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Contribution des habitats estuariens à la productivité et au fonctionnement du réseau trophique de la Seine Aval.

Impacts des aménagements et du changement global.

Par : Alexandre SCHICKELE

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Prénom :Alexandre
Adresse personnelle 7 rue du Cerf, 67115 Plobsheim:

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Remerciements

Arrivé au terme de mon stage de fin d’études, quoi de mieux qu’une traditionnelle page de remerciements pour débuter ce mémoire. Ce stage s’est déroulé dans le cadre du projet ANTHROPOSEINE financé par le programme SEINE-AVAL 5.

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Résumé étendu en français

Contribution des habitats estuariens à la productivité et au fonctionnement du réseau trophique de la Seine Aval. Impacts des aménagements et du changement global.

Contexte :

Les activités anthropiques côtières couplées au changement global exercent une pression croissante sur les environnements terrestres et marins. Les estuaires, situés à la conjonction des milieux marins et d'eau douce, jouent un rôle important dans les cycles biogéochimiques. Ils abritent également une forte production biologique malgré leur faible biomasse. Ceux-ci jouent un rôle crucial dans le maintien des ressources marines, notamment dû à leur fonction de nourricerie. L'estuaire de Seine est un estuaire méga-tidal, fortement anthropisé. Il a subi d'importants travaux d'endiguement et de dragage principalement depuis les années 1970. De 2002 à 2005, une nouvelle extension du port du Havre (Port 2000) a été construite, fermant une zone de 5 km² (20%) de la fosse Nord qui est une importante zone de nourricerie. En plus d'une réduction de débit de la rivière, d'autres aménagements ont vu le jour en parallèle de Port 2000 tel que la construction du pont de Normandie et la réhabilitation d'un méandre.

Plusieurs efforts de modélisation ont permis de montrer une altération du fonctionnement hydromorphologique de l'estuaire et une perturbation des communautés biologiques, notamment benthiques et suprabenthiques. D'autres études ont souligné des changements de composition sédimentaire, notamment un ensablement des fosses Nord et Sud. En parallèle, plusieurs modèles trophiques ont été appliqués à l'estuaire de Seine, de façon globale puis en considérant indépendamment les différents habitats le composant. Ceux-ci ont décrit l'écosystème comme immature et stressé. La fosse Nord a été caractérisée comme une zone soumise à de fortes pressions, ayant un recyclage important et des chaines trophiques courtes. La fosse Sud, quant à elle, semble peu anthropisée et ayant une forte activité biologique.

Objectifs :

Les précédents modèles trophiques ont été repris puis améliorés en considérant l'estuaire de Seine comme un réseau d'habitat interconnectés. Pour cela, deux modèles trophiques ont été construits selon une structure particulière utilisant l'approche de modélisation Ecopath sur les périodes avant (1996-2002) et après (2005-2012) la construction de Port 2000. Cette approche a permis l'étude du fonctionnement trophique de l'estuaire dans sa globalité ainsi qu'à l'échelle des habitats. L'étude présentée ci-après a pour objectif principal d'évaluer la contribution des différents habitats estuariens à la productivité et au fonctionnement trophique de la Seine Aval. Plus spécifiquement, ces modèles ont permis d'étudier la structure trophique de l'estuaire, d'estimer le rôle de nourricerie de chaque habitat ainsi que d'évaluer les interactions entre les différents habitats dans un contexte d'anthropisation.

Matériel et méthode :

- **Construction et structure du modèle**

Les modèles utilisés ont été construits en suivant l'approche Ecopath. Celle-ci permet une modélisation de l'ensemble du réseau trophique en suivant une hypothèse d'équilibre de masse au sein du système et de la période considérée. Les groupes fonctionnels, regroupant des espèces de caractéristiques trophiques homogènes, sont associés à une équation de production et de consommation permettant d'équilibrer le modèle. L'originalité de ce travail a été de construire un modèle semi-spatialisé en assignant les groupes de bas niveaux trophiques, sédentaires, à un compartiment spatial correspondant à un habitat particulier de l'estuaire. Les prédateurs supérieurs quant à eux, mobiles, ont été modélisé afin qu'ils soient libre de se nourrir dans tout l'estuaire et donc sur différents habitats. La matrice de régime alimentaire, permettant de modéliser les flux trophiques entre les groupes fonctionnels est également spatialisée selon une hypothèse de densité dépendance des relations prédateurs-proies. Les modèles ont été construits avec 66 groupes fonctionnels, incluant 11 groupes de prédateurs supérieurs et des groupes sédentaires répartis dans 6 habitats distincts : l'embouchure, le chenal de navigation et les zones Nord et Sud séparés en habitat intertidal et subtidale.

- **Evaluation de la contribution des habitats**

Chaque groupe fonctionnel de prédateur supérieur est dépendant des différents habitats en termes de consommation. La contribution de ces différents habitats au fonctionnement de l'estuaire a notamment été estimée par l'origine de la consommation des prédateurs supérieurs. Celle-ci a été calculée en prenant en compte les chaines directes (proies) et indirectes (proies de proies). L'étude de la contribution nous a notamment permis d'estimer l'importance de chaque habitat en termes de fonction de nourricerie. En parallèle, nous avons analysé l'efficacité écotrophique (dans notre cas, la part de la production d'un niveau trophique consommée par les niveaux trophiques supérieurs) moyenne par habitat afin de déterminer leur capacité à supporter la prédation.

- **Indicateurs de santé de l'écosystème**

L'importance de chaque groupe fonctionnel et indirectement des différents habitats estuariens a également été estimée en analysant les impacts trophiques. La matrice des Impacts Trophiques Mixtes couplée à l'indice de Keystoneness nous a permis de déterminer les groupes trophiques ayant un rôle majeur dans l'écosystème. Cette analyse a été complétée par différents indices de santé de l'écosystème afin de mieux caractériser le niveau de stress, le niveau d'activité et la maturité de l'estuaire de Seine dans sa globalité. Ces indices ont notamment servi de point de comparaison entre les deux périodes considérées et entre différents estuaires français. Enfin, une analyse d'incertitude a été menée sur ces indicateurs afin d'estimer le niveau de confiance dans ces résultats.

Résultats :

Les résultats ont rapidement montré l'importance des communautés benthiques en termes de biomasses, de flux et d'impact trophiques dans le système. Ces groupes fonctionnels sont les proies principales des prédateurs supérieurs mais sont également les principaux prédateurs des niveaux trophiques inférieurs, influençant fortement leurs habitats respectifs par un contrôle top-down. Concernant les prédateurs supérieurs, le Merlan (*Merlangius merlangus*) ainsi que les oiseaux marins jouent un rôle structurant important dans l'écosystème. Concernant les différents habitats, les zones Nord et Sud ont une forte contribution à la consommation des prédateurs supérieurs comparés à leur faible surface. Ceci peut être interprété comme une forte attractivité de ces zones de nourriceries.

D'un point de vue temporel, ces modèles complètent les changements mis en évidence par les précédents modèles trophiques. La comparaison des modèles avant et après la construction de Port 2000 montre notamment une forte chute de biomasse du suprabenthos alors que les biomasses benthiques ont augmentées. Ces changements de composition en termes de biomasses ont impacté les contributions de chaque habitat ainsi que les impacts trophiques des différents groupes. En effet, l'augmentation des biomasses benthiques a entrainé une hausse de la prédation au sein des différents habitats alors que la prédation des groupes mobiles (prédateurs supérieurs) a diminuée. Ceci a conforté l'importance des communautés benthiques, déjà très présentes dans l'estuaire de Seine. La comparaison des deux modèles a également mis en évidence un report de prédation (et donc un changement de contribution des habitats) de l'embouchure vers le chenal de navigation ainsi que des domaines subtidaux vers les domaines intertidaux. Ceci reflète d'une part des changements de biomasses, d'autre part, un possible décalage de l'estuaire vers l'aval.

Enfin, les indicateurs de santé des écosystèmes ont montré une augmentation du recyclage et des flux de consommation et de respiration entre les deux périodes. L'omnivorie a, quant à elle, diminué, indiquant une augmentation du stress et une diminution de la maturité de l'écosystème.

Conclusion :

Ce travail a permis de compléter les précédentes modélisations trophiques de l'estuaire de Seine en intégrant une dimension spatiale, de l'estuaire aux habitats. De plus, les modèles construits durant ce stage permettent une estimation des impacts dus aux aménagements liés à Port 2000 et au changement de débit de la Seine. L'hypothèse de densité dépendance des relations prédateurs-proies a permis de modéliser l'opportunisme et l'adaptation des prédateurs à cet environnement changeant. Ainsi, les modèles ont montré un report de prédation vers les zones intertidales durant la deuxième période considérée. De plus, les communautés benthiques ont été caractérisées comme jouant un rôle structurant important dans l'écosystème. De futures études des communautés ou une modélisation trophique plus large incluant la Baie de Seine permettrait notamment de replacer l'estuaire dans son environnement plus large et d'y inclure les activités de pêche et d'autres facteurs environnementaux.

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1. Introduction

Coastal development, anthropogenic disturbances and global climate change are exerting a growing pressure on marine and freshwater ecosystems (Halpern *et al.* 2008). These various disturbances are altering the biochemical cycles by modifying the soil, the water and the atmospheric composition (Doney 2010). Estuaries are located between marine and freshwater ecosystems and are playing a key role for biochemical cycles especially in carbon, nitrogen and phosphorous recycling (Doney 2010). They are known for being among the most productive ecosystems worldwide despite hosting a relatively low biomass and diversity comparing to other coastal ecosystems (McLusky & Elliott 2004). Estuaries are also important for marine resources by providing habitat and food to juvenile fish and seabirds (Elliott & Hemingway 2002; Wilson 2002). Estuarine environments are under high human pressures and at the same time, are also providing highly valuable ecosystem services to a large part of the human population worldwide (McLusky & Elliott 2004).

The Seine estuary, located in Northern France is a mega-tidal estuary, discharging its waters into the Eastern English Channel. It is the third largest French estuary and it is also known for being highly modified compared to its natural state (Meybeck *et al.* 1998). Several channeling works for navigation purposes and flood protection have been done during the last century, especially after 1970. These infrastructures significantly increased maritime traffic but altered the natural water flow and hydrological and sedimentary functioning of the estuary and its adjacent bay (Dauvin & Desroy 2005; Cuvilliez *et al.* 2009). Coastal and estuarine ecosystems have recently been included into European water policies through the Water Framework Directive which requires a “good ecological status” of all European waters (European Council 2000). Therefore, several measures have been taken, for example a large part of the Seine estuary has been set under Natura 2000 status. However, they are no concrete protections in the Seine estuary and the eastern Seine Bay.

From 2002 to 2005, a new extension of Le Havre harbour called Port 2000 has been built next to the existing harbour, closing out an average 5 km² area of the Northern flank (Tecchio *et al.* 2016). The Port 2000 construction was done along with other works on the estuary including dredging in the channel and the flanks, dykes opening and the construction of the Normandy Bridge, modifying once again the water flow in the estuary. All these works generally improved the water circulation for navigation in the estuary but recent studies showed that Port 2000’s construction had a negative impact on the estuarine communities. For example, diversity and density losses have been highlighted for suprabenthic communities (Dauvin *et al.* 2010). Other studies showed changes in the sedimentary composition of the estuary and the adjacent bay especially in the Northern flank facing siltation while muddy sediment are exported further in the bay (Dauvin *et al.* 2006; Cuvilliez *et al.* 2009).

In parallel of sedimentary and single community approaches, some researches focused on the food web structure and functioning of the Seine estuary through ecosystem approaches. The first food web modelling showed high level of stress and low system maturity in the downstream part of the estuary during the 1996 to 1999 time period

(Rybarczyk & Elkaïm 2003). Since then, other estuary food web studies have been done concerning the period before Port 2000's construction. The previous model has been improved by considering the Seine estuary as a set of distinct habitats having their own food web functioning instead of considering the whole estuary at one time (Vincent *et al.* 2006). This new approach has been taken up by Tecchio *et al.* (2015) with more recent data and the use of Ecological Network Analysis (ENA). This model concerned the 1996 to 2002 time period and included 6 functional habitats located in the Seine estuary and the Eastern part of the Seine bay. The Ecological Network Analysis showed important differences between the various habitats. The navigation channel and the Northern flank were identified as the most pressured habitat contrary to the Southern part of the estuary considered as less stressed and having the highest system activity. The impact of Port 2000 was assessed by comparing both 1996-2002 and 2005-2012 time period (Tecchio *et al.* 2016). These models highlighted an increase in detritivory activity and carbon recycling after 2005 in different habitats. However, ENA patterns were inconclusive about the direct impact of Port 2000.

Modelling approaches thus considered the Seine estuary either as a unique food web or as a set of different independent habitats accounting for data or modelling considerations. The habitat approach is important to understand the heterogeneity of the estuary and one of the main interest of the work presented here after, is to replace these structural and functional differences within the global functioning of the estuary. This point of view would help to have a detailed assessment of the impact of Port 2000's construction on the ecosystem, from the habitat to the estuary scale. My work during these six month internship within the EABX-FEE team at IRSTEA Bordeaux follows the studies presented above, especially Tecchio *et al.* (2015, 2016). This work focused more particularly on the contribution of the different spatial habitats of the Seine estuary to the whole estuary food web functioning and productivity. Several underlying questions arise from this problematic:

- How to describe the spatial structure and functioning of Seine estuary food web at both estuary and habitat scales?
- How can we describe the nursery efficiency of each estuarine habitat?
- How does each habitat influence the others and therefore which one has to be preferentially protected or restored through different scenarios?
- Which level of confidence is associated to these food web models?

The food web modelling was realized with the Ecopath software in order to use the previous models (*e.g.*Tecchio *et al.* 2015) as a baseline. However, the classic Ecopath modelling approach does not take account for spatial compartments. Therefore, a more complex model structure (Guénette *et al.* 2014; Piroddi *et al.* 2015) was adapted to our spatial estuary modelling. The models were constructed step by step. First we used strictly the input parameters, functional groups and spatial compartment of Tecchio *et al.* (2015). Then we clarified the functional group structure and finally we adapted the spatial compartment in order to meet homogeneous habitat within each spatial compartment. The following report presents the two food web models constructed both for the 1996 to 2002 and 2005 to 2012 time periods in order to assess the questions asked above.

2. Material and methods

2.1.Study area: the Seine estuary

The Seine estuary is a mega-tidal estuary located in Northern France (**fig.1**), discharging the waters of the Seine basin into the Eastern English Channel. The estuary is 170 km long, going from Le Havre harbour to the Poses dam, 40 km upstream of Rouen harbour. The Seine estuary is draining the water of a 79,000 km² area concentrating 40 % of the French industry and population of which 80 % live in urban areas (Guézennec 1999). The Seine basin includes Paris and two of the main commercial harbour of the country, Le Havre (2nd) and Rouen (6th). In this study, we will focus on the marine part of the estuary downstream of the Tancarville Bridge which corresponds to the average brackish water upstream limit. The estuary is mainly tide influenced with an average tidal range of 8 m at the estuary mouth (Guézennec 1999).

The mean annual river flow at Poses dam is 410 $m^3.s^{-1}$ (ranging from 81 to 2,000 $m^3.s^{-1}$ depending on the season) which is lower than the Gironde estuary (915 $m^3.s^{-1}$ at the confluence of the Garonne and Dordogne river) (Guézennec 1999; Girardin *et al.* 2014). The conjunction of the tides and the river flow creates a maximum turbidity zone (MTZ) in the estuary where the particles are merging. This MTZ, located between Le Havre harbour and the Tancarville Bridge can shift upstream to Vieux-Port during ebb tide or downstream into the Seine Bay during low tide (Dauvin et al., 2010). The maximum turbidity zone traps between 20,000 and 400,000 tons of particular material (Guézennec 1999). It is considered as a major detritus pool even if the Seine river has a relatively low mean particular material flow comparing to other European estuaries (675,000 tons per year at the Poses dam comparing to 2,000,000 tons per year for the Gironde) (Guézennec 1999; Le Hir 2001; Lobry *et al.* 2008).

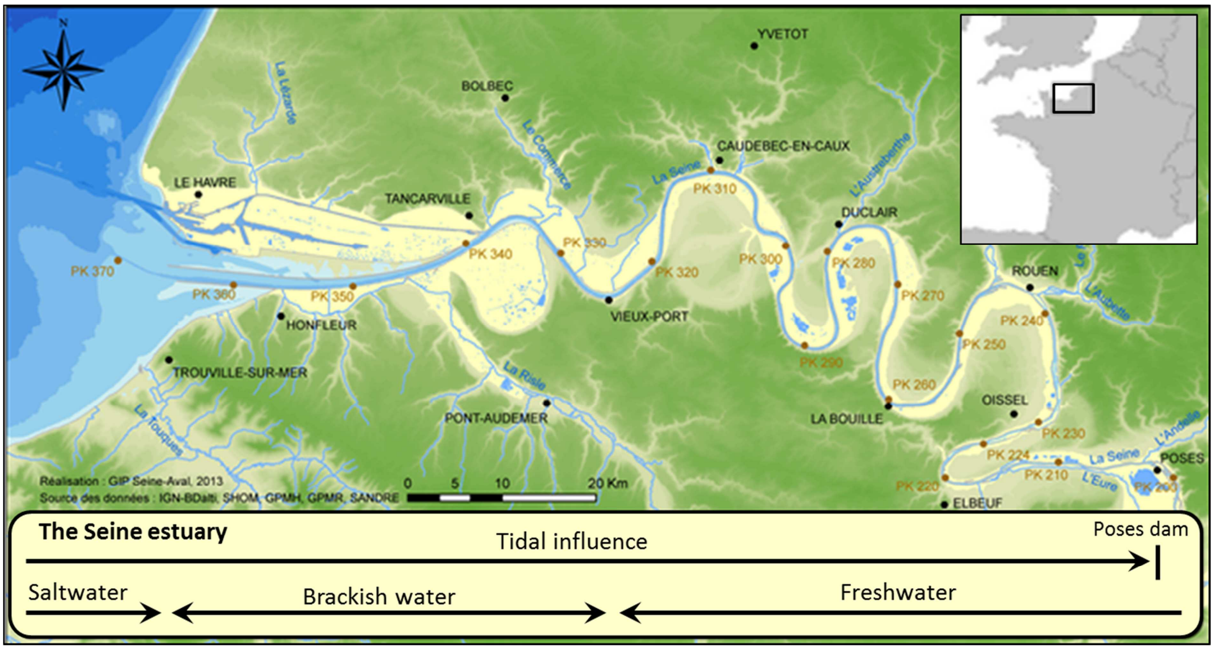


Figure 1: Map of the Seine estuary (according to GIP Seine Aval, 2013)
PK: kilometric point; PK 0 starting at Notre Dame de Paris

The Seine estuary's location makes it a major entrance point for commercial trading with Paris and its surroundings. This led to an important industrial development over the past century. The first channeling campaign started in the mid- 19th century with the construction of dykes from Tancarville to Rouen harbour 120 km upstream together with dredging of the shallow sandbars in order to have a minimum draught of 3.2 meters (Foussard 2010). In the 20th century, these works have been continued by consolidating the dykes and increasing the draught from the estuary to Rouen. The estuary started to silt up, causing the decline of Honfleur harbour and the need to extend the dykes further in the estuary to stabilize the navigation channel (Foussard 2010). In 1970, the development of Le Havre harbour led to extend the dykes to the estuary mouth which completely artificialized the estuary.

Resulting of 150 years of man alteration, the Seine Estuary and the Seine River morphology have been highly modified, with more than 80 % of the river banks being man modified nowadays and most of the islands partially erased to let a straight navigation channel (Foussard 2010). The estuary had a natural intertidal surface of 130 km², providing an important nursery ground for flatfishes which was reduced to 30 km² by the dykes and the general silting, particularly in the Northern intertidal mudflats (Dauvin *et al.* 2010). The industrial development along the river increased water pollution levels up to the highest in Europe and caused frequent hypoxic events until up the 2000's (Tecchio *et al.* 2016). Finally, the fisheries operating in the marine part of the estuary have nowadays collapsed probably due to the water and habitat quality in the estuary (Dauvin 2008).

2.2.Ecopath modelling approach

Generalities and model development

In order to estimate the carbon flows and the structure of the Seine estuary food web, we used the Ecopath with Ecosim approach and software developed by(Christensen & Walters 2004).

Ecopath is a software and a modelling approach that allow estimating the carbon flows and the food web functioning within an ecosystem. This modelling approach uses knowledge of the ecosystem's component instead of the carbon flows themselves. Therefore it is similar to inverse modelling (Lobry 2004). The model estimates are based on several quantitative parameters for each ecosystem functional group and for the whole ecosystem without explicitly modelling the underlying processes. This modelling approach was initiated by (Polovina 1984) to study tropical coral ecosystems. It has been used together with several theoretical ecology concepts developed by Ulanowicz (1986) as the basis of the Ecopath steady state modelling approach (Christensen & Pauly 1992). A time dynamic version of Ecopath, Ecosim emerged in 1995 (Walters *et al.* 1997, 2000) and a spatial dynamic package, Ecospace was developed in 1999 (Walters *et al.* 1999) leading to the integrated software package "Ecopath with Ecosim" (EwE). The software has been completed by several integrated routine, for example, Ecotroph which allows studying a given ecosystem through its trophic structure and variability (Gascuel & Pauly 2009).

This modelling approach has been widely used worldwide to describe food webs (Christensen & Walters 2004). Initially developed for studying marine ecosystem food webs, it has also been applied to the large North American bays (*e.g.*Monaco & Ulanowicz 1997) and more recently to temperate European coastal and mega-tidal estuaries ecosystems (*e.g.*Rybarczyk & Elkaïm 2003; Lobry *et al.* 2008; Prado *et al.* 2013; Tecchio *et al.* 2015).

Model functioning and basic equations

Ecopath is a single solution model, relying on a mass-balance hypothesis and using linear equations to estimate flows between a numbers of functional groups established *a priori* (Christensen & Walters 2004). A functional group is composed of a unique species or several species of similar trophic behavior pooled together. The model supposes that the system is mass balanced during the time period considered.

Each group is parameterized with, at least, its biomass (B, t.km^{-2}), its production rate over biomass (P/B, year^{-1}), its consumption rate over biomass (Q/B, year^{-1}), its assimilation efficiency or excretion rate (U/Q, -) and the interactions with its prey(s) and predator(s) in the form of a diet matrix (DC$_{ij}$, -) which also establishes the identity of the trophic flows (Christensen & Pauly 1992). Two linear equations are solved for each functional group to ensure the mass balance (**eq. 1**) and the energy balance (**eq. 2**)(Christensen & Pauly 1992; Christensen & Walters 2004). The mass-balance equation gives the production (P) of the ith group as a function of the predation of the jth predator, fishing mortality (Y), net migration (E), biomass accumulation (BA) and natural mortality (1-EE):

Production *= Total capture + Predation + Net migration + Other mortality + Accumulation*

$$B\left(\frac{P}{B}\right)_i = \sum_j B_j\left(\frac{Q}{B}\right)_j DC_{ij} + Y_i + E_i + BA_i + B_i\left(\frac{P}{B}\right)_i(1 - EE_i) \qquad \textbf{(eq. 1)}$$

The energy balance equation (also named consumption equation) gives the consumption (Q) of the ith group as a function of its production (P), respiration (R) and excretion (U):

Consumption = ***Production*** *+ Respiration + Unassimilated food*

$$Q_i = P_i + R_i + U_i \qquad \textbf{(eq. 2)}$$

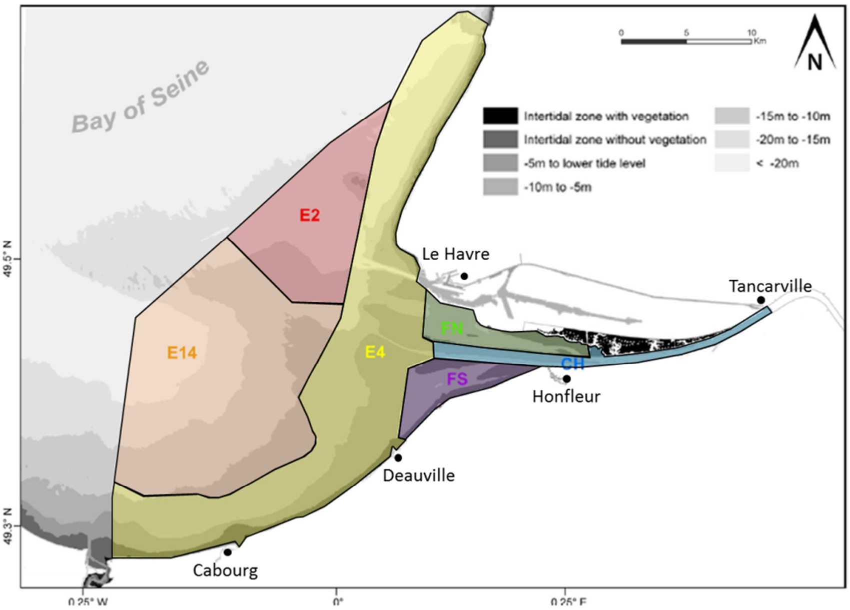
A system of linear mass balance and energy balance equation (one for each functional group present in the model) is solved to estimate the carbon flow between each trophic group. If only one parameter is missing *a priori* in the model, it is estimated by the model except for the diet matrix and, if it is the case, for the catch data which cannot be estimated. Due to the uncertainty and the different sources of data used to estimate the parameters a priori, the model is often not mass balanced at first time. This is reflected by ecotrophic efficiencies “out of balance” (EE>1) which means that the biomass produced by the trophic group is not enough to sustain the predation and/or fishing occurring on this group.

To ensure the mass balance, we applied a manual “trial and error” procedure on the different *a priori* parameters, following a top-down approach. We tried to change the parameters associated with higher uncertainty, *i.e.* the diet matrix first, followed by P/B and Q/B and if necessary the biomass (Christensen & Walters 2004). The changes made on each parameter were based on its uncertainty and on expert knowledge of the area studied and the species ecology. The Ecopath models were considered mass balanced when (1) Ecotrophic Efficiencies were <1; (2) food conversion efficiency (P/Q) was <0.5 (usually between 0.1 and 0.3) and (3) respiration over assimilation rate (R/A) was <1 (Christensen & Walters 2004; Piroddi *et al.* 2015).

2.3.Model structure

Models used as a basis for the spatial approach

The Seine estuary has first been considered as a network of habitats by Vincent *et al.* (2006) followed by Tecchio *et al.* (2015, 2016) using respectively an Ecopath and a LIM-MCMC approach. These works were used as a baseline for the spatial modelling approach I worked on during my internship and are presented hereafter.



N°	Group name
1	Seabirds
2	Fish, piscivores
3	Fish, planktivores
4	Fish, benthos feeders
5	Fish, endobenthic feeders
6	Benthic predators
7	Benthic filter feeders
8	Benthic deposit feeders
9	Suprabenthos
10	Meiofauna
11	Zooplankton
12	Bacteria
13	Microphytobenthos
14	Phytoplankton
15	Detritus

Figure 2: Functional groups and habitats used by Tecchio *et al.* (2015; 2016).
With FN (Northern flank), CH (Navigation channel), FS (Southern flank) and E4, E2 and E14 (Seine bay habitats)

Tecchio *et al.* (2015) used the Ecopath with Ecosim approach together with Ecological Network Analysis to model the food web structure in 6 spatial compartments. The spatial units included the Seine estuary and the adjacent part of the Seine bay as shown in **fig. 2** above. Each spatial compartment has been modelled separately during the time period from 1996 to 2002. The functional groups used for each model included 5 predator groups, 3 secondary consumer groups, 3 consumer groups, 2 primary producer groups and a detritus group as shown in **fig. 2**. The Ecological Network Analysis showed that the navigation channel and the Northern flank were in a stressed state and had a detritus based food web whereas a strong top down control was highlighted in the other habitats. The Southern channel showed the highest system activity and the marine habitats hosted most of the fish biomass together with high transfer efficiency.

The modelling approach used in Tecchio *et al.* (2015) focused only on each of the three estuarine compartments during the period 1996-2002 then 2005-2012 in order to study the impact of Port 2000. The functional groups remained the same as in **fig. 2**. The result showed an increasing of the trophic specialization in the Southern flank. They also highlighted an increase in detritivory and carbon recycling. However, in general, patterns of ENAs were inconclusive about the direct impact of Port 2000.

Model structure and hypotheses

The models built by Tecchio *et al.* (2015, 2016) highlighted heterogeneity between the various spatial compartments composing the Seine estuary, probably due to diversity in habitats (*e.g.* sediments, bathymetry). However, no relationships between these spatial units were modelled at this time. Yet, one of the main objectives of this work is to replace these structural and functional differences within the global functioning of the Seine estuary. Two Ecopath models have been built respectively for the 1996-2002 and 2005-2012 time period. They should be able to quantify the contribution of each spatial unit to the estuarine production and to describe the relations between the various spatial compartments and the impact of Port 2000.

The classic Ecopath modelling approach does not include a spatial approach. However, Ecopath has recently been used to assess the impact of a marine protected area (Guénette *et al.* 2014) or to model regional seas within a larger ecosystem (Piroddi *et al.* 2015). Both models include different spatial compartments[1] and are standing on a particular functional group[2] structure that we adapted for this work. It is explained here after and in **fig.3**.The trophic boxes are separated into two categories:

- **Sedentary boxes**: corresponds to the species associated to a unique habitat or spatial compartment, in general benthic groups. It is translated into the model by one trophic box per species group per habitat.
- **Mobile boxes**: corresponds to the species capable to move across the various habitats, in general pelagic groups and/or top predators. It is translated into the model by a unique trophic box per species group.

Such a model structure also involves changes in the way to link the various spatial compartments through the diet matrix. The sedentary boxes diets have been taken from the models from Tecchio *et al.* (2015). There are slight differences between the various spatial compartments according to their species biomass composition. Concerning the mobile boxes, the basic diets have been taken from different Seine estuary models (*e.g.*Raoux *et al.* (in prep.); Rybarczyk & Elkaïm 2003; Tecchio *et al.* 2015). See **Appendix 1** for the detailed Ecopath parameter references and **Appendix 2** for the complete diet matrix. The mobile boxes are exerting predation on various preys and spatial compartments. Hence, their diets have to be split between those different spatial units.

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[1] "Compartments" or "units" will refer to the spatial divisions of the model.

[2] "Boxes" or "groups" will refer to the Ecopath trophic boxes. In this model they are either considered sedentary or mobile.

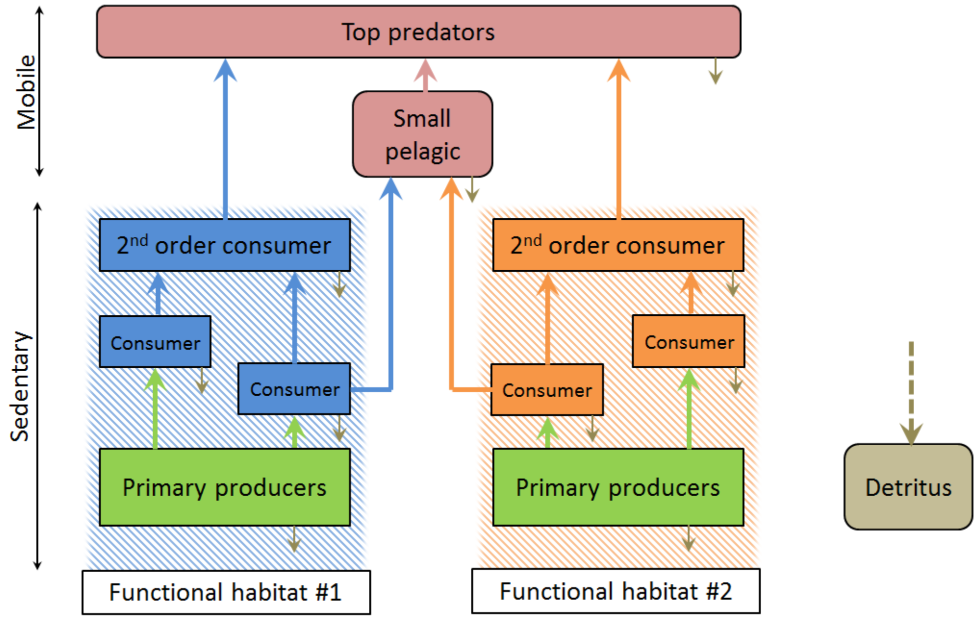


Figure 3: Synoptic diagram illustrating a simplified pattern of the spatial structure used for the Ecopath model

The "Optimal Foraging Theory", despite being partially contested, assumes that patch choice depends on the potential energy gain of this patch (Pyke 1984).The energy gain can be either influenced by the trophic limitation, the habitat selection and predator avoidance (Pyke 1984). Although, according to Le Pape & Bonhommeau (2015), the trophic limitation is the primary factor determining the habitat suitability in estuaries and coastal nurseries.

Another underlying assumption is that on a medium to long term period, predator distribution matches with the prey distribution in coastal and estuary nurseries (Le Pape & Bonhommeau 2015). The Seine estuary underwent several changes in the recent years, impacting the various biological communities (Dauvin & Desroy 2005; Dauvin *et al.* 2006, 2010). Therefore, we assume that the predator distribution has not completely matched with the prey distribution yet. This assumption is translated into the diet matrix by allocating the mobile group diets between the various spatial units according to their prey density instead of the predator density itself. The following equation (**eq. 3**) explains this modelling choice with DC (Diet) and B (biomass) for the jth predator, ith prey and hth habitat:

$$DC_{ijh} = DC_{ij} \times \frac{B_{ih}}{B_i} \qquad \textbf{(eq. 3)}$$

Main assumptions and modelling choices:
- *Functional groups are separated whether they are considered sedentary or mobile.*
- *The sedentary groups are allocated to a habitat (one group per habitat) and their diets are slightly different depending on the habitat biomass composition.*
- *The mobile groups are unique and their diets are allocated to each habitat according to their prey density in each of these habitats.*

2.4.Model parametrization and functional groups

Functional habitats

Estuaries are hosting a high diversity of habitats and functions notably due to the salinity gradient and the sedimentary and flow variations between the channel and the very shallow parts (McLusky & Elliott 2004). In the highly modified Seine estuary, the various man-made infrastructures, especially dykes, tend to isolate the different habitats from each other. Therefore, we could split the Seine estuary into 6 functional habitats as illustrated in **fig. 4**. Each habitat is supposed to be homogenous in terms of water flow, anthropogenic pressure and sedimentary and biological composition.

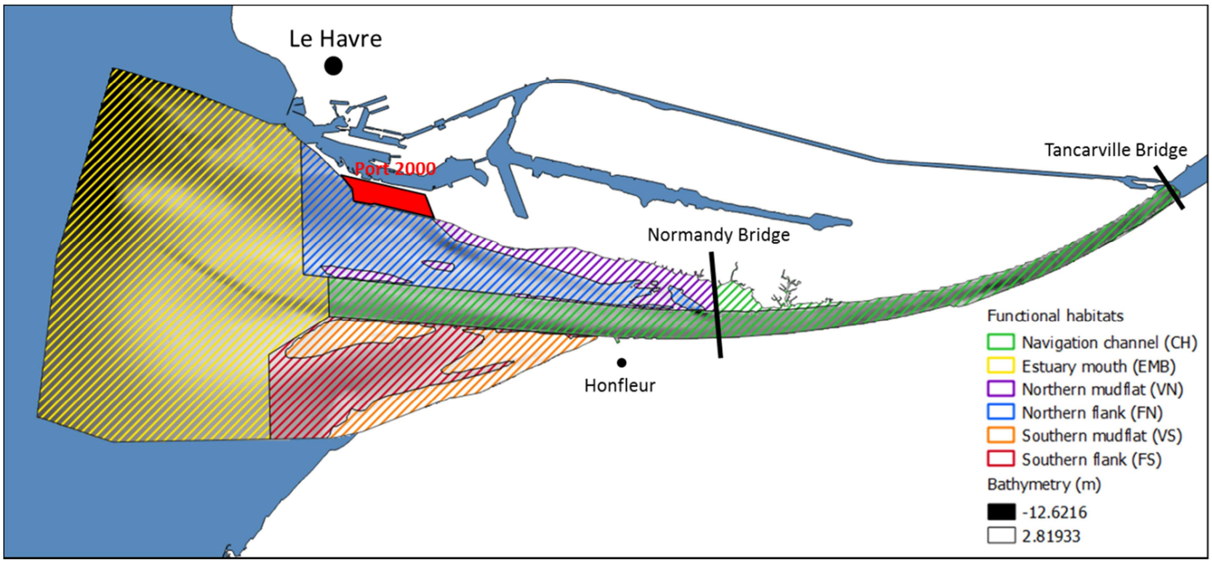


Figure 4: Map of the functional habitats (according to GIP Seine Aval, 2012).
With VN (Northern mudflat), VS (Southern mudflat), FN (Northern flank), FS (Southern flank), CH (Navigation channel) and EMB (Estuary mouth)

The spatial compartment chosen in (Tecchio *et al.* 2015) were used in an intermediate Ecopath model and were also taken as a baseline for the final Ecopath model. Concerning the estuarine part of the model, the intertidal and subtidal areas were considered in previous published models as part of the same functional unit despite having structural and functional differences. In order to respect homogeneity within each habitat, we choose in the present work to allocate the intertidal and subtidal areas in distinct functional units instead of keeping the previous Northern and Southern flank. Concerning the marine part of the model, we choose to only consider the estuary mouth because the model is heavily estuary focused. These modelling choices made us consider the following spatial compartments for the final Ecopath model:

- **VN (Northern intertidal mudflat):** intertidal mudflat pressured by habitat loss due to the Havre harbour and the Normandy Bridge.
- **FN (Northern subtidal flank):** subtidal, muddy-sandy bottom, subject to sedimentation and heavily modified by the Normandy Bridge.
- **VS (Southern intertidal mudflat):** large intertidal mudflat considered as the least pressured habitat (Tecchio *et al.* 2015).

- **FS (Southern subtidal flank):** subtidal, muddy-sandy bottom, subject to sedimentation and considered as low pressured.
- **CH (navigation channel):** year round dredged channel separated from the flanks by submerged dykes.
- **EMB (estuary mouth):** subtidal, muddy-sandy bottom, subject to indirect pressure coming from the estuary and granulate extraction.

Each spatial unit is distinguished from each other by various anthropogenic pressures. These might cause structural and functional responses between the various habitats.

Trophic groups

The various species are aggregated in functional groups which have homogenous trophic characteristics. Moreover, depending either on the mobile or sedentary aspect of these groups, they are associated to a spatial compartment or not. The functional groups used for the final model are presented in **table 1** below and the detail of the species per group can be found in **Appendix 3**.

Table 1: Functional groups used for the final Ecopath model

Mobile groups			**Sedentary groups (one by habitat)**		
1	SBD	Seabirds	**12-17**	IPR	Benthic predators
2	WHI	Whiting	**18-23**	IFF	Benthic filter feeders
3	FPI	Other fish piscivores	**24-29**	IDF	Benthic deposit feeders
4	FPV	Fish planktivores	**30-35**	SUP	Suprabenthos
5	SBA	European Seabass	**36-41**	MEI	Meiofauna
6	FBF	Other fish benthos feeders	**42-47**	ZOO	Zooplankton
7	SOL	Common Sole	**48-53**	BAC	Bacteria
8	PLA	European Plaice	**54-59**	MPB	Microphytobenthos
9	FLO	European Flounder	**60-65**	PHY	Phytoplankton
10	FLA	Other flatfishes			
11	CEP	Cephalopods	**66**	DET	Detritus

The groups used by Tecchio *et al.* (2015, 2016) were taken as a baseline for a first Ecopath meta-model. The trophic boxes repartition has been clarified since then by separating the cephalopods from the invertebrate benthic predators due to their diet and trophic parameters being highly different from families like *Asteriidae* or *Ophiuroidae*. Third, the top predators were detailed by separating important fishery species having nursery grounds in the Seine estuary and for which accurate data were available. This choice concerns *Merlangius merlangus* (Whiting), *Dicentrarchus labrax* (European Sea Bass), *Solea solea* (Common Sole), *Pleuronectes platessa* (European Plaice) and *Platichtys flesus* (European Flounder). Other modelling choices could have been done, notably a separation between benthic and pelagic cephalopods, more details on the top predators or on the benthic communities (as in Raoux *et al.* (in prep.)). However, we chose to have synthetic functional groups, particularly concerning the sedentary groups because it would have induced many interpretation difficulties.

Model parametrization

Two Ecopath food web model were constructed respectively for the 1996 to 2002 and 2005 to 2012 time periods. These periods were chosen in order to assess the Port 2000's (and associated modifications related to compensatory measures for instance) impact. Both time periods also corresponds to a shift in the water flow of the Seine (Dauvin & Pezy 2013). Several quality data collections were available starting in 1996 up to 2012 or 2013 depending on the functional group.

The biomasses were available from sampling surveys which, for many of them, occurred several times a year (*e.g.* COLMATAGE, Benthoseine) in the Seine estuary. Detailed biomass data were not available for some functional groups (*e.g.* meiofauna) and have been estimated from literature review of the previous Seine estuary models (Rybarczyk & Elkaïm 2003; Vincent *et al.* 2006; Tecchio *et al.* 2015). The trophic input parameters (production over biomass rate, consumption over biomass rate, excretion rate) were obtained from literature in similar ecosystems, either directly from the Seine estuary or the nearby Bay of Biscay or North Sea. When no literature or data were available, we used empirical equations to determine these parameters (Pauly 1980; Pauly *et al.* 1993). The detailed input and output parameters and biomasses are presented in **Appendix 1**.

2.5.Model outputs analysis

Contribution of the habitats to the consumption

Each mobile functional group (group 1-11) is dependent of the different habitats in terms of consumption. Based on the method used in Guénette *et al.* (2014), the contribution of the various habitats to the functioning of the Seine estuary has been notably calculated as the fraction of the consumption of predators occurring in each habitat. The **fig. 5** below presents the calculation method for a given habitat.

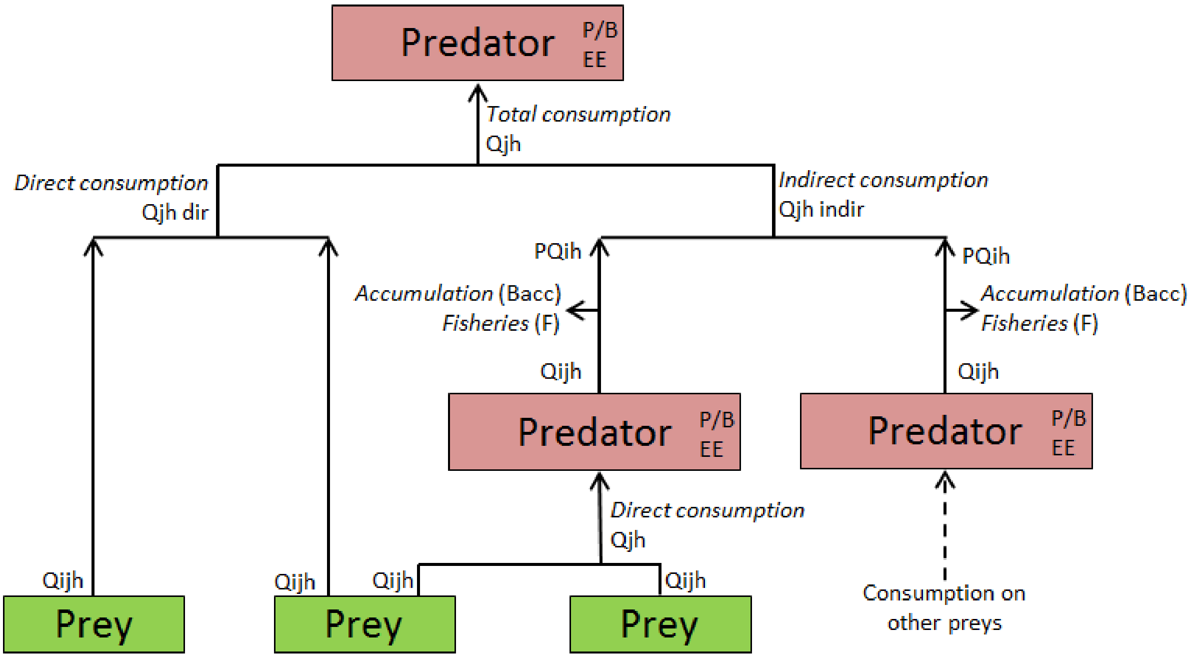


Figure 5: Synoptic diagram illustrating the consumption calculations.
Predators refer to the mobile functional groups and preys refer to the sedentary functional groups.

The consumption was calculated for direct pathways namely consumption of a predator on sedentary groups and for indirect pathways namely the consumption of a predator on species that feeds on the various sedentary groups. The direct consumption Q_{jh} of a predator *j* on preys *i* in a habitat *h* is calculated as follows:

$$Q_{jh}^{dir} = \sum_{i=1}^{Nh} Q_{ijh} \qquad \textbf{(eq. 4)}$$

The habitat contribution to the estuary functioning also takes account of the predator's consumption on the various habitats through indirect pathways. Indirect consumption was calculated step by step. First, we calculated the production of predator *j* based on direct consumption in each habitat, which can be considered as the production of predator *j* originating from these different habitats:

$$P_{jh}^{dir} = Q_{jh}^{dir} \times (P/Q)_j \qquad \textbf{(eq. 5)}$$

Second, the fraction of this production of predator j consumed by secondary predators namely the fraction of production not going to detritus (EE_j), not fished ($1-F_j$) and not accumulated ($1-Bacc_j$). In our case, (F_j) and ($Bacc_j$) were equal to zero.

$$PQ_{jh} = P_{jh}^{dir} \times EE_j \times \left(1 - F_j\right) \times \left(1 - Bacc_j\right) \qquad \textbf{(eq. 6)}$$

Hence, the indirect consumption originating from the various habitats (*i.e.* the consumption of secondary predator now named *j* on predators now named *i* which are feeding on the different habitats *h*) can be calculated as following:

$$Q_{jh}^{indir} = \sum_{i} \left(PQ_{ih} \times Q_{ijh} \Big/ \sum_{j} Q_{ijh} \right) \qquad \textbf{(eq. 7)}$$

Finally, the total consumption originating from each habitat for a given predator can be expressed as:

$$Q_{jh} = Q_{jh}^{dir} + Q_{jh}^{indir} \qquad \textbf{(eq. 8)}$$

The contribution of each habitat to the consumption of the predators on each of these habitats is given by the fraction of consumption (direct and indirect) originating from these habitats. It is given by the following equations:

$$pQ_{jh}^{dir} = Q_{jh}^{dir} \Big/ \sum_{h} Q_{jh}^{dir}; \; pQ_{jh}^{indir} = Q_{jh}^{indir} \Big/ \sum_{h} Q_{jh}^{indir} \qquad \textbf{(eq. 9)}$$

Trophic spectra analysis

Parts of the functional and structural changes can also be presented using trophic spectra (Gascuel *et al.* 2005) which are based on the mean trophic level and the biomass from Ecopath. The trophic spectrum, generally represented as a biomass spectrum, represents the biomass distribution of the whole ecosystem across trophic levels. In our case, the biomass spectra are used to highlight differences between habitats and time period in terms of biomass composition and more importantly mean trophic level shifts. The trophic spectra, as built in the Ecotroph routine, are constructed by spreading the biomass of each Ecopath functional group across the nearby trophic levels by a log-normal function centered on each species' mean trophic level (Gascuel *et al.* 2009 in Guénette *et al.* 2014). This method allows representing trophic level variability which can reflect diet variability within a given group or eventually variations in the species biomass composition within a given spatial compartment. The trophic spectrum for a given habitat can either be represented by superposed polygons corresponding to each group's trophic spectra or by a synthetic curve corresponding to the sum of all Ecopath groups' spectra.

Ecological network analysis

As a complementary approach we also performed Ecological Network Analysis on the Ecopath outputs. This routine provides various indices based on theoretical ecology and system maturity theory (Ulanowicz 1986). The several indices used are presented hereafter.

The **Mixed Trophic Impact (MTI)** is a routine used to highlight trophic interactions between each functional group (Ulanowicz & Puccia 1990; Christensen *et al.* 2008). It quantifies the relative change in each functional group induced by a slight biomass change in a single group. The MTI is calculated for each group in form of a MTI matrix giving the impact of each group on each group. The negative effect of a group on another is calculated following **eq. 10** for the jth prey and ith predator and kth compartment of the system:

$$f_{ij} = \frac{B_i (Q/B)_i DC_{ij}}{\sum_{k=1}^{n} B_k (Q/B)_k DC_{kj}} \qquad \textbf{(eq. 10)}$$

The positive effect of a prey *j* on a predator *i* can be expressed as: $g_{ij} = DC_{ij}$
Therefore the net effect is: $q_{ij} = g_{ij} - f_{ij}$
Each q_{ij} are part of a square matrix of k dimensions which is the effect matrix Q. This matrix is used to calculate the impact matrix M after varying the biomasses of each group. Negative MTI are associated with top-down effects while positive ones to bottom-up effects (Libralato *et al.* 2006).

The **Keystoneness Index (KS)** defines species which are playing a structuring role in the system. It is based on a given group's trophic impact (MTI) and biomass (B). Different KS index are proposed by the Ecopath routine. The first KS developed by Power *et al.* (1996) has been criticized for being strongly influenced by a group's biomass. The index currently used (which is also used in our models) is less sensitive to biomass and might therefore be more relevant given the biomass differences between our various habitats (Libralato *et al.* 2006). Finally, a third KS index has been developed by Valls *et al.* (2015) using the biomass rank instead of the biomass.

$$\varepsilon_i = \sqrt{\sum_{j \neq i}^{n} m_{ij}^2} \ ; \ p_i = \frac{B_i}{\sum_k B_k} \ ; \ KS_i = log[\varepsilon_i (1 - p_i)] \qquad \textbf{(eq. 11)}$$

Where ε_i is the total impact and p_i the contribution of the functional group to the total biomass of the food web (Power *et al.* 1996).

The **Total System Throughput (T..)** is defined as the sum of all flows occurring in the system. It is generally interpreted as an indicator of system activity and maturity (Latham 2006).

The **System Omnivory Index (SOI)** is calculated as the mean of the omnivory indices of each consumer group weighted by the logarithm of their respective consumptions. The SOI indicates the dietary adaptation of consumer groups. Therefore, an increasing of the SOI would indicate a response to an external pressure or stress (Fagan 1997; Libralato 2008).

The **Finn's Cycling Index (FCI)** corresponds to ratio of the flows generated by cycling and the total system throughput (Finn 1976, 1980). The FCI is generally interpreted as an indicator of stress and external pressure on the system.

Ascendancy is calculated as the Average Mutual Information (AMI) scaled by the Total System Throughput. It is an indicator of the ecosystem growth and development (Ulanowicz & Abarca-Arenas 1997). Therefore **Relative ascendancy (A/C)** is an indicator of the level of organization of the system compared to its total capacity (C). The **relative internal ascendancy (Ai/Ci)** takes only the internal flows in accounting. According to(Baird *et al.* 1991), a strong difference between these two ratios indicates the level of dependency of the system to external connections.

These various ENA indices can theoretically characterize the ecological state of a given ecosystem. Several modelling efforts using ENA have been done on various French estuaries (Selleslagh *et al.* 2012). Therefore, our two Seine estuary models have been integrated in a PCA analysis using the several ENA indices presented above as active variables. This analysis aims to complete the assessment of the Seine estuary evolution by comparing both 1996-2002 and 2005-2012 ecological state to the other French estuaries.

2.6.Assessing model uncertainty

Ecosystem modelling allows describing the structure and the functioning of a whole system through various theoretical indicators. These are providing estimations of the system's health, its maturity and its responses to external pressures (*e.g.* Selleslagh et al., 2012). However, when based on an Ecopath approach, these ecological indicators and the resulting interpretations are mostly relying on a single value. Therefore, no uncertainty is associated either to these indicators or the input parameters, despite the measurement uncertainty related to the data. A first method of uncertainty assessment in ecosystem models is to study the scientific question by using various modelling approach (Fulton 2010). For example, we could have used the Ecopath modelling approach in parallel of LIM-MCMC modelling as in Tecchio *et al.* (2015, 2016). Another approach would consist of incorporating directly uncertainty into Ecopath model by building several models each representing a mass balance solution within the given uncertainty range of the data (Kearney *et al.* 2012; Guesnet *et al.* 2015). A Matlab suite was developed by Kearney *et al.* (2012) and taken up by Guesnet *et al.* (2015) in order to provide a set of Ecopath output parameters and ENA distribution while still meeting the mass and energy balance requirements.

This uncertainty calculation method uses an Ecopath model and its pedigree (*i.e.* uncertainty range on the input parameters relative to the data source and quality (Pauly 2000; Christensen & Walters 2004) as input. The Ecopath model which is saved as a Microsoft Access 2003 database is first imported to the Matlab routine. All necessary input parameters (*i.e.* basic inputs, multi-stanza group parameters, diet compositions, fleet catches and discards) are compiled into the EwE input structure (Guesnet *et al.* 2015).

In a second step, the uncertainty range associated to each input parameters are imported into the Matlab routine. The pedigree, defined in Ecopath is exported to an Excel spreadsheet template which is then imported into the Matlab routine (Guesnet *et al.* 2015). Uncertainty is defined as a percentage of variation around the parameters single values and uncertainty range limits are calculated as below:

Limits = single value ± (uncertainty percentage × single value) **(eq. 12)**

The pedigree is defined for each input parameter, associating an uncertainty based on their origin (Pauly 2000; Christensen & Walters 2004). These uncertainty ranges are defined in a table for each parameter. An example is given for the biomass parameter in **table 2** below and the detailed pedigree used for both models is given in **Appendix 4**:

Table 2: uncertainty associated to the biomass parameter (Christensen *et al.,* 2008)

Biomass parameter

Category	Index	Confidence interval (± %)
Estimated by Ecopath	0,0	80
From other model	0,0	80
Guesstimate	0,0	80
Approximate or indirect method	0,4	50
Sampling/locally, low precision	0,7	30
Sampling/locally, high precision	1,0	10

The ENAtool Matlab routine generates a defined number of balanced Ecopath models using the pedigree as a prior parameter distribution. The models parameter are sampled either in a uniform distribution within the uncertainty limits defined as above or in a log-normal distribution with the mean and standard deviation according to the pedigree (Guesnet *et al.* 2015). In our case, the sampling was done using a Monte Carlo method and a uniform distribution for the prior parameters. Once a set of prior parameters is sampled, the routine calculates the missing parameters using a “stripped down” version of the Ecopath calculation algorithm by solving the production and consumption equation. Each model is checked whether it meets the ecotrophic efficiency balance (EE < 1) or not. We choose to sample a set of 100 balanced model in order to calculate the basic estimates and the ENA indices. This choice was a compromise between the high calculation time, given our model complexity and constrained ecotrophic efficiency and a sufficient number of balanced models according the sensitivity analysis in Guesnet *et al.* (2015). Finally, the ENAtool routine calculates a set of 13 ENA indices of which we chose to use the three presented in the previous part. Each ENA is calculated as a set of values or distribution which can be used in further statistical approaches. The set of ensembles provided by the ENAtool routine was used for a multi-factor ANOVA in order to complete Ecopath outputs presented hereafter.

3. Results

3.1.Data quality and model balancing

The pedigree index has been calculated for both 1996-2002 and 2005-2012 models using the routine proposed by Ecopath. The pedigree indices were 0.492 for both models, which are medium range value according to the Ecopath literature (Morissette 2007). The main uncertainties are due to several P/B and Q/B rate estimated by the Ecopath model. In general, biomasses were well documented in the Seine estuary and have therefore lower uncertainties than other parameters. The detailed pedigree values per functional groups can be found in **Appendix 4**.

Despite being constructed using the models from Tecchio *et al.* (2015, 2016) as a baseline, the new models structure caused several mass balance difficulties. The density-dependence hypothesis on the predator-prey relationship between the various habitats allowed respecting the mass balance requirement for most of the functional groups. However, several groups were not balanced, either due to this modelling choice or important biomass changes between the two periods which will be explained further. Both models were balanced according to the method presented in paragraph 2.2., following a top-down approach. The changes are presented in **table 3** below:

Table 3: Model mass balancing choices for each unbalanced group.
See table 1 for the function groups' abbreviations

Functional group	1996-2002	2005-2012
FPV	The predator fishes biomass composition changed compared to Tecchio et al. (2015; 2016). Therefore we had to modify the diet matrix by a major predation decrease from SBD, WHI, FPI and CEP. We also slightly increased the P/B rate from 1.2 to 1.3.	
FBF		The predation from FPI, CEP and canibalism had to be slightly decreased.
IPR	During the first time period, the IPR biomasses in the estuary were very low compared to the predators biomass. Therefore we had to decrease the predation from FBF and CEP on the estuary, reporting the predation in the estuary mouth.	
IFF	The predation from IPR was too important for various habitats due to their biomass increase. Therefore we had to slightly decrease the predation rate on IFF.	
IDF	The estuarine biomasses were not enough to sustain the predation rate. Therefore we had to slightly decrease the estuarine predation from FBF and FLO, reporting it in the estuary mouth. We also decreased the predation from IPR within the concerned habitats, reporting it on the other functional groups.	Due to biomass changes, we had to slightly decrease the IPR predation in the estuary mouth, reporting it on other functional groups.
SUP	The canibalism and the predation rate from IPR had to be slightly decreased for some habitats.	The SUP biomass significantly decreased. Therefore, we had to modify the diet matrix, mostly reducing the predation from IPR
MEI		The predation rates from IPR, IFF and IDF were slightly decreased due to the relative biomass increase of these groups compared to the MEI.
PHY	The predation from ZOO was slightly decreased and the P/B rate was increased of 10% for some habitats.	

According to Christensen & Walters (2004) a functional group is considered mass balanced when its ecotrophic efficiency is less than one. However, high ecotrophic efficiencies (between 0.9 and 1) can be considered as ecologically unlikely for some functional groups. Therefore, we considered the model balanced with slightly lower ecotrophic efficiencies (≈ 0.9). This modelling choice also improved the Monte Carlo sampling efficiency used for the uncertainty routine by having a less constrained models.

The predator-preys relationships were modelled following a density dependence hypothesis. However, the various changes made in order to meet the mass balance requirements are reflecting other ecological processes within the estuary. During the first time period, the estuarine benthic biomasses were very low and could not sustain the fish predation compared to the estuary mouth. The various infrastructures built after 1970 together with high river outflow during this time period shifted the nursery areas towards the estuary mouth (Dauvin & Pezy 2013) which could explain the biomass repartition. The fish diets reporting in the estuary mouth can be interpreted as a predation reporting due to the saturation of the estuarine nursery habitats in terms of nursery capacity. During the second time period, Port 2000's construction together with low river outflow completely changed the biomass structure of the estuary, especially the benthic and suprabenthic communities (Dauvin *et al.* 2010). Therefore, the diet used for the previous model had to be updated, reflecting possible changes or opportunistic behavior concerning predator foraging. These various assumptions will be discussed and completed further.

3.2.Structure and composition of the system

Biomass structure and composition

Ecosystem modelling approach allows studying a given food web ecological functioning in a given environmental and anthropic context. It is also used as a powerful tool to represent the food web structure and therefore the heterogeneity within a system. Environmental and anthropogenic pressures, especially salinity and turbidity, can affect the various estuarine communities from top predators to primary producers, creating variability within the ecosystem (*e.g.* Cabral *et al.* 2001; McLusky & Elliott 2004; Selleslagh *et al.* 2009; Gameiro & Brotas 2009; Eick & Thiel 2014). The Seine estuary with its various man-made infrastructures, altering sediment and flow dynamic, could create variability in the biomass composition of each functional habitat. The biomass corresponding to each functional groups and habitats are represented in **fig. 6** hereafter.

Due to very long calculation time (over 1 month) the uncertainty assessment has not been done on the models including 6 functional habitats which are presented below. However, an uncertainty assessment has been done on intermediate Ecopath models (with 4 habitats), aggregating both Northern intertidal and subtidal areas and both Southern intertidal and subtidal areas, using the same input parameters as for the final models. This assessment will be discussed further and the corresponding ENAtool output can be found in **Appendix 5**.The production over biomass rate decreases with the trophic level, therefore the global tendencies are the same as for the biomass and will not be discussed in details here. The detailed productions per functional group output are presented in **Appendix 6**.

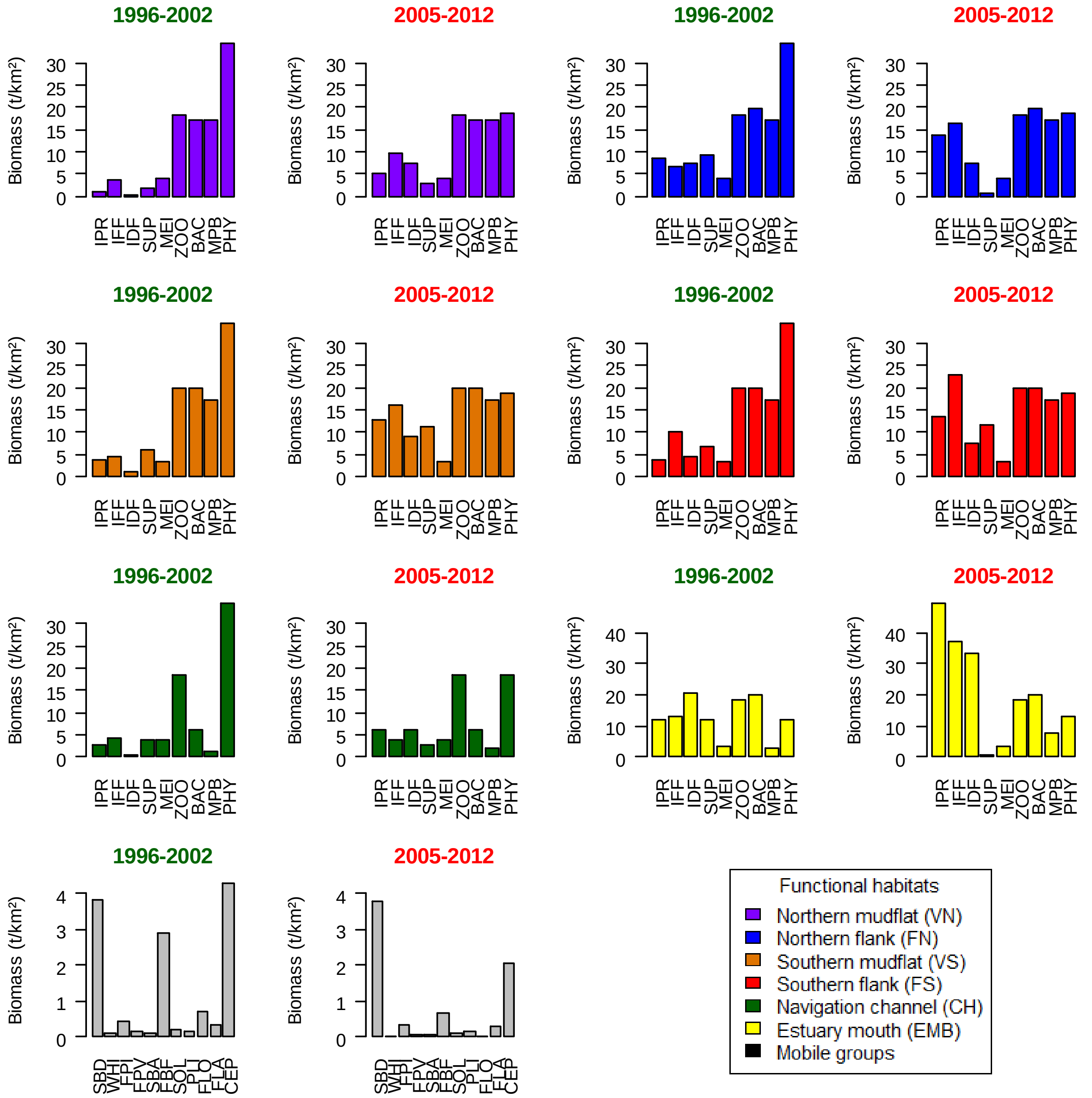


Figure 6: Biomass variability across habitats and time period

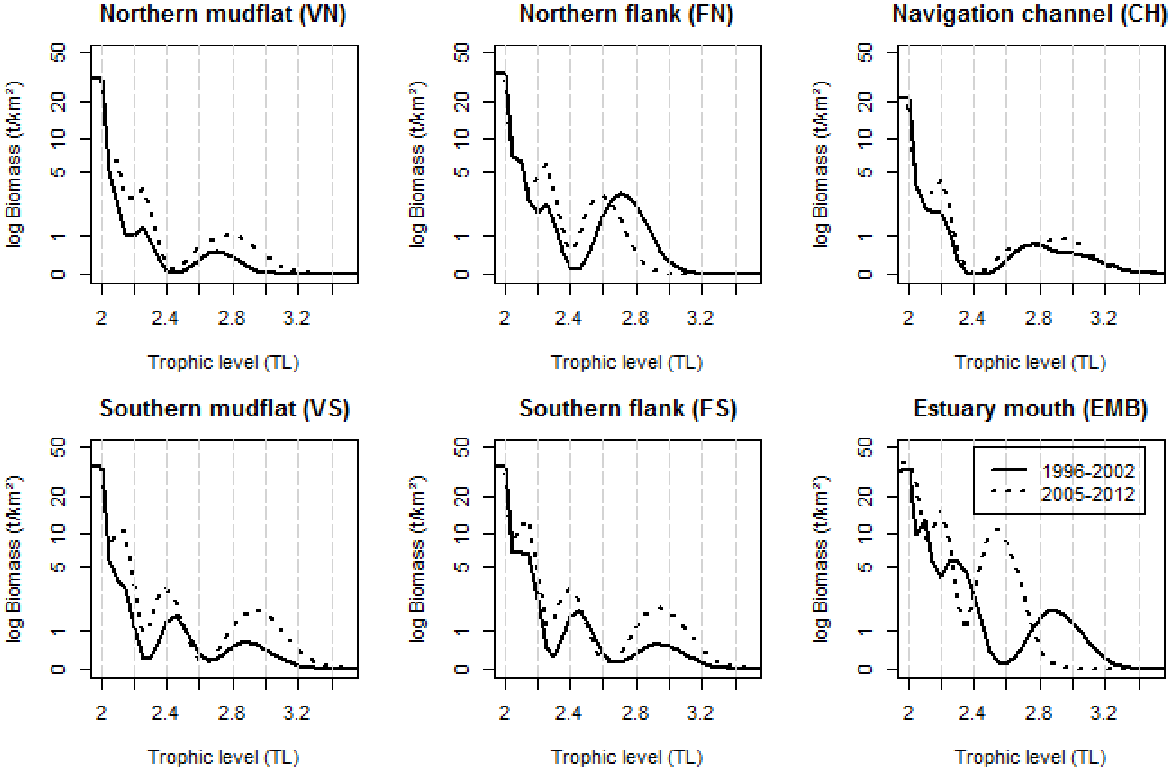
The **fig. 6** highlights variability between each habitat and time period considered, especially for the benthic consumer groups. Concerning the first time period, the primary producers, the bacteria and zooplankton groups have larger biomass pools and lower variability across the habitats than the other consumer groups. However, these biomasses are probably still underestimated and are the most uncertain data with an average standard deviation (hereafter "RSD") around the mean value of 20 % (see **Appendix 5**). In contrary, the benthic and suprabenthic consumer groups have lower biomass pools but higher variability probably due to the distinct pressures impacting the benthic habitat within the estuary. A comparison between the various habitats highlights common biomass patterns between both Northern and Southern intertidal mudflats and both Northern and Southern subtidal flanks. The navigation channel has the lowest biomasses which can be related to the yearly dredging occurring in this area (Tecchio *et al.* 2016) while the estuary mouth is hosting the highest benthic consumers' biomass pool.

A shift towards higher benthic biomass has been observed for the second time period while the suprabenthos' biomass collapsed. The benthic consumers' biomass has been multiplied by 3 for most of the functional habitats. Only the navigation channel remains at the same average biomass level. The primary production has been lowered, especially for phytoplankton. Finally, concerning the top predators, a general decrease in the biomass appears for most of the functional groups, suggesting less predation on the benthic habitats. All these changes are probably related to functional changes which will be assessed in the following part.

The ANOVA showed a significant effect of habitat, the group and the time period on the biomass (see **Appendix 5**). The habitat effect explained over 50% of the variability while the group effect explained 35% of the variability. The time period effect explained a small part of the variability but is part of significant interactions. Concerning the detailed habitat effect, a Tukey test showed significant differences for every pair of spatial compartment except between estuary mouth and Northern area. The greatest differences were observed between the navigation channel and the other spatial compartments. These differences concern only the intermediate models. We can assume that the results would be similar for the final models. However, this uncertainty assessment did not take account for the possible differences between intertidal and subtidal areas which present graphical differences in biomass composition.

Trophic spectra analysis

The biomass distribution across trophic levels resulting from the Ecotroph routine analysis is summarized in **fig. 7** below. The detailed trophic spectra per functional group are given in **Appendix 7**.



Northern mudflat (VN)

Northern flank (FN)

Navigation channel (CH)

Southern mudflat (VS)

Southern flank (FS)

Estuary mouth (EMB)

Figure 7: Biomass repartition across trophic levels per habitat

The trophic spectra revealed the same biomass shifts as before. Moreover, this representation also highlighted mean trophic level (hereafter MTL) differences between the various habitats and shifts between both time periods. For the first time period, a comparison between each functional habitat reveals lower MTL in the Northern area than in the other habitats. A decrease of the MTL can be interpreted as a response to external pressures, the Northern area being considered as the most impacted by Port 2000's construction (Gascuel *et al.* 2005; Tecchio *et al.* 2016). A MTL shift can also be observed by comparing both time periods for the Northern flank and the estuary mouth. Indeed, after Port 2000's construction, the benthic predators' MTL (≈2.8 during the first period) decreased down to an average trophic level of 2.5. Therefore, we can assume that the Northern flank and the estuary mouth were stressed during the second time period, either due to Port 2000's construction or flow alterations.

Flow diagram

The Seine estuary spatial food web structure can be presented through the flow diagrams in **fig. 8**, following the same structure as explained in **fig. 3**. The functional boxes are pooled by functional habitat and aggregated functional groups (in colored frames) for representation reasons.

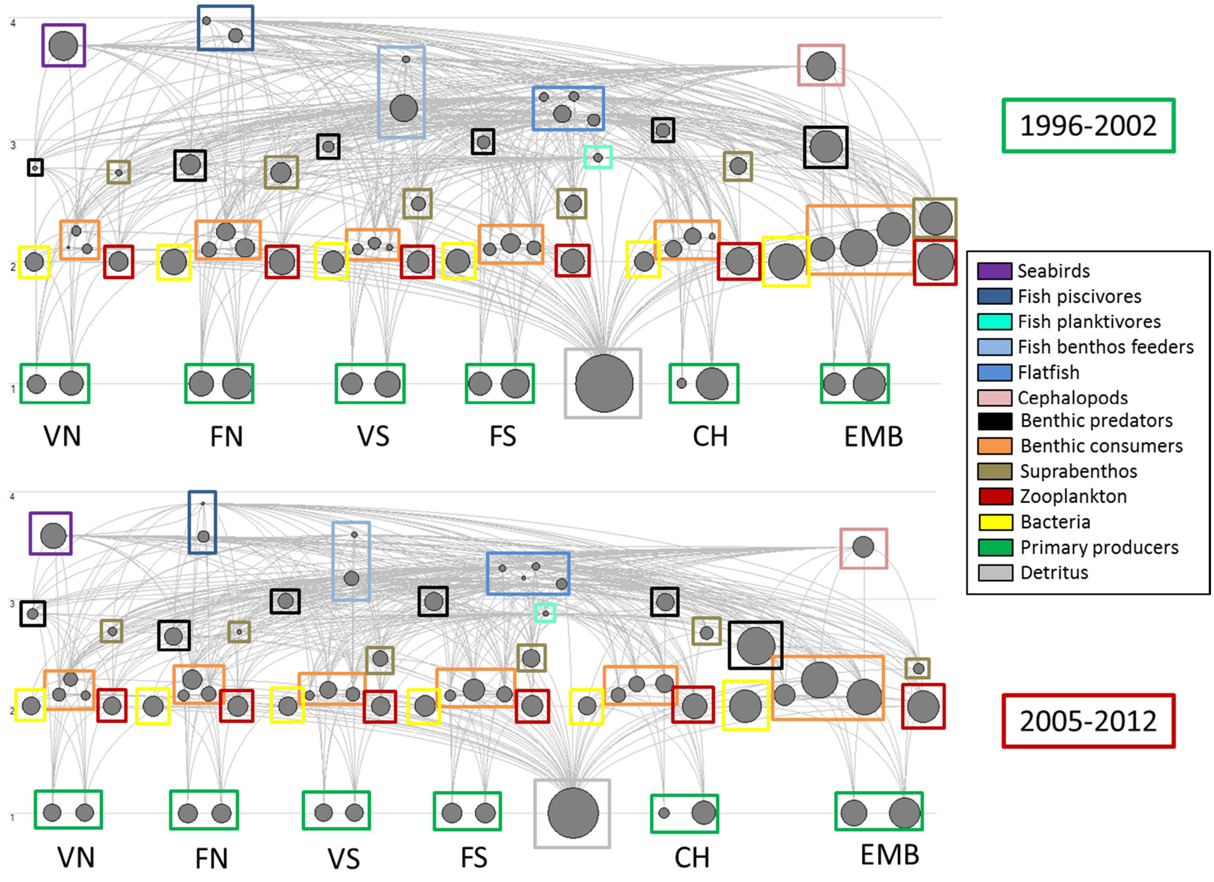


Figure 8: Flow diagrams

Each functional group is shown as a circle proportional to the log of its biomass and is drawn at its corresponding mean trophic level on the y-axis. The grey lines represent the predator-prey relationships within the food web.

The flow diagrams represent the spatial structure of the Ecopath model, each habitat having its proper food web ranging from the primary producers (TL = 1) to the benthic predators (TL ≈ 3). Each habitat's food web is indirectly connected to the other habitats through predator-prey relationships with the mobile functional groups. The top predators are playing a pivot role for the high and medium trophic level while most of the lower trophic levels are connected to the detritus pool.

Despite having no mobile functional group with an average mean TL of 2.5, the mobile-sedentary group relationships are concerning the whole food web, from the benthic predators to the primary producers. Each functional group of a given habitat is indirectly connected to each other habitat through these relationships. The planktivorous fish, the flatfishes and the cephalopods seems to play an important pivot role between the various habitats. On the other hand, the **fig. 8** illustrates the biomass shifts explained before. We note in particular that the suprabenthos' and top predators' biomasses decreased while the benthic consumers' biomasses increased. The primary producers remained with the highest biomasses. The mean trophic level shifts presented above are also observed in the flow diagrams.

3.3.Spatial functioning and trophic relationships

Habitat contribution to the predators' consumption

The biomass composition shifts presented before induces consumptions changes due to the density dependent hypothesis on the predator-prey relationships. This hypothesis allows modelling the adaptation or the opportunism of the functional group diets to their prey availability. The **fig. 9** hereafter represents the relative consumption in each habitat in comparison with the absolute total consumption of the functional group. Relative habitat contribution function of their surfaces and absolute consumption per functional group are presented in **Appendix 8 and 9**.

Concerning the first time period, the relative consumption in each habitat highlights the importance of the estuary mouth for most functional groups. Indeed, in average, the estuary mouth was contributing to 50 % of the mobile groups' consumption. This functional habitat was larger than the estuarine habitats and had relative similar biomass densities which explain this result. However, the Northern and Southern areas (which refer to the Northern and Southern subtidal and intertidal areas) were also contributing to an important part of the predators' consumption despite their smaller surfaces. The Northern area contributed to 22.5 % (respectively 4.5 % for the intertidal mudflat and 18 % for the flank) of the predators' consumption and the Southern area to 20 % (respectively 7 % for the intertidal mudflat and 12.5 % for the flank). If we take account of the habitat surfaces, both Northern and Southern areas seems the more attractive habitats of the system in terms of trophic availability (see **Appendix 8**). The navigation channel contributed only to 6 % of the mobile groups' consumption despite having a similar surface than the Northern area. This can reflect the high level of stress and the yearly dredging and flow alteration occurring in this area (Tecchio *et al.* 2016).

Within the same period, we also note that the planktivorous fishes and the various flatfishes were slightly more attracted by the Northern and Southern areas. Indeed, during young ages, it has been shown that these flatfishes had a habitat preference for shallow muddy-sandy areas as found in both areas (Van der Veer *et al.* 1991, 2001; Pihl & Van der Veer 1992).

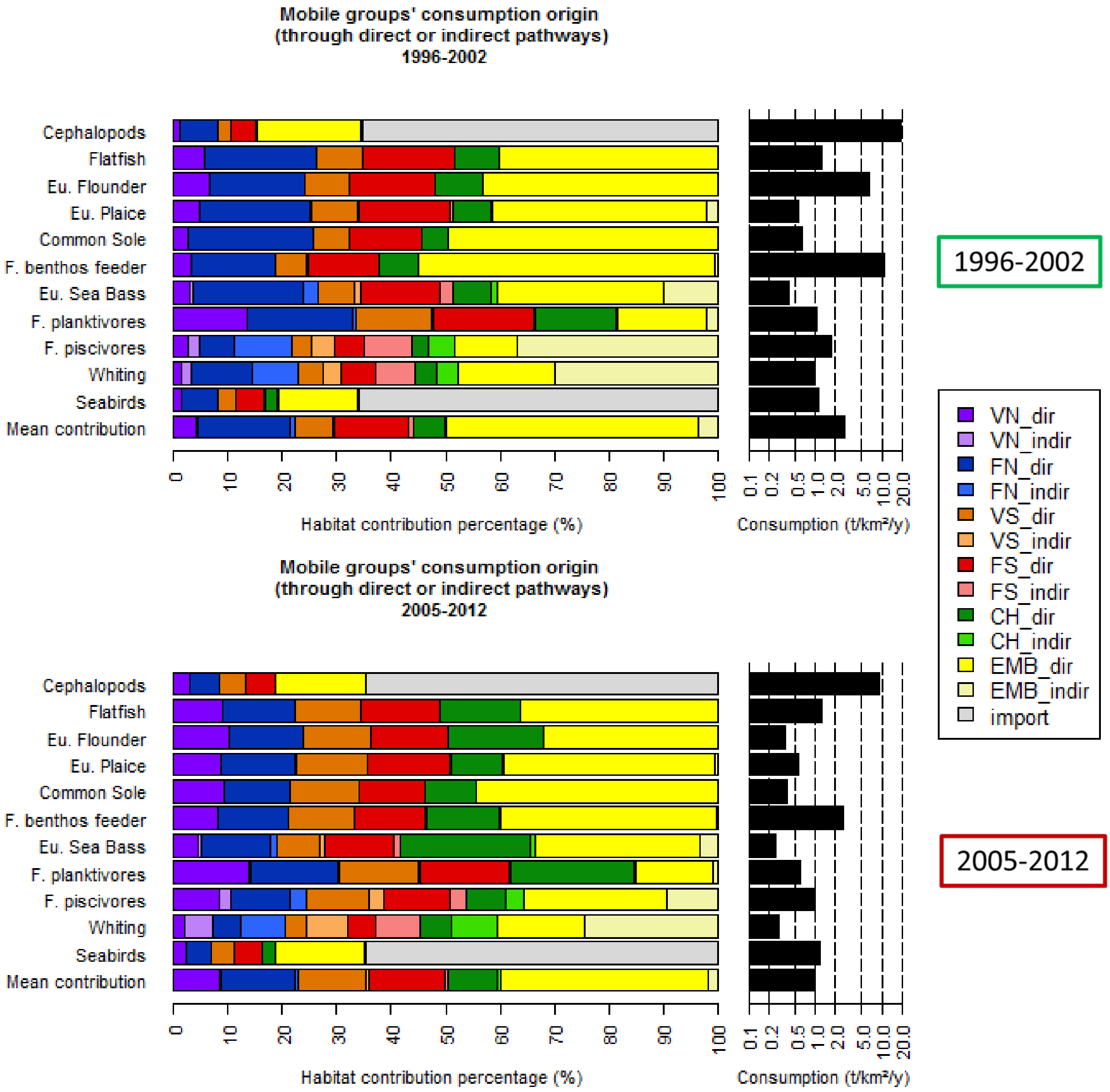


Figure 9: Habitat contribution to the mobile groups' consumption

The left part of the diagram represents the relative consumption occurring in each habitat while the right part represents the total consumption of a mobile group in the system. Import has not been taken account in the mean contribution calculation.

The benthos feeder fishes and Flounder had the highest absolute consumption during the first time period (Cephalopods had a large import component). During the 2005 to 2012 time period, the absolute consumption of most mobile groups was in average divided by 2 despite the increasing of the benthic biomasses. Concerning the relative contribution during the second time period, the contribution of the estuary mouth decreased from 50 % to 40 %.

The navigation channel contribution increased up to 10 % but still decreased in terms of absolute consumption (see **Appendix 9**). The relative contribution of the Northern area remained constant. However, the contribution of the subtidal flank decreased from 18 % to 14 % while the contribution of the intertidal mudflat increased up to 9 %. The Southern area increased its contribution up to 27 % with the same observation between intertidal and subtidal as for the Northern area. The relative contribution to indirect pathways generally decreased between both time periods except for Sea Bass.

These relative contribution changes are revealing predation reports from the estuary mouth towards the navigation channel and the Northern and Southern mudflats. The Northern mudflat has not been directly impacted by Port 2000's construction and has been partially restored. However this result was not expected and further results are needed to explain this predation report. Concerning the Southern mudflat, it has been characterized as the most attractive and least stressed area (Tecchio *et al.* 2015, 2016). Therefore we assume than the maximum trophic capacity (*i.e.* the maximum prey potentially consumable in the habitat) was not reached which could explain the predation report to this habitat.

Key points:

- *The estuary mouth contributes for a large part of the mobile groups' consumption while the Northern and Southern areas seem to be the most attractive habitats.*
- *The absolute consumption decreased between both time periods.*
- *During the second period, the relative contribution of the estuary mouth was partially reported towards the Southern area and the channel. Both flanks contribution was also partially reported towards their adjacent mudflats.*

Ecotrophic efficiency

In our models, the ecotrophic efficiency represents the consumed part of a functional group's biomass by the higher trophic levels because of the absence of fisheries and export. At a habitat scale, the mean ecotrophic efficiency would represent the capacity of a given habitat to provide preys to the higher trophic levels. Therefore, ecotrophic efficiency could be an indicator of habitat saturation in terms of prey availability. The calibration biases were considered to be the same for all habitats which allowed a comparison between the various habitats. The mean ecotrophic efficiency per habitat was calculated as following:

$$\overline{EE_{Habitat}} = \sum_i \left(EE_{Group\,i} \times \frac{B_{Group\,i}}{B_{Habitat}} \right) \qquad \textbf{(eq. 13)}$$

The mean ecotrophic efficiencies (referred as MEE hereafter) are represented with their habitats' corresponding biomass in **fig. 10** hereafter. Concerning the first time period, several variations can be observed between each habitats' MEE. The Northern flank and the estuary mouth were the most saturated habitat while the Southern areas and the Northern mudflat had the lowest MEE. When considering only the consumer groups having a TL > 2 (*i.e.* excluding zooplankton and bacteria which had very low ecotrophic efficiencies), the $MEE_{TL>2}$ showed that the higher trophic level within each habitat were under higher saturation, especially in the Southern area.

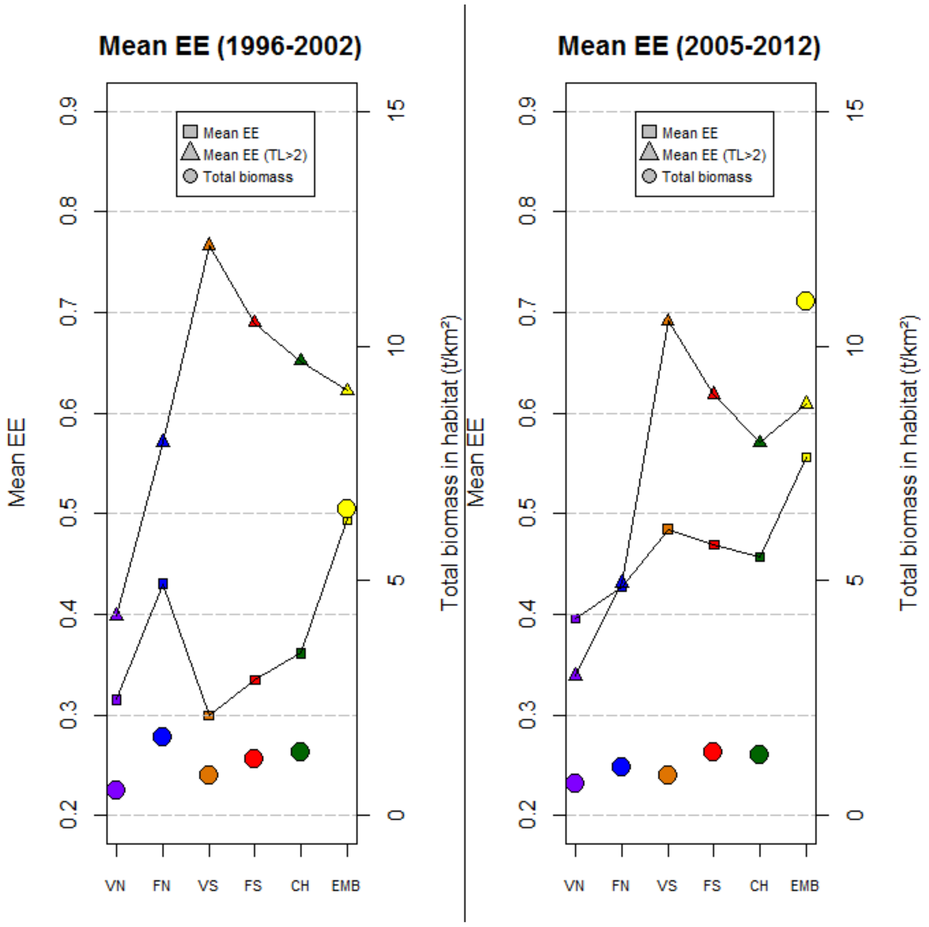


Figure 10: Mean ecotrophic efficiency evolution

During the second time period, the MEE increased for most of the habitats, except the Northern flank. The highest increase was observed for the Southern mudflat, followed by the Southern flank which had also the highest predation increase according the relative habitat contribution. However, if we compare both time periods, the mobile groups' predation decrease and the biomass increase in the various habitats should have been reflected by a MEE decrease. The $MEE_{TL>2}$ decreased in the second time period, keeping the same pattern as before between the various habitats. This result would be in accordance with the biomass and predation changes, however, other incoherencies are observed between the various habitats.

The MEE is reflecting the habitat saturation and should theoretically follow the same tendencies as the relative habitat contributions. However, the various interpretations are inconclusive about the relationships between relative contribution and MEE. Therefore, a more complex pattern might lead to these MEE changes. The main assumption is that another functional group is exerting high predation rates within the various habitats. Indeed, as observed before in **fig. 6**, the benthic predators' biomass highly increased between both time periods. This functional group is exerting high predation rates on the lower trophic levels and is one of the main preys of the mobile groups'. The benthic predators' biomass increase would therefore explain the MEE increase between both time periods because of the predation within each habitat. The $MEE_{TL>2}$ decrease would be explained by the conjunction of the benthic predators' biomass increase and the mobile groups' predation decrease.

This interpretation assumes that the benthic communities especially the benthic predators have a high influence on the other functional group. Further analysis would be able to assess the importance of the benthic communities in the Seine estuary.

Key points:

- *The MEE increased during the second time period, especially for the Southern area while the* $MEE_{TL>2}$ *decreased.*
- *The predation exerted by the mobile groups' decreased in favor of the benthic predators which exerted high predation rates within the various habitats during the second time period and strongly influenced the MEE.*
- *The results were inconclusive about the direct effect of the predation report on the ecotrophic efficiency.*

3.4.Ecological network analysis

Mixed trophic impact and Keystoneness index

The detailed Mixed Trophic Impact (MTI) results, presenting the impact of a given group on each other can be found in **Appendix 10** for the both time periods considered. Negative MTI are associated with top-down effects while positive ones to bottom-up effects (Libralato *et al.* 2006). Similar patterns can be observed within each habitat for both time periods. Most predators, especially benthic predators had a negative impact on their direct prey due to their diet preferences. Functional group negatively impacted themselves due to cannibalism and trophic competition. These Ecopath models have relatively aggregated functional group which increases the competition and cannibalism components within a given group. The benthic predators, suprabenthos and meiofauna groups exert the highest impact on the other groups (either negative or positive). The predator groups also exert a positive impact on their prey's prey which highlights an important top down component in the ecosystem trophic relationships. The lower trophic level (primary producers and zooplankton) exert a positive impact on their predators, revealing the bottom up control exerted by these groups.

A top down pattern is also observed within the mobile groups. It concerns particularly the seabirds, the piscivorous fishes and the cephalopods which had a strong negative impact on the other mobile groups. Concerning the trophic impacts occurring between each functional habitat, the mobile groups had mostly a negative impact on the benthic communities. The benthos feeder fishes and cephalopods had a strong top down control on the benthic predators, especially in the Northern mudflat and the estuary mouth. On the other hand, the detritus group had a strong positive impact on the other functional groups, revealing the importance of the detritus pool. The estuary mouth had a slight positive impact on the mobile group, probably due to the importance of this functional habitat in terms of prey production. Concerning the second time period, the same patterns remained. However, the benthic predator had a stronger negative impact on their prey and the suprabenthos had less impact (either positive or negative), probably due to the biomass changes. The top down control exerted by the top predators also slightly decreased in accordance with their biomass.

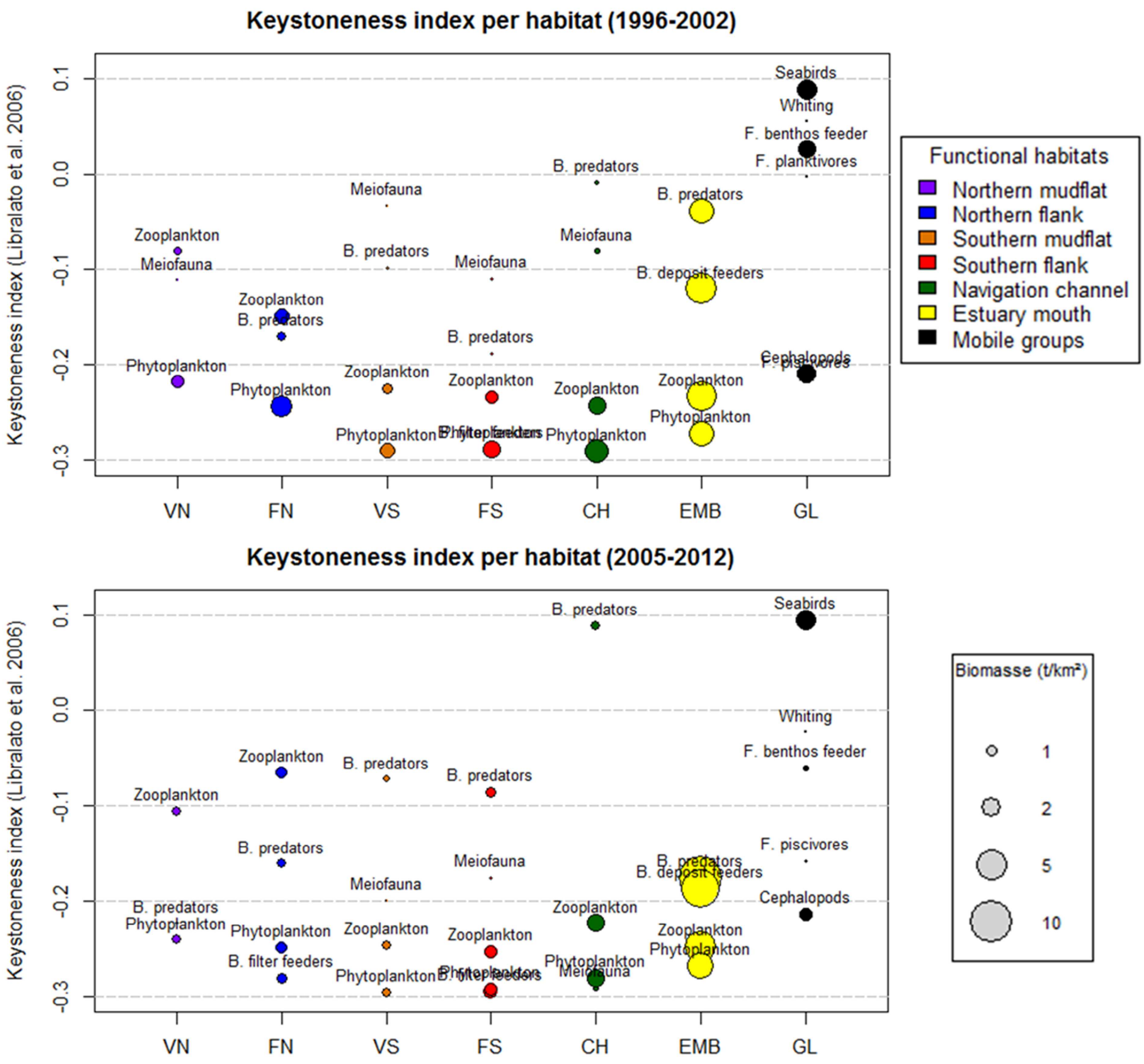


Figure 11: Keystoneness index per habitat (calculated using Libralato *et al.* 2006)

The area of the circles is proportional to the log of each group biomass. Only the high keystoneness groups are represented.

The keystoneness index (KS) presented in **fig. 11** above shows the importance of the benthic communities during the two time periods considered. Indeed, the benthic predators, meiofauna, zooplankton and in a lesser extent phytoplankton are represented as high keystoneness groups in most functional habitats. During the first time period, meiofauna had a high KS in the Southern mudflat, the Southern flank and in the navigation channel, revealing the importance of sediment driven processes in these habitats. Similar results were found in previous modelling efforts, highlighting the importance of detritus-driven dynamics (Tecchio *et al.* 2015). However, the benthic predators had also an important role in most habitats excepting in the Northern mudflat. Their high KS may reflect the top-down structuration in these habitats, already showed though the MTI analysis. Zooplankton and phytoplankton had also high KS values, probably reflecting the importance of these groups in terms of production and contribution to the mobile groups' consumption.

Mobile groups were represented by seabirds, whiting, benthos feeder fishes and planktivorous fishes. Seabirds and whiting were the two top predators of the system, exerting a strong top-down control on the other mobile groups. They were also found as high KS groups in previous models (Tecchio *et al.* 2015). Benthos feeder and planktivorous fishes were playing a pivot role in the system though their various trophic relationships with the lower trophic level in the different habitats.

During the second time period, the same functional groups were represented. However, the benthic predators had much higher KS than during the first time period, especially in the navigation channel and the Southern area. Indeed, the conjunction of the strong benthic predators' biomass increase and their high KS value are revealing the importance of benthic communities during the second time period. Moreover, it is reflecting the strong top-down structuration of the system as shown in the MTI analysis.

Key points:

- *The various habitats are mostly linked together through top-down relationships with the mobile groups.*
- *The KS reflected the important role of benthic communities, especially the increasing top-down structuration due to benthic predators.*

Assessing ecosystem stress

A set of 13 ecological indicators can be calculated by the ENAtool routine. However, due to the calculation difficulties explained before, we choose to only compare a few indices given as Ecopath outputs in order to assess the level of stress between both time periods. These are given in **table 4** below. The ENAtool outputs corresponding to the intermediate 4 habitats model are given in **Appendix 11**.

Table 4: Indices summary of the two models

	Seine estuary (1996-2002)	(% T..)	Seine estuary (2005-2012)	(% T..)
Sum of all consumption	4599,8	34,1	5099,6	43,4
Sum of all exports	2755,1	20,4	1394,1	11,9
Sum of all respiratory flows	1460,4	10,8	1751,5	14,9
Sum of all flows into detritus	4684,2	34,7	3513,2	29,9
Total system throughput T..	13499,5	100	11758,4	100
B/T..	0,009		0,013	
Connectance Index CI	0,127		0,128	
System Omnivory Index SOI	0,176		0,163	
Relative ascendancy A/C	26,3		25,8	
Relative intern ascendancy Ai/Ci	15,6		17,2	
Finn's cycling index FCI	10,7		13,8	

The Total System Throughput (T..), generally interpreted as an indicator of Ecosystem size and maturity (Latham 2006) decreased between both time periods despite the biomass increase. This result is contrary to Tecchio *et al.* (2016). However, both models do not completely overlap and we used more recent data for some functional groups, which could explain this result. Moreover, the T.. range presented in **Appendix 11** is relatively large.

Changes in the T.. composition can be observed between both time periods, in particular concerning the consumption and detritus components. Indeed, the 2005-2012 models had lower flows into detritus whereas the consumption flows were almost 10% higher. This composition differences might be explained by the benthic biomass increase which had low flows into detritus while phytoplankton which were one of the main detritus flow decreased.

The Connectance Index remained fairly constant between both time periods. It is strongly influenced by the food web structure which did not change between the two models. The System Omnivory Index slightly decreased. It can be interpreted as a system resistance to the recent pulse perturbations (Tecchio *et al.* 2016). Relative ascendancy A/C slightly decreased. It is usually interpreted as the quantity of information exchanged in the system and therefore system maturity (Christensen *et al.* 2008) which explains its correlation with the Total System Throughput. The relative intern ascendancy Ai/Ci decreased. It only takes account of the internal flows and is therefore highly correlated with the important consumption flows in the system. Finally, the Finn's Cycling Index increased between both time periods. It is generally interpreted as an indicator of system stress (Baird *et al.* 1991). The derived predatory cycling index which do not take account of the detritus cycles and is therefore more related to higher trophic level increased even more (from 0.37 to 0.51$\%_{T..}$). As in the previous modelling efforts (Rybarczyk & Elkaïm 2003; Tecchio *et al.* 2016), the Seine estuary showed low maturity and increasing levels of stress. We assume that these conclusions are directly or indirectly due to Port 2000's construction. However, further assessment should be done in order to distinguish the impacts induced from these constructions and the general flow decreasing these last years.

An uncertainty assessment has been done on the ENA outputs of the intermediate model in order to complete the results presented above. The set of ensemble provided by the ENAtool routine allowed us to perform Student tests for each ENA indices between both time periods considered (see **Appendix 11**). The results showed significant differences between both time periods for each ENA except for Internal Ascendancy and Overhead. Because the single ENA values between the intermediate and the final models are highly similar, we can assume that the uncertainty assessment would have given similar results for the ENA indices presented in **table 4**.

Comparison with other French estuaries

The various results and interpretations presented above revealed changes in the Seine estuary food web between both time periods. A comparison between different estuaries would replace the observed changes observed for this ecosystem in a global context. We used the data from Selleslagh *et al.* (2012)and our model outputs in a principal component analysis in **fig 12**. The detailed data are presented in **Appendix 12**. The total amount of variability represented by the two first dimensions of the PCA is 82.95 % with a relatively even contribution from every variable.

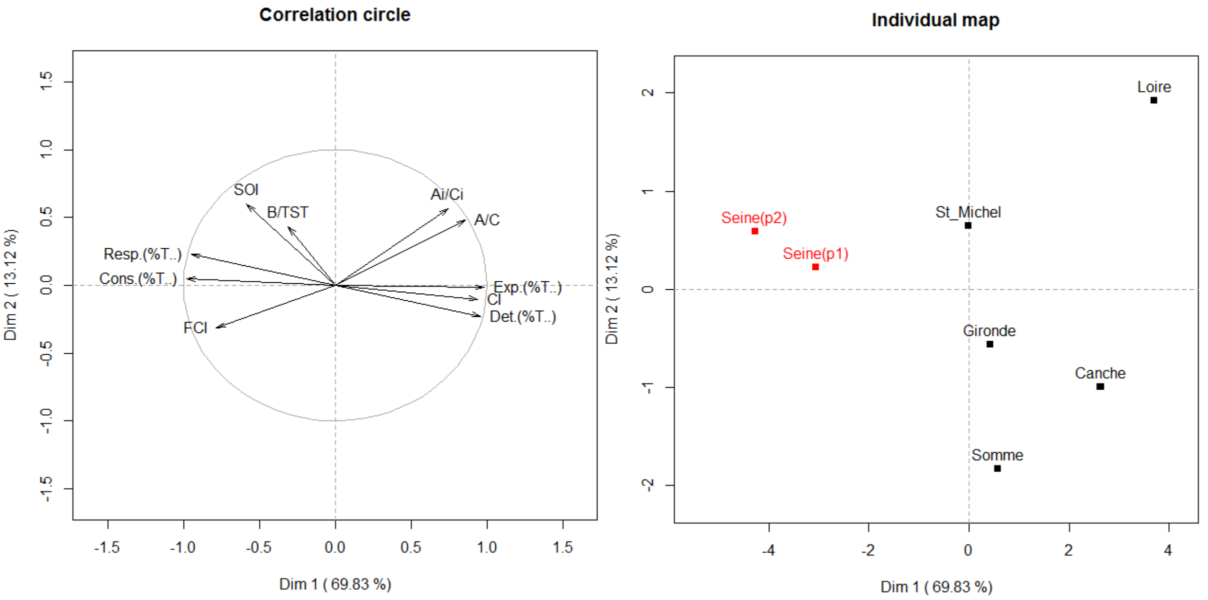


Figure 12: Principal component analysis (PCA) on various French estuaries

The data on the other French estuaries were taken from Selleslagh *et al.* (2012). B/TST, relative system throughput; CI, Connectance Index; SOI, System Omnivory Index; A/C , Relative Ascendancy; Ai/Ci, Relative Intern Ascendancy; FCI, Finn's Cycling Index; Cons (%T..), part of the Consumption flows; Exp (%T..), part of the Export flows; Resp (%T..), part of the Respiration flows; Det (%T..), part of the Detritus flows.

First, the PCA highlights the heterogeneity in the various estuarine ecosystems considered. The Seine estuary models (in red) were relatively distinct from the other estuaries. They were characterized by a large part of consumption and respiration flows in their Total System Throughput, a high Omnivory Index and recycling compared to other French estuaries. These results were partially found in previous studies (Selleslagh *et al.* 2012; Tecchio *et al.* 2016). These can be explained by the large biomass of benthic communities. On a temporal point of view, the Seine estuary slightly shifted towards higher consumption flow, respiration flow, omnivory and recycling which can be interpreted as a increasing of the level of stress in the system. This tendency was already characteristic of the first time period.

4. Discussion

This study is in line with recent studies assessing the ecological functioning of the Seine estuary ecosystem while trying to integrate different spatial scales in a present and past Port 2000's construction coherent food web models.

4.1.Model quality

Data quality

Relatively detailed local, temporal and spatial data were available for most of the input parameters. However, we are aware that data gaps still exists, especially concerning diets and production rate changes between habitats and time periods. Further sampling campaigns should help to decrease the model uncertainty by providing updated data. Both

1996-2002 and 2005-2012 food web models had a pedigree index of 0.492 which is a medium range value according to the 150 balanced EwE models assessed by Morissette (2007). This value can be explained by the use of local and high quality data coming from multiannual survey programs, for example the COLMATAGE, BENTHOSEINE or the various GIP Seine Aval and Le Havre harbor programs. A detailed database was created including spatial and temporal biomass data by aggregating these different data sources. The sampling programs included the Seine estuary downstream of Tancarville (see **Fig. 1**) and the adjacent Seine bay, thus covering the whole estuarine-coastal gradient from which we could study the estuarine ecosystem both at a global and habitat scale.

Despite the relatively local and detailed survey available, data gaps still exist, for example on the meiofauna where biomasses were estimated according to other models (see Tecchio *et al.* 2015, supp. material). These high uncertainties in biomass densities were also found for Zooplankton, Bacteria and Microphytobenthos for both time periods. The data from other models were available for each habitat, allowing us to estimate the spatial repartition of the concerned groups. Some of these functional groups had a medium to high keystoneness (KS) index and trophic impact on their respective habitats food web. The detritus based processes highlighted by the meiofauna's KS and the important bottom up control of the phytoplankton and zooplankton remains. However, the absolute value of the KS index associated with each functional group might change in within their respective uncertainty which could be modelled using ENAtools. Other gaps concerning the spatial repartition of the biomass were found for several functional groups. The Suprabenthos and Microphytobenthos biomasses were estimated by Ecopath for one or more spatial compartment. Biomasses of Zooplankton and Bacteria were initially calculated for larger areas and therefore we had to extrapolate the biomass to several spatial compartments. This concerns mostly the Northern intertidal and subtidal areas and the Southern intertidal and subtidal areas.

The other Ecopath input parameters (diet, production and consumption rates), as shown in **Appendix 1**, have been collected mostly from local or similar ecosystem models or sampling. The medium pedigree value is partially due to several P/B or Q/B rate estimated by the model as we preferred to fix the P/Q rate. This mostly concerned the benthic communities' Q/B which were calibrated according to J.C. Dauvin's expertise.

Difficulties in accounting for uncertainty in the modelling results

Initially, we planned to assess part of the impact of uncertainty on Ecopath inputs on the basic estimates (B, P/B, Q/B, EE and diet) and a set of 13 ENA outputs using the ENAtool routine (Kearney *et al.* 2012; Guesnet *et al.* 2015). However, due to long calculation time (estimated to be several weeks per model), we were not able to run the Matlab routine in time on both 1996-2002 and 2005-2012 models presented in the manuscript. The Matlab routine uses a Monte-Carlo algorithm to build a set of 100 (in our case) mass balanced models. The algorithm draws successively each input parameter in a uniform distribution defined by the parameter's *a priori* uncertainty range (Kearney *et al.* 2012). The drawn model is kept if it meets the mass balance requirements.

In our case, each model had 66 functional groups and about 15 to 20 of them were highly constrained depending on the time period, *i.e.* they had an Ecotrophic Efficiency value over 0.8. For a constrained group, there are statistically less possible input parameter combinations respecting the mass balance requirement. Therefore, the mean number of parameters sampled necessary to have one mass balanced model is directly linked to the number of functional groups, especially the number of constrained functional groups. Since the model parameters are all drawn and checked simultaneously for each group, the number of necessary samples is notably function of the number of functional groups, especially the constrained group, raised to a power factor. Therefore, the calculation time highly increased with the number of constrained functional groups which is the main limiting factor for uncertainty assessment on Ecopath models using this routine.

The modeling choice concerning the balancing with EE<0.9 permitted to have less constrained group. It decreased the calculation time of the uncertainty routine for the intermediate model. However it was insufficient for the final model. As they were only 9 trophic boxes per habitat, we could not aggregate them more for homogeneity reasons. Therefore, we chose to run the uncertainty on aggregated models (with 4 spatial compartments: Navigation channel, Estuary mouth, Southern area (FS+VS) and Northern area (FN+VN)) using the same input parameters as for the models presented above. The uncertainty results for these models are presented in **Appendix 5 and 11**.

4.2.Modelling choices and limitations

Despite the highly detailed biomass data on the benthic functional groups, their distribution were extremely extended towards positive values with several biomass values considered as ecologically aberrant (over 500 t/km² of wet weight). These outliers can be a consequence of the sampling method which was done using grabs (*e.g.* Van Veen samplers) (Dauvin *et al.* 2012). The grab allows sampling organisms living on sandy-muddy sediment like echinoderms, bivalve or worms. However, the main species found in the Seine estuary are aggregative. If the sample occurs on an aggregation, the biomass density will have a high value and might be an outlier. As the mean is very sensitive to extreme values, the outliers tended to significantly increase the mean biomass per group and spatial compartment. The survey biomass data distribution approaches an inverse-gamma distribution where the outliers are generally defined as the 5% higher values. Therefore, when calculating the mean biomass density per group, spatial compartment and time period, we only took in account the values between the quantile 0 and 0.95. This choice has only been made on the benthic predator, filter feeders and deposit feeders groups which had the most ecologically aberrant values. The other main modelling choice induced by the data concerns the cephalopods. Indeed, the data were detailed according to the spatial component. However, the survey only occurred in September, when this functional group has his abundance peak (Jereb *et al.* 2015; expert advice of J.P. Robin). Moreover, the cephalopods occur during only 5 month in the estuary area. Therefore, the calculated biomass was biased and we chose to allocate 60% of the diet to the import component in order to balance this bias. Another method would have been to reduce or estimate the input biomass in Ecopath.

The models interpretations are strongly dependent of the spatial compartments' definition. Indeed, the estuary division has been a compromise between detailed spatial compartments and model complexity. The aim was to focus on homogeneous habitats within each spatial compartment. In previous studies, the Northern mudflat was assumed to be the most impacted habitat (Tecchio *et al.* 2015, 2016). Therefore, the spatial compartments' definition is very similar to the previous modelling efforts for comparison reasons. However, we simplified the Seine bay's spatial compartments as the processes occurring in the bay were not of major interest in the present work. A more detailed set of spatial compartments could have been done following the salinity gradient (*e.g.* separation between oligo- and mesohaline areas in the navigation channel) or the substratum (*e.g.* separation between sandy and muddy areas). However, such a detailed division would have increased the model complexity and led to difficulties in the model structure and interpretations. In this case, a spatial modeling approach using Ecospace would have been more relevant to use, provided times series were available for each spatial compartment as Ecospace is a spatial version of Ecosim.

On the other hand, the available data included biomass density per age class which could have been used to detail the mobile trophic boxes. Indeed, multi-stanza groups could have been implanted for a few species, especially for *Solea solea*, *Dicentrarchus labrax*, *Platichtys flesus* for which the data were the most abundant. Multi-stanza groups would have induced difficulties linked to the density dependent hypothesis, notably for flatfishes. Indeed, in early juvenile stages, habitat preference has been shown for intertidal areas together with lower mobility and inter-specific trophic competition in comparison to older juvenile stages (Van der Veer *et al.* 1991, 2001; Pihl & Van der Veer 1992; Mariani *et al.* 2011). Therefore, in addition to the density dependence hypothesis, a habitat preference parameters should have been taken in account. However, these age classes do not represent a large part of the trophic box biomass. Hence, the functional groups' diet is not influenced by these early ages.

Finally, the most structuring modelling choice in this work concerned the density dependence hypothesis of the predator-prey relationships. Indeed, the whole food web structure relies on this assumption which is based on the optimal foraging theory and literature review (Pyke 1984; Le Pape & Bonhommeau 2015). As the species biomass composition changes, the diet matrix reflects the opportunism or adaptive behavior relied on these given changes. An alternative model has been built for each time period considered. This model relies on the contrary hypothesis which is that the predators forage where they are. So, this led to spatially distribute the fish in the model in relation to the place they were caught during the surveys. When comparing both hypotheses for a same model, we observe highly similar -or at best the same- EE values. This can be interpreted by a match between the predator location and its prey location. It also indicates that, despite the several recent changes which occurred in the estuary, the predator repartition has already changed according to their prey repartition.

4.3. Estuary ecology

The results presented before showed the high importance of benthic communities in terms of biomass, flows and keystoneness in the system. Indeed, benthic predators and, to a lesser extent, benthic filter feeders and deposit feeders dominated the medium TL flows and were the main prey for the mobile groups. They were also exerting important predation rates on the lower trophic level, influencing each habitat as it is shown by their keystoneness index. Their important role has already been highlighted in previous ecosystem models (Tecchio *et al.* 2015). Despite the relatively sediment and particulate organic matter inputs in the Seine estuary (Guézennec 1999; Le Hir 2001), the detritus pool participates to a large part in the estuarine trophic flows. At the top of the food web, Whiting, despite its low biomass and Seabirds are the top predators of the Seine estuary. They are exerting a strong top down control on their direct and indirect preys. They are notably influencing the high TL within each habitat, playing keystone predator role on a habitat scale. Previous keystoneness and MTI results already presented these species as playing an important role in the system (Tecchio *et al.* 2015).

At habitat scale, the estuary mouth presented the largest production and contribution to the mobile groups' consumption which is partially due to the density dependence hypothesis. However, this habitat requires an important role, especially in the diets in order to meet the mass balance requirements of the model. The importance of the estuary mouth reflects a possible shift of the estuarine nurseries downstream. A more detailed model, for example including multi-stanza groups, would allow determining each age class repartition. We assume that the younger ages are feeding in the inner estuary (Van der Veer *et al.* 1991, 2001; Pihl & Van der Veer 1992). The Northern intertidal and subtidal areas were supposed to be the most perturbed habitats (Dauvin *et al.* 2006; Cuvilliez *et al.* 2009; Tecchio *et al.* 2015). Stress has been highlighted by high recycling and omnivory in these habitats, revealing shorter food chains and low maturity (Tecchio *et al.* 2015). Together with the Southern area, these habitats were also shown as the most attractive in terms of prey availability for mobile groups compared to their small area. The Southern area, low pressured, has previously been characterized by high system activity compared to the other habitats (Tecchio *et al.* 2015). Finally, the navigation channel has been characterized with low biomass, production and contribution to the mobile groups' consumption. In general the results highlighted by the keystoneness index and the habitat contribution analysis in the present models reflected the ENA outputs discussed in previous assessment of the Seine estuary. The spatial Ecopath models complement the previous ENA analysis per habitat by integrating each habitat into the global functioning of the system. The contribution of each habitat allows studying another point of view in terms of habitat importance and structuring role in the system.

On a temporal point of view, the models also completed the shifts highlighted in previous modelling efforts (Tecchio *et al.* 2016). The present models showed important shifts in benthic and suprabenthic biomasses as highlighted by Dauvin *et al.* (2010). These changes impacted the trophic composition, the habitat contribution and the keystoneness index. Indeed, the benthic biomasses increase also raised their predation rate within each habitat as, in parallel, the mobile groups' predation decreased. Therefore, the various habitats were more influenced by the benthic predators than by the mobile groups. The keystoneness index reflected this process by highlighting a major increase of the benthic predators' KS index. The global ENA assessment showed an increase of recycling processes as in Tecchio *et al.* (2016). The omnivory index decreased, revealing lower maturity (Odum 1969). At habitat scale, predation reports have been highlighted from the flanks to the mudflats and from the estuary mouth to the inner estuary, especially the navigation channel. Despite its yearly dredging this habitat has still a significant role in the estuary. In case of a lower maritime traffic towards Rouen harbor, it would be interesting to study this habitat recovering potential. However, these various changes are only partially related to Port 2000's construction. The remediation works notably increased the intertidal surface in the Northern area while Port 2000's was built on the subtidal domain. This could explain the predation report from the Northern flank to the Northern mudflat.

The PCA analysis on the various ENA indices suggested that Port 2000's construction together with the shift in river flow decreased system maturity, omnivory and detritus flows in the system. Indeed, Port 2000 and the various remediation works changed the water circulation in the estuary, altering the flows and cycle and therefore decreased its maturity.

Estuarine quality paradox refers to the difficulty to discriminate the effects related to human driven pressures from natural environmental stress which is common in estuarine ecosystems (Dauvin 2007; Elliott & Quintino 2007). In our case, the North Atlantic Oscillation caused an important decrease in the Seine river discharge (Dauvin & Pezy 2013) which potentially masked or increased human driven processes between both time periods considered. For example, the benthic activity increase observed in the estuary, especially in the navigation channel, could have been caused by an upstream shift of the maximum turbidity zone in this habitat, increasing potential development of benthic communities. Further assessment should determine the impact of Port 2000's construction and remediation works on the benthic communities compared to the changes induced by natural processes.

4.4. Management perspective for the estuary

Estuaries are at the interface between marine and terrestrial ecosystem. Hence there is a need of adapted management in these systems because of the various services provided to the human population and the important human, industrial and commercial activities. Estuaries have recently been integrated in a spirit of Integrated Coastal Zone Management in accordance with several national and European policies, *e.g.* the Water Framework Directive (Dauvin 2007; Ducrotoy & Dauvin 2008). However, estuarine ecosystems are also natural stressed systems because of their location and complexity and at the same time are under various anthropogenic pressures which lead to a mixture of contradictory features defined by the Estuarine Quality Paradox (McLusky & Elliott 2004; Dauvin 2007). Therefore, the conjunction of an adapted coastal management and the prosperity of the various anthropogenic activities need a re-examination of the management policies in accordance with the actual knowledges of the ecosystem (Dauvin 2007).

Various surveys and rehabilitation programs already started with Port 2000's construction, notably restoring a river meander in the Northern subtidal area. Indeed, important habitat loss started since the beginning of the 19th century and further loss should be prevented or at least the consequences should be predicted.

The Ecopath models presented above assessed the various changes in the structure and functioning of the Seine estuary potentially induced by Port 2000's construction. On another point of view, they could be seen as the result of a habitat loss scenario. Indeed, between both time period considered, the Northern flank lost an average surface of 5 km² (Tecchio *et al.* 2015), modifying once again its composition and its contribution to the mobile groups' consumption. The Northern flank has been shown as more stressed than the Southern flank and more stressed in the 2002-2012 period than in the 1996-2002 period. Despite these changes, it remains an important habitat in terms of productivity and contribution. The direct impact of Port 2000's construction on the Northern flank and its adjacent mudflat is not very clear in our results. Either Port 2000 did not have a large impact or the remediation works were efficient. However, it is clear that the habitat loss is influencing its contribution and that the highly stressed state might lead to long term changes which could not be assessed in this study.

Concerning habitat restoration, especially nursery areas, the models showed the high importance of both Northern and Southern intertidal mudflats which had an important prey productivity and contribution to the mobile groups' consumption compared to their respective surface areas. Despite its stressed state, the Northern mudflat had a large trophic capacity due to low mean ecotrophic efficiency. In contrary, the Southern mudflat was shown as the least stressed habitat while its trophic capacity is lower due to high predation. We assume that the stressed state in the Northern mudflat either induces the development of opportunistic and highly productive benthic communities or induces a predation report towards the Southern mudflat. Therefore, the intertidal habitats should be part of future rehabilitation or habitat creation measures.

5. Conclusion

The spatial Ecopath models presented above provided a better understanding of the structural and functional differences in the Seine estuary ecosystem between both 1996-2002 and 2005-2012 time periods. The ecosystem was considered here as a network of interacting habitats completing the previous studies done by Tecchio *et al.* (2015, 2016). Each habitat has been designed with its own food web structure including the main estuarine organisms, from low to high TLs.

The results highlighted several structural and functional changes between and within each time period. The Seine estuary has been characterized by the strong contribution of the estuary mouth to the mobile groups' consumption and an important role of the intertidal mudflats as nursery grounds. Port 2000's construction, habitat loss and low river flow caused predation reports from the estuary mouth to the navigation channel and from the subtidal areas to the intertidal areas, therefore increasing their importance. The benthic communities are playing a pivot role in the ecosystem, providing prey to the mobile groups and regulating their respective habitats by a top-down control. The system stress increased during the second time period, highlighted by higher recycling, omnivory and benthic dependence.

The trophic models are improving the actual knowledges on the Seine estuary ecology at various scales and could therefore complete the various management tools. However, the observed changes can be completed by other modelling approaches, *e.g.* community approaches in order to assess the composition changes in detail within the various habitats. A modelling effort replacing the Seine estuary in the larger Seine bay ecosystem (*e.g.* Ecospace) should help understanding the interactions between the estuarine ecosystem, its adjacent marine habitats and the various pressures induced by fisheries. Finally, further Ecopath modeling could be done using the 2005-2012 model as a baseline in order to assess the effect of a potential increase in benthic biomasses or the maximum trophic capacity of both Northern and Southern mudflat.

References

Baird, D., McGlade, J. M. & Ulanowicz, R. E. (1991) The Comparative Ecology of Six Marine Ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences* **333**: 15–29.

Cabral, H. N., Costa, M. J. & Salgado, J. P. (2001) Does the Tagus estuary fish community reflect environmental changes? *Climate Research* **18**: 119–126.

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. & Walters, C. J. (2004) Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* **172**: 109–139.

Christensen, V., Walters, C. J. & Forrest, R. (2008) Ecopath with Ecosim version 6 User Guide. : 235.

Cuvilliez, A., Deloffre, J., Lafite, R. & Bessineton, C. (2009) Morphological responses of an estuarine intertidal mudflat to constructions since 1978 to 2005: The Seine estuary (France). *Geomorphology* **104**: 165–174.

Dauvin, J. C., Desroy, N., Janson, A. L., Vallet, C. & Duhamel, S. (2006) Recent changes in estuarine benthic and suprabenthic communities resulting from the development of harbour infrastructure. *Marine Pollution Bulletin* **53**: 80–90.

Dauvin, J. C., Brind'Amour, A., Cuvilliez, A., Dancié, C., Desroy, N., Le Hir, P., Lesour, S., Mear, Y. & Morin, J. (2012) Rapport Seine-Aval 4 COLMATAGE. *Seine-Aval Scientific Report*: 210.

Dauvin, J.-C. (2007) Paradox of estuarine quality: benthic indicators and indices, consensus or debate for the future. *Marine Pollution Bulletin* **55**: 271–281.

Dauvin, J.-C. (2008) The main characteristics, problems, and prospects for Western European coastal seas. *Marine Pollution Bulletin* **57**: 22–40.

Dauvin, J.-C. & Desroy, N. (2005) The food web in the lower part of the Seine estuary: a synthesis of existing knowledge. *Hydrobiologia* **540**: 13–27.

Dauvin, J.-C. & Pezy, J.-P. (2013) Long-term changes of the Seine estuary suprabenthos (1996–2012). *Journal of Experimental Marine Biology and Ecology* **448**: 93–103.

Dauvin, J.-C., Alizier, S., Vallet, C. & Ruellet, T. (2010) Does the Port 2000 harbour construction have an effect on the Seine estuary suprabenthic community? *Estuarine, Coastal and Shelf Science* **86**: 42–50.

Doney, S. C. (2010) The growing human footprint on coastal and open-ocean biogeochemistry. *science* **328**: 1512–1516.

Ducrotoy, J.-P. & Dauvin, J.-C. (2008) Estuarine conservation and restoration: the Somme and the Seine case studies (English Channel, France). *Marine Pollution Bulletin* **57**: 208–218.

Eick, D. & Thiel, R. (2014) Fish assemblage patterns in the Elbe estuary: guild composition, spatial and temporal structure, and influence of environmental factors. *Marine Biodiversity* **44**: 559–580.

Elliott, M. & Hemingway, K. (2002) *Fishes in Estuaries*. Oxford.

Elliott, M. & Quintino, V. (2007) The Estuarine Quality Paradox, Environmental Homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Marine Pollution Bulletin* **54**: 640–645.

European Council (2000) *Directive 2000/60/EC of the European Parliament and the Council*.

Fagan, W. F. (1997) Omnivory as a stabilizing feature of natural communities. *The American Naturalist* **150**: 554–567.

Finn, J. T. (1976) Measures of Ecosystem Structure adn Function Derived from Analysis of Flows. *Journal of Theoretical Biology* **56**: 363–380.

Finn, J. T. (1980) Flow Analysis of Models of the Hubbard Brook Ecosystem. *Ecology* **61**: 562–571.

Foussard, V. (2010) Evolution morphologique d’un estuaire anthropisé de 1800 à nos jours. *Seine-Aval Scientific Report* **2.3**: 48.

Fulton, E. A. (2010) Approaches to end-to-end ecosystem models. *Journal of Marine Systems* **81**: 171–183.

Gameiro, C. & Brotas, V. (2009) Patterns of Phytoplankton Variability in the Tagus Estuary (Portugal). *Estuaries and Coasts* **33**: 311–323.

Gascuel, D. & Pauly, D. (2009) EcoTroph: Modelling marine ecosystem functioning and impact of fishing. *Ecological Modelling* **220**: 2885–2898.

Gascuel, D., Bozec, Y.-M., Chassot, E., Colomb, A. & Laurans, M. (2005) The trophic spectrum: theory and application as an ecosystem indicator. *ICES Journal of Marine Science: Journal du Conseil* **62**: 443–452.

Gascuel, D., Tremblay-Boyer, L. & Pauly, D. (2009) EcoTroph (E.T): a trophic level based software for assessing the impacts of fishing on aquatic ecosystems. *Vancouver, BC: Canada* **17**: 82.

Girardin, M., Castelnaud, G. & Lobry, J. (2014) Surveillance halieutique de l’estuaire de la Gironde -Suivi des captures 2013 -Etude de la faune circulante 2013. *Rapport pour EDF CNPE du Blayais, Irstea, Centre de Bordeaux, Cestas*: 238.

Guénette, S., Meissa, B. & Gascuel, D. (2014) Assessing the Contribution of Marine Protected Areas to the Trophic Functioning of Ecosystems: A Model for the Banc d’Arguin and the Mauritanian Shelf (KI Stergiou, Ed.). *PLoS ONE* **9**: e94742.

Guesnet, V., Lassalle, G., Chaalali, A., Kearney, K., Saint-Béat, B., Karimi, B., Grami, B., Tecchio, S., Niquil, N. & Lobry, J. (2015) Incorporating food-web parameter uncertainty into Ecopath-derived ecological network indicators. *Ecological Modelling* **313**: 29–40.

Guézennec, L. (1999) Seine-Aval : un estuaire et ses problèmes. *Seine-Aval Scientific Report* **1.1**: 29.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D’Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R. & Watson, R. (2008) A Global Map of Human Impact on Marine Ecosystems. *Science* **319**: 948–952.

Jereb, P., Allcock, A. L., Lefkaditou, E., Piatkowski, U., Hastie, L. C. & Pierce, G. J. (2015) Cephalopod biology and fisheries in Europe: II. Species Accounts. *ICES Cooperative Research Report*: 360.

Kearney, K. A., Stock, C., Aydin, K. & Sarmiento, J. L. (2012) Coupling planktonic ecosystem and fisheries food web models for a pelagic ecosystem: Description and validation for the subarctic Pacific. *Ecological Modelling* **237**–**238**: 43–62.

Latham, L. G. (2006) Network flow analysis algorithms. *Ecological Modelling* **192**: 586–600.

Le Hir, P. (2001) Courants, vagues et marées : les mouvements de l’eau. *Seine-Aval Scientific Report*: 32.

Le Pape, O. & Bonhommeau, S. (2015) The food limitation hypothesis for juvenile marine fish. *Fish and Fisheries* **16**: 373–398.

Libralato, S. (2008) System Omnivory Index A2 - Jørgensen, Sven Erik. *Encyclopedia of Ecology* (B. D. Fath, ed): pp. 3472–3477. Oxford: Academic Press.

Libralato, S., Christensen, V. & Pauly, D. (2006) A method for identifying keystone species in food web models. *Ecological Modelling* **195**: 153–171.

Lobry, J. (2004) Quel référentiel de fonctionnement pour les écosystèmes estuariens? Le cas des cortèges de poissons fréquentant l’estuaire de la Gironde.

Lobry, J., David, V., Pasquaud, S., Lepage, M., Sautour, B. & Rochard, E. (2008) Diversity and stability of an estuarine trophic network. *Marine Ecology Progress Series* **358**: 13–25.

Mariani, S., Boggan, C. & Balata, D. (2011) Food resource use in sympatric juvenile plaice and flounder in estuarine habitats: Food resource use in plaice and flounder. *Marine Ecology* **32**: 96–101.

McLusky, D. & Elliott, M. (2004) *The Estuarine Ecosystem : Ecology, Threats and Management*. New York.

Meybeck, M., De Massily, G. & Fustec, E. (1998) *La Seine en son bassin : fonctionnement écologique d'un système fluvial anthropisé*. Paris.

Monaco, M. E. & Ulanowicz, R. E. (1997) Comparative ecosystem trophic structure of three U.S. mid-Atlantic estuaries. *Marine Ecology Progress Series* **161**: 239–254.

Morissette, L. (2007) Complexity, cost and quality of ecosystem models adn their impact on resilience : A comparative analysis, with emphasis on marine mammals and the Gulf of St. Lawrence.

Odum, E. P. (1969) The Strategy of Ecosystem Development. *Science* **164**: 262–270.

Pauly, D. (1980) On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil* **39**: 175–192.

Pauly, D. (2000) Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES Journal of Marine Science* **57**: 697–706.

Pauly, D., Bartz, M. L. S. & Palomares, M. L. D. (International C. for L. A. R. M. (1993) Improved construction, parametrization and interpretation of steady-state ecosystem models. *ICLARM Conference Proceedings (Philippines)* p. ICLARM.

Pihl, L. & Van der Veer, H. W. (1992) Importance of exposure and habitat structure for the population density of 0-group plaice, Pleuronectes platessa L., in coastal nursery areas. *Netherlands Journal of Sea Research* **29**: 145–152.

Piroddi, C., Coll, M., Steenbeek, J., Macias Moy, D. & Christensen, V. (2015) Modelling the Mediterranean marine ecosystem as a whole: addressing the challenge of complexity. *Marine Ecology Progress Series* **533**: 47–65.

Polovina, J. J. (1984) Model of a coral reef ecosystem. *Coral reefs* **3**: 1–11.

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., Daily, G., Castilla, J. C., Lubchenco, J. & Paine, R. T. (1996) Challenges in the Quest for Keystones Identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems. *BioScience* **46**: 609–620.

Prado, P., Ibáñez, C., Caiola, N. & Reyes, E. (2013) Evaluation of seasonal variability in the food-web properties of coastal lagoons subjected to contrasting salinity gradients using network analyses. *Ecological Modelling* **265**: 180–193.

Pyke, G. (1984) Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology and Systematics* **15**: 523–575.

Raoux, A., Tecchio, S., Pezy, J. P., Lassalle, G., Degraer, S., Wilhelmsson, D., Cachera, M., Ernande, B., Le Guen, C., Haraldsson, M., Grangeré, K., Le Loc'h, F., Dauvin, J. C. & Niquil, N. ((in prep.)) Benthic and fish aggregation inside an offshore wind farm : Which effects on the trophic web functioning? *Ecological Indicators*.

Rybarczyk, H. & Elkaïm, 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.

Selleslagh, J., Amara, R., Laffargue, P., Lesourd, S., Lepage, M. & Girardin, M. (2009) Fish composition and assemblage structure in three Eastern English Channel macrotidal estuaries: A comparison with other French estuaries. *Estuarine, Coastal and Shelf Science* **81**: 149–159.

Selleslagh, J., Lobry, J., Amara, R., Brylinski, J.-M. & Boët, P. (2012) Trophic functioning of coastal ecosystems along an anthropogenic pressure gradient: A French case study with emphasis on a small and low impacted estuary. *Estuarine, Coastal and Shelf Science* **112**: 73–85.

Tecchio, S., Rius, A. T., Dauvin, J.-C., Lobry, J., Lassalle, G., Morin, J., Bacq, N., Cachera, M., Chaalali, A., Villanueva, M. C. & Niquil, N. (2015) The mosaic of habitats of the Seine estuary: Insights from food-web modelling and network analysis. *Ecological Modelling* **312**: 91–101.

Tecchio, S., Chaalali, A., Raoux, A., Tous Rius, A., Lequesne, J., Girardin, V., Lassalle, G., Cachera, M., Riou, P., Lobry, J., Dauvin, J.-C. & Niquil, N. (2016) Evaluating ecosystem-level anthropogenic impacts in a stressed transitional environment: The case of the Seine estuary. *Ecological Indicators* **61**: 833–845.

Ulanowicz, R. E. (1986) *Growth and Development: Ecosystems Phenomenology.* New York.

Ulanowicz, R. E. & Abarca-Arenas, L. G. (1997) An informational synthesis of ecosystem structure and function. *Ecological Modelling* **95**: 1–10.

Ulanowicz, R. E. & Puccia, C. J. (1990) Mixed Trophic Impacts in Ecosystems. *Coenoses* **5**: 7–16.

Valls, A., Coll, M. & Christensen, V. (2015) Keystone species: toward an operational concept for marine biodiversity conservation. *Ecological Monographs* **85**: 29–47.

Van der Veer, H., Bergman, M., Dapper, R. & Witte, J. (1991) Population dynamics of an intertidal 0-group flounder Platichthys flesus population in the western Dutch Wadden Sea. *Marine Ecology Progress Series* **73**: 141–148.

Van der Veer, H. W., Dapper, R. & Witte, J. I. (2001) The nursery function of the intertidal areas in the western Wadden Sea for 0-group sole Solea solea (L.). *Journal of Sea Research* **45**: 271–279.

Vincent, L., Rybarczyk, H. & Dauvin, J. C. (2006) Analyse du fonctionnement du réseau trophique de l'estuaire de la Seine et des structures spatiales qui la constituent. *Seine-Aval Scientific Report*: 61.

Walters, C., Christensen, V. & Pauly, D. (1997) Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in fish biology and fisheries* **7**: 139–172.

Walters, C., Pauly, D. & Christensen, V. (1999) Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* **2**: 539–554.

Walters, C., Pauly, D., Christensen, V. & Kitchell, J. F. (2000) Representing Density Dependent Consequences of Life History Strategies in Aquatic Ecosystems: EcoSim II. *Ecosystems* **3**: 70–83.

Wilson, J. G. (2002) Productivity, Fisheries and Aquaculture in Temperate Estuaries. *Estuarine, Coastal and Shelf Science* **55**: 953–967.

Appendix 1: Ecopath input and output parameters value and references

Group	Biomass	P/B and Q/B	Diet
SBD Seabirds	From Rybarczyk and Elkaïm (2003) model using data from Sueur and Triplet (1999)	From Rybarczyk and Elkaïm (2003)	From Rybarczyk and Elkaïm (2003); Tecchio et al. (2015)
WHI Whiting	Ifremer, CSLN, Le Havre port authority sampling programs (Liteau, Port2000, Grand Canal, COLMATAGE 2008-2009-2010, and GIP Seine-Aval	From Raoux et al. (in prep)	From Raoux et al. (in prep)
FPI Other fish piscivores		FishBase; Mackinson and Daskalov (2007); Carpentier et al. (2009)	Lobry et al. (2008); Selleslagh et al. (2012)
FPV Fish planktivores			
SBA European Seabass		From Rybarczyk and Elkaïm (2003)	From Rybarczyk and Elkaïm (2003)
FBF Other fish benthos feeders		FishBase; Mackinson and Daskalov (2007); Carpentier et al. (2009)	Lobry et al. (2008); Selleslagh et al. (2012)
SOL Common Sole		From Raoux et al. (in prep)	From Raoux et al. (in prep)
PLA European Plaice		Raoux et al. (in prep)	Raoux et al. (in prep)
FLO European Flounder		Rybarczyk and Elkaïm (2003)	Rybarczyk and Elkaïm (2003)
FLA Other flatfishes		FishBase; Mackinson and Daskalov (2007); Carpentier et al. (2009)	Lobry et al. (2008); Selleslagh et al. (2012)
CEP Cephalopods	PECTOW, BENTHOSEINE and COLMATAGE projects, Le Havre port authority, and GIP Seine-Aval	Raoux et al. (in prep) and Lassalle et al. (2011)	Raoux et al. (in prep) and Lassalle et al. (2011)
IPR Benthic predators		Rybarczyk and Elkaïm (2003); Brey (2001); Le Loc'h (2004)	Hunt (1925); Janson (2007); Mouny et al. (1998); Rybarczyk and Elkaïm (2003)
IFF Benthic filter feeders			
IDF Benthic deposit feeders			
SUP Suprabenthos	National Natural History Museum Paris, Wimereux marine station, Caen University, Le Havre port authority, and GIP Seine-Aval sampling programs	Brey (2001); Carpentier et al. (2009); Le Loc'h (2004)	Qualitative estimation from Lobry et al. (2008)
MEI Meiofauna	Le Guellec and Bodin (1992); Ratsimbazafy (1998); Spilmont (2004)	Chardy and Dauvin (1992); Le Loc'h (2004)	Tecchio et al. (2015) and general knowledge
ZOO Zooplankton	From Rybarczyk and Elkaïm (2003)	Rybarczyk and Elkaïm (2003)	Tecchio et al. (2015) and general knowledge
BAC Bacteria	Chardy (1987); Chardy and Dauvin (1992)	Mackinson and Daskalov (2007)	Chardy and Dauvin (1992); Tecchio et al. (2015)
MPB Microphytobenthos	Spilmont (2004); Napoléon et al. (2012)	Spilmont (2004)	-
PHY Phytoplankton	SURVAL database (http://envlit.ifremer.fr/resultats/surval)	Souissi (2007)	-
DET Detritus	Seine-Aval sampling program	-	-

Basic estimates for the 1996-2002 model

Group name	Trophic level	Habitat area (fraction)	Biomass in habitat area (t/km²)	Biomass (t/km²)	Production / biomass (/year)	Consumption / biomass (/year)	Ecotrophic efficiency	Production / consumption	Unassimil. / consumption
Seabirds	3,774	1,000	3,839	3,839	0,013	**0,325**	**0,000**	0,040	0,2
Whiting	3,978	1,000	0,117	0,117	1,735	7,635	**0,107**	0,227	0,2
Other Fish piscivores	3,855	1,000	0,430	0,430	0,533	3,500	**0,804**	0,152	0,2
Fish planktivores	2,851	1,000	0,157	0,157	1,300	6,700	**0,896**	0,194	0,2
European Sea Bass	3,661	1,000	0,105	0,105	0,530	3,140	**0,431**	0,169	0,2
Other Fish benthos feeders	3,255	1,000	2,914	2,914	1,360	**4,690**	**0,662**	0,290	0,2
Common Sole	3,352	1,000	0,196	0,196	0,700	3,200	**0,479**	**0,219**	0,2
European Plaice	3,349	1,000	0,162	0,162	0,950	3,380	**0,196**	**0,281**	0,2
European Flounder	3,212	1,000	0,719	0,719	1,753	8,861	**0,106**	**0,198**	0,2
Other flatfish	3,161	1,000	0,326	0,326	1,159	4,570	**0,014**	**0,254**	0,2
Cephalopods	3,606	0,840	4,280	3,595	2,000	**5,714**	**0,087**	0,350	0,2
Benthic predators VN	2,767	0,050	0,898	0,045	3,000	**15,000**	**0,898**	0,200	0,2
Benthic predators FN	2,791	0,120	8,458	1,015	3,000	**15,000**	**0,687**	0,200	0,2
Benthic predators VS	2,947	0,070	3,922	0,275	3,000	**15,000**	**0,922**	0,200	0,2
Benthic predators FS	2,976	0,090	3,726	0,335	3,000	**15,000**	**0,876**	0,200	0,2
Benthic predators CH	3,076	0,160	2,680	0,429	3,000	**15,000**	**0,369**	0,200	0,2
Benthic predators EMB	2,946	0,520	11,876	6,176	3,000	**15,000**	**0,394**	0,200	0,2
Benthic filter feeders VN	2,250	0,050	3,487	0,174	3,500	**16,667**	**0,401**	**0,210**	0,3
Benthic filter feeders FN	2,250	0,120	6,644	0,797	3,500	**16,667**	**0,331**	**0,210**	0,3
Benthic filter feeders VS	2,152	0,070	4,596	0,322	3,500	**16,667**	**0,908**	**0,210**	0,3
Benthic filter feeders FS	2,152	0,090	10,178	0,916	3,500	**16,667**	**0,574**	**0,210**	0,3
Benthic filter feeders CH	2,205	0,160	4,099	0,656	3,500	**16,667**	**0,822**	**0,210**	0,3
Benthic filter feeders EMB	2,265	0,520	12,815	6,664	3,500	**16,667**	**0,436**	**0,210**	0,3
Benthic deposit feeders VN	2,112	0,050	0,230	0,012	4,000	**18,182**	**0,901**	0,220	0,3
Benthic deposit feeders FN	2,112	0,120	7,473	0,897	4,000	**18,182**	**0,575**	0,220	0,3
Benthic deposit feeders VS	2,112	0,070	1,039	0,073	4,000	**18,182**	**0,918**	0,220	0,3
Benthic deposit feeders FS	2,112	0,090	4,329	0,390	4,000	**18,182**	**0,881**	0,220	0,3
Benthic deposit feeders CH	2,205	0,160	0,478	0,076	4,000	**18,182**	**0,909**	0,220	0,3
Benthic deposit feeders EM	2,115	0,520	20,412	10,614	4,000	**18,182**	**0,692**	0,220	0,3
Suprabenthos VN	2,724	0,050	1,776	0,089	6,300	**31,500**	**0,832**	0,200	0,3
Suprabenthos FN	2,724	0,120	9,246	1,110	6,300	**31,500**	**0,830**	0,200	0,3
Suprabenthos VS	2,474	0,070	**5,890**	**0,412**	6,300	**31,500**	0,900	0,200	0,3
Suprabenthos FS	2,474	0,090	**6,900**	**0,621**	6,300	**31,500**	0,900	0,200	0,3
Suprabenthos CH	2,778	0,160	3,857	0,617	6,300	**31,500**	**0,924**	0,200	0,3
Suprabenthos EMB	2,358	0,520	11,769	6,120	6,150	**30,750**	**0,892**	0,200	0,3
Meiofauna VN	2,100	0,050	3,922	0,196	15,000	**75,000**	**0,057**	0,200	0,3
Meiofauna FN	2,100	0,120	3,922	0,471	15,000	**75,000**	**0,114**	0,200	0,3
Meiofauna VS	2,100	0,070	3,448	0,241	15,000	**75,000**	**0,128**	0,200	0,3
Meiofauna FS	2,100	0,090	3,448	0,310	15,000	**75,000**	**0,169**	0,200	0,3
Meiofauna CH	2,100	0,160	3,681	0,589	12,000	**60,000**	**0,350**	0,200	0,3
Meiofauna EMB	2,100	0,520	3,250	1,690	15,000	**75,000**	**0,770**	0,200	0,3
Zooplankton VN	2,000	0,050	18,424	0,921	**45,000**	150,000	**0,093**	0,300	0,4
Zooplankton FN	2,000	0,120	18,424	2,211	**45,000**	150,000	**0,321**	0,300	0,4
Zooplankton VS	2,000	0,070	19,816	1,387	**38,400**	128,000	**0,147**	0,300	0,4
Zooplankton FS	2,000	0,090	19,816	1,783	**38,400**	128,000	**0,180**	0,300	0,4
Zooplankton CH	2,000	0,160	18,424	2,948	**45,000**	150,000	**0,117**	0,300	0,4
Zooplankton EMB	2,000	0,520	18,424	9,580	**39,000**	130,000	**0,256**	0,300	0,4
Bacteria VN	2,000	0,050	16,970	0,849	26,790	**53,580**	**0,040**	0,500	0,35
Bacteria FN	2,000	0,120	19,970	2,396	26,790	**53,580**	**0,053**	0,500	0,35
Bacteria VS	2,000	0,070	19,970	1,398	26,790	**53,580**	**0,026**	0,500	0,35
Bacteria FS	2,000	0,090	19,970	1,797	26,790	**53,580**	**0,030**	0,500	0,35
Bacteria CH	2,000	0,160	6,182	0,989	26,790	**53,580**	**0,093**	0,500	0,35
Bacteria EMB	2,000	0,520	19,970	10,384	26,800	**53,600**	**0,061**	0,500	0,35
Microphytobenthos VN	1,000	0,050	17,250	0,863	35,000		**0,775**		0
Microphytobenthos FN	1,000	0,120	17,250	2,070	35,000		**0,896**		0
Microphytobenthos VS	1,000	0,070	17,200	1,204	35,000		**0,172**		0
Microphytobenthos FS	1,000	0,090	17,200	1,548	35,000		**0,221**		0
Microphytobenthos CH	1,000	0,160	**1,109**	**0,177**	33,000		0,900		0
Microphytobenthos EMB	1,000	0,520	**2,574**	**1,339**	35,000		0,900		0
Phytoplankton VN	1,000	0,050	34,595	1,730	150,000		**0,314**		0
Phytoplankton FN	1,000	0,120	34,595	4,151	150,000		**0,329**		0
Phytoplankton VS	1,000	0,070	34,595	2,422	150,000		**0,352**		0
Phytoplankton FS	1,000	0,090	34,595	3,114	150,000		**0,363**		0
Phytoplankton CH	1,000	0,160	34,595	5,535	150,000		**0,398**		0
Phytoplankton EMB	1,000	0,520	12,000	6,240	165,000		**0,853**		0
Detritus	1,000	1,000	190,000	190,000			**0,412**		0,2

Values not entered as input parameters and therefore estimated by the model are indicated in bold.

Basic estimates for the 2005-2012 model

Group name	Trophic level	Habitat area (fraction)	Biomass in habitat area (t/km²)	Biomass (t/km²)	Production / biomass (/year)	Consumption / biomass (/year)	Ecotrophic efficiency	Production / consumption	Unassimil. / consumption
Seabirds	3,596	1,000	3,783	3,783	0,013	**0,325**	**0,000**	0,040	0,2
Whiting	3,890	1,000	0,026	0,026	1,735	7,635	**0,164**	0,227	0,2
Other Fish piscivores	3,582	1,000	0,352	0,352	0,533	3,500	**0,825**	0,152	0,2
Fish planktivores	2,862	1,000	0,091	0,091	1,300	6,700	**0,861**	0,194	0,2
European Sea Bass	3,600	1,000	0,077	0,077	0,530	3,140	**0,478**	0,169	0,2
Other Fish benthos feeders	3,190	1,000	0,657	0,657	1,360	**4,690**	**0,924**	0,290	0,2
Common Sole	3,294	1,000	0,119	0,119	0,700	3,200	**0,333**	**0,219**	0,2
European Plaice	3,307	1,000	0,166	0,166	0,950	3,380	**0,206**	**0,281**	0,2
European Flounder	3,202	1,000	0,040	0,040	1,753	8,861	**0,060**	**0,198**	0,2
Other flatfish	3,142	1,000	0,316	0,316	1,159	4,570	**0,056**	**0,254**	0,2
Cephalopods	3,487	0,830	2,071	1,719	2,000	**5,714**	**0,092**	0,350	0,2
Benthic predators VN	2,862	0,060	5,004	0,300	3,000	**15,000**	**0,704**	0,200	0,2
Benthic predators FN	2,647	0,080	13,952	1,116	3,000	**15,000**	**0,765**	0,200	0,2
Benthic predators VS	2,983	0,060	12,778	0,767	3,000	**15,000**	**0,321**	0,200	0,2
Benthic predators FS	2,977	0,090	13,326	1,199	3,000	**15,000**	**0,250**	0,200	0,2
Benthic predators CH	2,969	0,170	5,914	1,005	3,000	**15,000**	**0,033**	0,200	0,2
Benthic predators EMB	2,564	0,540	49,412	26,682	3,000	**15,000**	**0,263**	0,200	0,2
Benthic filter feeders VN	2,250	0,060	9,660	0,580	3,500	**16,667**	**0,125**	**0,210**	0,3
Benthic filter feeders FN	2,250	0,080	16,498	1,320	3,500	**16,667**	**0,178**	**0,210**	0,3
Benthic filter feeders VS	2,152	0,060	16,025	0,961	3,500	**16,667**	**0,889**	**0,210**	0,3
Benthic filter feeders FS	2,152	0,090	22,749	2,047	3,500	**16,667**	**0,658**	**0,210**	0,3
Benthic filter feeders CH	2,205	0,170	4,009	0,682	3,500	**16,667**	**0,862**	**0,210**	0,3
Benthic filter feeders EMB	2,240	0,540	36,847	19,897	3,500	**16,667**	**0,839**	**0,210**	0,3
Benthic deposit feeders VN	2,112	0,060	7,537	0,452	4,000	**18,182**	**0,276**	0,220	0,3
Benthic deposit feeders FN	2,112	0,080	7,550	0,604	4,000	**18,182**	**0,472**	0,220	0,3
Benthic deposit feeders VS	2,112	0,060	9,051	0,543	4,000	**18,182**	**0,736**	0,220	0,3
Benthic deposit feeders FS	2,112	0,090	7,494	0,674	4,000	**18,182**	**0,827**	0,220	0,3
Benthic deposit feeders CH	2,205	0,170	6,118	1,040	4,000	**18,182**	**0,598**	0,220	0,3
Benthic deposit feeders EM	2,085	0,540	33,391	18,031	4,000	**18,182**	**0,836**	0,220	0,3
Suprabenthos VN	2,694	0,060	**2,965**	**0,178**	6,300	**31,500**	0,900	0,200	0,3
Suprabenthos FN	2,694	0,080	0,737	0,059	6,300	**31,500**	**0,847**	0,200	0,3
Suprabenthos VS	2,442	0,060	**11,339**	**0,680**	6,300	**31,500**	0,900	0,200	0,3
Suprabenthos FS	2,442	0,090	**11,669**	**1,050**	6,300	**31,500**	0,900	0,200	0,3
Suprabenthos CH	2,687	0,170	2,747	0,467	6,300	**31,500**	**0,833**	0,200	0,3
Suprabenthos EMB	2,348	0,540	0,611	0,330	6,150	**30,750**	**0,838**	0,200	0,3
Meiofauna VN	2,100	0,060	3,922	0,235	15,000	**75,000**	**0,096**	0,200	0,3
Meiofauna FN	2,100	0,080	3,922	0,314	15,000	**75,000**	**0,152**	0,200	0,3
Meiofauna VS	2,100	0,060	3,448	0,207	15,000	**75,000**	**0,344**	0,200	0,3
Meiofauna FS	2,100	0,090	3,448	0,310	15,000	**75,000**	**0,378**	0,200	0,3
Meiofauna CH	2,100	0,170	3,681	0,626	12,000	**60,000**	**0,877**	0,200	0,3
Meiofauna EMB	2,100	0,540	3,250	1,755	15,000	**75,000**	**0,899**	0,200	0,3
Zooplankton VN	2,000	0,060	18,424	1,105	**45,000**	150,000	**0,163**	0,300	0,4
Zooplankton FN	2,000	0,080	18,424	1,474	**45,000**	150,000	**0,190**	0,300	0,4
Zooplankton VS	2,000	0,060	19,816	1,189	**38,400**	128,000	**0,289**	0,300	0,4
Zooplankton FS	2,000	0,090	19,816	1,783	**38,400**	128,000	**0,312**	0,300	0,4
Zooplankton CH	2,000	0,170	18,424	3,132	**45,000**	150,000	**0,104**	0,300	0,4
Zooplankton EMB	2,000	0,540	18,424	9,949	**39,000**	130,000	**0,333**	0,300	0,4
Bacteria VN	2,000	0,060	16,970	1,018	26,790	**53,580**	**0,064**	0,500	0,35
Bacteria FN	2,000	0,080	19,970	1,598	26,790	**53,580**	**0,064**	0,500	0,35
Bacteria VS	2,000	0,060	19,970	1,198	26,790	**53,580**	**0,036**	0,500	0,35
Bacteria FS	2,000	0,090	19,970	1,797	26,790	**53,580**	**0,034**	0,500	0,35
Bacteria CH	2,000	0,170	6,182	1,051	26,790	**53,580**	**0,154**	0,500	0,35
Bacteria EMB	2,000	0,540	19,970	10,784	26,800	**53,600**	**0,093**	0,500	0,35
Microphytobenthos VN	1,000	0,060	17,250	1,035	35,000		**0,828**		0
Microphytobenthos FN	1,000	0,080	17,250	1,380	35,000		**0,843**		0
Microphytobenthos VS	1,000	0,060	17,200	1,032	35,000		**0,367**		0
Microphytobenthos FS	1,000	0,090	17,200	1,548	35,000		**0,375**		0
Microphytobenthos CH	1,000	0,170	**1,918**	**0,326**	33,000		0,900		0
Microphytobenthos EMB	1,000	0,540	**7,455**	**4,026**	35,000		0,900		0
Phytoplankton VN	1,000	0,060	18,600	1,116	150,000		**0,616**		0
Phytoplankton FN	1,000	0,080	18,600	1,488	150,000		**0,657**		0
Phytoplankton VS	1,000	0,060	18,600	1,116	150,000		**0,697**		0
Phytoplankton FS	1,000	0,090	18,600	1,674	150,000		**0,718**		0
Phytoplankton CH	1,000	0,170	18,600	3,162	150,000		**0,723**		0
Phytoplankton EMB	1,000	0,540	13,000	7,020	165,000		**0,881**		0
Detritus	1,000	1,000	190,000	190,000			**0,603**		0,2

Values not entered as input parameters and therefore estimated by the model are indicated in bold.

Appendix 2: Diet matrix

1996 to 2002 time period (1/3)

	Prey \ predator	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
1	Seabirds																	
2	Whiting	0,016	0,002															
3	Other Fish piscivores	0,059	0,007	0,001								0,005						
4	Fish planktivores	0,022	0,042	0,051								0,002						
5	European Sea Bass		0,009		0,001		0,001											
6	Other Fish benthos feeders		0,244	0,565	0,020	0,033	0,043		0,010			0,046						
7	Common Sole		0,038		0,003							0,001						
8	European Plaice		0,031		0,002													
9	European Flounder		0,138		0,010													
10	Other flatfish				0,005													
11	Cephalopods											0,030						
12	Benthic predators VN	0,003	0,009	0,003		0,012	0,003	0,008	0,006	0,001	0,002	0,002	0,020					
13	Benthic predators FN	0,030	0,084	0,021	0,003	0,111	0,043	0,075	0,055	0,014	0,019	0,030		0,032				
14	Benthic predators VS	0,014	0,039	0,009	0,001	0,052	0,019	0,035	0,026	0,007	0,022	0,012			0,013			
15	Benthic predators FS	0,014	0,037	0,009	0,001	0,049	0,024	0,033	0,024	0,007	0,021	0,015				0,011		
16	Benthic predators CH	0,009	0,027	0,007	0,001	0,035	0,026	0,024	0,017	0,004	0,006							
17	Benthic predators EMB	0,063	0,117	0,030	0,004	0,157	0,163	0,105	0,078	0,020	0,111	0,112						0,023
18	Benthic filter feeders VN	0,009	0,003	0,007		0,003	0,004	0,003	0,028	0,009	0,024	0,001	0,034					
19	Benthic filter feeders FN	0,018	0,006	0,013		0,006	0,009	0,006	0,054	0,016	0,047	0,003		0,032				
20	Benthic filter feeders VS	0,012	0,003	0,009		0,004	0,005	0,004	0,037	0,011	0,022	0,001			0,185			
21	Benthic filter feeders FS	0,027	0,008	0,021		0,010	0,013	0,010	0,083	0,024	0,050	0,004				0,243		
22	Benthic filter feeders CH	0,011	0,004	0,008		0,004	0,005	0,004	0,033	0,010	0,029						0,257	
23	Benthic filter feeders EMB	0,024	0,010	0,026		0,012	0,016	0,012	0,104	0,030	0,038	0,006						0,102
24	Benthic deposit feeders VN				0,001	0,001	0,001	0,004	0,002	0,002	0,002		0,015					
25	Benthic deposit feeders FN	0,012	0,012	0,021	0,021	0,024	0,032	0,133	0,071	0,054	0,069	0,015		0,043				
26	Benthic deposit feeders VS	0,002	0,001	0,003	0,003	0,003	0,004	0,018	0,010	0,006	0,008	0,003			0,020			
27	Benthic deposit feeders FS	0,007	0,006	0,012	0,011	0,014	0,026	0,076	0,041	0,033	0,041	0,010				0,085		
28	Benthic deposit feeders CH	0,001	0,001	0,001	0,001	0,002	0,003	0,008	0,005	0,007	0,004						0,028	
29	Benthic deposit feeders EMB	0,047	0,040	0,056	0,012	0,066	0,212	0,362	0,195	0,280	0,134	0,043						0,249
30	Suprabenthos VN		0,003		0,008	0,019	0,005	0,001	0,003	0,009	0,005	0,001	0,213					
31	Suprabenthos FN		0,019		0,041	0,098	0,027	0,005	0,015	0,044	0,025	0,010		0,204				
32	Suprabenthos VS		0,003		0,008	0,019	0,005	0,001	0,003	0,009	0,004	0,001			0,365			
33	Suprabenthos FS		0,019		0,041	0,098	0,027	0,005	0,015	0,044	0,020	0,010				0,309		
34	Suprabenthos CH		0,009		0,018	0,041	0,011	0,002	0,006	0,018	0,015						0,204	
35	Suprabenthos EMB		0,028		0,055	0,125	0,034	0,007	0,019	0,056	0,048	0,012						0,286
36	Meiofauna VN				0,007			0,010	0,007		0,011	0,006	0,022					
37	Meiofauna FN				0,007			0,010	0,007		0,011	0,006		0,022				
38	Meiofauna VS				0,006			0,009	0,006		0,010	0,004			0,052			
39	Meiofauna FS				0,006			0,009	0,006		0,010	0,004				0,044		
40	Meiofauna CH				0,007			0,010	0,007		0,010						0,284	
41	Meiofauna EMB				0,006			0,009	0,006		0,007	0,004						0,045
42	Zooplankton VN			0,021	0,060		0,012		0,003	0,047	0,003		0,281					
43	Zooplankton FN			0,021	0,060		0,012		0,003	0,047	0,003			0,269				
44	Zooplankton VS			0,022	0,064		0,013		0,003	0,050	0,003				0,091			
45	Zooplankton FS			0,022	0,064		0,013		0,003	0,050	0,003					0,077		
46	Zooplankton CH			0,021	0,060		0,012		0,003	0,047	0,003						0,057	
47	Zooplankton EMB			0,021	0,067		0,012		0,003	0,047	0,003							0,057
48	Bacteria VN																	
49	Bacteria FN																	
50	Bacteria VS																	
51	Bacteria FS																	
52	Bacteria CH																	
53	Bacteria EMB																	
54	Microphytobenthos VN												0,191					
55	Microphytobenthos FN													0,183				
56	Microphytobenthos VS														0,209			
57	Microphytobenthos FS															0,177		
58	Microphytobenthos CH																0,057	
59	Microphytobenthos EMB																	0,068
60	Phytoplankton VN				0,059													
61	Phytoplankton FN				0,059													
62	Phytoplankton VS				0,059													
63	Phytoplankton FS				0,059													
64	Phytoplankton CH				0,059													
65	Phytoplankton EMB				0,019													
66	Detritus						0,163				0,153		0,224	0,215	0,065	0,055	0,113	0,170
67	Import	0,600										0,600						

1996 to 2002 time period (2/3)

	Prey \ predator	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
1	Seabirds																		
2	Whiting																		
3	Other Fish piscivores																		
4	Fish planktivores																		
5	European Sea Bass																		
6	Other Fish benthos feeders																		
7	Common Sole																		
8	European Plaice																		
9	European Flounder																		
10	Other flatfish																		
11	Cephalopods																		
12	Benthic predators VN																		
13	Benthic predators FN																		
14	Benthic predators VS																		
15	Benthic predators FS																		
16	Benthic predators CH																		
17	Benthic predators EMB																		
18	Benthic filter feeders VN																		
19	Benthic filter feeders FN																		
20	Benthic filter feeders VS																		
21	Benthic filter feeders FS																		
22	Benthic filter feeders CH																		
23	Benthic filter feeders EMB																		
24	Benthic deposit feeders VN																		
25	Benthic deposit feeders FN																		
26	Benthic deposit feeders VS																		
27	Benthic deposit feeders FS																		
28	Benthic deposit feeders CH																		
29	Benthic deposit feeders EMB																		
30	Suprabenthos VN													0,049					
31	Suprabenthos FN														0,049				
32	Suprabenthos VS															0,050			
33	Suprabenthos FS																0,050		
34	Suprabenthos CH																	0,100	
35	Suprabenthos EMB																		0,031
36	Meiofauna VN							0,020											
37	Meiofauna FN								0,020										
38	Meiofauna VS			0,020						0,020									
39	Meiofauna FS				0,020						0,020								
40	Meiofauna CH					0,050						0,050							
41	Meiofauna EMB						0,050						0,050						
42	Zooplankton VN	0,200						0,050						0,631					
43	Zooplankton FN		0,200						0,050						0,631				
44	Zooplankton VS			0,130						0,050						0,400			
45	Zooplankton FS				0,130						0,050						0,400		
46	Zooplankton CH					0,100						0,050						0,600	
47	Zooplankton EMB						0,200						0,010						0,316
48	Bacteria VN	0,050						0,040						0,010					
49	Bacteria FN		0,050						0,040						0,010				
50	Bacteria VS									0,040									
51	Bacteria FS										0,040								
52	Bacteria CH					0,050						0,100							
53	Bacteria EMB						0,010						0,050						
54	Microphytobenthos VN	0,050						0,290						0,049					
55	Microphytobenthos FN		0,050						0,290						0,049				
56	Microphytobenthos VS			0,080						0,290						0,220			
57	Microphytobenthos FS				0,080						0,290						0,220		
58	Microphytobenthos CH					0,100						0,200							
59	Microphytobenthos EMB						0,040						0,130						
60	Phytoplankton VN	0,600						0,100											
61	Phytoplankton FN		0,600						0,100										
62	Phytoplankton VS			0,550						0,100									
63	Phytoplankton FS				0,550						0,100								
64	Phytoplankton CH					0,600						0,100							
65	Phytoplankton EMB						0,600						0,110						0,232
66	Detritus	0,100	0,100	0,220	0,220	0,100	0,100	0,500	0,500	0,500	0,500	0,500	0,650	0,262	0,262	0,330	0,330	0,300	0,421
67	Import																		

1996 to 2002 time period (3/3)

	Prey \ predator	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**
1	Seabirds																		
2	Whiting																		
3	Other Fish piscivores																		
4	Fish planktivores																		
5	European Sea Bass																		
6	Other Fish benthos feeders																		
7	Common Sole																		
8	European Plaice																		
9	European Flounder																		
10	Other flatfish																		
11	Cephalopods																		
12	Benthic predators VN																		
13	Benthic predators FN																		
14	Benthic predators VS																		
15	Benthic predators FS																		
16	Benthic predators CH																		
17	Benthic predators EMB																		
18	Benthic filter feeders VN																		
19	Benthic filter feeders FN																		
20	Benthic filter feeders VS																		
21	Benthic filter feeders FS																		
22	Benthic filter feeders CH																		
23	Benthic filter feeders EMB																		
24	Benthic deposit feeders VN																		
25	Benthic deposit feeders FN																		
26	Benthic deposit feeders VS																		
27	Benthic deposit feeders FS																		
28	Benthic deposit feeders CH																		
29	Benthic deposit feeders EMB																		
30	Suprabenthos VN																		
31	Suprabenthos FN																		
32	Suprabenthos VS																		
33	Suprabenthos FS																		
34	Suprabenthos CH																		
35	Suprabenthos EMB																		
36	Meiofauna VN																		
37	Meiofauna FN																		
38	Meiofauna VS																		
39	Meiofauna FS																		
40	Meiofauna CH																		
41	Meiofauna EMB																		
42	Zooplankton VN	0,050																	
43	Zooplankton FN		0,050																
44	Zooplankton VS			0,050															
45	Zooplankton FS				0,050														
46	Zooplankton CH					0,050													
47	Zooplankton EMB						0,050												
48	Bacteria VN	0,050																	
49	Bacteria FN		0,050																
50	Bacteria VS			0,050															
51	Bacteria FS				0,050														
52	Bacteria CH					0,050													
53	Bacteria EMB						0,050												
54	Microphytobenthos VN	0,150						0,150											
55	Microphytobenthos FN		0,150						0,150										
56	Microphytobenthos VS			0,150															
57	Microphytobenthos FS				0,150														
58	Microphytobenthos CH					0,100													
59	Microphytobenthos EMB						0,050												
60	Phytoplankton VN	0,100						0,500											
61	Phytoplankton FN		0,100						0,500						0,200				
62	Phytoplankton VS			0,100						0,650						0,100			
63	Phytoplankton FS				0,100						0,650						0,100		
64	Phytoplankton CH					0,100						0,700						0,200	
65	Phytoplankton EMB						0,100						0,500						0,200
66	Detritus	0,650	0,650	0,650	0,650	0,700	0,750	0,350	0,350	0,350	0,350	0,300	0,500	0,400	0,400	0,520	0,520	0,400	0,400
67	Import													0,400	0,400	0,380	0,380	0,400	0,400

2005 to 2012 time period (1/3)

	Prey \ predator	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
1	Seabirds																	
2	Whiting	0,006	0,001															
3	Other Fish piscivores	0,050	0,008	0,002								0,009						
4	Fish planktivores	0,020	0,040	0,040								0,002						
5	European Sea Bass		0,029		0,002		0,004											
6	Other Fish benthos feeders		0,244	0,343	0,018	0,030	0,020		0,009			0,027						
7	Common Sole		0,054		0,004							0,001						
8	European Plaice		0,075		0,005							0,001						
9	European Flounder		0,018		0,001													
10	Other flatfish				0,010							0,001						
11	Cephalopods											0,032						
12	Benthic predators VN	0,006	0,017	0,006		0,021	0,014	0,014	0,010	0,002	0,003	0,010	0,100					
13	Benthic predators FN	0,016	0,047	0,017	0,001	0,058	0,040	0,039	0,029	0,007	0,010	0,028		0,123				
14	Benthic predators VS	0,015	0,043	0,017	0,001	0,053	0,037	0,036	0,026	0,006	0,022	0,026			0,021			
15	Benthic predators FS	0,015	0,045	0,017	0,001	0,055	0,038	0,037	0,027	0,007	0,023	0,028				0,021		
16	Benthic predators CH	0,007	0,019	0,008	0,001	0,025	0,016	0,016	0,012	0,003	0,004							
17	Benthic predators EMB	0,086	0,167	0,063	0,005	0,205	0,140	0,138	0,101	0,024	0,140	0,101						0,048
18	Benthic filter feeders VN	0,010	0,004	0,013		0,004	0,005	0,004	0,031	0,008	0,025	0,001	0,030					
19	Benthic filter feeders FN	0,019	0,006	0,021		0,006	0,008	0,006	0,053	0,014	0,044	0,003		0,037				
20	Benthic filter feeders VS	0,017	0,006	0,021		0,006	0,008	0,006	0,052	0,014	0,029	0,003			0,244			
21	Benthic filter feeders FS	0,026	0,007	0,029		0,009	0,011	0,009	0,073	0,020	0,042	0,004				0,248		
22	Benthic filter feeders CH	0,005	0,002	0,004		0,002	0,002	0,002	0,013	0,003	0,011						0,134	
23	Benthic filter feeders EMB	0,028	0,012	0,046		0,014	0,017	0,014	0,119	0,032	0,041	0,007						0,145
24	Benthic deposit feeders VN	0,006	0,006	0,017	0,010	0,012	0,034	0,064	0,034	0,046	0,032	0,007	0,040					
25	Benthic deposit feeders FN	0,006	0,006	0,017	0,010	0,012	0,034	0,064	0,034	0,046	0,032	0,007		0,049				
26	Benthic deposit feeders VS	0,007	0,006	0,019	0,011	0,014	0,040	0,076	0,041	0,055	0,038	0,010			0,105			
27	Benthic deposit feeders FS	0,006	0,005	0,015	0,009	0,012	0,034	0,063	0,034	0,045	0,032	0,007				0,106		
28	Benthic deposit feeders CH	0,010	0,006	0,013	0,008	0,009	0,027	0,052	0,028	0,037	0,021						0,152	
29	Benthic deposit feeders EMB	0,038	0,034	0,069	0,009	0,052	0,148	0,281	0,153	0,201	0,101	0,035						0,147
30	Suprabenthos VN		0,002		0,005	0,011	0,003	0,001	0,002	0,005	0,003	0,001	0,190					
31	Suprabenthos FN		0,012		0,025	0,058	0,014	0,003	0,009	0,024	0,014	0,006		0,007				
32	Suprabenthos VS		0,002		0,005	0,011	0,003	0,001	0,002	0,005	0,002	0,001			0,294			
33	Suprabenthos FS		0,012		0,025	0,058	0,014	0,003	0,009	0,024	0,012	0,006				0,284		
34	Suprabenthos CH		0,052		0,091	0,215	0,055	0,012	0,032	0,090	0,079						0,113	
35	Suprabenthos EMB		0,012		0,020	0,048	0,012	0,003	0,007	0,020	0,018	0,004						0,003
36	Meiofauna VN				0,007			0,010	0,007		0,011	0,006	0,020					
37	Meiofauna FN				0,007			0,010	0,007		0,011	0,006		0,025				
38	Meiofauna VS				0,006			0,009	0,006		0,010	0,004			0,042			
39	Meiofauna FS				0,006			0,009	0,006		0,010	0,004				0,043		
40	Meiofauna CH				0,007			0,010	0,007		0,010						0,335	
41	Meiofauna EMB				0,006			0,009	0,006		0,007	0,004						0,024
42	Zooplankton VN			0,033	0,059		0,011		0,003	0,043	0,003		0,250					
43	Zooplankton FN			0,033	0,059		0,011		0,003	0,043	0,003			0,307				
44	Zooplankton VS			0,036	0,063		0,012		0,003	0,046	0,003				0,073			
45	Zooplankton FS			0,036	0,063		0,012		0,003	0,046	0,003					0,075		
46	Zooplankton CH			0,033	0,059		0,011		0,003	0,043	0,003						0,067	
47	Zooplankton EMB			0,033	0,067		0,011		0,003	0,043	0,003							0,119
48	Bacteria VN																	
49	Bacteria FN																	
50	Bacteria VS																	
51	Bacteria FS																	
52	Bacteria CH																	
53	Bacteria EMB																	
54	Microphytobenthos VN												0,170					
55	Microphytobenthos FN													0,209				
56	Microphytobenthos VS														0,168			
57	Microphytobenthos FS															0,170		
58	Microphytobenthos CH																0,067	
59	Microphytobenthos EMB																	0,157
60	Phytoplankton VN				0,055													
61	Phytoplankton FN				0,055													
62	Phytoplankton VS				0,055													
63	Phytoplankton FS				0,055													
64	Phytoplankton CH				0,055													
65	Phytoplankton EMB				0,033													
66	Detritus						0,152				0,146		0,200	0,245	0,052	0,053	0,134	0,357
67	Import	0,600										0,600						

2005 to 2012 time period (2/3)

	Prey \ predator	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**
1	Seabirds																		
2	Whiting																		
3	Other Fish piscivores																		
4	Fish planktivores																		
5	European Sea Bass																		
6	Other Fish benthos feeders																		
7	Common Sole																		
8	European Plaice																		
9	European Flounder																		
10	Other flatfish																		
11	Cephalopods																		
12	Benthic predators VN																		
13	Benthic predators FN																		
14	Benthic predators VS																		
15	Benthic predators FS																		
16	Benthic predators CH																		
17	Benthic predators EMB																		
18	Benthic filter feeders VN																		
19	Benthic filter feeders FN																		
20	Benthic filter feeders VS																		
21	Benthic filter feeders FS																		
22	Benthic filter feeders CH																		
23	Benthic filter feeders EMB																		
24	Benthic deposit feeders VN																		
25	Benthic deposit feeders FN																		
26	Benthic deposit feeders VS																		
27	Benthic deposit feeders FS																		
28	Benthic deposit feeders CH																		
29	Benthic deposit feeders EMB																		
30	Suprabenthos VN													0,021					
31	Suprabenthos FN														0,021				
32	Suprabenthos VS															0,021			
33	Suprabenthos FS																0,021		
34	Suprabenthos CH																	0,020	
35	Suprabenthos EMB																		0,021
36	Meiofauna VN							0,020											
37	Meiofauna FN								0,020										
38	Meiofauna VS			0,020						0,020									
39	Meiofauna FS				0,020						0,020								
40	Meiofauna CH					0,050						0,050							
41	Meiofauna EMB						0,021						0,021						
42	Zooplankton VN	0,200						0,050						0,650					
43	Zooplankton FN		0,200						0,050						0,650				
44	Zooplankton VS			0,130						0,050						0,412			
45	Zooplankton FS				0,130						0,050						0,412		
46	Zooplankton CH					0,100						0,050						0,653	
47	Zooplankton EMB						0,206						0,010						0,319
48	Bacteria VN	0,050						0,040						0,010					
49	Bacteria FN		0,050						0,040						0,010				
50	Bacteria VS									0,040									
51	Bacteria FS										0,040								
52	Bacteria CH					0,050						0,100							
53	Bacteria EMB						0,010						0,052						
54	Microphytobenthos VN	0,050						0,290						0,050					
55	Microphytobenthos FN		0,050						0,290						0,050				
56	Microphytobenthos VS			0,080						0,290						0,227			
57	Microphytobenthos FS				0,080						0,290						0,227		
58	Microphytobenthos CH					0,100						0,200							
59	Microphytobenthos EMB						0,041						0,134						
60	Phytoplankton VN	0,600						0,100											
61	Phytoplankton FN		0,600						0,100										
62	Phytoplankton VS			0,550						0,100									
63	Phytoplankton FS				0,550						0,100								
64	Phytoplankton CH					0,600						0,100							
65	Phytoplankton EMB						0,618						0,113						0,234
66	Detritus	0,100	0,100	0,220	0,220	0,100	0,103	0,500	0,500	0,500	0,500	0,500	0,670	0,270	0,270	0,340	0,340	0,327	0,426
67	Import																		

2005 to 2012 time period (3/3)

	Prey \ predator	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**
1	Seabirds																		
2	Whiting																		
3	Other Fish piscivores																		
4	Fish planktivores																		
5	European Sea Bass																		
6	Other Fish benthos feeders																		
7	Common Sole																		
8	European Plaice																		
9	European Flounder																		
10	Other flatfish																		
11	Cephalopods																		
12	Benthic predators VN																		
13	Benthic predators FN																		
14	Benthic predators VS																		
15	Benthic predators FS																		
16	Benthic predators CH																		
17	Benthic predators EMB																		
18	Benthic filter feeders VN																		
19	Benthic filter feeders FN																		
20	Benthic filter feeders VS																		
21	Benthic filter feeders FS																		
22	Benthic filter feeders CH																		
23	Benthic filter feeders EMB																		
24	Benthic deposit feeders VN																		
25	Benthic deposit feeders FN																		
26	Benthic deposit feeders VS																		
27	Benthic deposit feeders FS																		
28	Benthic deposit feeders CH																		
29	Benthic deposit feeders EMB																		
30	Suprabenthos VN																		
31	Suprabenthos FN																		
32	Suprabenthos VS																		
33	Suprabenthos FS																		
34	Suprabenthos CH																		
35	Suprabenthos EMB																		
36	Meiofauna VN																		
37	Meiofauna FN																		
38	Meiofauna VS																		
39	Meiofauna FS																		
40	Meiofauna CH																		
41	Meiofauna EMB																		
42	Zooplankton VN	0,050																	
43	Zooplankton FN		0,050																
44	Zooplankton VS			0,050															
45	Zooplankton FS				0,050														
46	Zooplankton CH					0,050													
47	Zooplankton EMB						0,050												
48	Bacteria VN	0,050																	
49	Bacteria FN		0,050																
50	Bacteria VS			0,050															
51	Bacteria FS				0,050														
52	Bacteria CH					0,050													
53	Bacteria EMB						0,050												
54	Microphytobenthos VN	0,150						0,141											
55	Microphytobenthos FN		0,150						0,133										
56	Microphytobenthos VS			0,150															
57	Microphytobenthos FS				0,150														
58	Microphytobenthos CH					0,100													
59	Microphytobenthos EMB						0,050												
60	Phytoplankton VN	0,100						0,505						0,2					
61	Phytoplankton FN		0,100						0,510						0,200				
62	Phytoplankton VS			0,100						0,650						0,100			
63	Phytoplankton FS				0,100						0,650						0,100		
64	Phytoplankton CH					0,100						0,680						0,200	
65	Phytoplankton EMB						0,100						0,500						0,200
66	Detritus	0,650	0,650	0,650	0,650	0,700	0,750	0,354	0,357	0,350	0,350	0,320	0,500	0,400	0,400	0,520	0,520	0,400	0,400
67	Import													0,400	0,400	0,380	0,380	0,400	0,400

Appendix 3: General species composition per functional group

Group	Composition
SBD Seabirds	Mainly gulls, kittiwakes, gannets and auks
WHI Whiting	Merlangius merlangius
FPI Other fish piscivores	Gadidae, *Scyliorhinus canicula, Scomber scombrus, Zeus faber*
FPV Fish planktivores	Clupeidae, Engraulidae, *Atherina presbyter*
SBA European Seabass	*Dicentrarchus labrax*
FBF Other fish benthos feeders	Rays, Eels, Blenniidae, Gobiidae, Triglidae
SOL Common Sole	*Solea solea*
PLA European Plaice	*Pleuronectes platessa*
FLO European Flounder	*Platichthys flesus*
FLA Other flatfishes	Mainly *Psetta maxima, limanda limanda*
CEP Cephalopods	*Alloteuthis, Loliginidae, Sepia officinalis, Sepiola* spp.
IPR Benthic predators	Mainly echinoderms (*Asteridae* and *Ophiuridae*) and mollusc gastropods
IFF Benthic filter feeders	Mainly *Acanthicardia* spp., *Actinia* spp., *Cerastoderma edule, Mya* spp., *Mytilus edulis,* and Pectinidae
IDF Benthic deposit feeders	Mainly *Abra alba*, *Buccinum undatum*, annelids, and echinoderms (*Echinocardium cordatum*, *Thyone fusus*)
SUP Suprabenthos	Crustacean decapods (dominated by *Crangon crangon*), amphipods, mysidiacea, cumacea
MEI Meiofauna	Mosly nematodes
ZOO Zooplankton	-
BAC Bacteria	-
MPB Microphytobenthos	-
PHY Phytoplankton	-
DET Detritus	-

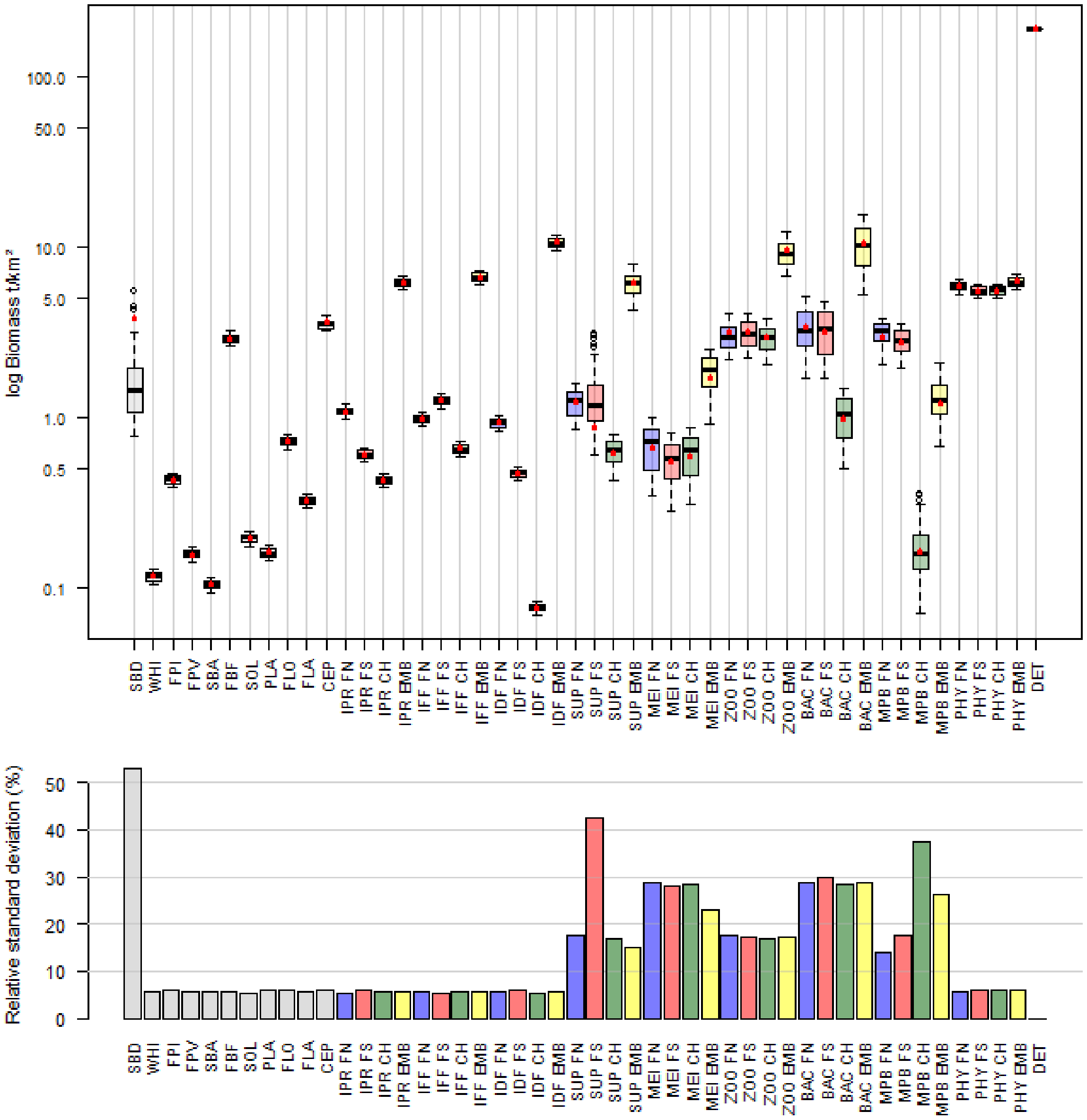
Appendix 4: Model pedigree

The pedigree index is given as an uncertainty rate around the mean value. The parameters estimated by the models are indicated in grey.

Functional group	Biomass in habitat area	P/B	Q/B	Diet
1 Seabirds	0,8	0,5	0	0,6
2 Whiting	0,1	0,4	0,4	0,3
3 Other Fish piscivores	0,1	0,3	0,3	0,3
4 Fish planktivores	0,1	0,3	0,3	0,3
5 European Sea Bass	0,1	0,3	0,3	0,3
6 Other Fish benthos feeders	0,1	0,3	0	0,3
7 Common Sole	0,1	0,4	0,4	0,3
8 European Plaice	0,1	0,4	0,4	0,3
9 European Flounder	0,1	0,3	0,3	0,3
10 Other flatfish	0,1	0,3	0,3	0,3
11 Cephalopods	0,1	0,4	0	0,5
12 Benthic predators VN	0,1	0,6	0	0,3
13 Benthic predators FN	0,1	0,6	0	0,3
14 Benthic predators VS	0,1	0,6	0	0,3
15 Benthic predators FS	0,1	0,6	0	0,3
16 Benthic predators CH	0,1	0,6	0	0,3
17 Benthic predators EMB	0,1	0,6	0	0,3
18 Benthic filter feeders VN	0,1	0,6	0	0,3
19 Benthic filter feeders FN	0,1	0,6	0	0,3
20 Benthic filter feeders VS	0,1	0,6	0	0,3
21 Benthic filter feeders FS	0,1	0,6	0	0,3
22 Benthic filter feeders CH	0,1	0,6	0	0,3
23 Benthic filter feeders EMB	0,1	0,6	0	0,3
24 Benthic deposit feeders VN	0,1	0,6	0	0,3
25 Benthic deposit feeders FN	0,1	0,6	0	0,3
26 Benthic deposit feeders VS	0,1	0,6	0	0,3
27 Benthic deposit feeders FS	0,1	0,6	0	0,3
28 Benthic deposit feeders CH	0,1	0,6	0	0,3
29 Benthic deposit feeders EMB	0,1	0,6	0	0,3
30 Suprabenthos VN	0,3	0,5	0	0,5
31 Suprabenthos FN	0,3	0,5	0	0,5
32 Suprabenthos VS	0	0,5	0	0,5
33 Suprabenthos FS	0	0,5	0	0,5
34 Suprabenthos CH	0,3	0,5	0	0,5
35 Suprabenthos EMB	0,3	0,5	0	0,5
36 Meiofauna VN	0,5	0,5	0	0,6
37 Meiofauna FN	0,5	0,5	0	0,6
38 Meiofauna VS	0,5	0,5	0	0,6
39 Meiofauna FS	0,5	0,5	0	0,6
40 Meiofauna CH	0,5	0,5	0	0,6
41 Meiofauna EMB	0,5	0,5	0	0,6
42 Zooplankton VN	0,3	0	0,3	0,5
43 Zooplankton FN	0,3	0	0,3	0,5
44 Zooplankton VS	0,3	0	0,3	0,5
45 Zooplankton FS	0,3	0	0,3	0,5
46 Zooplankton CH	0,3	0	0,3	0,5
47 Zooplankton EMB	0,3	0	0,3	0,5
48 Bacteria VN	0,5	0,4	0	0,6
49 Bacteria FN	0,5	0,4	0	0,6
50 Bacteria VS	0,5	0,4	0	0,6
51 Bacteria FS	0,5	0,4	0	0,6
52 Bacteria CH	0,5	0,4	0	0,6
53 Bacteria EMB	0,5	0,4	0	0,6
54 Microphytobenthos VN	0,3	0,3		
55 Microphytobenthos FN	0,3	0,3		
56 Microphytobenthos VS	0,3	0,3		
57 Microphytobenthos FS	0,3	0,3		
58 Microphytobenthos CH	0	0,3		
59 Microphytobenthos EMB	0	0,3		
60 Phytoplankton VN	0,1	0,6		
61 Phytoplankton FN	0,1	0,6		
62 Phytoplankton VS	0,1	0,6		
63 Phytoplankton FS	0,1	0,6		
64 Phytoplankton CH	0,1	0,6		
65 Phytoplankton EMB	0,1	0,6		
66 Detritus				

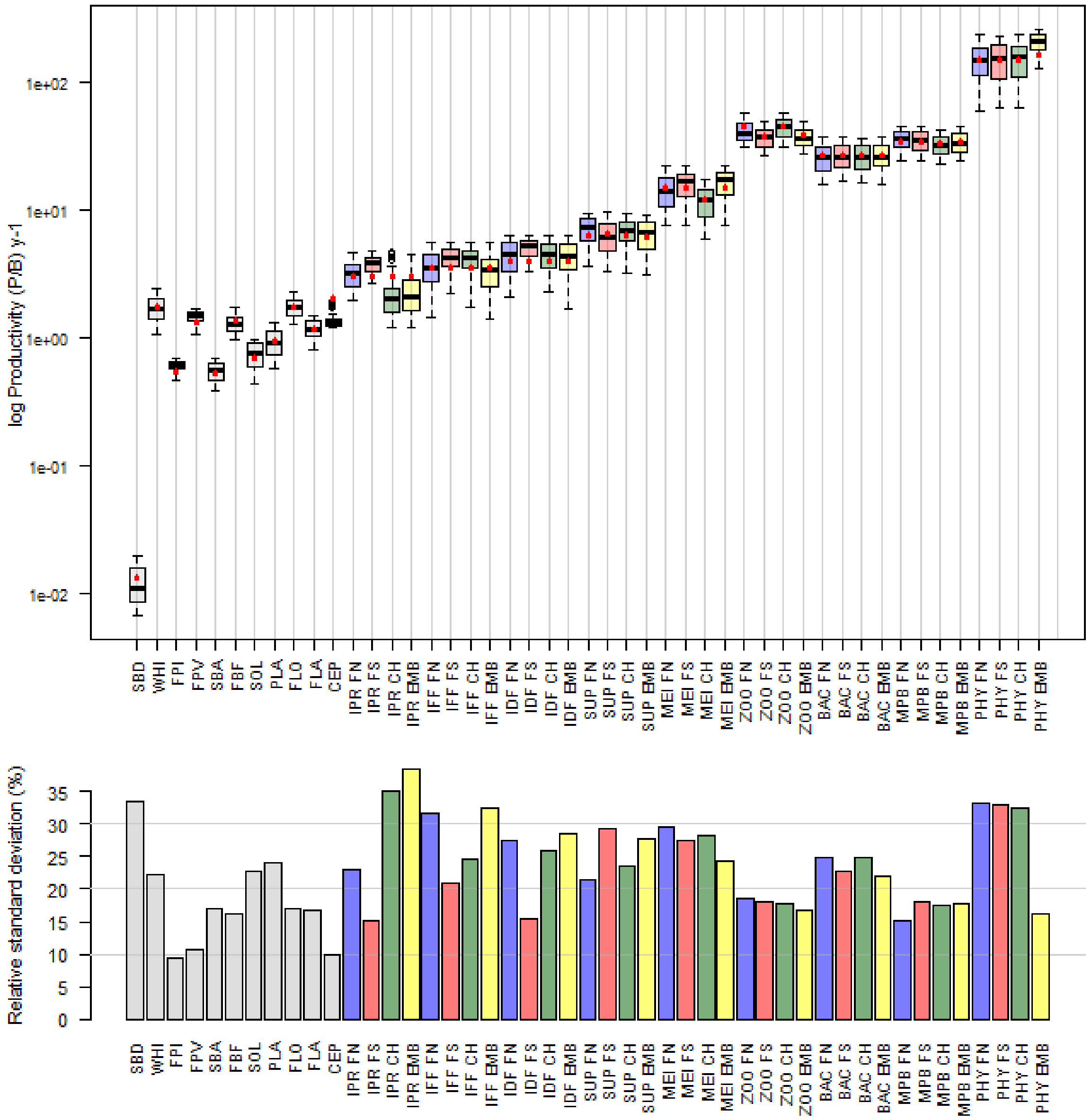
Appendix 5: ENAtool outputs for Ecopath output parameters

1996 to 2002 time period – Biomass



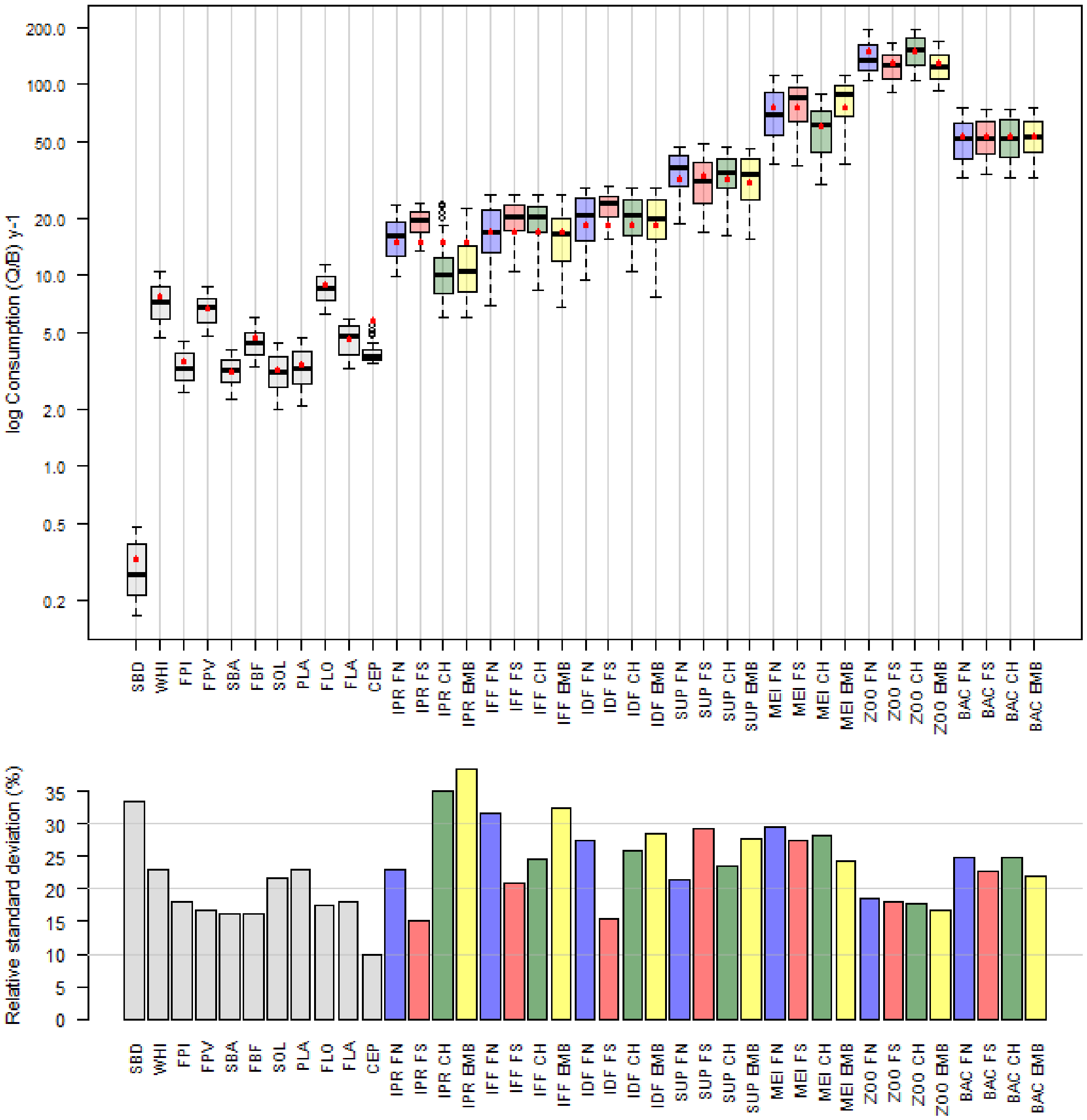
Mobile groups are represented in grey, the aggregated Northern intertidal and subtidal area in blue, the aggregated Southern intertidal and subtidal area in red, the navigation channel in green and the estuary mouth in yellow.

1996 to 2002 time period – Production over biomass rate



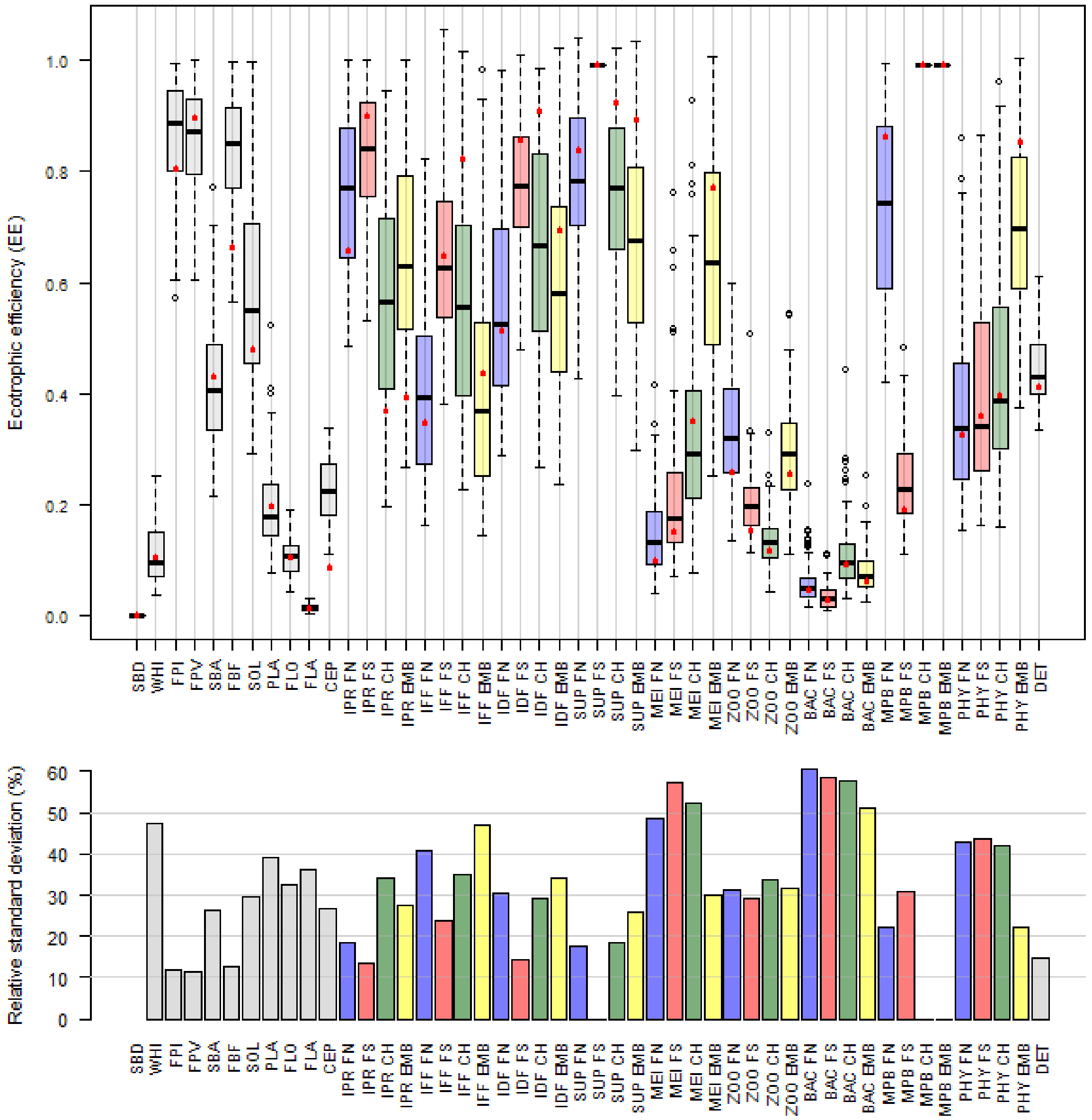
Mobile groups are represented in grey, the aggregated Northern intertidal and subtidal area in blue, the aggregated Southern intertidal and subtidal area in red, the navigation channel in green and the estuary mouth in yellow.

1996 to 2002 time period – Consumption over biomass rate



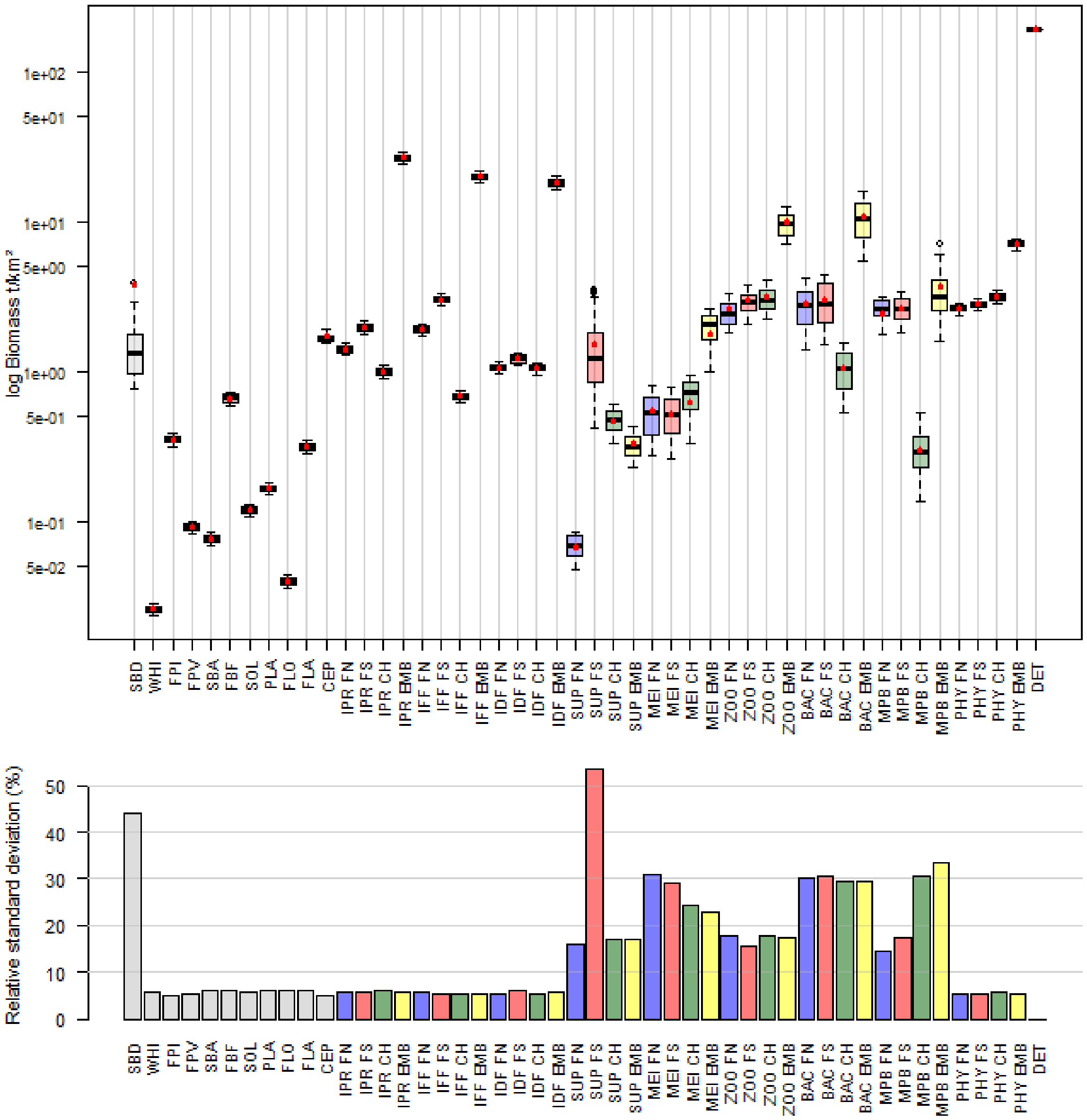
Mobile groups are represented in grey, the aggregated Northern intertidal and subtidal area in blue, the aggregated Southern intertidal and subtidal area in red, the navigation channel in green and the estuary mouth in yellow.

1996 to 2002 time period – Ecotrophic efficiency



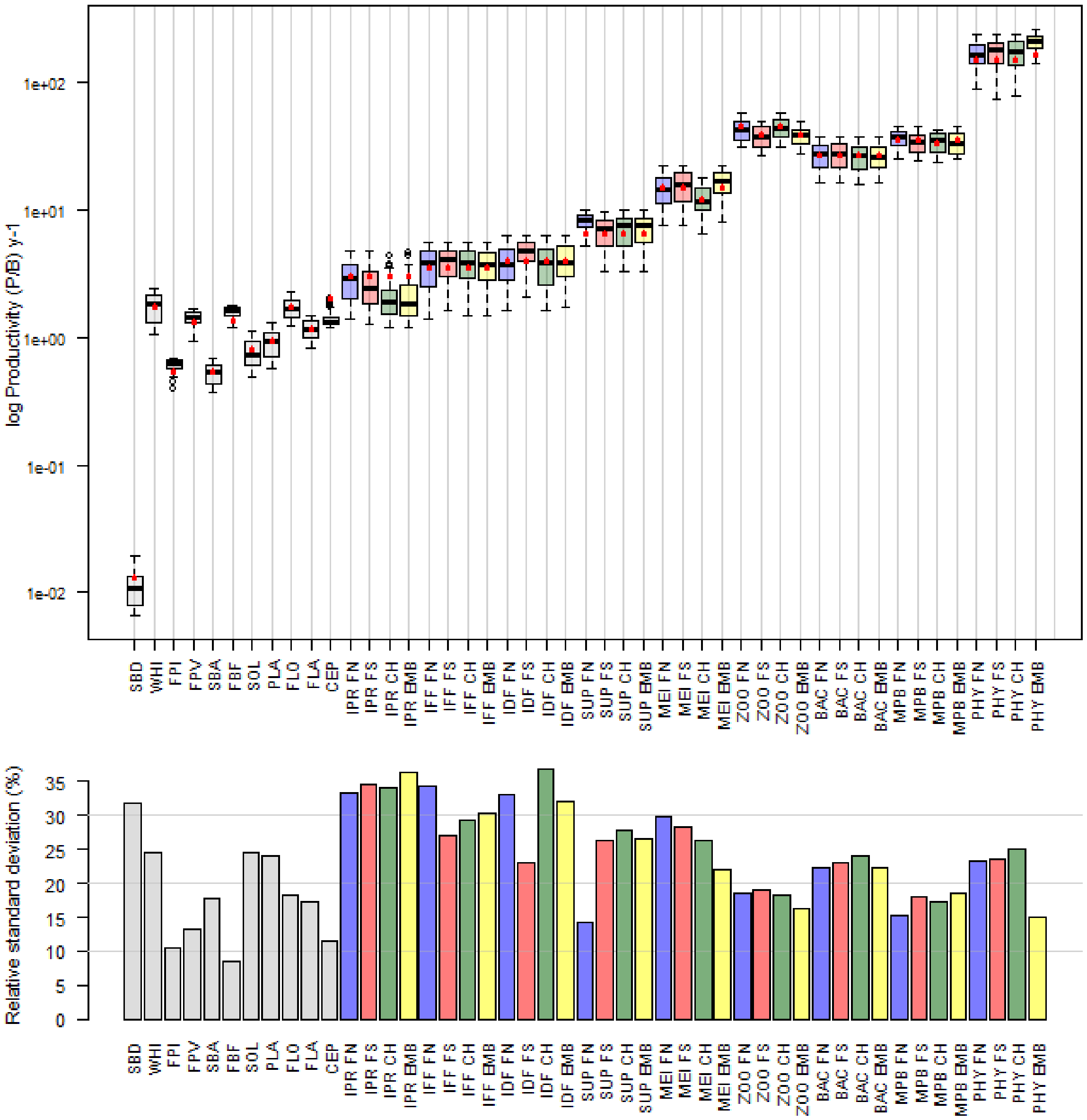
Mobile groups are represented in grey, the aggregated Northern intertidal and subtidal area in blue, the aggregated Southern intertidal and subtidal area in red, the navigation channel in green and the estuary mouth in yellow.

2005 to 2012 time period – Biomass



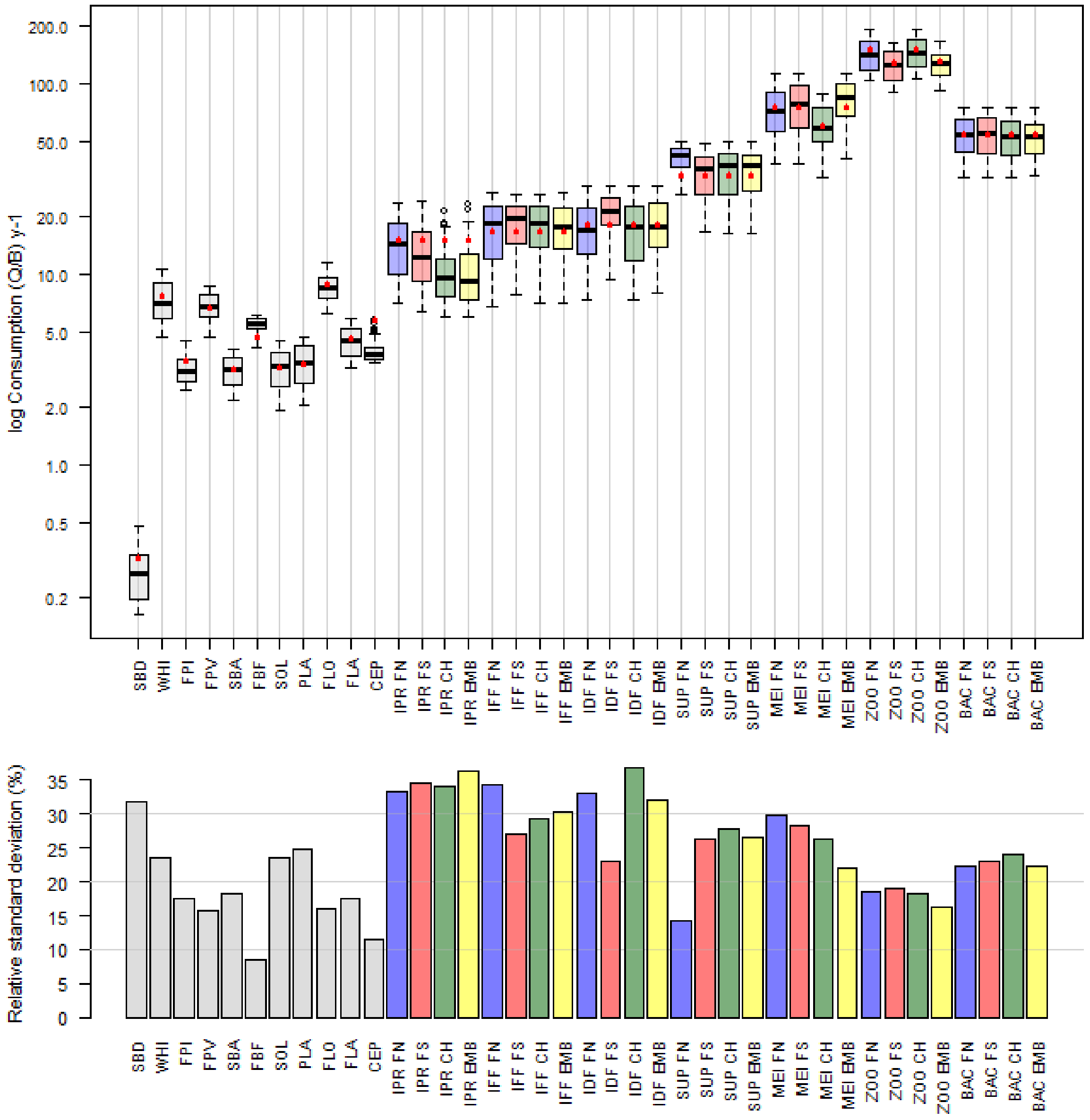
Mobile groups are represented in grey, the aggregated Northern intertidal and subtidal area in blue, the aggregated Southern intertidal and subtidal area in red, the navigation channel in green and the estuary mouth in yellow.

2005 to 2012 time period – Production over biomass rate



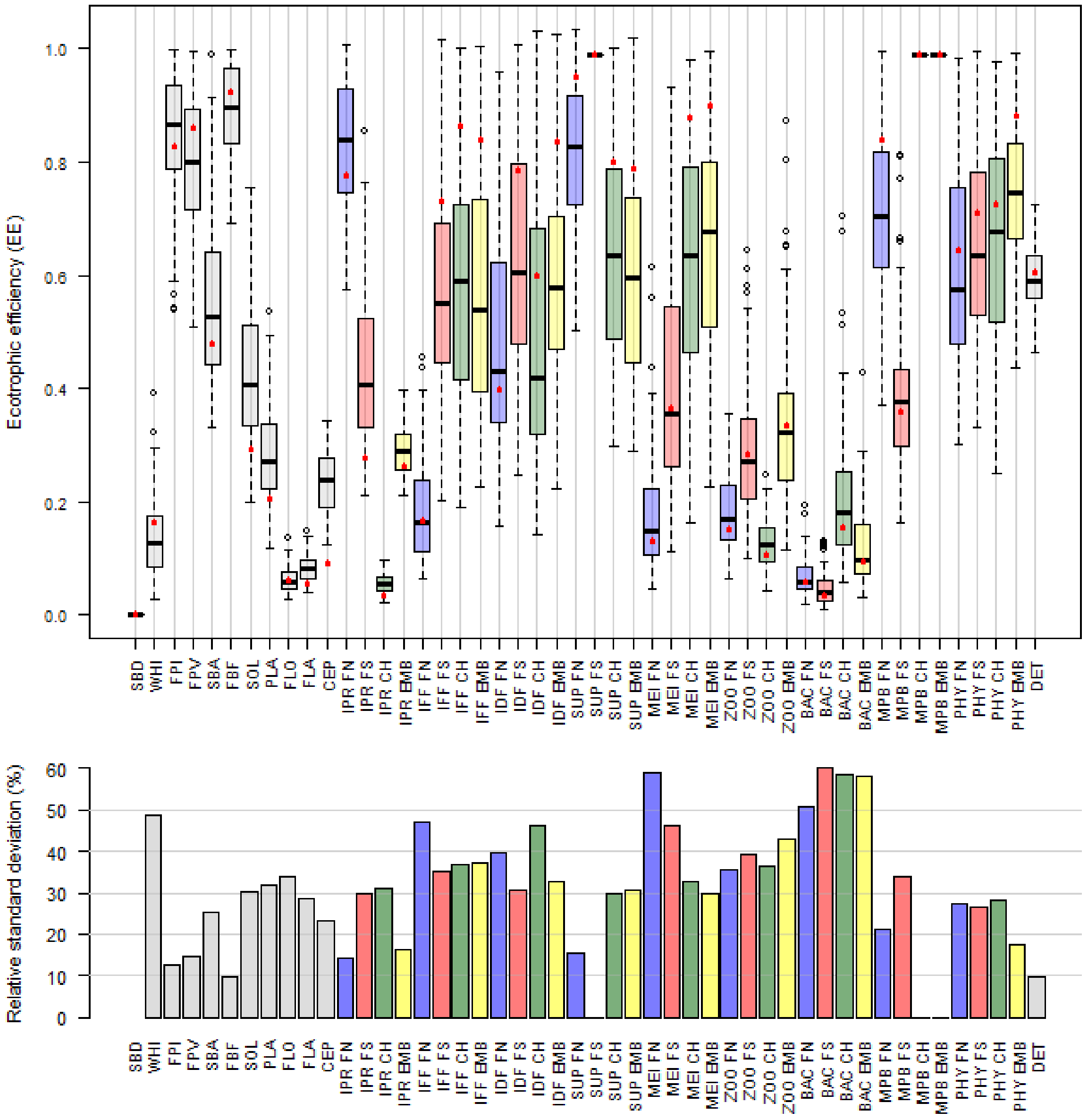
Mobile groups are represented in grey, the aggregated Northern intertidal and subtidal area in blue, the aggregated Southern intertidal and subtidal area in red, the navigation channel in green and the estuary mouth in yellow.

2005 to 2012 time period – Consumption over biomass rate



Mobile groups are represented in grey, the aggregated Northern intertidal and subtidal area in blue, the aggregated Southern intertidal and subtidal area in red, the navigation channel in green and the estuary mouth in yellow.

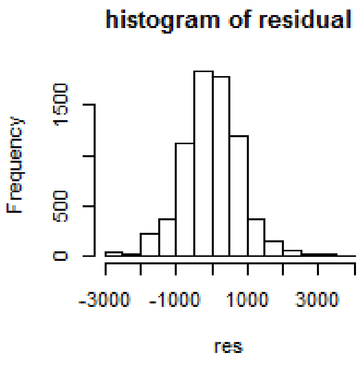
2005 to 2012 time period – Ecotrophic efficiency

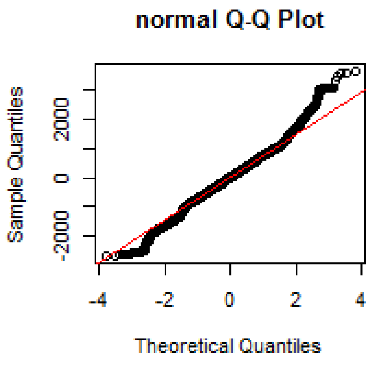


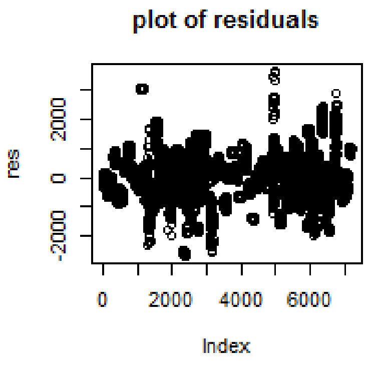
Mobile groups are represented in grey, the aggregated Northern intertidal and subtidal area in blue, the aggregated Southern intertidal and subtidal area in red, the navigation channel in green and the estuary mouth in yellow.

ANOVA and Tukey test results for the uncertainty assessment on biomass

```
> res<-aov(b.all ~ grp + hab + per + (grp*hab) + (grp*per) + (hab*per), data=b.all)
> anova(res)
Analysis of Variance Table

Response: b.all
            Df     Sum Sq    Mean Sq  F value    Pr(>F)    
grp          8 1.1355e+10 1419418871 2182.003 < 2.2e-16 ***
hab          3 6.0776e+09 2025869428 3114.270 < 2.2e-16 ***
per          1 2.5761e+07   25761124   39.601 3.299e-10 ***
grp:hab     24 4.0024e+09  166764790  256.359 < 2.2e-16 ***
grp:per      8 1.5146e+09  189320805  291.034 < 2.2e-16 ***
hab:per      3 5.3187e+08  177289394  272.538 < 2.2e-16 ***
Residuals 7152 4.6525e+09     650512                       
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> summary(glht(res,linfct=mcp(hab="Tukey")))

         Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts


Fit: aov(formula = b.all ~ grp + hab + per + (grp * hab) + (grp * 
    per) + (hab * per), data = b.all)

Linear Hypotheses:
              Estimate Std. Error t value Pr(>|t|)    
EMB - CH == 0  2123.04      85.02  24.972   <1e-05 ***
FN - CH == 0   2189.33      85.02  25.752   <1e-05 ***
FS - CH == 0   2718.68      85.02  31.978   <1e-05 ***
FN - EMB == 0    66.28      85.02   0.780    0.864    
FS - EMB == 0   595.64      85.02   7.006   <1e-05 ***
FS - FN == 0    529.35      85.02   6.226   <1e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- single-step method)
```

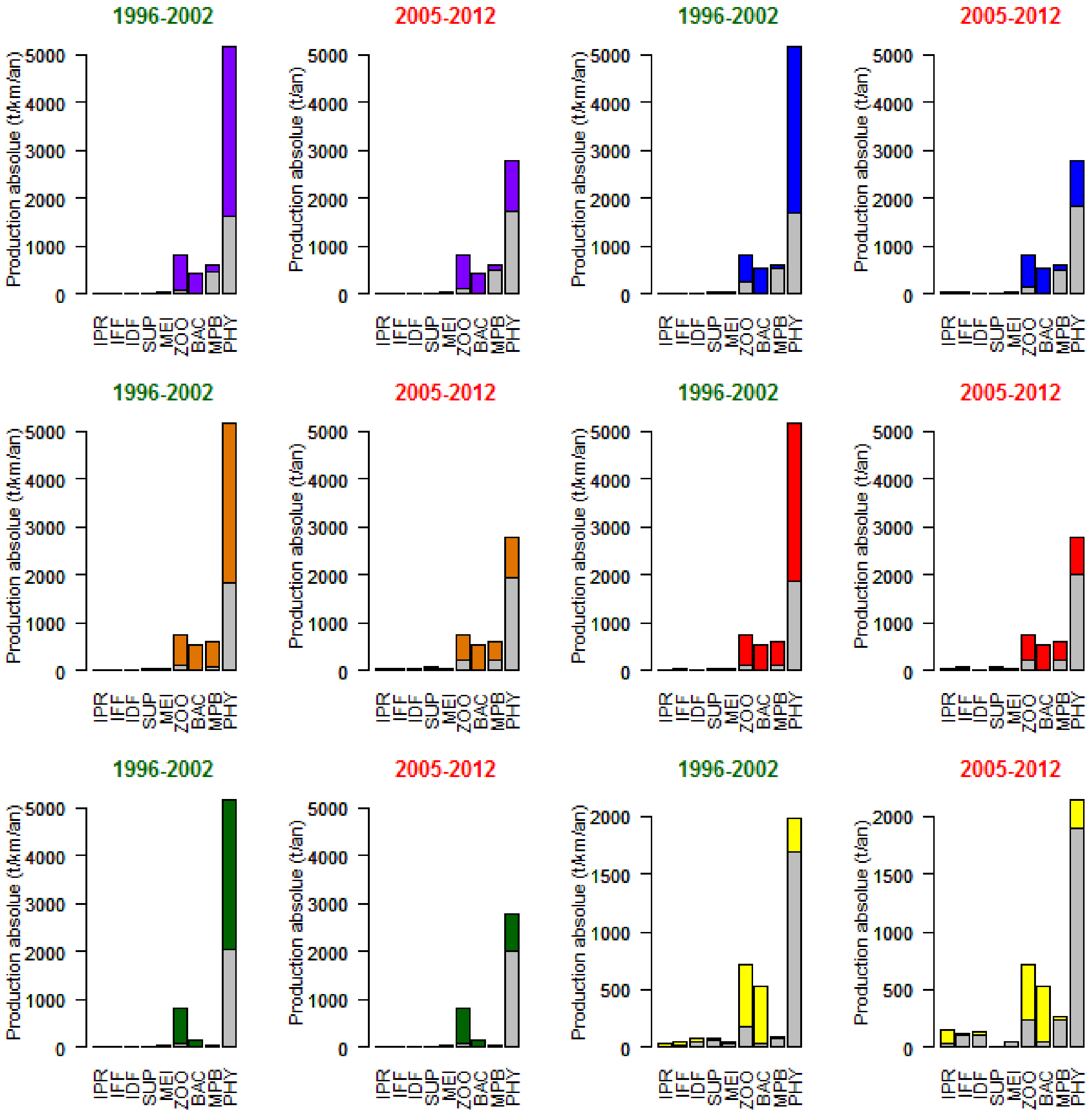

histogram of residual


normal Q-Q Plot


plot of residuals

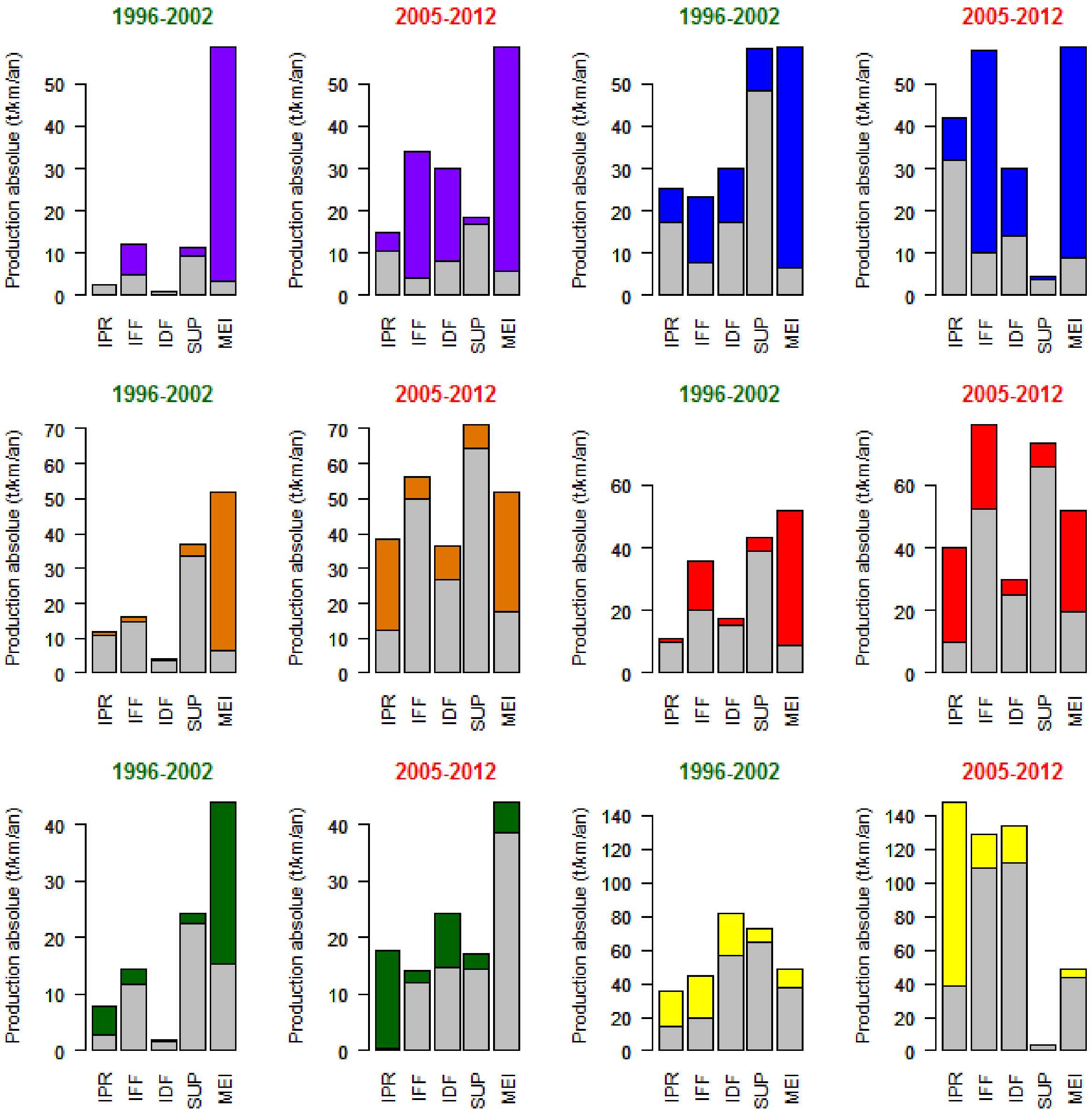
The residual distribution seams to follow a normal distribution regarding of the histogram and the Q-Q plot. However, the Q-Q plot shows a deviation compared to a normal distribution for high values. Finally, the residuals are equally and relatively homogeneously distributed between positive and negative values as shown in the residual plot.

Appendix 6: Detailed production per functional group



The habitats are represented as following: VN (violet), FN (blue), VS (orange), FS (red), CH (green), EMB (yellow). The grey represents the consumed part of the production = P x EE

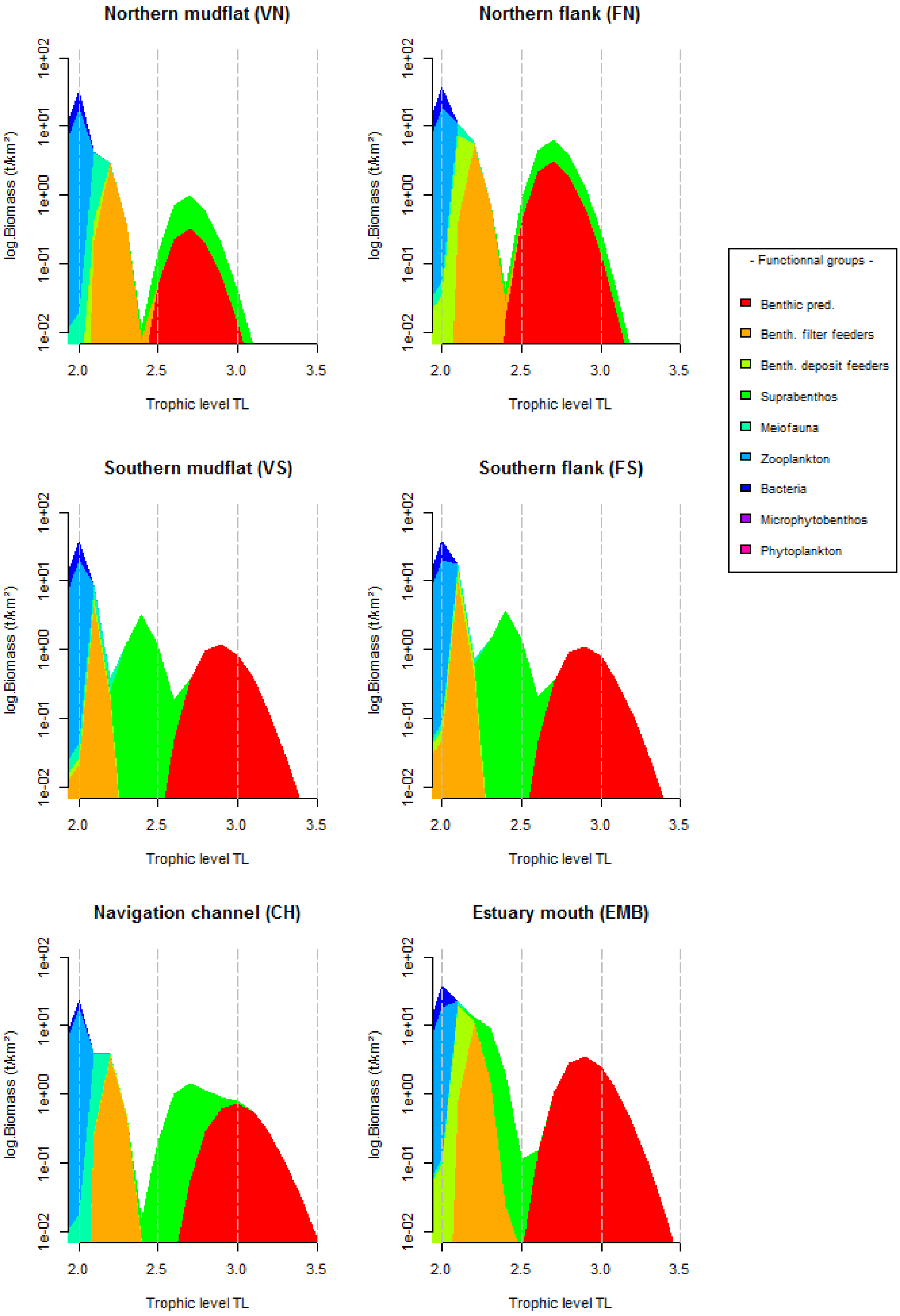
Details on the benthic compartments



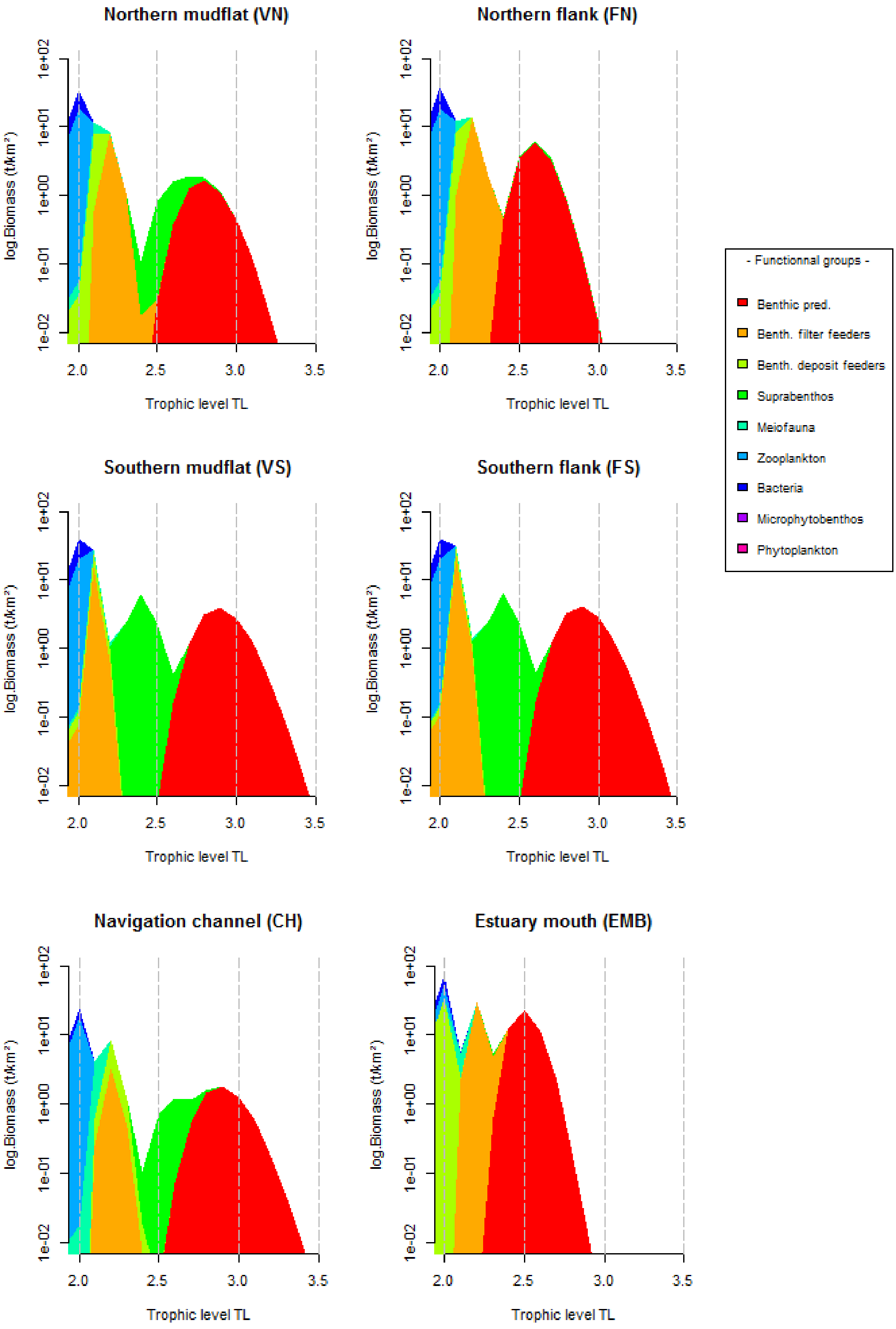
The habitats are represented as following: VN (violet), FN (blue), VS (orange), FS (red), CH (green), EMB (yellow). The grey represents the consumed part of the production = P x EE

Appendix 7: Detailed trophic spectra per habitat

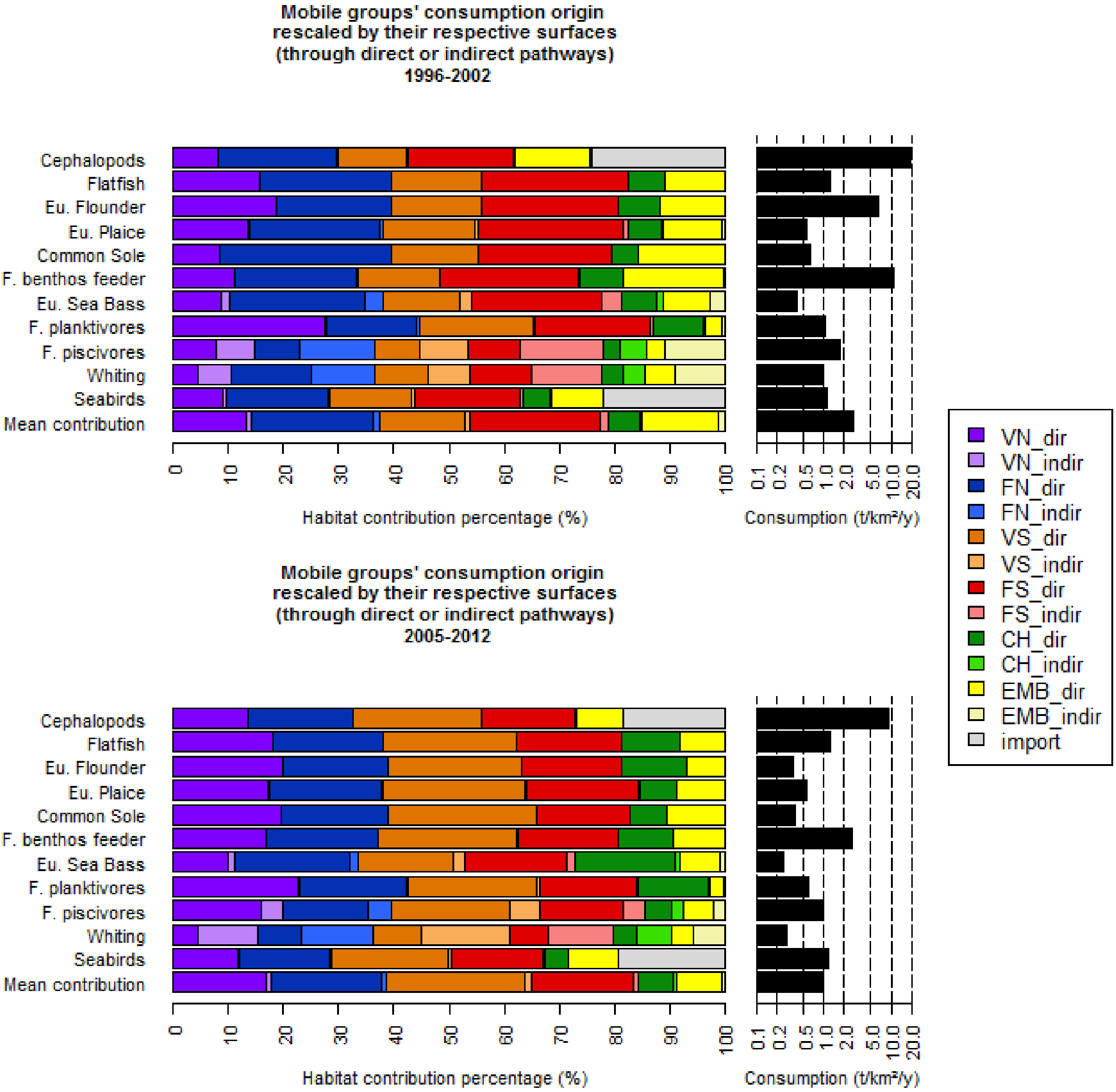
1996 to 2002 time period



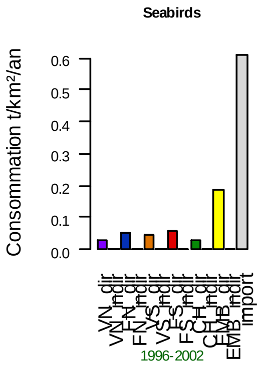
2005 to 2012 time period

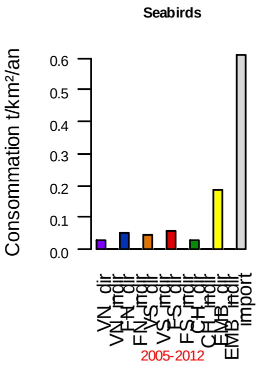


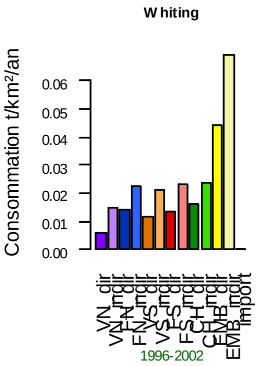
Appendix 8: Contribution to the mobile groups' consumption rescaled by each habitats' surface

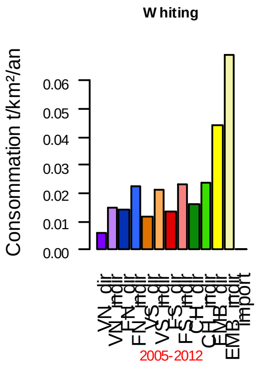


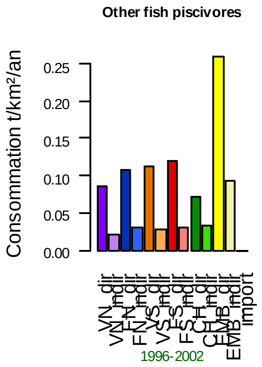
Appendix 9: Absolute consumption per mobile group

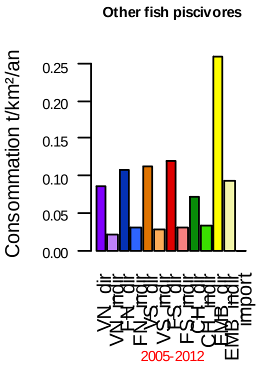

Seabirds

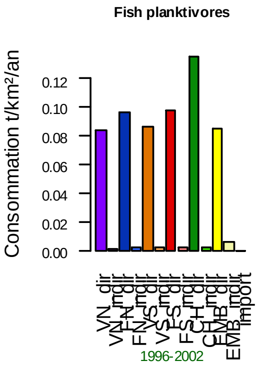

Seabirds

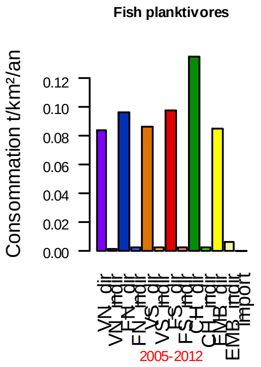

Whiting

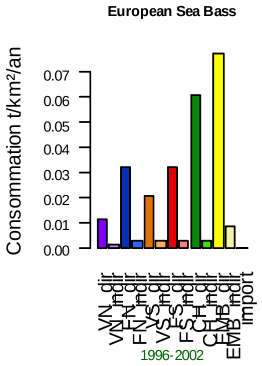

Whiting

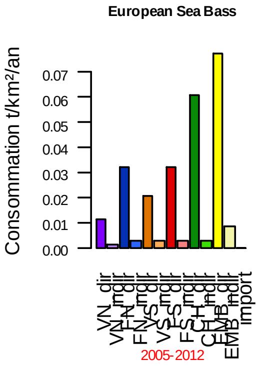

Other fish piscivores

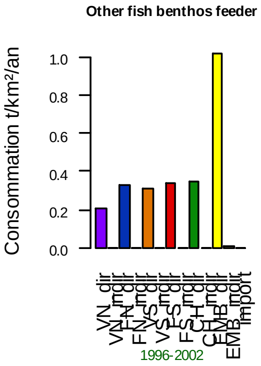

Other fish piscivores

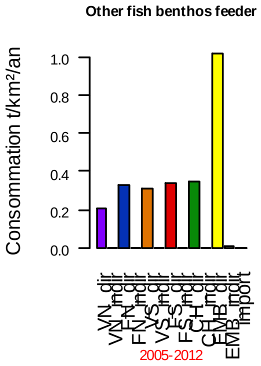

Fish planktivores

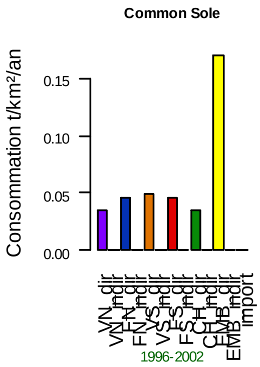

Fish planktivores

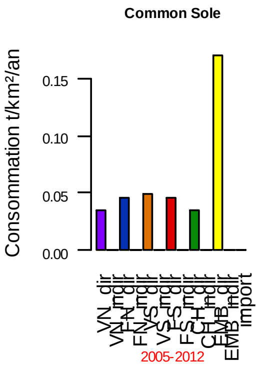

European Sea Bass

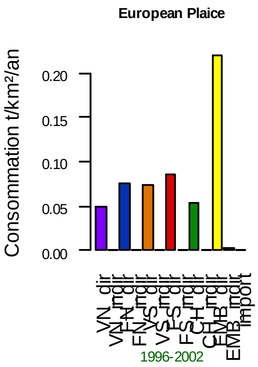

European Sea Bass

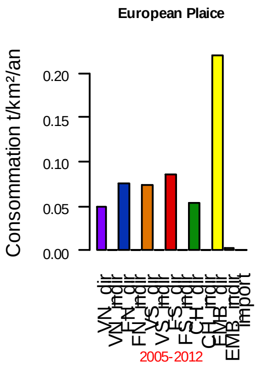

Other fish benthos feeder

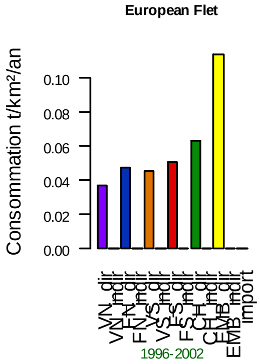

Other fish benthos feeder

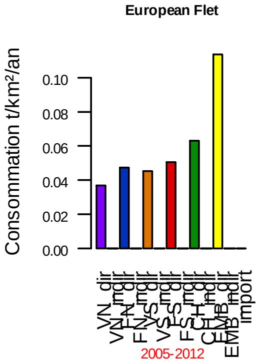

Common Sole
Consommation t/km²/an
0.15
0.10
0.05
0.00
VN_dir
VN_indir
FN_dir
FN_indir
VS_dir
VS_indir
FS_dir
FS_indir
CH_dir
CH_indir
EMB_dir
EMB_indir
import
1996-2002

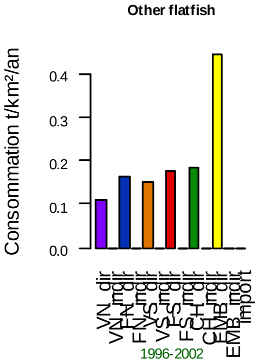

Common Sole
Consommation t/km²/an
0.15
0.10
0.05
0.00
VN_dir
VN_indir
FN_dir
FN_indir
VS_dir
VS_indir
FS_dir
FS_indir
CH_dir
CH_indir
EMB_dir
EMB_indir
import
2005-2012

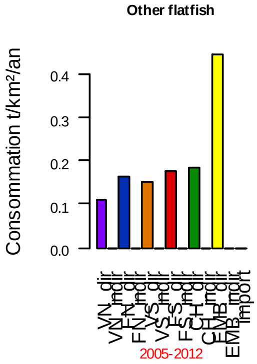

European Plaice
Consommation t/km²/an
0.20
0.15
0.10
0.05
0.00
VN_dir
VN_indir
FN_dir
FN_indir
VS_dir
VS_indir
FS_dir
FS_indir
CH_dir
CH_indir
EMB_dir
EMB_indir
import
1996-2002

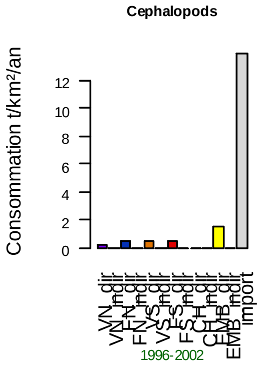

European Plaice
Consommation t/km²/an
0.20
0.15
0.10
0.05
0.00
VN_dir
VN_indir
FN_dir
FN_indir
VS_dir
VS_indir
FS_dir
FS_indir
CH_dir
CH_indir
EMB_dir
EMB_indir
import
2005-2012

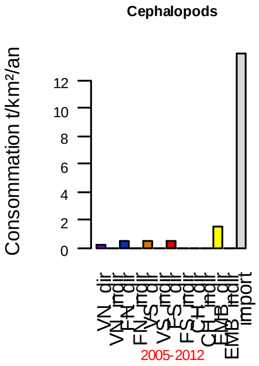

European Flet
Consommation t/km²/an
0.10
0.08
0.06
0.04
0.02
0.00
VN_dir
VN_indir
FN_dir
FN_indir
VS_dir
VS_indir
FS_dir
FS_indir
CH_dir
CH_indir
EMB_dir
EMB_indir
import
1996-2002


European Flet
Consommation t/km²/an
0.10
0.08
0.06
0.04
0.02
0.00
VN_dir
VN_indir
FN_dir
FN_indir
VS_dir
VS_indir
FS_dir
FS_indir
CH_dir
CH_indir
EMB_dir
EMB_indir
import
2005-2012

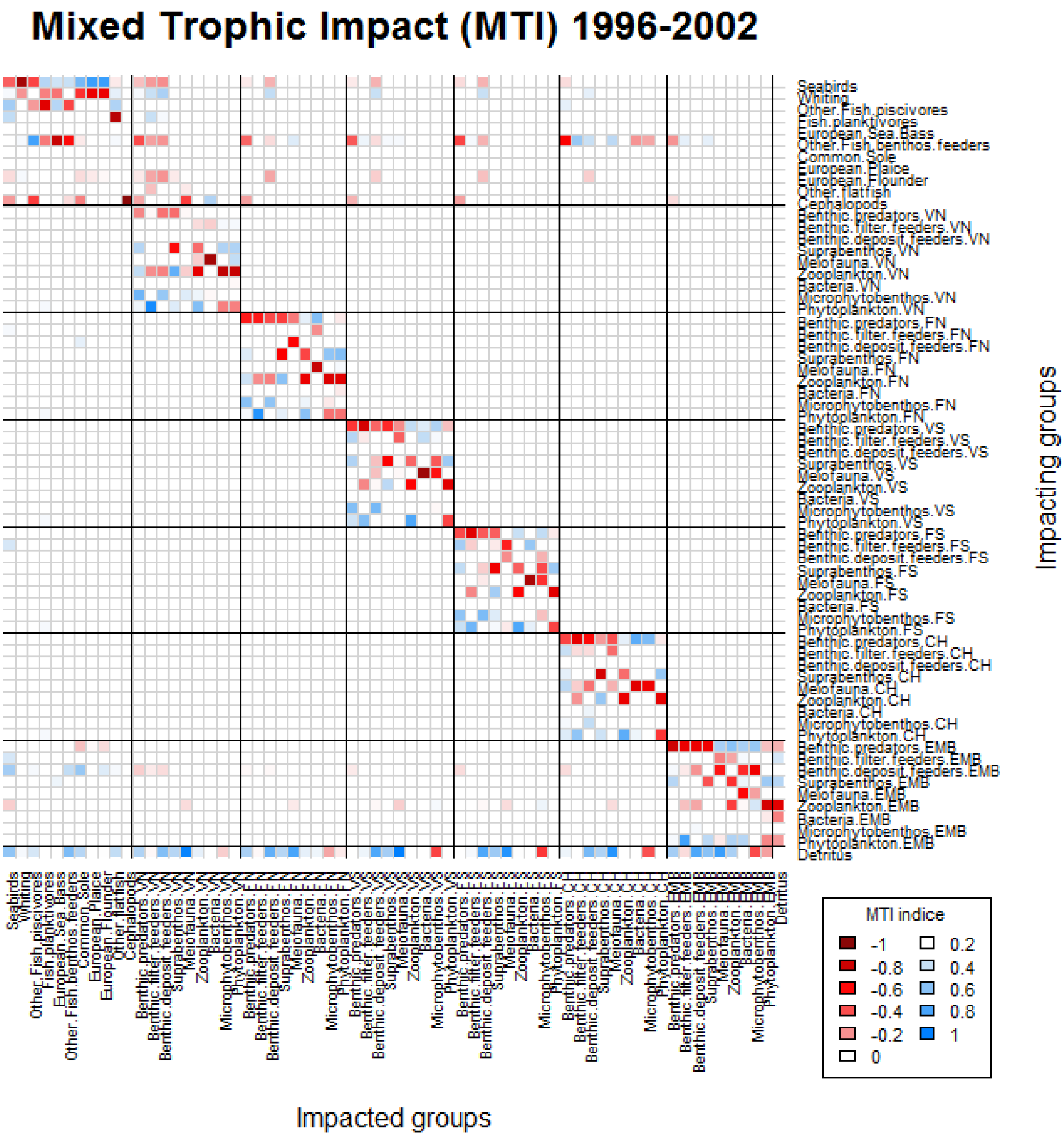

Other flatfish
Consommation t/km²/an
0.4
0.3
0.2
0.1
0.0
VN_dir
VN_indir
FN_dir
FN_indir
VS_dir
VS_indir
FS_dir
FS_indir
CH_dir
CH_indir
EMB_dir
EMB_indir
import
1996-2002


Other flatfish
Consommation t/km²/an
0.4
0.3
0.2
0.1
0.0
VN_dir
VN_indir
FN_dir
FN_indir
VS_dir
VS_indir
FS_dir
FS_indir
CH_dir
CH_indir
EMB_dir
EMB_indir
import
2005-2012

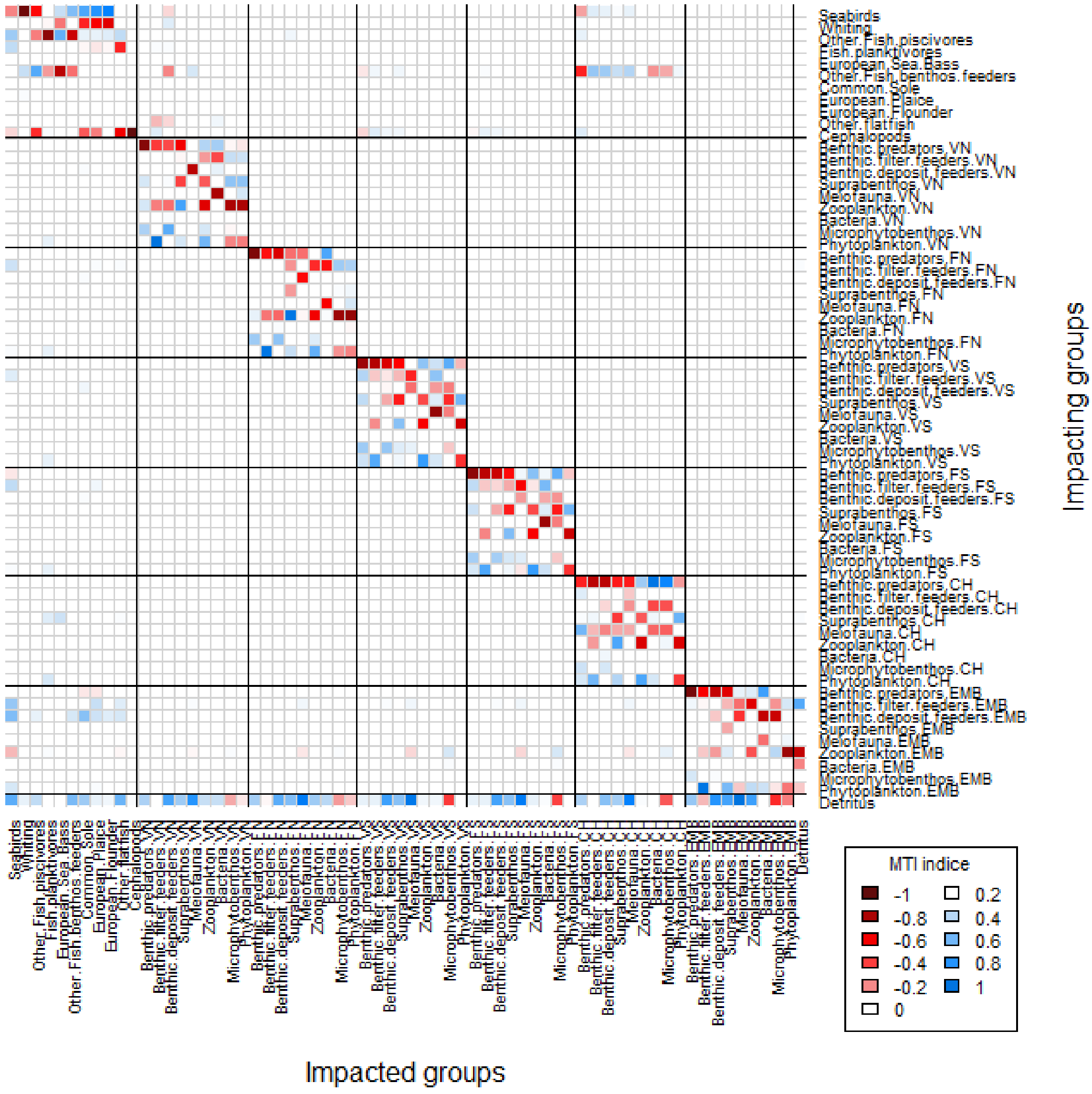

Cephalopods
Consommation t/km²/an
12
10
8
6
4
2
0
VN_dir
VN_indir
FN_dir
FN_indir
VS_dir
VS_indir
FS_dir
FS_indir
CH_dir
CH_indir
EMB_dir
EMB_indir
import
1996-2002


Cephalopods
Consommation t/km²/an
12
10
8
6
4
2
0
VN_dir
VN_indir
FN_dir
FN_indir
VS_dir
VS_indir
FS_dir
FS_indir
CH_dir
CH_indir
EMB_dir
EMB_indir
import
2005-2012

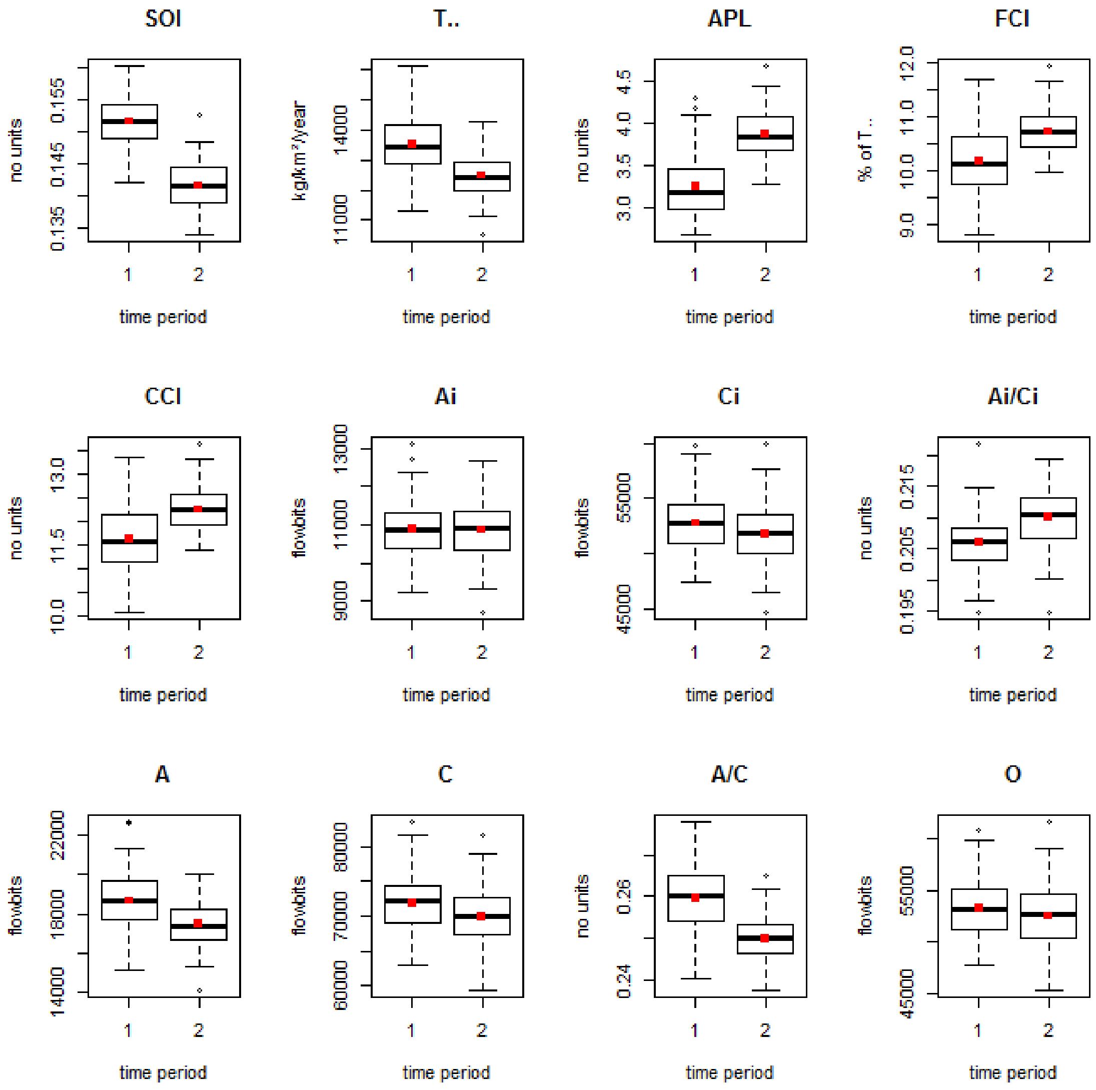
Appendix 10: Mixed Trophic Impact matrix



Mixed Trophic Impact (MTI) 2005-2012



Appendix 11: ENAtool outputs for ENA indices



Corresponding Student test outputs for each ENA between both time periods:

ENA	t	df	p-value
SOI	19.09	196.28	<2.2E-16
T..	9.23	186.53	<2.2E-16
APL	-13.52	185.72	<2.2E-16
FCI	-7.88	178.79	3.04E-13
Ai	0.13	197.58	0.89
Ci	2.75	196.00	6.40E-4
Ai/Ci	-6.22	197.21	2.93E-09
A	6.89	189.67	7.78E-11
C	3.46	197.88	6.77E-4
A/C	10.04	172.59	<2.2E-16
O	1.818	196.10	0.07

Appendix 12: Principal component analysis input values

	ENA									
Estuary	B/TST	CI	SOI	A/C	Ai/Ci	FCI	Cons.(%T..)	Exp.(%T..)	Resp.(%T..)	Det.(%T..)
Seine(p1)	0,009	0,127	0,176	26,3	15,6	10,69	34,1	20,4	10,8	34,7
Seine(p2)	0,013	0,128	0,163	25,8	17,2	13,84	43,4	11,9	14,9	29,9
Canche	0,003	0,33	0,04	53,6	35,6	0,8	3,2	46,9	1,5	48,4
Somme	0,01	0,25	0,01	35	24,7	12,2	14	36,2	1,7	48,1
St_Michel	0,02	0,17	0,06	44	27,4	0,64	11,6	39,4	7,8	41,3
Loire	0,01	0,34	0,12	90	80	0,19	0,7	49,3	0,4	49,7
Gironde	0,003	0,27	0,12	48	17	3,99	14	36,7	5,8	43,4

Diplôme : Ingénieur agronome

Spécialité : Sciences Halieutiques et Aquacoles

Spécialisation / option : Ressources et Ecosystèmes Aquatiques

Enseignant référent : M. Didier Gascuel

Auteur(s) : Alexandre Schickele

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Maître de stage : M. Jérémy Lobry

Titre français : Contribution des habitats estuariens à la productivité et au fonctionnement du réseau trophique de la Seine Aval. Impacts des aménagements et du changement global.

Titre anglais : Contribution of the estuarine habitats to the productivity and the food web functioning of the Seine Aval. Impact of the infrastructures and global change.

Résumé :

Les estuaires sont des milieux productifs, important pour le maintien des ressources marines et très exposés aux pressions anthropiques et environnementales. L'estuaire de Seine est un écosystème fortement altéré, notamment suite à la récente construction de Port 2000. Deux modèles écosystémiques (1996-2002 et 2005-2012) spatialisés utilisant l'approche Ecopath ont été construits afin d'estimer la contribution des différents habitats estuariens au fonctionnement du réseau trophique ainsi que l'impact de ces aménagements. Ces modèles s'appuient sur une structure particulière incluant des groupes trophiques sédentaires liés aux habitats et des prédateurs supérieurs mobiles. Les relations prédateurs-proies sont modélisées selon une hypothèse de densité dépendance permettant de prendre en compte l'opportunisme et l'adaptation des prédateurs. Ces modèles ont mis en évidence le rôle structurant des communautés benthiques ainsi que l'attractivité des zones Nord et Sud de l'estuaire malgré les pressions anthropiques. Un report de prédation vers l'aval et les zones intertidales a été observé durant la seconde période. Différents indicateurs de santé des écosystèmes ont également mis en évidence une diminution de la maturité et une augmentation du stress de cet estuaire déjà fortement stressé.

Abstract :

Despite being highly exposed to various anthropogenic and environmental pressures, estuaries are productive and important areas for the maintaining of marine resources. The Seine estuary is a largely altered ecosystem, particularly after Port 2000's construction. Two spatial ecosystem models (1996-2002 and 2005-2012) using the Ecopath modelling approach have been built. They aimed to estimate the contribution of the various estuarine habitats to the global food web functioning and the impact of the various recent infrastructures. These models are relying on a particular structure, including sedentary trophic group which are associated to a particular habitat and mobile trophic group, corresponding to the top predators. The predator-prey relationships are modelling following a density dependence hypothesis which takes account of the predators' opportunism and the adaptation. The two models highlighted the structuring role of the benthic communities and the high attractiveness of the Northern and Southern areas in terms of nursery. A predation report has been shown from downstream to upstream and from subtidal areas to intertidal areas during the second time period. Finally, Ecosystem Network Analysis indicated a maturity decrease and an increase of stress in this already stressed estuary.

Mots-clés : Ecopath, estuaire de Seine, trophique, spatialisé, impacts anthropiques, habitats.

Key Words: Ecopath, Seine estuary, trophic, spatial, anthropic impacts, habitats.

* *Elément qui permet d'enregistrer les notices auteurs dans le catalogue des bibliothèques universitaires*