
Network analysis and inter-ecosystem comparison of two intertidal mudflat food webs (Brouage Mudflat and Aiguillon Cove, SW France)

Delphine Leguerrier^a, Delphine Degré^{a, b} and Nathalie Niquil^{a, *}

^aCentre de Recherche sur les Ecosystèmes Littoraux Anthropisés (CRELA, UMR 6217 CNRS-IFREMER-Université de La Rochelle), Pôle Sciences et Technologie, avenue Michel Crépeau, 17042 La Rochelle Cedex 1, France

^bOffice National de la Chasse et de la Faune Sauvage, Réserve Naturelle de la Baie de l'Aiguillon, Ferme de la Prée Mizottière, 85450 Sainte-Radegonde des Noyers, France

*: Corresponding author : Niquil N., email address : [nniquil@univ-lr.fr](mailto:niquil@univ-lr.fr)

Abstract:

Network analysis was used to analyse steady-state models of the food webs of two intertidal mudflat ecosystems: Aiguillon Cove and Brouage Mudflat, on the South-Western Atlantic Coast of France. The aim was to highlight emergent properties of food-web functioning in these two ecosystems and to compare these properties with other coastal ecosystems. Both ecosystems imported detritus in parallel to a high benthic primary production. They were characterised by a high diversity of resources. Both also exported living material, leading to a high quality production, quantified as export of Exergy. This export was mainly composed of cultivated bivalves during the cold season for Brouage Mudflat, and of the migration of grazing fish in Aiguillon Cove during the warm season. Their internal organization was characterised by short pathways, high recycling, high redundancy and low net ecosystem production, compared to the other systems selected. These characteristics, encountered in many estuaries, presented less extreme values.

Keywords: food web; ecosystem comparison; inverse analysis; network analysis; intertidal mudflat; Atlantic coast

Introduction

In coastal management, it is necessary to have an overview of ecosystem functioning which is necessarily done through a holistic description (Jørgensen and Müller, 2000a). One way to gather all the information on an ecosystem's biocenosis and assess the relationships between its various components is to build its food web (Winemiller and Polis, 1996). As it is difficult to comprehend the nature of complex food webs through direct observation, indices characterizing food web properties through an overall vision of its structure and its functioning have been developed (Ulanowicz, 1986; Kay et al., 1989).

The aims of network analysis indices are to characterise the overall structure of the ecosystem and to assess both direct and indirect relationships between compartments (Szyrmer and Ulanowicz, 1987). A "goal function" is supposed to tend to an optimum as the system evolves (Bendoricchio and Jørgensen, 1997), but if there is a preferred state or goal for the ecosystem, it is not often well defined (Fath, 2004). Various hypotheses have been proposed, such as a maximizing Power output (Lotka 1924 in Bendoricchio and Jørgensen, 1997; Odum and Pinkerton, 1955), Ascendency (Ulanowicz 1986), Emergy (Odum 1988), Exergy (stored, Jørgensen 1999 or dissipated, Schneider and Kay 1994), ratio of Emergy/Exergy (Bastianoni and Marchettini 1997). Many properties of the ecosystems, in terms of energy utilization, organization, synergism, or homogenization due to indirect effects have also been used (Higashi et al. 1993, Patten 1995, Fath and Patten 1998, 1999). Exergy, Emergy, Power, Ascendency and indirect effects seem to present a common basis (Patten 1995). Even though they cannot be unified in one single theory (Jørgensen and Müller, 2000b), they are mutually consistent (Fath et al., 2001). They can then be used to compare ecosystems and to describe their relative evolutions. Indeed, considering that the mean ecosystem computed as a static food web represents a stabilized system under certain constraints, it is possible to compute some indices on the basis of some goal functions (adapted originally to study the evolution of simulation models or to evaluate systems, e.g. Exergy – Marques et al., 1997; Fath et al., 2004). Baird et al. (1991) showed that ecosystem comparison based on network analysis indices can be used for a better characterization of ecosystems.

European intertidal mudflats are among the most biologically productive areas in the world (McLusky and Elliott, 2004). Along the French Atlantic coast, Aiguillon Cove and Brouage Mudflat are macrotidal ecosystems mainly composed of extended mudflats. They are similar in terms of their benthic fauna. Both are major European sites for shellfish (oyster and mussel) culture (Gouilletquer and Le Moine, 2002). They differ by the presence of a salt-marsh adjacent to the large mudflat in Aiguillon Cove, absent in Brouage, and by the extension of the shellfish structures, much more extended in Brouage than in Aiguillon Cove. The shape of the coast and the location of rivers also present differences. Aiguillon Cove has a longer residence time and a direct river input, differing from the Brouage Mudflat.

In this study, we examined how these similarities and differences impacted food web functioning. This functioning was characterised through the calculation of network analysis indices and was compared between the two sites. In order to place these results in the context of coastal ecosystems in general, network indices from AC and BM were then compared to those of published food webs from the literature that had similar structures. Our hypothesis was that these two European type soft-bottom semi-enclosed coastal ecosystems, under estuarine influence, would have common characteristics, but that their slight, especially morphological, differences would also result in differences in food-web functioning, which could be elucidated by a network analysis approach.

The Brouage Mudflat has been annually modelled by Leguerrier et al. (2003, 2004), and compared to Aiguillon Cove by a direct observation of the food-web flows (Degré et al., 2006). The method used for estimating missing values of the carbon flows was inverse analysis (Vézina and Platt, 1988). Degré et al. (2006) modified this approach for coupling two seasons. Based on ecological modifications of the communities, the "summer" season was defined as mid-March to mid-October, and the "winter" season as the rest of the year.

The objective of the present paper was to go further in the trophic functioning description of these two close ecosystems. Network indices (Ulanowicz, 1986; Kay et al., 1989) of these two food webs were estimated and used to compare the functioning of these systems between summer and winter. Then indices were calculated on a mean annual basis and compared to computable or published indices in several food webs models available in marine scientific literature.

1. Material and Methods

1.1. Study sites and model construction

[Figure 1]

Located on the South-Western Atlantic French coast (Figure 1), the Charentais Sounds (Pertuis) are semi enclosed macrotidal areas protected from the ocean influence by islands (Ile de Ré and Ile d'Oléron) and influenced by estuarine transport through the Charente and Sèvre Niortaise rivers. They are characterized by the presence of large mudflats, which are the sites of an extensive shellfish culture (Gouilletquer and Héral, 1997), juvenile fish nurseries (Le Pape et al., 2003) and feeding grounds for wintering shorebirds (Triplet et al., 2001).

The Brouage mudflat is located on the eastern part of the Marennes-Oléron Bay. It covers 40 km² (Gouleau et al., 2000); with a flat bottom slope (1:1000) and a very wide (4.5 km) tidal area. The current speed varies from 0.2 to 0.6 m s⁻¹ (Bassoullet et al., 2000; Le Hir et al., 2000). Oyster culture on racks covers 16% of the intertidal area, located on the lower part (Lemoine, pers. comm.).

The Aiguillon Cove is a large intertidal area (Verger, 1968), constituted mainly of large mudflats (33 km²) and surrounded by salt-marshes (11 km²). This cove is a semi-circular sedimentation basin for silts and clays (Verger, 1968). It has a gentler bottom slope and a larger mudflat on the southern than of the northern part (1.5:1000 vs. 1.8:1000 and 3.5 vs. 3 km, respectively). Current speeds average 0.2-0.6 m s⁻¹ (SHOM, 2001). The mudflat was considered as composed of 97% of "free" mudflat, 2% of mussel cultures and 1% of oyster racks.

A previous study of these two systems (Degré et al., 2006) estimated carbon flows on an average square meter of mudflat using inverse analysis. Two seasons ("summer": mid-March to mid-October, and "winter": the rest of the year) were distinguished. This partition has been chosen to take into account: (1) the wintering of migratory birds (which arrive in October and depart by March); (2) the gastropoda *Hydrobia ulvae*, which begin to reproduce in March (Haubois et al., 2004); (3) the nematodes, which are more numerous in winter (Rzeznik-Orignac et al., 2003); and (4) the microphytobenthos which usually begins their high primary production in March (Guarini et al., 2004).

The inverse analysis, as developed by Vézina and Platt (1988), was adapted by Degré et al. (2006) in order to compute simultaneously the two seasonal food webs. Biomass was considered constant over the annual period. A biomass variation was considered between the two seasons, when documented. Available information on the flows included field estimates (e.g. bacterial production), experiments (e.g. grazing of diatoms by nematods) and validated-model results (net primary production). The input and output flows of plankton and detritus by hydrodynamic transport were estimated using simple physical equations. Unknown flows were constrained with inequalities from literature data.

In the Aiguillon Cove and the Brouage Mudflat, Degré et al. (2006) described 16 compartments: microphytobenthos, phytoplankton and resuspended microphytobenthos, benthic foraminifers, nematodes, bivalves (mainly *Scrobicularia plana* and *Macoma balthica*), annelids (mainly *Hediste diversicolor*, *Neanthes succinea* and *Nephtys hombergii*), gastropods (mainly *Hydrobia ulvae*), arthropods, shellfish culture (*Crassostrea gigas* in the Brouage mudflat and *Mytilus edulis* in the Aiguillon cove), pelagic microzooplankton (ciliates and flagellates), mesozooplankton (mainly copepods), fish juveniles (mainly carnivorous fishes, especially juvenile flat fish *Solea solea*), adult grazing fish (mainly mullet *Liza ramada*), and shorebirds (mainly Dunlins *Calidris alpina*, Knot *Calidris canutus* and black-tailed Godwit *Limosa limosa*), and benthic and pelagic detritus, which also include the free and attached bacteria.

A total of 106 carbon flows (see Figure 3 in Degré et al., 2006) were calculated between the compartments. The same food web structure was taken into account in summer and in winter. Because there was more extensive data for the Brouage Mudflat, the conceptual models of inverse analysis were slightly different: the BM detritus compartments were divided into dissolved organic carbon (DOC), particulate organic carbon (POC) and bacteria. Then, these 3 compartments were aggregated for the Network Analysis, so that the structure of the model would be the same in the 2 studied ecosystems.

1.2. Inter-ecosystem comparisons

[Figure 2] [Table 1]

In order to compare the functioning of the 2 French intertidal mudflats with other ecosystems, 14 coastal sites were chosen (Table 1, Figure 2), according to the availability in the literature of a static model either built with inverse analysis (Vézina and Platt, 1989) or with ECOPATH (Christensen and Pauly, 1992) and that coupled benthic and pelagic layers. All models were annually averaged. Biomass-based model values were converted into gC with the assumption that 1 g wet weight = 0.04 Gc. All results are expressed in $\text{gC}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$. Models were selected according to their level of aggregation of species into compartments considered similar to the one of the French mudflats. The models chosen had from 12 to 24 compartments. More detailed models (St Mark in the Apalachee Bay, in Florida, 51 compartments, Baird et al., 1998; Sylt-Rømø Bight, Wadden Sea, 59 compartments, Baird et al., 2004) were included in the discussion for the indices that were less sensitive to the model structure, but they were excluded from the quantitative analysis in order to limit structural differences between the studied models.

[Three upwelling systems were selected. The Peruvian upwelling system (Figure 2) is a part of the larger Humbolt Current System in the south-western Pacific (Baird et al., 1991). It supports one of the most productive fisheries in the world (Baird et al., 1991). The Benguela upwelling system is situated along the West coast of Africa in the South-East Atlantic Ocean (Heymans et al., 2004). The northern Benguela ecosystem is bounded by the Angolan gyre in the north and by the Lüderitz upwelling centre in the south. The Tongoy Bay is located in the management area of Puerto Aldea, Chile. Four subtidal habitats from Tongoy Bay were studied (Ortiz and Wolff, 2002): (1) seagrass meadows from 0 to 4 m depth, (2) sand-gravel between 4 and 10 m, (3) sand between 10 and 14 m, and (4) mud > 14 m depth.

The two African estuaries are located (Baird and Ulanowicz, 1993) on the Indian Ocean coasts. The Swartkops estuary discharges into the Indian Ocean through a constricted inlet. The estuary is small (4 km², with 1.82 km² of *Spartina maritima* dominated salt marshes), shallow (1.6 m of tidal amplitude), turbid and well-mixed (Baird and Ulanowicz, 1993). The Kromme estuary discharges into the St Francis Bay through a constricted inlet. The estuary is small (3 km², with 0.8 km² of *Spartina maritima* dominated salt marshes), shallow (1.6 m of tidal amplitude), and well-mixed (Baird and Ulanowicz, 1993).

Three American estuaries were compared (Monaco and Ulanowicz, 1997), all of which are under anthropogenic influence. While the Narragansett Bay has three entrances from west to east: the West Passage, the East Passage, and the Sakonnet River, the Delaware Bay mixes freshwater from the Schuylkill River at the port of Philadelphia with salt water from the Atlantic Ocean at Cape May and Cape Henlopen. The Chesapeake Bay is the largest drowned river valley estuary in the USA (Baird et al., 1991). The mesohaline region, studied by Baird et al. (1991), encompasses about 48 % of the total area of the Bay and receives large amounts of pollutants and nutrients in runoff.

The brackish Baltic Sea is characterized by a latitudinal gradient of salinity, nutrients, hydrographic conditions, temperature and light intensity, that influences abundance, distribution, composition and diversity of species. Sandberg et al. (2000) compared three sites of the Baltic Sea: the low saline and oligotrophic Bothnian Bay, the Bothnian Sea and the Baltic proper, where salinity and nutrient levels are higher.

Three European estuaries were included in the comparison. The Ythan estuary, located about 20 km north of Aberdeen, Scotland, is a maximum 620 m wide estuary. The habitats studied by Baird and Milne (1981) are comprised of 71 ha of subtidal areas and 185 ha of intertidal areas (115 ha of mud and mud-sand mixture, particularly in upper reaches, and 70 ha of sand, mussels beds, and stones, particularly in mouth and lower reaches). Baird and Ulanowicz (1993) studied the whole Ythan estuary that receives about 2000 m³ of primary treated sewage per day from upstream towns. The Ems estuary is a shallow semi-diurnal tidal estuary draining into the Wadden Sea, including 245.7 km² of large tidal flats composed by sand in the mouth and clay sediment in the middle and upper reaches (Baird and Ulanowicz, 1993). The Ems estuary (Baird et al., 1991) exhibits gradients of tidal amplitude and salinity. It receives large amounts of nutrients, but shows little eutrophication or pollution. The Seine Estuary is located at the interface between the French River Seine and the Eastern Channel (Rybarczyk and Elkaim, 2003). The downstream sector with mudflats (polyhaline or mesohaline, 10-25 ‰) is separated from the upstream sector (mesohaline or oligohaline, 0.5-10 ‰), near Honfleur.]

1.3. Synthetic Indices

1.3.1. Throughput and production indices

The Total System Throughput (TST) of an ecosystem is the sum of all its fluxes and hence depends on the aggregation level chosen for its representation (Kay et al., 1989). The Net System Production ($\text{gC}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$) is the sum of all migratory (i.e. not the gross primary production) inputs to the system minus all the exports of the system (Rybarczyk and Elkaïm, 2003). Based on Exergy (Jørgensen et al., 1995) goal functions, we established an index that defines the qualitative assessment of exchanges with the outside of the systems. We called it Net System Quality Production (units of energy). It was computed by multiplying each of those exchange fluxes by a coefficient representing the quality of the material involved in Exergy computation (Jørgensen et al., 1995). The Detritivory/Herbivory ratio was also computed.

1.3.2. Cycling and trophic indices

Other indices attempt to summarise all the possible pathways between compartments, and hence are based on the calculation of the integral interaction matrix which accounts for both direct and indirect relations between compartments: the Leontief matrix (Szyrmer and Ulanowicz, 1987). Based on this matrix, various indices can be computed, among which Average Path Length (APL) and the Finn Cycling Index (FCI). The APL (Finn, 1976) represents the mean number of steps that a particle entering the system will take before exiting. Originally, the FCI (Finn, 1976) gave the proportion of material cycling in the system versus straightforward flows that do not cycle. It was reformulated by Ulanowicz (1986) who chose to normalize it by the TST and computed it by removing one by one the cycling elements of the networks, hence calculating also the number of cycles and their average length.

The Lindeman representation of a food web aims to visualize it as a food chain (Lindeman, 1942), with primary producers and detritus at the first level. According to their diets, compartments are dispatched amongst integer number Trophic Levels between which Transfer Efficiencies can be computed (Ulanowicz, 1986). Compartments are also given an index which represents their average Trophic Level.

1.3.3. Energy flowing indices

The use of thermodynamic functions has allowed energy flowing thorough ecosystems to be quantified. Ascendancy (A) is a measure of the amount of information flowing within a system, multiplied by the TST (Ulanowicz, 1986). Its upper bound is the Development Capacity (C) and the gap between the two is composed of 'overheads': on imports, on exports, dissipative (respiratory) and pathway redundancy (Ulanowicz, 1997). Relative Ascendancy (A/C), relative Redundancy (Redundancy/C) and internal relative Ascendancy (Ascendancy/internal Development Capacity) were also calculated.

1.3.4. Inter-ecosystem comparisons

The comparisons focused on two 2-dimensional indices: Net System Production and Net System Quality Production, and non-dimensional indices: FCI, Detritivory / Herbivory ratio, Primary Production Efficiency (net primary production / herbivory), relative Ascendancy and Redundancy, internal relative Ascendancy, Net Primary Production / total Biomass (productivity), Gross Primary Production / total System Respiration, APL and number of trophic level. When possible, indices have been computed from results described in the articles, either using `netwrk.exe`[®] (Ulanowicz, 1999: <http://www.cbl.umces.edu/~ulan/ntwk/network.html>) concerning the counting of cycles within the food webs), or by direct calculation from indices described above, when they were recorded, or flux-diagram results when they were precise enough.

To examine the relationships between the indices and to characterise the different ecosystems, Spearman rank correlations were calculated and a principal component analysis (PCA) was performed on the table of the indices for the different ecosystems. In order to suppress missing values, the Tongoy Bay and Northern Benguela upwelling were not taken into account in these

analysis, nor the number of trophic levels and the primary production efficiency. These analyses were performed with XLSTAT[®].

2. Results

2.1. Comparison of the two seasons in the two French intertidal mudflats

[Table 2]

The Brouage Mudflat showed two contrasting seasons (Table 2). The contrast between summer and winter was higher in Brouage Mudflat than in Aiguillon Cove for the net system quality production and for all the non-dimensional indices computed (FCI, Detritivory/Herbivory, relative Ascendency and Redundancy, internal relative Ascendency, APL and number of trophic levels). The net system production was negative for both seasons in the two systems. The net system import was higher (higher absolute values) in Aiguillon Cove than in Brouage Mudflat. For each site, the net system import was higher in summer than in winter.

The enrichment in high quality material (measured by net system quality production) observed was not the same either: while Aiguillon Cove exports were more enriched during summer than winter, it was the opposite in Brouage Mudflat. In Brouage, the high winter quality production was connected to the seasonality of the oyster production, mainly harvested in winter, and in Aiguillon, with the high migration of grazing fish in summer.

The Brouage Mudflat was characterised, from summer to winter, by the decrease of APL, FCI, number and length of cycles, and number of trophic levels and the increase in A/C, internal relative Ascendency and Net System Quality Production, while these indices were equivalent for the two seasons in Aiguillon Cove. The difference between A/C and internal relative Ascendency was similar in Brouage Mudflat and Aiguillon Cove during the two seasons.

Different pathways occurred during the two seasons for Brouage Mudflat, whereas the diets of each compartment remained approximately the same in Aiguillon Cove. The nekton juveniles in Aiguillon Cove, for instance, had a diet exclusively composed of bivalves, while they changed their diet at Brouage Mudflat from predation of 50% on bivalves, 25% on gastropods, and 25% on arthropods in summer, to 75% on bivalves and 25% on gastropods in winter (Degré et al., 2006). Grazing fish from Aiguillon Cove had a mixed diet of microphytobenthos and detritus at both seasons, while at Brouage Mudflat they switched from an exclusively herbivorous diet in summer to prey on nematofauna in winter. They then entered into competition with carnivorous annelids. Overall, diets were more based on detritus than on primary production, with a Detritivory/Herbivory ratio higher in winter than in summer for the two ecosystems.

The loss of one Trophic Level and increase of the Trophic Efficiency from level 2 to level 3 was due to the combined decrease production efficiency of annelids and increase in that of the nematodes: there was a change in the carbon pathways in Brouage Mudflat, which did not occur in Aiguillon Cove. Indeed, the nematode populations were more numerous in winter than in summer in Brouage (Rzeznik-Orignac et al., 2003), contrary to what is observed for macrofauna.

2.2. Annual properties and inter-ecosystem comparisons

[Table 3]

The annual models of Brouage Mudflat and Aiguillon Cove were compared to several ecosystems from the literature (Table 3). Brouage Mudflat and Aiguillon Cove had a very low Net System Production. These negative values were due to high material import mainly composed of detritus. Negative values were also found for Swartkops estuary, Kromme estuary and Chesapeake Bay. In contrast, the Net System Quality Production was very high compared to the other systems. This corresponded to the export of living material (phytoplankton, zooplankton, bird, fish and commercial export of bivalve production).

Brouage Mudflat and Aiguillon Cove were characterised by short pathways as shown by the low values of Average Path Length and number of trophic levels. These two indices presented wide variations among ecosystems, and even among estuaries.

The recycling intensity in Brouage Mudflat and Aiguillon Cove, measured by FCI, was close to the mean value of the different ecosystems. Estuaries were the most highly recycling systems. Compared to them, the FCI of Brouage Mudflat and Aiguillon Cove was low.

Concerning Detritivory/Herbivory, the values in Brouage Mudflat and Aiguillon Cove were close to the mean value. Most of the high values were encountered in estuaries.

Brouage Mudflat and Aiguillon Cove had values of A/C lower than the mean value. These values were in the lower part of the range covered by estuaries. The Relative Redundancy or importance of parallel pathways inside the food web was high in Brouage Mudflat and Aiguillon Cove, as for most of the other estuaries.

The Brouage Mudflat and Aiguillon Cove presented a high value of productivity and this primary production was efficiently driven to herbivores (high Primary Production Efficiency values).

[Table 4]

The correlation matrix between all network indices (Table 4) presented a complex pattern of interactions. The strong negative correlation between Relative Ascendency and Redundancy was directly linked to the calculation of these indices. The same was true for the positive correlation between total Relative Ascendency and internal Relative Ascendency. The negative correlation observed between productivity and FCI could be related to the fact that recycling and matter input were the two possible ways of increasing the flows in a system (Borrett and Osidele, 2006). Moreover, the recycling (FCI), by decreasing the proportion of the flows derived from the production, increased the APL (Christensen, 1995; Borrett and Osidele, 2006). FCI was also positively related to redundancy, expressed as its ratio to development capacity. The gross primary production/respiration naturally correlated to Net System Production, and was negatively correlated to Detritivory /Herbivory as a high gross primary production enhances herbivory. The net system production also positively correlated with internal Ascendency, which could correspond either to a enhancement of internal flows or of their organisation. Cycling played a central role in the multiple correlations observed (Borrett and Osidele, 2006).

The principal component analysis of these indices constructed a first component (34% of the variance) positively correlated with recycling (FCI contributed to 16% of the variance and was the dominating factor in the first axis construction), and redundancy (contribution: 14%) and negatively correlated to Ascendency (13%) and the net system production (13%). On the first axis, all estuaries models were located on the right hand side, with the exception of the first Ythan model and the Seine model. This corresponded to the fact that most of the estuaries presented a high FCI, high redundancy and a low net production and A/C. Brouage Mudflat and Aiguillon Cove showed the same tendency as estuaries, with less extreme values than that of Narragansett Bay, Kromme or Swartkops estuaries.

The second principal component (that explained 20% of the variance) was positively correlated to the internal relative Ascendency (contribution: 28%, dominating variable on this axis), and negatively correlated to the difference between total and internal relative Ascendency (22%, linked to the sensitivity to external exchanges) and to the production of quality (14%). Brouage Mudflat and Aiguillon Cove were located at the extreme low values of this axis, with high quality production and high dependency to external exchanges.

[Figure 3]

3. Discussion

3.1. Seasonal variations:

According to our model, the Brouage Mudflat was characterized by a higher level of organization in winter than in summer. This would be linked to a higher redundancy of the flows in summer. This higher level of organization in winter implies a lower adaptation capacity (Heymans et al., 2002). This seasonal difference was not observed in Aiguillon Cove, but as this model presented more gaps in seasonal data, no conclusion will be drawn from it.

Comparing the Relative Ascendency and the internal Relative Ascendency quantifies the dependency on external factors. Indeed, the computation of internal Ascendency and development capacity does not consider the exchanges with the outside (Ulanowicz and Norden, 1990): hence, the gap between the two consists only of the internal Redundancy. The comparison between total and internal relative Ascendency represents a degree of dependency on the exogenous connections to adjacent ecological and physical systems (Baird et al., 1991). This difference remained constant during the two seasons, at both study sites, implying a constant dependency to external exchanges.

The drop in APL, FCI, the number of cycles and their mean length suggest a diminution of stress for Brouage Mudflat during winter (Baird and Ulanowicz, 1989). The loss of one trophic level in Brouage Mudflat was associated with higher transfer efficiency between the two

preceding ones, a lower trophic level of nekton juveniles but a higher one of grazing fish. Indeed, very different pathways occurred in summer and winter for Brouage Mudflat, whereas the diets of each compartment remained approximately the same in Aiguillon Cove.

The loss of one Trophic Level and increase of the Trophic Efficiency from level 2 to level 3 was due to the combined decrease in annelid efficiency and increase in nematode efficiency: there was a change in the carbon pathways in Brouage Mudflat, which does not occur in Aiguillon Cove. Indeed, as opposed to macrofauna, nematodes were more abundant in winter than in summer (Rzeznik-Orignac et al., 2003). The nematode dynamics have been studied in Brouage Mudflat (Rzeznik-Orignac et al., 2003), but not in Aiguillon Cove, and the sensitivity analyses showed that grazing by nematodes has a significant impact on the results (Degré et al., 2006): we can wonder if, with more information on this peculiar compartment, different patterns would be observed in Aiguillon Cove.

These observations underline the interest of coupling two seasons in the modelling of a food web, provided that enough information is available to characterize the seasonal patterns of the populations. The key role of nematodes is also shown in the food web dynamics. It had already been demonstrated that nematodes were an important compartment for benthic communities (Gerlach, 1971), at the detrital level (Escaravage et al., 1989), in the transfer of material towards higher trophic levels (Coull, 1990), and in food-web functioning (Leguerrier et al., 2003), but it is emphasized here that they may also play a structural role by forcing the trophic organization of the ecosystem. Schmid-Araya et al. (2002) suggested that meiofauna play a key role as intermediate between trophic levels, and adding this compartment in a conceptual model increased its complexity. Hence, meiofauna is an important compartment to consider in the choice of aggregation level in the conceptual model.

All these comparisons were done in tendency, without testing the significance of the observed differences. The lack of information on the variability of the numerous processes estimated, and on the biomass of some compartments, did not allow processing this statistical analysis (Bondavalli et al., 2006).

3.2. Annual system properties

Even though overall activity (TST) in Brouage Mudflat was 1.5 times higher than in Aiguillon Cove, the two mudflats showed similar global functioning, with net import from the ocean, net export of primary production, a predominance of benthic primary production over pelagic primary production due to its high turbidity (Blanchard and Cariou Le Gall, 1994), and dominating consumption of detritus. In parallel to a high benthic primary production, they both import material from the water column. To go further in this overall comparison, we will compare our two food-web results with those concerning other similarly modelled food webs.

3.3. Advantages and limits of the inter-ecosystem comparison

The use of network analysis for comparing ecosystem properties has been the subject of numerous articles bringing interesting ideas to coastal ecology. However, the dangers of such a comparison have also been highlighted. Early comparative studies using network analysis (Baird et al. 1991, 1993) emphasized that the degree of aggregation among the compartments had to be essentially the same in order to avoid artificial dissimilarities. Christensen (1995) has shown that several network indices were sensitive to the level of aggregation. This is why the selection made here was based on the number of compartments, and on the similarity in this level. Moreover, the comparison was only made on carbon-based or mass models translated into carbon. Models in phosphorus or nitrogen currency were not taken into account as they would involve processes specific to these currencies. However, some differences would remain between the compared models as shown in Appendix 1. Only Brouage and Aiguillon Cove had exactly the same structure. Others varied in the number of non-living compartments and micro-meiofaunal living compartments. Both have been shown to be sensitive when using network analysis (microbial loop: Abarca-Arenas & Ulanowicz 2002, non-living material: Allesina et al. 2005). This is why the comparison of the two systems Aiguillon Cove and Brouage with the other systems will be done considering tendencies and not exact values.

3.4. Systems importing quantity but exporting quality

Even though the two study sites import material, as opposed to most of the other systems (Table 4), the quality of imports is lower than that of exports. The quality of a unit of material is

linked to the information embodied in its components. Marques et al. (1997) have followed the simplification proposed by Jørgensen et al. (1995) to compute Exergy: the simple multiplication of the compartment's biomass by a weighting factor using the detritus at the basic reference-level gives, in arbitrary units, the quality embodied in the biomass considered. The yearly gains in quality were 304% and 123% of the yearly quality inputs for Aiguillon Cove and Brouage Mudflat, respectively, and each season had also a positive net quality production. Hence, the two systems were "producing quality" all over the year. Moreover, they were, amongst the most quality-productive systems (Table 4). The Kromme Estuary imports quality, all the others (when quality could be computed from the published results) export quality, but only the Peruvian upwelling exports more quality than Aiguillon Cove and Brouage Mudflat.

3.5. Systems under low stress

The FCI can be used for comparison purposes, even though it is subject to discussion (Allesina and Ulanowicz 2004) concerning its absolute value which may not include all flows involved in cycling. However, the new method they introduced (comprehensive cycling index, CCI) appears to be linearly related to FCI, in their analysis of 23 ecosystem models. As CCI is computationally intensive to determine, and appears as a linear multiple of FCI, most of recent studies remain focused on FCI (e.g. Borrett and al., 2006).

Monaco and Ulanowicz (1997) associated high FCI and APL values with a high efficiency in retaining particulate matter within the food web. FCI has also been related to positive feedbacks in ecosystems that contribute to stability, and has been observed inversely correlated with system recovery time (Vasconcellos et al., 1997). According to Baird and Ulanowicz (1989), however, a paucity of cycles coupled with a high FCI index indicates a disturbed system. Baird et al. (1991) also associated a high FCI with a stressed system more than with a stable one. These findings may not be incompatible, and one could argue that stressed conditions could enhance rapid ecosystem adaptation. Here, even if the FCI was higher than in particular systems such as upwelling systems, they remain relatively low. The values of Brouage Mudflat and Aiguillon Cove are close to the mean FCI value of St Mark National Wildlife Refuge seagrass ecosystem (18 %: Baird et al., 1998) and of the Sylt-Rømø Bight ecosystem in the Wadden Sea (17%: Baird et al. 2004). The low FCI of Brouage Mudflat and Aiguillon Cove associated with a great number of cycles, might reveal a poorly stressed system.

In Brouage Mudflat, the FCI is higher than in Aiguillon Cove. This is related to a more important shellfish culture. This could be interpreted as the fact that Brouage Mudflat, would be more stressed and adaptive than Aiguillon Cove.

The amount of overheads is also believed to indicate system resilience and strength in reserve (Heymans et al., 2002): low values of A/C were observed for Brouage Mudflat and Aiguillon Cove. Both presented a high adaptation capacity.

3.6. A large diversity of resources

The detritivory/herbivory ratio of both Aiguillon Cove and Brouage Mudflat was within the range observed for estuaries and bays, being closest to that of Delaware and Chesapeake bays. Values of detritivory/herbivory were in the low part of this range in the models of St Mark (1.8; Baird et al., 1998) and Sylt-Rømø Bight (1.4; Baird et al, 2004). Relatively low for Aiguillon Cove, the D/H ratio was higher in Brouage Mudflat, meaning that detritivory was an essential process there.

The efficiency of transfer of the primary production toward herbivores in Aiguillon Cove was higher than in Brouage Mudflat, and both of them were superior to the average observed for estuaries and bays and to values observed in the models of St Mark (46.6%; Baird et al., 1998) and Sylt-Rømø Bight (57.5%; Baird et al, 2004).

Hence, we can conclude that Brouage Mudflat and Aiguillon Cove benefit from a large diversity of resources in comparison to other systems. Indeed, it is known that those two mudflats receive material from different origins: river-borne detritus, neritic phytoplankton, microphytobenthos and "true" phytoplankton constitute a great variety of resources, used in the food web with efficiency (Riera, 1998; Guarini et al., 2004; Haubois et al., 2005).

Brouage Mudflat was, amongst all the compared ecosystems, the one that had the largest difference between total and internal Relative Ascendency values. Aiguillon Cove's indices showed also a large difference, comparable to that in the Seine Estuary. Hence, we can conclude that our two systems appeared to be very dependent on external conditions, with a higher dependence for Brouage Mudflat.

3.7. An intermediate maturity

According to Christensen (1995), neither Maturity nor Stability can be defined consistently. Ulanowicz (1986), and then Baird et al. (1991) and Ulanowicz and Abarca-Arenas (1997) linked Maturity *sensu* Odum (1969) with Ascendency, observing that an increasing Ascendency was structurally linked to a higher species richness, more retention of resources within the system, and a tendency towards trophic specialization. Hence, in the absence of major perturbation, ecosystems should exhibit a propensity to increase their Ascendency. This has been discussed by Christensen (1995), as he found a negative correlation between Ascendency and Maturity. Perez-España and Arregun-Sanchez (1999) proposed an index of Maturity that they first linked to Stability and then, with dynamic simulations, found to be inversely correlated with stability (Perez-España and Arregun-Sanchez 2001). We will here evaluate the maturity of a system according to the coupled observation of net primary production / biomass (NPP/B) and gross primary production / system respiration (GPP/R) indices, following Odum's (1969) explanations in our interpretation.

The combined observations of NPP/B and GPP/R would suggest a more advanced maturity for Brouage Mudflat than for Aiguillon Cove, while the two systems should be, because they are under estuarine influence, relatively juvenile in comparison to other marine ecosystems (Frontier and Pichod-Viale, 1995).

The low APL and number of trophic levels could be partly due to the fact that the bacteria were merged with the detritus in a single compartment, whereas in most of the presented systems (Baird et al., 1991; Baird and Ulanowicz, 1993; Monaco and Ulanowicz, 1997; Sandberg et al., 2000), free pelagic bacteria are separated (Annexe 1). Indeed, the computation of the number of trophic levels for the Brouage Mudflat system in which bacteria were separated showed 5 trophic levels, and the Baird and Milne (1981) model of the Ythan estuary, which did not include separate bacterial compartment, showed 4 trophic levels. However, bacteria were not separately included by Rybarczyk and Elkaim (2003) or Heymans et al. (2004), which present systems with at least 5 trophic levels. Moreover, the computation of the APL for Brouage Mudflat with bacterial compartments did not give a higher value (it was even lower: 1.63 was obtained). According to Valandro et al. (2003), the number of energy transformation levels in trophic webs is usually below 5, but the number is greater in aquatic ecosystems. The transfer efficiencies are also very low for Aiguillon Cove and Brouage Mudflat in comparison to other systems values, which generally exceed 30% and can easily reach 70% for the first step.

Frontier and Pichod-Viale (1995) described the maturation of ecosystems in terms of gains in accumulated organic matter, in diversity of species and of ecological niches, in complexity, recycling, and organization, and proposed structural interpretation of rank-frequency diagrams. In Aiguillon Cove and Brouage Mudflat, such an interpretation of the rank-frequency diagrams of species showed a less mature system for Aiguillon Cove, as only 2 species, *Scrobicularia plana* and *Hydrobia ulvae*, dominate the populations, whereas the diagram is more equilibrated in Brouage Mudflat (Degré, unpublished results).

Conclusion

The network indices of the different ecosystems, synthesised by the principal component analysis, underlined the high similarity of functioning of Aiguillon Cove and Brouage Mudflat. Both presented general trends of most of the analysed estuaries (high redundancy, high recycling, low net production compared to the others) but these characteristics were less extreme than in most of the estuaries. Their only extreme position concerned their high quality production, and especially the export of living material: cultivated shellfish, grazing fish, and their dependency on external exchanges, linked to a high diversity of resources.

Acknowledgements

This work was supported by two grants from ONCFS on shorebirds and benthos interactions (D. Degré PhD grant), from ACI/ECCO (J.M. Guarini Program grant), and from the French Ministry of Agriculture – ENGREF (D. Leguerrier PhD grant). The authors thank Tammi Richardson, Anne-Gaëlle Haubois, Pierre-Guy Sauriau and Ian Jenkinson for English corrections and for useful comments.

References

- Abarca-Arenas, L.G., Ulanowicz, R.E., 2002. The effects of taxonomic aggregation on network analysis. *Ecological Modelling* 149, 285-296.
- Allesina, S., Ulanowicz, R.E., 2004. Cycling in ecological networks: Finn's index revisited. *Ecological Modelling* 28, 227-233.
- Allesina, S., Bondavalli, C., Scharler, U.M., 2005. The consequences of the aggregation of detritus pools in ecological networks. *Ecological Modelling* 189, 221-232.
- Baird, D., McGlade, J.M., Ulanowicz, R.E., 1991. The comparative ecology of six marine ecosystems. *Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences* 333, 15-29.
- Baird, D., Milne, H., 1981. Energy flow in the Ythan Estuary, Aberdeenshire, Scotland. *Estuarine Coastal and Shelf Science* 13, 455-472.
- Baird, D., Ulanowicz, R.E., 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecological Monographs* 59, 329-364.
- Baird, D., Ulanowicz, R.E., 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. *Marine Ecology Progress Series* 99, 221-237.
- Baird, D., Luczkovich, J., Christian, R.R., (1998). Assessment of spatial and temporal variability in ecosystem attributes of the St Marks national wildlife refuge, Apalachee Bay, Florida. *Estuarine, Coastal and Shelf Science* 47, 329-349.
- Baird, D., Asmus, H., Asmus, R., 2004. Energy flow of a boreal intertidal ecosystem, the Sylt-Rømø Bight. *Marine Ecology Progress Series* 279, 45-61.
- Bassoullet, P., Le Hir, P., Gouleau, D., Robert, S., 2000. Sediment transport over an intertidal mudflat: field investigations and estimation of fluxes within the "Baie de Marennes-Oléron" (France). *Continental Shelf Research* 20, 1635-1653.
- Bastianoni, S., Marchettini, N., 1997. Emergy/exergy ratio as a measure of the level of organization of systems. *Ecological Modelling* 99, 33-40.
- Bendoricchio, G., Jørgensen, S.E., 1997. Exergy as goal function of ecosystems dynamic. *Ecological Modelling* 102, 5-15.
- Blanchard, G.F., Cariou-Le Gall, V., 1994. Photosynthetic characteristics of microphytobethos in Marennes-Oléron Bay, France: preliminary results. *Journal of Experimental Marine Biology and Ecology* 182, 1-14.
- Bondavalli, C., Bodini, A., Rossetti, G., Allesina, S., 2006. Detecting stress at the whole-ecosystem level: The case of a mountain lake (Lake Santo, Italy). *Ecosystems* 9, 768-787.
- Borrett, S.R., Whipple, S.J., Patten, B.C., Christian, R.R. 2006. Indirect effects and distributed control in ecosystems. Temporal variability of indirect effects in a seven-compartment model of nitrogen flow in the Neuse River Estuary (USA): time series analysis. *Ecological Modelling* 194, 178-188.
- Borrett, S.R., Osidele, O.O., 2007. Environ indicator sensitivity to flux uncertainty in a phosphorus model of Lake Sidney Lanier, USA. *Ecological Modelling* 200, 371-383.
- Christensen, V., Pauly, D., 1992. ECOPATH II - a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling*, 61, 169-185.
- Christensen, V., 1995. Ecosystem maturity - towards quantification. *Ecological Modelling* 77, 3-32.
- Coull, B.C., 1990. Are members of the meiofauna food for higher trophic levels? *Transactions of the American Microscopical Society* 109, 233-246.
- Degré, D., Leguerrier, D., Arminot du Chatelet, E., Rzeznik, J., Auguet, J.-C., Dupuy, C., Marquis, E., Fichet, D., Struski, C., Joyeux, E., Sauriau, P.-G., Niquil, N., 2006. Comparative analysis of the food webs of two intertidal mudflats during two seasons using inverse modelling: Aiguillon Cove and Brouage Mudflat, France. *Estuarine, Coastal and Shelf Science*, 69, 107-124.
- Escaravage, V., Garcia, M.E., Castel, J., 1989. The distribution of meiofauna and its contribution to detritic pathways in tidal flats (Arcachon Bay, France). *Topics in marine biology*. Ros J.D. (ed) 53, 551-559.
- Fath, B.D., 2004. Distributed control in ecological networks. *Ecological Modelling* 179, 235-245.
- Fath, B.D., Jørgensen, S.E., Patten, B.C., Straškraba, M., 2004. Ecosystem growth and development. *BioSystems* 77, 213-228.
- Fath, B.D., Patten, B.C., 1998. Network synergism: Emergence of positive relations in ecological systems. *Ecological Modelling* 107, 127-143.

- Fath, B.D., Patten, B.C., 1999. Quantifying resource homogenisation using network flow analysis. *Ecological Modelling* 123, 193-205.
- Fath, B.D., Patten, B.C., Choi, J.S., 2001. Complementarity of Ecological Goal Functions. *Journal of Theoretical Biology* 208, 493-506.
- Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. *Journal of Theoretical Biology* 56, 363-380.
- Frontier, S., Pichod-Viale, D., 1995. *Ecosystèmes. Structure, Fonctionnement, Evolution*. Masson, Paris, 447 pp.
- Gerlach, S.A., 1971. On the importance of meiofauna for benthos communities. *Oecologia* 6, 176-190.
- Gouleau, D., Jouanneau, J.M., Weber, O., Sauriau, P.G., 2000. Short- and long-term sedimentation on Montportail-Brouage intertidal mudflat, Marennes-Oléron Bay, France. *Continental Shelf Research* 20, 1513-1530.
- Gouletquer, P., Héral, M., 1997. Marine molluscan production trends in France: from fisheries to aquaculture. In: MacKensie, C.L., Bunell, V.G., Rosenfield, A. (Eds.), *The history, present condition, and future of the Molluscan fisheries of North America and Europe*. NOAA Technical Report NMFS 129, Department of Commerce, Seattle, Washington, pp. 137-164.
- Gouletquer, P., Le Moine, O., 2002. Shellfish farming and Coastal Zone Management (CZM) development in Marennes-Oléron Bay and Charentais Sounds (Charente-Maritime, France): A review of recent developments. *Aquaculture International* 10, 507-525.
- Guarini, J.-M., Gros, P., Blanchard, G., Richard, P., Fillon, A., 2004. Benthic contribution to pelagic microalgal communities in two semi-enclosed, European-type littoral ecosystems (Marennes-Oléron Bay and Aiguillon Bay, France). *Journal of Sea Research* 52, 241-258.
- Haubois, A.-G., Guarini, J.-M., Richard, P., Hemon, A., Arotcharen, E., Blanchard, G.F., 2004. Differences in spatial structures between juveniles and adults of the gastropod *Hydrobia ulvae* on an intertidal mudflat (Marennes-Oléron Bay, France) potentially affect estimates of local demographic processes. *Journal of Sea Research* 51, 63-68.
- Haubois, A.-G., Guarini, J.-M., Richard, P., Fichet, D., Radenac, G., Blanchard, G.F., 2005. Ingestion rate of the deposit-feeder *Hydrobia ulvae* (Gastropoda) on epipellic diatoms: effect of cell size and algal biomass. *Journal of Experimental Marine Biology and Ecology* 317, 1-12.
- Heymans, J.J., Shannon, L.J., Jarre, A., 2004. Changes in the northern Benguela ecosystem over three decades: 1970s, 1980s and 1990s. *Ecological Modelling* 172, 175-195.
- Heymans, J.J., Ulanowicz, R.E., Bondavalli, C., 2002. Network analysis of the South Florida Everglades graminoid marshes and comparison with nearby cypress ecosystems. *Ecological Modelling* 149, 5-23.
- Higashi, M., Patten, B.C., Burns, T.P., 1993. Network trophic dynamics: the modes of energy utilization in ecosystems. *Ecological Modelling* 66, 1-42.
- Jørgensen, S.E., 1999. State-of-the-art of ecological modelling with emphasis on development of structural dynamic model. *Ecological Modelling* 120, 75-96.
- Jørgensen, S.E., Müller, F., 2000a. Towards a unifying theory. In: Jørgensen, S.E., Müller, F. (Eds.) *Handbook of ecosystem theories and management*. Lewis Publisher, CRC Press LLC, pp. 465-471.
- Jørgensen, S.E., Müller, F., 2000b. Ecosystems as complex systems. In: Jørgensen, S.E., Müller, F. (Eds.) *Handbook of ecosystem theories and management*. CRC Press LLC, pp. 5-20.
- Jørgensen, S.E., Nielsen, S.N., Mejer, H., 1995. Emergy, environ, exergy and ecological modelling. *Ecological Modelling* 77, 99-109.
- Kay, J., Graham, L.A., Ulanowicz, R.E., 1989. A detailed guide for network analysis. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.) *Network analysis in marine ecology. Methods and applications*. Springer-Verlag, Berlin, pp. 15-61.
- Le Hir, P., Roberts, W., Cazaillet, O., Christie, M., Bassoulet, P., Bacher, C., 2000. Characterization of intertidal flat hydrodynamics. *Continental Shelf Research* 20, 1433-1459.
- Le Pape, O., Holley, J., Guérault, D., Désaunay, Y., 2003. Quality of coastal and estuarine essential fish habitats: estimations based on the size of juvenile common sole (*Solea solea* L.). *Estuarine, Coastal and Shelf Science* 58, 793-803.
- Leguerrier, D., Niquil, N., Boileau, N., Rzeznik, J., Sauriau, P.-G., Le Moine, O., Bacher, C., 2003. Numerical analysis of the food web of an intertidal mudflat ecosystem on the Atlantic coast of France. *Marine Ecology Progress Series* 246, 17-37.
- Leguerrier, D., Niquil, N., Petiau, A., Bodoy, A., 2004. Modeling the impact of oyster culture on

- a mudflat food web in Marennes-Oléron Bay (France). *Marine Ecology Progress Series* 273, 147-162.
- Marques, J.C., Pardal, M.A., Nielsen, S.N., Jørgensen, S.E., 1997. Analysis of the properties of exergy and biodiversity along an estuarine gradient of eutrophication. *Ecological Modelling* 102, 155-167.
- McLusky, D.S., Elliott, M., 2004. *The Estuarine Ecosystem: ecology, threats and management*. OUP, Oxford, pp. 214.
- Monaco, M.E., Ulanowicz, R.E., 1997. Comparative ecosystem trophic structure of three US mid-Atlantic estuaries. *Marine Ecology Progress Series* 161, 239-254.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science* 164, 732-731.
- Odum, H.T., 1988. Self-organization, transformity and information. *Science* 242, 1132-1139.
- Odum, H.T., Pinkerton, R.C., 1955. Time's speed regulator. *American Scientist* 43, 321-343.
- Ortiz, M., Wolff, M., 2002. Trophic model of four benthic communities in Tongoy Bay (Chile): comparative analysis and preliminary assessment of management strategies. *Journal of Experimental Marine Biology and Ecology* 268, 205-235.
- Patten, B.C., 1995. Network integration of ecological extremal principles: exergy, emergy, power, ascendancy, and indirect effects. *Ecological Modelling* 79, 75-84.
- Pérez-España, H., Arregùn-Sánchez, F., 1999. A measure of ecosystem maturity. *Ecological Modelling* 119, 79-85.
- Riera, P., 1998. $\delta^{15}\text{N}$ of organic matter sources and benthic invertebrates along an estuarine gradient in Marennes-Oléron Bay (France): implications for the study of trophic structure. *Marine Ecology Progress Series* 166, 143-50.
- Rybarczyk, H., Eilkaïm, B., 2003. An analysis of the trophic network of a macrotidal estuary: the Seine Estuary (Eastern Channel, Normandy, France). *Estuarine, Coastal and Shelf Science* 58, 775-791.
- Rzeznik-Orignac, J., Fichet, D., Boucher, G., 2003. Spatio-temporal structure of the nematode assemblages of the Brouage mudflat (Marennes-Oléron Bay, France). *Estuarine, Coastal and Shelf Science* 58, 77-88.
- Sandberg, J., Elmgren, R., Wulff F., 2000. Carbon flows in Baltic Sea food webs - a re-evaluation using a mass-balance approach. *Journal of Marine Systems* 25, 249-260.
- Schmid-Araya, J.M., Hildrew, A.G., Robertson, A., Schmid, P.E., Winterbottom, J., 2002. The importance of meiofauna in food webs: evidence from an acid stream. *Ecology* 83, 1271-1285.
- Schneider, E.D., Kay, J.J., 1994. Manifestation of the second law of thermodynamics. *Mathematical and Computer Modelling* 19, 25-48.
- SHOM, 2001. *Courants de marée de la côte ouest de France de Saint-Nazaire à Royan*. Service Hydrographique et Océanographique de la Marine (Ed.), Brest, 72 pp.
- Szyrmer, J., Ulanowicz, R.E., 1987. Total flows in ecosystems. *Ecological Modelling* 35, 123-136.
- Triplet, P., Le Dréan-Quéneec'hdu, S., Mahéo, R., 2001. Incidence des infrastructures portuaires et des activités humaines sur l'abondance et la répartition des limicoles sur le littoral français. In: Drévès, L., Chaussepied, M. (Eds.), *Restauration des écosystèmes côtiers*. Ifremer, Brest, pp. 243-255.
- Ulanowicz, R.E., 1986. *Growth and development: ecosystem phenomenology*. Springer-Verlag, New York, 203 pp.
- Ulanowicz, R.E., 1997. *Ecology, the ascendant perspective*. Columbia University Press, NY, 201 pp.
- Ulanowicz, R.E., 1999. NETWRK 4.2 a package of computer algorithms to analyse ecological flow networks. <http://www.cbl.umces.edu/~ulan/ntwk/network.html>
- Ulanowicz, R.E., Abarca-Arenas, L.G., 1997. An informational synthesis of ecosystem structure and function. *Ecological Modelling* 95, 1-10.
- Ulanowicz, R.E., Norden, J.S., 1990. Symmetrical overheads in flow networks. *Int J Systems Sci* 21, 429-437.
- Valandro, L., Caimmi, R., Colombo, L., 2003. What is hidden behind the concept of ecosystem efficiency in energy transformation? *Ecological Modelling* 170, 185-191.
- Vasconcellos, M., Mackinson, S., Sloman, K., Pauly, D., 1997. The stability of trophic mass-balance model of marine ecosystems: A comparative analysis. *Ecological Modelling* 100, 125-134.
- Verger, F., 1968. *Marais et wadden du littoral français*. Biscaye frères, Bordeaux, 541 pp.
- Vézina, A.F., 1989. Construction of flow networks using inverse methods. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.), *Network analysis in marine ecology. Methods and applications*. Springer-Verlag, Berlin.
- Vézina, A.F., Platt, T., 1988. Food web dynamics in the ocean. I. Best estimates using inverse

methods. *Marine Ecology Progress Series* 42, 269-287.

Winemiller, K.O., Polis, G.A., 1996. Food webs: what do they tell us about the world? In: Polis, G.A., Winemiller, K.O. (Eds.), *Food webs. Integration of patterns and dynamics*. Chapman and Hall, New York, pp. 1-22.

Table 1: Description of the sites of the inter-system comparison and bibliographic references: 1- Baird et al. 1991, 2- Ortiz and Wolff 2002, 3- Heymans et al. 2004, 4- Baird and Ulanowicz 1993, 5- Rybarczyk and Elkaïm 2003, 6- Monaco and Ulanowicz 1997, 7- Sandberg et al. 2000, 8- Baird and Milne 1981, 9- Degré et al. 2006. When a reference is cited by new authors, the new reference is after (exponent into brackets) the original one.

ref	site	lat - long	ocean or sea	localisation	dimension	description
1	Peruvian upwelling	4°S-81°W 14°S-77°W	Pacific	Peru	2100 km long - 370 km wide	upwelling system
2	Tongoy Bay	30°15' S - 71°31' W	Pacific	Coquimbo, Chile	16 km long, including 2 km in Puerto Aldea	Seagrass meadows (0-4 m depth) Sand-gravel (4-10 m depth) sand (10-14 m depth) mud (>14 m depth) total
1						Southern System (500 m depth)
3	Benguela upwelling	15°S - 5°E 27°S - 15°E	South-Eastern Atlantic	Namibia - Southern Africa	179 000 km ²	Northern System ; 70s Northern System ; 80s Northern System ; 90s
1 ^(4,5)	Swartkops estuary	32°52' S – 25°39' E	Indian	southeast of Southern Africa	15 km long 4 km ²	salt marshes and sand flats, shallow, temperate, turbid, salinity gradient (10 - 35), sediment gradient (fine grained sand and mud - coarse sand)
4	Kromme estuary	34°08' S – 24°51' E	Indian	southeast of Southern Africa	14 km long 3 km ²	salt marshes and sand flats, shallow, well- mixed and temperate, salinity gradient (below 32), sediment gradient (organic rich mud - sand)
6 ⁽⁵⁾	Narragansett Bay	41°35' N – 71°22' W	North- Western Atlantic	West and East Passages, Sakonnet River, USA	48 km long - 4.8 to 19 km wide	anthropogenically stressed, 30 to 32 of salinity
6 ⁽⁵⁾	Delaware Bay	39°02' N – 75°06' W	North- Western Atlantic	Cape May - Cape Henlopen, Schuylkill River, USA	84 km long	anthropogenically stressed, 0 to 35 of salinity
6 ⁽⁵⁾ 1	Chesapeake Bay	36°50' to 39°40' N – 76°10' W	North- Western Atlantic	Susquehanna and Potomac Rivers, USA	320 km long - 4.8 to 48 km wide	mesohaline region (salinity from 6 to 18), pollutants and nutrients in runoff
7	Bothnian Bay	65° N - 23° E		Northern Bay in the Balthic Sea	36 000 km ²	low saline and oligotrophic
7	Bothnian Sea	62° N - 19° E		Middle Bay in the Balthic Sea	79 000 km ²	mesohaline, non tidal estuary
7 1	Baltic proper	56° N - 19° E		Southern Bay in the Balthic Sea	210 000 km ²	higher levels of salinity and nutrient
8 4	Ythan Estuary	57°20' N - 2°00' W	North Sea	Aberdeen, Scotland	71 ha subtidal + 185 ha intertidal areas	salinity gradient (0-35), sediment gradient (mud and mud-sand, sand, mussels beds, and stones), 2000m ³ .d ⁻¹ primary treated sewage
1 ⁽⁴⁾	Ems Estuary	53°26' N – 6°54' E	Wadden Sea	Netherlands	500 km ²	shallow semi-diurnal tidal estuary, shallow, large tidal flats, salinity (14 - 34), large amounts of nutrients, little eutrophication or pollution
5	Seine Estuary	49°25' N – 00°14' E	Eastern Channel	River Seine, Honfleur, France	106 km long - 34.34 km wide	poly- or mesohaline mudflats (10-25), meso- or oligohaline upstream (0.5-10)
9	Aiguillon Cove	46°15' N - 1°10' W	North-Eastern Atlantic	Breton Sound, Sèvre Niortaise river, France	3.5 km wide in Charente- Maritime, 3 km wide in Vendée	semi-enclosed macrotidal bay, extended mudflats, estuarine influence, neighbouring salt-marshes
9	Brouage Mudflat	45°55' N - 1°08' W	North-Eastern Atlantic	Marennes-Oléron Bay, Charente river, France	4.5 km wide	eastern extended mudflat, estuarine influence, 'ridges and runnels' bedforms

Table 2: Network analysis indices. TST = Total System Throughput. NSP = Net System Production ($\text{gC.m}^{-2}.\text{y}^{-1}$), NSQP = Net System Quality Production, N(TL) = number of trophic levels, TE(1→2) = Trophic Efficiency from trophic level 1 to level 2 (calculated from the Lindeman Spine aggregation into a linear chain), TE(2→3) = idem for level 2 to 3, TE(3→4) = idem from level 3 to 4, D/H = detritivory/herbivory, APL = Average Path Length, FCI = Finn Cycling Index, N cycles = Number of cycles, <Length> = mean length of cycles, A = Ascendancy, C = Development Capacity, A/C = Relative Ascendancy (Ascendancy/Development Capacity), R/C = Relative Redundancy, Ai/Ci = internal Relative Ascendancy (internal Ascendancy/internal Development Capacity), Dimensional indices are given in $\text{gC.m}^{-2}.\text{month}^{-1}$ for the seasonal models and in $\text{gC.m}^{-2}.\text{y}^{-1}$ for the year models.

	AC summer	AC winter	BM summer	BM winter	AC annual	BM annual
	$\text{gC.m}^{-2}.\text{month}^{-1}$				$\text{gC.m}^{-2}.\text{y}^{-1}$	
TST	751	607	1 026	1 139	8 295	12 874
NSP	-64	-45	-24	-19	-673	-263
NSQP	2 481	2 040	384	2 150	27 562	12 734
NNTL	4	4	4	3	4	4
TE(1→2)	28.50%	24.30%	16.50%	15.80%	27%	16.20%
TE(2→3)	5.69%	6.32%	4.47%	7.02%	5.89%	5.60%
TE(3→4)	0.04%	0.11%	4.54%	0	0.06%	2.30%
D/H	4.77	5.01	5.98	7.50	4.85	6.55
APL	1.89	1.96	1.82	1.62	1.92	1.73
FCI	13.6%	14.1%	23.0%	11.3%	14.9%	19.2%
N cycles	25	24	44	31	26	48
<Length>	2.68	2.55	3.5	2.93	2.65	3.46
A	1 015	803	1 308	1 578	10 878	16 615
C	3 199	2 631	3 949	3 952	35 847	48 301
R/C	32.6%	33.5%	37.6%	31.4%	33.5%	36.1%
A/C	31.7%	30.5%	33.1%	39.9%	30.3%	34.4%
Ai/Ci	20.4%	19.2%	15.3%	22.2%	18.7%	16.3%
A/C - Ai/Ci	11.3%	11.3%	17.8%	17.7%	11.6%	18.1%

Table 3: Comparison of indices of Network Analysis for various ecosystems (same bibliographic and food web references than in the table 1). The indices presented are the following ones: Net System Production (NSP: $\text{gC}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$), Net System Quality Production (NSQP: energy unit), Average Path Length (APL) and Number of trophic levels ($N_{(\text{TL})}$), Total Finn Cycling Index (FCI), fluxes to Detritus / Total System Throughput (FtoD/TST), detritivory/herbivory (D/H), Relative Ascendancy (Ascendancy/Development Capacity: A/C), Redundancy normalized by the Development Capacity (R/C), internal relative ascendancy (Ascendancy/internal Development: A_i/C_i), Primary Production Efficiency (PPEff: net primary production / herbivory), Net Primary Production / total Biomass (without detritus) (NPP/B), Gross Primary Production / total System Respiration (GPP/R), Net Primary Production / non-primary producers Respiration (NPP/R). When the computation was possible, values not given in the cited articles have been computed (values in italics), when it was not possible, the corresponding cells are left blank. Coloured cells correspond to values that are superior to the mean data for the studied systems.

ref	site	description	abb. PCA	NSP	NSQP	APL	$N_{(\text{TL})}$	FCI	D/H	A/C	R/C	A_i/C_i	PP Eff	NPP/B	GPP/R
1	Peruvian upwelling	upwelling system	Pupw	1 990	49 870	2,2	8	4%	0,4	48%	27%	45%	78%	47,2	1,6
		Seagrass meadows		202		2,4	6	3%		31%	1%	21%		10,6	
2	Tongoy Bay	Sand-gravel		380		2,4	6	2%		30%	1%	21%		9,4	
		sand		-148		2,6	6	4%		27%	1%	19%		0,2	
		mud		178		2,5	6	4%		33%	1%	22%		31,7	
		total		215		2,4	6	3%		28%	2%	20%		12,2	
1		Southern System	Bupw	99	381	2,5	8	2%	3,5	51%	28%	45%	24%	37,9	1,8
3	Benguela upwelling	Northern System 70s		245		2,3	4	3%		42%	0%			27,0	5,0
		Northern System 80s		50		3,3	4	22%		24%	0%			20,0	1,2
		Northern System 90s		178		2,6	4	10%		32%	0%			16,0	3,6
1 ^(4,5)	Swartkops estuary	saltmarsh, sandflat	SW	-363	1 968	4,0	6	44%	10,2	28%	36%	30%	40%	1,7	0,7
4	Kromme estuary	saltmarsh, sandflat	K	-203	-78	2,4	6	26%	22,5	34%	34%	29%	91%	4,0	0,1
6 ⁽⁵⁾	Narragansett Bay	estuary	N	87	399	4,2		48%	8,1	34%	42%	32%		24,2	1,3
6 ⁽⁵⁾	Delaware Bay	estuary	D	78	205	2,8		37%	3,4	33%	39%	31%		28,2	1,3
6 ⁽⁵⁾	Chesapeake Bay	estuary	Ca	-292	142	3,3		24%	6,9	31%	36%	30%		30,3	0,5
1			Cb	-256	3 697	3,6	6	30%	12,1	50%	28%	35%	41%	24,9	0,7
7	Bothnian Bay	oligohaline	BOa	13	34	2,3	7	13%	1,3	44%	31%	36%	47%	25,9	1,7
7	Bothnian Sea	mesohaline	BOb	42	1 244	3,2	7	27%	1,8	43%	34%	42%	52%	13,4	1,5
7			BAa	83	267	2,8	7	21%	1,3	43%	33%	41%	47%	18,9	1,8
1	Baltic proper	polyhaline	BAb	-4,3	60	3,3	7	23%	1,5	56%	22%	40%	71%	16,7	1,0
8	Ythan Estuary	estuary	Ya	424	1 354	2,5	4	27%	15,2	58%	25%	49%	26%	1,0	0,6
4			Yb	340	841	2,9	6	26%	13,3	34%	34%	34%	8%	4,8	1,7
1 ⁽⁴⁾	Ems Estuary	estuary	E	23	61	3,4	5	30%	2,1	38%	36%	38%	98%	11,1	1,3
5	Seine Estuary	estuary	SE	230	99 343	4,0	5	16%	2,5	35%	28%	23%		38,3	1,4
9	Aiguillon Cove	extended mudflat	AC	-673	27 562	1,9	4	15%	4,9	30%	34%	19%	85%	22,5	0,4
9	Brouage Mudflat	extended mudflat	BM	-263	12 734	1,7	4	19%	6,6	34%	36%	16%	63%	20,8	0,7
			mean:	102	11 116	2,8	6	18%	6,5	37%	23%	31%	55%	19,2	1,4

values superior to the mean

Table 4: Matrix of Spearman rank correlations between all network indices (Table 3), calculated from the 18 models taken into account in the PCA (those with a PCA abbreviation in Table 3).

	NSP	NSQP	APL	FCI	D/H	A/C	R/C	Ai/Ci	NPP/B	GPP/R	A/C-Ai/Ci
NSP	1	0.146	0.015	-0.133	-0.183	0.497	-0.356	0.606	0.172	0.608	-0.145
NSQP		1	-0.024	-0.166	0.063	-0.045	-0.227	-0.139	0.220	-0.047	0.217
APL			1	0.606	0.152	-0.147	0.215	-0.051	-0.026	0.069	-0.392
FCI				1	0.482	-0.317	0.562	-0.082	-0.517	-0.318	-0.456
D/H					1	-0.306	0.274	-0.356	-0.472	-0.607	-0.062
A/C						1	-0.780	0.786	0.054	0.374	0.402
R/C							1	-0.541	-0.132	-0.222	-0.500
Ai/Ci								1	-0.057	0.534	-0.151
NPP/B									1	0.303	0.271
GPP/R										1	-0.294
A/C-Ai/Ci											1

Annexe 1: Structure of the selected models for the inter-system comparison. DOC=Detritic Organic Carbon, POC=Particular Organic Carbon, bacteria and primary producers. The blank cells mean that the compartment does not exist in the model. The non empty cells contain either information when details about compartment contents are given or an asterisk when the compartment is described only by the heading of each column. Number of compartments ('non fauna' (including det, DOC, POC, bacteria and primary producers), micro-meio-fauna (including zooplankton, meiofauna and foraminifera), invertebrate fauna (benthos and epifauna) or vertebrate fauna (fish, birds and mammals)) in each food web model (same bibliographic references as in table 1).

ref	site	description	detritus	DOC	suspended POC	sediment POC	pelagic producers	benthic producers	pelagic bacteria	Numbers of food web compartments				
										non-fauna	micro-meio	invertebrates	vertebrates	total
1	Peruvian upwelling	upwelling system		*	*	*	*	*	*	6	3	1	6	16
2	Tongoy Bay	seagrass meadows					phytoplankton + rodophyta + <i>Chondrocanthus chamissoi</i> + <i>Ulva sp.</i> + <i>Heterozostera tasmanica</i>		*	6	1	10	0	17
		sand-gravel					phytoplankton + rodophyta + <i>C. chamissoi</i> + <i>U. sp.</i>		*	5	1	13	0	19
		sand					phytoplankton + rodophyta + <i>C. chamissoi</i> + <i>U. sp.</i>		*	5	1	10	0	16
		mud					phytoplankton		*	2	1	9	0	12
		total					phytoplankton + rodophyta + <i>C. chamissoi</i> + <i>U. sp.</i> + <i>H. tasmanica</i>		*	6	1	17	0	24
1	Benguela upwelling	Southern system		*	*		phytoplankton		*	4	2	0	10	16
3		Northern system 70s	*				phytoplankton	*		3	2	1	11	17
3		Northern system 80s	*				phytoplankton	*		3	2	1	11	17
3		Northern system 90s	*				phytoplankton	*		3	2	1	11	17
1 ^(4,5)	Swartkops estuary	saltmarsh, sandflat		*	*	*	*	*	*	6	3	2	4	15
4	Kromme estuary	saltmarsh, sandflat		*	*	*	*	benthic microalgae, macrophytes	*	7	3	2	4	16
6 ⁽⁶⁾	Narragansett Bay	estuary	*			POC+bacteria	phytoplankton	benthic algae	*	5	2	5	2	14
6 ⁽⁶⁾	Delaware Bay	estuary	*			POC+bacteria	phytoplankton	benthic algae	*	5	2	5	2	14
6 ⁽⁶⁾	Chesapeake Bay	estuary	*			POC+bacteria	phytoplankton	benthic algae	*	5	2	4	2	13
1				*	*		POC+bacteria	phytoplankton	benthic algae	*	6	3	4	2
7	Bothnian Bay	oligohaline		*		*	*	*	*	5	3	2	2	12
7	Bothnian Sea	mesohaline		*		*	*	*	*	5	3	2	2	12
7	Baltic proper	polyhaline		*		*	*	*	*	5	3	2	2	12
1				*	*		*	*	*	*	6	3	4	2
8	Ythan Estuary	estuary			*	POC+benthic microflora	phytoplankton	benthic macrophytes (<i>Enteromorpha spp.</i> , <i>Chaetomorpha linum</i> , <i>Ulva lactuca</i> , <i>Fucus spiralis</i> , <i>Vaucheria sp.</i>)		5	2	2	3	12
4	Ems Estuary	estuary	*	*	*	*	phytoplankton	idem	*	6	3	2	3	14
1 ⁽⁴⁾				*	*	*	*	*	*	*	6	3	4	2
5	Seine Estuary	estuary				POC+detritus	phytoplankton	phytobenthos (microphytobenthos, chlorophytes and pheophytes)		3	1	7	4	15
9	Aiguillon Cove	extended mudflat	benthic detritus + bacteria				phytoplankton and resuspended microphytobenthos	microphytobenthos	pelagic detritus + bacteria	4	4	5	3	16
9	Brouage Mudflat	extended mudflat	benthic detritus + bacteria				phytoplankton and resuspended microphytobenthos	microphytobenthos	pelagic detritus + bacteria	4	4	5	3	16

Figures

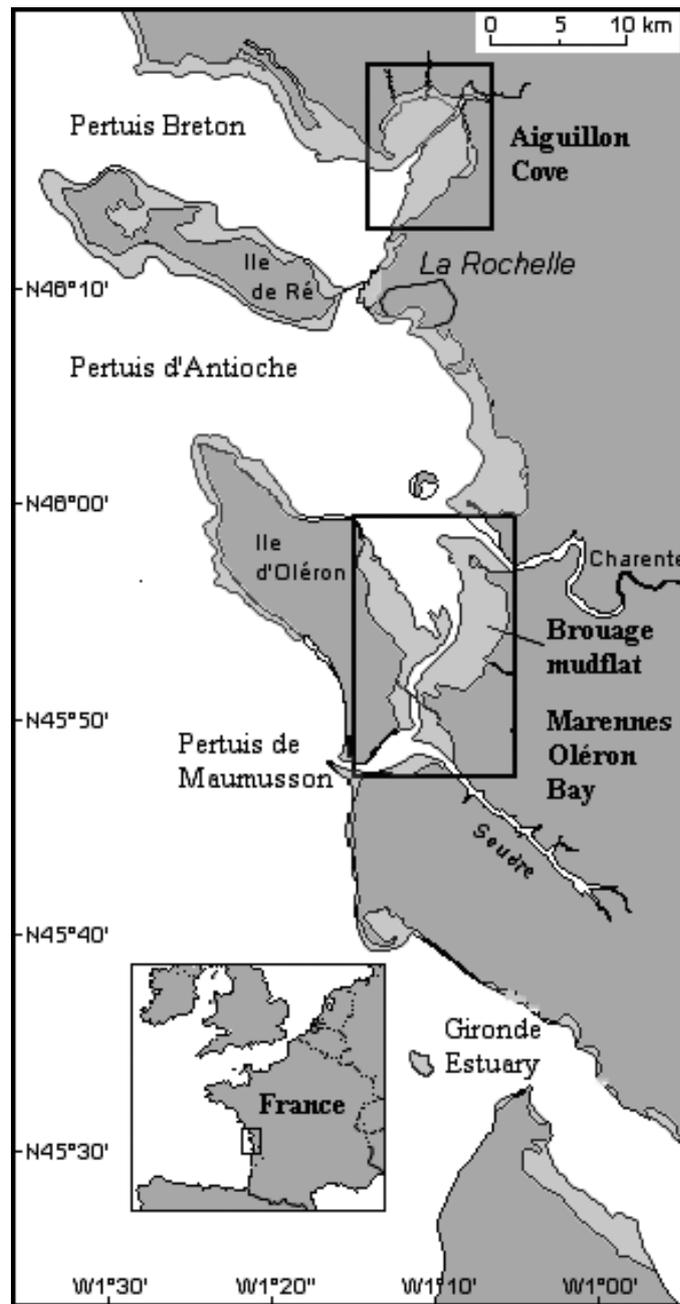


Fig. 1. Map of the Charentais Sounds (Pertuis) showing the location of the two study sites: the Aiguillon Cove and the Brouage Mudflat (from Degré et al., 2006)

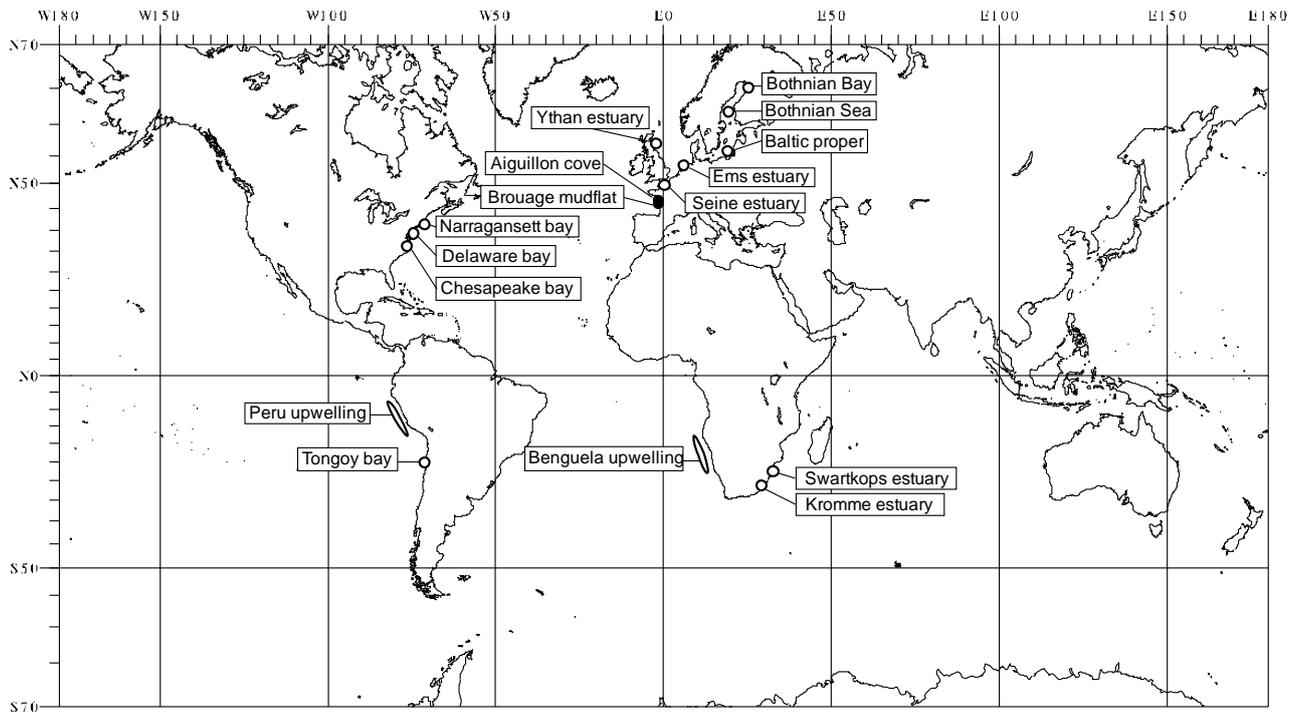


Fig. 2. Map of the world with the 2 French intertidal mudflats (Aiguillon and Brouage, black points), and the 14 compared sites (3 Baltic sites, 3 North-European estuaries, 3 American estuaries, 3 upwelling systems and 2 South-African estuaries, white points).

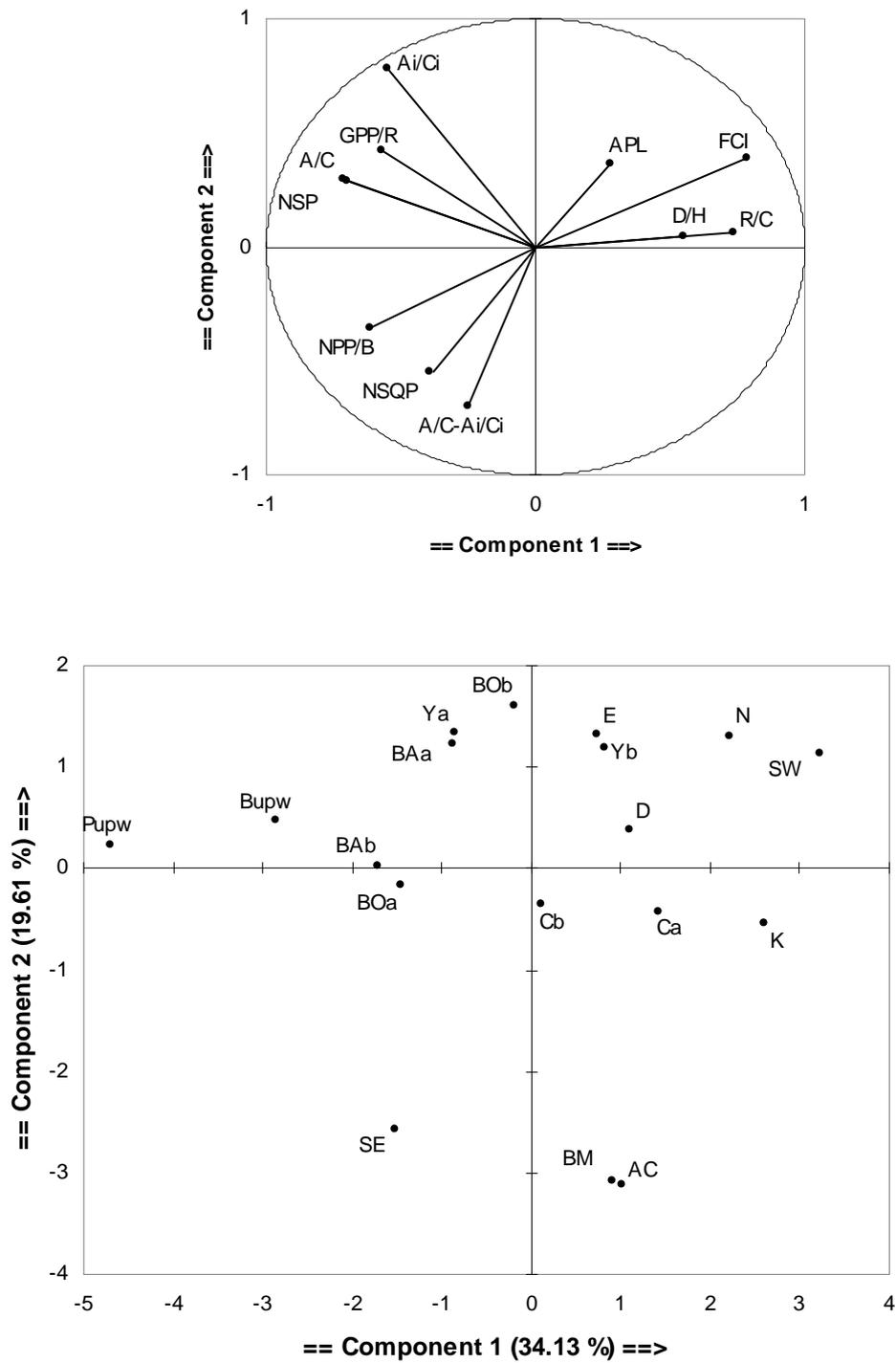


Fig. 3. Principal Component Analysis applied to the indices of Tab. 3. Upper part of the figure: scatter plot of the variables (network analysis indices) in the space defined by the 2 first components. Lower part of the figure: scatter plot of the observations (ecosystems). For indices and ecosystem abbreviations see Table 3.