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The European coastal zone: characterization and first assessment of ecosystem metabolism

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Abstract

The geomorphic, oceanographic, terrestrial and anthropogenic attributes of the European coastal zone are described and published data on ecosystem function (primary production and respiration) are reviewed. Four regions are considered: the Baltic Sea, Mediterranean Sea, Black Sea and the European Atlantic coast including the North Sea. The metabolic database (194 papers) suffers from a non-homogeneous geographical coverage with no usable data for the Black Sea which was therefore excluded from this part of our study. Pelagic gross primary production in European open shelves is, by far, the most documented parameter with an estimated mean of 41 mmol C m^{-2} d^{-1}, the lowest value is reported in the Mediterranean Sea (21 mmol C m^{-2} d^{-1}) and the highest one in the Atlantic/North Sea area (51 mmol C m^{-2} d^{-1}). Microphytobenthic primary production, mostly measured in shallow areas, is extrapolated to the entire 0–200 m depth range. Its contribution to total primary production is low in all regions (mean: 1.5 mmol C m^{-2} d^{-1}). Although macrophyte beds are very productive, a regional production estimate is not provided in this study because their geographical distribution along the European coastline remains unknown. Measurements of pelagic community respiration are clearly too sparse, especially below the euphotic zone, to yield an accurate picture of the fate of organic matter produced in the water column. With a mean value of 17 mmol C m^{-2} d^{-1}, benthic community respiration consumes approximately 40% of the pelagic organic matter production. Estuaries generally exhibit high metabolic rates and a large range of variation in all parameters, except microphytobenthic primary production. Finally, the problem of eutrophication in Europe is discussed and the metabolic data obtained in the framework of the Land–Ocean Interactions in the Coastal Zone (LOICZ) project are compared with available direct measurements of net ecosystem production.

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Keywords: ecosystems; global; metabolism; shelf; estuaries; primary production; respiration; Europe

1. Introduction

The coastal zone is a transition area between land and the open ocean. It receives considerable amounts of freshwater, nutrients, dissolved and particulate organic matter, sediment and contaminants. It also exchanges matter and energy with the open ocean. The coastal zone is, by definition, relatively shallow. This has two consequences: (1) light penetrates a significant portion of the water column, even reaching the bottom and (2) there is a strong coupling between pelagic and benthic processes. These inputs, together with its shallowness, make the coastal zone very active in terms of primary production and respiration. Coastal metabolism has been reviewed in a number of fairly recent papers (Smith and Hollibaugh, 1993; Alongi, 1998; Gattuso et al., 1998; Wollast, 1998).

The European coastal zone has geomorphic and metabolic characteristics similar to those of other coastal areas. Although these attributes have never been fully reviewed, local and thematic studies have received strong support and attention in the European research

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programs. A major reason is that the European Union (EU) has promoted inclusion of socio-economic aspects in the research projects reflecting the increasing significance of the coastal ocean in the EU and elsewhere in terms of fishing, aquaculture and recreation. The European Commission launched ELOISE (European Land–Ocean Interaction Studies) as a loose network of reasonably small coastal research projects. ELOISE is the European contribution to LOICZ (Land–Ocean Interaction in the Coastal Zone), a program element of the International Geosphere Biosphere program (IGBP).

Two of the initial goals of ELOISE (Cadée et al., 1994) were related to ecosystem function: (1) to determine the role of coastal seas in land-ocean interactions (including shelf-deep sea interactions along the shelf break) in the context of global change and (2) to determine the regional and global consequences of human impact through pollution, eutrophication and physical disturbance on land-ocean interactions in the coastal zone.

This paper has two aims. First, to review the geomorphic, oceanographic, terrestrial and anthropogenic attributes of the EU coastal zone using global databases recently accessible. Second, to review, synthesize and analyse published data on ecosystem function, essentially primary production and respiration.

2. Characterization of the European coastal zone

The continental shelf, continental margin, coastal ocean and coastal zone are fuzzy concepts for which various definitions have been proposed. It is outside the scope of this paper to review these definitions. The definition of the terms as commonly used was adopted and the operational definition applied here was explicitly mentioned.

The continental shelf is the area extending from the coast to the shelf break, which is usually defined by the 200 m depth isobath. The continental margin is the transition zone between the continental crust and the oceanic crust, including the coastal plain, continental shelf, slope and rise (Kennett, 1982). The coastal ocean is the portion of the global ocean where physical, biological and biogeochemical processes are directly affected by land. It is either defined as the part of the global ocean covering the continental shelf or the continental margin. The coastal zone usually includes the coastal ocean as well as the portion of the land adjacent to the coast that influences coastal waters. It can readily be appreciated that none of these concepts has a clear operational definition. The marine portion of the coastal zone was defined as the area with a depth of 200 m or less or, when the data are gridded with a large cell size, with at least one depth sounding of 200 m or less. The land portion of the coastal zone is the land area located in the 0.5° ×0.5° cell enclosing the coastline (see below).

Two major sources of information were used: the ETOPO2 data set for the depth attributes and the LOICZ environmental database for most other attributes. The gridded ETOPO2 data set was downloaded from the Data Support Section of the National Center for Atmospheric Research (http://dss.ucar.edu/datasets/ds759.3/data/) on 9 December, 2002. It blends satellite altimetry with ocean soundings and new land data to provide a global elevation and bathymetry on a $2' \times 2'$ grid. The UNIX version of the Generic Mapping Tool (gmt 3.4.2-3), with its full resolution coastline, was used to calculate surface area, volume, median and average depth.

The international program LOICZ has compiled atmospheric, geomorphic, terrestrial, oceanic, biogeochemical and human-related variables, and produced a gridded database freely accessible (http://hercules.kgs.ukans.edu/hexacoral/envirodata/main.htm) on the World Wide Web. The grid size (0.5° or about 55 km at the equator) is coarse for coastal areas, which exhibit major gradients in their environmental and ecological attributes at scales of 1 km or less. Importantly, data for many of the variables present in the LOICZ database are simply not available on a global scale and with a better geographical resolution. The choice of the grid size was then a compromise between the existing data and the objective of using the same grid size for all variables. This database is a very powerful tool, (1) to describe the attributes of coastal ocean at a global scale, more specifically its geomorphology, environmental setting and biogeochemical properties, and (2) to explore how the coastal zone is influenced by inputs from land the atmosphere, and by human activities.

Here, four regions were examined (Fig. 1): the Baltic Sea (including the Kattegat), the Mediterranean Sea, the Black Sea (including the Sea of Azov) and the European Atlantic coast (including the English Channel, the North Sea and the Skagerrak). While the Caspian Sea is often included as an EU sea (Mamaev, 2002), this area was not considered because it is not connected to an open ocean or marginal sea. Similarly, freshwater bodies were not considered.

2.1. Geomorphic attributes

2.1.1. Surface area and hypsometry

The European coastal zone covers 8.4% of the world coastal zone surface area (2.18 vs. 25.84×10^6 km^2; Table 1), with a similar median depth (60 vs. 46 m). The European Atlantic coast is the largest region (56% of the EU coastal zone) reflecting the large area of the North Sea and the extended shelf that surrounds the United Kingdom. The next largest region is the Mediterranean (21%). It has a relatively narrow shelf, except in the northern Adriatic Sea, representing only 18% of the total surface area. The coastal zones of the Baltic Sea and the

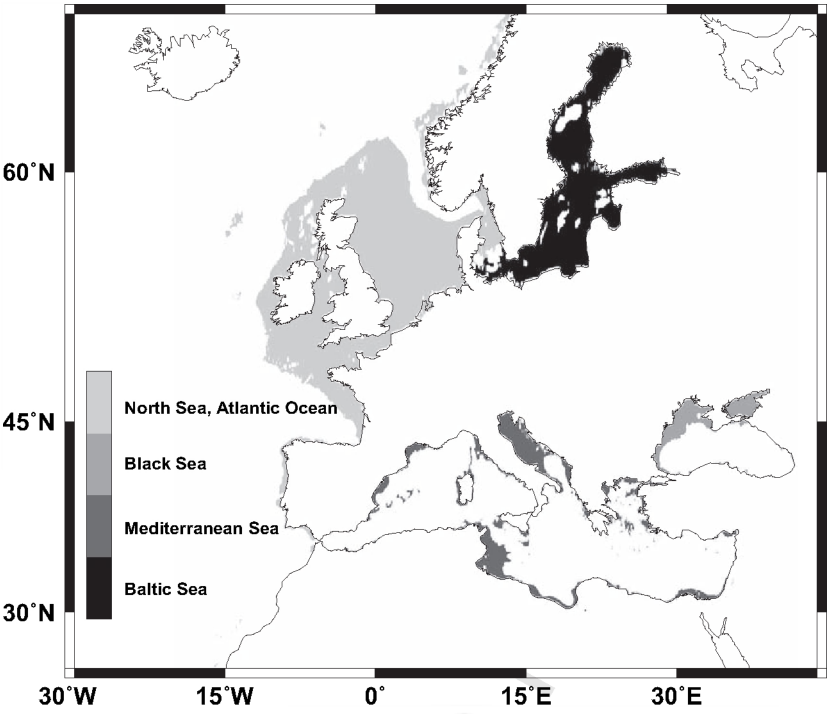

Fig. 1. Map of the European coastal zone with considered sub-regions.

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Black Sea (97% and 28% of their total surface area) include 17% and 6% of the EU coastal zone; they are the shallowest regions (median depth of 35 and 40 m). The European Atlantic region is the deepest (median depth: 73 m). Note that part of the Baltic Sea (Gulf of Bothnia and eastern part of Gulf of Finland) has a seasonal ice cover for up to half a year; the maximum annual ice cover ranges from 12% to 100% of the surface area (Gronvall and Seina, 1999).

The hypsometric curves (Fig. 2) show that the European Atlantic region has a much steeper slope than all other regions of the European coastal zone and is steeper than the mean value for the global coastal zone. About 34% of the Baltic Sea area is shallower than 20 m, 23% of the Black Sea, 19% of the Mediterranean Sea and only 11% of the European Atlantic Ocean, compared with a mean value of 26% for the global coastal zone.

Table 1
Geomorphic attributes of the European coastal zone

Geographical zone	Area (10^6 km^2)	Volume (10^6 km^3)	Mean depth±SD (m)	Median depth (m)
Baltic Sea	0.37	18.17	46±43	35
Mediterranean Sea	0.45	29.07	67±54	56
Black Sea	0.13	7.25	56±49	40
Atlantic, European	1.23	95.59	78±53	73
Total, mean and median depth (Europe)	2.18	150.06	69±53	60

2.1.2. Attributes of land adjacent to the coastal zone

Nearly 50% of total length of the European coastline (calculated at a nominal scale of 1:250 000) is in the Atlantic domain, 27% in the Baltic Sea, 20% in the Mediterranean Sea and less than 5% in the Black Sea (Table 2). The median elevation of land adjacent to the coast, that is comprised in the LOICZ coastal cells described above, is higher in the Mediterranean (194 m) than elsewhere in Europe (grand median, 112 m). The surface area of the coastal cells covered by crop land

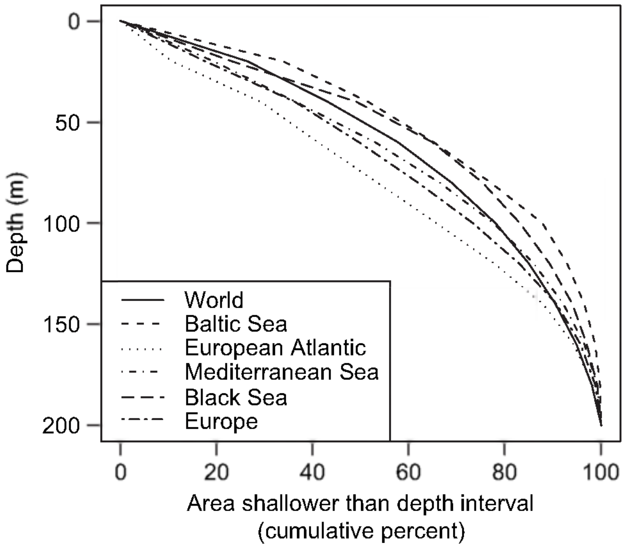

Fig. 2. Hypsometry of the European coastal ocean.

Table 2
Geomorphic attributes of the LOICZ database coastal cells

Variable	Baltic Sea	Mediterranean Sea	Black Sea	European Atlantic	Whole of Europe
Coastline length (km) [1]	77802	56650	10738	133357	278547
Median of mean land elevation (m) [2]	27	194	79	123	112
Median maximum elevation (m) [3]	68	650	227	380	331
Median of SD of elevation (m) [4]	14	138	46	80	68

Numbers in brackets refer to data sources listed in the appendix available at: http://www.obs-vlfr.fr/~gattuso/ECSS_app.htm.

ranges from 15% in the European Atlantic region to 42% in the Black Sea region (Fig. 3).

2.2. Atmospheric attributes

Some but not all atmospheric environmental parameters vary greatly depending on the zone considered. The median wind speed is higher in the European Atlantic region than in the Mediterranean region, with a difference of less than 2 m s^{-1} (Table 3). The median air temperature is 10.5 °C for all of Europe; the median, minimum and maximum monthly air temperatures range widely from -15.4 to 31.9 °C. The median annual precipitation is similar in the Baltic, Mediterranean and Black Sea regions (range, 671–720 mm yr^{-1}) but is significantly higher in the European Atlantic region (1022 mm yr^{-1}). The largest range of mean monthly precipitation is found in the Mediterranean region (0–484 mm month^{-1}).

2.3. Oceanic attributes

The median mean monthly sea surface temperature (SST) varies almost 3-fold between the geographical regions (7.7 °C in the Baltic Sea and 19.5 °C in the Mediterranean; Table 4). The range of mean monthly SST is >20 °C in the four regions. Sea surface salinity (SSS) is reported but some EU coastal areas are seasonally or permanently stratified. For example, according to Kautsky and Kautsky (2000) the central Baltic Proper is permanently stratified (salinities of 6–8 in the upper layer and 10–14 in the deeper layer). The median SSS differs considerably between geographical regions (6.4 in the Baltic Sea and 38.1 in the Mediterranean Sea). The median wave height is 3–4 times smaller in the Black Sea than in the other three regions; it is highest in the European Atlantic region. The median tidal range also differs largely between regions with values close to 0 m in the Baltic Sea and the Mediterranean Sea regions, and between 2 and 4 m in the European Atlantic region.

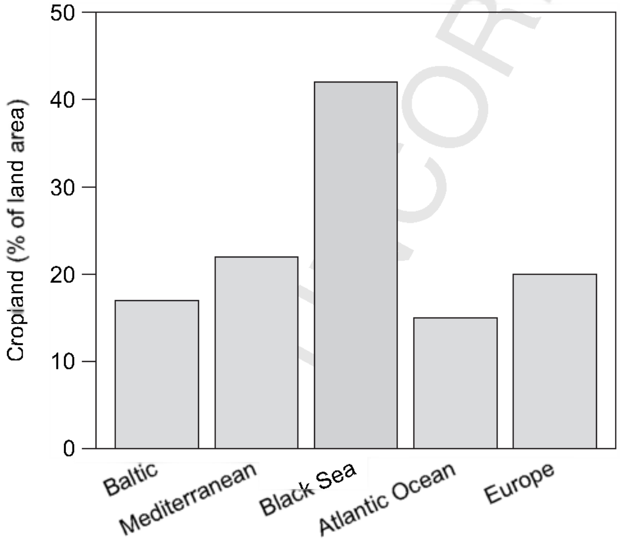

Fig. 3. Relative surface area (%) of cropland in the coastal cells. Data from the University of Maryland's 1 km global land cover product (Hansen et al., 2000) extracted from the LOICZ database.

2.4. River basin and coastal population attributes

In Europe, 58% of the total annual runoff comes from 35 large river basins (Fig. 4); individual runoff values range from 13.1 to 329 km^3 yr^{-1}. The calculated combined runoff is similar to that reported by Dai and Trenberth (2002). The European Atlantic region receives about the same total runoff as the Mediterranean Sea (Table 5), but the yield (runoff per unit of river basin area) is 3-times greater. The very large river basin area for the Mediterranean region is due to the Nile basin, which extends over 10 African countries and covers about 3×10^6 km^2. As a result, the total basin population is equally large with more than 360×10^6 inhabitants. European basins drain an area 7-times larger than the surface of the EU coastal zone (15.2 vs. 2.2×10^6 km^2). The rivers that drain Europe are small and carry little sediment (Milliman and Meade, 1983; Milliman and Syvitski, 1992). Only the Rhône, Po and Danube Rivers appear to have annual sediment discharge rates $>10\times10^6$ t. The Danube River, by far the largest in terms of its drainage area and water discharge volume, has a sediment discharge rate of 67×10^6 t yr^{-1}. The total sediment discharge from Europe is 230×10^6 t yr^{-1}. Estimates of nutrient loads, nitrogen (DIN) and phosphorus (DIP), from European drainage basins are based on the model of Smith et al. (2003). Nutrient yield from the European Atlantic river basin is about twice the average and more than 3 times the Mediterranean Sea value. The Baltic and Black Seas are each near the

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Table 3
Atmospheric attributes of all cells with at least one depth <200 m

Variable	Baltic Sea	Mediterranean Sea	Black Sea	European Atlantic	Whole of Europe
Median wind speed (m s^{-1}) [5]	7.4	6.5	–	8.3	7.2
Median of air temperature (°C) [6]	3.4	16.0	10.3	8.0	10.5
Minimum and maximum monthly averaged air temperature (°C) [7]	−11; 21.6	−8.5; 31.9	−7.4; 24.5	−15.4; 26.6	−15.4; 31.9
Median CV of 12 months average air temperature (°C) [8]	2.8	1.9	2.7	1.5	1.9
Median annual precipitation (mm yr^{-1}) [9]	720	679	671	1022	794
Minimum and maximum monthly averaged precipitation (mm) [10]	16; 222	0; 484	18; 277	0.1; 342	0; 484

Numbers in brackets refer data sources listed in the appendix available at: http://www.obs-vlfr.fr/˜gattuso/ECSS_app.htm.

average. The human attributes of the coastal cells are shown in Table 6. The population density is the highest in the Mediterranean coastal area (58.5 inhabitants km^{-2}), and minimal along the Baltic coast with a value of 13.1 inhabitants km^{-2}.

3. Metabolic performances of European coastal ecosystems

3.1. Construction, content and characteristics of the database

A database was constructed using references from the Aquatic Science and Fisheries Abstracts (ASFA) database and from review papers (Charpy-Roubaud and Sournia, 1990; Smith and Hollibaugh, 1993; Heip et al., 1995; Gattuso et al., 1998; Cahoon, 1999; Cebrián, 2002; Middelburg et al., in press). This database is available from the authors or on the World Wide Web (http://www.obs-vlfr.fr/eurotroph/). One of the striking outcomes of the literature search was that, while several hundred papers were returned for each search, a relatively small number of them could be used. Indeed, a large number of studies focused on the metabolism of single species rather than of the community. Such data were not considered here. Although budgets of air-sea CO_2 fluxes can be a reliable estimate of the trophic status of an ecosystem (Frankignoulle et al., 1998; Thomas and Schneider, 1999; Frankignoulle and Borges, 2001), this study only focuses on measured processes and LOICZ budgets. The following information has been compiled where available: latitude and longitude of the study site, time of the year, depth of the site and of sampling, salinity, temperature, nutrient concentrations, community primary production (net or gross), community respiration and the methods used to measure these processes. The database presently comprises 194 references. The database is certainly not exhaustive, but it is regularly updated. It also has a significant bias against papers published before 1978 because the ASFA database only lists references published after that date. However, our database is believed to be a relatively unbiased sample of the literature published after 1978.

The number of studies of EU coastal ecosystem function has steadily increased during the past decades (Fig. 5). The present rate of publication is about 10–15 papers per year. However, only some of these studies

Table 4
Oceanic attributes of all cells with at least one depth sounding <200 m

Variable	Baltic Sea	Mediterranean Sea	Black Sea	European Atlantic	Whole of Europe
Median of monthly averaged sea surface temperature [11]	7.7	19.5	14.7	10.6	15.3
Minimum and maximum monthly sea surface temperature [12]	−1.8; 21	6.5; 29.3	3.6; 27.2	−1.8; 24.8	−1.8; 29.3
Median of monthly averaged sea surface salinity [13]	6.4	38.1	18.0	34.9	35.2
Minimum and maximum monthly averaged sea surface salinity [14,15]	3.3; 23.1	17.7; 39.7	15; 19.1	3.3; 37	3.3; 39.7
Median wave height (scaled discrete classes) [15]	3	3	1	4	3
Median tidal range (scaled discrete classes) [16]	0	0	1	3	1

Classes for wave height are: 0 = permanent sea ice, 1 = 0–2.5 m, 3 = 2.5–3.5 m, 4 = 3.5–4.5 m, 6 = 4.5–6.5 m, 7 = >6.5 m. Classes for tidal range are: 0 = tideless, 1 = <2 m, 3 = 2–4 m, 6 = 4–8 m, 10 = >8 m. Numbers in brackets refer data sources listed in the appendix available at: http://www.obs-vlfr.fr/~gattuso/ECSS_app.htm.

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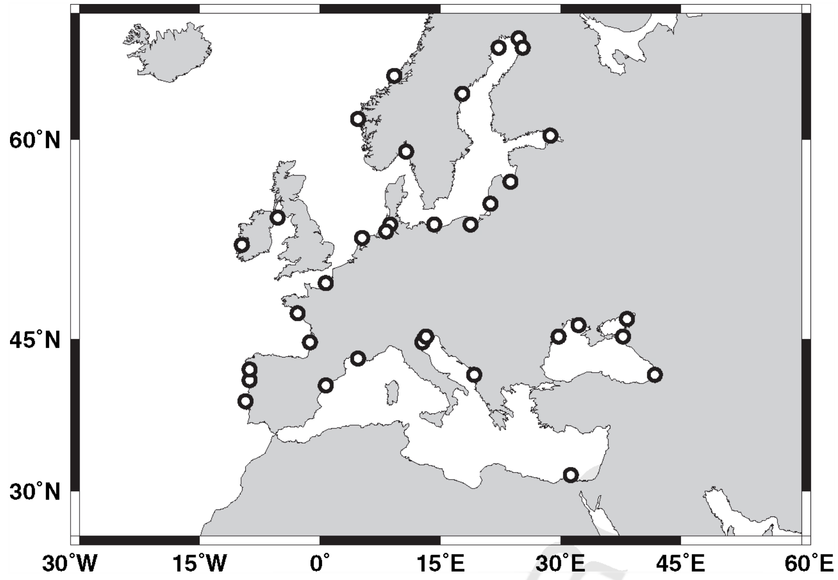

Fig. 4. Location of the 35 coastal cells that contribute most to coastal runoff.

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report yearly estimates of the processes, which limits their usefulness to derive the global properties of ecosystem function.

3.1.1. Methods and collection of data

The data were obtained using a wide range of techniques: change in the concentration of a tracer (^{14}C, CO_2 or O_2) during incubations carried out in situ or under in situ simulated conditions, or using large-scale budgeting (Gordon et al., 1996), but all are expressed in mmol C $m^{-2} d^{-1}$. The metabolic process measurements originally reported in oxygen units were transformed into carbon units by assuming that the photosynthetic and respiratory quotients equal 1. Although PQ seems to be higher than 1 in phytoplankton (Hedges et al., 2002), the paucity of available data and the general lack of recorded environmental conditions (including nutrient sources for photosynthesis) in the publications prevent assessment of the sensitivity of PQ in our evaluation.

Some papers report metabolic rates measured at only one depth and expressed in µmol C $l^{-1} d^{-1}$. These references were excluded from our assessment that considered only rates normalized per unit surface area, with the exception of pelagic community respiration data (see next section). A significant number of papers report hourly rates of primary production and/or respiration. Hourly pelagic and benthic respiration rates were converted into daily rates assuming constant values over 24 h. This neglects the fact that respiration can be higher in the light than in the dark in many photosynthetic organisms as reported recently for an algal-dominated reef maintained in a mesocosm (Langdon et al., 2003).

Incubations with the ^{14}C-tracer method were generally carried out around noon; multiplying these rates by the day length averaged over an annual period (12 h) can lead to an overestimation. The procedure of Cahoon (1999) was followed and a factor of 10 was used to convert hourly to daily rates for microphytobenthic gross primary production (GPP). The same approach was used for pelagic GPP estimates.

A large proportion of the annual primary production data (90% pelagic and 30% benthic) were measured using the ^{14}C technique during incubations ranging from 1 to 24 h. It is well recognized that the ^{14}C technique measures

Table 5
River basin attributes of the European coastal zone

Variable	Baltic Sea	Mediterranean Sea	Black Sea	European Atlantic	Whole of Europe
Total river basin area (10^6 km^2) [17]	1.86	8.68	2.49	2.19	15.22
Total runoff (km^3 yr^{-1}) [18]	429	788	413	793	2424
Total river basin population (10^6 inhabitants) [19]	92.6	360.8	187.2	251.8	892.4
Median river basin population density (inhabitants km^{-2}) [20]	19.14	45.44	42.0	34.1	34.3
DIN yield (10^3 mol m^{-2} yr^{-1})	10.2	6.1	11.2	20.1	9.5
DIP yield (10^3 mol m^{-2} yr^{-1})	0.5	0.3	0.6	1.1	0.5

Numbers in brackets refer data sources listed in the appendix available at: http://www.obs-vlfr.fr/~gattuso/ECSS_app.htm.

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Table 6
Human attributes of coastal cells

Variable	Baltic Sea	Mediterranean Sea	Black Sea	European Atlantic	Whole of Europe
Total coastal population (million inhabitants) [21]	14.9	133.0	20.5	74.7	243.1
Coastal population density (inhabitants per km^2 land area) [22]	13.1	58.5	30.9	19.4	30.0
Cell road density (road area divided by land area in %) [23]	0.12	0.16	0.17	0.13	0.14

Numbers in brackets refer data sources listed in the appendix available at: http://www.obs-vlfr.fr/~gattuso/ECSS_app.htm.

something between gross and net primary production (Peterson, 1980), depending on the incubation time: short incubation times are closer to GPP whereas long incubation times are closer to net primary production (NPP). Only the rates of ^{14}C uptake measured over an incubation period ≤6 h (90% of the total number of papers reporting ^{14}C primary production) have been considered. It was assumed that they yield rates comparable to GPP estimated by the oxygen technique.

Benthic and pelagic community respiration (CR) were mainly measured by the oxygen method. In coastal areas, and especially within sediments, the oxygen concentration is sometimes too low to allow a complete aerobic mineralization of the organic matter and alternative oxidants are used through anoxic metabolic pathways (Thamdrup and Canfield, 2000). When there is no net accumulation of reduced metabolites, i.e. when anaerobic respiration products are completely reoxidized when they reach the sediment surface, the oxygen method is a reliable estimate of total mineralization processes, both aerobic and anaerobic.

Another oxygen consuming process can occur in coastal ecosystems receiving high loads of ammonium. Nitrification, the conversion of ammonium to nitrate, is the process by which chemoautotrophic bacteria obtain their energy to fix carbon. Even though this process demands significant amounts of oxygen and may lead to suboxic conditions, especially in eutrophic estuaries, it is an inefficient autotrophic process (Heip et al., 1995) and was not considered in our study. As oxygen consumption (OC) values reported in eutrophic estuaries often include both respiration and nitrification processes, OC therefore can overestimate CR.

Sub-annual rather than annual values of processes are reported in about 30% of the studies; these were excluded from our analysis (see Figs. 5 and 6).

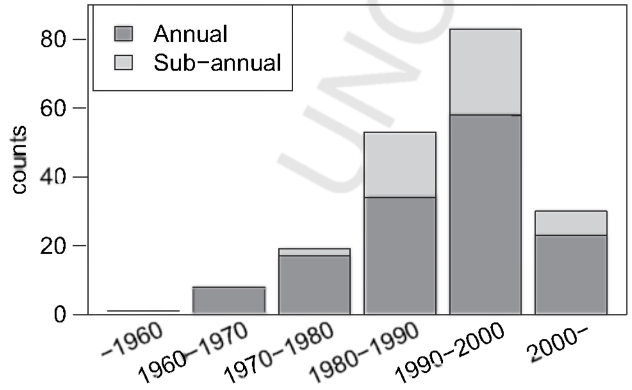

Fig. 5. Number of papers present in the database and year of publication.

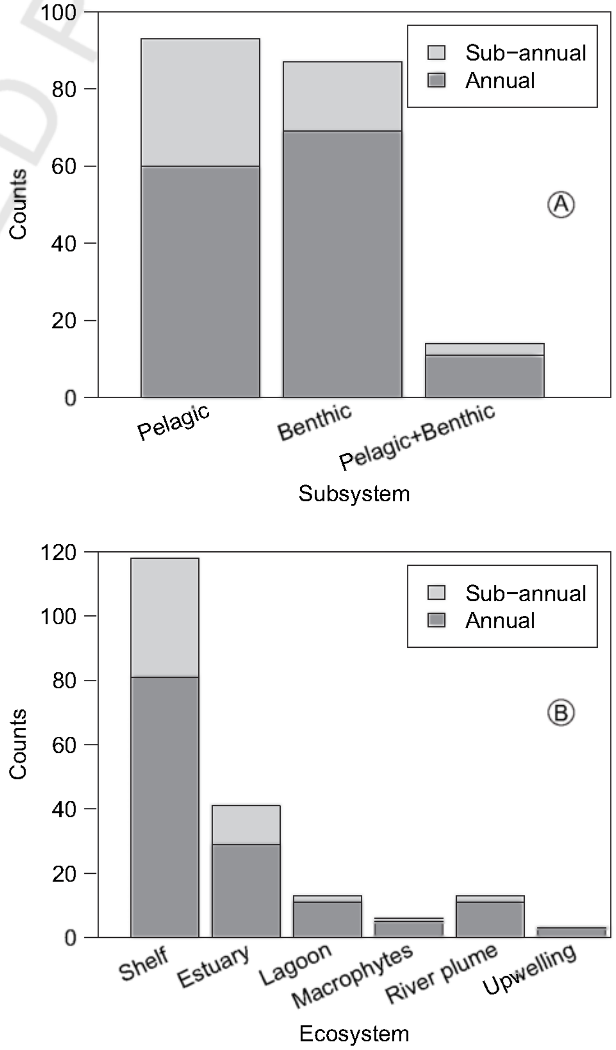

Fig. 6. (A) Number of papers according to ecosystem types. (B) Number of papers reporting annual or sub-annual metabolic data in the pelagos, benthos or both.

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Use of the criteria set forth above reduced the number of usable references from 194 to 129. Additional data for pelagic GPP in the North and Baltic Seas ($n = 73$) were obtained from MADS (Den National Database for Marine Data, National Environmental Research Institute, Denmark, http://www.dmu.dk/forside_en.asp) and BIOMAD (Database on Marine Biological Monitoring Data, Department of Systems Ecology, Stockholm University, Sweden, http://www2.ecology.su.se/dbbm/index.shtml) databases.

3.1.2. Geographical location of the data and systems considered

Not surprisingly, the study sites are not evenly distributed in the EU coastal zone (Fig. 7); many more measurements are available from the North Sea and the Kattegat than elsewhere. The database has relatively few data from the Mediterranean region. Most data are concentrated on specific areas, such are river plumes; there is only one site from the northern African coast and none from the Black Sea region. About the same number of data are available for the pelagos (93 references) and for the benthos (87 references; Fig. 6A), while more importantly, relatively few studies report processes from both the water column and the benthos (14 references). The study sites were distributed across different coastal ecosystems or physiographic zones, including: estuary, river plume and macrophyte-dominated ecosystems. Study sites that could not be assigned to one of these categories were grouped in a ‘shelf’ category which, for our analysis, also included coastal lagoons and upwelling areas. Most data were collected from the shelf (118) and estuaries (41), with few studies from other categories (3–13; Fig. 6B).

3.2. Coastal zone systems other than estuaries

Metabolic data for the European coastal zone were considered in three regions: the Baltic Sea, Atlantic Ocean/North Sea area and the Mediterranean Sea. Each of these regions was divided into sub-regions in order to group areas sharing similar environmental settings or metabolic properties. The Kattegat was grouped with the Baltic Sea, rather than with the North Sea as was done in Section 2, to enable comparison with previous regional estimates (Wasmund et al., 2001). The surface area of the Baltic Sea sub-regions were taken from HELCOM (1996). The Black Sea was not considered because none of the publications considered met the set of criteria described above. Estuaries are considered in a separate section because they exhibit a range of variation and a magnitude of metabolic parameters much larger than other coastal systems.

3.2.1. Pelagic gross primary production

The Baltic Sea is, by far, the most documented area in term of pelagic GPP rates in our database with 83 values including 28 in published papers and 55 extracted from the MADS and BIOMAD databases. Pelagic GPP is lowest in the Belt Sea (7.9 mmol C $m^{-2} d^{-1}$; MADS database) and highest in the plume of the Oder river (96 mmol C $m^{-2} d^{-1}$; Wasmund et al., 2001). Following the procedure of Wasmund et al. (2001), the Baltic was divided into five sub-regions (see Table 7) and the main river plumes (Vistula, Daugava and Oder river plumes) were considered separately. Our database does not include data for the Bothnian Bay and Bothnian Sea, both of which are said to be the least productive areas of the Baltic Sea (Elmgren, 1984; Kautsky and Kautsky,

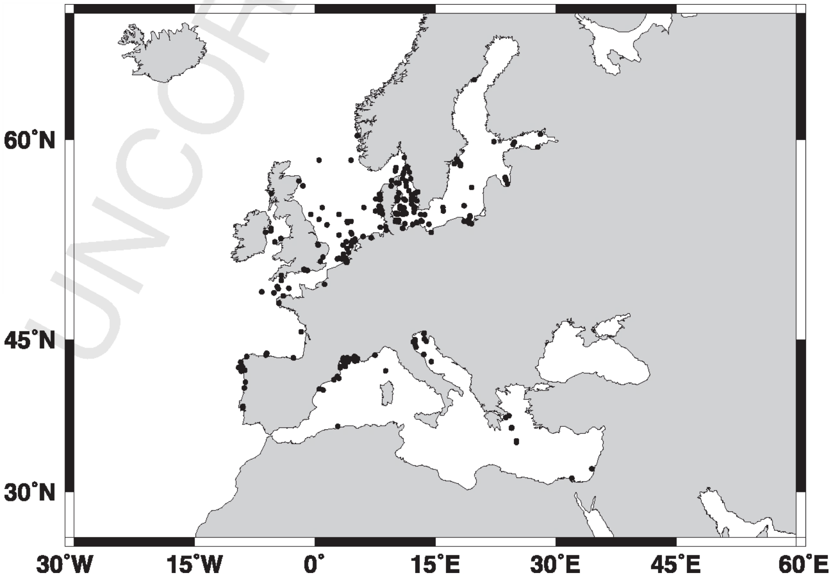

Fig. 7. Location of sites with one or more entry in the database.

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Table 7
Annual pelagic gross primary production (GPP) in European coastal regions

	Annual pelagic GPP (mmol C m^{-2} d^{-1})			Area (km^2)	Ref. no.
	Mean	SD	N		
Baltic Sea					
Sub-regions					
Kattegat/Belt Sea	37	14	55	42508	1–7
Baltic proper	43	13	15	211069	1, 8–15
Gulf of Finland	25	5	3	29600	16–18
Bothnian Sea	12	–	1	79256	14
Bothnian Bay	4	–	1	36260	14
River plumes				–	
Vistula plume	64	4	4	–	14, 19–21
Daugava plume	68	11	3	–	14, 22
Oder plume	96	–	1	–	14
Weighted average and total Baltic Sea region	31	–	83	398693	
European Atlantic and North Sea					
Sub-regions					
North Sea	48	13	28	454832	1, 23–30
English Channel	40	18	5	71175	31–34
Irish Sea	25	7	4	107051	35–38
Atlantic coast	60	12	5	594642	39–41
Upwelling					
Ría of Vigo	110	6	2	–	42, 43
Weighted average and total European Atlantic and North Sea regions	51	–	44	1227700	
Mediterranean Sea					
Sub-regions					
Western region	20	5	8	198163	44–51
Northern Adriatic Sea	48	–	1	72536	52
Eastern region	11	5	5	172871	53–57
River plumes					
Rhône river plume	160	70	2	–	58, 59
Po river plume	134	–	1	–	52
Coastal lagoons					
Gulf of Fos	150	–	1	–	60
Berre Lagoon	59	10	2	–	51, 61
Weighted average and total Mediterranean region	21	–	20	443570	
Weighted average and total European coastal zone	41		147	2069963	

The list of references is available at http://www.obs-vlfr.fr/~gattuso/ECSS_ref.htm.

2000; Wasmund et al., 2001). Therefore, the same values as Wasmund et al. (2001) were used for the Bothnian Sea (12 mmol C m^{-2} d^{-1}) and the Bothnian Bay (4 mmol C m^{-2} d^{-1}). The highest values of GPP were found in river plume areas. Due to their relative small surface area, these ecosystems will not be included in our estimation. Indeed, Wasmund et al. (2001) reported that a separate treatment of river plumes is not necessary for whole Baltic Sea primary production estimates. Pelagic GPP of the Kattegat and Belt Sea areas, based on 55 values, reaches 37 (±14) mmol C m^{-2} d^{-1}, a value slightly lower than the one used by Wasmund et al. (2001) which was based on only one reference (43 mmol C m^{-2} d^{-1}; Heilman et al., 1994). The mean GPP of the Baltic proper (15 values; 43±13 mmol C m^{-2} d^{-1}) is higher than that of the Kattegat and Belt Sea areas and consistent with the value used by Wasmund et al. (2001) in their global estimate, and with the estimate of Shaffer (1987). The mean value found for the Gulf of Finland, based on only 3 references, is about 25 (±5) mmol C m^{-2} d^{-1}. Our database does not include data from the Neva River plume entering the Gulf of Finland which was therefore excluded from our study. Considering the surface area and GPP values for each of these sub-regions, a weighted average of the whole Baltic Sea pelagic GPP of 31 mmol C m^{-2} d^{-1} is proposed. Wasmund et al. (2001) proposed a pelagic GPP of 34 mmol C m^{-2} d^{-1} for the whole Baltic Sea, based on their measurements between 1993 and 1997 in the south-eastern Baltic Sea as well as data from literature. The pelagic GPP values reported by Elmgren (1984) are also consistent with our estimate.

In the Atlantic/North Sea region, 44 values were found including 18 extracted from the MADS database. The lowest value was reported for western Scotland (16 mmol C m^{-2} d^{-1}; Wood et al., 1973) and the highest for Ría de Vigo, an upwelling area in north-western Spain (114 mmol C m^{-2} d^{-1}; Moncoiffé et al., 2000). This region was divided in 4 areas: North Sea, English Channel, Irish Sea and Atlantic coast. The North Sea is the most documented area in this region (28 measurements) but no data were found for the northern part; its mean GPP is 48 (±13) mmol C m^{-2} d^{-1} (Table 7). The mean GPP of the English Channel is about 40 (±18) mmol C m^{-2} d^{-1} (5 values). The Irish Sea is the least productive area in north-western Europe with a mean value of 25 (±7) mmol C m^{-2} d^{-1} based on four annual measurements. Upwelling areas should be considered separately but this is not possible at this stage because of the lack of data and also the unknown surface area covered by upwellings in European waters. Data from the Ría of Vigo were therefore excluded from the analysis in order to avoid a bias. The average annual value for the Atlantic coast is about 60 (±12) mmol C m^{-2} d^{-1}. A surface-weighted average pelagic GPP for the Atlantic/North Sea region of 51 mmol C m^{-2} d^{-1} was estimated. To the best of our knowledge, this is the first global estimate of pelagic GPP available for the region. In their review, Reid et al. (1990) estimated 40, 57 and 46 mmol C m^{-2} d^{-1}, respectively in the northern, central and southern North Sea. Also, Joint and Pomroy (1993) gave regional estimates based on the

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ICES sub-divisions of the North Sea, but their measurements (from 24 h incubations) were closer to NPP than GPP and thus, are not comparable with our estimate.

The Mediterranean Sea was divided into three basins: western (excluding the Rhône River plume), northern Adriatic Sea (excluding the Po River plume) and eastern basins. Pelagic GPP in the region is low, especially in the eastern basin which was characterized by Azov (1991) as a 'marine desert' resulting from phosphorus deficiency (Krom et al., 1991). The lowest value was found near the Israeli coast (4.3 mmol C m^{-2} d^{-1}; Berman and Townsend, 1984) and the highest in the Cretan Sea (18 mmol C m^{-2} d^{-1}; Psarra et al., 2000). The mean GPP for this area is based on 5 references and reaches a value of 11 (±5) mmol C m^{-2} d^{-1} (see Table 7). The northern Adriatic Sea is one of the most productive areas in the Mediterranean (Sournia, 1973), with a production rate of about 48 mmol C m^{-2} d^{-1}. It receives the discharge from the Po River and phosphorus recycling is supposed to be very fast, decreasing the phosphorus limitation in this part of the Mediterranean Sea (Ivancic and Degobbis, 1987). The plume of the Po River has a very high production rate (134 mmol C m^{-2} d^{-1}; Puddu et al., 1998). The north-western basin is the most documented in our database, with the lowest GPP reported along the Spanish coast (16 mmol C m^{-2} d^{-1}; Margalef and Ballester, 1967; San Feliu and Muñoz, 1970) and the highest in the Rhône dilution plume (205 mmol C m^{-2} d^{-1}; Lefèvre et al., 1997). In their recent review, Lefèvre et al. (1997) made an extensive compilation of available primary production data in the Gulf of Lions, dividing the coastal zone of this sub-region into three provinces based on hydrological features: (1) the Gulf of Marseille with a GPP of 20 mmol C m^{-2} d^{-1}, (2) the Rhône River plume with very high values (70–340 mmol C m^{-2} d^{-1}) and (3) the 'Rhône River dilution zone' with intermediate rates (26 mmol C m^{-2} d^{-1}). Furthermore, these authors reported no significant increase in GPP over the last 30 years, indicating that this part of the Mediterranean Sea is less influenced by catchment-based human activities than other coastal areas of Europe. The mean GPP (excluding the Rhône River plume) estimated from our database for this area is based on eight references and reaches a value of 20 (±5) mmol C m^{-2} d^{-1} (see Table 7). Coastal lagoons in this region exhibit higher production rates, i.e. 150 and 59 mmol C m^{-2} d^{-1} for the Gulf of Fos and the Berre lagoon, respectively (Minas, 1976; Kim, 1983; Barranguet et al., 1996), and considering their small area, are not considered in our global estimate. A wider study of the metabolic performance of coastal lagoons adjacent to the Mediterranean Sea is in progress using the LOICZ approach; see the LaguNet web site at http://www.dsa.unipr.it/lagunet/. The present version of the database does not include any data from the south-western basin. One data point was found (46 mmol C m^{-2} d^{-1}; Tellaï, 1969) but it was not included in the database because the original paper is not available to us and the data, obtained from a secondary source, could not be checked. Weighing these rates according to the surface areas represented by each sub-region, yielded a first estimation of pelagic GPP (21 mmol C m^{-2} d^{-1}) for the coastal Mediterranean Sea, confirming its oligotrophic status (Nixon, 1995).

Thus, a pelagic GPP in European coastal waters of about 41 mmol C m^{-2} d^{-1} was estimated (see Table 7 and Fig. 8A for frequency distribution). Smith and Hollibaugh (1993), Wollast (1998) and Gattuso et al. (1998) estimated the global GPP of continental shelves as 37, 46 and 49 mmol C m^{-2} d^{-1} respectively. Our estimate for European open coastal waters is consistent with these global estimates.

Most of the primary production values used in this review were estimated by the ^{14}C-tracer method and the difficulties for interpreting these data were discussed above. Moreover, almost all studies dealt only with particulate primary production. It is now well accepted that dissolved compounds released by phytoplankton can represent a significant portion of the produced organic matter. Indeed, Holligan (1989), Morán et al. (2002), Witek et al. (1999), and Larsson and Hagström (1982) reported dissolved primary production values of 10%, 16%, 5% and 14% of the total primary production in the North Sea, the north-western Mediterranean Sea, Gulf of Gdánsk and Baltic proper, while very high rates (up to 30%) were recorded in summer in the Gulf of Finland (Kuparinen, 1987). Dissolved production by phytoplankton on a global scale remains poorly known, but Morán et al. (2002) found a significant inverse relationship between PER (percent extracellular release) and total system productivity whereby there is higher PER in oligotrophic environments, confirming earlier results from Fogg (1983). Data on the relative contributions of dissolved and particulate production to GPP are too scarce to attempt an estimation of the importance of dissolved production in our value of GPP. However, our estimates clearly underestimate GPP, especially in low productivity waters, such as the eastern Mediterranean and Baltic Seas regions.

3.2.2. Microphytobenthic gross primary production

Fewer annual studies of benthic GPP in coastal areas of Europe were found in the literature compared with pelagic GPP. The database presently comprises 40 annual measurements (both in shallow and deep areas), but study sites are not well distributed within the region of interest. For instance, as already reported by Cahoon (1999), no data were found for the entire eastern Mediterranean Sea nor for the eastern Baltic Sea. Presumably these two regions have low GPP values due to light limitation in the eastern Baltic and nutrient limitation in the eastern Mediterranean Sea. Such lack of information

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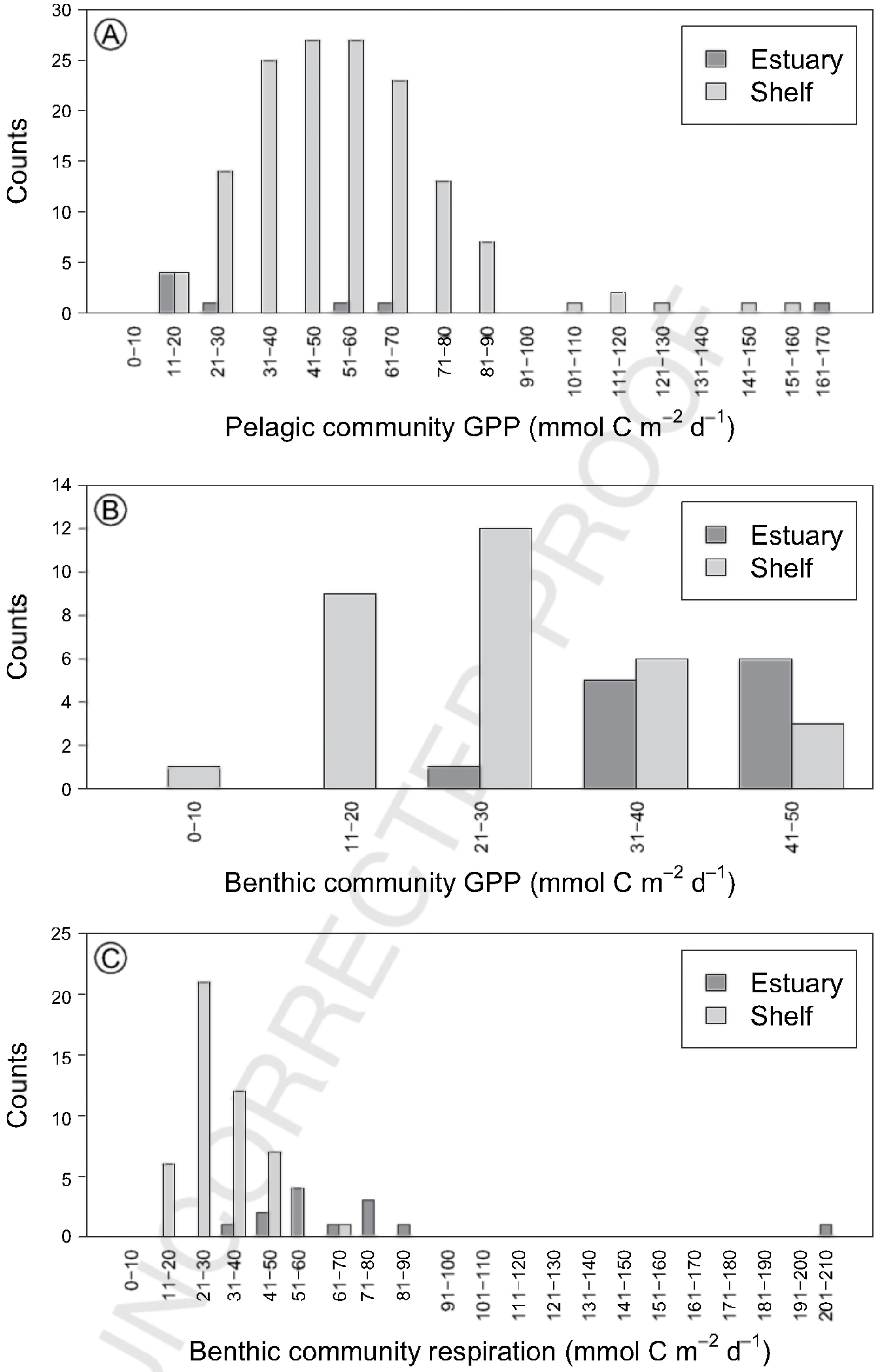

Fig. 8. Frequency distribution of (A) pelagic gross primary production, (B) benthic gross primary production, and (C) community respiration in estuaries (black bars) and open shelf systems (open bars).

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of course will negatively affect upscaling. In contrast with data on pelagic GPP, most of the studies are based on the oxygen method (70%).

Calculation of depth-integrated GPP requires either data across the depth range or information on the decrease of GPP as a function of depth, the deepest benthic production (6 mmol C m^{-2} d^{-1}) being measured in the Gulf of Trieste at a depth of 22 m (Herndl et al., 1989). However, very few studies have investigated the decrease of GPP with depth although benthic GPP is assumed to occur at depths greater than 20 m (Cahoon, 1999). Data for the three major regions show different

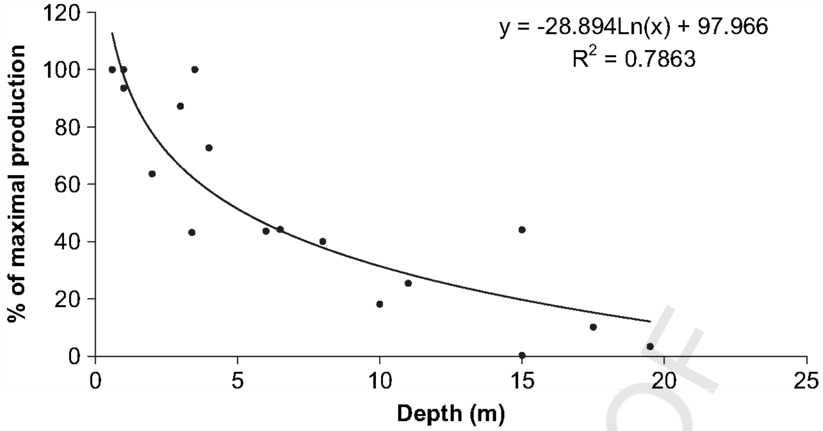

Fig. 9. Decrease with depth of microphytobenthic gross primary production (GPP) in the Baltic Sea, based on data from Gargas (1970), Sundbäck and Jönsson (1988), and Meyercordt and Meyer-Reil (1999).

depth ranges; 22 m in the Mediterranean Sea and 20 m in the Baltic Sea regions, but only 5 m in the Atlantic/North Sea region. In the latter and the Baltic Sea regions, the same function for decrease of benthic GPP with depth was used. Depth-integrated (0–200 m) GPP was calculated by the relationship between GPP (% of maximal value) and depth (see Fig. 9) derived in the Baltic Sea using data from Gargas (1970), Sundbäck and Jönsson (1988), and Meyercordt and Meyer-Reil (1999): $\%P_{max} = -28.894 \times LN\ (Depth) + 97.966$ ($r^2 = 0.7863$, $P < 0.01$, $n = 17$; LN is the natural logarithm).

In the Mediterranean Sea, where water column turbidity is lower, GPP was estimated at three depth ranges (0–5 m, 5–10 m and 10–30 m) from published data, and the depth-integrated GPP (0–200 m) was calculated assuming that GPP is 0 below 30 m.

Benthic GPP exhibits high geographical variations in the Baltic Sea, with no production found at 3.4 m in Kirr-Bucht, Darss-Zingst Bodden, southern Baltic Sea (Meyercordt and Meyer-Reil, 1999) and the highest value reported in Faellesstrand lagoon, Denmark (34 mmol C $m^{-2} d^{-1}$; Kristensen, 1993). Thus, the shallow (0–5 m) benthic production for this region (14±12 mmol C $m^{-2} d^{-1}$, Table 8) must be taken with caution. Averaged over the 0–20 m zone and weighted by the surface of the coastal areas with depths <20 m, the average microphytobenthic GPP of the Baltic Sea is about 2 mmol C $m^{-2} d^{-1}$ (Table 8), only 4% of the pelagic GPP. Our estimate is lower than that of Cahoon (1999) (4 mmol C $m^{-2} d^{-1}$) but similar to that of Elmgren (1984) (1.2 mmol C $m^{-2} d^{-1}$) for the whole Baltic Sea benthic compartment (including the macrophytobenthos).

The Atlantic/North Sea and Mediterranean regions are less documented than the Baltic Sea. Both regions exhibit low variation, with mean values of 22 (±5) mmol C $m^{-2} d^{-1}$ and 16 (±6) mmol C $m^{-2} d^{-1}$ in shallow areas of the Atlantic/North Sea and Mediterranean Sea regions (Table 8 and Fig. 8B for frequency distribution). Using the relationship described above, a microphytobenthic GPP in the Atlantic/North Sea of about 1 mmol C $m^{-2} d^{-1}$ (2% of the pelagic GPP) was estimated.

It must be stressed that few data are available for the Mediterranean Sea region and may not be representative of the whole area. The average benthic GPP in the Mediterranean Sea declines from 16 (±6) mmol C $m^{-2} d^{-1}$ in the depth range 0–5 m to 5 (±1) mmol C $m^{-2} d^{-1}$ at 10–30 m (Table 8). The depth-integrated benthic GPP is around 2.5 mmol C $m^{-2} d^{-1}$ in the Mediterranean Sea (13% of pelagic GPP), lower than the value estimated by Cahoon (1999) (4 mmol C $m^{-2} d^{-1}$). Cahoon (1999) and Charpy-Roubaud and

Table 8
Annual microphytobenthic gross primary production (GPP) in European coastal regions

	Annual microphytobenthic GPP (mmol C $m^{-2} d^{-1}$)			Area (km^2)	Ref. no.
	Mean	SD	N		
Baltic Sea					
0–5 m	14	12	17	61706	2, 13, 62–68
0–200 m	2	–	–	398693	
Atlantic/North Sea					
0–5 m	22	5	8	55750	27, 69–74
0–200 m	1	–	–	1227700	
Mediterranean Sea					
0–5 m	16	6	5	35632	60, 75, 76
5–10 m	11	9	2	16565	60, 77
10–30 m	5	1	3	71625	60, 77
0–200 m	2.5			443570	
Weighted average and total European coastal zone	1.5	–	–	2069963	

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Sournia (1990) reported mean values of benthic primary production for worldwide temperate shallow areas (all ecosystem types included) of around 20 mmol C m^{-2} d^{-1} and 23 mmol C m^{-2} d^{-1}, respectively. Our estimate (mean value for the 0–5 m depth range in European coastal waters: 17 mmol C m^{-2} d^{-1}) is slightly lower, and certainly due to our separate consideration of shelves and estuaries which present higher production values (see next section).

Finally, the average microphytobenthic GPP along European coastlines (0–200 m) is about 1.5 mmol C m^{-2} d^{-1} (Table 8; 3.6% of pelagic GPP), lower than values estimated for worldwide continental shelves by Cahoon (1999) for temperate regions and Charpy-Roubaud and Sournia (1990).

3.2.3. *Macrophytobenthic net primary production*

Macrophyte (seagrass and macroalgae) beds are expected to be very productive areas. Indeed, Charpy-Roubaud and Sournia (1990) reported NPP values in temperate regions from 100 to >450 mmol C m^{-2} d^{-1}, mainly from intertidal or shallow areas. They estimated a production value in the 0–50 m depth fringe of about 170 mmol C m^{-2} d^{-1} (vs. 11 mmol C m^{-2} d^{-1} for microphytobenthos), but their procedure for estimating the decrease in production with depth is not clear.

GPP by macrophytes was not uspscaled to the whole European coastal zone for three reasons: (i) very few annual studies were found in the literature for these areas (five to date), (ii) the distribution and production of macrophytes along the depth gradient is not resolved and (iii) the surface area covered by macrophytes in Europe is not yet estimated (Duarte, personal communication, 2003).

Also primary production by macrophytes seems to be relatively small in several European coastal systems. Wasmund (1986) estimated that micro- and macrophytobenthos contribute 7% of total NPP in shallow coastal lagoons of the Baltic Sea and Elmgren (1984) attributed 3% of total NPP to phytobenthos in the whole Baltic Sea. In the Wadden Sea (North Sea), where tidal flats represent approximately 50% of the surface area (Cadée and Hegeman, 1974), macroalgal production is negligible (Cadée, 1980).

The surface area potentially covered by the seagrass *Posidonia oceanica* in the Mediterranean Sea is about 0.035×10^6 km^2 (Pasqualini et al., 1998), or only 8% of the surface area of the Mediterranean coastal zone. This value is similar to that of Whittaker and Likens (1975) for the global distribution of macrophytes. The depth-integrated (0–200 m) NPP (leaves plus rhizomes) for *P. oceanica* is about 1 mmol C m^{-2} d^{-1} in the coastal Mediterranean Sea, based on data for 22 sites at three different depths (Pergent-Martini et al., 1994) and for the Bay of Calvi (Corsica) at 30 m (Bay, 1984) (see Table 9 for calculation details). It is difficult to compare this value to the total (pelagic+benthic) net primary production in the Mediterranean Sea region but, assuming that phytoplankton and microphytobenthos respiration (R) ranges between 5 and 50% of GPP, the contribution of *P. oceanica* to the total NPP was estimated to lie between 5 and 10%. This value contrasts strongly with the 40% of total NPP estimated for worldwide continental shelves (Charpy-Roubaud and Sournia, 1990).

Table 9
Annual net primary production by *Posidonia oceanica* (leaves plus rhizomes) in the Mediterranean coastal area based on values from Pergent-Martini et al. (1994) at 5, 10 and 20 m and Bay (1984) at 30 m

Depth range (m)	Measured depth (m)	Annual NPP (mmol C m^{-2} d^{-1})[a]	Area[b] (km^2)
0–7.5	5	73 (53–93)	3173
7.5–15	10	45 (35–55)	2340
15–25	20	20 (18–22)	2725
25–35	30	13.2[c]	2318
Weighted average and total Mediterranean Sea region	0–200	1	445883

[a] Assuming a dry weight carbon content of 40% (Mateo and Romero, 1997).

[b] Assuming that 8% of the Mediterranean coastline is covered by *P. oceanica* (Pasqualini et al., 1998).

[c] Leaf blades NPP was reported (12.4 mmol C m^{-2} d^{-1}). According to Pergent-Martini et al. (1994), rhizomes NPP represents 6.4% of leaf NPP.

3.2.4. *Pelagic community respiration*

Very few measurements of depth-integrated community respiration (CR) based on the oxygen incubation method, even in the euphotic zone, were found during our compilation of data. Moreover, in contrast to primary production, planktonic CR occurs throughout the water column (Williams, 1984), and it is therefore not possible to compare rates integrated over different depth ranges. Consequently, CR is shown in volumetric units in Table 10 (μmol C l^{-1} d^{-1}) when directly measured by the oxygen bottle method in the euphotic or aphotic zone (two references only for the latter). When only integrated values were reported, these were divided by the depth of the water column, assuming a constant rate over that depth range.

In the Baltic Sea, measurements of pelagic CR were made in the euphotic zone of the Gulf of Finland (Kuparinen, 1984; Kuparinen, 1987). These data, together with the GPP data discussed above, enable estimation of how much of GPP is remineralized in the upper water column. The euphotic CR represents 34% of the pelagic GPP integrated over the euphotic layer (10 m; GPP = 25 mmol C m^{-2} d^{-1}). Therefore, net community production (NCP = GPP–CR) in the euphotic zone is 66% of pelagic GPP. Furthermore, Kuparinen et al. (1984) speculated that pelagic CR in the aphotic zone

Table 10
Annual pelagic community respiration (CR) in European coastal regions

Region	Depth layer (m)	Annual pelagic CR (μmol C l^{-1} d^{-1})	Ref. no.
Baltic Sea			
Gulf of Finland	Euphotic (0–10 m)	0.9	16
Gulf of Finland	Euphotic (0–10 m)	0.8	17
Gulf of Gdánsk	Euphotic (0–7 m)	14.8	78
Gulf of Gdánsk	Euphotic (2.5 m)	11.2	79
Kattegat	Aphotic (15–30 m)	1.3	80
Kattegat	Aphotic (15–25 m)	2.2	4
Pomeranian Bay	Epipelagique (0–20 m)	4.3	15
Gulf of Gdánsk	Water column	2.7	19
Atlantic/North Sea			
North Sea	Euphotic (15 m)	2.6	81
North Sea	Water column (0–50 m)	2.4	82
Bay of Biscay	Euphotic (0–20 m)	1.8	41
Ría de Vigo	Euphotic (0–12 m)	4	42
Mediterranean Sea			
Bay of Blanes	Euphotic (15 m)	5.2	83
Bay of Calvi	Euphotic (0–15 m)	6.2	84
Gulf of Lions	Euphotic (0–60 m)	3.5	58

The list of references is available at http://www.obs-vlfr.fr/~gattuso/ECSS_ref.htm.

(>10 m) is 50% of the euphotic NCP (30% of pelagic GPP). Thus, the amount of organic matter remineralized in the whole water column is about 70% of pelagic GPP. This result is consistent with the one found by Elmgren (1984) who used data from sediment traps in the whole Baltic Sea to estimate organic matter utilization in the whole water column of about 60% of pelagic GPP. Rydberg et al. (1990) estimated CR rates in aphotic deep waters of the south-eastern Kattegat. Based on their results and pelagic GPP estimated for this region (36 mmol C m^{-2} d^{-1}), the amount of organic matter remineralized in the aphotic deep-water column is estimated to 30%. In the same area, using data from Granéli (1992), a somewhat higher value of 45% of pelagic GPP was found. Based on indirect methods in the Baltic proper, Shaffer (1987), Rahm (1987), and Pers and Rahm (2000) estimated organic matter mineralization in aphotic deep-waters below the S = 8 isohaline of 12, 11.5 and 10.5 mmol C m^{-2} d^{-1} (RQ = 1). This corresponds to about 25% of the pelagic GPP for this region and is consistent with the value found by Olesen and Lundsgaard (1995) in the Kattegat.

CR is much higher in the Gulf of Gdánsk (Witek et al., 1997; Witek et al., 1999; York et al., 2001) and the Pomeranian Bay (Witek et al., 2001), especially in surface waters. These systems receive high loads of organic matter from the Vistula and Oder rivers and CR integrated over the entire water column is higher than autochthonous production of organic matter over most of the year.

In the Atlantic/North Sea region, only four annual values were found, all measured in the euphotic zone. The lowest value was found in the Bay of Biscay (1.8 μmol C l^{-1} d^{-1}; Serret et al., 1999) and the highest value in the upwelling area of the Ría de Vigo (4 μmol C l^{-1} d^{-1}; Moncoiffé et al., 2000). CR data for the Mediterranean Sea region are high with the highest value reported for the Bay of Calvi (6.2 μmol C l^{-1} d^{-1}; Velimirov and Walenta-Simon, 1992). As these data were obtained in areas supporting relatively high rates of pelagic and benthic GPP, they may not be representative of the Mediterranean Sea region as a whole.

Measurements of pelagic CR in the European coastal zone are clearly too sparse to yield an accurate picture of the fate of organic matter produced in the water column. However, previous considerations of the Baltic Sea (excluding river plumes and mainly based on indirect methods) suggest that roughly 60% of pelagic GPP is consumed in the water column (30% in the euphotic and 30% in the aphotic zones). This is higher than previous estimates of coastal mineralization rates (Gattuso et al., 1998; Wollast, 1998) that indicate only 30% of the autochthonous production is consumed in the water column.

3.2.5. Benthic community respiration

The average benthic CR in the Atlantic/North Sea and Baltic Sea regions are 16 (±8, $n = 17$) and 17 mmol C m^{-2} d^{-1} (±8, $n = 20$; Table 11). Benthic CR rates from literature are not well distributed within regions, especially in the Baltic Sea where no data were found for the entire eastern Baltic Sea (Baltic proper, Gulf of Finland, Bothnian Sea and Bothnian Bay). Respiration rates are temperature-dependent but also controlled by the quality and quantity of organic matter available. Thus, lower rates should be found in these low productive regions, and our value of 17 mmol C m^{-2} d^{-1} may be slightly overestimated.

As with other metabolic parameters, few benthic CR measurements have been conducted in the Mediterranean Sea region (10 data points or sets were found), the most documented area being the northern Adriatic Sea (6 values) but no data were found for the most oligotrophic part (eastern basin). Thus, our estimates should be considered tentative and subject to uncertainty. The highest benthic CR rates were reported in coastal lagoons, Thau lagoon (31 mmol C m^{-2} d^{-1};

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Table 11
Annual benthic community respiration (CR) in European coastal regions

	Annual benthic CR (mmol C $m^{-2} d^{-1}$)			Area (km^2)	Ref. no.
	Mean	SD	N		
Baltic Sea	17	8	20	398693	4, 13, 19, 66–68, 80, 85–90
North Sea/Atlantic	16	8	17	1227700	28, 38, 87, 91–97
Mediterranean Sea	22	6	10	443570	60, 76, 77, 98–101
Weighted average and total European coastal zone	17			2069963	

The list of references is available at http://www.obs-vlfr.fr/~gattuso/ECSS_ref.htm.

Barranguet et al., 1994) in France and Saca di Goro (55 mmol C $m^{-2} d^{-1}$; Bartoli et al., 1996) in the northern Adriatic Sea. The benthic CR for the entire Mediterranean Sea region weighted according to surface area is 22 mmol C $m^{-2} d^{-1}$. The weighted average of the three regions provides a benthic CR value of 17 mmol C $m^{-2} d^{-1}$ for shelf areas in Europe (see also Fig. 8C for frequency distribution).

Based on a global benthic CR dataset, Middelburg et al. (in press) proposed a similar value for global coastal benthic CR (17 mmol C $m^{-2} d^{-1}$). Wollast (1998) and Gattuso et al. (1998) reported benthic mineralization of about 30% of pelagic GPP. The benthic CR rate estimated in our study represents 40% of the estimated pelagic GPP (41 mmol C $m^{-2} d^{-1}$). It should be noted that almost all the compiled data were collected in shallow areas where available organic matter and the rate of mineralization are probably higher. Since the ratio benthic:pelagic mineralization decreases with increasing depth (Jørgensen, 1983; Heip et al., 1995), a significant overestimation might be expected. On the other hand, several studies showed that the oxygen method can strongly underestimate total carbon mineralization rates in low oxygen environments because reduced metabolites cannot be completely reoxidized. For instance, Jørgensen (1982) estimated that sulfide burial resulting from net sulfate reduction can represent 10% of carbon mineralization. Overall, our estimate that benthic CR is 40% of pelagic GPP is the best present estimate of benthic mineralization in European coastal areas.

3.3. Estuaries

Estuaries are the main transition zone between the freshwater of the land and the salt water of the oceans (Heip et al., 1995). Receiving high amounts of nutrient, organic matter and suspended particles, estuaries are extremely dynamic systems usually characterized by strong physico-chemical gradients, enhanced biological activity, and intense sedimentation and resuspension (Ketchum, 1983). Our database contains metabolic values from 29 papers in which benthic measurements (GPP and CR) represent almost 70% of available annual values. One of the striking outcomes (Table 12 and Fig. 8) is the strong variability in pelagic GPP compared to intertidal or shallow benthic GPP. Pelagic values range from 1.7 (Ems-Dollard estuary; Van Es, 1977) to 153.3 mmol C $m^{-2} d^{-1}$ in the highly productive Urdaibaï estuary (Revilla et al., 2002). The smaller range of benthic GPP extends from 22.3 mmol C $m^{-2} d^{-1}$ in the Colne River estuary (Thornton et al., 2002) to 37.8 mmol C $m^{-2} d^{-1}$ in the western Scheldt estuary (Barranguet et al., 1998). The average benthic GPP of 31 (±5) mmol C $m^{-2} d^{-1}$ is almost twice the benthic GPP estimated in intertidal or shallow open shelf areas (see previous section). This supports our approach of investigating and synthesizing separately the open shelves and

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Table 12
Annual community metabolism rates in European estuaries (mmol C $m^{-2} d^{-1}$)

Site	Pelagic GPP	Benthic GPP	Pelagic CR	Benthic CR	Ref. no.
Western Scheldt	40.4	–	–	–	102
Western Scheldt	–	31	–	–	103
Western Scheldt	52.7	–	–	–	104
Western Scheldt	–	37.8	–	–	105
Western Scheldt	–	–	–	194.2	106
Eastern Scheldt	75.7	–	–	–	107
Eastern Scheldt	–	35.6	–	–	108
Ems-Dollard	1.7	26.7	20.8	44.7	109
Ems-Dollard	–	36	–	40.5	110
Ems-Dollard	–	22.6	–	–	111
Ems-Dollard	3	–	–	–	69
Ems-Dollard	–	36.4	–	47.5	112
Norsminde Fjord	–	–	–	40.1	113
Norsminde Fjord	–	–	–	52	114
Limforden	–	–	–	34	115
Bristol Channel	17	–	–	–	116
Ythan	–	26.5	–	–	117
Lynher	18.5	32.6	–	–	118
Thames	–	–	–	64	119
Colne	–	22.3	–	65.1	120
Colne	2	–	–	–	121
Southampton water	40.4	–	–	–	34
Great Ouse	–	–	–	79.5	122
Great Ouse (Upper)	–	–	–	64	123
Urdaibai	153.3	–	84.4	–	124
Douro	–	30	–	26.4	125
Tagus	–	35.6	–	–	126
Tagus	–	–	–	37.5	127
Elbe	–	26.4	–	–	128
Mean (SD)	40 (47)	31 (5)	53 (45)	61 (43)	
n	10	13	2	13	

The list of references is available at http://www.obs-vlfr.fr/~gattuso/ECSS_ref.htm.

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estuaries values. Moreover, the high values and the small variation in benthic GPP between estuaries suggest that most of the systems studied were eutrophic and not nutrient limited. It is noteworthy that all measurements were made on intertidal or very shallow sediments where there was little or no light limitation. Extrapolating these rates over the whole surface area of each estuary will lead to a much greater variation in values, reflecting differences in geomorphology (e.g. relative surface area of shallow and deep water) and light availability at the seafloor. This also suggests that GPP in the pelagic compartment of estuaries is mainly driven by physical parameters such as residence time, turbidity and vertical stratification rather than by nutrient concentrations (Boynton et al., 1982; Heip et al., 1995). Moreover, the production of organic matter by chemoautotrophic bacteria such as nitrifiers, which are reported to be very active in eutrophic estuaries (Heip et al., 1995), was not taken into account. van Spaendonk et al. (1993) estimated primary production by these organisms as 32% of the total primary production in the inner Scheldt estuary. The importance of this process generally decreased seaward, becoming negligible relative to phytoplankton production (Heip et al., 1995).

With only two references of depth-integrated pelagic CR (Van Es, 1977; Revilla et al., 2002), it is difficult to provide any conclusion about its magnitude in European estuaries. In contrast to benthic GPP, benthic CR exhibits large variability between sites with minimal values in estuaries of the Portuguese coast (Cabrita and Brotas, 2000; Magalhães et al., 2002) and a very high mean annual rate in the Scheldt estuary (Middelburg et al., 1996). Intermediate values (60–80 mmol C $m^{-2} d^{-1}$) were found in estuaries along the English coast (Colne, Great Ouse and Thames rivers). The average benthic CR in estuaries (61 ± 43 mmol C $m^{-2} d^{-1}$) is much higher than that on open shelves (17 mmol C $m^{-2} d^{-1}$, see previous section). Almost all the benthic CR data were measured in intertidal or very shallow areas. Benthic CR should decrease with increasing depth because of the absence of microphytobenthos and a decrease in available organic matter due to decomposition in the water column.

3.4. Metabolic balance

In this section, the metabolic balance (NCP) in both the pelagic and benthic compartments of open shelf areas and estuaries is examined, and 19 papers reporting such data in the European coastal zone were found. GPP is plotted as a function of CR in Figure 10. The data points above the 1:1 line are autotrophic with respect to carbon, whereas, those below that line are heterotrophic. Pelagic metabolic values for both open shelves and estuaries were integrated over the entire euphotic zone or the water column, if the depth was less than the euphotic zone. The database contains nine values of annual pelagic NCP for open shelf areas. Three sites had a heterotrophic euphotic zone, with minimal NCP in the Gulf of Gdánsk (−37 mmol C $m^{-2} d^{-1}$; Witek et al., 1999). The most productive area is the upwelling in the Ría de Vigo with a NCP of 65 mmol C $m^{-2} d^{-1}$. Large variations in the GPP/CR ratio in European shelves (1.5 ± 0.9) prevent any meaningful upscaling. Moreover, the pelagic GPP/CR ratio is certainly lower as this estimate only addresses the euphotic zone.

Only two studies of the metabolic balance in pelagic compartment of estuaries were found in the literature. The water column of the Urdaibaï estuary is autotrophic on an annual basis with a NCP of nearly 70 mmol C $m^{-2} d^{-1}$ (Revilla et al., 2002) while Van Es (1977) reported a value of −20 mmol C $m^{-2} d^{-1}$ in the Ems-Dollard estuary. This is clearly insufficient data from which to draw conclusions about the metabolic balance in European estuaries.

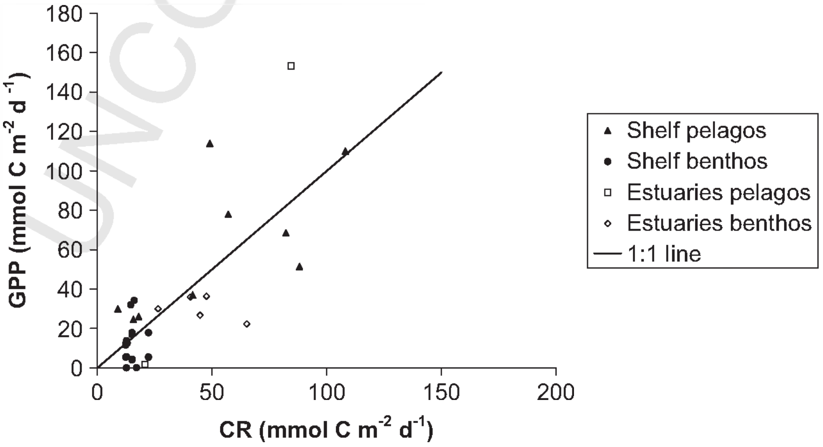

Fig. 10. Community gross primary production (GPP) as a function of community respiration (CR) in the benthos and pelagos of European estuaries and shelf environments.

A strong variation is also observed in the benthic compartment of shallow (0–5 m) European coastal areas (GPP/CR = 0.8 ± 0.7) with a minimal NCP reported in Kirr-Bucht (Darss-Zingst Bodden), a coastal lagoon of the south-western Baltic Sea (−17 mmol C $m^{-2} d^{-1}$; Meyercordt et al., 1999), and a maximal value in the west coast of Sweden (18 mmol C $m^{-2} d^{-1}$; Sundbäck and Miles, 2000).

Based on our global estimations of benthic GPP and CR over the 0–200 m depth range, benthic NCP is −15 mmol C $m^{-2} d^{-1}$ in the Baltic Sea and Atlantic/North Sea regions and −19.5 mmol C $m^{-2} d^{-1}$ in the Mediterranean Sea. These values must be considered as preliminary, considering the uncertainty in the estimation of both benthic GPP and CR due to the relatively poor spatial distribution especially in the Mediterranean Sea. Only one estuarine benthic area was found to be net autotrophic (Douro river estuary; Magalhães et al., 2002) while all the other sites were heterotrophic, with a minimal NCP value (−43 mmol C $m^{-2} d^{-1}$) measured in the Colne River estuary (Thornton et al., 2002). The benthic compartment in estuaries seems therefore to be heterotrophic even at shallow depths. Using the average benthic GPP and CR in estuarine shallow areas, a benthic NCP of −17 mmol C $m^{-2} d^{-1}$ is calculated. It must be stressed that this estimate, similar to that found in Baltic Sea and Atlantic/North Sea open shelves, only concerns shallow depths (< 5 m) and, then, cannot be extrapolated to the whole surface area of estuaries, due to the site-specific variation of both GPP and CR with depth. Another approach to assessing the metabolism of coastal ecosystems was developed through budgeting methods (Gordon et al., 1996). These budgets estimate net ecosystem production (NEP, expressed as *p-r* in the LOICZ terminology) and the balance between nitrogen fixation and nitrogen loss through denitrification (nfix-ndenit) from the non-conservative flux of nitrogen and phosphorus in a system. This procedure implies that the changes in dissolved inorganic phosphorus in a system depends on exchange processes with adjacent systems and on the difference between consumption by primary production and release by mineralization processes (NEP) assuming an elemental particulate organic matter C:P ratio. This procedure might be biased when applied in very turbid areas, where physico-chemical adsorption/desorption of phosphorus on or from particles is supposed to occur (Froelich, 1988).

The NEP data derived by the LOICZ method for European sites are summarized in Table 13 and show that most of sites are balanced, with net metabolism around zero. Three of the sites that depart from a balanced status are included in our database and offer the opportunity to determine consistency: the Ría of Vigo, the Gulf of Lions and the Gulf of Gdánsk. No direct measurement of ecosystem metabolism in these areas is available for comparison, although pelagic GPP and CR values reported by Lefèvre et al. (1997) and Moncoiffé et al. (2000) in the euphotic zone of the Gulf of Lions and the Ría of Vigo suggest an autotrophic status for these areas, in agreement with the LOICZ estimate. However, Witek et al. (1997) showed that pelagic CR exceeded depth-averaged pelagic GPP in the Gulf of Gdánsk in 1993, which is counter to the NEP estimated by the LOICZ method for the same period. It was estimated above (Section 3.2.4) that the pelagic CR in the Baltic Sea represents approximately 60% of pelagic GPP. Assuming that benthic CR is 40% of pelagic GPP, NEP should be about 0 in this area, an estimate that is consistent with that obtained with the LOICZ method.

Table 13
Net ecosystem production of the ‘preferred’ LOICZ budget sites in Europe

Location	NEP (mmol C $m^{-2} d^{-1}$)
Baltic Sea	
Baltic Proper	0.2
Belt Sea	0.0
Bothnian Bay	0.0
Bothnian Sea	0.0
Curonian lagoon	−1.4
Luleälven estuary	−10
Gulf of Gdánsk	17.4
Gulf of Riga	0.6
Szczecin lagoon	6.3
Baltic global	0.5
Kattegat	3.5
Atlantic/North Sea	
Southern North Sea	0.9
Irish Sea	1.9
Ría of Vigo	12.8
Lough Hyne	3.4
Solent estuary	10.7
Mediterranean Sea	
Sacca di Goro lagoon	−16
Valli di Comacchio	0
Gulf of Lions	16
Inner Thermaikos Gulf	5
Black Sea	
Malii Adzalik	19
Dnieper-Bug	−21
Dniester	11
Donuzlav	0.4

Downloaded from the LOICZ environmental database on 29 April, 2003: (http://hercules.kgs.ukans.edu/hexacoral/envirodata/main.htm).

3.5. Coastal ecosystems and the eutrophication problem

Eutrophication refers to an increase in the rate of supply of organic matter to an ecosystem, which most commonly is related to nutrient enrichment enhancing primary production (Nixon, 1995). Several papers recently reported such phenomena in European coastal

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areas. For example, inputs of nutrients to the Baltic Sea have drastically increased since the 1940s due to changes in land use, excessive use of fertilizers in agriculture, loss of wetlands, sewage outlets and emissions of nitrogen from fossil fuel burning (Larsson et al., 1985; Kautsky and Kautsky, 2000). This was also demonstrated in the North Sea (Cadée and Hegeman, 2002) although a recent decrease of nutrient loads in these areas was observed in the 1990s (Ducrotoy et al., 2000; HELCOM, 2002). The effect of these increases is a general enhancement of pelagic GPP in the Baltic (Renk et al., 1988; Richardson and Heilmann, 1995; Kaczmarek et al., 1997; Wasmund et al., 2001) and North Seas (Ducrotoy et al., 2000; Cadée and Hegeman, 2002), and intertidal microphytobenthos production increased in the Wadden Sea (Cadée, 1984). This enhanced phytoplankton production has several consequences: (1) increased water turbidity in several areas (Sandén and Hakansson, 1996; Cadée and Hegeman, 2002) decreasing light availability for benthic producers, and (2) higher sedimentation and respiration rates in deep waters leading to anoxic conditions in several places (Ducrotoy et al., 2000; Kautsky and Kautsky, 2000). Eutrophication in coastal areas has also resulted in changes in the macroalgal community, reduced biodiversity and appearance of toxic blooms (Kautsky et al., 1992; Ducrotoy, 1999; Ærtebjerg et al., 2001). In the Mediterranean Sea, Ærtebjerg et al. (2001) reported a general increase of nitrogen and phosphorus loading from rivers, although only one long-term pelagic GPP study was found in the literature which concluded that no systematic eutrophication in the Gulf of Lions due to the Rhône River outflow was evident over the last 30 years (Lefèvre et al., 1997).

4. Conclusion

Upscaling is the process of functional generalization of data at small spatial scale (well-studied sites) to a much larger area. It has two prerequisites: (1) a classification of the area under consideration (the EU coastal zone) and (2) a relatively unbiased database of parameters (in our case, primary production and respiration) collected at study sites which are well characterized with respect to the available typology. Once this information is available, the data obtained in each category of the typology may be upscaled using a bottom-up approach: the property measured at a small scale is multiplied by the surface area of the relevant category of the typology.

This approach has both inherent limitations and limitations which are specific to its application to coastal areas. The most critical limitation is the lack of a typology for the coastal zone of the EU or for the global CZ. This goal is being actively pursued at a global scale by LOICZ using its global environmental database and a classification tool (LOICZView; Maxwell and Buddemeier, 2002). Perhaps the major obstacle which, so far, has constrained development of a global functional typology is the lack of global datasets geo-referenced at a scale of 0.5° or less that describe biotic variables, such as the percent cover of submerged macrophytes or marine sediments. For example, the surface area of the EU coastal zone covered by, say, lagoons or macrophytes is unknown. Similarly, the proportion of vegetated vs. non-vegetated marine sediments is unknown.

Also, the community composition of the study sites cannot be considered as homogeneous both in space and time. Rather, they are mosaics of various communities, sometimes changing with time, each with distinct metabolic properties. For example, should a coastal lagoon harbouring extensive seagrass beds be classified into the lagoon or macrophytes-dominated category.

The diversity of habitats and communities in the coastal zone is very high. The classification used here, and in other recent reviews (Gattuso et al., 1998; Middelburg et al., in press), does have a functional basis but it is sometimes too simplistic. For example, all estuaries are grouped in a single category despite having attributes, such as turbidity and residence time, that can exhibit very large differences and result in distinct metabolic properties.

This first assessment of ecosystem metabolism in the European coastal zone enables identification of geographical areas and processes which are well- or poorly-documented. Indeed, much more data were found for the Baltic Sea and Atlantic/North Sea regions than for the Mediterranean Sea region. Moreover, available data are not evenly distributed within each region. For instance, relatively few information was found for the eastern parts of the Baltic and Mediterranean Seas and the northern North Sea.

Pelagic GPP on open shelves is, by far, the most documented parameter in our database. Problems related to the use of the ^{14}C-tracer method (net vs. gross, particulate vs. dissolved), which is the most used method to measure pelagic GPP were already discussed. Then, due to these methodological problems and to a non-perfect spatial coverage, our global estimate (41 mmol C $m^{-2} d^{-1}$) for the European coastal zone contains some uncertainties. Anyway, this value is believed to be the most robust estimate of our study. While microphytobenthic GPP is often believed to be an important metabolic process in coastal areas, a production averaged over the entire 0–200 m depth range of $<4\%$ of pelagic GPP (1.5 mmol C $m^{-2} d^{-1}$) is calculated. However, our procedure for estimating the decrease of production with depth is not ideal, especially in the Atlantic Ocean and the North Sea sub-regions, and adds more to the uncertainty in these first regional estimates than the limited geographical coverage of data. More

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relevant data are urgently needed to allow a better evaluation of benthic GPP on a global scale.

Macrophytes were not included in our study, mainly because of their unknown distribution along European coastlines. While Charpy-Roubaud and Sournia (1990) attributed 40% of total shelf production to macrophytobenthos, an estimate cannot be provided at this stage. However, many studies in European coastal areas suggest that this value is too high and cannot be applied to European shelves. As for benthic GPP, our estimation of open shelves benthic CR (17 mmol C $m^{-2} d^{-1}$) suffers from some uncertainties due to the insufficient geographical coverage, especially in the eastern Mediterranean and Baltic Seas regions and to the lack of data at depths greater than 100 m. Although this estimate is consistent with a previous one (Middelburg et al., in press), our value is believed to be slightly overestimated. Pelagic CR is clearly the least-documented metabolic process in our database, especially in the aphotic zone. Such data are required to have a better understanding of pelagic remineralization.

While benthic GPP in estuaries was found to be relatively constant between sites (mean value, 31 mmol C $m^{-2} d^{-1}$), pelagic GPP and benthic CR exhibited strong spatial variability. Moreover, as for open shelves, very few pelagic CR measurements were found in the literature.

Considering these various uncertainties, it is clearly not possible at this stage to upscale the available data and to obtain a meaningful metabolic balance estimate for the EU coastal zone.

5. Uncited reference

Soluri and Woodson, 1990.

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References

Alongi, D.M., 1998. Coastal Ecosystem Processes. CRC Press, Boca Raton, FL.

Azov, Y., 1991. Eastern Mediterranean – A marine desert? Marine Pollution Bulletin 23, 225–232.

Barranguet, C., Alliot, E., Plante-Cuny, M.R., 1994. Benthic microphytic activity at two Mediterranean shellfish cultivation sites with reference to benthic fluxes. Oceanologica Acta 17 (2), 211–221.

Barranguet, C., Plante-Cuny, M.R., Alivon, E., 1996. Microphytobenthos production in the Gulf of Fos, French Mediterranean coast. Hydrobiologia 333 (3), 181–193.

Barranguet, C., Kromkamp, J., Peene, J., 1998. Factors controlling primary production and photosynthetic characteristics of intertidal microphytobenthos. Marine Ecology Progress Series 173, 117–126.

Bartoli, M., Cattadori, M., Giordani, G., Viaroli, P., 1996. Benthic oxygen respiration, ammonium and phosphorus regeneration in surficial sediments of the Sacca di Goro (northern Italy) and two French coastal lagoons: A comparative study. Hydrobiologia 329 (1–3), 143–159.

Bay, D., 1984. A field study of the growth dynamics and productivity of *Posidonia oceanica* (L.) Delile in Calvi Bay, Corsica. Aquatic Botany 20 (1-2), 43–64.

Berman, T., Townsend, D., El Sayed, S.Z., Trees, C.C., Azov, Y., 1984. Optical transparency, chlorophyll and primary productivity in the Eastern Mediterranean near the Israeli coast. Oceanologica Acta 7 (3), 367–372.

Boynton, W.R., Kemp, W.M., Keefe, C.W., 1982. A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. In: Kennedy, V.S. (Ed.), Estuarine Comparisons. Academic Press, New York, pp. 69–90.

Cabrita, M.T., Brotas, V., 2000. Seasonal variation in denitrification and dissolved nitrogen fluxes in intertidal sediments of the Tagus Estuary, Portugal. Marine Ecology Progress Series 202, 51–65.

Cadée, G.C., Hegeman, J., 1974. Primary production of the benthic microflora living on tidal flats in the Dutch Wadden Sea. Netherlands Journal of Sea Research 8 (2), 260–291.

Cadée, G.C., 1980. Reappraisal of the production and import of organic carbon in the western Wadden Sea. Netherlands Journal of Sea Research 14 (3-4), 305–322.

Cadée, G.C., 1984. Has input of organic matter into the western part of the Dutch Wadden Sea increased during the last decade? Netherlands Institute of Sea Research Bubl. Series 10, 71–82.

Cadée, G.C., Hegeman, J., 2002. Phytoplankton in the Marsdiep at the end of the 20th century: 30 years monitoring biomass, primary production, and Phaeocystis blooms. Journal of Sea Research 48 (2), 97–110.

Cadée, N., Dronkers, J., Heip, C., Martin, J.-M., Nolan, C., 1994. ELOISE (European Land-Ocean Interaction Studies) Science Plan. Office for Official Publications of the European Communities, Luxembourg.

Cahoon, L.B., 1999. The role of benthic microalgae in neritic ecosystems. In: Ansell, A.D., Gibson, R.N., Barnes, M. (Eds.), Oceanography and Marine Biology: an Annual Review. Routledge, London.

Cebrián, J., 2002. Variability and control of carbon consumption, export, and accumulation in marine communities. Limnology and Oceanography 47 (1), 11–22.

Charpy-Roubaud, C., Sournia, A., 1990. The comparative estimation of phytoplanktonic, microphytobenthic and macrophytobenthic

UNCORRECTED PROOF

primary production in the oceans. Marine Microbial Food Webs 4 (1), 31–57.

Dai, A.G., Trenberth, K.E., 2002. Estimates of freshwater discharge from continents: Latitudinal and seasonal variations. Journal of Hydrometeorology 3 (6), 660–687.

Ducrotoy, J.-P., 1999. Indications of change in the marine flora of the North Sea in the 1990s. Marine Pollution Bulletin 38, 647–654.

Ducrotoy, J.-P., Elliott, M., De Jonge, V.N., 2000. The North Sea. Marine Pollution Bulletin 41 (1–6), 5–23.

Elmgren, R., 1984. Trophic dynamics in the enclosed, brackish Baltic Sea. Rapports et Procès-verbaux des Reunions, Conseil International pour l'Exploration de la Mer 183, 152–169.

Fogg, G.E., 1983. The ecological significance of extracellular products of phytoplankton photosynthesis. Botanica Marina 26, 3–14.

Frankignoulle, M., Abril, G., Borges, A., Bourge, I., Canon, C., DeLille, B., Libert, E., Théate, J.-M., 1998. Carbon dioxide emission from European estuaries. Science 282, 434–436.

Frankignoulle, M., Borges, A.V., 2001. European continental shelf as a significant sink for atmospheric carbon dioxide. Global Biogeochemical Cycles 15 (3), 569–576.

Froelich, P.N., 1988. Kinetic control of dissolved phosphate in natural rivers and estuaries: A primer on the phosphate buffer mechanism. Limnology and Oceanography 33 (4 pt 2), 649–668.

Gargas, E., 1970. Measurements of primary production, dark fixation and vertical distribution of the microbenthic algae in the Oresund. Ophelia 8, 231–253.

Gattuso, J.-P., Frankignoulle, M., Wollast, R., 1998. Carbon and carbonate metabolism in coastal aquatic ecosystems. Annual Review of Ecology and Systematics 29, 405–434.

Gordon, D.C.J., Boudreau, P.R., Mann, K.H., Ong, J.-E., Silvert, W.L., Smith, S.V., Wattayakorn, G., Wulff, F., Yanagi, T., 1996. LOICZ biogeochemical modelling guidelines. LOICZ Reports and Studies 5, 1–96.

Granéli, W., 1992. Below-halocline oxygen consumption in the Kattegat. Hydrobiologia 235–236, 303–310.

Gronvall, H., Seina, A., 1999. Towards optimal sea-ice monitoring in the Baltic Sea. ICES Journal of Marine Science 56 (Suppl. S), 165–171.

Hansen, M.C., DeFries, R.S., Townshend, J.R.G., Sohlberg, R., 2000. Global land cover classification at 1km spatial resolution using a classification tree approach. International Journal of Remote Sensing 21, 1331–1364.

Hedges, J.I., Baldock, J.A., Gelinas, Y., Lee, C., Peterson, M.L., Wakeham, S.G., 2002. The biochemical and elemental compositions of marine plankton: a NMR perspective. Marine Chemistry 78 (1), 47–63.

Heilman, J.P., Richardson, K., Aertebjerg, G., 1994. Annual distribution and activity of phytoplankton in the Skagerrak/Kattegat frontal region. Marine Ecology Progress Series 112, 213–223.

Heip, C.H.R., Goosen, N.K., Herman, P.M.J., Kromkamp, J., Middelburg, J.J., Soetaert, K., Ansell, A.D., Gibson, R.N., Barnes, M., 1995. Production and consumption of biological particles in temperate tidal estuaries. In: Ansell, A.D., Gibson, R.N., Barnes, M. (Eds.), Oceanography and Marine Biology: an Annual Review. Routledge, London, pp. 1–149.

HELCOM, 1996. Third periodic assessment of the state of the marine environment of the Baltic Sea, 1989–1993; background document. Baltic Sea Environment Proceedings 64, 1–252.

HELCOM, 2002. Environment of the Baltic Sea area, 1994–1998. Baltic Sea Environment Proceedings 82, 1–23.

Herndl, G.J., Peduzzi, P., Fanuko, N., 1989. Benthic community metabolism and microbial dynamics in the Gulf of Trieste (northern Adriatic Sea). Marine Ecology Progress Series 53 (2), 169–178.

Holligan, P.M., 1989. Primary productivity in the shelf areas of North-West Europe. Advances in Botanical Research 16, 193–252.

Ivancic, I., Degobbis, D., 1987. Mechanisms of production and fate of organic phosphorus in the Northern Adriatic Sea. Marine Biology 94, 117–125.

Joint, I., Pomroy, A., 1993. Phytoplankton biomass and production in the southern North Sea. Marine Ecology Progress Series 99, 169–182.

Jørgensen, B.B., 1982. Mineralization of organic matter in the sea bed: Role of sulfate reduction. Nature 296, 643–645.

Jørgensen, B.B., 1983. Processes at the sediment–water interface. In: Bolin, B., Cook, R.B. (Eds.), The Major Biochemical Cycles and their Interactions. Wiley, Chichester, pp. 477–509.

Kaczmarek, S., Koblentz-Mishke, O., Ochocki, S., Nakonieczny, J., Renk, H., 1997. Primary production in the eastern and southern Baltic Sea. Oceanologia 39 (2), 117–135.

Kautsky, H., Kautsky, L., Kautsky, N., Kautsky, U., Lindblad, C., 1992. Studies on the Fucus vesiculosus community in the Baltic Sea. Acta Phytogeographica Suecica 78, 33–48.

Kautsky, L., Kautsky, N., 2000. The Baltic Sea, including Bothnian Sea and Bothnian Bay. In: Sheppard, C. (Ed.), Seas at the Millenium: An Environmental Evaluation. Elsevier, Amsterdam.

Kennett, J.P., 1982. Marine Geology. Prentice-Hall, Englewood Cliffs, NJ.

Ketchum, B.H., 1983. Estuarine characteristics. In: Ketchum, B.H. (Ed.), Estuaries and Enclosed Seas. Elsevier, Amsterdam, pp. 1–14.

Kim, K.T., 1983. Primary pelagic production of the Etang de Berre in 1977–1978. Comparison with the marine environment (North-west Mediterranean). Marine Biology 73 (3), 325–341.

Kristensen, E., 1993. Seasonal variations in benthic community metabolism and nitrogen dynamics in a shallow, organic-poor danish lagoon. Estuarine, Coastal and Shelf Science 36 (6), 565–586.

Krom, M.D., Kress, N., Brenner, S., 1991. Phosphorus limitation of primary productivity in the eastern Mediterranean Sea. Limnology and Oceanography 36 (3), 424–432.

Kuparinen, J., 1984. Annual and seasonal fluctuation of primary productivity and overall respiration in a pelagic plankton community off Tvärminne, SW coast of Finland. Ophelia 3 (Suppl.), 11–121.

Kuparinen, J., Leppänen, J.-M., Sarvala, J., Sundberg, A., Virtanen, A., 1984. Production and utilisation of organic matter in a baltic ecosystem off Tvärminne, southwest coast of Finland. Rapports et Procès-verbaux des Reunions, Conseil International pour l'Exploration de la Mer 183, 180–192.

Kuparinen, J., 1987. Production and respiration of overall plankton and ultraplankton communities at the entrance to the Gulf of Finland in the Baltic Sea. Marine Biology 93 (4), 591–607.

Langdon, C., Broecker, W.S., Hammond, D.E., Glenn, E., Fitzsimmons, K., Nelson, N.G., Peng, T.-H., Hajdas, I., Bonani, G., 2003. Effect of elevated CO_2 on the community metabolism of an experimental coral reef. Global Biogeochemical Cycles 17, art.1011.

Larsson, U., Hagström, A., 1982. Fractionated phytoplankton primary production, exudate release and bacterial production in a Baltic eutrophication gradient. Marine Biology 67, 57–70.

Larsson, U., Elmgren, R., Wulff, F., 1985. Eutrophication and the Baltic Sea: Causes and consequences. Ambio 14 (1), 9–14.

Lefèvre, D., Minas, H.J., Minas, M., Robinson, C., Williams, P.J.L.B., 1997. Review of gross community production, primary production, net community production and dark community respiration in the Gulf of Lions. Deep Sea Research Part II 44 (3–4), 801–832.

Magalhães, C.M., Bordalo, A.A., Wiebe, W.J., 2002. Temporal and spatial patterns of intertidal sediment-water nutrient and oxygen fluxes in the Douro River estuary, Portugal. Marine Ecology Progress Series 233, 55–71.

Margalef, R., Ballester, A., 1967. Fitoplancton y produccion primaria de la costa catalana, de junio de 1965 a junio de 1966. Investigaciones Pesqueras 31 (1), 165–182.

Mateo, M.A., Romero, J., 1997. Detritus dynamics in the seagrass Posidonia oceanica: Elements for an ecosystem carbon and nutrient budget. Marine Ecology Progress Series 151, 43–53.

UNCORRECTED PROOF

Maxwell, B.A., Buddemeier, R.W., 2002. Coastal typology development with heterogenous data sets. Regional Environmental Change 3 (1–3), 1.

Meyercordt, J., Gerbersdorf, S., Meyer-Reil, L.A., 1999. Significance of pelagic and benthic primary production in two shallow coastal lagoons of different degrees of eutrophication in the southern Baltic Sea. Aquatic Microbial Ecology 20 (3), 273–284.

Meyercordt, J., Meyer-Reil, L.A., 1999. Primary production of benthic microalgae in two shallow coastal lagoons of different trophic status in the southern Baltic Sea. Marine Ecology Progress Series 178, 179–191.

Middelburg, J.J., Klaver, G., Nieuwenhuize, J., Wielemaker, A., de Haas, W., Vlug, T., van de Nat, J.W.A., 1996. Organic matter mineralization in intertidal sediments along an estuarine gradient. Marine Ecology Progress Series 132, 157–168.

Middelburg, J.J., Duarte, C.M., Gattuso, J.P., 2004. Respiration in coastal benthic communities. In: del Giorgio, P.A., Williams, P.J.L.B. (Eds.), Respiration in Aquatic Ecosystems. Oxford University Press, Oxford, in press.

Milliman, J.D., Meade, R.H., 1983. World-wide delivery of river sediment to the oceans. Journal of Geology 91 (1), 1–21.

Milliman, J.D., Syvitski, J.P.M., 1992. Geomorphic/tectonic control of sediment discharge to the ocean: the importance of small mountainous rivers. Journal of Geology 100, 525–544.

Minas, M., 1976. Primary organic production in a brackish eutrophic environment (Etang de Berre). Effects of strong dilution (diversion of the waters of the Durance). Marine Biology 35 (1), 13–29.

Moncoiffé, G., Alvarez-Salgado, X.A., Figueiras, F.G., Savidge, C., 2000. Seasonal and short-time-scale dynamics of microplankton community production and respiration in an inshore upwelling system. Marine Ecology Progress Series 196, 111–126.

Morán, X.A.G., Estrada, M., Gasol, J.M., Pedrós-Alió, C., 2002. Dissolved primary production and the strength of phytoplankton bacterioplankton coupling in contrasting marine regions. Microbial Ecology 44 (3), 217–223.

Nixon, S.W., 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia 41, 199–219.

Olesen, M., Lundsgaard, C., 1995. Seasonal sedimentation of autochthonous material from the euphotic zone of a coastal system. Estuarine, Coastal and Shelf Science 41 (4), 475–490.

Pasqualini, V., Pergent-Martini, C., Clabaut, P., Pergent, G., 1998. Mapping of Posidonia oceanica using aerial photographs and side scan sonar: application off the island of Corsica (France). Estuarine, Coastal and Shelf Science 47, 359–367.

Pergent-Martini, C., Rico-Raimondino, V., Pergent, G., 1994. Primary production of *Posidonia oceanica* in the Mediterranean basin. Marine Biology 120, 9–15.

Pers, C., Rahm, L., 2000. Changes in apparent oxygen removal in the Baltic proper deep water. Journal of Marine Systems 25, 421–429.

Peterson, B.J., 1980. Aquatic primary productivity and the ^{14}C-CO$_2$ method: a history of the productivity problem. Annual Review of Ecology and Systematics 11, 359–385.

Psarra, S., Tselepides, A., Ignatiades, L., 2000. Primary productivity in the oligotrophic Cretan Sea (NE Mediterranean): seasonal and interannual variability. Progress in Oceanography 46 (2–4), 187–204.

Puddu, A., Ferla, R.L., Allegra, A., Bacci, C., Lopez, M., Oliva, F., Pierotti, C., 1998. Seasonal and spatial distribution of bacterial production and biomass along a salinity gradient (northern Adriatic Sea). Hydrobiologia 363 (1–3), 271–282.

Rahm, L., 1987. Oxygen consumption in the Baltic proper. Limnology and Oceanography 32 (4), 973–978.

Reid, P.C., Lancelot, C., Gieskes, W.W.C., Hagmeier, E., Weichart, G., 1990. Phytoplankton of the North Sea and its dynamics: a review. Netherlands Journal of Sea Research 26 (2–4), 295–331.

Renk, H., Nakonieczny, S., Ochocki, S., 1988. Primary production in the Southern Baltic in 1985 and 1986 compared with long-term seasonal variation. Kieler Meeresforschungen Sonderheft 6, 203–209.

Revilla, M., Ansotegui, A., Iriarte, A., Madariaga, I., Orive, E., Sarobe, A., Trigueros, J.M., 2002. Microplankton metabolism along a trophic gradient in a shallow-temperate estuary. Estuaries 25 (1), 6–18.

Richardson, K., Heilmann, J.P., 1995. Primary production in the Kattegat: Past and present. Ophelia 41, 317–328.

Rydberg, L., Edler, L., Floderus, S., Granéli, W., 1990. Interaction between supply of nutrients, primary production, sedimentation and oxygen consumption in SE Kattegat. Ambio 19 (3), 134–141.

San Feliu, J.M., Muñoz, F., 1970. Hidrografia y fitoplancton de las costas de Castellon, de julio 1967 à junio 1968. Investigación Pesquera 34 (2), 417–449.

Sandén, P., Hakansson, B., 1996. Long-term trends in Secchi depth in the Baltic Sea. Limnology and Oceanography 41, 346–351.

Serret, P., Fernández, E., Sostres, J.A., Anadón, R., 1999. Seasonal compensation of microbial production and respiration in a temperate sea. Marine Ecology Progress Series 187, 43–57.

Shaffer, G., 1987. Redfield ratios, primary production, and organic carbon burial in the Baltic Sea. Deep-Sea Research 34 (5–6), 769–784.

Smith, S.V., Hollibaugh, J.T., 1993. Coastal metabolism and the oceanic organic carbon balance. Reviews of Geophysics 31 (1), 75–89.

Smith, S.V., Swaney, D.P., Talaue-McManus, L., Bartley, J.D., Sandhei, P.T., McLaughlin, C.J., Dupra, V.C., Crossland, C.J., Buddemeier, R.W., Maxwell, B.A., Wulff, F., 2003. Humans, hydrology, and the distribution of inorganic nutrient loading to the ocean. Bioscience 53 (3), 235–245.

Soluri, E.A., Woodson, V.A., 1990. World vector shoreline. International Hydrographic Review 67, 27–36.

Sournia, A., 1973. La production primaire planctonique en Méditerranée. Essai de mise à jour. Bulletin de l'étude en Commun de la Méditerranée 5, 1–128.

Sundbäck, K., Jönsson, B., 1988. Microphytobenthic productivity and biomass in sublittoral sediments of a stratified bay, SE Kattegat. Journal of Experimental Marine Biology and Ecology 122, 63–81.

Sundbäck, K., Miles, A., 2000. Balance between denitrification and microalgal incorporation of nitrogen in microtidal sediments, NE Kattegat. Aquatic Microbial Ecology 22, 291–300.

Tellaï, S., 1969. Détermination de la production organique à l'aide du carbone 14, dans les parages d'Alger. NATO Technical Reports of the Sub-committee for Oceanographic Research 47, 56–63.

Thamdrup, B., Canfield, D.E., 2000. Benthic respiration in aquatic sediments. In: Sala, O.E., Jackson, R.B., Mooney, H.A., Howarth, R.W. (Eds.), Methods in Ecosystem Science. Springer, New York, pp. 86–103.

Thomas, H., Schneider, B., 1999. The seasonal cycle of carbon dioxide in Baltic Sea surface waters. Journal of Marine Systems 22, 53–67.

Thornton, D.C.O., Dong, L.F., Underwood, G.J.C., Nedwell, D.B., 2002. Factors affecting microphytobenthic biomass, species composition and production in the Colne Estuary (UK). Aquatic Microbial Ecology 27 (3), 285–300.

Van Es, F.B., 1977. A preliminary carbon budget for a part of the Ems estuary: the Dollard. Helgolander Wissenschaftliche Meeresuntersuchungen 30, 283–294.

van Spaendonk, J.C.M., Kromkamp, J.C., de Visscher, P.R.M., 1993. Primary production of phytoplankton in a turbid coastal plain estuary, The Westerschelde (The Netherlands). Netherlands Journal of Sea Research 31 (3), 267–279.

Velimirov, B., Walenta-Simon, M., 1992. Seasonal changes in specific growth rates, production and biomass of a bacterial community in the water column above a Mediterranean seagrass system. Marine Ecology Progress Series 80 (2-3), 237–248.

Wasmund, A., Andrushaitis, A., Lysiak-Pastuszak, E., Müller-Karulis, B., Nausch, G., Neumann, T., Ojaveer, H., Olenina, I., Postel, L.,

UNCORRECTED PROOF

Witek, Z., 2001. Trophic status of the South-Eastern Baltic Sea: a comparison of coastal and open areas. Estuarine, Coastal and Shelf Science 53 (6), 849–864.

Wasmund, N., 1986. Ecology and bioproduction in the microphytobenthos of the chain of shallow inlets (Boddens) south of the Darss-Zingst peninsula (southern Baltic Sea). International Revue der gesamten Hydrobiologie 71 (2), 153–178.

Whittaker, R.H., Likens, G.E., 1975. The biosphere and man. In: Lieth, H., Whittaker, R.H. (Eds.), Primary Productivity of the Biosphere. Springer, Berlin, pp. 305–328.

Williams, P.J.L.B., 1984. A review of measurements of respiration rates of marine plankton populations. In: Hobbie, J.E., Williams, P.J.L.B. (Eds.), Heterotrophic Activity in the Sea. Plenum, New York, pp. 357–389.

Witek, Z., Ochocki, S., Maciejowska, M., Pastuszak, M., Nakonieczny, J., Podgorska, B., Kownacka, J.M., Mackiewicz, T., Wrzesinska-Kwiecien, M., 1997. Phytoplankton primary production and its utilization by the pelagic community in the coastal zone of the Gulf of Gdansk (southern Baltic). Marine Ecology Progress Series 148 (1–3), 169–186.

Witek, Z., Ochocki, S., Nakonieczny, J., Podgorska, B., Drgas, A., 1999. Primary production and decomposition of organic matter in the epipelagic zone of the Gulf of Gdansk, an estuary of the Vistula. Ices Journal of Marine Science 56 (Suppl.), 3–14.

Witek, Z., Drgas, A., Ameryk, A., Ochocki, S., 2001. Production and mineralization of organic matter in the Pomeranian Bay (Baltic Sea). Bulletin of the Sea Fisheries Institute, Gdynia 154 (3), 49–69.

Wollast, R., 1998. Evaluation and comparison of the global carbon cycle in the coastal zone and in the open ocean. In: Brink, K.H., Robinson, A.R. (Eds.), The Sea, Vol. 10, Wiley. New York, pp. 213–252.

Wood, B.J.B., Tett, P.B., Edwards, A., 1973. An introduction to the phytoplankton, primary production and relevant hydrography of Loch Etive. Journal of Ecology 61, 569–585.

York, J.K., Witek, Z., Labudda, S., Ochocki, S., Aas, E., 2001. Comparison of primary production and pelagic community respiration rate in the coastal zone of the Gulf of Gdansk (Baltic Sea, Poland). Oceanologia 43 (3), 365–378.

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