Benthic fluxes, net ecosystem metabolism and seafood harvest: completing the organic carbon balance in the Ría de Vigo (NW Spain)

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Abstract

Simultaneous direct measurements of primary production, pelagic and benthic respiration and vertical fluxes allowed, for the first time, the evaluation of the carbon metabolism in the Ría de Vigo (NW Spain) on seasonal and annual scales. With this aim, a total of 16 oceanographic cruises covering the main oceanographic conditions were carried out between April 2004 and January 2005. In addition, a 2D carbon budget, including extraction from mussel culture and fisheries activities, is proposed. The pelagic system was net autotrophic during the spring and summer periods and autotrophic or almost in balance during autumn and winter. Vertical fluxes of organic carbon were higher than net community production (NCP) during autumn and winter periods, probably due to resuspension processes and inputs of organic matter from continental runoff. Benthic mineralization is an important process in the Ría de Vigo, which gains significance during autumn and winter when benthic respiration accounts for 40% and 45% of the total respiration, respectively. The Ría de Vigo is net autotrophic on annual basis ($317 \pm 113 \text{ g C m}^{-2} \text{ yr}^{-1}$) even though the benthic metabolism reduces the NCP by 23%. Total annual carbon seafood harvest amounted 3% of the net ecosystem metabolism and it is dominated by mussel culture (89%). However, based on mean energy transfer efficiency between trophic levels of 10%, it is estimated that mussel culture and reported fish catches require up to 38% of the NCP. The organic carbon produced *in situ* at the Ría de Vigo and available for export to the adjacent shelf or to be buried in the sediment represents $\frac{1}{4}$ of the gross primary production and it is favoured during summer upwelling.

Highlights

An annual carbon budget including benthic fluxes and seafood harvest is proposed.

The Ría de Vigo is net autotrophic on annual basis ($317 \pm 113 \text{ g C m}^{-2} \text{ yr}^{-1}$).

Benthic remineralization reduces the autotrophy of the system by 23 %.

Mussel culture and fisheries require 38 % of the net community production.

Shelf carbon export and sediment burial account for ¼ of the gross primary production.

Keywords: benthic fluxes, primary production, respiration, carbon budget, coastal upwelling, net ecosystem metabolism, mussel harvest, wild catch fisheries

1. Introduction

Coastal zones contribute disproportionately large amounts of production and respiration in relation to their areas covered over the global ocean (Wollast, 1998). In these regions, production (P) and respiration (R) processes are magnified due to the influence of hydrodynamic events, such as upwelling and continental inputs, combined with the proximity of the sediment remineralizing environment (Zeldis, 2004). To provide a better understanding of the functioning of these biogeochemically active regions, studies of ecosystem metabolism are necessary. Net ecosystem metabolism (NEM) represents the balance between primary production and total respiration in an ecosystem and can be measured as the summation of anabolic and catabolic rates of all the organisms in the system (Kemp et al., 1997), where catabolic rates represent the sum of the respiratory processes (Testa et al., 2012). The term net community production (NCP) is often used when just the microbial pelagic community metabolism is being measured (Staehr et al., 2012). The balance between net autotrophy and heterotrophy will depend on the nature of exogenous inputs (Caffrey et al., 1998) and so, coastal systems receiving high inorganic nutrient inputs tend to be net autotrophic ($P > R$) while those ones with high organic inputs tend to be net heterotrophic ($R > P$). Measurements of ecosystem metabolism indicate the trophic status of the ecosystem (Odum, 1956) as well as to give an idea of how the system processes nutrients and organic matter (Smith and Hollibaugh, 1997). This information is essential to nourish food web models and to partition biogeochemical processes among the different aerobic and anaerobic pathways (Hopkinson et al., 1999). Among the different methods used to calculate NEM, direct rate measurements allow partitioning of production and respiration processes into shares of different habitats (Testa et al.,

2012), i.e. they have the advantage of estimating the relative contribution to total ecosystem metabolism by pelagic and benthic components (Staehr et al., 2012).

Several factors can regulate the trophic status in a coastal system such as inputs of inorganic nutrients, exchange rate with the adjacent seaward region and loading rates of organic carbon. Organic matter produced by phytoplankton not respired in the water column may be transferred to higher trophic levels, transported offshore, exported vertically towards the sediment and mineralized or buried in the sediment. High *in situ* primary production in many coastal systems provides the substrate of autochthonous organic matter that contributes to secondary production either directly or indirectly (Hyndes et al., 2014) and is then, available to higher trophic levels such as predators and scavengers. Therefore, primary production is an important factor on the production of marine fishes as it supports food to fisheries harvest (Kemp et al., 1997; Pauly and Christensen, 1995). Harvest and migration of marine organisms may represent potentially significant losses in the organic carbon budget of a coastal ecosystem (Houde and Rutherford, 1993) and so, overharvesting of marine organisms reduces the abundance of consumers and so it reduces the carbon transfer towards higher trophic levels (Hyndes et al., 2014).

The Galician Rías Baixas (NW Iberian Peninsula; Fig. 1) comprise four V-shaped coastal inlets located in the unique coastal upwelling system of Europe. In this region, the upwelling of subsurface cold and nutrient rich Eastern North Atlantic Central Water (ENACW) promotes high phytoplankton abundance able to support the highest mussel production (*Mytilus galloprovincialis* Lamark) in Europe. This activity renders a total

estimated production of $243 \times 10^6 \text{ kg yr}^{-1}$ (Figueiras et al., 2002). The Ría de Vigo sustains 474 suspended mussel rafts and provides approx. 15 % of the total mussel production of the Rías Baixas. Studies dealing with the biogeochemical fluxes and net budgets of organic carbon in the Rías Baixas have been mainly derived from stationary box models of inorganic nutrients (Prego, 1994, 1993), which then developed to non-stationary box models (Álvarez-Salgado et al., 1996; Dale and Prego, 2002; Gilcoto et al., 2001; Rosón et al., 1999). Later on, Piedracoba et al., (2008) included direct measurements of vertical fluxes and water column production/respiration experiments incubated at laboratory. These studies have inferred that mineralization of the organic matter in the sediments of the rías must have a major importance in the net ecosystem metabolism, but up to date none of them have measured *in situ* benthic measurements.

The first goal of this manuscript is to explore the importance of benthic respiration in the Ría de Vigo and to evaluate in what extent it determined the trophic status of the ecosystem. With this aim, benthic respiration was analysed in relation to *in situ* and simultaneously measured primary production, pelagic respiration rates (Arbones et al., 2008) and vertical export of particles (Zúñiga et al., 2011) during four seasonal campaigns carried out in the framework of the FLUVBE project (Coupling of benthic and pelagic fluxes in the Ría de Vigo). Bringing together all these measurements, the main objective of the manuscript was to determine the Net Ecosystem Metabolism in the Ría de Vigo on seasonal and annual basis. From here, an annual carbon budget including potential carbon inputs from continental sources and losses from the system in the form of mussel harvest, wild catch fisheries and shellfishing has been built. In

this way, this manuscript presents an integrative view of the ecosystem carbon trade off, increasing our general knowledge of coastal system responses to different combination of environmental changes (Carpenter et al., 2009; Hobbie, 2000; Kemp and Boynton, 2012; Rhoten et al., 2009).

2. Methods

2.1. Study area

The study site was located in the Ría de Vigo, a temperate coastal embayment and one of the four Rías Baixas of the NW Iberian Peninsula. The Ría is oriented NE-SW, widens seawards, and is partially enclosed by the Cíes Islands (Fig. 1). From May to October, prevailing northerly winds cause the upwelling of cold nutrient-rich subsurface ENACW, which enters into the Ría. During upwelling conditions, primary production is increased (Fraga, 1981), as it is the potential export of biogenic carbon to the sediment and the adjacent shelf (Álvarez-Salgado et al., 2001). During the other half of the year, downwelling conditions, associated with prevailing southerly winds, are favoured.

2.2. Sampling strategy and water sampling

In the framework of the Spanish project FLUVBE, 16 oceanographic cruises were carried out at FLUVBE station, located in the main channel of the Ría de Vigo (Fig. 1). The sampling strategy of the cruises, which covered the period between April 2004 and January 2005, was intended to capture the predominant oceanographic conditions in the study area; i.e. spring bloom (April), summer upwelling-stratification (July), autumn bloom (October) and winter mixing (January). During each period, the station was visited twice a week during a 15 days period. Arbones et al. (2008) explained in detail

the measurements that they are briefly described below. Measurements of plankton community gross primary production (GPP), NCP, and dark community respiration (DCR) were determined by 24h *in situ* light-dark bottle oxygen incubations at 4 depths in the photic layer and 1 depth in the aphotic zone of the water column. Samples were taken with 10 L PVC Niskin bottles mounted on a rosette with a SBE 911 CTD. At each of the 4 photic depths, 4 light and 4 dark bottles were placed in a specially constructed plexiglass holder. For the aphotic depth, only 4 dark samples were incubated. A further set of 4 replicates at each depth was fixed at time 0. Dissolved oxygen was determined by an automated Winkler titration system. Net *in vitro* changes in the light and dark bottles gave NCP and DCR, respectively. Production and respiration rates were calculated as follows: NCP = ΔO_2 in light bottles in relation with the initial oxygen concentration; DCR = ΔO_2 in dark bottles in relation with the initial oxygen concentration; GPP = NCP + DCR. In order to convert oxygen production and oxygen consumption to carbon units a photosynthetic quotient and an O_2/TCO_2 ratio for pelagic respiration of 1.4 were assumed following Fraga et al. (1998).

The upwelling index was estimated using the component $-Q_x$ of the Ekman transport following Bakun's (1973) method:

$$-Q_x = (\rho_{air} C_D |V| V_y) / (f \rho_{sw})$$

where ρ_{air} is the density of air (1.22 kg m⁻³ at 15°C), C_D is an empirical dimensionless drag coefficient (1.4 x 10⁻³ according to Hidy 1972), f is the Coriolis parameter (9.946 x 10⁻⁵ at 43°N), ρ_{sw} is the density of seawater (1025 kg m⁻³) and $|V|$ and V_y , are the

average daily modulus and northerly component of the geostrophic winds centred at 43°N, 11°W, respectively. Average daily geostrophic winds were estimated from surface atmospheric pressure charts. Positive values of $-Q_x$ indicate upwelling and correspond to predominance of northerly winds.

Continental runoff into the Ría de Vigo is dominated by the discharge from the river Oitavén-Verdugo at the inner part of the ría (Fig. 1). Its flow is a combination of regulated and natural flow. Daily flows were provided by the company in charge of the management of urban waters. The Eiras reservoir controlled 23 ± 12 % of the total flow during the study year. The natural component of the flow per unit area was calculated following Ríos et al. (1992).

2.3. Vertical Fluxes

Vertical particle fluxes towards the sediment were estimated using a homemade multitrap collector system. It was composed by 4 PVC trap baffled cylinders of 28 cm² collecting area and aspect ratio of 10.8. Sediment traps were deployed at FLUVBE site at approximately 16 m depth (approx. 5 metres above sea bottom) for a 24 hour period, filled with filtered seawater with additional 5 PSU in excess per liter and without the addition of any preservatives. A subsample of 200 mL of the material collected in each cylinder was used for analysis of particulate organic carbon (POC). Filters were vacuum dried and frozen (-20 °C) before analysis. Samples were vaporized with HCl (32%) for 24 h to eliminate inorganic carbon. A Perkin Elmer 2400 CHN analyzer was used for measurements of POC, using an acetanilide standard daily. The precision of the method is ± 3.6 mg C m⁻³.

In order to determine phytoplankton derived carbon settled in the traps (C_{phyto}), a fraction of 100 mL preserved in Lugol's iodine was employed for microplankton determination. Depending on the chl *a* concentration, a volume ranging from 10 to 50 mL was sedimented in a composite sedimentation chamber and observed through an inverted microscope. The phytoplankton organisms were counted and identified to species level. Dimensions were taken to calculate cell biovolumes after approximation to the nearest geometrical shape (Hillebrand et al., 1999) and cell carbon was calculated following Strathmann (1967) for diatoms and dinoflagellates, Verity et al. (1992) for other flagellates ($> 20 \mu\text{m}$) and Putt & Stoecker (1989) for ciliates. Unfortunately, subsamples for C_{phyto} were not available for the spring period.

2.4. Benthic fluxes

Fluxes of dissolved oxygen, total alkalinity and pH at the sediment-water interface were measured *in situ* by means of a benthic chamber, placed by a diver directly on the sediment surface. The equipment consisted of a PVC opaque cylindrical chamber, which incubated 140 L of overlying seawater, and covered 0.64 m^2 of sediment surface. Inside the chamber, sensors for temperature (SBE39), turbidity (Seapoint Turbidity Meter) and dissolved oxygen (SBE43) gave a continuous recording of these variables during the incubation time (approx. 8 h) (Ferrón et al., 2008). Discrete samples were withdrawn from the chamber at prefixed times with a multiple water KC Denmark sampler provided with 12 syringes of 50 ml capacity.

Total alkalinity was determined by potentiometric titration with HCl to a final pH of 4.4 (Pérez and Fraga, 1987) and adapted for small sampling volume of 5 mL. The measurements of pH were analyzed spectrophotometrically following Clayton & Byrne (1993). Total CO₂ was estimated from pH and total alkalinity using the carbonic system equations with the carbonic and boric acid dissociations constants of Lueker et al. (2000). Benthic fluxes were estimated by empirical linear fittings based on changes in concentration over time. Alkalinity fluxes were corrected for the influence of ammonium and nitrate fluxes by adding the fluxes of NO₃⁻ and subtracting the NH₄⁺ fluxes. Assuming that calculated TCO₂ fluxes account for organic carbon remineralization and net dissolution of CaCO₃, it can establish an upper limit of the amount of carbon oxidized as the calculated TCO₂. As Ca⁺² fluxes were not measured, an estimate of the maximum dissolution of CaCO₃ was calculated as ½ alkalinity fluxes following Berelson et al. (1998). Consequently, the lower limit of the carbon oxidation was obtained subtracting maximum CaCO₃ dissolution rates from measured TCO₂ fluxes. Based on these assumptions, carbon oxidation rates (Cox_{avg}) were calculated as the average between the upper and lower limit. Uncertainties of the fluxes account for the fit of the data to a linear function and the propagation of random errors.

3. Results & Discussion

3.1. Hydrographic conditions, pelagic production and respiration rates

The seasonal sampling for the study year captured the most relevant hydrodynamic conditions for this coastal upwelling system, as explained in detail by Villaceros-Robineau et al. (2013). Here, the main hydrographic features of each seasonal period are described. During the spring period there was a transition from downwelling to

upwelling as observed by $-Q_x$ values and temporal evolution of temperature (Fig. 2). There was also a shift in the continental runoff, with the highest values associated with downwelling-favouring southerly winds. Biological properties responded to this transition situation with an increase of the NCP as upwelling waters entered. The summer period was characterized by constant upwelling conditions and low values of continental runoff ($< 20 \text{ m}^{-3} \text{ s}^{-1}$). Pelagic autotrophy dominated during this period as NCP reached the highest values for the whole year ($> 300 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$), pointing to *in situ* produced organic carbon potentially available to be exported to the continental shelf, to the sediment or to higher trophic levels. Under upwelling conditions, outwelling of waters from the Ría are favoured (Álvarez-Salgado et al., 2000), and consequently the offshore export of organic matter is enhanced (Álvarez-Salgado et al., 1997; Fraga, 1981). The autumn period started with upwelling conditions though a strong downwelling pulse ($-Q_x < -4000 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$) between the 1st and 2nd sampling days, homogenized the water column, bringing warmer waters ($>15 \text{ °C}$) towards sea bottom. Continental runoff increased after the downwelling pulse and maintained high values until the end of the period ($> 40 \text{ m}^3 \text{ s}^{-1}$). NCP and respiration decreased after the downwelling pulse, and the water column was basically in metabolic balance for these last days. Finally, during the winter period, there was a thermal inversion associated with the winter cooling and NCP reached its minimum as expected (Cermeño et al., 2006).

There was a clear seasonal pattern for both NCP and DCR in the water column with maximum values during summer and spring periods, when phytoplankton community was dominated by large cells ($> 20 \text{ }\mu\text{m}$). The pelagic system of the Ría de Vigo was net

autotrophic during the spring and summer seasons and autotrophic or almost in balance during the winter and autumn periods (Arbones et al., 2008).

3.2 Vertical fluxes of organic carbon

The annual vertical fluxes of organic carbon, which averaged $1.08 \pm 0.15 \text{ g C m}^{-2} \text{ d}^{-1}$, were of the same order as previous values reported for the Galician coast (Bode et al., 1998; Piedracoba et al., 2008; Varela et al., 2004) and did not show any significant seasonal variations ($p > 0.1$) (Fig. 3). However, there was a seasonal variability on the fluxes of phytoplankton derived carbon (C_{phyto}) with maximum values during summer upwelling ($0.26 \pm 0.21 \text{ g C m}^{-2} \text{ d}^{-1}$, Fig 3.) decreasing in autumn and reaching minimum values during winter ($0.03 \pm 0.01 \text{ g C m}^{-2} \text{ d}^{-1}$). Therefore, the average percentage of phytoplankton carbon flux over the total organic carbon varied seasonally, decreasing from 26 % during summer to 9 % during autumn and finally 2 % during winter. According to Zúñiga et al. (2011), the seasonality in the C_{phyto} fluxes towards the sediment is influenced by the phytoplankton community structure of the water column.

Based on the data from primary production, vertical fluxes and pelagic respiration, a 1D carbon budget for each season was built (Fig. 4). During spring, half of the GPP (52 %) is respired in the photic zone, a value comparable to the 43 % obtained by Moncoiffé et al. (2000) during the upwelling season. Organic carbon vertical fluxes are of the same order of magnitude as the NCP, which means that vertical export is favoured over offshore transport. The fact that the spring period comprised a transition from downwelling to upwelling, constrained on average the export to the

adjacent shelf, being a situation similar to a weak upwelling scenario as described by Torres-López et al. (2005). The summer upwelling period is characterized by the highest GPP ($4.12 \text{ g C m}^{-2} \text{ d}^{-1}$) of the year, from which the photic zone is able to respire just 15 %. Vertical organic carbon fluxes represented 32 % of the integrated NCP. These values were very similar to those obtained during an upwelling/relaxation cycle in the Ría de Vigo (30 %, Piedracoba et al. 2008), and close to the 14-26 % obtained by Olli et al. (2001) on the shelf of the Iberian Upwelling system. Approximately 70 % of the NCP is available to be transferred to higher trophic levels or exported to the adjacent continental shelf. This last process is favoured by the positive circulation of the Ría during the upwelling season. During autumn and winter, vertical fluxes of organic carbon exceeded by far NCP (2.5 and 7 fold higher, respectively), suggesting that there are additional sources of organic carbon to the fluxes others than *in situ* primary production, as advection, resuspension processes or organic matter from continental runoff. Villacieros-Robineau et al. (2013), studying the hydrodynamics of the bottom boundary layer in the Ría de Vigo by means of a downwards looking Acoustic Doppler Current Profiler, found that bottom shear stress was strong enough for the autumn period to cause the resuspension of sea surface sediments. The presence of allochthonous material in the settling particles explained the lower contribution of C_{Phyto} to the vertical organic carbon fluxes during autumn and winter compared to the summer period. Furthermore, higher C:N ratios of the material for winter than the other seasons (11.3 ± 3 and 7.2 ± 0.4 respectively, Alonso-Pérez & Castro 2014) reflected less labile organic matter, more characteristic from continental runoff (Kemp et al., 1997) or resuspended material.

On annual average, vertical organic carbon flux represented approx. 91 % of the integrated NCP. Although these data might contrast with Prego (1993), who found that the Ría de Vigo exports offshore 1/3 of the annual net community production, it has to be taken into account that during autumn and winter a major proportion of organic carbon is from allochthonous origin and not produced inside the Ría.

3.3 Benthic fluxes

Benthic respiration may be measured either as oxygen consumption or carbon dioxide production, and so most researchers measure one of both parameters and assume a BRQ (benthic respiration quotient) = 1 and Redfield C:N:P stoichiometry for the organic matter (Hopkinson and Smith, 2005). However, BRQ of benthic systems varies widely across studies and dissolved inorganic carbon flux may exceed oxygen consumption when organic matter is mainly anaerobically degraded, reaching values of BRQ as high as 2.15 in Tomales Bay (Dollar et al., 1991). In the present study, both oxygen taken up and inorganic carbon production were measured. Benthic fluxes of Cox_{avg} showed a similar trend to oxygen uptake (Fig. 5) being the two variables highly correlated (r : -0.78, $p < 0.01$, $n = 15$), with no significant differences among spring, summer and autumn but significantly lower during winter. Thus, it is suggested that benthic inorganic carbon fluxes at the Ría de Vigo are also influenced by the upwelling/downwelling events and the arrival of labile organic matter to the sediment as it was previously found for the oxygen fluxes (Alonso-Pérez and Castro, 2014). Likewise, averaged BRQ was 0.76 ± 0.23 which can be considered low compared to values reported by Hopkinson & Smith (2005) from different estuaries worldwide, and values obtained by Forja et al. (2004) at 5 different coastal sites in the Iberian

Peninsula (1.1 to 3.1). These low BRQ values point to the preference of aerobic catabolic processes in the degradation of organic matter at the sediment surface.

Taking into account the vertical fluxes, 26 % of the organic carbon is remineralized in the sediment and only 7 % in the aphotic layer of the water column (Fig. 4). This benthic share was similar to the average of 24 % compiled by Hopkins & Smith (2005) for different estuaries worldwide. The percentage of the vertical fluxes remineralized in the sediment is higher during spring, summer and autumn (approx. 30 %) and descends to 16 % during winter (Fig. 4), when benthic fluxes were lower and the highest values of relatively refractory material were registered in the sediment trap. Respiration at the aphotic water column reaches its maximum (17 % of the vertical fluxes) during summer upwelling coinciding with the highest contribution of C_{Phyto} to the vertical fluxes, though it remains low during the whole year. In contrast, Piedracoba et al. (2008) obtained a contribution of 61% of the aphotic respiration at the Ría de Vigo during upwelling conditions, based on P/R oxygen measurements incubated at laboratory.

Overall, benthic respiration appears to be an important metabolic process in the Ría de Vigo, averaging 34 % of the total respiration, which includes it in the upper range for estuaries (23 % to 37 %, Hopkins & Smith 2005). There is a dominance of pelagic respiration during spring and summer periods (75 % and 73 %, respectively) while benthic mineralization gains importance during autumn and winter periods, reaching values of 40 % and 44 % of the total respiration, respectively.

3.4 NEM: importance of benthic fluxes, mussel culture and fisheries

The unique opportunity of simultaneous measurements of production and pelagic and benthic respiration allowed to establish an assessment of Net Ecosystem Metabolism (GPP – total respiration) for the Ría de Vigo on seasonal and annual scales. On a seasonal scale, the proportion of NEM over the calculated GPP reaches its maximum during summer (72%) and reduces to -6 % for the winter period (Fig. 4), with an annual average NEM sharing 49% of GPP. Smith & Hollibaugh (1993) in a study including 22 coastal ecosystems obtained an inverse relationship between GPP and NEM, where most productive systems had the most heterotrophic metabolism. This relationship was attributed to the fact that most of the nutrients delivered to these systems were derived from terrestrial organic matter. In contrast to coastal sites highly influenced by riverine inputs, NEM in the Ría de Vigo was positively correlated with *in situ* GPP ($r:0.98$), due to the major contribution of inorganic nutrients advected into the Ría by upwelled waters (Fraga 1981). The seasonal variability of NEM also remarks the importance of the benthic respiration on the autotrophy of the ecosystem. As previously indicated, the pelagic domain of the Ría de Vigo is autotrophic or in balance (Arbones et al., 2008). When the benthic respiration is included to evaluate the trophic status of the system, averaged NEM for spring is still autotrophic, though not significant ($0.43 \pm 0.53 \text{ g C m}^{-2} \text{ d}^{-1}$, $p > 0.05$), autumn NEM is in balance ($0.09 \pm 0.82 \text{ g C m}^{-2} \text{ d}^{-1}$), and averaged NEM during winter is even negative ($-0.03 \pm 0.13 \text{ g C m}^{-2} \text{ d}^{-1}$).

Based on data collected in this study and estimations from the literature, a 2D annual carbon budget for the Ría de Vigo has been built (Fig. 6), including the carbon extracted from the system by mussel culture, wild catch fisheries and shellfishing.

Inputs and outputs of carbon from the system were normalized to the area of the Ría (117 km²) as delimited in Fig. 1. Calculations were based on wet weight catches and wet weight: carbon ratios for each of the faunal groups using referenced data as shown in the first 3 columns of Table 1. Continental inputs were obtained from Evans et al. (2011).

The main feature of the budget is that the Ría de Vigo is net autotrophic on annual basis ($317 \pm 113 \text{ g C m}^{-2} \text{ yr}^{-1}$) in contrast to the majority of estuaries that on average appear to be net heterotrophic (Hopkinson & Smith 2005), including coastal sites affected by upwelling processes as Tomales bay (Smith and Hollibaugh, 1997). In fact, the annual NEM value of the Ría de Vigo appeared to be high compared with systems as Chesapeake bay ($47 \text{ g C m}^{-2} \text{ yr}^{-1}$, Kemp et al. 1997) and some Australian coastal sites ($11\text{-}21 \text{ g C m}^{-2} \text{ yr}^{-1}$, Eyre & McKee 2002, Ferguson & Eyre 2010). Our result is closer to the value of NCP obtained by Dale & Prego (2005) at the Ría de Pontevedra ($210\text{-}314 \text{ g C m}^{-2} \text{ yr}^{-1}$) using a non-stationary state mass balance. Another important highlight from the budget is that benthic remineralization in this coastal system ($104 \pm 20 \text{ g C m}^{-2} \text{ yr}^{-1}$) reduces the autotrophy of the system (NCP) by 23%. Input of continental runoff of particulate organic carbon ($4.1 \text{ g C m}^{-2} \text{ yr}^{-1}$) represented only about 1.3 % of the NEM, of which $2.8 \text{ g C m}^{-2} \text{ yr}^{-1}$ derived from sewage treatment plants (Evans et al., 2011). If dissolved organic carbon (DOC) is also considered from the fluvial discharges, the input of continental runoff will reach 2.3% (Gago et al., 2005). Carbon extracted from mussel harvest ($8.9 \text{ g C m}^{-2} \text{ yr}^{-1}$) represented 89 % of the total annual harvest in the Ría de Vigo, followed by wild catch of fishes ($0.8 \text{ g C m}^{-2} \text{ yr}^{-1}$) and shellfishing ($0.4 \text{ g C m}^{-2} \text{ yr}^{-1}$). The result means that mussel may uptake approx. 2% of the NCP generated annually at

the Ría de Vigo. Figueiras et al. (2002) already estimated that 12 % of the NCP was incorporated by mussel at the Ría de Arousa. Although the Ría de Arousa has a surface 1.3 times higher than in the Ría de Vigo, this percentage of NCP taken up by mussels does not differ substantially between both Rías if it is taken into account that the number of mussel rafts in the Ría de Arousa is 5 times higher than in the Ría de Vigo (Labarta, 1999). Total harvest in the Ría de Vigo extracted $10 \text{ g C m}^{-2} \text{ yr}^{-1}$ from the Ría (Table 1), which comprised 3 % of the NEM. Kemp et al. (1997) obtained a carbon loss rate from fish wild catches in Chesapeake Bay very similar ($8 \text{ g C m}^{-2} \text{ yr}^{-1}$), but in this case it represented larger proportion of the NEM (17%). When analysing the contribution of seafood harvest in terms of primary production required (PPR) to sustain these mussel culture and fisheries activities, this low 3% value shifts to a larger share of PPR. For doing this, it has to be taken into account that the energy transfer efficiency between trophic levels is $\pm 10 \%$ and estimate PPR following Pauly & Christensen (1995):

$$\text{PPR} = C_i \times 10^{(\text{TLi}-1)}$$

C_i : Organic carbon from each species harvested

TLi: Trophic Level of each species harvested

Mussel harvest at the Ría de Vigo requires approx. 20 % of the annual NCP, wild catch of fishes 17 % and shellfishing 0.8 % (Table 1). Total mussel culture and fishing requires 38 % of the NCP, surpassing the value of 25.1 % for upwelling areas and the 8.3 % for coastal/reef systems, obtained by Pauly & Christensen (1995).

If the PPR from fisheries and mussel culture harvest ($168 \text{ g C m}^{-2} \text{ yr}^{-1}$) is extracted to the NEM, the organic carbon produced *in situ* at the Ría de Vigo and available for export to the adjacent shelf or to be buried in the sediment is $149 \text{ g C m}^{-2} \text{ yr}^{-1}$, which is approx. 1/4 of the GPP. This proportion is higher during spring and summer, when export/advection of organic material to the adjacent shelf is favoured by means of outwelling events and be an important food for the shelf benthic communities (López-Jamar et al., 1992).

Overall, this first assessment of the NEM of the Ría evidences the strong autotrophic state of this ecosystem. However, there are still important uncertainties that must be resolved to accurately evaluate the trophic state and complete the carbon budget in the ría. The FLUVBE station was located in the central axis of the Ría, an area covered by muddy sediment, which is the most abundant sediment type in the Ría de Vigo (Vilas et al., 2005). Moreover, the Ría de Vigo is an upwelling driven system which acts as an extension of the continental shelf and channels the 3D variability of the adjacent ocean into a 2D-circulation along the Ría main channel which, in last term, modulates the hydrodynamic and biogeochemical responses (Figueiras et al., 2002). Taking into account both circumstances, our study site can be considered representative of the subtidal regime in the Ría, though it has to be recognized that there are different specific benthic habitats in the Ría (Casal et al., 2013; López-Jamar & Cal, 1990; Rodil et al., 2009) mainly driven by sea surface sediment type (Vilas et al. 2005). As a future remark, it has been shown that changes in atmospheric pressure fields and associated wind patterns may decrease the intensity of upwelling-induced ecosystem production along many coastal systems (Barth et al., 2007). For the NW Iberian coastal upwelling

system, several studies demonstrated an interannual weakening of northerly winds (Barton et al., 2013; Pardo et al., 2011) which leads to a decrease in the occurrence and diminishing of the upwelling of cold and nutrient-rich subsurface waters into the rias. If continuing this trend, the potential upwelled waters entering into the rias will be warmer and not so nutrient rich. These warmer temperatures will favour benthic fluxes but on the other hand a decrease on primary production is expected, ending up in less autotrophy of this coastal upwelling system.

4. Acknowledgements

The authors thank the crew of the 'R/V Mytilus' and the members of the Department of Oceanography from the Instituto de Investigaci3n Mariñas of Vigo (IIM-CSIC) for their valuable help. Financial support came from CICYT project REN 2003-04458. F.A-P. was funded by a fellowship from the Spanish Ministerio de Ciencia y Tecnología. D.Z. was funded by a postdoctoral fellowship (Plan I2C) from Xunta de Galicia (Spain).

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Figure captions

Figure 1. Map of the Ría de Vigo, showing the location of the sampling station FLUVBE and boundary limits (solid lines) used for the calculations of carbon budget.

Figure 2. Time series of upwelling index ($-Q_x$, solid line) and daily averaged runoff (Q_R , bars) (a), temperature (b), Net Community Production (NCP) and Dark Community Respiration (DCR) both in the photic layer and aphotic layer (c).

Figure 3. Seasonal vertical fluxes of particulate organic carbon (POC) and carbon derived phytoplankton (C_{Phyto}). No data for spring C_{Phyto} . Units in $\text{g C m}^{-2} \text{d}^{-1}$.

Figure 4. Seasonal carbon budgets. Benthic respiration obtained from alkalinity and pH benthic fluxes (Cox_{avg}). Units in $\text{g C m}^{-2} \text{d}^{-1}$. Errors presented as the SD of the mean for each season. Pelagic respiration and NCP were converted to carbon units using a $R_c = 1.4$ (Fraga et al. 1998).

Figure 5. Sediment oxygen uptake (vertical bars) and benthic carbon oxidation fluxes (Cox_{avg} , open circles). Fluxes are in $\text{mmol m}^{-2} \text{d}^{-1}$. Error bars are based on the propagation of random errors from measured benthic fluxes.

Figure 6. Annual carbon budget for the Ría de Vigo presented as a summary of mean annual organic carbon fluxes. Rates in $\text{g C m}^{-2} \text{yr}^{-1}$. Upper left corner represents the carbon extraction rate from wild catch fisheries, shellfishing and mussel harvest, respectively. NEM: net ecosystem metabolism. GPP: gross primary production. PhoR: photic respiration. NCP: net community production. AphoR: aphotic respiration. BeR: benthic respiration. Runoff: inputs from continental runoff obtained from Evans et al. (2011).

Table 1. Summary of annual harvest for each faunal group, ratio Wet Weight (WW) : Organic Carbon (C), Carbon extracted from the system (Carbon flux) trophic level (TL), primary production required to sustain catches (PPR) and percentage of net community production (NCP) represented by PPR, in mussel raft culture, fisheries and shellfishing at the Ría de Vigo. Data were averaged for the area covered by the Ría de Vigo (117 km²), excluding San Simón Bay.

		Harvest Tn WW yr ⁻¹	Ratio WW/C	Carbon flux g C m ⁻² yr ⁻¹	TL	PPR g C m ⁻² yr ⁻¹	% PPR/ NCP
Mussel Raft	Mussel	34502^(a)	33.3 ^(c)	8.85	2	88.5	19.80
Fisheries		819^(b)		0.76		76.1	17.03
	Fish	528	8.7 ^(d)	0.52	3	51.8	11.59
	Cephalopod	214	10.8 ^(e)	0.17	3	16.9	3.78
	Crustacean	77	8.9 ^(f)	0.07	3	7.4	1.66
Shellfishing		1264^(b)		0.35		3.5	0.80
	Bivalves	992	33.3 ^(g)	0.25	2	2.5	0.57
	Sea Urchin	192	66.2 ^(h)	0.02	2	0.2	0.06
	Goose barnacle	80	8.9 ^(f)	0.08	2	0.8	0.17
Total		36585		9.96		168.1	37.63

^(a) Number of rafts: 474, annual production per raft: 72.18 Tn yr⁻¹ (Labarta, 1999)

^(b) Annual wild catches in 2006 (Peleteiro et al., 2008)

^(c) Pérez-Camacho & González (1984)

^(d) Czamanski et al. (2011)

^(e) Clarke et al. (1994)

^(f) Vinogradov (1953); Walve & Larsson (1999)

^(g) Ansell (1974)

^(h) Vinogradov (1953)

Fig. 1

Fig. 2

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6