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Habitat partitioning and trophic levels of terrestrial macroinvertebrates of a Tyrrhenian coastal ecosystem (Grosseto, Italy)

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Abstract. A study was conducted on a Tyrrhenian sandy beach ecosystem to examine habitat partitioning of macroinvertebrates in relation to the abiotic factors and to the vegetation and to assess links with trophic webs. The study site was located in the Maremma Regional Park, in an area where the beach was undergoing a process of aggradation and thus was in a continuous dynamic state. The site was characterised by a dune slack that could be periodically flooded by heavy rain or invaded by marine water during violent sea storms. Monthly surveys were carried out for an entire year along two transects regularly set from the shoreline to the retrodune. Plants were assessed through quadrat sampling whereas macroinvertebrates were caught with pitfall traps perpendicular to the shoreline. Species diversity (α and β diversity), richness and abundance were calculated together with mean zonations for both plants and terrestrial invertebrate species. Using Hierarchical cluster analysis plants were grouped into two clusters according to the abiotic factors whereas macroinvertebrates into four, according to abiotic factors and to the vegetation. For the most abundant species isotopic signature of $\delta^{13}C$ and $\delta^{15}N$ were assessed and cluster analysis was again preformed. Multi-source mixing models were used to identify trophic levels and the relative contribution of each food sources to the diets of each group of macroinvertebrates. The results of the annual α diversity value indicated a very rich invertebrate community highly correlated to the complexity of the habitat and a β diversity value that showed changes in the composition of the community every 40 m. The influence of marine subsides in the food web decreased at increasing distance from the sea and distinctive food webs were found according to the species zonation patterns. Some species mainly depended upon marine subsides (wrack debris), others, although inhabiting beach areas, were tied to both marine and terrestrial food sources whereas dune slack species were linked to terrestrial items. The work showed that in a spatially limited but complex environment, as is a beach - dune - slack system, marine wracks mainly subsided macroinvertebrates species of the eulittoral and contributed very little to the energy budget of more terrestrial species.

Key words: Mediterranean coastal ecosystem, ecological indices, energy flux, terrestrial macroinvertebrates, stable isotopes.

Résumé. ***Fractionnement de l'habitat et niveaux trophiques des macroinvertébrés terrestres d'un écosystème côtier tyrrhénien (Grosseto, Italie).*** Une étude a été menée sur un écosystème tyrrhénien de plage sableuse pour examiner le fractionnement de l'habitat des macroinvertébrés en fonction des facteurs abiotiques et de la végétation et évaluer les liens avec les réseaux trophiques. Le site d'étude est localisé dans le Parc Régional de Maremma, dans une région où la plage subissait un processus de progradation et se trouve dans un état dynamique continu. Le site était caractérisé par des marais de l'arrière dune qui pouvaient être inondés périodiquement par les fortes pluies ou envahis par l'eau marine pendant les tempêtes violentes. Les études mensuelles ont été exécutées sur une année entière le long de deux transects régulièrement mis en place du rivage jusqu'à l'arrière dune. Les plantes ont été évaluées à travers des quadrats d'échantillonnage tandis que les macroinvertébrés ont été capturés avec des pièges disposés perpendiculairement au rivage. La diversité spécifique (diversités α et β), richesse et abondance ont été calculées ensemble avec les zonations moyennes des plantes et des espèces d'invertébrées terrestres. En utilisant une analyse hiérarchique, les plantes ont été assemblées dans deux groupes en rapport avec les facteurs abiotiques alors que les macroinvertébrés se sont répartis en quatre groupes en rapport avec les facteurs abiotiques et la végétation. Pour les espèces les plus abondantes, la signature isotopique de $\delta^{13}C$ de $\delta^{15}N$ a été évaluée et l'analyse hiérarchique a été effectuée de nouveau. Les modèles 'Multi-source mixing' ont été utilisés pour identifier les niveaux trophiques et la contribution relative de chaque source de nourriture à l'alimentation de chaque groupe de macroinvertébrés. Les résultats annuels des valeurs de la diversité α ont montré une communauté d'invertébrés très riche et hautement corrélée à la complexité de l'habitat et une valeur de la diversité β qui a montré des changements dans la composition de la communauté chaque 40 m. L'influence des laisses marines dans le réseau trophique décroît avec la distance croissante de la mer et des réseaux trophiques distincts ont été trouvés en fonction des modèles de zonation des espèces. Quelques espèces dépendent principalement des laisses marines (dépôts, débris), d'autres, en peuplant des secteurs de plage, ont été liées aux sources alimentaires tant marines que terrestres, tandis que les espèces des marais de l'arrière dune ont été liées à la matière organique terrestre. Le travail a montré également que dans un espace limité, mais avec un environnement complexe, comme c'est le cas du système plage – marais de l'arrière dune, les varechs marins permettent le maintien des espèces de macroinvertébrés de l'étage eulittoral et contribuent très peu au budget d'énergie à plus d'espèces terrestres.

Mots clés: Ecosystème côtier méditerranéen, indices écologiques, flux d'énergie, macroinvertébrés terrestres, isotopes stables.

INTRODUCTION

Cross-habitat fluxes have long been a central focus of ecosystem ecology and recently it has become clear that ecosystems are both donors and recipients of allochthonous inputs. Both physical and biotic vectors transfer the subsidies, which can be the direct result of feedback processes between the donor system and the

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recipient ("recipient controlled") or the transfer processes can be independent of the recipient ("donor controlled") (Polis *et al.* 1997). Recently attention has been drawn on how these spatial subsidies affect food webs dynamics and the availability of resources for consumers (Polis & Hurd 1995, 1996a,b). Ecologist have discovered that allochthonous subsidies vary greatly over space and time (Huxel *et al.* 2002, Anderson & Polis 2004) and that donor controlled nutrient additions can affect primary productivity and can lead to bottom-up control of trophic dynamics that bring to higher growth rates of populations and higher carrying capacities (DeAngelis 1992). In coastal environments an important determinant of the transfer rate is the perimeter:area ratio of the ecosystem, particularly where physical vectors transfer the subsidy (Polis *et al.* 1997). Coastal terrestrial ecosystems have large P:A ratio thus the effect of the subsidy is proportionally large (Vanni *et al.* 2004). These allochthonous inputs can change food webs in recipient habitats through arrays of interactions affecting food web stability according to which trophic position subsidies enter a food web (Huxel *et al.* 2002) Furthermore, the general effects of subsidies are strongest where differences in productivity between donor and recipient habitat is high (Polis *et al.* 1997) or where recipient habitats have low productivity and much work has been conducted in this direction (Polis & Hurd 1996a, Stapp & Polis 2003, Wait *et al.* 2005, Catenazzi & Donnelly 2007a). In another recent paper on marine-terrestrial resource flows Paetzold *et al.* (2008) analysed a forest island, where terrestrial primary productivity was high and comparable to that occurring in the surrounding marine ecosystem. The study showed that stranded wrack was less important for recipient terrestrial consumers and was mainly confined to intertidal specialist consumers and mobile consumers that opportunistically forage in intertidal habitats.

In environments relatively opened to neighbouring ecosystems, such as beaches, strong effects of subsidies have been described. Subsidy quantity and rate of delivery is mediated by physical and biotic feature of landscapes (Witman *et al.* 2004) and by the nature of the boundaries between habitats (Cadenasso *et al.* 2004). Also biotic vectors can be crucial in determining the amount of a subsidy that arrives in a recipient habitat (Witman *et al.* 2004). Stranding of shore drift (detached seagrass, macroalgae and carrion) represents the main conduit of marine subsidies to the terrestrial environment (Kirkman & Kendrick 1997, Colombini & Chelazzi 2003). These accumulations support the food chain starting from primary consumers, mainly scavengers and detritivores (Inglis 1989), which attract predators, such as carnivorous beetles, spiders and scorpions (Anderson & Polis 1998) and in turn may be preyed upon by vertebrate species, such as lizards, birds and rodents (Polis & Hurd 1996b, Polis *et al.* 1997, Castilla *et al.* 2008).

In recent years there has been a growing interest in assessing trophic pathways of sandy beach ecosystems with the use of stable isotopes of carbon and nitrogen. Recent papers have shown that marine macrophytes are intrinsically linked to the food web of beach invertebrates (Adin & Riera 2003, Ince *et al.* 2007, Catenazzi & Donnely 2007b, Paetzold *et al.* 2008), although these studies analysed invertebrates directly associated to the wracks. Instead relatively little is known about the trophic pathway of arthropod communities inhabiting the entire beach dune system and to what extent inland terrestrial arthropods derive energy from marine subsidies. The present paper aims to elucidate trophic pathways of the most abundant macroinvertebrates using stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) and to evaluate the relative contribution of marine vs. terrestrial sources of energy for consumers. We focused on answering the questions: to what degree do the most abundant terrestrial arthropods derive energy from stranded shore wrack and how far inland do marine resources penetrate the beach dune system through biotic vectors?

MATERIAL AND METHODS

Study site

To the south of the Ombrone river in the Maremma Regional Park (Grosseto, Italy) lies a sandy beach dune ecosystem characterised by a high degree of instability as it is continuously experiencing a severe erosion process in areas close to the river mouth and a phenomenon of accretion in the southern section of the beach (Colombini *et al.* 2006). Consequently proceeding from north southwards there is an increasing beach width associated to a decreasing dune height. The site chosen for the study was located in the southern section at a 6 km distance from the river mouth (42°37'52.8''N, 11°4'42.3''E). This area consisted in an exposed beach (Marques *et al.* 2003) with a wide, flat eu- (aphital zone) and supralittoral with the first pioneer plants (40 m in width). This was followed by a low dune (1.10 m in height) covered by a typical Mediterranean maquis and a dune slack, a low lying depression between the first and second dune belt characterised by a typical salt marsh vegetation and flooded by superficial sea water during storms.

Sampling procedures

From October 2006 to September 2007 an ecological study was carried out at the selected site. To capture terrestrial macroinvertebrates two line transects, at a 25 m distance, were set perpendicularly to the shoreline and proceeded landwards for 150 m to the back dune up to the pinewood vegetation. The transects consisted of a series of pitfall cross traps set at a 5 m interval from which fauna samples were collected during four seasons (October, January, April, July). Arthropods were then counted and identified to species level.

Qualitative and quantitative assessment of the vegetation was carried out in the four different seasons using quadrats (50 x 50 cm) of above-ground vegetation. Samples were taken externally from the two transects at 1m (October), 2 m (January), 3 m (April) and 4m (July) distance from the pitfall traps. Plants were identified and the surface vegetation was cut and stored in plastic bags. Once in the laboratory plants were weighed after oven drying at 70°C until constant weight. Mean plant biomass, expressed in dw kg m^{-2}, was calculated pooling data from quadrats sampled from 35 m to 90 m (dune) and from 95 m to 150 m (wet dune slack).

During sampling periods the chemical and physical characteristics of the substrate (moisture, pH conductivity, organic matter, grain size, water table depth, pH and conductivity of the water table) were also collected.

At the study site beach wracks mainly consisted of rhizomes of the marine angiosperm *Cymodocea nodosa* because there was a consistent seagrass meadow directly in front of the site. Other marine organic material, such as *Posidonia oceanica* and/or red, brown and green macroalgae was, instead, quite rare. To determine the annual stranding of *C. nodosa* and to assess marine biomass reaching the shore in that particular section of the beach 5 transects were set perpendicular to the shoreline. These consisted of strips of sand (2 m in width and at a 10 m interval) ranging from the sealine limits to the first pioneer plants (about 30 m inland) within which seagrass was collected at the sand surface. Monthly samples were collected always in the same spots. In the laboratory seagrass was weighed after oven drying at 70°C until constant weight.

Collection and procedures for stable isotope analysis

For stable isotope determination terrestrial macroinvertebrates were collected from the pitfall traps whereas fliers associated to the vegetation were caught using hand nets. Only for some insect species both the preimaginal and adult stages were examined because both occurred in the pitfalls. Of the intertidal fauna only three species were selected to assess the possibility of marine components entering the terrestrial food web. All captured species were kept alive for 24 h to allow gut evacuation and then were frozen at -20°C and dried at 70°C until constant weight.

Plants of the dune and dune slack were collected to assess the terrestrial-derived component entering the food web. For isotopic analysis the most abundant vascular plants were chosen and only green leaf material from five individuals of each species was used. To assess intraspecific differences species with a wide sea-land distribution pattern such as *Inula crithmoides* and *Sporobolus pungens*, isotopic analysis was made on samples collected at two different distances from the sea.

To study the marine allochthonous material reaching the beach at the study site fresh leaves of *Cymodocea nodosa* and of *Posidonia oceanica* were collected together with thalli of macroalgae (*Ulva lactuca*, red and brown algae). Seston and diatoms were collected with plancton nets (mesh size 200 μm) at sea and in beach foam deposits, respectively. All material was immediately frozen and then oven dried at 70°C except for seagrasses leaves that were gently scraped to eliminate epiphytes before oven drying.

To assess sand parameters and sediment organic matter (SOM) surface sediment samples (up to 10 cm in depth) were collected at 10 m, 30 m, 50 m, 70 m, 90 m, 110 m, 130 m, 150 m. The sand was dried and sieved with an automatic shaker using sieves with meshes up to 63 μm. To assess other sources of allochthonous organic matter faeces of cattle, fallow deer and of seagull were also collected.

For each macroinvertebrate and plant species, 5 individuals were separately ground with mortar and pestle and two replicates were made from each individual. The elimination of carbonates by acidification prior to isotopic analysis was considered for marine derived macrophytes and animals, intertidal crustacean species and SOM (Mateo *et al.* 2008, Serrano *et al.* 2008). Non-acidified aliquots were used for $\delta^{15}N$ determination. Subsamples were then individually oxidised in a Carlo Erba 1110 elemental analyser (Carlo Erba Instruments, Milan, Italy) coupled to a Finnigan Delta Plus mass spectrometer. Isotope ratios ($\delta^{13}C$, $\delta^{15}N$) in per mil (‰) were obtained using this formula:

$$\delta \text{sample} = [(\text{Rsample}/\text{Rstandard}) - 1]\ \ 1000$$

$R = {}^{13}C/{}^{12}C$, or $R = {}^{15}N/{}^{14}N$). The δ values reflected the ratio of heavy and light isotopes in the samples compared with standard reference materials, namely Vienna PeeDee Belemnite (PDB) carbonate and atmospheric air nitrogen.

Data analysis

For each macroinvertebrate species a mean zonation was calculated using species capture frequency at the single trap. For plant species the mean zonation was calculated on a presence/absence basis of the different plants in the quadrats.

Hierarchical cluster analysis using Ward's method and the Euclidean distance was used to group plants according to the abiotic parameters of the site.

This analysis was also employed to identify groups of plants, macroinvertebrates and allochthonous items on the base of stable isotopic carbon and nitrogen ratio values. For each group the mean $\delta^{13}C$ and $\delta^{15}N$ and Hotelling's confidence ellipses (Batschelet 1981) were calculated at a 95% level of probability. A mean zonation was calculated for each group and a one-way analysis of variance, followed by a Tukey HSD test, was performed.

To estimate how far inland marine derived elements enter in the food web the proportion of marine diet calculated for each species was plotted against their mean zonation pattern. The proportion of each primary source was calculated with the multi source mixing model (Phillips & Gregg 2003, Philips *et al.* 2005) using IsoSource software. This procedure is designed to use isotopic signatures (ratios) to determine the range of feasible source contributions to a mixture when there are too many sources to allow a unique solution. All possible combinations of each source contribution (0-100%) are examined in small increments (e.g., 1%). Medians and 1–99 percentile ranges were taken into account.

Three basal sources of marine origin were chosen: seagull faeces, marine seagrasses (mean value between *Cymodocea nodosa* and *Posidonia oceanica*) and marine organisms (mean value between algae and marine macroinvertebrates), whereas for sources of terrestrial origin two basal sources were used: terrestrial plants (mean value of all species) and sediment organic matter (mean value of all distances).

As $\delta^{15}N$ values provide an indication of the trophic position of a consumer, Lubetkin and Simenstad, (2004) equation was used to estimate the trophic level of each macroinvertebrate species.

$$L=f_1L_1+f_2L_2+f_3L_3+f_4L_4+f_5L_5+1$$

where f_1s are the fractions each food contributes to the consumer's diet, the L_1s are the trophic levels of those foods and L is the trophic level of the species of interest.

Basal sources were: seagull faeces (assumed trophic position, a.t.p., L_1=4), marine seagrasses (L_2=1), marine organisms (including algae, marine invertebrates and seston, a.t.p. L_3=1.4), terrestrial plants (a.t.p. L_4=1) and sediment organic matter (a.t.p. L_5=1).

RESULTS

Ecosystem energy sources

During the sampling period beach stranding of *C. nodosa* varied monthly reaching its highest level in February and March (0.072 and 0.080 dw kg m^{-2}, respectively) (Fig. 1). An annual value of 0.458 dw kg m^{-2} y^{-1} was calculated for seagrass stranding for the entire sampling period.

Regarding terrestrial primary production a total of 40 terrestrial plant species were identified in the system. Pioneer plants such as *Cakile maritima, Sporobolus pungens* and *Inula crithmoides* occurred on the foredune whereas *Ammophila arenaria* and *Euphorbia paralias* were most abundant on the dune. Considering the beach fascia ranging from 35 m to 90 m from the sealine limits, a mean plant biomass of 0.21 dw kg m^{-2} was calculated whereas in the dune slack a value of 0.98 dw kg m^{-2} was obtained. Here the dominant plant species were *Juncus acutus*, and *Schoenus nigricans*, but also *Limonium etruscum*, *S. pungens* and *I. crithmoides* occurred. Species richness was 8.8 species m^{-2} (0.3 SE). Using hierarchical cluster analysis plants were grouped into 2 clusters according to the abiotic factors. These groups corresponded to dune species on the one hand and to dune slack species on the other as shown by their zonation pattern.

Macroinvertebrate abundance, richness and diversity

During the ecological study 334 arthropod species were collected for a total of 47580 individuals (Table I). The most abundant species belonged to areas of the beach and were represented by the amphipod *Talitrus saltator*, the coleopteran staphylinid *Phytosus nigriventris*, the isopod *Tylos europaeus* and the tenebrionid *Phaleria provincialis* (39.8%, 11.2%, 10.9% and 10.0% of total captures respectively). On the dune an unidentified ant species, the spider *Arctosa cinerea* and the coleopteran tenebrionid *Halammobia pellucida* were instead sampled as most abundant (1.6%, 0.7%, and 0.6% of total captures respectively). In the dune slack an unidentified springtail, the amphipod *Orchestia gammarellus*, the spider *Arctosa perita* and the coleopteran Carabidae *Calomera littoralis* occurred as most abundant species (5.8%, 1.8%, 0.5% and 0.4% of total captures respectively).

Regarding diversity indices variations occurred in the four seasons for the α diversity index with higher values in April (Table I). A fairly high value was also obtained for the annual value which was definitively higher than other study sites of the Mediterranean (Colombini *et al.* 2003, Chelazzi *et al.* 2005). Pielou's evenness index was fairly constant in all four seasons reaching an annual value of 0.42 (Fig. 2). In both plants and animals 50% of the community changed approximately every 40 metres as show by the β diversity index. When abundance, species richness and α diversity were correlated with the distance from the sea (in metres) there was a significant decrease in species abundance proceeding towards land ($y = 0.015x + 7.799$ $R^2=0.524$ $p<0.001$) associated to a significant increase in species richness ($y=0.069x + 51.179$ $R^2=0.143$ $p<0.05$) and in α diversity ($y=0.071x + 9.805$ $R^2=0.450$ $p<0.001$).

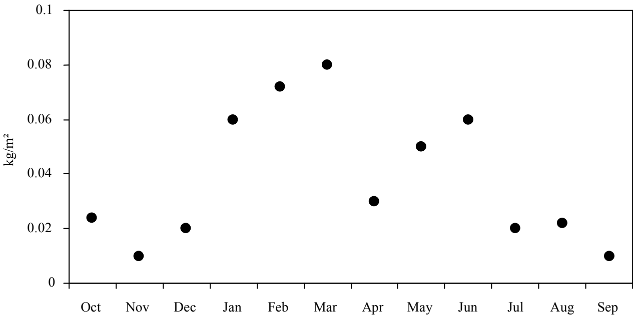

Figure 1: Monthly stranding of *Cymodocea nodosa* wracks (dry weights) from October 2006 to September 2007 at the Maremma Regional Park.

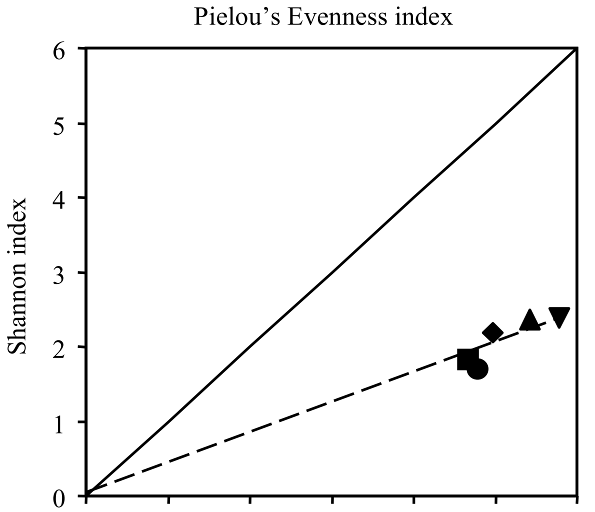

Figure 2: Pielou's evenness index shown in the four seasons and on the total (October= solid circle, January=solid square, April=solid triangle July=solid rhomb, total=solid downward triangle).

Table I: Abundance, species richness, diversity indices of macroinvertebrates; 1/β represents metres at which 50% of the arthropod and plant communities change.

	Oct	Jan	Apr	Jul	Tot
Arthropods					
n	8413	3270	24716	11181	47580
species	120	107	226	145	334
α diversity	19.83	21.21	34.35	23.51	48.48
J'	0.35	0.39	0.43	0.44	0.42
L	0.34	0.39	0.21	0.18	0.20
1/β (m)	71.57	37.95	40.71	61.61	36.57
Plants					
1/β (m)	53.00	35.23	36.96	37.00	40.96

Stable isotope analysis and zonation patterns

Stable isotope analysis was carried out on a total of 27 plants, 66 macroinvertebrate species and several allochthonous items that could contribute to an energy input of the system (Tables II, III). Among terrestrial plants δ^{13}C values ranged from -32.7‰ (*Anthemis maritima*) to -13.2‰ (*Erianthus ravennae*) whereas δ^{15}N values from -8.3‰ (*Erica multiflora*) to 1.2‰ (*Limonium etruscum.* Among the terrestrial macroinvertebrates *Tachyporus* sp. and the larva *Phytosus nigriventris* had the lowest (-28.1‰) and highest (-6.5‰) δ^{13}C values, respectively, while the silverfish Machilidae gen. sp. and the larvae of the dipteran Drosophilidae gen. sp. were the species with the most depleted (-5.3‰) and enriched (14.1‰) δ^{15}N values, respectively. The analysis of the isotopic signatures of marine allochthonous inputs of algae, seston, diatoms and marine organisms presented δ^{13}C values varying from -21.1 to -17.0‰ and δ^{15}N from 3.5 to 8.0‰. δ^{13}C values of SOM were more depleted compared to items of marine origins and varied from -28.3 to -25.1‰. A mean value with standard error of -26.9 ± 0.3‰ was obtain when all points were pooled and this did not differ (*df*= 1.36 *F*=0.081 *NS*) from the overall mean value of the plants (-26.3 ± 1.1‰). On the other hand nitrogen values of SOM had a mean value of 1.3 ± 0.2‰ and was significantly different (*df*= 1.36 for δ^{15}N *F*=23.787 *P*<0.001) from that of the plants (-2.6 ± 0.4 S.E.‰) indicating an organic input of different origin. Faeces of fallow deer and cattle differed significantly for carbon values but not for those of nitrogen (*df*=1.17 for δ^{13}C *F*=40.862 *P*<0.001; for δ^{15}N *F*=0.249 *NS*).

Table II: Mean isotopic signatures of plants, two vertebrate species and other allochthonous inputs with standard errors. Groups (P) found with cluster analysis are reported together with sample numbers (n) and mean zonations or actual distances (m = meters from the shore line). S.E. = standard error, a = associated to M. remyi, s = stranded, I = intertidal, sz = surf zone, nl = not localised.

		δ^{13}C		δ^{15}N			
species	P	mean	S.E.	mean	S.E.	*n*	m
Plants							
Juniperus oxycedrus	3	-28.3	0.2	-5.9	0.6	5	102
Pancratium maritimum	3	-29.7	0.2	-2.8	0.4	5	70
Ammophila arenaria	2	-28.0	0.4	-1.7	0.4	5	63
Elymus farctus	3	-28.0	0.5	-3.0	0.5	5	64
Erianthus ravennae	1	-13.2	0.1	-2.8	0.3	5	137
Sporobolus pungens	1	-14.4	0.3	0.2	0.5	5	45
Sporobolus pungens	1	-14.0	0.3	-4.1	0.5	5	123
Schoenus nigricans	2	-29.0	0.5	-1.3	0.4	5	122
Juncus acutus (stem)	2	-26.1	0.3	-1.0	1.0	5	122
Juncus acutus (leaf)	3	-27.3	0.6	-4.4	0.3	5	122
Salicornia fruticosa	2	-26.6	0.3	0.6	0.4	5	123
Salsola kali	1	-13.7	0.1	0.7	0.9	5	55
Silene colorata	3	-29.4	0.3	-2.8	0.4	5	78
Limonium etruscum	2	-28.8	0.4	1.2	0.5	5	106
Euphorbia paralias	3	-27.5	0.4	-2.8	0.5	5	57
Euphorbia peplis	1	-14.1	0.2	-4.3	0.6	5	60
Medicago litoralis	3	-29.6	0.3	-2.9	0.1	5	85
Ononis variegata	3	-30.3	0.2	-3.0	0.2	5	75
Cakile maritima	2	-30.7	0.5	1.1	0.6	5	40
Erica multiflora	3	-27.4	0.4	-8.3	0.2	5	145
Blackstonia perfoliata	3	-27.8	0.3	-3.2	0.2	5	107
Plantago coronopus	3	-30.7	0.5	-3.0	0.6	5	123
Echinophora spinosa	3	-28.6	0.4	-4.9	0.3	5	50
Pseudorlaya pumila	2	-30.0	0.2	-1.2	0.4	5	72
Anthemis maritima	3	-32.7	0.4	-6.1	0.5	5	68
Dittrichia viscosa	2	-29.7	0.4	-1.3	0.2	5	125
Helichrysum stoechas	3	-29.4	0.4	-3.3	0.6	5	85
Inula crithmoides	2	-28.8	0.2	-1.2	0.3	5	50
Inula crithmoides	3	-27.1	0.9	-3.9	0.3	5	125
Xanthium italicum	2	-27.0	0.5	-2.0	0.3	5	62

	δ^{13}C		δ^{15}N			
species	mean	S.E.	mean	S.E.	*n*	m
Others						
Bacillariophyceae gen. sp.	-20.2	0.3	4.5	0.2	5	s
Phaeophyceae gen. sp.	-20.8	0.7	3.2	0.2	5	s
Ulva lactuca	-19.7	0.5	7.0	1.2	4	s
Rhodophyta gen. sp.	-20.8	1.2	3.5	0.2	5	s
Cymodocea nodosa	-10.2	0.2	3.4	0.6	5	s
Posidonia oceanica	-12.9	0.6	0.4	0.4	5	s
Donax trunculus	-21.1	0.1	4.8	0.3	5	i
Ophelia radiata	-17.0	0.1	8.0	0.1	5	i
Eurydice sp.	-18.4	0.2	7.7	0.1	5	s
Larus cachinnans faeces	-19.0	0.7	16.6	2.9	5	nl
Dama dama faeces	-32.3	0.1	1.2	0.6	5	nl
Bos taurus faeces	-27.4	1.2	0.9	0.3	5	nl
Seston	-20.6	0.3	4.5	0.2	5	sz
Wood debris	-27.5	0.1	0.2	0.1	5	s
Stranded wood (a)	-27.8	0.2	-1.6	0.7	5	s
SOM	-28.3	0.4	1.7	0.3	5	10
SOM	-26.7	0.2	1.8	0.5	5	30
SOM	-26.9	0.2	1.1	0.5	5	50
SOM	-27.3	0.2	0.2	0.3	5	70
SOM	-27.3	0.2	2.1	0.1	5	90
SOM	-26.0	0.1	1.7	0.1	5	110
SOM	-25.1	0.2	1.3	0.2	5	130
SOM	-27.4	0.1	0.3	0.1	5	150

Data of stable isotopes of δ^{13}C and δ^{15}N relative to terrestrial plants, macroinvertebrates and allochthonous items were analysed separately with hierarchical cluster analysis. At a dissimilarity level of 50% plants were pooled into three groups (P1, P2 and P3), whereas macroinvertebrates into four (A1, A2, A3 and A4) (Tables II & III, Fig. 3). Cluster analysis clearly segregated C_4 plants (P1) with enriched δ^{13}C such as *Erianthus* *ravennae*, *Sporobolus pungens*, *Salsola kali* and *Euphorbia peplis* from the rest of the C_3 plants The C_3 plants were then grouped in two different clusters on the base of the $\delta^{15}N$. For the allochthonous items three clusters were found which included seagull faeces (with the highest $\delta^{15}N$ value), marine organisms (including algae, marine invertebrates and seston,) and SOM + mammal faeces (Fig. 3).

Table III: Mean isotopic signatures of terrestrial macroinvertebrates with standard errors. Groups (A) found with cluster analysis are reported together with sample numbers (n) and mean zonations (m = metres from the shoreline). S.E. = standard error

		$\delta^{13}C$		$\delta^{15}N$			
Species	A	mean	S.E.	mean	S.E.	*n*	m
Hygromiidae							
Trochoidea trochoides (a)	3	-25.7	0.6	1.2	0.5	5	106
Trochoidea trochoides (b)	4	-25.8	0.5	-1.4	0.2	5	122
Helicidae							
Eobania vermiculata	3	-25.0	0.4	1.7	1.1	5	25
Phalangiidae							
Phalangium opilio	3	-25.2	0.6	1.6	0.8	4	116
Pseudoscorpionida gen. sp.	2	-20.6	0.3	3.8	0.5	4	73
Lycosidae							
Arctosa cinerea	2	-21.6	0.8	7.1	1.0	5	51
Arctosa perita	2	-22.6	1.4	4.1	0.6	4	88
Thomisidae							
Thomisus onustus	2	-24.6	0.2	5.3	0.3	5	122
Tylidae							
Tylos europaeus ad.	2	-20.5	0.6	7.6	0.2	5	14
Tylos europaeus juv.	2	-21.9	0.5	6.5	0.2	5	6
Porcellionidae							
Agabiformius obtusus	2	-23.4	0.2	2.3	0.5	5	79
Talitridae							
Macarorchestia remyi	2	-20.7	0.6	2.7	0.5	5	30
Orchestia gammarellus ad.	4	-24.7	0.3	-1.1	0.1	5	124
Orchestia gammarellus juv.	4	-25.1	0.2	-1.0	0.2	5	123
Talitrus saltator ad.	2	-22.8	0.4	5.6	0.2	5	8
Talitrus saltator juv.	2	-22.0	0.4	6.6	0.2	5	3
Geophilidae							
Geophilus sp.	2	-22.4	0.4	7.2	0.4	5	42
Collembola gen. sp.	4	-26.1	0.2	-1.9	0.2	2	113
Machilidae gen. sp.	4	-24.7	0.0	-5.3	0.2	5	106
Blattellidae							
Loboptera decipiens	4	-26.6	0.2	-1.1	0.4	5	92
Rhinotermitidae							
Reticulitermes lucifugus	3	-24.4	0.1	0.9	0.2	5	60
Acrididae							
Oedipoda caerulescens	2	-20.0	1.6	1.2	0.3	5	45
Aiolopus strepens	3	-25.2	1.2	3.3	0.1	3	90
Labiduridae							
Labidura riparia	3	-24.9	0.5	4.0	0.7	5	107
Miridae							
Lygus pratensis	2	-25.5	0.7	6.1	0.8	5	73
Lygaeidae							
Beosus maritimus	3	-25.1	0.3	2.5	0.4	5	106
Carabidae							
Cicindela campestris	3	-25.7	0.3	1.8	0.4	4	127
Cylindera trisignata	2	-22.1	0.7	6.4	0.4	5	0
Calomera littoralis	3	-24.8	0.4	2.6	0.4	5	100
Eurynebria complanata	2	-21.4	0.3	9.7	0.1	4	23
Eurynebria complanata l.	2	-20.1	0.2	6.6	0.0	1	16
Scarites buparius	2	-22.5	2.0	3.6	0.6	4	35
Parallelomorphus laevigatus	2	-21.7	0.7	10.9	0.2	4	5
P. laevigatus l.	1	-17.3	1.1	8.4	0.5	5	7
Licinus sp.	4	-24.5	0.3	-1.9	0.5	4	123
Histeridae							
Hypocaccus dimidiatus	1	-13.8	0.8	9.7	0.2	5	2
Staphylinidae							
Quedius sp.	3	-26.7	0.6	3.5	0.2	4	122
Mycetoporus sp.	2	-23.0	0.4	11.7	0.5	3	20
Tachyporus sp.	2	-28.1	0.4	7.8	1.0	5	20
Phytosus nigriventris	1	-16.5	0.5	7.6	0.3	5	11
Phytosus nigriventris l.	1	-6.5	0.1	7.4	0.2	5	11
Atheta sp. 1	1	-22.5	0.7	12.4	0.6	5	23
Atheta sp. 2	2	-11.7	0.5	9.7	0.4	3	12
Atheta sp. 3	2	-25.2	1.5	7.5	0.6	5	25
Geotrupidae							
Thorectes intermedius	3	-25.6	0.5	4.0	0.4	4	88
Cetonidae gen. sp. l.	3	-25.4	0.9	4.2	0.8	3	40
Elateridae							
Isidus moreli	2	-22.5	0.7	5.1	0.6	5	31
Isidus moreli l.	1	-17.3	1.8	6.2	0.4	5	32
Buprestidae							
Acmaeodera quadrifasciata	4	-23.1	0.2	-3.8	0.5	5	75
Coccinellidae							
Adalia decempunctata	2	-26.5	0.3	6.4	1.9	5	122
Oedemeridae							
Oedemera flavipes	4	-22.9	0.3	-3.7	0.6	5	75
Stenostoma rostratum	2	-23.3	0.9	1.6	0.4	5	75
Anthicidae							
Cyclodinus constrictus	2	-26.3	0.7	7.5	1.1	5	122
Tenebrionidae							
Tentyria grossa	3	-26.1	0.1	2.8	0.2	5	84
Stenosis brenthoides	3	-25.5	0.1	3.4	0.5	5	81
Pimelia bipunctata	2	-25.9	0.2	5.6	0.6	5	64
Pimelia bipunctata l.	3	-24.5	0.5	3.3	0.6	2	60
Gonocephalum pusillum	3	-25.6	0.3	2.5	0.3	5	97
Trachyscelis aphodioides	1	-9.8	0.2	5.0	0.4	5	24
Phaleria provincialis	1	-16.7	1.4	6.8	0.5	5	18
Phaleria provincialis l.	1	-15.0	1.2	6.9	0.3	5	21
Halammobia pellucida	2	-24.3	0.7	5.5	0.3	5	47
Xanthomus pellucidus	2	-22.8	1.0	3.0	0.3	5	42
Bruchidae gen. sp.	4	-26.5	0.2	-5.1	0.5	4	27
Curculionidae							
Mesites pallidipennis	3	-25.2	0.2	0.4	0.3	5	25
Myrmeleontidae							
Acanthaclisis baetica l.	2	-26.2	0.8	6.8	1.0	4	56
Ascalaphidae							
Libelloides coccajus	3	-25.8	0.3	2.8	0.2	5	125
Sepsidae gen. sp.	3	-27.0	0.3	3.0	0.5	4	99
Heleomyzidae gen. sp.	2	-23.4	0.9	8.0	0.9	4	18
Drosophilidae gen. sp.	2	-24.2	0.7	14.1	0.7	5	40
Diptera gen. sp. l.	1	-9.3	0.3	10.0	0.7	5	20
Braconidae							
Apanteles sp.	3	-25.8	0.2	2.4	0.9	5	29
Scoliidae							
Scolia sexmaculata	3	-24.7	0.6	3.1	0.8	5	106
Mutillidae							
Smicromyrme viduata	3	-24.8	0.4	3.3	1.1	5	73
Formicidae gen. sp.	3	-26.2	0.2	0.3	0.3	5	75
Pompilidae							
Pompilus cinereus	2	-21.3	0.9	9.7	0.5	5	30

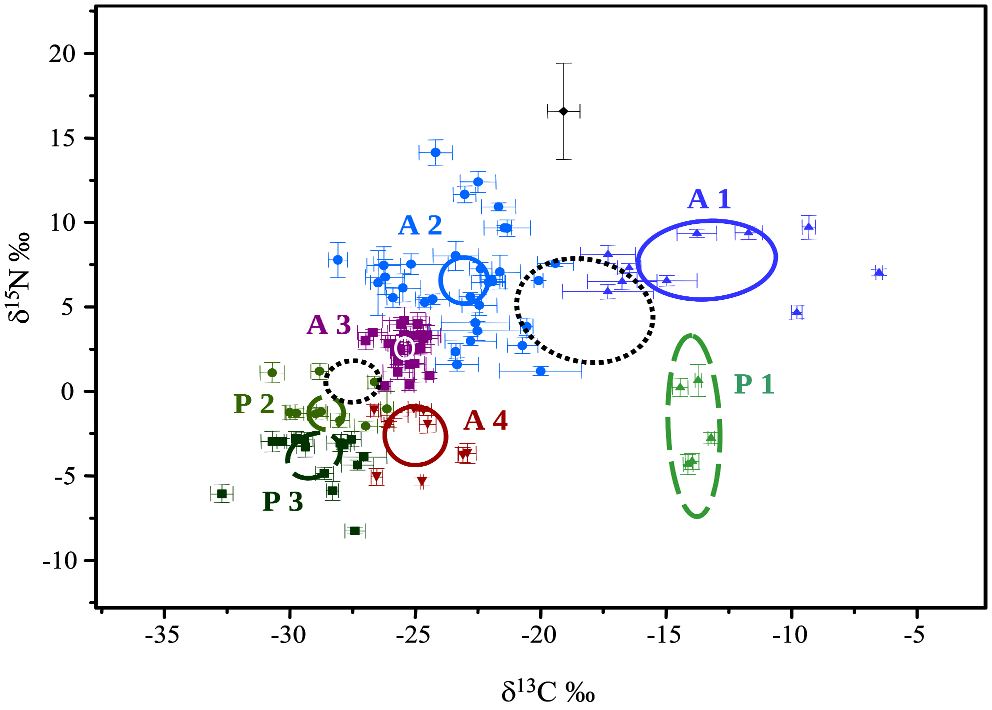

Figure 3: Stable isotopes of δ13C and δ15N (with standard errors) relative to terrestrial plant and macroinvertebrate species analysed with hierarchical cluster analysis. For plant species three groups are indicated (P1 light green empty triangles, P2 pea green empty circles, P3 dark green empty squares), for macroinvertebrates four groups are shown (A1 blue full triangles, A2 light blue full circles, A3 purple full squares, A4 red inverted full triangles). Hotelling's confidence ellipses at a 95% level of probability are also shown for plants (dashed line ellipses), macroinvertebrates (continuous line ellipses) and for allochthonous material (dotted line). For the latter points are not shown except for sea gull faeces (solid rhomb).

For macroinvertebrates the four groups (A1, A2, A3 and A4), segregated by cluster analysis, differed in both isotopic signatures δ^{13}C and δ^{15}N in all cases except for A3 vs. A4 for δ^{13}C and A1 vs. A2 for δ^{15}N, where no differences occurred.

The analysis of the spatial distribution patterns along the sea-land axis of the macroinvertebrate species belonging to the four groups obtained with cluster analysis showed different mean zonations. A1 group pooled species strictly related to the eulittoral area of the beach (mean zonation with standard error 16.6 ± 2.8 m) together with other species linked to seagrass wrack material. Instead, A2 group had a mean zonation of 43.5 ± 6.0 m and pooled both beach and fore dune species. Adults and juveniles of crustaceans species of beach and tenebrionids of the dune were pooled together with spiders and coleopteran carabids. A3 group pooled species inhabiting the back dune (mean zonation 86.6 ± 6.0 m) such as molluscs, earwigs, coleopteran carabids and tenebrionds. Finally A4 group (mean zonation 107.5 ± 6.3 m) pooled species inhabiting the dune slack such as amphipods, springtails, silverfish and oedemerids. Differences between the mean zonation patterns (ANOVA df=3,72 F=26.098 $P<0.001$) of the macroinvertebrate groups were significant in four cases when comparing beach groups (A1 or A2) with the more terrestrial groups (A3 or A4) (Tukey tests $P<0.05$) but not when comparisons were made within groups (between A1 and A2 groups or between A3 and A4 groups).

Marine vs terrestrial trophic sources in macro-invertebrates and trophic levels

The proportion of marine items in diets was estimated for macroinvertebrate species with the multi-source mixing model (Table IV). Only for the A1 group the proportion of marine food items was higher than that of terrestrial origin. In all other groups the opposite occurred. When the proportion of marine items was correlated with the spatial distribution pattern of the different species a significant decrease was obtain proceeding landwards (Fig. 4).

Trophic levels (Table IV) calculated for macro-invertebrates of beach dune ecosystems showed three trophic levels (TL 2, TL 3, TL 4). The trophic levels of the A1 group corresponded to primary consumers (tenebrionids and elaterids, TL 2) and to those of predator species (staphylinids, carabids, and histerids, TL 3). Instead the A2 group included primary consumers, such as amphipods, tenebrionids, oedemerids, and scavengers, such as amphipods, isopods, tenebrionids, which were all included in the TL 2. The TL 3 included predators such as staphylinids, hymenopterans, carabids or dipterans feeding on carrion, whereas the TL 4 included top predators (*Atheta* sp. 1). On the other hand in the dune slack macroinvertebrates of the A3 group showed only one trophic levels (TL 2), which included a variety of species belonging to different trophic guilds (primary consumers, scavengers and predators) indicating different basal sources. The species belonging to the A4 group were excluded from the isosource model as their basal sources were different from those put into the model.

Table IV: Proportion of terrestrial vs. marine food items entering the trophic web of macroinvertebrates. Trophic levels (TL) were obtained with multi-source mixing model based on five basal resources (seagull faeces, marine seagrasses, marine organisms, terrestrial plants and sediment organic matter).

beach dune species	land	sea	TL
A1			
I. moreli l.	0.27	0.73	2
P. provincialis l.	0.16	0.84	2
P. provincialis ad.	0.20	0.80	2
P. nigriventris	0.15	0.85	3
P. laevigatus l.	0.16	0.84	3
H. dimidiatus	0	1	3
A2			
S. rostratum	0.83	0.17	2
M. remyi	0.64	0.36	2
A. obtusus	0.80	0.20	2
X. pellucidus	0.74	0.26	2
Pseudoscorpida gen. sp.	0.58	0.42	2
S. buparius	0.70	0.30	2
A. perita	0.69	0.31	2
P. bipunctata	0.93	0.07	2
T. onustus	0.82	0.18	2
I. moreli	0.64	0.36	2
H. pellucida	0.78	0.22	2
L. pratensis	0.88	0.12	2
T. saltator ad.	0.63	0.37	2
E. complanata l.	0.40	0.60	2
C. trisignata	0.53	0.47	2
T. europaeus juv.	0.52	0.48	2
T. saltator juv.	0.52	0.48	2
A. cinerea	0.47	0.53	3
T. europaeus ad.	0.35	0.65	3
Geophilus sp	0.55	0.45	3
Heleomyzidae gen. sp.	0.66	0.34	3
P. cinereus	0.41	0.59	3
E. complanata	0.41	0.59	3
P. laevigatus	0.43	0.57	3
Mycetoporus	0.55	0.45	3
Atheta sp. 1.	0.49	0.37	4
A3			
T. grossa	1.00	0.00	2
T. trochoides	0.98	0.02	2
C. campestris	0.53	0.47	2
Apanteles sp.	0.98	0.02	2
L. coccajus	0.96	0.04	2
E. vermiculata	0.92	0.08	2
P. opilio	0.93	0.07	2
G. pusillum	0.55	0.45	2
T. intermedius	0.94	0.06	2
S. brenthoides	0.94	0.06	2
A. strepens	0.91	0.09	2
B. maritimus	0.90	0.10	2
C. littoralis	0.98	0.02	2
S. sexmaculata	0.87	0.13	2
S. viduata	0.87	0.13	2
L. riparia	0.87	0.13	2
P. bipunctata	0.84	0.16	2

DISCUSSION

The analysis of the energy inputs in the coastal ecosystem clearly indicated a substantial quantity of marine subsidies irregularly deposited on the eulittoral throughout the year. These mainly consisted of *Cymodocea nodosa* that occurred as a conspicuous seagrass bed in the shallow waters in front of the study site. Annual biomass stranding was twice the size of the autochthonous plant biomass present in the area. The relatively low terrestrial plant biomass was related to the particular instability of this section of the coast. The continuous evolution of the beach's state, with high wind velocities associated to a rapid beach progradation, prevented the formation of a stable and densely vegetated dune (Hesp 1989). Another factor influencing the system was the presence of *Ammophila arenaria* plants, which grew rapidly, colonising seaward beach surfaces by rhizome growth and initially formed low but wide dunes (Rodriguez-Echeverria *et al.* 2008). In fact in coasts experiencing progradation, *A. arenaria* traps sand very rapidly and builds dunes at rates that exceed the threshold of tolerance of other local species (Hilton *et al.* 2005).

Vegetation biomass of the dune slack was definitively higher than that of the adjacent fore dune but lower than that of other dune slacks that had reached the climax stage. McLachan *et al.* (1987) in Algoa Bay, South Africa, reported an above ground mean dry biomass of about 69 g m^{-2}, whereas Berendse *et al.* (1998) on Terschelling island showed that in a 5-year old plot of a dune slack the biomass was only 150 dw g m^{-2} but that in the 76 year-old plot it increased to 1344 dw g m^{-2}. At the study site the dune slack probably would never have reached its climax stage as it was continuously undergoing changes. Furthermore, the hydrological conditions created particular chemical and physical features as it received freshwater surface run-offs from the inland Uccellina hills and sea water during the winter storms. With the summer season the water table dropped approximately 1 m (Colombini *et al.* 2009b) below the soil surface and the basophilous pioneer vegetation, represented by *Schoenus nigricans* and *Juncus acutus*, was in its middle colonization phase (Grootjans *et al.* 1991, Sykora *et al.* 2004). High levels of pH (in our case over 9) are known to reinforce nitrogen mineralization, and to prevent a rapid build-up of organic material (Etherington 1982). This stage reaches a maximum age of ca. 35 years (Lammert & Grootjans 1998) and is phosphorous-limited because of high pH. In fact, *S. nigricans* is able to accumulate large amounts of biomass that, with prolonged wet periods, tend to accelerate the acidification process in the dune slack and eventually bring to shifts in the dominant plant species (Grootjans *et al.* 1991).

Due to the complexity of the abiotic conditions, the number of plant species was quite high even considering that the sea-land fascia is spatially restricted (150 m) and included a large non-vegetated area (eu- and supralittoral). As a consequence macroinvertebrate richness was elevated. However this was not entirely due to the presence of the vegetation (both in species and biomass) but also to the conspicuous presence of wrack debris in the non-vegetated area. In accordance to other studies (McLachlan & Brown 2006, Fallaci *et al.* 1994, Chelazzi *et al.* 2005) macroinvertebrate abundance scored the highest values for beach areas thanks to amphipods, isopods. Other abundant species on the beach were the coleopteran staphylinids and the tenebrionids that were intrinsically tied to the wrack debris (Colombini *et al.* 2000, 2009a). On the dune and dune slack areas species abundance was quite low including that of *O. gammarellus*. In these two areas other species such as spiders of the *Arctosa* genus were found dominant together with predator carabids.

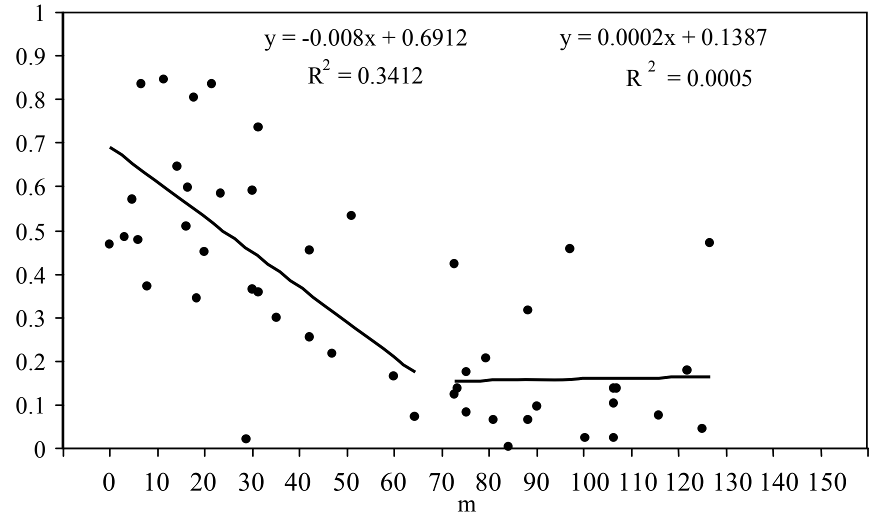

Figure 4: Proportion of marine food sources present in the diet of different macroinvertebrate species (calculated with the multi-source mixing model) and plotted against their mean zonation (in metres). Regression equations and probability levels (P) are also shown for the two areas.

The significant difference that appeared in the isotopic signatures of plants with C_3 and C_4 photosynthetic pathways was clearly demonstrated by the results. C_4 plants (P1 group and seagrasses) more enriched in $\delta^{13}C$ compared to the C_3 plants (P2 and P3 groups) were thus provided with an important adaptive mechanism to survive in hot environments (Bjorkman *et al.* 1974) with low soil fertility (Brown 1978). The intraspecific differences of $\delta^{13}C$ and $\delta^{15}N$ occurring in a C_3 plant (*Inula crithmoides*) and of $\delta^{15}N$ in a C_4 plant (*Sporobolus pungens*) can be explained considering that the plants were sampled in areas with different soil conductivity values (Colombini *et al.* 2009a). It has been shown that elevated levels of N availability can lead to increased rates of N-cycling and that this increase in turn results in ^{15}N enrichment of the soil pool. Plants accessing to this soil pool can then become relatively ^{15}N-enriched over time (Dawson *et al.* 2002) and plants lying at different positions within a site can show differences. Furthermore, Guy *et al.* (1980) demonstrated that C_3 plants of inland saline wetlands showed salinity-induced changes in $\delta^{13}C$ values due to a shift in the balance between the relative activities of the two primary enzymes of CO_2 fixation.

Analysing the zonation patterns of the macroinvertebrate species that made up the four groups pointed out by cluster analysis, it appeared clear that these groups include eu- and supralittoral species (A1 and A2 groups) on the one hand and extralittoral species (A3 and A4 groups) on the other. The decrease in the proportion of marine food sources in the diets of the different macroinvertebrate species when proceeding landwards indicated that the influence of marine subsides was limited to beach dune areas. A similar result was obtained by Paetzold *et al.* (2008) that showed the relatively low contribution of marine-derived resources to the diet of terrestrial arthropod consumers of a productive temperate island. As shown by the two trophic levels that were obtained, the species belonging to the A1 group are mainly primary and secondary consumers, the latter foraging on preys found within the stranded wracks. A2 group was more heterogeneous and exhibited species belonging to trophic guilds grouped into three trophic levels. Primary consumers (herbivores feeding on vascular plants of marine and terrestrial habitats), scavengers, predators and top predators mainly belonged to the beach and to the seaward face of the dune. However, other more mobile species (fliers or spiders) occupied the landward face of the dune. A3 group pooled species inhabiting the backdune and showed only one trophic level which includes a variety of species belonging to different trophic guilds (primary consumers, scavengers and predators). The fact that some predator species of the A2 and A3 groups occupied lower trophic levels can be an indication that these predators belonged to different trophic chains with preys belonging to lower trophic levels. The A4 group included species feeding on pollen and others soil arthropods (collembolans, amphipods and mud snails) which fed on items such as monocellular algae, bacteria and fungi (Schmidt *et al* 2004, Chahartaghi *et al.* 2005), for which isotopic signatures were not evaluated.

In conclusion the study shows that allochthonous marine derived material mainly subsidizes macroinvertebrates species inhabiting the eulittoral and contributes very little to the food chains of more terrestrial species. The effects of inputs on stability in well established food chain models has been assessed by McCann & Yodis (1995), that showed that at low levels of allochthonous inputs food web dynamics are stabilized. The complexity of the areas backing up the beach and the presence of a dune slack rich in plant species probably are sufficient to provide autochthonous resources to macroinvertebrates living in the area. Resource partitioning of autochthonous and allochthonous resources may allow a trophic level to persist by compartmentalizing food webs and thus greatly influences the stability of the food webs. More information is needed to understand on how mosses, lichens, algae and bacteria species might be an important missing link to the picture.

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