

From ecological relevance of the ecosystem services concept to its socio-political use. The case study of intertidal bare mudflats in the Marennes-Oléron Bay, France

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From ecological relevance of the ecosystem services concept to its socio-political use. The

case study of intertidal bare mudflats in the Marennes-Oléron Bay, France.

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Highlights

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- Bare mudflats are the place of a high primary production based on benthic microalgae
- 41 Bare mudflats provide numerous ecosystem services, some of them remaining unknown
- Monetary assessments of ecosystem services—core of this approach—are restrictive
- Marennes-Oléron Bay case study illustrates these limits (e.g. unknown functions)
- Despite spreading out, the ecosystem service based approach needs to be reconsidered

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Keywords

- 47 Coastal ecosystem; intertidal bare mudflats; ecosystem services; economic valuation; socio-
- 48 political use.

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Abstract

Assessments based on monetary valuation of ecosystem services have been increasingly used as a tool to highlight the connection between ecosystems and society. The dissemination of this approach is leading to difficulties and ambiguities related to the use of such assessments in the socio-political realm. Such limits can be stressed using the case study of intertidal bare mudflats. These coastal habitats indeed provide many ecological functions—several being related to the high production of benthic microalgae—but also remain poorly known for some other aspects. The major users of these habitats (i.e. oyster farmers) are still unaware about the trophic role of benthic microalgae, limiting contingent valuation survey methods. Moreover, economic valuation cannot take into account the potentials of mudflats (i.e. undescribed functions) like positive feedbacks related to shellfish farming and provision of bioactive compounds. The lack of physical boundaries in marine systems also strongly reduces the effectiveness of assessments. Lastly, there are concerns that monetary valuation can lead to a commodification of the nature or to the economization of the environment (e.g. appropriation of the environment by users, creation of artificial thresholds). The evaluation of the functions of a socio-ecosystem should not only be restricted to a monetary assessment of its ecosystem services, as this framework may be more reductive than integrative. Some other descriptors not based on currencies—should be used for ecosystem description.

1. Introduction

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Coastal ecosystems host a high biodiversity, play a central role in the biogeochemical cycles of several major elements (e.g. carbon, nitrogen, silica), and are the place of a high biological production (up to 30% of the yearly total production on Earth) (Teal, 1962; Odum, 1980; Day et al., 1989; Valiela, 2010). These high diversity and productivity support key economic activities closely connected to coastal ecosystem functioning (e.g. aquaculture, fisheries). Tourism and business activities also highly developed in coastal areas during the last decades due their attractiveness, leading to the development of large infrastructures (e.g. harbors, cities) (Timmerman and White, 1997) and the increase of anthropogenic pressures, having a strong impact on the functioning of these ecosystems (e.g. drying-up by damming, discharges from the catchment basin) (Millennium Ecosystem Assessment (MEA), 2005; OSPAR Commission, 2009). In addition, coastal ecosystems can be highly affected by acute environmental pressures (e.g. storms) as well as global climate change (Ferns, 1983; Breilh et al., 2014). Therefore, management of coastal ecosystems has to be enhanced to better take into account Human-Nature interdependencies in environmental planning. In this aim, managers and stakeholders are in need of integrated (i.e. merging information from ecosystems and societies) and understandable measures that can be used to highlight the importance of ecosystems to the public and policy makers (Niemi and McDonald, 2004).

The concept of ecosystem services (ES) appeared to be a relevant approach to highlight Human-Nature interdependencies and the importance of coastal ecosystems for human societies. ES are the varied benefits that humans freely gain from the natural environment and from a properly-functioning ecosystem (MEA, 2005). The concept was introduced in the late 1980s as part of a new approach to considering the environment, developed within the ecological economics movement (de Groot, 1987; Costanza and Daly, 1992; Daily, 1997). The aim was to support an instrumental line of reasoning to demonstrate the dependence of human societies on an all-encompassing biosphere, and its indispensable contribution to all economic activities. Economic valuation of ES was indeed developed to warn societies about costs related to the lack of conservation measures (Costanza et al., 1997). A major strength of such an approach is that it can be used to consider the functioning of a socio-ecosystem on its whole. ES-based approaches were widely used as a reference in numerous scientific studies, particularly in the fields of economy (e.g. Farber et al., 2002; Sagoff, 2011; de Groot et al., 2012; Tuya et al., 2014), as well as in ecology (Barbier et al., 2011; Smale et al., 2013; zu Ermgassen et al., 2013; Seitz et al., 2014). As a result, the interest of economic valuation of ES quickly spread through diverse international and national initiatives following an anthropocentric and utilitarian approach (NRC, 2005; MEA, 2005; TEEB, 2010), as it was thought it could be used towards better environmental decision-making. However, as the concept of ES was developed in the aim to manage socio-ecosystems in a more sustainable way, it is of importance to highlight the limits and ambiguities related to this concept for its use in a socio-political framework.

Several studies and opinion papers already provide a critical view related to the monetary valuation of ES in ecosystem assessments (e.g. Spash, 2008; Norgaard, 2010; Gomèz-Baggethun and Ruiz-Pérez, 2011; Kallis et al. 2013; Gomèz-Baggethun and Muradian, 2015). Even if some of these papers rely on concrete illustrations (e.g. Kallis et al. 2013; Fisher and Brown, 2015; Rode et al., 2015; Rode et al., 2017), most of them remain quite conceptual, potentially restricting their audience to environmental economists, while, in the meantime, there is still a raise of interest of researchers in ecology and environmental planners in the use of ES based approaches to highlight the role of ecosystems. In this manuscript, we follow a more pragmatic path to complete the conceptual approaches criticizing the monetary valuation of ES that have been carried out for several years: We use a coastal habitat as a case study to first highlight the ecological functions it provides, as well as those that are still poorly known. We then carry out a critical analysis of the monetary valuation of ES referring to this factual ecological approach, and question the usefulness and the relevance of monetary valuation of ES from the viewpoint of its initial aim (i.e. highlight the dependence of human societies to the Nature).

The coastal habitat used as a case study are the intertidal bare mudflats, a typical and very widespread habitat in estuaries (Mc Lusky, 1989) (Fig. 1) especially along the European coasts (Scott et al., 2014). A particular focus will be put on the Marennes-Oléron bay mudflats, as this bay hosts the largest network of intertidal bare mudflats in France and has been studied for more than 30 years (Héral et al., 1989; Riera and Richard, 1996; Guarini et al., 2000; Leguerrier et al., 2007; Saint-Béat et al., 2014) (Fig. 2 and 3A). Intertidal bare mudflats play a major role in the functioning of coastal areas due to their high biological productivity (Cahoon, 1999; Blanchard et al., 2006; Kromkamp and Forster, 2006) and their central location among habitats in coastal areas, which supports the enrichment of adjacent terrestrial and marine ecosystems. Important economic activities (e.g. shellfish-farmers, fishermen, shellfish gatherers, tourists, birders) are closely related to the ecological functions provided by intertidal bare mudflats (Atkins et al., 2011; Böhnke-Henrichs et al., 2013; Liquete et al., 2013). The concentration of these activities on a relatively small area, in addition to expanding coastal urbanization,

generates a high pressure on this system; specifically, resource (e.g. water) and landscape use conflicts have been a crucial recurrent problem (Rivaud and Cazals, 2013; Sauzeau, 2014).

To highlight the functions (known and supposed) provided by intertidal bare mudflats, a first part of this manuscript describes the functioning of this habitat, with a particular focus on ecological functions. In a second part, we focus on the socio-political use of the concept of ES reviewing the way it changed how societies apprehend Human-Nature relationships, relying on the case study of mudflats. We then question the fundamental issues and ambiguities related to economic valuation of ES.

2. The case study of intertidal bare mudflats in the Marennes-Oléron Bay

2.1 A defining feature of intertidal bare mudflats: The high biological productivity of the microbial biofilm

Intertidal bare mudflats are characterized by a very high productivity (Blanchard et al., 2006; Kromkamp and Forster, 2006; Saint-Béat et al., 2013, 2014; Van Colen et al., 2014) and production can reach up to 390 g C m⁻² year⁻¹ in the Marennes-Oléron Bay (Guarini et al., 2000). Primary production comes from benthic microalgae, which size ranges from 10 to 150 µm (Fig. 3C) and which are mainly composed of diatoms (i.e. unicellular brown algae) in temperate intertidal bare mudflats (Haubois et al., 2005; Ribeiro et al., 2013).

In fine cohesive sediments (i.e. 'mud'), as in the Marennes-Oléron Bay, the high biological production rate is supported by a unique combination of physical, chemical and biological traits (Underwood and Kromkamp, 1999; Paterson and Hagerthey, 2001): 1. the high concentrations in nutrients in the sediment pore-water, as well as the peculiar light availability and the temperature modulations at the surface and in the sediment; 2. the behavioral adaptation of a major growth form of benthic diatoms (i.e. epipelon, Round et al., 1990) to this peculiar environment: epipelic diatoms can move freely between sediment particles—a unique ability in the plant kingdom—and typically form biofilms at the sediment surface (Fig. 3B); 3. the essential coupling between benthic (i.e. sediment) and pelagic (i.e. water column) physical and biological processes according to tidal and fortnightly cycles (Saint-Béat et al., 2014).

Epipelic diatoms show upward and downward migrations as a function of tidal cycle and photoperiod with a fine tuning by light, temperature and nutrient availability (Admiraal, 1984) (Fig. 4). During emersion, they can form a dense biofilm at the surface of the sediment, where they accumulate the energy they need for their metabolism (i.e. photosynthesis) (Fig. 4). When their energy quota is reached and/or when the timing for the next submersion of the mudflat is

close, they move downward into the sediment where they use nutrients and produce new biomass by dividing (Saburova and Polikarpov, 2003). Nevertheless, due to tidal currents and waves, part of the benthic diatoms can be resuspended in the water column on a daily basis, and contribute up to one third of the phytoplankton biomass in the Marennes-Oléron Bay (Guarini et al., 2004). Both the biological cycle occurring in the sediment and its coupling with the water column processes are essential in continuously stimulating the microalgal production (Guarini et al., 2006; Saint-Béat et al., 2014).

2.2 Roles of benthic microalgae in the functioning of intertidal bare mudflats and ecosystems: the known

2.2.1 Role of benthic microalgae in the functioning of mudflat and estuarine food webs

During emersion, the highly productive surficial algal biofilm (Fig. 3 and 4) fuels a large diversity of trophic groups of consumers: grazers (e.g. *Hydrobia ulvae*), suspension deposit feeders (e.g. *Scrobicularia plana*, *Macoma balthica*), harpacticoid copepods and epistrate feeder nematodes (Plante-Cuny and Plante, 1986; Riera et al., 1996; Haubois et al., 2005; Rzeznik-Orignac et al., 2008), which can themselves reach very high biomasses (Sauriau, 1987; Bocher et al., 2007). Benthic microalgae are a food resource of high quality (Cebrián, 1999) so they are more easily assimilated by consumers than benthic detrital material coming from seagrass or continental inputs (Lebreton et al., 2011). All meiofauna and macrofauna which rely on benthic microalgae are prey species for higher trophic level consumers like shrimps, fish (i.e. mullets, seabasses, flat fishes) (Kostecki et al., 2012; Carpentier et al., 2014) and birds (Saint-Béat et al., 2013), at both juvenile and adult stages, making intertidal bare mudflats essential nurseries for some of these species. These consumers themselves are resources for recreational and professional fishermen, as well as for hunters and birders (Owen and Williams, 1976; Feldman et al., 2000; Vasconcelos et al., 2010). Production rates of microalgae may thus directly benefit to the economic activity of professional fisheries and tourism.

During immersion, benthic microalgae are resuspended into the water column due to waves and tidal currents, which generates a strong link between benthos and pelagos (Saint Béat et al., 2014) (Fig. 4). As a result, benthic microalgae become available to suspension feeders (Riera and Richard, 1996; Choy et al., 2008) among which some are farmed and/or collected by shellfish farmers, professional fishermen and recreational gatherers (e.g. *Crassostrea gigas, Mytilus edulis, Tapes phillipinarum, Cerastoderma edule*). Benthic algae also largely support the pelagic food web when resuspended into the water column, by increasing phytoplanctonic

and bacterial productions (MacIntyre et al., 1996; Saint-Béat et al., 2014) that are very likely used by suspension feeders too. Additionally, resuspension of benthic algae allows their export to adjacent ecosystems and habitats (Saint Béat et al., 2014), where they can fuel other food webs.

As a result, benthic microalgae support the functioning of habitats (i.e. intertidal bare mudflats) often protected due to their value as a natural heritage (e.g. marine protected areas, nature reserves for migratory birds, hunting reserves), which contribute to the building of a strong territorial image, sometimes of international reputation (ecotourism, birding, gastronomy...). The importance of the ecological functions of the Marennes-Oléron Bay—and particularly of intertidal bare mudflats—has been recognized through the creation of the "natural marine reserve of the Gironde Estuary and of the Charentais Sounds" which covers 6500 km² and along 800 km of coastline (decree No. 2015-424 of April 15th, 2015 from the French Ministry of Ecology, Sustainable Development and Energy). Two national nature reserves have also been created in order to preserve large surfaces of intertidal bare mudflats: the Moëze-Oléron nature reserve, located in the Marennes-Oléron Bay, and the Aiguillon Bay nature reserve, located in the north of the Marennes-Oléron Bay (Fig. 2), covering large surfaces of intertidal bare mudflats as well.

2.2.2 Importance of benthic microalgae production in supporting shellfish farming

Benthic microalgae are a major food resource for oysters farmed in and close to intertidal bare mudflats (Riera and Richard, 1996; Kang et al., 2003). Oyster farming has a central role in the attractiveness of coastal areas and strongly participates to the identity of the Marennes-Oléron Bay and its associated intertidal bare mudflats. Oyster farming for business purpose has been carried out on the intertidal bare mudflats of the Marennes-Oléron Bay since the last third of the 19th century. Since 1853, the French government started to consider intertidal bare mudflats as maritime public domain and allowed oyster farmers to use them under a rental regime (Sauzeau, 2005). Nowadays, oyster farming is an important social and economic activity of the Charente Maritime French department (6 864 km²) from which the Marennes-Oléron Bay belongs to (Fig. 2), with yearly revenues of more than 300 million € after the Regional Authority for Food, Agriculture and Forests of Poitou-Charentes (Direction Régionale de l'Alimentation, de l'Agriculture et de la Forêt de Poitou-Charentes, 2012). At the national level, the Charente Maritime department is the first area for shellfish farming, both in terms of employments and farmed areas (Girard et al., 2009). The Charente Maritime department hosts the highest number (i.e. one third) of shellfish farming businesses in France, with 90 % (i.e. 908

businesses) dedicated to oyster farming after the Regional Committee for Shellfish Farming (Comité Régional de la Conchyliculture de Poitou Charentes, 2011). At the European level, the Charente Maritime department is at the first rank for the commercialization of the Pacific cupped oyster (*Crassostrea gigas*). The Charente Maritime department is also the only area in France where all the steps requested in the oyster production cycle can be carried out, from the collection of the spat in intertidal areas (Fig. 5A and B) to the fattening in ponds (Fig. 5F), until commercialization. Large areas of intertidal bare mudflats are used for oyster farming, where oysters are grown in plastic bags on metal trestles (Fig. 5C and D). Natural oyster reefs are also common at the vicinity of intertidal bare mudflats (Fig. 5E).

This historical importance of oyster farming led to multiple and complex connections with the territory. This activity indeed leads to the production of a product of high traditional value (i.e. oysters), symbolizing a specific corporate image and the healthy quality of the environment where oyster farming takes place (Grelon, 1978). Oysters farmed in the Marennes-Oléron bay are indeed certified, based on two national quality labels and a protected geographical indication (i.e. a certification of origin and of quality for agricultural products and foodstuffs awarded by the European Union). Such quality labels and certifications highlight the crucial economic importance of the oyster farming in the Marennes-Oléron Bay at both national and international levels. They obviously strengthen the identity and the patrimonial dimension of shellfish farming in the Marennes-Oléron Bay and in Charente-Maritime (Bérard et al., 2008).

2.3 Roles of benthic microalgae in the functioning of intertidal bare mudflats and ecosystems: the unknown

The studies carried out on the functioning of the intertidal bare mudflats during the last decades have provided a large amount of information about their functioning. But there are still important fields of research to develop on this habitat, some related to new research topics, and some related to the connection of this habitat with coastal ecosystems on their whole. Our aim here is not to provide an exhaustive review of research topics related to intertidal bare mudflats, but to highlight that knowledge is still lacking in some scientific fields.

2.3.1 Potentially valuable bioactive compounds provided by benthic microalgae

Benthic diatoms display a high degree of taxonomic, phylogenetic and functional diversity (Kooistra et al., 2007), including several growth forms mainly characterized by their habitat (i.e. more or less cohesive sediments) and their ecophysiology (Barnett et al., 2015). Related to this diversity, they synthesize a large range of molecules, which some are bioactive compounds,

with an obvious potential to identify and develop new drugs or innovative products (Hess et al., 2018). Uses include the synthesis of carbon neutral biofuels, pharmaceuticals, health foods, bioactive compounds, materials relevant to nanotechnology, and for bioremediation of contaminated water (Bozarth et al., 2009). While applications in biofuel (Levitan et al., 2014) and nanotechnology (Dolatabi, 2011) activities have recently received a major interest, this is less the case for bioactive compounds and their potential applications in human health and food, animal feed, cosmetics and nutraceutics industries. We identified two types of bioactive compounds synthesized by benthic diatoms that appear of special interest for future biotechnological or pharmaceutical applications: exopolysaccharides (EPS) and pigments.

EPS are extracellular polymeric substances containing different types of complex assemblages of polysaccharides and proteins (Urbani et al., 2012). Beyond their role in stabilizing sediment and counteracting the sediment erosion in bare mudflats (Stal, 2010), EPS from benthic diatoms are well known to having anti-bacterial properties (Amin et al., 2012). For instance, the diatom *Navicula phyllepta*, which is the dominant species of epipelic diatom in the mudflat of the Marennes-Oléron Bay (Haubois et al., 2005), has a specific anti-bacterial activity (i.e. inhibition of biofilm formation) on Flavobacterium sp., a genus of bacteria inhabiting bare mudflats, and known to be involved in cold water disease in wild and farmed salmonid fish (Duchaud et al., 2007; Dohgri et al., 2017). Diatom EPS could consequently be of potential interest in food and feed industries, and in medical and pharmaceutical applications. Two types of diatom inhabit intertidal habitats: epipelic diatoms, which use EPS to support their motility in cohesive sediment, and epipsammic diatoms, which use EPS to more or less firmly attach to less cohesive (i.e. sandier) sediment (Underwood and Paterson, 2003). Because of their different behavior in the sediment, these two types of benthic diatoms are likely to synthesize different quantities and types of EPS as previously observed for different growth forms of planktonic diatoms (Amin et al., 2012), making intertidal habitats, and especially Marennes-Oléron mudflats (de Brouwer et al., 2003), a potentially large reserve of a high diversity of bioactive compounds.

These distinct behaviors among benthic diatoms additionally drive differential responses to their light, temperature and salinity environment (Barnett et al., 2015; Laviale et al., 2015; Juneau et al., 2015) including synthesis of different quantities of 'photoprotective' pigments such as carotenoids. Precisely, xanthophyll carotenoids (e.g. diadinoxanthin, diatoxanthin), which are quasi-exclusive to diatoms (Kuczynska et al., 2015), are in higher amounts in epipsammic than in epipelic diatoms (Barnett et al., 2015; Blommaert et al., 2017). Xanthophyll carotenoids are well-known antioxidants (i.e. scavengers of intracellular oxygen radicals) and

are thus bioactive compounds of special interest for many profitable industries (Guedes et al., 2011; Christaki et al., 2012) including foods and feeds (Christaki et al., 2011), medical and pharmaceutical applications (e.g. cancer phototherapy, prevention of age-related macular degeneration) (Picot, 2014) and dermocosmetics (i.e. sun protection, aging prevention) (Abida et al., 2013).

2.3.2 Importance of mudflats in global carbon and nutrient cycles

Microalgae contribute to production of atmospheric O₂ through photosynthesis and can mitigate the on-going atmospheric CO₂ increase (Raven, 2017)—that drives global warming—as they use it for their growth. It is likely that benthic microalgae have a strong role in this function due to their very high production rate (Guarini et al., 2000), even if areas of intertidal bare mudflats are only located along shorelines. Information about the role of benthic microalgae in this cycle exists at the scale of the habitat (Underwood and Kromkamp, 1999) but there is now a need to assess this role at a more global scale, likely through modeling. Such assessments are complex to carry out due to methodological issues, as they rely on large spatial datasets, implying considerable sampling efforts.

Benthic diatoms also play a very important role in nutrient cycles, especially N and Si, as the frustule of benthic diatoms is made of silica. Intertidal bare mudflats are located at the mouth of estuaries, where high loads of nutrients (i.e. nitrogen) can be released. Thanks to their high production rate, benthic microalgae can reduce eutrophication, and therefore limit the blooms of toxic phytoplankton and macroalgae (Valiela et al., 1997; Anderson et al., 2002). As for CO₂ trapping, it is of high need to assess at the ecosystem scale the role of intertidal bare mudflats in the trapping of these nutrients. As for CO₂ trapping, such assessments are challenging as they rely on accurate estimations of biomasses and production at a large spatial scale.

Recent advances in satellite remote sensing based on microalgal pigment reflectance now enable to decipher the spatial and temporal dynamics of microalgal biomass at the scale of an entire mudflat, and may therefore be very useful for large scale assessments (Méléder et al., 2010) (Fig. 6). This ecosystem-scaled approach recently permitted to understand 1. the seasonal and interannual variations of microalgal biomass (van der Wal et al., 2010; Benyoucef et al., 2014), 2. the negative impact of extreme climate events such as heat waves (Brito et al., 2013), 3. the tight relationship between microalgal biomass and human activities, such as oyster farming (Kazemipour et al., 2012). The successful launch of the European Space Agency Sentinel-2 satellite with its high resolution optical sensors and high revisit frequency (Gernez et al., 2017) will certainly increase the capability to analyze macro-scale spatio-temporal

variations of benthic microalgae. However, the most promising advances will probably come from hyperspectral sensors that will soon be available onboard satellite. High spectral resolution has the potential to discriminate the main groups of benthic microalgae, as well as macroalgae and aquatic plants (Barillé et al., 2017), and to infer primary production (Méléder et al., 2018).

3. Socio-political use of the ES concept

In view of this presentation, the ES concept appears to be an analytical framework that can be easily mobilized to highlight the functions provided by coastal ecosystems to human societies: e.g., the primary production of benthic microalgae as a supporting service, the nitrogen removal as a regulating service (Table 1). Nevertheless, the conversion of ecological functions into ES could be perilous. Given that the ES concept is clearly and intrinsically linked to the objective of the sustainable management of socio-ecosystems, it is essential to question the socio-political use of the ES concept. Indeed, what can be said regarding the mobilization of ES in the framework of public policies and institutional reforms that aim to integrate the environmental challenge into the development model of contemporary society?

3.1. From ecological concerns to a tool used for ecosystem assessment

The aim of the ES approach, developed within the ecological economics movement (de Groot, 1987; Costanza and Daly, 1992; Daily, 1997), was to demonstrate the dependence of human societies on biosphere and its indispensable contribution to all economic activities. The objective was to propose, as part of a systemic approach, a series of conceptual innovations to reformulate the analytic frameworks of environmental economics, which were considered as too simplistic and often unrealistic (Norgaard, 1989). As previously described using the intertidal bare mudflats of the Marennes-Oléron Bay as a case-study, the application of this concept involves consideration of ecosystems for their functions as well as the services provided to society by these functions.

However, there has been a more specific nature of the socio-political use of the ES concept since the late 1990s, following the publication of the well-known article by Costanza et al. (1997). Adopting the language of monetary valuation, Costanza et al. (1997) estimated the annual value of ES to be about US\$33 trillion in 1995 dollars, which would have equated to US\$46 trillion in 2007 dollars (this value was updated to US\$125 trillion in 2007 dollars in Costanza et al. (2014)). The aim of this calculation of substantial economic value of ES was intended to alert policymakers to the fundamental role of wildlife for human well-being and the need to curb environmental damage.

In doing so, the pragmatic nature of the economic valuation of ES struck a chord in the academic world, and from the 2000s it emerged as a language that was considered relevant in the political arena. Major initiatives carried out at the international level—such as the MEA (2005), which provides a reference classification for ES, or TEEB (2010) with its focus on "making nature's value visible" to support public decision-making—are more or less along these lines and use ES as a framework. Several monetary valuation exercises on the market and non-market values of ES have been carried out at various scales (Breeze et al., 2015; Remme et al., 2015; D'Amato et al., 2016). In addition to its use as a mean of raising awareness among human societies, as endorsed and reaffirmed by Costanza et al. (2014), economic valuation is progressively seen as an essential tool of governance assistance: "You cannot manage what you do not measure" (TEEB, 2010).

Moreover, by demonstrating the value of nature, the ES economic valuation exercise transforms the relationship between the socio-economic sphere and the environment. The integration of environmental concerns is no longer viewed solely from the perspective of an obligation (i.e. a system to preserve), but can also be seen as an economic opportunity (i.e. a system to exploit) (Girouard, 2010). This shift corresponds to the emergence of the idea of the green economy, which is less exploitative and damaging in terms of the environment, while also potentially providing a source of investment and innovation, which is progressively becoming part of an inclusive growth concept encompassed by the term "Green Growth" (The World Bank, 2012).

As a result, economic valuation of ES became a cornerstone in the scientific and political arenas for the understanding of sustainability issues (Prévost, 2016). The large range of aims of the economic valuation of ES is nevertheless questioned in both the academic literature and in public debate. Beyond the argument of pragmatism related to ES valuation developed during the last 20 years, our aim is to question more precisely how ES valuation has changed the representation and the construction of human-nature relationships. To this end, we based our analysis on diverse international environmental conventions. These conventions can indeed be considered as a system for the production of formal social rules, with the purpose of organizing interactions between human activities and the environment. This step in the reasoning process is a prerequisite to further question the benefits of the ES concept within the framework of the Marennes-Oléron bay intertidal bare mudflat case study.

3.2. An evolution of the representation of human-nature relationships

The dissemination of the ES concept is part of a significant evolution of the relationship between society and nature, a first sign of which was identified at the Rio United Nations Conference on Environment and Development in 1992. While this conference put environmental and development issues at the forefront of the international community's concerns, it also marked a break in the definition of the value of nature, which until then had been considered independently of its direct value to humans. Indeed, international conventions adopted after the 1972 Stockholm Conference emphasized the heritage aspect of nature and the intrinsic dimension of its value: the 1979 Bonn Convention on Migratory Species recognizes in its preamble that "wild animals (...) are an irreplaceable part of the earth's natural systems"; the Bern Convention on the Conservation of European Wildlife and Natural Habitats, also signed in 1979, states that "wild flora and fauna constitute a natural heritage of aesthetic, scientific, cultural, recreational, economic and intrinsic value"; the World Charter for Nature proclaimed in 1982 explicitly acknowledged that "every form of life is unique, warranting respect regardless of its worth for humans, and, to accord other organisms such recognition humans must be guided by a moral code of action". The aim of all these texts is to emphasize, from a perspective known as ecocentric, the value of nature per se, and on the moral dimension of the recognition of this value as applied to all living organisms (Prévost et al., 2016).

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The change in perspective that occurred in 1992 during the Rio conference concerns the introduction of an anthropocentric foundation as a motive for conservation and environmental management. In the Convention on Biological Diversity that resulted from this conference, the intrinsic value of nature is not entirely denied. Indeed it is stated in the preamble that the contracting parties are "conscious of the intrinsic value of biological diversity and of the ecological, genetic (...) values of biological diversity and its components". However, an important part of the debate has concerned the economic losses related to the erosion of biodiversity and, on the other hand, the economic opportunities related to its exploitation. Recognizing for each state "the sovereign right to exploit their own resources pursuant to their own environmental policies, and the responsibility to ensure that activities within their jurisdiction or control do not cause damage to the environment of other States or of areas beyond the limits of national jurisdiction" (Article 3), the Convention ultimately contains a major contradiction with regard to the consideration according to which biodiversity is "a common good of humanity, a world heritage, etc." (Tsayem Demaze, 2009). Thus, the text places great emphasis on the utility or economic and industrial value of biodiversity and biotechnologies, to the detriment of the preservation of ecosystems as a habitat for fauna and flora. In this text, biodiversity is not granted with the status as a common heritage of humanity.

In this specific context, the introduction and dissemination of the ES concept carries an anthropocentric representation of human-nature relationships. It also provides an analytical framework leading to a new definition of the value of the nature (McCauley, 2006; Sagoff, 2008). This value would fundamentally depend on the benefits derived from ecosystems by and for humans for their survival and/or well-being. In other words, the concept of the intrinsic value of nature is progressively being replaced by a utilitarian acceptance of value, which was reaffirmed in the 2010 Nagoya Protocol on Access to genetic resources and the fair and equitable sharing of benefits arising from their utilization. This protocol recognizes that the public awareness of the economic value of ecosystems and biodiversity, as well as the sharing of this economic value with "the custodians of biodiversity are key incentives for the conservation of biological diversity" (Preamble). As a result, this protocol potentially challenges the mechanisms and the tools used in environmental management, as these tools are issued from the fundamental principles of prevention and precaution (Naim-Gesbert, 2014; Prieur, 2011). These mechanisms and tools are questioned in favor of a procedure highlighting and protecting ES. This procedure is based on incentive and contractual management instruments, which fall under the category of Market Based Instruments (Gómez-Baggethun and Muradian, 2015).

By applying this reasoning to the case study of the Marennes-Oléron Bay intertidal bare mudflats, we emphasize the decisive role of scientific knowledge on the functioning of the ecosystem to envisage management measures based on ES. At present, although we are able to accurately describe various ecosystem functions, as demonstrated above, the scientific community acknowledges that all of the mechanisms of interaction between humans and the environment are not perfectly understood. For example, a good account has been made of the benthic microalgae-based food web (Leguerrier et al., 2007; Saint-Béat et al., 2014), which makes it possible to state that this habitat is favorable to the development of oyster farming and satellite remote sensing has recently shown that oysters have a positive impact on benthic microalgae (Echappé et al., 2018). In contrast, knowledge about the impact of human activities on primary production (i.e. the feedback effects) is in its infancy. For instance, would a change in the use of the foreshore by oyster farmers have an impact on production and on the microalgae biomass on mudflats¹? As a result, the issue of preservation in the name of existing

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¹ A research program (2015-2018) funded by the Fondation de France is currently underway on this issue "DYCOFEL: Human-Nature Interdependencies: Dynamic analysis of the relationships between changes of practices in shellfish farming and functioning of coastal ecosystems".

services is becoming restrictive. Similarly, the largely unexplored potential of mudflats in terms of valuable bioactive compounds for health, for example, are related to future scientific discoveries and therefore difficult to take into account when assessing ecosystem services. One of the questions that accompanies the development of the ES-based approach ultimately relates to the key role of expertise in our understanding of human-nature relationships (Carpenter et al., 2009), and consequently to the ability of this analytical framework to take into account functions and services that are not yet known at the time of the description of a given ecosystem.

In addition, the evolution of society's relationship to nature, which has led to the latter being evaluated and accounted for in terms of the benefits derived from ecosystems, implies that the values obtained, particularly through economic analysis, are sufficiently meaningful to inform public decisions. At this stage, it is important to highlight the difficulties and even ambiguities that persist around the production of these economic values and their use.

3.3. From difficulties to ambiguities of the monetary assessment of ES

As we have already underlined, the economic and monetary assessment of ES raises high hopes for environmental management (NRC, 2005). This evaluation is based on a sequential logic, in which life sciences reveal the functions of ecosystems in terms of supply, regulation and/or support, for which economists seek to translate the functional value into monetary units using technical equipment that is supposedly neutral and objective (i.e. methods that have been used in the field of environmental economics since the 1970s, which aim to show the preferences of economic agents for nature). The economic and monetary valuation of ecosystems thus produced would have several applications (Laurans et al., 2013) as summarized in table 2.

While economic valuation is now a major component of the way in which environmental issues are addressed in the perspective of ES, it is however subject to major criticism. Without attempting to be exhaustive, given the abundant literature on the subject (e.g. Chee, 2004; Gómez-Baggethun and Ruiz-Pérez, 2011), it seems that the debate on the monetary assessment of ES revolves around two main themes: 1. The capacity of the economy and its tools to produce a meaningful value for nature; and 2. The purpose of the economic value produced. In this section we aim to illustrate these two lines of criticism using the case study of the intertidal bare mudflats of the Marennes-Oléron Bay.

3.3.1. The difficulties of ES valuation

The first theme reflects the long-running criticism of the environmental assessment methods of neoclassical economics (Daly, 1992) and relates to several difficulties, the most important ones, in relation to our study, are discussed here.

Firstly, most valuation methods concerning ES are based on the contingent valuation survey methods. The main objective of these methods is to give a price to environmental goods or services in cases where either the market fails to do so, or there is simply no relevant market. To some extent, these methods are a substitute for markets and they reproduce the same mechanism, i.e. the expression of an informed choice after a rational trade-off between gains and losses regarding the different alternative choices. It refers to individual preferences, either revealed by actual behavior or stated in surveys. Yet, the main failures of individual choice concerning the value of ES are due to a lack and asymmetry of information: economic agents may have no familiarity with a particular service, or have no understanding of its benefits (Pritchard et al., 2000; Salles, 2011). Moreover, agents may misinterpret or lack knowledge about the ecological processes they have an involvement with and, as a result, may not be able to assess their whole mechanisms and effect of their choices on these ecological processes. Such a limitation may be extended to include a lack of knowledge concerning the impact of ecological processes on the well-being of other individuals, and that of future generations (Medvecky, 2012). This limitation is striking in the case of intertidal bare mudflats as even the shellfish farmers—who are the major economic agents in intertidal bare mudflats—do not suspect any role of the benthic microalgae and of intertidal bare mudflats in oyster farming processes.

Secondly and more broadly, economic evaluation is limited by the state of scientific knowledge at a time *t* on the functioning of ecosystems and on the nature of the dependencies with human societies, as mentioned in 3.2. In other words, such an evaluation cannot take into account the potential of ecosystems in terms of functions that are yet to be described, related to ecological processes that are less well known, which runs the risk of underestimating their importance. This is typically the case for habitats like intertidal bare mudflats, the functioning of which has been much less studied than some other types of coastal or terrestrial habitats. To our knowledge, the first systemic descriptions of intertidal bare mudflat functioning were done in the late 1970s (Warwick et al., 1979; Admiraal, 1984; Asmus and Asmus, 1985), in contrast to other coastal habitats that have been studied for much longer (e.g. salt marshes, seagrass beds...) (Teal, 1962; Thayer et al., 1975; Kikuchi and Pérès, 1977). The first ecosystem valuation of a coastal habitat was thus carried out in marshes in 1974 (Gosselink et al., 1974; Odum and Odum, 2000). As a result, there is much less scientific knowledge about intertidal bare mudflats even though they also provide very important functions (see 2). The lower level

of interest shown by human societies, including scientists, is very likely related to the microscopic size of its main primary producers (i.e. benthic microalgae) and of some very important groups of consumers (e.g. microfauna, nematodes, benthic copepods) which makes these systems less attractive and much more complex to study. Even though some people (e.g. shellfish farmers, professional and recreational fishermen) are highly dependent on the ecological functions of microalgae in bare mudflats, they do not take these microorganisms into consideration, nor do they even know their role or existence, because they are not directly observable. Changes to the population structures of microalgae or its consumers are therefore usually invisible to almost all users of this habitat. Moreover, the identification of ES and of human-nature interdependencies is getting more complex in ecosystems highly connected to adjacent ones and which boundaries are sometimes difficult to define, as functioning of these systems also relies on larger scale processes (e.g. freshwater inflows, meteorological processes, animal migrations). This is typically the case in coastal ecosystems like intertidal bare mudflats, as their functioning is generally very complex due to tight connections to open waters and drainage basin, leading to important flows of matter and energy between these systems. Another issue is the structure of coastal ecosystems which is strongly based on gradients (e.g. salinity gradients in estuaries, nutrient gradients in water), which means there is a lack of clear boundaries between systems (Day et al., 1989; McLusky, 1989).

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Along these lines we can mention, thirdly and finally, that a significant part of the criticism concerns the fact that economic assessment methods are more or less unable to take into account factors such as system complexity, time, uncertainty, threshold effects and potential irreversibility (Georgescu-Roegen, 1971; Daily et al., 2000; Daly and Farley, 2004). This is particularly true for coastal ecosystems, as their functioning is driven by many abiotic parameters (e.g. light, temperature, nutrient concentrations...) leading to complex temporal variations that range from daily (i.e. tides) to annual (i.e. seasons) and decadal (i.e. North Atlantic Oscillation, El Niño Southern Oscillation) fluctuations. Coastal ecosystems are also highly sensitive to irreversible impacts, such as diseases (Den Hartog, 1987), invasive species (Daehler and Strong, 1996) that can easily spread through these systems following their introduction via aquaculture or ballast waters, or as a consequence of species migration related to global change (Bax et al., 2003). Moreover, it is acknowledged that if the different components of an ecosystem are studied individually, the combination of the attributes of each component does not reflect the overall attributes. Some attributes of an ecosystem, known as emergent properties, can indeed only be revealed when assessing the ecosystem on its whole (Leguerrier et al., 2007). However, the approach that aims to evaluate ES necessarily involves segmentation, which only provides a partial representation of the system (Turnhout et al., 2013). As a result, issues related to a piecemeal approach, which is potentially disconnected from the functioning of complex ecosystems, incur a risk that should be highlighted.

3.3.2. Pricing: for what purpose?

By placing the issue of economic value at the heart of the environmental challenge, and by building on the analytical reference tool that exists in the field of standard economic theory, the ES approach is ultimately limited (Norgaard, 2010). While economic modeling should not necessarily be avoided on the grounds that it involves major simplifications of a complex reality, we should, particularly in relation to nature, use the results of such modeling with extreme caution (Costanza et al., 2014). This observation leads us to the second theme of the debate, which is triggered by the development of the economic valuation of ES.

Some of the literature indeed highlights a concern for the purpose of the economic value generated (Gómez-Baggethun and Ruiz-Pérez, 2011; Arsel and Büscher, 2012). There is a particular emphasis on the fear that the monetary assessment of ES is a first step towards the commodification of the environment (McCauley, 2006; Turnhout et al., 2013). The promotion of conservation instruments such as payments for ES plays a significant role in the expression of this fear (Karsenty and Ezzine de Blas, 2014). More broadly, the growing use of market-based instruments based on the monetary assessment of nature is sometimes regarded as part of the commodification of the environment, which is part of an extension of the neoliberal logic (Parr, 2015; Knox-Hayes, 2015). It should however be noted that this particular criticism is based on the superficial equation of economic theory with its practical implementation and the tendency to label the whole system as neoliberal, ranging from research to decision-making bodies, while the practical application of this type of instrument shows that the market is only rarely called upon (Vatn, 2010; Muradian and Rival, 2012). Such misconceptions generate confusion, weakening the initial aim of economic valuation of nature, which was to highlight the importance of the environment to human societies (Prévost, 2016).

While the monetary assessment of ES does not necessarily imply the commodification of nature, the importance of the economic value of ES in the construction of environmental public choices seems to leave aside at least three important societal issues. The first relates to the rationale of the appropriation of the value of ES, a subject that remains little studied. We are still at the point of discovery regarding the economic value of services from ecosystems. However, through the use of economic valuation, the preservation of ecosystems tends to be part of a rationale of financial incentives to adopt practices for the benefit of the environment.

If, for example, an economic assessment was to be carried out on the positive effects of oyster farming (e.g. increase of water quality, coastline protection) (Grabowski et al., 2012) on the Marennes-Oléron Bay ecosystem, would oyster farmers request payments in return for the services that they consider they provide to this ecosystem, in the same way as European farmers are remunerated for agricultural multifunctionality? (Potter and Tilzey, 2007). In the absence of a democratic debate on large-scale property rights, it is quite possible that the development of pricing metric approaches may open new spaces of appropriation (Dempsey and Robertson, 2012).

The second issue is that monetary valuation creates artificial thresholds for funding ecosystem conservation and restoration actions. Many ecosystem services are likely difficult to price (see 3.3.1), for example, ecosystem protection is often driven by cultural services (e.g. sense of place), which may carry less weight than provisioning services (e.g. food production) when translated to economic terms. Incomplete monetary valuation of ecosystem services can result in insufficient funds to compensate for habitat or ecosystem loss; in this case, the value for restoring an area of habitat is unequal to the amount that area of habitat is worth (Fisher and Brown, 2015).

The last issue relates to the effective power of the monetary value of ES in the context of environmental degradation. Recent experimental work (Rode et al., 2017) highlighted the fact that monetary justifications do not systematically play their intended role of raising the alarm. Indeed, the authors point out that arguments citing the loss of ES (without attaching a monetary value) significantly reduce the approval rating of experiment participants regarding the construction of environmentally damaging infrastructure, while moral-ecological arguments seem even more likely to lead to the rejection of proposed developments (a combination of the two argument types leads to the highest rejection rates for infrastructure installation). Taking the monetary values of ES into account, on the other hand, can either decrease or increase the approval for the installation of infrastructure (Rode et al., 2017). Therefore, it seems legitimate for us to question the necessity of monetary valuation for environment and ecosystem protection, especially since the values obtained are highly debatable.

4. For a return to the use of non-monetary synthetic descriptors

While monetary valuation of ES does not appear as a good tool for management and decision making (Table 3), there is still a real need to use synthetic descriptors of ecosystem functioning. We suggest that such descriptors should not be based on anthropocentric units such as currencies. Such non-antropocentric units have already been developed for a long time, such

as the "emergy" (spelled with an "m"), which is a descriptor taking into account all the energy used or transformed to product a good or a service. This descriptor can also be described as the "memory of the energy used to produce something", leading to the term emergy (see more in Odum and Odum, 2000). Foundation of this approach is based on the principle that an ecosystem is producing goods and services in their whole, contrary to valuation methods which are based on their usefulness as seen by users, which is very relative. Ecological network analyses and their related indices (Baird, 2011; Niquil et al., 2011) are also very promising approaches to better assess the functions provided by a habitat or an ecosystem as these approaches are systemic and can be carried out at the ecosystem scale. It has been recently, and successfully, used for intertidal bare mudflats (Saint-Béat et al., 2013, 2014). Such approaches could therefore be used to describe the functioning of ecosystems, as well as their importance to societies, without relying on monetary assessments.

5. Conclusion

In theory, the concept of ES appears as providing an interesting framework to highlight the significance of ecosystems to human societies, and the use of ES-based approaches for the valuation of ecosystems and of their functions is tempting. Nevertheless, a cautious position should be adopted regarding this approach. The concept of ES itself has been already largely criticized in the literature. Beyond these epistemological considerations, the case study of intertidal bare mudflats points out issues related to the assessment of the monetary value of ES in their whole. This habitat indeed provides many ecological functions, among which many of them are not yet known. As a result, comprehensive analyses of such socio-ecosystems cannot be restrained to an ES-based approach, which is more reductive than holistic, and then may be risky. In the case of intertidal bare mudflats, such an approach would indeed not take into account some important but barely known—or even undescribed—, ecological potentials of this habitat. It would be relatively reductive as well because the transfer of knowledge about ecological functions of this habitat to economical agents has not yet been done. We therefore recommend researchers and environmental planners to rely on other synthetic descriptors that are not based on currencies.

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Tables

Category			
Supporting services	- Primary production: Production of marine food resources of high quality that		
	support, e.g., shellfish farming and gathering, fisheries, aquaculture.		
	- Nutrient cycling (carbon, nitrogen, silicates).		
	- Atmospheric O2 production.		
Provisioning services	- Bio- and chemo-diversity: Production of bioactive compounds used in, e.g.,		
	biotechnology, pharmacology, food and feed industry, cosmetics.		
Regulating services	- Global climate regulation: fixation of atmospheric and water dissolved CO2.		
	- Quality of coastal waters: bioremediation of contaminated water (e.g. nitrogen		
	fixation).		
	- Reduction of coastal erosion: production of cohesive exopolysaccharides.		
Cultural services	- Support the ecosystem functioning in protected patrimonial areas: e.g. marine parks, migratory shorebird reserves.		
	- Support the regional identity with international scope, e.g., gastronomy, tourism.		
	- Specific landscape and buildings related to recreational fisheries and oyster		
	farming.		

Table 1. Examples of ecosystem services provided by intertidal bare mudflats as categorized by the Millenium Ecosystem Assessment (2005).

Decisive AESV (for a specific decision)	AESV for trade-offs "By proposing a monetary value for ecosystem services, AESV can help factor related concerns into the cost-benefit analysis that underpins the trade-offs made by decision-makers" Participative AESV "Economic analysis [is considered] as a negotiation language" AESV as a criterion for environmental management "Given the limited budgets allocated to the protection of ecosystem services, AESV can help prioritize conservation efforts within an organization, in an optimal way". It can facilitate the identification of options that are most likely to maximize benefits, or of which territories contribute most to ecosystem
"Technical" AESV (for the design of an instrument)	services. Investment priorities may then be defined accordingly." AESV for establishing levels of damage compensation "An agent responsible for the degradation of ecosystem services may be obliged to pay compensation for such damage. () AESV provides guidance for administrative decisions or court rulings that determine the amounts to be paid out." AESV for price-setting "In cases where an economic instrument has been decided, AESV can be used to determine the amounts payable on the basis of a willingness-to-pay or willingness-to-receive logic, such as payments made by the beneficiaries of services in the case of payments for ecosystem services, entrance fees to protected areas, etc."
Informative AESV (for decision- making in general)	AESV for awareness-raising "Informative AESV may be seen as the vector for a broad message concerning the preferences that should be mainstreamed into society, particularly to ensure that ecosystem services considerations are integrated into public and privates choices." AESV for justification and support "An Informative AESV can be used by a stakeholder to promote a given course of action, as opposed to AESV for trade-offs where valuations are deemed neutral and inform an optional choice." AESV for producing 'accounting indicators' "Informative AESV are applied in situations where valuation is designed to ensure that decision-makers, or the general public, remain informed of the state of natural capital. This information can be taken into consideration for decision-making in general."

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Table 2. The different applications of ecosystem services valuation (AESV), after Laurans et

al. (2013), modified.

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Ecosystem services framework	Main criticism	Illustration based on the Marennes-Oléron Bay case study	Sections
Promotion of an anthropocentric argument for ecosystem preservation	Conservation approaches limited to ecosystems already well described by scientists	Potentialities related to unknown bioactive compounds Lack of knowledge about positive feedbacks of oyster farming on ecosystem functioning	2.3.1 & 3.2
Monetary valuation	Economic assessment methods more or less unable to take into account factors such as system complexity, time, uncertainty, threshold effects and potential irreversibility	Functioning of mudflats driven by several abiotic parameters, leading to complex temporal variations ranging from day to decades High sensitivity of coastal ecosystems to irreversible impacts (e.g. invasive species like Spartina anglica; decline of Zostera marina due to the wasting disease)	3.3.1
	Combination of the attributes of each component which does not reflect the overall attributes of an ecosystem when all different components are studied individually	Emergent properties of mudflats can only be determined based on holistic approaches	3.3.1
Promotion of the contingent survey method	Tightly connected to individual preferences: lack and asymmetry of information	Lack of knowledge of users (e.g. oyster farmers) about the role of benthic microalgae in the functioning of mudflats	3.3.1
	Limited by scientific knowledge: evaluation cannot take into account the potentials of ecosystems for undescribed functions	Potentialities related to unknown bioactive compounds Lack of knowledge about positive feedbacks of oyster farming on ecosystem functioning Difficulties related with approaches at the ecosystem scale (costs, methodological locks)	2.3.1 & 3.3.1
	Limited by scientific knowledge: Knowledge improvement can depend on methodological issues	Microscopic size of benthic diatoms Accessing to mudflats is challenging	3.3.1
	Risk of commodification of the environment	No market based instrument in the Marennes-Oléron Bay	3.3.2
Market based instruments	Risk of instrumentalization of ecosystem protection	No market based instrument in the Marennes-Oléron Bay e.g. would oyster farmers request payments in return for the services that they consider they provide to coastal ecosystems?	3.3.2
	Risk of setting-up of artificial thresholds for funding ecosystem conservation and restoration actions	No market based instrument in the Marennes-Oléron Bay	3.3.2
	Higher weight of moral ecological arguments compared to monetary arguments	No market based instrument in the Marennes-Oléron Bay	3.3.2

Table 3. Synthesis of the main criticisms about the ecosystem services framework and the monetary valuation using the intertidal bare mudflats of the Marennes-Oléron as a case study.

1181 Figure captions

- Fig. 1. Examples of intertidal bare mudflats throughout tropical, temperate and polar zones
- illustrating their worldwide distribution.

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- Fig. 2. Map of the Charentais Sounds displaying the location of the Marennes-Oléron Bay, the
- Aiguillon Bay, the intertidal zone and the areas used for shellfish farming.

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- Fig. 3. A. Intertidal bare mudflat in the Marennes-Oléron Bay during low tide. Details of the
- biofilm of microphytobenthos at the sediment surface (B) and of the pennate diatoms
- 1190 constituting the biofilm (C, optic microscopy, X 100).

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- Fig. 4. Conceptual diagram of the processes leading to microphytobenthos primary production
- on intertidal bare mudflats in relation with the alternance of tides: Upward migration of diatoms
- during low tide and process of suspension of benthic diatoms in the water column at high tide
- 1195 (modified from Blanchard, 2006).

1196

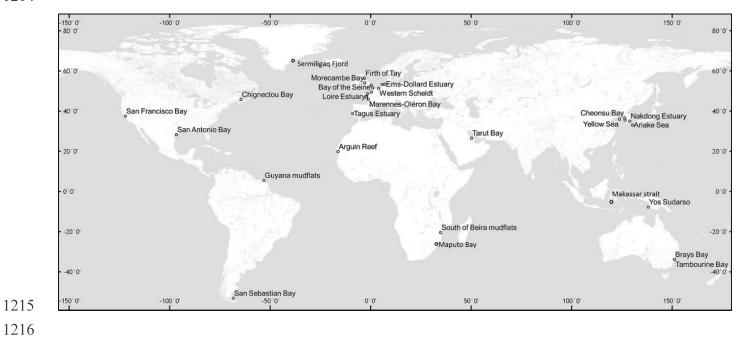
- Fig. 5. Specificities of oyster farming in the Marennes-Oléron Bay: Artificial collectors: PVC
- dishes (A) and tubes (B) used for natural settlement of the spat of *Crassostrea gigas*. Oysters
- growing in plastic bags on metal trestles (C and D). Natural oyster reef formed by clusters of
- vertically-growing oysters (E). Web of salt marsh ponds used for the fattening of oysters (F):
- square ponds in the foreground and in the background have been modified by oyster farmers
- while the larger diversity of pond shapes in the middle of the picture indicates those still have
- their initial salt flat shape.

1204

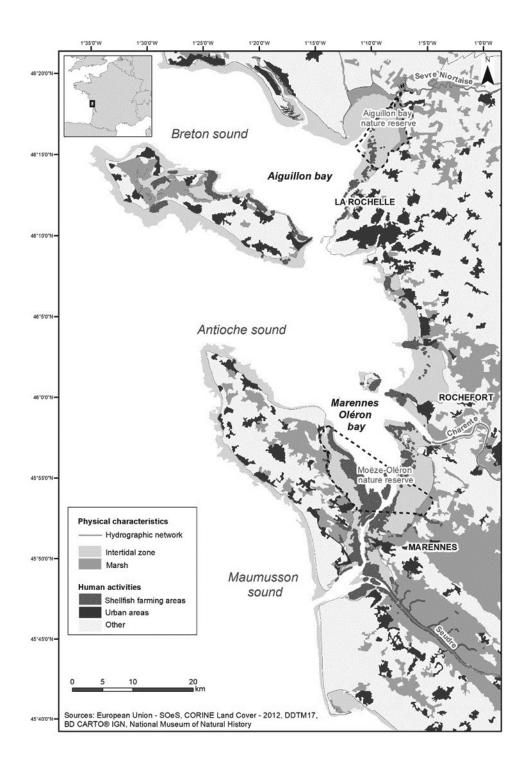
- Fig. 6. Satellite remote sensing image of the eastern side of the Marennes-Oléron Bay in
- 1206 September 2012. Microphytobenthos is identified with a normalized difference vegetation
- index (NDVI), with a threshold between 0 and 0.3. Red color indicates the highest level of
- biomass. The dotted polygons represent shellfish farming areas. SPOT 5 satellite image with a
- spatial resolution of 20 m.

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1217 Figure 2

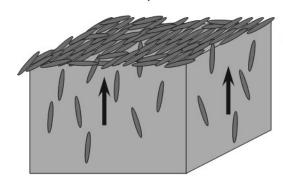




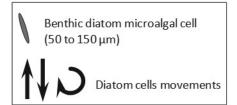
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Diurnal emersion

Sediment upward migration Biofilm formation Photosynthesis



Food for benthic consumers



Diurnal immersion

Sediment downward migration Cell division

Resuspension in the water column

Water column

Sediment

- ➡ Production of new microalgal biomass
- Food for pelagic consumers

