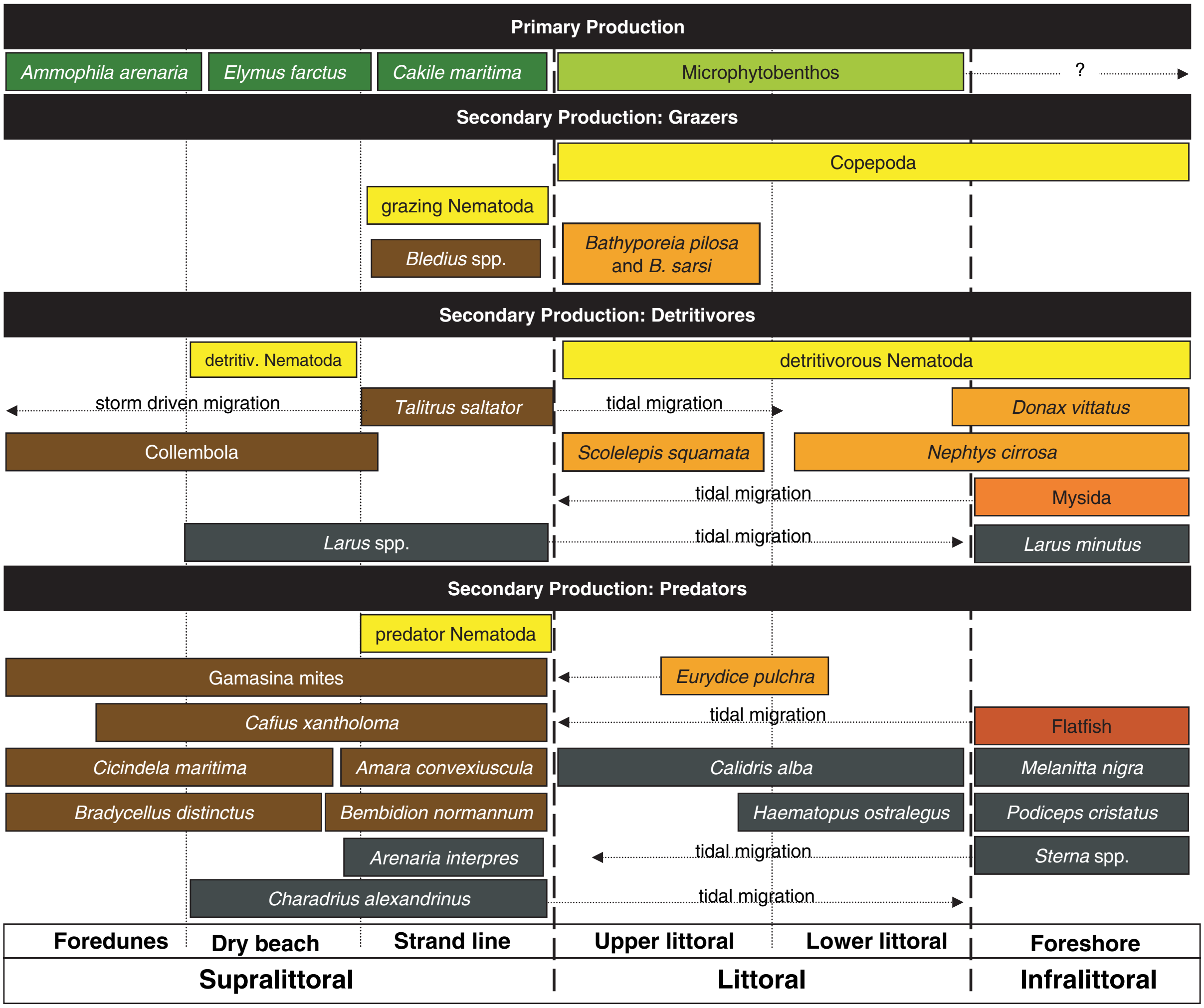

Fig. 3. Productivity allocation on Belgian beaches represented by some abundant taxa.

While biodiversity may be lower on Belgian beaches than in some other ecosystems, each biological component plays a key role in the functioning of this highly productive ecosystem, specifically adapted to life in a dynamic physical environment. Sandy beaches can certainly no longer be regarded as biological deserts. Therefore, management of beaches should involve more caution than is often the case. Although many beach biota are adapted to the naturally high environmental stress of tides, waves and winds, this adaptations have their limits. Several types of recreation, beach management and commercial activities pose the main threats that sandy beaches face along the Belgian coast.

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