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Original article

Benthic microbial loop functioning in coastal lagoons: a comparative approach

Boucle microbienne benthique dans les lagunes côtières : approche comparative

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Abstract

Coastal lagoons are highly variable and dynamic systems that have been rarely investigated in terms of benthic microbial loop. We present here the results of a comparative study aimed at investigating factors and benthic processes potentially affecting microbial loop functioning in three lagoon systems (Goro, Lesina and Marsala lagoons). The three lagoons were characterised by different geo-morphological, trophic and ecological features. We determined organic matter quantity and biochemical composition, exo-enzymatic activities, bacterial biomass and bacterial carbon production together with heterotrophic nanoflagellate and meiofauna biomass. These variables allowed providing estimates of biomass ratios between different benthic compartments and gathering information on C transfer in different systems. The results of this study indicate that organic matter composition played a primary role on microbial loop ability of channelling C-biomass to higher trophic levels. In coastal lagoons, indeed, quantity and quality of sediment organic matter control rates of organic matter degradation, turnover rates (through breakdown of large macromolecules) and utilisation by benthic heterotrophic organisms (bacterial C production). Exo-enzymatic activities in all lagoons investigated were generally low, when compared to coastal marine systems, and lowest rates were observed in systems characterised by refractory organic pools. Our results indicate that the autotrophic contribution to the biopolymeric carbon pools, which influences the ratio of autotrophic to heterotrophic biomass, is a key factor regulating the functional efficiency of the benthic system. The structure of the benthic microbial loop varied according to the different characteristics of the lagoons: from a classical "detritus sink" system (i.e., the Marsala lagoon, where organic matter was highly refractory), to the "source" system (Lesina lagoon, which displayed an efficient C transfer to higher trophic levels, mediated by benthic bacteria).

Résumé

Très peu d'études existent sur la boucle microbienne dans les lagunes côtières, systèmes dynamiques à grande variabilité. Nous présentons ici les résultats d'une étude comparée s'intéressant aux facteurs du milieu et aux processus benthiques qui affectent le fonctionnement du réseau microbien dans trois systèmes lagunaires (Goro, Lesina et Marsala). Ces trois lagunes présentent des aspects géomorphologiques, trophiques et écologiques différents. Nous avons mesuré la teneur en matière organique et la composition biochimique, les activités exo-enzymatiques, la biomasse bactérienne et la production bactérienne carbonée ainsi que la biomasse de la méiofaune et des flagellés hétérotrophiques. Nous avons ainsi pu estimer les taux de transfert de biomasse et donc les flux de carbone entre les différents compartiments benthiques. La composition en matière organique joue un rôle primordial sur l'aptitude de la boucle microbienne à canaliser la biomasse de carbone vers les échelons supérieurs. Dans les lagunes côtières, la qualité et la quantité de matière organique sédimentaire contrôlent le taux de dégradation de la matière organique, les taux de renouvellement (par destructuration des grosses molécules) et l'utilisation par les hétérotrophes benthiques (production carbonée bactérienne). Dans les trois lagunes étudiées, les activités exo-enzymatiques sont faibles comparé aux écosystèmes marins côtiers ; les taux les plus bas se rencontrent dans les systèmes caractérisés par un pool organique réfractaire. Aussi, les taux de mobilisation de la matière organique sont-ils bas. Ces résultats montrent que la contribution autotrophique aux pools de carbone des biopolymères qui influencent le rapport biomasse autotrophe / biomasse hétérotrophe constitue un facteur de régulation essentiel

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de l'efficience de la boucle microbienne. La structure de ce réseau microbien varie d'une lagune à l'autre entre deux situations opposées : d'un classique « puits à détritus » (par exemple la lagune de Marsala où la matière organique est hautement réfractaire) à un système « source » (la lagune de Lesina avec un transfert efficace du carbone vers les niveaux trophiques supérieurs par l'intermédiaire des bactéries benthiques).

Keywords: Benthic microbial loop; Organic detritus; Coastal lagoons

Mots clés : Boucle microbienne benthique ; Détritus organiques ; Lagunes côtières

1. Introduction

Coastal lagoons are generally characterised by important physical and chemical gradients that make these systems highly unstable and subjected to unpredictable fluctuating conditions (Clavier et al., 1995; Pusceddu et al., 1996). Lagoons can act either as a sink for organic matter (OM) accumulation, or as reservoirs able to fertilise adjacent coastal areas, through organic and inorganic nutrient export (Pusceddu et al., 1999, 2003; Barnes, 1994). Besides physical factors, the balance between OM export and its accumulation is dependent upon degradation and heterotrophic utilisation of the organic matter pools. These processes, largely mediated by the benthic microbial loop (Deming and Barross, 1993; Caumette, 1992), are important for understanding the relationship between the lagoon and the adjacent coastal zone.

Despite several investigations focusing on the role of environmental gradients (e.g., salinity or temperature gradients, according to confinement theory, Guelorget and Perthuisot, 1983), the study on factors controlling the benthic microbial loop functioning and the organic C transfer to higher trophic levels in coastal lagoons is extremely limited (Ekebom, 1999). The primary step of organic matter breakdown is mediated by extracellular enzymatic activities that make organic macromolecules available for bacterial uptake. Sediment organic matter can be channelled to higher trophic levels both directly (e.g., through deposit-feeding meiofauna and macrofauna) and/or indirectly (i.e., through bacterial uptake, bacterial C production, and subsequent consumption by bacterial-grazers, such as protozoa and bacterivorous meiofauna, Montagna, 1985; Bott and Borchardt, 1999). We estimated the ability of the different lagoon systems in transferring organic detritus to higher trophic levels, by means of a sequential step of analyses including the biochemical composition of sedimentary organic matter followed by the potential rates at which the protein and carbohydrate pools were mobilised (by means of exo-enzymatic activities, i.e., aminopeptidase and β-glucosidase). Then we estimated the fraction of the protein pool potentially incorporated into bacterial biomass (i.e., measuring bacterial carbon production, BCP). Finally, we investigated heterotrophic nanoflagellates (HNF) and meiofauna assemblages in order to evaluate the potential of these systems in supporting higher trophic levels of the benthic microbial food web. This approach allowed elaborating a conceptual model describing the balance between organic matter accumulation, autotrophic vs. heterotrophic biomass and bacterial C production of coastal lagoons characterised by different trophic and environmental conditions.

This research help in providing comparative information on: (i) the biomass ratios of the different microbial benthic components; (ii) the balance between organic matter degradation, utilisation and transfer (mediated by bacteria); (iii) factors and processes potentially affecting organic matter diagenesis and benthic microbial loop functioning.

2. Materials and methods

2.1. Study sites and sampling

This study was carried out at three Italian lagoons located at different latitudes (Fig. 1): Sacca di Goro in the northern Adriatic Sea, Lesina lagoon in the central–southern Adriatic Sea and Stagnone di Marsala, the southernmost site, located in the western sector of Sicily.

The Sacca di Goro lagoon, the southernmost basin of the wider Po deltaic system (Fig. 1a) (average water depth of 1.5 m), is subjected to continuous natural subsidence phenomena and large anthropogenic loads. The basin is connected to the sea by means of both natural and artificial canals and is characterised by clear seasonal fluctuations of temperature and salinity and, during summer, may experience sub-oxic/anoxic conditions due to dystrophic crises characterised by anomalous macrophyte blooms (Ulva and Gracilaria; Viaroli et al., 1993).

The Lesina lagoon is characterised by shallow depths (on average 0.8 m depth; Fig. 1b), is connected to the sea through two channels and receives freshwater from two minor rivers. In the last few years, the Lesina lagoon experienced a progressive eutrophication followed by occasional dystrophic crises due to the abnormal proliferation of the green algae *Valonia utricularis*. Large parts of the lagoon are also covered by *Zostera noltii* and *Ruppia* sp.

The Marsala lagoon is connected to the sea by means of two large channels (Fig. 1c). The northern canal is 450-m wide and is characterised by evident seawater mixing. The southern canal, 1450 m wide, allows a continuous seawater inflow. The current speed typically ranges from 2 to 5 cm s^{-1} (Mazzola and Sarà, 1995). The average water depth is ca 1 m. In the central and northern sector of the lagoon, an extended seagrass meadow (Posidonia oceanica) influences water circulation. No major continental inputs are present.

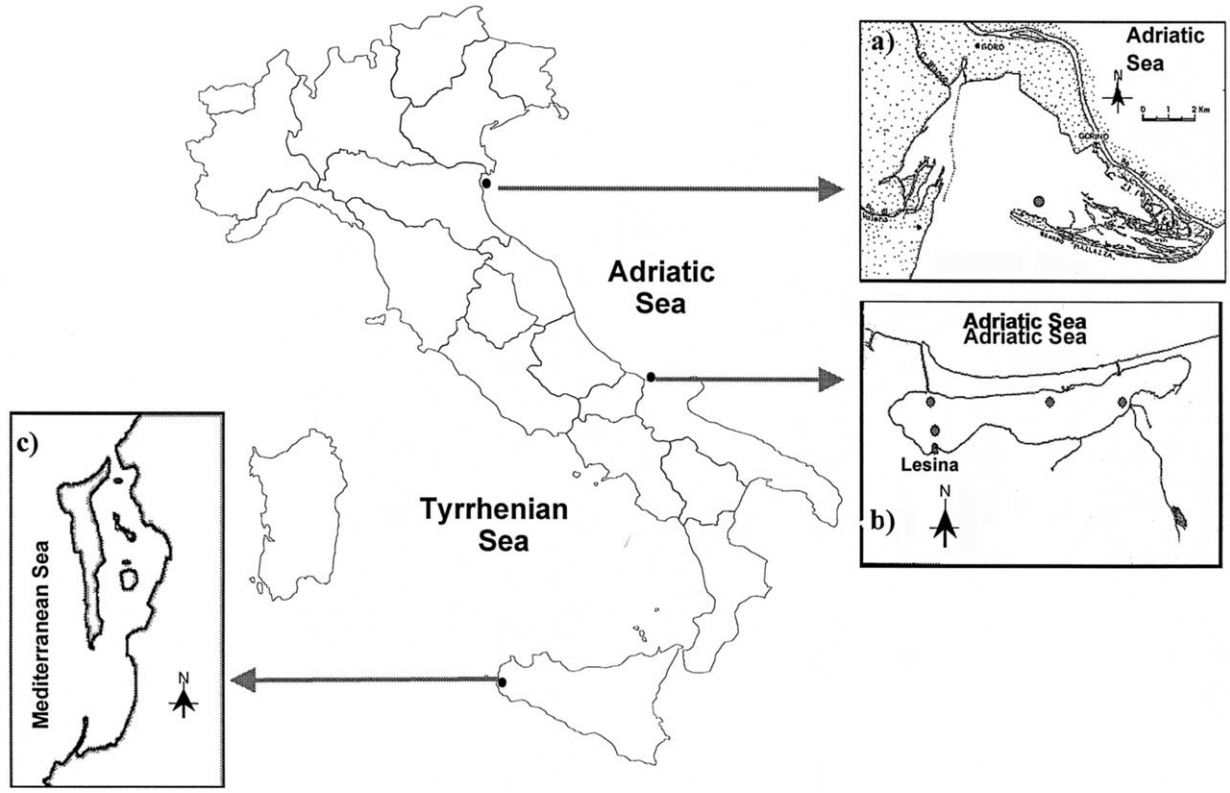

Fig. 1. Sampling areas and station locations in the three lagoons: (a) Sacca di Goro; (b) Laguna di Lesina; (c) Stagnone di Marsala.

2.2. Sediment sampling

Four seasonal samplings were carried out in both Lesina (four stations) and Marsala lagoons (two stations), whereas sediment sampling in the Sacca di Goro (two stations) was carried out only in summer. In order to obtain information representative of the average ecological conditions, station locations were defined on the basis of previous studies (Pusceddu et al., 1999; Viaroli et al., 1993), according to salinity gradients, distance from the sea, algal coverage and the different hydrodynamic properties.

Temperature and salinity were determined at each sampling, using a multi-parametric probe. Sediment samples (top 0–1 cm) were collected manually using Plexiglas tubes (i.d. 4.7 cm). Ten replicate cores per station were brought back to the laboratory and processed within 4 h. The top 1 cm of three cores was immediately frozen at –20 °C and stored until analysis. Samples for bacterial and heterotrophic nanoflagellate counting (about 1 cm^3) were immediately fixed with buffered formaldehyde for bacteria (2% final concentration) and with buffered glutaraldehyde for nanoflagellates (1.5% final concentration) and stored at 4 °C until analyses. Biochemical determinations and bacterial and nanoflagellate counting were carried out within two weeks from sampling. For meiofaunal analysis, three replicate cores (each 10.7 cm^2 surface area) were taken down to a depth of 10 cm and fixed with buffered 4% formaldehyde solution.

2.3. Photosynthetic pigments

Chloroplastic pigments (chlorophyll-a and phaeopigments) were extracted from about 1 g of sediment with 5 ml of 90% acetone and determined fluorometrically in order to estimate chlorophyll-a and subsequently acidified with 200 µl of 0.1 N HCl to estimate phaeopigments (Lorenzen and Jeffrey, 1980). Chloroplastic pigment equivalents (CPE) were defined as the sum of chlorophyll-a and phaeopigments. Primary organic carbon was calculated by converting chlorophyll-a concentration to carbon content (CChla), using a conversion factor of 40 (de Jonge, 1980).

2.4. Biochemical composition of the sedimentary organic matter

Total protein (PRT) concentration was determined on sediment sub-samples according to Hartree (1972). Protein concentrations were expressed as bovine serum albumin (BSA) equivalents. Total carbohydrates (CHO) were analysed according to Gerchakov and Hatcher (1972) and expressed as glucose equivalents. Total lipids (LIP) were extracted from the sediment by direct elution with chloroform–methanol (1:1 v/v) according to Bligh and Dyer (1959) and then determined according to Marsh and Weinstein (1966). Analyses were performed spectrophotometrically. For each biochemical assay, blanks were obtained using pre-combusted sediments (450 °C for 4 h). All analyses were performed in three to five replicates on about 1 g of

sediment. Carbohydrate, protein and lipid concentrations were converted into carbon equivalents using the conversion factors 0.40 and 0.49 and 0.75 mgC mg^{-1}, respectively, and normalised to sediment dry weight (Fabiano et al., 1995). The sum of total protein, carbohydrate and lipid carbon equivalents was reported as biopolymeric organic carbon (BPC, Pusceddu et al., 2000).

2.5. Bacterial and heterotrophic nanoflagellate abundance and biomass

For bacterial counting, sediment sub-samples were sonified three times (Branson Sonifier 2200; 60 W for 1 min) and diluted 500 times with sterile and 0.2 µm pre-filtered formaldehyde (2% final concentration). Sub-samples were then stained for 5 min with Acridine Orange (final concentration 5 mg l^{-1}) and filtered on black Nuclepore polycarbonate (pore size 0.2 µm) filters. The filters were analysed as described by Fry (1990) using epifluorescence microscopy (Zeiss Axioskop2, × 1000). For each slide, at least 10 microscope fields were observed and a total of at least 400 cells were counted. Bacterial biovolume was estimated using a micrometer ocular (as maximal length and width) assigning bacterial cells to different size classes (Fry, 1990). Bacterial biovolume was converted into carbon content assuming 310 fgC μm^{-3} (Fry, 1990). The average cell carbon content was calculated as the ratio of total bacterial biomass to total bacterial abundance. Bacterial abundance and biomass were normalised to dry weight after desiccation (60 °C, 24 h).

HNF were extracted from sediments using a Percoll gradient centrifugation, according to Epstein (1995). HNF counting was carried out under epifluorescence microscopy using the double staining (DAPI and FITC) technique (Sherr et al., 1993). Only cells with a major axis comprised between 2 and 20 µm and with a definite nucleus were counted, whereas cells with bizarre shapes, those associated with other cells or those having a harder outer membrane or shell were excluded (Bak and Niuewland, 1989, Bak et al., 1991, Hondeveld et al., 1994). HNF biovolume was estimated on all counted cells (as maximal length and width) using a micrometer ocular. At least 100 cells per slide were counted. HNF biomass was estimated converting cell biovolume using a conversion factor 200 fgC μm^{-3} (Børsheim and Bratbak, 1987; Ekebom, 1999).

2.6. Bacterial secondary production and exo-enzymatic activities

Benthic bacterial production was measured by ^{3}H-leucine incorporation following the procedure described by van Duyl and Kop (1994). Sediment sub-samples (200 µl), added to a saturating aqueous solution of ^{3}H-leucine (6-µCi final concentration per sample), were incubated for 1 h in the dark at in situ temperature. After incubation, bacterial C incorporation was stopped with 1.7 ml of 80% ethanol before scintillation counting. Sediment blanks were made adding ethanol immediately before ^{3}H-leucine addition. Data were normalised to sediment dry weight after dessication (60°, 24 h). We calculated organic bacterial protein contribution to the overall protein pool assuming a C:N = 4 for bacterial C-biomass and then we converted bacterial N into bacterial protein content assuming: protein = 6.25 × N (see Danovaro et al., 1999a).

Extracellular enzymatic activity of β-D-glucosidase (MFU-β-glucopyranoside, Glu-MUF) and aminopeptidase activity (L-Leucine-4-methylcoumarinyl-7-amide, Leu-MCA) was measured immediately after sediment retrieval (Meyer-Reil, 1987; Meyer-Reil and Koster, 1992). Extracellular enzymatic activity measurement was carried out in triplicate by adding 150 µl of Glu-MUF and Leu-MCA to 1 ml of a slurry prepared using 1:1 volumes of water and sediment (final concentration 200 µM, after determination of saturating concentration; Poremba, 1995). Substrate incubations were performed in the dark at in situ temperature for 1 h (enzymatic activities increased linearly with time up to 3 h). After incubation, the slurries were centrifuged (3000 rpm, 5 min) and supernatants were analysed fluorometrically (at 365 nm excitation, 455 nm emission for MFU-glu; Hoppe, 1993 and 380 nm excitation, 440 nm emission for Leu-MCA; Meyer-Reil, 1986). Data were normalised to sediment dry weight (60 °C, 24 h) and reported as nanomolar of MUF or MCA released per gram of sediment dry weight h^{-1}. Aminopeptidase and β-glucosidase activities were converted into equivalents of C mobilised assuming that 1 nmol of substrate hydrolysed enzymatically corresponded to 72 ng of mobilised C. Bacterial efficiency in using the mobilised C source was estimated as the ratio of bacterial C production to C potentially mobilised enzymatically. Bacterial efficiency in utilising enzymatically mobilised proteins was calculated as the ratio between bacterial protein production and proteins potentially mobilised.

2.7. Meiofaunal parameters

Meiofaunal samples were sieved through 1000 and 32-µm meshes, extracted by centrifugation in Ludox HS (density 1.18 g cm^{-3}), counted and classified per taxon under a microscope, after staining with Rose Bengal (0.5 g l^{-1}). After measurement of a representative sub-sample, referred to the biomass of nematodes and copepods (which all together accounted for >90% of the total meiofaunal biomass at all sampling sites), meiofaunal biomass was estimated assuming an average biomass of 1 µgC ind.$^{-1}$ (Gambi et al., 2003).

2.8. Statistical analyses

For all variables, differences among sampling periods and sites were assessed by Anova analysis, followed by post-hoc Newman–Keuls (NK) test.

Table 1
Comparison of main environmental parameters (e.g., temperature, salinity and grain size) and of photosynthetic pigment concentrations (e.g., chlorophyll-a, phaeopigment and CPE) in different lagoons

Sites	Seasons	Stations	Temperature	Salinity	Sand	Chlorophyll-a		Phaeopigments		CPE	
			°C	psu	%	μg g^{-1}	std	μg g^{-1}	std	μg g^{-1}	std
Goro lagoon	Summer	1	25.0	28.0	84.3	0.8	0.1	9.2	0.5	10.0	1.0
		2	25.0	28.0	85.8	2.6	1.3	15.5	0.7	18.1	3.0
		Summer mean (±SE)	25.0±0.0	28.0±0.0	85.0±0.5	1.7±0.6		12.3±2.2		14.1±3.2	
Lesina lagoon	Summer	1	23.5	38.0	78.2	20.1	0.0	36.6	6.4	46.7	3.6
		2	23.5	33.0	88.6	20.5	1.9	6.1	0.3	26.5	1.5
		3	23.9	28.0	93.7	24.2	6.0	23.2	4.3	47.4	9.7
		4	24.0	10.0	75.2	28.6	3.4	14.9	2.4	43.5	5.7
	Autumn	1	22.0	41.0	83.5	13.1	1.5	19.6	2.9	32.7	4.3
		2	21.0	44.0	89.5	18.5	5.4	26.1	6.0	38.5	13.8
		3	20.0	35.0	87.3	38.3	7.6	41.2	6.7	79.4	14.2
		4	17.0	11.0	87.8	51.1	17.6	25.2	1.5	76.3	19.1
	Winter	1	12.0	35.0	92.5	27.6	1.0	31.1	6.1	49.5	18.7
		2	12.0	36.5	91.2	28.9	5.4	20.0	1.0	48.9	4.4
		3	11.0	26.0	97.9	54.0	12.6	19.8	2.7	73.8	15.4
		4	13.0	12.0	86.0	41.9	4.9	44.4	5.3	86.3	10.2
	Spring	1	23.0	21.0	85.0	20.1	4.3	27.5	5.8	47.6	9.8
		2	23.0	15.0	92.2	41.4	2.8	28.3	7.2	69.8	10.0
		3	22.0	15.0	94.9	35.7	5.2	24.6	1.1	60.3	6.4
		4	17.0	5.0	81.6	86.9	11.2	59.0	4.8	145.9	12.9
		Summer mean (±SE)	23.7±0.1	27.5±5.3	83.9±3.8	23.3±1.7		20.2±5.6		41.0±4.3	
		Annual mean(±SE)	19.2±1.2	25.3±3.1	87.8±1.5	34.4±4.4		28.0±3.1		60.8±6.9	
Marsala lagoon	Summer	1	25.9	48.9	93.8	2.6	0.4	1.5	0.1	4.1	0.5
		2	28.5	52.4	84.7	4.4	1.4	4.7	1.4	9.1	2.8
	Autumn	1	20.0	nd	92.6	0.1	0.0	0.1	0.0	0.1	0.0
		2	22.0	nd	90.8	0.0	0.0	0.1	0.0	0.2	0.0
	Winter	1	14.0	36.7	93.6	1.8	0.1	0.8	0.1	2.6	0.2
		2	13.6	37.9	89.0	6.6	2.6	3.1	1.1	9.6	3.3
	Spring	1	18.8	41.3	86.3	3.1	0.	1.9	0.3	5.0	0.7
		2	16.7	41.4	84.9	5.7	2.0	3.2	1.1	7.2	2.4
		Summer mean (±SE)	27.2±0.9	50.7±1.2	89.2±3.2	3.5±0.6		3.1±1.2		6.6±1.8	
		Annual mean (±SE)	19.9±1.8	43.1±2.0	89.5±1.3	3.0±0.8		1.9±0.5		4.7±1.2	

3. Results

3.1. Environmental variables and phytopigment concentration

Data on temperature, salinity, sediment grain size and phytopigment concentration are reported in Table 1. In all lagoons, during the investigated periods, temperature displayed clear seasonal patterns. Annual and summer mean temperatures were similar at the three sites (15.1 °C -Mistri, pers. comm., and 25.0 °C at Goro, 19.2 and 23.7 °C at Lesina and 19.9 and 27.2 °C at Marsala, respectively). Conversely, salinity displayed significant differences among sites: highest values were observed at Marsala (range 36.7–52.4 psu; Anova, $P < 0.05$) and lowest at Lesina (range 5.0 and 44.0 psu, respectively). In all the systems, sediment grain size displayed the dominance of the sandy fraction (generally >80%).

At all sampling periods, surface sediments of the Lesina lagoon exhibited the highest chlorophyll-a concentrations (23.3 ± 1.7 μg g^{-1} in summer). Significantly lower values were observed in the other two sites (1.7 ± 0.6 and 3.5 ± 0.6 μg g^{-1} in summer for Goro and Marsala, respectively; Anova, $P < 0.001$; NK test: Goro < Marsala < Lesina). Chlorophyll-a contribution to total phytopigment concentrations (CPE) ranged from 11% (Goro lagoon) to >50% in Lesina and Marsala lagoons.

3.2. Sedimentary biopolymeric organic carbon (BPC)

The three sites displayed clear differences in terms of quantity and biochemical composition of sedimentary organic matter (Table 2). Lesina and Marsala displayed the highest biopolymeric carbon concentrations (in summer 8.1 ± 1.2 and 6.5 ± 3.4 mgC g^{-1}, respectively), whereas Goro displayed values ca. 5–7 times lower. Carbohydrates represented the dominant biochemical class of organic compounds at Goro and Lesina (accounting for 42–54% of total BPC concentration, respectively), whereas lipids dominated at Marsala (41% of total BPC). In Lesina and Goro, lipid concentration was generally low contributing to 14–18% to total BPC concentration. The protein to carbohydrate ratios in all the lagoons were always <1.

Table 2
Comparison of biochemical composition of organic matter (e.g. protein, carbohydrate and lipid concentrations), biopolymeric organic carbon (BPC) and ratio between proteins (PRT) and carbohydrates (CHO) in different sampling lagoons

Sites	Seasons	Stations	Proteins		Carbohydrates		Lipids		Biopolymeric carbon		PRT:CHO
			mg g^{-1}	std	mg g^{-1}	std	mg g^{-1}	std	mgC g^{-1}	std	
Goro lagoon	Summer	1	0.9	0.0	0.7	0.1	0.3	0.0	0.9	0.1	1.3
		2	1.2	0.0	2.4	1.4	0.3	0.0	1.8	0.6	0.5
		Summer mean (±SE)	1.0 ± 0.1		1.6 ± 0.6		0.3 ± 0.03		1.4 ± 0.3		0.9 ± 0.3
Lesina lagoon	Summer	1	5.5	1.0	14.2	2.3	1.5	0.1	9.6	1.5	0.4
		2	2.5	0.8	6.5	1.6	0.3	0.0	4.0	1.1	0.4
		3	5.1	0.6	14.9	3.3	2.3	0.3	10.2	1.9	0.3
		4	3.9	0.4	16.0	1.1	0.7	0.0	8.8	0.6	0.2
	Autumn	1	4.6	0.5	11.3	3.2	1.0	0.2	7.5	1.6	0.4
		2	3.8	0.6	9.9	1.4	0.6	0.3	6.3	1.0	0.4
		3	7.4	0.6	22.7	5.0	3.7	0.1	15.5	2.3	0.3
		4	6.5	0.5	25.5	4.4	1.6	0.2	14.6	2.1	0.3
	Winter	1	7.2	0.8	12.7	3.4	2.9	0.1	10.8	1.8	0.6
		2	3.8	0.8	10.6	1.9	1.3	0.3	7.0	1.4	0.4
		3	4.2	1.0	14.3	1.5	1.7	0.3	9.1	1.3	0.3
		4	6.2	0.4	29.0	7.8	3.2	0.6	17.0	3.7	0.2
	Spring	1	8.0	0.8	5.2	0.9	2.2	0.1	7.7	0.8	1.5
		2	4.8	0.7	2.7	0.6	1.0	0.1	4.2	0.7	1.8
		3	7.1	0.6	5.3	1.0	2.1	0.4	7.2	0.9	1.3
		4	5.9	0.7	6.5	1.1	2.4	0.3	7.4	1.0	0.9
		Summer mean (±SE)	4.2 ± 0.6		12.9 ± 1.9		1.2 ± 0.4		8.1 ± 1.2		0.3 ± 0.03
		Annual mean(±SE)	5.4 ± 0.4		13.0 ± 1.8		1.8 ± 0.2		9.2 ± 0.9		0.6 ± 0.1
Marsala lagoon	Summer	1	0.9	0.2	0.7	0.1	1.3	0.2	1.7	0.3	1.2
		2	6.8	0.8	8.2	0.0	6.5	0.7	11.2	0.9	0.8
	Autumn	1	0.2	0.0	0.8	0.0	0.2	0.0	0.6	0.0	0.3
		2	0.5	0.1	1.3	0.2	1.4	0.1	1.8	0.2	0.3
	Winter	1	0.8	0.1	0.7	0.1	2.1	0.1	2.2	0.1	1.4
		2	2.9	0.6	3.5	1.3	2.6	0.6	4.7	1.2	1.2
	Spring	1	0.9	0.1	1.6	0.1	0.4	0.1	1.4	0.1	0.6
		2	2.2	0.3	5.3	0.8	0.9	0.2	3.8	0.5	0.4
		Summer mean (±SE)	3.9 ± 2.1		4.5 ± 2.6		3.9 ± 1.9		6.5 ± 3.4		1.0 ± 0.1
		Annual mean (±SE)	1.9±0.7		2.8±0.9		1.9±0.7		3.4±1.1		0.8±0.1

3.3. Benthic bacteria, nanoflagellates and meiofauna

Bacteria, nanoflagellate, meiofauna density and biomass at the three sampling sites are reported in Table 3. In summer, bacterial density in surface sediments of the Marsala lagoon ($10.7 \pm 2.2 \times 10^9$ cell g^{-1}) was 2–53 times higher than at Lesina and Goro (0.2 ± 0.01 and $4.5 \pm 1.0 \times 10^9$ cell g^{-1}, respectively). At all the sites, lower bacterial densities were observed in winter. Bacterial biomass displayed similar temporal and spatial patterns with highest values at the Marsala lagoon (3–12 times higher than at Lesina and Goro, respectively).

In the Marsala lagoon, HNF density ($16.3 \pm 8.9 \times 10^5$ g^{-1}) and biomass (12.4 ± 5.6 µgC g^{-1}) were 4–6 times higher than at the other two sites (Lesina: 4.5 ± 0.7 n $\times 10^5$ g^{-1} and 2.8 ± 0.6 µgC g^{-1}, respectively, for density and biomass; Goro: 2.8 ± 0.3 n $\times 10^5$ g^{-1} and 2.2 ± 0.3 µgC g^{-1}, respectively, for density and biomass).

Meiofaunal density and biomass displayed an opposite pattern, with significantly lower values in the Marsala lagoon (90 ± 29 ind 10 cm^{-2} and 4.1 ± 1.3 µgC g^{-1}, respectively, for abundance and biomass) than in the two other sites (Lesina: 1 273 ± 490 ind 10 cm^{-2}, 57.3 ± 22.1 µgC g^{-1} and Goro: 2 713 ± 347 ind 10 cm^{-2} and 122.1 ± 15.6 µgC g^{-1}, respectively, for abundance and biomass) (Anova, all $P < 0.01$; NK test: Goro > Lesina > Marsala).

3.4. Exo-enzymatic activity and bacterial secondary production

Exo-enzymatic activities (aminopeptidase and β-glucosidase) and bacterial secondary production at the three sites are reported in Table 4. On average, aminopeptidase (Leu-MCA) and β-glucosidase (β-Glu) activities were significantly higher in the Lesina lagoon than in the two other sites (Anova, $P < 0.001$; NK test: Lesina > Goro > Marsala). Aminopeptidase activity was always higher than

Table 3
Comparison of bacterial, HNF and meiofauna abundance and biomass in different sampling lagoons

Sites	Seasons	Stations	Total bacteria		Bacteria biomass		HNF		Nano biomass		Total meio		Meio biomass	
			cell × 10^9 g^{-1}	std	µgCg^{-1}	std	n × 10^5 g^{-1}	std	µgC g^{-1}	std	ind × 10 cm^2	std	µgC g^{-1}	std
Goro	Summer	1	0.2	0.1	61.1	12.1	3.2	0.3	2.6	0.6	2222	166	100.0	7.5
		2	0.2	0.0	63.3	9.4	2.3	0.1	1.8	0.2	3203	1173	144.2	52.8
		Summer mean (±SE)	0.2 ± 0.01		62.2 ± 0.8		2.8±0.3		2.2±0.3		2713 ± 347		122.1 ± 15.6	
Lesina	Summer	1	3.0	0.6	132.9	11.1	4.8	0.2	2.0	0.1	855	87	38.5	3.9
		2	3.5	0.7	170.2	1.0	2.0	0.5	1.2	0.2	900	577	40.5	25.9
		3	8.1	0.5	375.2	11.7	5.7	0.9	3.6	0.9	400	116	18.0	5.2
		4	3.6	1.5	234.3	5.7	5.6	0.1	4.5	1.3	2937	837	132.1	37.7
	Autumn	1	2.7	0.1	126.4	13.4	2.7	0.6	1.9	0.8	1983	641	89.2	28.9
		2	2.4	0.9	134.4	12.5	4.0	0.3	2.9	0.3	1073	634	48.3	28.5
		3	1.5	0.1	100.9	0.6	6.7	0.5	4.4	0.0	515	237	23.2	10.7
		4	2.0	0.2	122.8	14.6	3.0	0.5	1.9	0.3	287	98	12.9	4.4
	Winter	1	2.3	0.2	129.5	19.1	2.2	0.3	1.1	0.3	2998	628	134.9	28.3
		2	2.2	0.3	123.3	5.2	3.7	0.2	1.4	0.1	2767	709	124.5	31.9
		3	1.1	0.3	67.7	3.5	8.7	3.5	6.9	3.1	1198	505	53.9	22.7
		4	2.1	0.0	153.6	4.7	10.0	2.4	5.7	1.9	1033	495	46.5	22.3
	Spring	1	4.1	0.6	254.6	5.2	4.1	1.8	2.4	0.0	2310	984	104.0	44.3
		2	3.6	0.8	202.2	10.8	3.3	1.0	2.1	0.1	2636	1335	118.6	60.1
		3	3.1	0.3	190.4	4.4	1.8	0.4	0.8	0.2	2600	1523	117.0	68.6
		4	4.9	1.0	342.4	9.9	5.0	1.2	4.2	2.3	712	157	32.0	7.1
		Summer mean (±SE)	4.5 ± 1.0		228.2 ± 46.2		4.5±0.7		2.8±0.6		1273 ± 490		57.3 ± 22.1	
		Annual mean (±SE)	3.1 ± 0.4		178.8 ± 20.7		4.6±0.6		2.9±0.4		1575 ± 240		70.9 ± 10.8	
Marsala	Summer	1	13.8	1.0	990.7	250.0	3.6	0.7	4.5	0.9	88	37	4.0	1.7
		2	7.6	1.6	526.5	125.0	28.9	4.8	20.2	2.7	11	10	0.5	0.0
	Autumn	1	9.4	0.7	468.1	160.0	1.5	0.2	4.3	0.8	37	10	1.7	0.5
		2	6.9	1.1	331.8	98.0	8.0	1.4	6.4	1.0	20	8	0.9	0.4
	Winter	1	0.5	0.1	32.6	5.8	2.0	0.2	3.5	0.7	130	15	5.9	0.7
		2	1.2	0.3	61.7	16.9	29.1	4.2	21.2	3.0	83	42	3.7	1.9
	Spring	1	4.1	1.0	256.6	62.6	2.4	0.3	6.1	1.1	49	58	2.2	1.6
		2	1.8	0.2	105.8	12.1	9.7	1.0	11.9	1.6	302	88	13.6	4.0
		Summer mean (±SE)	10.7 ± 2.2		758.6 ± 164.1		16.3±8.9		12.4±5.6		50 ± 27		2.2 ± 1.2	
		Annual mean (± SE)	5.7 ± 1.5		346.7 ± 105.2		10.7±3.9		9.8±2.4		90 ± 31		4.1 ± 1.4	

β-glucosidase activity. In surface sediments, aminopeptidase activity ranged from 0.6 to 609.5 nmol g^{-1} h^{-1}, whereas β-glucosidase activity ranged from 0.3 to 142.8 nmol g^{-1} h^{-1}. In summer, the ratio Leu-MCA:β-Glu displayed the highest values at Goro (7.1 vs. 3.5 and 3.3 at Lesina and Marsala, respectively). The rates of protein mobilisation (expressed as C equivalents) at Lesina (18.8 µgC g^{-1} h^{-1}) and Goro (4.2 µgC g^{-1} h^{-1}) were significantly higher than those at Marsala (0.2 µgC g^{-1} h^{-1}).

BCP showed a pattern similar to those observed for enzymatic activities. BCP at Lesina was, on average, 4–5 times higher than at Goro and Marsala, respectively. In the sediment of Lesina lagoon, bacterial C production ranged from 0.6 ± 0.2 to 2.6 ± 0.4 µgC g^{-1} h^{-1}, whereas at Goro and Marsala, the BCP ranged from 0.3 ± 0.1 to 0.5 ± 0.1 µgC g^{-1} h^{-1} and from 0.2 ± 0.01 to 0.3 ± 0.01 µgC g^{-1} h^{-1}, respectively.

4. Discussion

4.1. Quantity and quality of sedimentary organic matter

The biochemical composition of sediment organic matter is generally used to gather information on the origin, quality and availability of the deposited organic material (Danovaro et al., 1993), and is important both in a biogeochemical perspective (as organic matter degradation rates affect its burial in the sediments; Hartnett et al., 1998) and from a trophodynamic point of view (as organic matter quality influences metabolism and distribution of benthic assemblages; Graf, 1992; Dell'Anno et al., 2002).

Comparing the three investigated lagoons in summer period, Lesina and Marsala displayed the highest biopolymeric carbon (BPC) concentrations, with values 5–6 times higher than those at Goro. The quantitative contribution of the autotrophic fraction to the sediment organic matter was esti-

Table 4
Comparison of extracellular enzymatic activity (aminopeptidase and β-glucosidase), aminopeptidase and β-glucosidase ratio (L-MCA/β-Glu), BCP, potentially mobilised proteins (M-PRT) and carbohydrates (M-CHO), protein (PRTt) and carbohydrate (CHOt) turnover in the three investigated lagoons

Sites	Seasons	Stations	L-MCA		β-Glu		L-MCA/	BCP		M-PRT	M-CHO	PRTt	CHOt
			nmol g^{-1} h^{-1}	std	nmol g^{-1} h^{-1}	std	β-Glu	µgC g^{-1} h^{-1}	std	µgC g^{-1} h^{-1}	µgC g^{-1} h^{-1}	d	d
Goro	Summer	1	66.7	44.0	9.9	0.0	6.7	0.3	0.1	4.8	0.7	3.9	16.7
		2	51.2	8.2	6.9	1.3	7.4	0.5	0.1	3.7	0.5	6.4	17.1
		Summer mean (± SE)	59.0 ± 5.5		8.4 ± 1.0		7.1 ± 0.2	0.4 ± 0.1		4.2 ± 0.4	0.6 ± 0.07	5.1 ± 0.9	16.9 ± 0.2
Lesina	Summer	1	230.2	67.4	109.1	9.0	2.1	1.5	0.2	16.6	7.9	6.8	30.2
		2	330.4	142.0	43.4	12.6	7.6	0.6	0.2	23.8	3.1	2.1	34.5
		3	169.4	19.1	142.8	15.4	1.2	2.4	0.3	12.2	10.3	8.6	24.2
		4	310.5	174.1	95.2	26.4	3.3	2.0	0.0	22.4	6.9	3.5	38.9
	Autumn	1	61.5	0.0	55.9	7.8	1.1	1.2	0.2	4.4	4.0	21.3	46.7
		2	169.4	49.7	35.2	17.5	4.8	0.8	0.1	12.2	2.5	6.4	65.1
		3	609.5	110.6	86.0	29.6	7.1	1.0	0.1	43.9	6.2	3.5	61.2
		4	169.3	70.7	41.0	10.4	4.1	1.1	0.1	12.2	3.0	10.9	143.8
	Winter	1	190.9	0.0	41.6	13.8	4.6	1.1	0.1	13.7	3.0	10.7	70.9
		2	9.6	0.4	27.8	13.7	0.3	0.8	0.1	0.7	2.0	110.7	88.1
		3	70.0	24.4	13.9	5.9	5.1	0.7	0.3	5.0	1.0	17.2	238.3
		4	304.7	52.8	57.4	5.5	5.3	1.1	0.0	21.9	4.1	5.8	116.8
	Spring	1	320.5	81.9	40.6	4.7	7.9	0.9	0.1	23.1	2.9	7.1	29.7
		2	112.5	78.5	33.6	1.1	3.3	1.2	0.0	8.1	2.4	12.1	18.7
		3	368.1	182.5	29.0	11.1	12.7	1.5	0.1	26.5	2.1	5.5	42.3
		4	488.4	155.7	32.0	4.0	15.3	2.6	0.4	35.2	2.3	3.5	47.4
		Summer mean (± SE)	260.2 ± 32.2		97.6 ± 17.9		3.5 ± 1.2	1.6 ± 0.3		18.8 ± 2.3	7.0 ± 1.3	5.3 ± 1.3	31.9 ± 2.7
		Annual mean (± SE)	244.7 ± 38.8		55.3 ± 8.5		5.4 ± 1.0	1.3 ± 0.1		17.6 ± 2.8	4.0 ± 0.6	14.7 ± 6.3	68.5 ± 13.7
Marsala	Summer	1	2.6	0.4	2.9	0.4	0.9	0.3	0.1	0.2	0.2	102.8	59.2
		2	2.9	0.4	0.5	0.3	5.8	0.3	0.1	0.2	0.0	666.6	3786.6
	Autumn	1	17.3	4.1	1.2	0.4	14.5	0.2	0.0	1.2	0.1	4.0	147.8
		2	7.7	0.9	0.3	0.1	26.2	0.2	0.0	0.6	0.0	19.1	1037.7
	Winter	1	3.6	1.2	2.1	0.9	4.7	0.3	0.0	0.3	0.1	65.3	74.0
		2	0.6	0.1	3.1	1.0	0.3	0.2	0.0	0.0	0.2	1464.2	262.4
	Spring	1	19.2	4.0	16.1	4.3	1.4	0.2	0.0	1.4	1.2	13.9	23.6
		2	12.7	5.0	4.3	1.8	4.1	0.2	0.1	0.9	0.3	48.6	282.2
		Summer mean (± SE)	2.7 ± 0.1		1.7 ± 0.9		3.3 ± 1.7	0.3 ± 0.02		0.2 ± 0.01	0.1 ± 0.06	401.8 ± 199.3	604 ± 301.0
		Annual mean (± SE)	8.3 ± 2.4		3.8 ± 1.7		7.2 ± 2.9	0.2 ± 00.2		0.6 ± 0.2	0.3 ± 0.1	65.5 ± 38.0	168.1 ± 115

mated as the C-Chl to BPC ratio. In the Lesina lagoon, chlorophyll-a carbon accounted for a large fraction of total biopolymeric carbon pools (ca 12%; Fig. 2), whereas at the other two lagoons, a much lower contribution was observed (4% and 2% at Goro and Marsala, respectively). In addition, the ratio of chlorophyll-a C to total heterotrophic C (as bacteria, nanoflagellates and meiofauna biomass) was 2.7, 0.3 and 0.2, respectively, at Lesina, Goro and Marsala. Therefore, it could be concluded that different lagoons were characterised by clear differences in the ratio of autotrophic to total heterotrophic carbon biomass (Dell'Anno et al., 2002).

The accumulation of biopolymeric carbon is the result of the balance between in situ production, allochthonous inputs, utilisation/degradation and export. These processes are reflected by changes in the biochemical composition of the BPC pools. Our results showed a marked difference in the

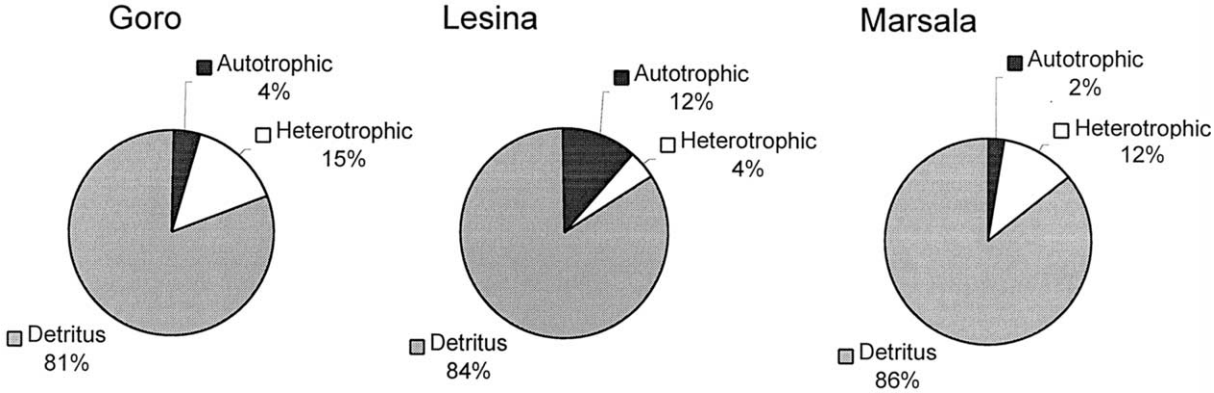

Fig. 2. Proportions (%) of autotrophic (e.g., chlorophyll-a concentration), heterotrophic (e.g., bacterial, nanoflagellate and meiofauna biomass) and detritus carbon in summer period.

biochemical composition of organic matter at the three study sites. Carbohydrates dominated at the lagoon of Lesina (accounting for 63% of BPC) as a result of the large contribution of the autotrophic carbon (C Chl-a) to total biopolymeric carbon. A protein to carbohydrate ratio <1 is a typical feature of lagoon sediments (Danovaro, 1996; Pusceddu et al., 1999). However, Marsala and Goro lagoons, being characterised by a low autotrophic C contribution to BPC, displayed a protein to carbohydrate ratio close to 1. Biopolymeric C pools in the Marsala lagoon were largely accounted by lipid-C (45%), whereas in Goro lagoon, carbohydrate and protein-C contribution to BPC was ca 40%. Such a difference in the biochemical composition of organic matter, in these lagoons, indicates a different origin of the organic detritus (Pusceddu et al., 2000). Being a large fraction of sediment OM generally originated from primary production, differences in the biochemical composition of OM are likely to be the result of different primary producers in different lagoons. Seagrasses are known to characterise benthic systems accumulating large quantities of refractory-structural carbohydrates and generally display a lower protein content (Danovaro, 1996) than fresh macroalgal detritus (Pusceddu et al., 2003). In fact, the three systems were characterised by a different composition of primary producers: while Lesina lagoon was characterised by the presence of large Zostera noltii meadows (associated with Valonia), a large portion of the Marsala lagoon was covered by the seagrass Posidonia oceanica, the Goro lagoon was characterised by the presence of the macroalgae Ulva and Gracilaria.

4.2. Balance between organic matter mobilisation and bacterial uptake

In aquatic sediments, the determination of the enzymatic activities (as well as the ratio of aminopeptidase to glucosidase activity) provides important indications on the potential organic matter flow through the microbial loop and on the quality of the organic matter available to heterotrophs (Fabiano and Danovaro, 1998). In this study, despite high protein and carbohydrate concentrations being observed, aminopeptidase and glucosidase activities were low (especially at Marsala and Goro) when compared to values reported in the literature for coastal sediments (Meyer-Reil, 1986; King, 1986; Danovaro et al., 2002). The highest aminopeptidase activities and protein turnover rates (calculated as the ratio of enzymatically mobilised proteins to total protein content) were observed at Goro and Lesina lagoons, with values up to two orders of magnitude higher than at Marsala. Such differences suggest the presence of a much higher refractory composition of the organic matter in the sediment of the Marsala lagoon. These results are consistent with previous studies carried out by Pusceddu et al. (2003) that reported, in the Marsala lagoon sediments, only a small fraction of protein and carbohydrate pool (about 4%) was enzymatically degradable and, therefore, available for heterotrophic metabolism. Therefore, at both Goro and Lesina, the entire protein pool was potentially degraded in ca 5 d, whereas at the Marsala lagoon, 402 d were required. These data suggest a lower efficiency in OM mobilisation with consequent higher retention and possible burial at the Marsala lagoon when compared to the other two systems.

It is recognised that the amount of available protein and carbohydrate pools in marine sediments (i.e., enzymatically hydrolysable, sensu Danovaro et al., 2001; Dell'Anno et al., 2000) is an important factor influencing bacterial activity and distribution (Danovaro et al., 1993, 1999a). The Marsala lagoon displayed also the lowest bacterial C production. However, despite low enzymatic activities and protein turnover rates, the highest bacterial biomass was observed. This could indicate that a large fraction of the bacterial assemblages is dead or dormant (Luna et al., 2002), and that the scarce nutritional quality (highly refractory composition) of the sediment organic matter in the Marsala lagoon is reflected more by functional bacterial parameters (i.e., bacterial C production) than by bacterial abundance and biomass alone.

Organic matter potentially mobilised by exo-enzymatic activities can be utilised both by benthic metazoans and bacteria. If bacteria out compete metazoan for the utilisation of the available trophic sources (i.e., limiting metazoan secondary production by uptaking most of the available organic pools), the transfer of organic C to higher trophic levels is likely to be less efficient and dependent upon bacterial grazing (Manini et al., 1999). We estimated that, at both Lesina and Goro lagoons, only ca 10% of the mobilised protein pools were converted into bacterial proteins, while the remaining 90% was unutilised and, therefore, potentially directly available to other benthic consumers (i.e., higher trophic levels). In contrast, at Marsala, ca 50% of the enzymatically mobilisable protein pool was converted into bacterial biomass. This fact, coupled with the evidence that the absolute amount of protein mobilised was the lowest among the three lagoons (Table 4), suggests that at Marsala, the quantity of unutilised proteins available for direct utilisation by benthic consumers was 10–40 times lower than that at the other two sites. These factors are likely to control the transfer of carbon towards the higher trophic levels (i.e., metazoa) thus influencing the relative importance of the different benthic components involved in the microbial loop functioning.

4.3. Comparison between bacteria, nanoflagellates and meiofauna standing stocks

The distribution of the different components involved in the benthic microbial loop (bacteria, nanoflagellates and meiofauna) varies in response to a complex array of variables (Danovaro, 2000), and it has been recently demonstrated that the relative importance of bacteria, nanoflagellate, meiofauna and macrofauna change in response to the organic enrichment and benthic trophic state (Albertelli et al., 1999; Danovaro et al., 1999b). Given the quantity and quality of the different organic matter in three lagoons investigated, differences in relative importance of bacteria, nanoflagellates and meiofauna are expected. The ratio of bacterial to nanoflagel-

late abundance displayed values one to two orders of magnitude higher at Marsala and Lesina than at Goro.

Bacterial and nanoflagellate biomasses in the sediments of the Marsala lagoon are among the highest reported in the literature for shallow coastal environments (Hansen et al., 1992; Tibbles et al., 1992). HNF are essentially bacterivorous and, therefore, are expected to remove a certain fraction of the benthic bacterial biomass (Patterson et al., 1989; Hondeveld et al., 1994; Epstein and Shiaris, 1992). Also meiofauna can remove a fraction of bacterial biomass, but at a relatively low efficiency (Danovaro et al., 2000; Castel, 1992; Manini et al, 1999); hence, generally, meiofauna is more dependent upon the actual amounts of food available in the sediment (Findlay, 1981; Montagna et al., 1982; Danovaro et al., 1999b; Gambi et al., 2003).

In this study, bacteria, nanoflagellate and meiofauna biomass displayed strong differences between sites considering their contribution to total heterotrophic C-biomass (summer mean 34, 1, and 65%, respectively, for Goro; 66, 1 and 33%, respectively, for Lesina; 97.5, 2 and <1%, respectively, for Marsala). The relatively larger importance of bacteria and nanoflagellate with respect to meiofauna at Marsala suggests that the bioavailable fraction of OM is utilised by bacteria and nanoflagellates and then "sequestered" into these small components of the microbial food web, since it is not transferred to meiofauna (i.e., to higher trophic levels). This system acts as a sink for organic carbon pools in the sediment. Conversely, at Goro and to a lesser extent at Lesina, meiofauna reached a relatively higher importance when compared to bacteria and nanoflagellates, indicating that organic C was more efficiently transferred to higher trophic levels. This was apparently the result of the higher nutritional quality of the sedimentary organic matter and of the weaker competition for food resources with benthic bacteria.

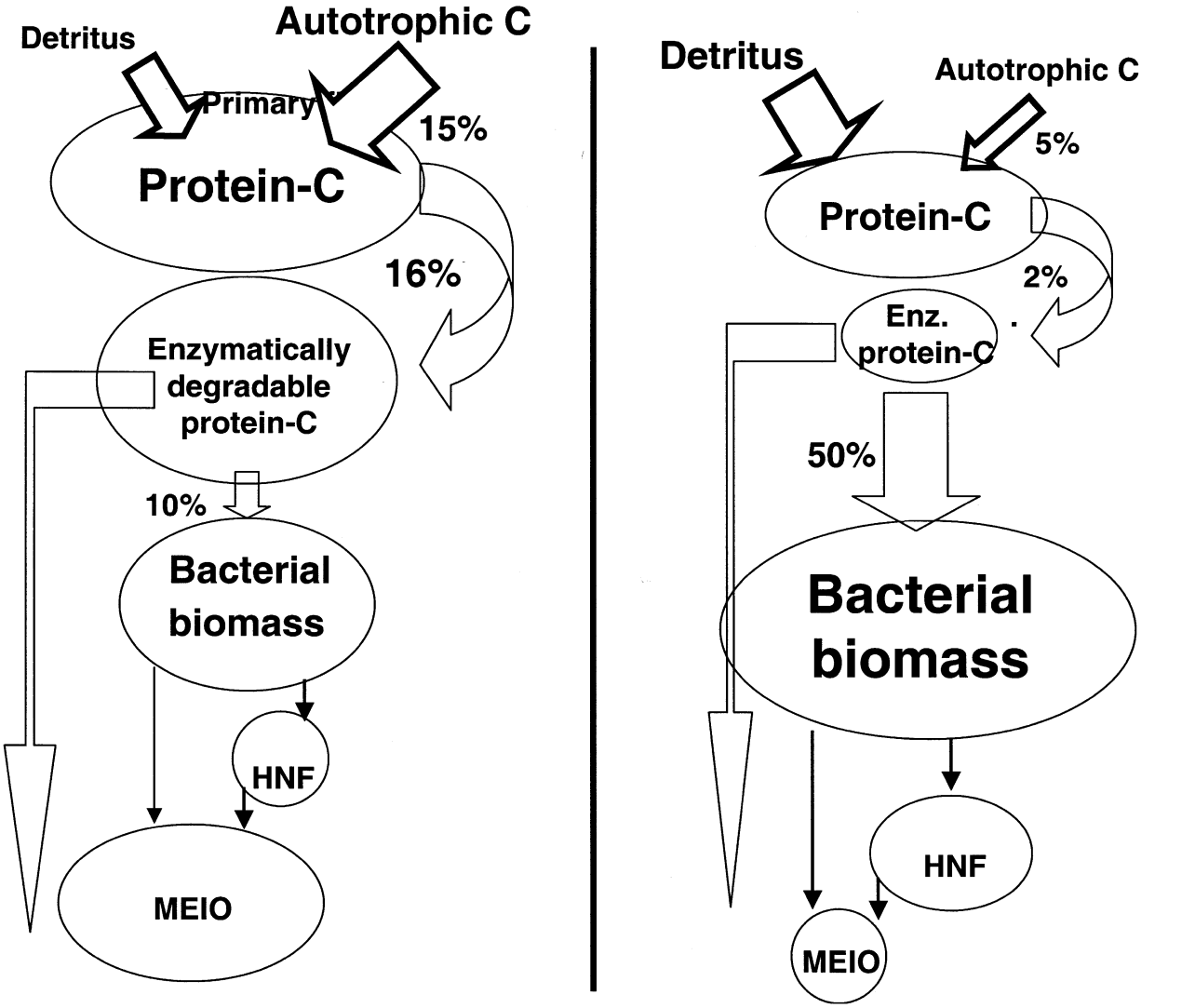

Fig. 3. Simplified scheme of the protein-carbon pools and flows (annual mean) in two lagoon systems (Lesina and Marsala), with focus on inputs (organic detritus and autotrophic carbon), mobilisation (enzymatically degradable carbon) and potential export (bacteria, nanoflagellates and meiofauna biomass are expressed as protein-C). In order to visualise differences among systems better, differences in box and arrow sizes are proportional to difference in carbon quantity and flows among compartments.

4.4. Conceptual model of microbial loop functioning in different lagoon systems

Using the data set available for Lesina and Marsala, we elaborated, using semi-quantitative indications, a conceptual model of OC flow through the benthic microbial loop (Fig. 3). This study supports the conclusion that the origin and composition of sedimentary organic matter played a primary role in regulating the efficiency of the lagoons in channelling detrital C to higher trophic levels, and indicates that Lesina was the lagoon displaying the highest efficiency. Such conditions are primarily reflected by the capability of mobilising rapidly a large fraction of primary (i.e., autotrophic, CChl-a) organic matter (here expressed as protein-C concentrations). At Lesina, despite the high aminopeptidase activity and protein turnover, high protein accumulation was due to the much higher organic matter input due to primary producers. Conversely, at Marsala, the limiting step was represented by the inability of the benthic system of mobilising the protein pools (only 2% daily, calculated as ratio between enzymatically degradable protein-C and protein-C pool per m^2).

In the most efficient system (Lesina), only 10% of the mobilised protein carbon was converted into bacterial biomass (calculated as [bacterial protein production]/[mobilised proteins] × 100), while the remaining 90% was potentially available at higher trophic levels (nanoflagellates and meiofauna) or exported from the system. In contrast, at Marsala, the highly refractory composition of the sediment organic matter was coupled with a bacterial component able to utilise 50% of the protein pool mobilised. The dominance of bacteria in this system reduced the amounts of proteins bioavailable to meiofauna or potentially exportable, acting as a sink for biopolymeric carbon. These conditions allowed the Lesina system to support the highest (absolute and relative) meiofaunal biomass, while at Marsala, meiofaunal biomass values were among the lowest reported in the literature, and indeed, comparable to deep-sea oligotrophic systems (Danovaro et al., 1999b). Therefore, in the investigated lagoons, the main factors limiting the transfer of carbon to higher trophic levels are represented by the source and quality of the organic input, the capability of the system of mobilising organic matter pools and the benthic bacterial ability of converting the mobilised carbon into bacterial biomass.

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