

**Trophodynamic variations
on microtidal North
Mediterranean sandy
beaches**

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KEYWORDS

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Abstract

Trophic models of the micro and meiobenthic community of six sandy beaches on the Ligurian coast (north-western Mediterranean Sea) have been performed to assess variations in structure and function of the ecosystem. A novel approach based on the determination of the feeding predisposition of the benthic community revealed that there is a significant shift in the trophodynamics of the system with respect to environmental constraints. Along an emerged-submerged gradient the benthic community displayed a clear trend from a fundamentally detritus-dependent structure to an autotrophic, more balanced and diversified one. The trends analysed focus on the importance of the swash zone as a transitional area between the land and the sea that is characterised by a high diversity and activity of the trophic network.

1. Introduction

Beaches and coastal zones worldwide represent one of the most vulnerable and seriously endangered environments (Defeo & de Alava 1995, Lubchenco et al. 1995, Zann 1997, Lercari & Defeo 1999, Schoeman et al. 2000). In recent decades, Mediterranean beach environments have been subjected to different stress factors, above all by strong human pressure in the form of elevated pollution of coastal waters, urbanisation, erosion and the continuously rising numbers of tourists (Fabiano et al. 2002). It has thus

The complete text of the paper is available at <http://www.iopan.gda.pl/oceanologia/>

become necessary to understand how a beach environment can react to such disturbances and modify its structure and functionality to adapt to changing conditions and increasing stress.

Simulating the trophic network of the sandy beach habitat is a novel approach for assessing variations in the structure and function of the benthic system (Heymans & Baird 1995, Heymans & McLachlan 1996, Ortiz & Wolff 2002, Leguerrier et al. 2003, Fabiano et al. 2004b). In this study we focused on the micro- and meiobenthic community structure to search for a tool with which to compare different beach environments. The microbenthic loop is a major sub-system within the marine food chain and its role in affecting ecosystem function has aroused increasing interest since it was first described in 1983 (Azam et al. 1983). The simulation of the micro- and meiobenthic network provided a tool for assessing the real trophic attitude of the subsystems under consideration here.

2. Material and methods

In order to determine the feeding predisposition of the benthic community, it was necessary to set up a trophic network model of the beach environments. In this study we analysed data on organic matter, bacteria, microphytobenthos and meiofauna collected from six different beaches along the whole Ligurian Coast (Ligurian Sea, Italy) in the north-western Mediterranean: Lavagna (LAV), Pietra Ligure (PIE), Loano (LOA), Albisola (ALB), Varazze (VAE), Varigotti (VAI) (Fig. 1). These beaches represent a good sample of the typical Ligurian sandy beach – short, with a slope of < 5%. Two replicate transects were sampled on each beach in March, June and October 2000; the June campaign was not carried out at the Albisola and Varigotti beaches, and only one transect was sampled at Loano in March and June. Transects were oriented perpendicular to the coastline and were spaced 500 m apart. On each transect 4 stations were situated along the gradient across the beach (Fig. 1): station 1 (Sta. 1) located 1–1.5 m above the extreme limit of wave run up; station 2 (Sta. 2) located in the swash zone, station 3 (Sta. 3) located in the surf zone (depth ~ -1 m) and station 4 (Sta. 4) located in the submerged beach zone (depth ~ -5 m).

The models for each study area were created using Ecopath with Ecosim 5.0 software (<http://www.ecopath.org/>). Ecopath bases its parameterisation on the assumption of mass balance over an arbitrary period, in this case one year. Ecopath parameterisation is based on two master equations, one for production and one for the energy balance, which have to be solved for each group (array of species with a similar ecological attitude) in the simulation (Christensen et al. 2000).

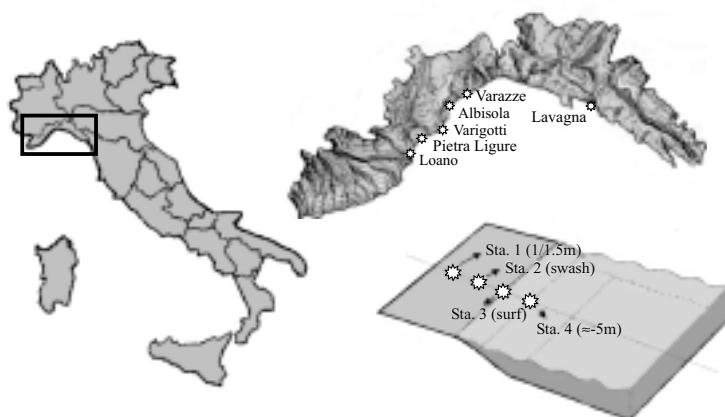


Fig. 1. Sampling stations and transect scheme

The groups involved in the simulations are reported in Table 1 along with their respective laboratory methodologies of analysis.

To perform a simulation, the software needs four basic parameters: biomass, production/biomass ratio, consumption/biomass ratio, and ecotrophic efficiency. If only three of the basic parameters are entered

Table 1. Benthic parameters and groups utilised for the Network analysis and the trophodynamic determination. Methodologies of analysis are reported as references in the third column

Benthic parameter	Group	Reference
chlorophyll <i>a</i>	microphytobenthos	Plante-Cuny 1974
bacteria biomass	bacteria	Meyer-Reil 1983
	nematodes	Wieser 1960, Warwick & Price 1979, Romeyn & Bowman 1983
meiofauna	copepods	Wieser 1960, Warwick & Price 1979
	polychaetes	Wieser 1960, Warwick & Price 1979
	turbellarians	Wieser 1960, Warwick & Price 1979
	others	Wieser 1960, Warwick & Price 1979
total organic matter	detritus	Parker 1983

(in our case, the ecotrophic efficiency was never estimated), the following parameters are needed for each group: catch rate, net migration rate, biomass accumulation rate, assimilation rate and diet composition. For a basic parameterisation, a balanced procedure involving certain changes in the original diet matrix is often necessary (Table 2) until the ecotrophic efficiency for each group in the simulation has a value of < 1 . For a complete description of the simulation methodologies involved in this study, readers are referred to Fabiano et al. (2004b).

From the application of the resulting balanced diet matrix it is possible to obtain real values of the trophic attitude of the networks analysed and, when a simulation is possible, a complete network analysis can be carried out.

Network analysis

The balanced food webs were examined using network analysis, which quantifies cycling (Finn 1976), through-flows, storage, information-theoretical indices of whole-system status (Ulanowicz 1986) and indirect diet relationships. Analysis of the trophic network allows whole-system indices to be obtained. In this study we considered:

- Total System Throughput (TST) – this is simply the sum of all transfer processes occurring in the system. $TST = \sum_{i,j} T_{ij}$ for all possible fluxes T_{ij} , where i and j can represent either a system component or the external environment. It measures the extent of the total activity in the system (Heymans et al. 2002).
- Ascendency, which quantifies both the level of system activity and the degree of organisation with which the material is being processed in the system. The Ascendency (ASC) is calculated as the product of TST and the Average Mutual Information (AMI). This latter measures the average amount of constraint exerted upon an arbitrary quantum of currency as it is channelled from any one compartment to the next (Ulanowicz 1997). The Ascendency is formulated as follows:

$$ASC = TST \times AMI = \sum_{i=1}^n \sum_{j=1}^n T_{ij} \log(T_{ij} B^2 / B_i B_j T).$$

An increase in ASC is linked to the growth and to the development of the system (Ulanowicz 1986, 2004).

- The Carrying Capacity is the diversity of the system flows scaled by the total system Throughput. It is expressed by $C = \sum_{i,j} T_{ij} \log \left[\frac{T_{ij}}{T..} \right]$ and represents the upper limit to the growth of the ASC.

Table 2. Original diet matrix

		Predator (j)										
		1	2	3	4	5	6	7	8	9		
Prey (i)	1	microphytobenthos			0.10	0.80			0.10		0.10	$DC_{1,j}$
	2	bacteria			0.20		0.70	0.20	0.20	0.80	0.20	$DC_{2,j}$
	3	nematodes			0.10			0.05	0.05		0.05	$DC_{3,j}$
	4	copepodes			0.10			0.05	0.05		0.05	$DC_{4,j}$
	5	nauplia			0.10			0.05	0.03		0.03	$DC_{5,j}$
	6	polychaetes						0.05	0.05		0.05	$DC_{6,j}$
	7	turbellarians						0.05	0.05		0.05	$DC_{7,j}$
	8	gastrotricha			0.10			0.05	0.03		0.03	$DC_{8,j}$
	9	others						0.05	0.05		0.05	$DC_{9,j}$
	10	detritus		1.00	0.30	0.20	0.30	0.45	0.39	0.20	0.39	$DC_{10,j}$
	import	1.00									$DC_{imp,j}$	
	Sum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00		
		$DC_{i,1}$	$DC_{i,2}$	$DC_{i,3}$	$DC_{i,4}$	$DC_{i,5}$	$DC_{i,6}$	$DC_{i,7}$	$DC_{i,8}$	$DC_{i,9}$		

Trophodynamic determination

A novel approach for determining the trophic attitude of the ecosystems considered here has been developed in this study. The biomass of each group presented in the system is first divided into five fractions in order to assess the biomass of the particular group that is behaving as Detritivorous (Det), Herbivorous (Her), Bacterivorous (Bat), Carnivorous (Car) or Autotrophic (Aut). This is done by multiplying the biomass of each group by the percentage of its own diet belonging to every trophic attitude. Then for each one of the five different behaviours the divided biomasses are summed to obtain the total biomass in the system that displays that kind of trophic propensity. Finally, the five different biomasses are divided by the total biomass of the system to obtain the percentage of the system representing that trophic attitude.

As far as the diet matrix is concerned (an example is shown in Table 2), the following formulation was employed:

$$\text{Det} = \frac{\sum_{j=1}^{n-1} B_j \times DC_{10,j}}{\sum_{i=1}^{n-1} B_i}; \quad \text{Her} = \frac{\sum_{j=1}^{n-1} B_j \times DC_{1,j}}{\sum_{i=1}^{n-1} B_i}; \quad \text{Bat} = \frac{\sum_{j=1}^{n-1} B_j \times DC_{2,j}}{\sum_{i=1}^{n-1} B_i};$$

$$\text{Car} = \frac{\sum_{i=3}^{n-1} \sum_{j=1}^{n-1} B_j \times DC_{i,j}}{\sum_{i=1}^{n-1} B_i}; \quad \text{Aut} = \frac{B_1 \times DC_{imp,1}}{\sum_{i=1}^{n-1} B_i}.$$

It is a logical consequence of the above formulation that the resulting values are pure numbers, and that the sum of the five values is 1 (Det + Her + Bat + Car + Aut = 1). The values obtained depend on the number of variables that have been supplied to the system, such as biomass composition, production and consumption rates, percentage of unassimilated food, and the composition of the balanced diet matrix.

Statistical analysis

Analysis of Variance (ANOVA) was used to investigate the overall differences between the transects, beaches, periods and stations for each investigated variable. A two-tailed *F*-test was used to assess whether the two 'main effects' were significant against the residuals. Prior to the analysis, the homogeneity of variance was assessed by Cochran's test and, when necessary, data were appropriately transformed. All statistical tests and correlation analyses were carried out using the R12 statistics toolbox of MATLAB.

3. Results

We applied the ANOVA test to all the stations to ascertain whether there were any differences between the transects, beaches, periods and stations. Neither transects nor beaches displayed any significant variations, either in the biological data (Fabiano et al. 2004a) or in the network indicators (Table 3). As a consequence, for each period and each station an average value was obtained for the different beaches and transects so as to achieve a general model of the sandy beach of the Ligurian coast and a general trend of the microbenthic loop subsystem with respect to seasonal variations and the physical influence of the sea.

Table 3. ANOVA table for the investigated spatial and temporal variability of network indicators on Ligurian beaches

	Source of variation	Sum of squares	DF	Mean square	<i>F</i> -ratio	<i>P</i> -value
Ascendency	transect	1.93 e+06	1	1.93 e+06	0.09	0.77
	beach	5.14 e+07	5	1.03 e+07	0.47	0.80
	station	4.83 e+08	3	1.61 e+08	7.29	0.00
	season	1.23 e+08	2	6.14 e+07	2.78	0.07
Information	transect	0.9 e-04	1	0.9 e-04	0.01	0.92
	beach	0.1625	5	0.0325	3.81	0.00
	station	0.1025	3	0.0342	4.01	0.01
	season	0.0551	2	0.0275	3.23	0.04
Throughput	transect	1.14 e+06	1	1.14 e+06	0.06	0.81
	beach	3.79 e+07	5	7.57 e+06	0.39	0.86
	station	4.44 e+08	3	1.48 e+08	7.55	0.00
	season	2.22 e+08	2	6.10 e+07	3.11	0.05
Capacity	transect	5.35 e+15	1	5.35 e+15	0.39	0.53
	beach	4.03 e+16	5	8.06 e+15	0.59	0.71
	station	1.11 e+17	3	3.69 e+16	2.71	0.05
	season	5.96 e+16	2	2.98 e+16	2.19	0.12

Network analysis

Global attributes

Ascendency values ranged from 2640.6 to 10137.0 tonne km⁻² year⁻¹ at autumn station 1 and winter station 4 respectively, and displayed a general trend with an increase that followed the emerged-submerged gradient

(Fig. 2). Winter and autumn stations also showed a peak at station 2, whereas in spring this station displayed the lowest seasonal value.

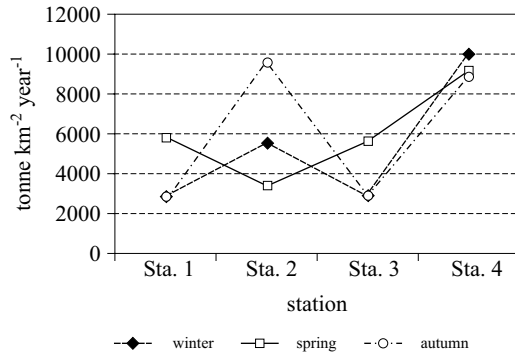


Fig. 2. Spatial pattern of Ascendency in the seasons considered

Throughput accounted for the greatest part of the Ascendency values and displayed the same temporal and spatial pattern ($\rho = 98.75$, $n = 12$, $p < 0.001$). The Information displayed generally low values ranging from 0.931 bits at spring station 2 to 1.235 bits in winter station 2. The spatial trend of Information differed from that of Ascendency and Throughput, correlations being insignificant (Fig. 3).

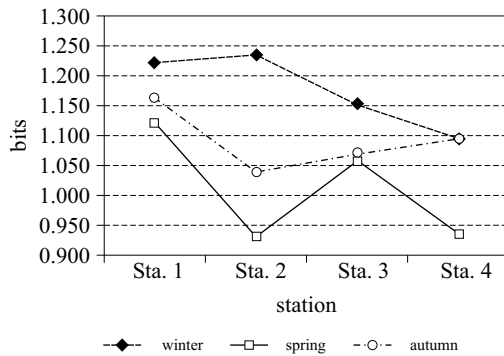


Fig. 3. Spatial trend of Information in the seasons considered

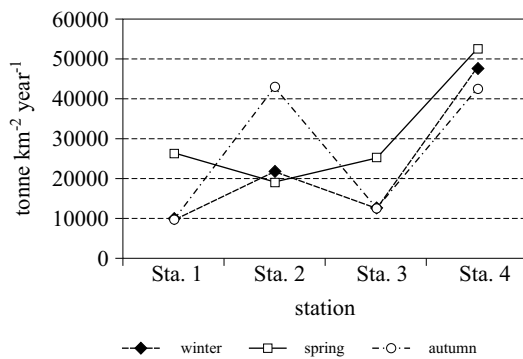


Fig. 4. Capacity trend in the three different seasons

The Carrying Capacity displayed values ranging from 9661.4 to 52462.9 tonne km⁻² year⁻¹ at autumn station 1 and spring station 4 respectively, with a spatial pattern (Fig. 4) following that of the Ascendency and with high correlation values ($\rho = 97.71$, $n = 12$, $p < 0.001$).

Lindeman trophic analysis

The Lindeman transformation matrices are based on a knowledge of the dietary ratios of all the compartments in the ecosystem. The rows of this matrix represent the apportionment of the corresponding species among the integer trophic levels, which are depicted by the columns. Table 4 lists the percentage of total activity at each trophic level (the cumulative percentage is reported) obtained by the sum of the contributors of all the groups in the simulations.

Table 4. Cumulative percentage of total activity at each trophic level. Roman numerals identify trophic levels detected for each simulation

		Trophic level							
		I	II	III	IV	V	VI	VII	VIII
autumn	station 1	59.59	97.50	99.88	99.99	100.00	100.00		
	station 2	58.59	95.80	99.73	99.98	100.00	100.00		
	station 3	56.59	94.90	99.70	99.98	100.00	100.00	100	
	station 4	55.10	92.28	99.15	99.91	99.99	100.00	100.00	100.00
winter	station 1	58.32	93.99	99.31	99.92	99.99	100.00	100.00	100.00
	station 2	57.79	94.64	99.48	99.95	100.00	100.00	100.00	
	station 3	63.23	96.34	99.66	99.97	100.00	100.00	100.00	100.00
	station 4	62.63	95.38	99.60	99.96	100.00	100.00	100.00	100.00
spring	station 1	57.10	93.40	99.30	99.93	99.99	100.00	100.00	
	station 2	61.98	93.91	99.38	99.94	99.99	100.00	100.00	100.00
	station 3	59.59	95.42	99.76	99.99	100.00	100.00	100.00	
	station 4	59.68	94.23	99.57	99.97	100.00	100.00	100.00	100.00

Table 4 shows that the simulation detected from six to eight different trophic levels (Lindeman 1942), but that the changes in beaches, seasons and stations are all practically insignificant. Ligurian sandy beaches constantly displayed the greatest part of the trophic activity, which acted on the first two trophic levels (> 92.28%), thus showing a strong dependence on detritus in all the seasons considered.

System trophodynamics

The analysis revealed the same behaviour in all the beaches; this showed the clear dominance of the dissipative and autotrophic attitudes (Fig. 5). Detritivorous behaviour was absolutely dominant at the first three stations, whereas autotrophic dynamics became more and more important along the emerged-submerged gradient, until the fourth station, where it assumed the greatest relevance in the trophic network. Considering the trend across the beach, it was clear that the detritivorous behaviour and consequently the dependence on detritus followed the emerged-submerged gradient linearly, decreasing with increasing depth and marine input. The autotrophic attitude showed the opposite behaviour and increased with increasing depth, indicating a strong dependence on marine input. This latter trend is strictly

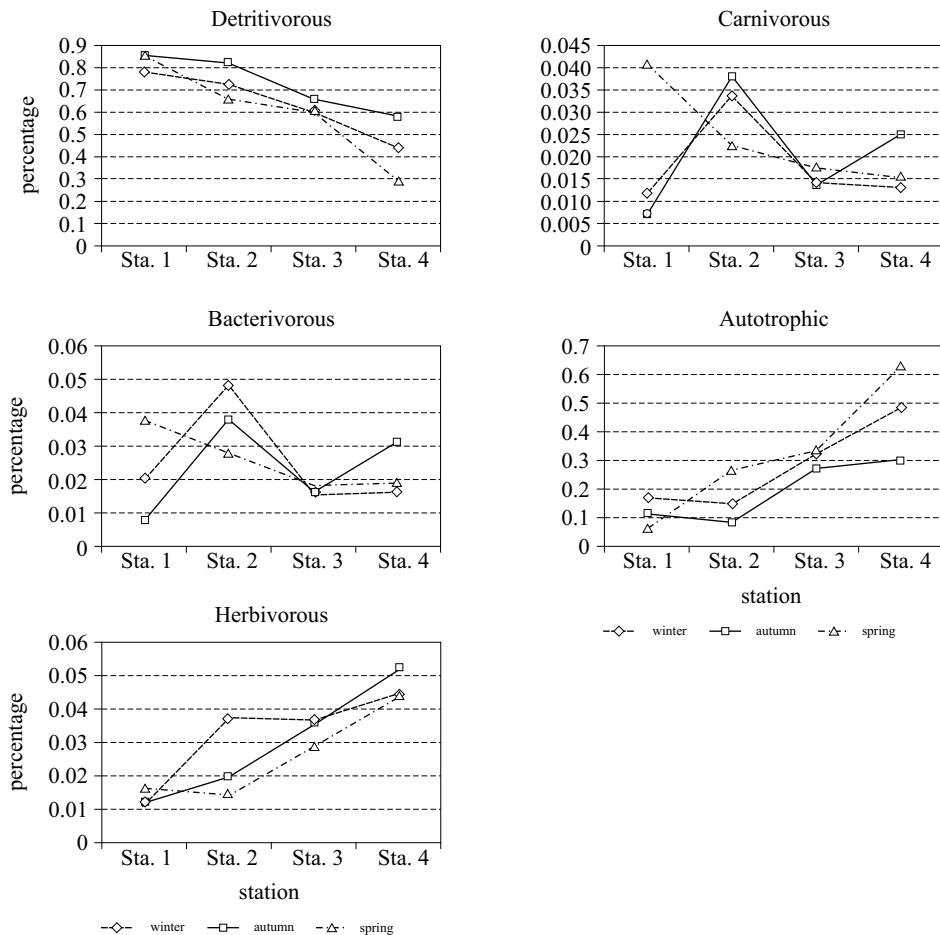


Fig. 5. Percentage of trophic attitude along transects in each season

related to the herbivorous one, which displayed a similar trend. Also, carnivorous and bacterivorous dynamics displayed a similar trend, except at station 1 in spring, where the activity is higher as compared to the other seasons.

4. Discussion

The similarities displayed by the beaches covered by this study allowed us to consider the averaged model as a general model of Ligurian sandy beaches. Ascendency, Capacity and Throughput values were very much lower in comparison with what was observed for the micro- and meiobenthic subsystem in coastal Ligurian zones (Fabiano et al. 2004b) or in Mediterranean coastal zones (Vassallo et al., in press), confirming the strongly oligotrophic nature of the beach system. As further confirmation, both trophodynamic and Lindeman trophic analysis revealed that this system is basically a detritus-dependent system, and showed that the major part of the activity in the beach benthic environment was related to consumption and dissipation within the detritus compartment. However, trophodynamic analysis was more sensitive to changes in trophic structure and function, and allowed us to distinguish between different situations in the spatial and temporal pattern.

Network analysis showed that Ascendency, Throughput and Capacity were closely related to each other, with similar autumn and winter trends, and a spring trend with some partial differences, in particular at the emerged or semi-emerged stations. It also revealed an increase in total activity and functionality of the system along the emerged-submerged gradient, displaying higher values of Ascendency, Throughput and Capacity on moving from the beach to the sea (from station 1 to station 4).

On the other hand, Information displayed the opposite behaviour, with values decreasing along the land-sea transect. Moreover, Information showed values generally decreasing from spring to autumn and finally to winter, indicating a strong seasonal dependence not shown up by the other network-oriented indicators.

Ligurian sandy beaches displayed increasing values of general activity and functionality of the system with increasing influence of the sea, but this has to be related to a decrease in the efficiency of resource exploitation. Thus, the microbenthic subsystem increases its activity with rising input, in particular with increasing marine input, but optimises resource exploitation when the external input of natural resources is low, as is the case at the emerged stations or in the driest season.

Ligurian sandy beaches displayed the same trophodynamic trend along the environmental beach gradient across the swash zone. They were char-

acterised by a strong detritus dependence at the most emerged station. Becoming weaker and weaker with the increasing influence of the sea, this strictly detritus-dependent attitude was replaced by autotrophic behaviour and a more diversified and balanced trophic network. The trophodynamics of these beaches did not reveal any major seasonal variations; all the trophic attitudes except for Carnivorous and Bacterivorous behaviour in spring displayed similar trends in the three seasons analysed. At the station farthest from the water-line the Carnivorous and Bacterivorous attitudes showed an increase in consuming activity that could be related to favourable climatic conditions or to the initial activities of the beach operators whilst preparing beaches for the summer season by moving and mixing the topmost layer of the sand.

For the majority of the indicators, this analysis has shown that the widest variability and the highest values were detected for station 2, located in the swash zone. Along the emerged-submerged gradient, station 2 displayed the widest seasonal variations in the network indicators, as well as the most active and lively trophic network with the highest values of predatory and more generally consuming behaviour. These latter results confirmed the importance of the swash zone as a transitional area between land and sea characterised by a high diversity and trophic network activity.

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