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Quantity and bioavailability of sediment organic matter as signatures of benthic trophic status

Antonio Pusceddu[1,*], Antonio Dell'Anno[1], Mauro Fabiano[2], Roberto Danovaro[1]

[1]Department of Marine Sciences, Polytechnic University of Marche, Via Brecce Bianche, 60131 Ancona, Italy
[2]Department for the Study of the Territory and its Resources, University of Genoa, Corso Europa, 26, 16100 Genova, Italy

ABSTRACT: Tools used for assessing marine trophic status are generally based on water column characteristics, which, however, may provide unreliable classification of the benthic trophic status. Here, we provide evidence from the literature that quantity and bioavailability of sediment organic matter are reliable proxies to assess benthic marine trophic status. We compiled data on the protein, carbohydrate and lipid concentration of sediments from different oceanic and coastal regions and varying water depths. The concentration of these 3 components as a whole (biopolymeric carbon) was found to be significantly correlated ($r = 0.84$) with the total organic carbon concentration, suggesting that the biopolymeric fraction is representative of the total organic carbon pool. However, the systematic variation of the biopolymeric fraction was higher than that of total organic carbon concentrations, suggesting that biopolymeric carbon is a more sensitive proxy of benthic trophic status than is the total carbon pool. Furthermore, biopolymeric carbon was significantly correlated to the amount of phytopigments, indicating that biopolymeric carbon accumulation in the sediment is related to inputs of algal carbon. Biopolymeric carbon concentrations were also positively correlated to the sediment community oxygen consumption, suggesting that the progressive accumulation of biopolymeric carbon could be an additional co-factor potentially responsible for hypoxic or anoxic events. The enzymatically digestible and algal fractions of biopolymeric carbon decreased in sediments with increasing biopolymeric carbon content (i.e. eutrophic systems), suggesting that organic carbon in eutrophic sediments is mostly refractory in nature. We propose that a biopolymeric carbon concentration in the sediment of >2.5 mg C g^{-1}, being associated with a bioavailable fraction of $<10\%$, can be considered as a threshold level at which benthic consumers may experience mostly refractory organic carbon.

KEY WORDS: Marine sediments · Organic matter · Trophic status

INTRODUCTION

Eutrophication is a frequent and widespread phenomenon associated with the human utilisation of coastal areas of oceans, and its development is generally described using 'input-response' models (Cloern 2001). These models assume that an increase in nutrient concentrations causes an increase of primary production that, if surpassing certain threshold levels, primes detrimental effects on the ecosystem (Pinckney et al. 2001).

The trophic status of marine ecosystems is generally assessed through chemical measurements (e.g. inorganic nitrogen and phosphorus) and/or surrogate measurements of algal biomass in the water column (Stefanou et al. 2000). These proxies may fail in detecting the consequences of increased nutrient loads on benthic systems (Dell'Anno et al. 2002) since they cannot provide any predictive information on the rate of organic matter inputs to the benthos (i.e. benthic trophic status; Jørgensen & Richardson 1996).

Benthic trophic status can be assessed in terms of total organic carbon (TOC) supply rate to the sea bottom (as g C m^{-2} yr^{-1}; Nixon 1995). However, this is difficult to assess since the magnitude of the organic carbon fluxes is not always directly linked to the primary production in the water column, and the assessment of all of the possible inputs of organic carbon is difficult to

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*Email: a.pusceddu@univpm.it

achieve synoptically on large spatial and temporal scales (Lee et al. 1988). Another approach uses biological indicators such as presence and/or abundance of benthic diatoms and macroalgae (Duarte 1995, Kelly 1998), but the applicability of this method is limited to those systems characterised by the presence or dominance of living photosynthetic primary producers. Moreover, it does not provide any indication of the possible consequences of eutrophication at higher trophic levels of the benthic food web. However, the consequences of changing trophic status reach all hierarchical levels of the ecosystem organisation.

The response of consumers to increased organic matter supply is influenced more by organic matter quality (e.g. bioavailability) rather than by bulk concentration in the ecosystem (Cebrián et al. 1998, Huxel 1999). Thus, the assessment of the trophic status needs to be extended to a more comprehensive description of the organic matter available for heterotrophic nutrition, and should include indicators of the quantity and bioavailability of all (including detrital) resources (Grall & Chauvaud 2002). This is particularly important for the assessment of the benthic trophic status, where the largest reservoir of food for benthic consumers is deposited (detrital) organic matter (Jørgensen & Richardson 1996).

Studies aiming at providing a reconstruction of long-term changes in the productivity of a given system have used stratigraphic analyses of organic carbon, nitrogen and phosphorus concentrations coupled with ^{210}Pb geochronology (Cornwell et al. 1996), foraminifera distributions (Duijnstee et al. 2004), and stable isotopic and lipid biomarker signatures in sediments (Zimmerman & Canuel 2002). These features allowed an assessment of historical changes in the trophic status of aquatic ecosystems only if analysed as a suite of indicators, since no indicator alone provided adequate information concerning the multiple, interrelated components of the ecosystems (Turner et al. 2006).

Alternatively, recent changes in the benthic trophic status through time can be detected by means of an analysis of organic carbon in superficial sediments. Several studies have provided evidence that eutrophication is associated with a net accumulation or burial of organic carbon in the sediment (Cornwell et al. 1996, Emeis et al. 2000, Farías 2003). Other studies reported decreasing values of the C/N ratio in eutrophic sediments (Sampou & Oviatt 1991).

Organic matter in marine sediments is composed of compounds exhibiting different levels of bioavailability for consumers, ranging from labile (i.e. immediately digestible, sensu Mayer et al. 1995) to refractory (recalcitrant to decomposition). Refractory compounds (such as humic and fulvic acids, structural carbohydrates and ‘black’ carbon) generally account for most of the sedimentary organic matter, and due to very low degradation rates, accumulate in marine sediments (Middelburg et al. 1999). In contrast, highly labile compounds, representing the fraction of organic matter that is rapidly digested by benthic consumers, are subjected to greater temporal and spatial changes (Mayer et al. 1995). However, between these 2 opposite levels of bioavailability, there is a continuum of characteristics, which passes through intermediate levels of bioavailability. Unfortunately, the assessment of the lability of sediment organic carbon is not an easy task, and generally implies several operational assumptions.

The biopolymeric fraction of sediment organic carbon, measured as the sum of protein, carbohydrate and lipid carbon (BPC), has often been reported as the fraction of TOC potentially available to benthic consumers (Fabiano et al. 1995, Bianchelli et al. 2008). More recent investigations reported that only a fraction (5 to 30%) of these biopolymers is enzymatically digestible by consumers (Pusceddu et al. 2003).

In this work, we tested the following hypotheses: (1) BPC (sensu Fabiano et al. 1995) is related to TOC in marine sediments, (2) the algal fraction of BPC changes in sediments exhibiting different BPC concentrations, (3) temporal variability in BPC concentration in the sediment changes under different benthic trophic status conditions, (4) sediment community oxygen consumption is related to BPC concentrations and (5) the enzymatically digestible fraction of BPC varies in sediments characterised by different trophic status.

Our goals were, thus, to (1) provide evidence that the quantity and bioavailability of BPC are reliable proxies for marine benthic trophic status, and (2) identify potential threshold levels of key organic carbon-related variables indicating trophic status shifts. To achieve these goals, we examined data from the published literature for relationships between BPC and TOC concentrations in marine sediments from different oceanic and coastal regions and water depths, including intertidal shallow waters and hadal depths. Then we explored the relationships between the quantity of BPC and (1) the algal carbon fraction associated with phytopigments, (2) the sediment community oxygen consumption (SCOC) and (3) the bioavailable (i.e. enzymatically digestible) fraction of sediment organic carbon (BAC).

MATERIALS AND METHODS

We compiled data published over the last 20 yr on phytopigment (chlorophyll *a* [chl *a*] and phaeopigment), protein, lipid, carbohydrate, BPC and TOC concentrations in surface marine sediments worldwide (Table 1). Because of the multiple different sources of these data, we noticed that not all variables have been measured in all studies. All of the data used in this study were obtained from the scientific literature (see Table 1) using similar analytical methods. Possible biases due to different devices used for sediment sampling and/or the use of different analytical protocols were accurately checked (details are described later).

Sediment samples (top 2 cm) were collected from coastal to hadal depths (i.e. from 0 to 7800 m water depth) using manual corers, Van Veen grabs, box-corers or multiple corers (Table 1). Previous studies have demonstrated that the quantity and biochemical compositions of sediment organic matter collected using multiple corers and box-corers display some differences (Shirayama & Fukushima 1995, Danovaro et al. 1998). However, since the differences in the concentration of organic matter in sediments collected using different sampling devices are of the same order of magnitude as are the differences in organic matter concentrations determined on sediment replicates collected using the same sampling device (Danovaro et al. 1998), the data used in this study were not corrected.

The concentrations of sedimentary chl *a*and phaeopigments were determined spectrophotometrically or spectrofluorometrically, according to standard protocols (Lorenzen & Jeffrey 1980). Total sedimentary lipids were extracted in chloroform:methanol (1:1, vol:vol; Bligh & Dyer 1959) and the resulting fraction, after evaporation in a dry hot bath at 80 to 100°C for 20 min, was quantified according to the sulfuric acid carbonisation procedure (Marsh & Weinstein 1966). Data on total lipids presented in this study were expressed in tripalmitine equivalents. The lipid fraction determined using this protocol allows the quantification of total lipid concentrations, but does not permit discriminating between different classes of lipids, which is different from chromatographic methods generally used in organic geochemistry (Volkman 2006). However, this was not the main interest of the present study.

Total protein concentrations were determined according to Lowry et al. (1951) as modified by Hartree (1972) and Rice (1982) to compensate for phenol interference and are expressed as bovine serum albumin (BSA) equivalents. Bradford's (1976) protocol, used in some of the studies, provides results similar to Lowry et al.'s (1951) protocol (Berges et al. 1993) and, therefore, no corrections were applied. Total carbohydrate concentrations, expressed in glucose equivalents, were obtained according to the Gerchacov & Hatcher (1972) protocol based on the phenol and concentrated sulfuric acid reaction with saccharides. The fractions of protein and carbohydrate enzymatically digestible were assessed according to Danovaro et al. (2001), modified for coastal sediments by Pusceddu et al. (2003), and reported as BSA and glucose equivalents, respectively. Briefly, enzymatically digestible proteins were determined as the difference between protein contents of intact sediments and sediments added with a solution of proteinase-K and protease after a 1 h incubation at 37°C. Protein analyses from these samples were carried out according to Lowry et al. (1951). Enzymatically digestible carbohydrates were determined as the difference between carbohydrate quantities released by sediment added with a mixture of enzymes (α-amylase, β-glucosidase, proteinase-K, lipase) and by intact sediments after 1 h incubation at room temperature. Carbohydrates from all supernatants and from intact sediments were analyzed according to Gerchacov & Hatcher (1972). Sediment subsamples muffled at 550°C for 4 h and processed as described previously were used as blanks. Concentrations of enzymatically digestible proteins and carbohydrates were normalized to sediment dry weight.

Total organic C concentrations in the sediment were determined according to Hedges & Stern (1984). BPC concentrations were calculated as the sum of protein, carbohydrate and lipid carbon equivalents, using conversion factors obtained from the elemental analysis of standard molecules (0.49, 0.4 and 0.75 µg C μg^{-1}, respectively, for BSA, glucose and tripalmitine; Fabiano et al. 1995). Bioavailable carbon (BAC) concentration was calculated as the sum of digestible proteins and carbohydrates converted into carbon equivalents by using the same factors as for their total pools (Danovaro et al. 2001). The algal carbon contribution to BPC was calculated as the percentage of chl *a* to BPC concentrations, after converting chl *a* concentration into carbon equivalents using a mean value of 40 µg C μg^{-1} chl *a* (Pusceddu et al. 1999).

Statistical analyses. The relationships between the different fractions of sediment organic matter were assessed using either Type-I or Type-II regression analyses (Legendre & Legendre 1998). In particular, the Type-II regression analysis was carried out to avoid the underestimation of the slope of linear relationships between variables containing errors (Legendre & Legendre 1998). The Type-II regression analysis was carried out using the major axis regression method, since in all of the cases in the present study the variables were expressed in the same physical units or were dimensionless (Jolicoeur 1990). Type-II regression analyses were performed using the MODEL-II.exe routine (Legendre 2001).

The statistical differences between slopes and intercepts obtained from Type-I regressions testing for the relationships between variables in different environmental contexts were assessed by means of an analysis of covariance (ANCOVA). When slopes were found to be heterogeneous we used Tukey's multiple comparison tests (Zar 1984) to determine which combinations of ecosystems differed.

Table 1. Mean value and range of protein, carbohydrate, lipid, chl *a* and total organic carbon (TOC) concentrations in marine sediments worldwide. DW = dry weight, na = not available, nd = not determined

Location	Sampling period	Sampling device	Station depth (m)	Proteins (mg g DW^{-1})		Carbohydrates (mg g DW^{-1})		Lipids (mg g DW^{-1})		Chlorophyll *a* (µg g DW^{-1})		Total organic carbon (mg g DW^{-1})		Source
				Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	
Barents Sea	na	USNEL spade corer	0–500	6.0	5.2–6.7	0.4	0.3–0.5	nd	nd	0.07	0.01–0.14	nd	nd	Pfannkuche & Thiel (1987)
Barents Sea	na	USNEL spade corer	501–1000	5.4	5.4	0.37	0.37	nd	nd	0.06	0.06	nd	nd	〃
Barents Sea	na	USNEL spade corer	1001–3920	3.4	2.1–4.7	0.30	0.26–0.35	nd	nd	0.06	0.006–0.14	nd	nd	〃
Baltic Sea	Sep 1981, Jun 1982	Grab	18	na	3.8–7.7	nd	0.4–4.0	nd	nd	nd	nd	nd	nd	Meyer Reil (1983)
Baltic Sea (Kiel Bight)	Sep 1981, Apr 1982	Grab	na	7.1	6–8	2.3	0.7–3.4	nd	nd	nd	nd	nd	nd	Meyer Reil & Graf (1986)
Gulf of St. Lawrence	May–Jul 1988	Box-corer	350	0.3	0.2–0.4	9.8	8.5–10.8	1.1	0.9–1.4	14.4	10.7–16.3	20.6	18.0–23.3	Colombo et al. (1996)
NE Atlantic (Porcupine Abyssal Plain)	Sep 1996, Mar 1997, Oct 1997	Multicorer	4800	0.7	0.3–1.4	1.5	0.9–2.2	0.19	0.04–0.78	nd	nd	nd	nd	Danovaro et al. (2001)
Gulf of Gascogne	Fall 1984	Box-corer	2100	1.9	na	2.4	na	0.2	na	nd	nd	nd	nd	Khripounoff et al. (1985)
Barraña, Galicia	Jan 1997, Jan 1998	Manual corer	Intertidal	1.1	0.4–3.3	0.28	0.03–0.67	0.12	0.02–0.31	nd	nd	2.3	0.6–5.4	Cividanes et al. (2002)
Gulf of Lions	Oct 1983, Dec 1985	Box-corer	26	1.1	0.1–2.3	0.77	0.3–4.3	nd	nd	nd	nd	4.8	2.4–7.3	Buscail et al. (1995)
Gulf of Fos	Sep 1985, Oct 1986	Manual corer	6–17	1.6	1.0–2.6	3.2	2.4–4.1	0.23	0.07–0.66	1.9	0.4–5.9	11.1	6.9–15.8	Fichez (1991)
Ligurian Sea (Zoagli)	Feb 1990, Feb 1993	Manual corer	10	0.03	0.02–0.07	0.3	0.13–0.67	0.1	0.02–0.21	3.6	2.6–5.3	1.9	1.6–2.9	Fabiano et al. (1995)
Ligurian Sea (Prelo)	Feb 1990, Jan 1991	Manual corer	4	0.2	0.05–1.6	0.8	0.3–3.6	0.24	0.10–1.08	0.7	0.1–1.8	3.4	1.7–16.1	Danovaro et al. (1994)
Ligurian Sea	Jul 1990	Grab	5–135	0.3	0.01–0.7	1.3	0.2–3.0	0.35	0.09–0.88	2.3	0.6–7.1	nd	nd	Albertelli et al. (1999)
Ligurian Sea (Harbour)	Sep–Oct 1996	Manual corer	5	6.5	5.8–8.0	13.2	8.6–17.7	1.2	1.0–1.4	8.0	5.8–10.1	nd	nd	Danovaro et al. (1999c)
Ligurian Sea	Jan 1991, Jan 1992	Manual corer	4	0.1	0.02–0.3	0.9	0.3–5.3	0.23	0.09–0.63	3.4	2.4–5.2	3.0	2.0–6.1	Danovaro & Fabiano (1997)
Northern Adriatic Sea	Jun 1996, Feb 1997	Manual corer	15–55	1.4	0.2–4.1	0.18	0.07–0.42	0.35	0.07–1.07	1.46	0.4–3.9	nd	nd	Danovaro et al. (2002)
Northern Adriatic Sea	Jun 1996, Feb 1997	Manual corer	15–55	1.8	0.9–3.7	0.22	0.09–0.64	0.33	0.14–0.62	1.14	0.6–2.2	nd	nd	〃
Tyrrhenian Sea	Nov 1989	Grab	20–60	0.7	0.2–1.7	0.89	0.3–1.9	0.01	0.001–0.025	3.6	0.3–7.4	nd	nd	Fabiano & Danovaro (1994)
Tyrrhenian Sea	Jul 1997, Feb 1998	Manual corer	10	2.4	1.6–3.3	1.3	0.5–2.8	1.06	0.3–2.1	nd	nd	nd	nd	Mazzola et al. (1999)
Tyrrhenian Sea	Jun 1993, May 1994	Manual corer	0.5–2.5	6.0	2.2–12.1	12.8	0.8–70.5	1.6	0.3–4.5	4.6	0–77.6	nd	nd	Pusceddu et al. (1999)
Ionian and Aegean seas	Sep 1989	Box-corer	0–500	0.12	0.11–0.15	1.8	1.6–2.3	0.12	0.09–0.14	nd	nd	nd	nd	Danovaro et al. (1993)
Ionian and Aegean seas	Sep 1989	Box-corer	501–1000	0.11	0.07–0.16	2.0	1.4–2.3	0.08	0.05–0.16	nd	nd	nd	nd	〃
Ionian and Aegean seas	Sep 1989	Box-corer	1001–2401	0.11	0.07–0.13	1.9	1.2–2.5	0.10	0.05–0.19	nd	nd	nd	nd	〃

Table 1 (continued)

Location	Sampling period	Sampling device	Station depth (m)	Proteins (mg g DW^{-1})		Carbohydrates (mg g DW^{-1})		Lipids (mg g DW^{-1})		Chlorophyll *a* (µg g DW^{-1})		Total organic carbon (mg g DW^{-1})		Source
				Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	
Northern Aegean Sea	Mar–Apr 1997	Multicorer	0–500	2.2	0.4–3.5	3.9	1.2–5.9	0.47	0.3–0.8	3.8	1.0–7.9	nd	nd	Danovaro et al. (1999b)
Northern Aegean Sea	Mar–Apr 1997	Multicorer	501–1000	4.0	1.8–6.6	5.0	3.6–6.5	0.67	0.5–0.8	4.2	0.3–10.1	nd	nd	"
Northern Aegean Sea	Mar–Apr 1997	Multicorer	1001–1271	4.7	4.5–5.0	6.9	6.4–7.3	1.2	1.1–1.3	3.3	1.0–5.7	nd	nd	"
Southern Aegean Sea	Aug–Sep 1997	Multicorer	500–1000	1.3	0.6–2.1	5.5	4.2–6.8	0.3	0.3–0.4	1.7	0.6–2.9	nd	nd	Danovaro et al. (1999b)
Southern Aegean Sea	Aug–Sep 1997	Multicorer	1001–2270	1.6	0.5–3.5	6.2	1.0–11.6	0.33	0.1–0.7	3.8	0.2–11.4	nd	nd	"
Aegean Sea	Sep 1989	Box-corer	na	0.2	0.1–0.2	2.4	1.7–3.0	0.09	0.02–0.16	nd	nd	nd	nd	Danovaro et al. (1995)
Cretan Sea	Sep 1995	Multicorer/ box-corer	40–500	0.6	0.5–0.7	1.0	0.6–1.5	0.25	0.11–0.35	1.1	0.1–2.6	nd	nd	Danovaro et al. (1998)
Cretan Sea	Sep 1995	Multicorer/ box-corer	501–1000	0.2	0.1–0.3	0.7	0.5–1.0	0.11	0.07–0.15	0.06	0–0.1	nd	nd	"
Cretan Sea	Sep 1995	Multicorer/ box-corer	1001–1540	0.2	0.2	0.8	na	0.11	0.11	0.05	0.05	nd	nd	"
Cretan Sea	Aug 1994, Mar 1995, May 1995, Sep 1995	Multicorer	40–1540	1.0	0.2–3.0	1.9	0.2–7.9	0.17	0.03–0.69	0.54	<0.05–3.1	5.0	3.0–9.0	Tselepides et al. (2000)
Ionian Sea	Jun 1993	Multicorer	500–1000	0.12	0.08–0.16	nd	nd	nd	nd	nd	nd	5.5	5.2–5.8	Boetius et al. (1996)
Ionian Sea	Jun 1993	Multicorer	1001–4617	0.06	0.04–0.07	nd	nd	nd	nd	nd	nd	4.6	4.1–5.3	"
Levantine Sea	Jun 1993	Multicorer	0–500	0.06	0.06	nd	nd	nd	nd	nd	nd	4.2	4.2	"
Levantine Sea	Jun 1993	Multicorer	501–1000	0.09	0.09	nd	nd	nd	nd	nd	nd	6.2	6.2	"
Mactan, Philippines	na	na	na	na	0.5–1.3	na	0.7–1.6	nd	nd	nd	nd	nd	nd	Graf & Meyer Reil (1985)
Demerara Abyssal Plain	Sep 1981	Box-corer	4440	2.4	na	1.8	na	0.3	na	nd	nd	nd	nd	Sibuet (1984)
Atlantic Ocean	Sep 1981	Box-corer	4850	1.9	na	1.7	na	0.3	na	nd	nd	nd	nd	"
South Pacific (Atacama Trench)	Sep 1997	Box-corer	1061–1355	3.4	1.6–6.2	1.9	0.7–4.3	1.0	0.6–1.9	6.1	2.8–11.8	nd	nd	Danovaro et al. (2003)
South Pacific (Atacama Trench)	Sep 1997	Piston corer	7800	2.6	2.6	0.3	na	0.6	0.6	2.0	2.0	nd	nd	Danovaro et al. (2003)
Ross Sea (Antarctica)	Jan–Feb 1995	Grab	37–223	1.9	1.0–4.9	5.4	2.2–13.3	0.22	0.12–0.40	10.2	1.9–27.8	nd	nd	Pusceddu et al. (2000)
Mediterranean coastal lagoon	May 1995–Feb 1996	Manual corer	2	4.8	0.2–8.5	6.5	0.1–12.0	0.9	0.1–1.5	4.1	0.5–20.0	nd	nd	Pusceddu et al. (2003)
Southern Adriatic and Ionian seas	Mar–Sep 2000	Grab/ multicorer	10–50	1.5	01–14.0	3.7	0.1–12.2	0.3	0.04–2.4	13.3	1.2–43.5	nd	nd	Dell'Anno et al. (2002)
Alicante, Spain (fish farm sediments)	Sep 2003	Manual	27–30	2.0	1.8–2.3	8.3	6.1–12.7	0.5	0.3–0.7	11.3	6.5–18.5	7.0	5.8–9.3	Pusceddu et al. (2007a)
Pachino, Italy (fish farm sediments)	Sep 2002	Manual	30	1.1	0.4–2.0	4.3	1.9–6.6	0.2	0.1–0.4	1.6	0.8–2.5	3.8	1.2–5.0	"
Sounio, Greece (fish farm sediments)	Jul 2003	Manual	20–25	0.9	0.6–1.2	4.8	0.5–11.2	0.5	0.3–0.7	0.5	0.1–0.8	4.3	0.0–8.3	"
Cyprus (fish farm sediments)	Jul 2002	Manual	30–35	3.0	1.5–5.3	3.8	1.9–5.4	0.7	0.4–1.1	2.8	2.0–2.4	5.3	3.0–8.3	"
Ross Sea (Antarctica)	Nov 1994, Jan 1995	Box-corer	439–567	2.1	0.2–3.4	0.59	0.4–0.8	0.21	0.01–0.38	0.3	0.2–0.4	nd	nd	Fabiano & Danovaro (1998)

Systematic variations in BPC and TOC concentrations and temporal variability in concentration of BPC in different ecosystems were assessed as the value of mean squares after a 1-way ANOVA was performed using sampling time as a single source of variance, separately for each data set.

PRIMARY PRODUCTION AND SEDIMENT ORGANIC ENRICHMENT

Relatively few studies have reported synoptic determinations of TOC and BPC concentrations. Using a reduced data set available from a few studies carried out in the Mediterranean Sea, we found that BPC is significantly related to TOC (Fig. 1). The BPC represents 71% of the TOC variance, while the remaining 29% is ascribed to other factors such as the variable composition and importance of the refractory fractions (Middelburg et al. 1999). However, whilst the biopolymeric fraction undergoes rapid changes in quantity and composition during early diagenesis, TOC generally exhibits a more conservative nature (Fabiano et al. 1995). This suggests that changes in the quantity of BPC might respond to changes and/or differences in the systems' productivity more promptly than TOC.

To test this hypothesis, we examined the relationship between proxies of primary production and BPC. The input of primary organic matter to the sea bottom (together with the benthic algal biomass, if present) is generally assessed using phytopigment concentrations in surface sediments (Pfannkuche et al. 2000). In our analysis, the total phytopigment concentrations (the sum of chl *a* and phaeopigments, expressed as carbon equivalents) explained only about 13% of BPC variance (Type-I regression: $r^2 = 0.127$, $n = 124$, $p < 0.01$), with the remaining 87% being ascribed to other sources, including non-marine sources, of organic matter entering the system. Since photosynthetic pigments are labile compounds (Lee et al. 2000), their concentration in surface sediments may reflect primary production processes only at shallow water depths. In contrast, their progressive depletion during particle sinking through the water column will generally result in a progressive decrease of the phytopigment concentration in deep-sea sediments in moving from bathyal to abyssal depths (Fabiano et al. 2001). The weak relationship that we observed between phytopigment concentrations and BPC concentration is, therefore, potentially biased by the data collected at deeper depths. The analysis of different types of coastal ecosystems, in fact, indicates a much closer relationship between total phytopigment and BPC concentrations (Fig. 2a), with significant changes seen in the slope of the linear regressions (Table 2). Despite the fact that the 3 selected areas represent only part of the primary production levels found worldwide, the observed pattern suggests that the BPC in oligotrophic coastal systems (e.g. Ligurian Sea) is more closely dependent upon the input of primary organic matter than that in eutrophic systems (e.g. Adriatic Sea).

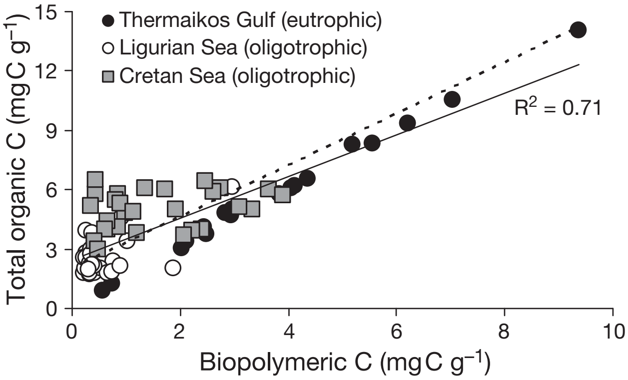

Fig. 1. Type-I (continuous line) and Type-II (dashed line) linear regressions between TOC and BPC concentrations in Mediterranean sediments. Data are extracted from Fabiano et al. (1995) for Ligurian Sea, Tselepides et al. (2000) for Cretan Sea and Pusceddu et al. (2005) for Thermaikos Gulf. R^2 is the coefficient of Type-I regression

We observed decreasing algal carbon contributions to the BPC pools with increasing BPC concentrations in the sediment (Fig. 2b). The comparison of environments characterised by diverse organic matter input and different productivities indicates that increasing accumulation of BPC in marine sediments is associated even in highly productive systems (such as estuaries, ponds and fish farm sediments) with low algal carbon contributions to BPC. This suggests that, in eutrophic sediments characterised by high BPC concentrations and benthic algal biomass, algal carbon is progressively diluted in a complex and heterogeneous organic matrix. In this regard, however, it must be considered that the carbon:chl *a* ratio of living algae can vary from 10 to about 100 (Banse 1977). Since we used a ratio of

Table 2. Output of the analysis of covariance (ANCOVA) testing for differences between slopes and intercepts of Type-I regressions illustrated in Fig. 2a. $^{***}p < 0.001$, $^{*}p < 0.05$, ns = not significant, na = not applicable

ANCOVA comparison	*F* Slope	*F* Intercept	Multiple comparisons Slope	Multiple comparisons Intercept
Liguran Sea (L) vs Ross Sea (R)	32.20***	0.37 ns	L > R	na
Ross Sea (R) vs Adriatic Sea (A)	4.21*	5.86*	R > A	R < A
Ligurian Sea (L) vs Adriatic Sea (A)	4.04*	0.006 ns	L > A	na

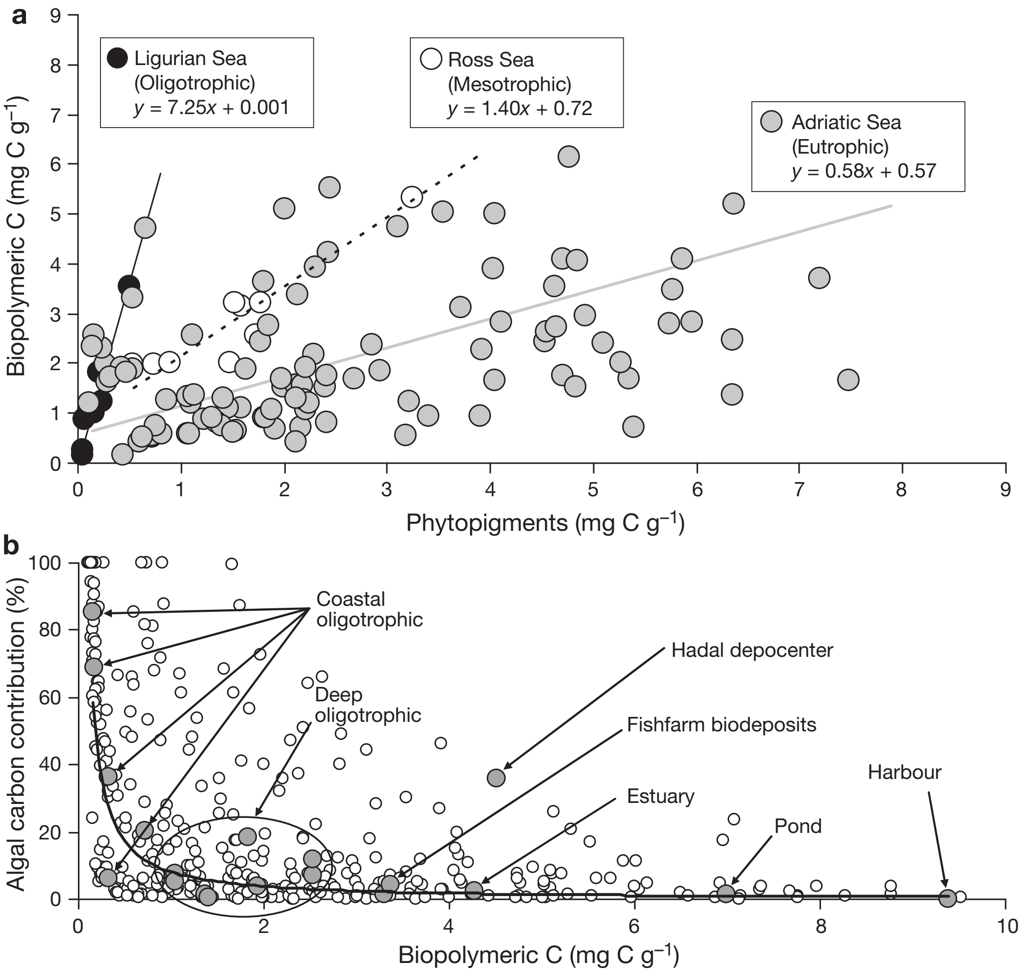

Fig. 2. Type-II regressions between phytopigment (chl *a* and phaeopigment in C equivalents) and BPC concentrations in marine sediments in 3 coastal ecosystems with (a) different primary productivity levels, and (b) relationship between the fraction of BPC that is made up by phytopigments (= algal carbon contribution, expressed as the percentage of chl *a* carbon equivalents) and BPC concentrations in marine sediments. Data for (a) are extracted from Fabiano et al. (1995) for Ligurian Sea, Pusceddu et al. (2000) for Ross Sea and Danovaro et al. (2002) for Adriatic Sea. In (b), grey circles represent the mean values of representative sediments characterised by increasing BPC concentrations, whereas open circles represent all data

40, our estimates of the algal carbon contribution to BPC are potentially biased by a factor of up to 2 to 4. Moreover, we compared systems characterised by a wide variability in depositional regimes, so that the values of the algal carbon contribution to BPC should be considered with some caution.

Sediments exhibiting different BPC loads are also characterised by different temporal variability patterns. Marine sediments characterised by high BPC loads, such as coastal lagoons and organically enriched sediments beneath cages at fish farms, display a more pronounced temporal variability. Conversely, benthic systems characterised by lower BPC contents are characterised by a much lower temporal variability (Fig. 3). This result suggests that under ‘eutrophic’ conditions (i.e. high primary productivity) the inputs of organic carbon widely fluctuate, determining strong and sudden shifts of background levels of sediment organic matter concentrations. Conversely, in oligotrophic systems, the seasonal organic carbon input during algal blooms does not detectably alter background concentrations of organic matter in the sediment.

BIOPOLYMERIC CARBON AND OXYGEN DEMAND

Organic matter reaching the sediment surface stimulates benthic metabolism (Witbaard et al. 2001). This has been used for carrying out a worldwide estimate of particulate organic carbon fluxes to the deep ocean (>1000 m in depth) from benthic oxygen flux estimates (Jahnke 1996). In turn, the accumulation of organic carbon in the sediment is also a function of organic carbon reactivity with the available oxygen (Dauwe et al.

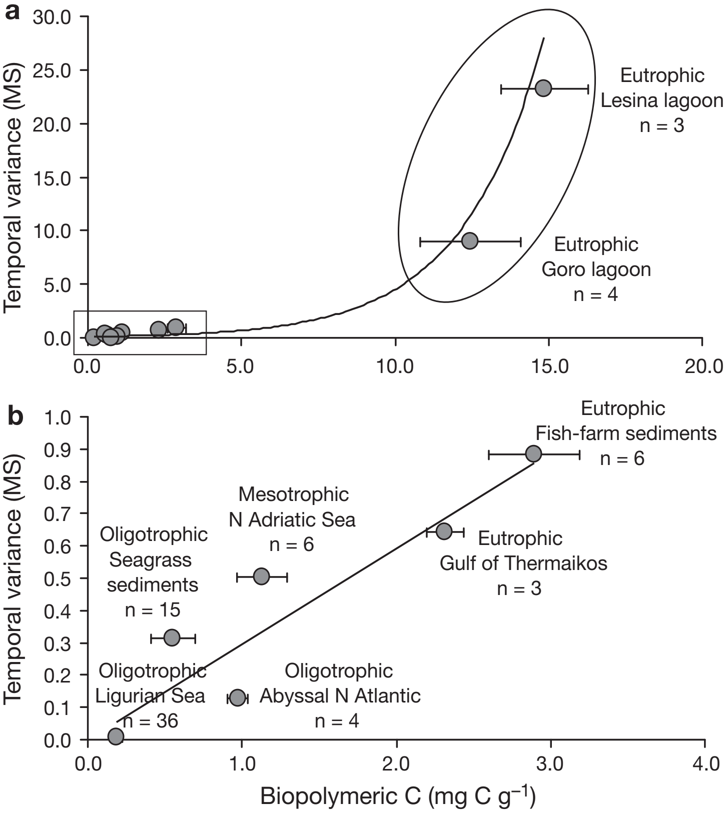

Fig. 3. Relationship between BPC sediment content and its temporal variability in different marine environments. Temporal variability is reported as mean squares (MS) derived after a 1-way ANOVA performed using sampling time as a single source of variance, separately for each data set; (b) is an enlarged view of the inset in (a). Horizontal bars indicate SE values. Data plotted refer to Manini et al. (2003) for coastal lagoons, Mazzola et al. (1999) for fish farm sediments, Pusceddu et al. (2005) for Thermaikos Gulf, Danovaro et al. (2002) for N Adriatic Sea), Danovaro et al. (1994) for seagrass sediments, Fabiano et al. (1995) for Ligurian Sea, and Danovaro et al. 2001 for Atlantic sediments

2001). When the sediment experiences an excessive organic input, oxygen can be completely depleted, with anaerobic processes prevailing.

We have found significant relationships between *in situ* measurements of SCOC and synoptic measurements of TOC and BPC concentration of the sediment (Fig. 4). The results of Type-I regression indicated that concentrations of both pools explained significant proportions of the variance of oxygen consumption rates, but whilst total organic carbon explained 61% of SCOC variance, BPC alone can explain 79% of SCOC variance. From the linear equations calculated using Type-II regression, it can be calculated that an increase of 1 mol C m^{-2} in sediment BPC concentration would enhance SCOC by about 100 µmol m^{-2} h^{-1}, which is about 2-fold higher than the SCOC increase obtained by an equal increase in TOC concentration (about 53 µmol m^{-2} h^{-1}). These results indicate that the BPC is more labile towards degradation than is the total carbon pool and suggest that an enrichment in the BPC concentration, more than in TOC, will shift the system towards conditions of higher oxygen demand.

The ecological consequences of excessive organic accumulation in the sediment will also depend upon the hydrodynamic regime and other environmental constraints (e.g. water mixing, temperature, salinity, pressure, biological activity), to which the remaining 21 to 39% of the unexplained variance in the relationships outlined previously can be ascribed. Nonetheless, our results suggest that high BPC concentrations in surface sediments might be an additional co-factor potentially responsible for the development of hypoxic and/or anoxic events (Dell'Anno et al. 2008).

BIOPOLYMERIC AND BIOAVAILABLE ORGANIC CARBON RELATIONSHIPS: TROPHIC CONSEQUENCES

Since BPC may contain molecules that become available to consumers only after microbial reworking, the use of BPC as a proxy for labile organic carbon depends also on its origin and molecular composition. The amount of labile (bioavailable) organic matter in marine sediments can be extrapolated according to

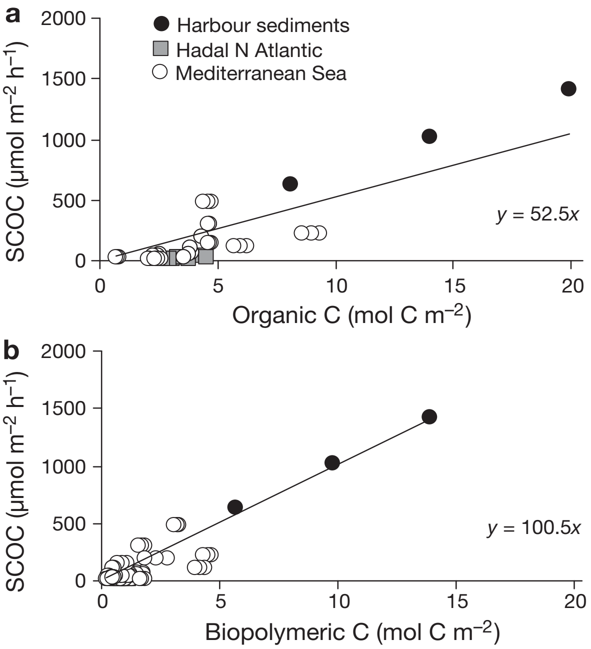

Fig. 4. Relationships between sediment community oxygen consumption (SCOC) and (a) total organic carbon and (b) BPC concentrations in the sediment. Data are summarised from Danovaro et al. (1999a, 2002), Witbaard et al. (2000), Duineveld et al. (2000), Tselepides et al. (2000) and Lykousis et al. (2002). Type-II regression equations are reported

mathematical models based on the exponential decrease of organic carbon with increasing depth in the sediments (Rice & Rhoads 1989). Such models, however, assume that different classes of organic compounds undergo degradation and utilisation at similar rates (Danovaro et al. 2001).

A number of studies demonstrated that only a certain fraction of BPC in marine sediments can actually be degraded enzymatically and, thus, is readily available for heterotrophic nutrition (Dauwe & Middelburg 1998, Dauwe et al. 1999a,b, Dell'Anno et al. 2000, Danovaro et al. 2001). Based on this background, we investigated the relationship between concentrations of BPC and bioavailable carbon (BAC) in sediments characterised by different productivity levels (Fig. 5a). As expected from the linear relationship between BPC and the sediment community oxygen consumption, BAC is positively correlated with BPC, suggesting that eutrophic (i.e. enriched in BPC concentration) sediments are characterised also by high concentrations of rapidly digestible material. However, increasing BPC concentrations in the sediment also display a progressive decrease of the percentage contribution of the bioavailable carbon to BPC (Fig. 5b). This finding would indicate that benthic environments subjected to changes in trophic status may experience relevant changes in the relative importance of the labile and refractory fractions of sediment organic carbon. These changes could be also the result of differences in sediment particle characteristics, which are known to play a major role in the preservation (and, thus, lability) of the different pools of sediment organic matter (Keil et al. 1994). Nevertheless, our results are in agreement with previous studies indicating that eutrophic systems, subjected to the accumulation of large amounts of organic matter in subsurface sediments, could be

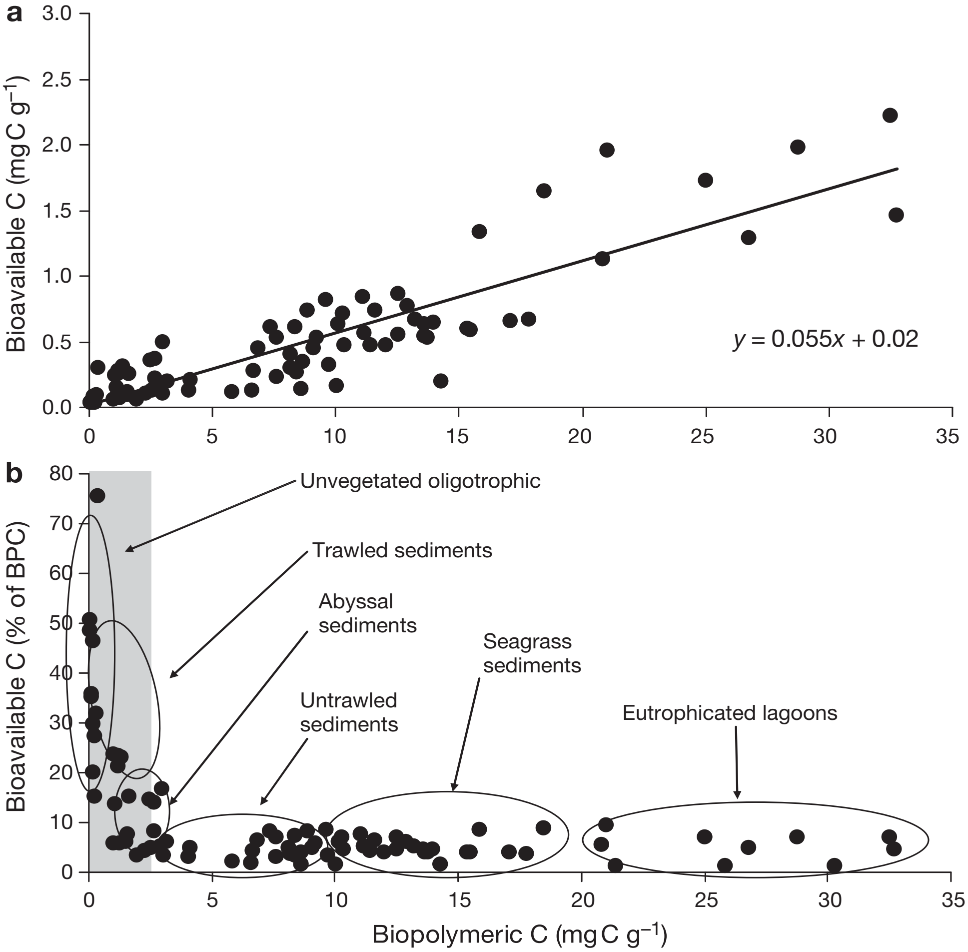

Fig. 5. Relationships between (a) BPC and BAC quantities and (b) the bioavailable (enzymatically digestible) fraction of BPC versus BPC quantity in marine sediments. Data are extracted from Danovaro et al. (2001) for the Porcupine Abyssal Plain (4850 m depth), Pusceddu et al. (2003) for the western Mediterranean Sea (2 m depth), Pusceddu et al. (2005) for the eastern Mediterranean Sea (30 to 86 m depth) and Pusceddu et al. (2007b) for the Goro and Lesina lagoons. The light grey area encloses values of BPC concentrations less than 2.5 mg C g^{-1}, which correspond to values of the bioavailable fraction >10%. The equation in (a) is derived by Type-II regression analysis

characterised by an enhancement of the complexation of buried organic molecules with the inorganic matrix, thus making them less 'available' to heterotrophic nutrition (the so-called 'sorptive preservation hypothesis'; Mayer 1994). This could be also due to an 'encapsulation' mechanism of potentially labile molecules (such as proteins) in organically enriched sediments (such as those buried in the sapropel layers; Knicker & Hatcher 1997). The accumulation of mostly refractory organic matter in organically enriched sediments appears to be the case of transitional (lagoonal) ecosystems (e.g. Pusceddu et al. 2003).

From these relationships, it can also be seen that when BPC concentrations in the sediment exceed 2.5 mg C g^{-1}, its bioavailable fraction is always less than 10%. These 2 values, when verified contemporarily in the same area, can, thus, be proposed as threshold levels out of which accumulation of BPC leads to altered organic matter bioavailability to benthic consumers.

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