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**PRODUCTION PRIMAIRE ET FONCTIONNEMENT ÉCOLOGIQUE EN
MILIEU ESTUARIEN TURBIDE
Cas de l'estuaire de la Gironde (France)**

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CHAPITRE 1

INTRODUCTION GÉNÉRALE

1.1 Contexte de l'étude

Les zones côtières consistent en une mosaïque d'écosystèmes inter-connectés par des flux de composés dissous, de matières détritiques et d'organismes. Elles sont reconnues comme des régions très actives d'un point de vue biogéochimique. Ces zones occupent une superficie très modeste puisqu'elles couvrent approximativement 7,5 à 8,5 % de la surface totale des océans (Sverdrup et al., 1942; Menard and Smith, 1966; Costanza et al., 1998). Malgré cette surface relative très restreinte, elles sont le siège d'une activité de minéralisation très intense. Middelburg et al. (2005) ont en effet estimé que cette activité dans les sédiments côtiers représenterait près de la moitié de la minéralisation totale s'effectuant dans l'ensemble des sédiments marins. Cette intense activité biogéochimique est alimentée par des flux de matière dérivant d'une importante production primaire autochtone ainsi que d'apports allochtones. La production primaire des systèmes côtiers est en effet très importante, elle représenterait, à elle seule, entre 14 et 30 % de la production primaire océanique totale (Gattuso et al., 1998; Duarte et al., 2004). Les apports allochtones d'origine continentale sont convoyés vers la zone côtière par les systèmes estuariens. Ces estuaires, en milieu tempéré sont définis par Day (1981) comme « *des masses d'eau côtières partiellement fermées étant reliées à l'océan de manière permanente ou périodique et au sein desquelles il existe des variations mesurables de salinité dues au mélange des eaux marines avec les eaux douces continentales* ».

Chaque année ces estuaires transporteraient vers les océans environ 0,4-0,9 Gt ($Gt=10^{15}g$ ou 10^9 tonnes) de carbone organique issu des continents dont 0,15 à 0,17 Gt est sous forme particulaire (Ludwig et al., 1996; Hedges et al., 1997). Les écosystèmes estuariens sont également très impliqués dans les flux d'organismes entre écosystèmes puisqu'ils constituent des zones de nourricerie particu-

lièrement importantes pour de nombreux juvéniles de poissons marins (Boehlert and Mundy, 1988), des zones de passage obligatoires pour les espèces de poissons migrateurs anadromes et catadromes (Brosse et al., 2000; Elliott et al., 2007) mais aussi pour les oiseaux limicoles (Gross-Custard, 1985). Finalement, les écosystèmes estuariens représenteraient 20% de la valeur économique des écosystèmes marins et 60% de celle des zones côtières (Mantoura et al., 1991; Pauly and Christensen, 1995; Costanza et al., 1998).

La définition du terme « estuaire » a longtemps été basée sur les travaux et observations réalisés dans les régions tempérées (ex : Pritchard 1967), de sorte que ces définitions ne prenaient pas en compte certaines caractéristiques telles que la fermeture temporaire de la connexion à la mer et les conditions d'hypersalinité pouvant être observées durant la saison sèche dans certaines zones, notamment en Afrique du Sud ou dans le Sud-Ouest de l'Australie. Ainsi, Potter et al. (2010) ont récemment proposé une définition beaucoup plus large pour ce terme. Selon ces auteurs, un estuaire consiste en « *une masse d'eau côtière partiellement fermée qui est en relation permanente ou périodique avec l'océan ouvert et qui reçoit, au moins périodiquement, des apports d'eau douce par des rivières* ». Si l'on adopte cette dernière définition, le terme d'estuaire inclut une large gamme d'écosystèmes aux caractéristiques physiques, chimiques et biologiques très variées (Figure 1.1), impliquant, malgré un grand nombre de points communs, des modes de fonctionnement différents. Le présent travail de thèse s'est intéressé au fonctionnement écologique d'un estuaire européen « classique » (selon Potter et al., 2010), l'estuaire de la Gironde. Selon Dame (2009), cet estuaire correspondrait au type géomorphologique « Riverine estuary ».

Au sein de ce type d'estuaire du nord de l'Europe, il existe des variations importantes des caractéristiques susceptibles de déterminer leur mode de fonctionnement à l'échelle de la zone côtière adjacente. Les facteurs environnementaux qui sont susceptibles de déterminer le mode de fonctionnement d'un système estuarien sont multiples. Effet, les estuaires sont connus pour modifier les transferts, depuis les rivières vers les eaux océaniques, des composés aussi bien dissous que particulaires (Billen et al., 1991). Au cours de leur passage à travers les eaux estuariennes, les particules organiques sont en effet soumises aux cycles de sédimentation et de remise en suspension qu'accompagnent des oscillations anoxiques et oxiques (Abril, 2000). Une partie de ce matériel organique est piégée dans les sédiments estuariens et/ou est minéralisée dans l'estuaire par l'activité des organismes hétérotrophes. Les estuaires ont un effet de filtre (Schulbel and Kennedy, 1984) sur les transferts de matière entre continent et océan de telle sorte que seule une fraction des apports terrestres atteindrait finalement les côtes (Abril et al., 2002). La signification quantitative des processus estuariens dans la modification de la spéciation et finalement dans l'atténuation des flux des composés azotés par exemple, vers les océans côtiers a reçu une attention particulière (Abril, 2000; Vanderborght et al., 2007; Wollast,

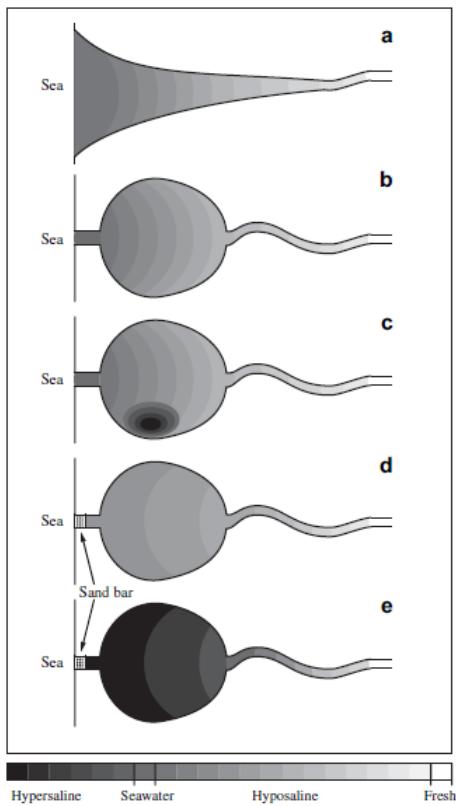


FIGURE 1.1 – Exemples stylisés (a) d'un estuaire macrotidal classique de l'hémisphère nord avec un gradient longitudinal de salinité et (b-e) d'estuaires du Sud-Ouest Australien qui comprend typiquement un chenal d'entrée court et étroit, un vaste bassin central relié à la partie aval d'une rivière. (b) estuaire ouvert de manière permanente sur l'océan présentant un gradient longitudinal de salinité ; (c) estuaire ouvert de manière permanente sur l'océan présentant un gradient longitudinal de salinité mais aussi une zone d'hypersalinité ; (d) estuaire fermé saisonnièrement par une barre sableuse (en tirets) mais demeurant hyposalins et (e) estuaire fermé saisonnièrement par une barre sableuse et qui est hypersalin en raison de l'évaporation intense. (issu de Potter et al., 2010)

1983).

Parmi les processus qui affectent la dynamique du fonctionnement de l'estuaire, la production primaire peut avoir un effet majeur puisqu'elle va agir sur la dynamique des composés dissous tels que l'oxygène dissous en augmentant sa concentration et en diminuant celles de l'azote inorganique et du phosphore dissous de la colonne d'eau. Deux moteurs importants peuvent de ce fait affecter la production primaire dans les estuaires : i) la turbidité, qui limite fortement la photosynthèse (Cole et al., 1992; Irigoien and Castel, 1997a), détermine pour une part très importante le statut trophique (autotrophe/hétérotrophe) du système et ii) le temps de résidence des eaux dans un système estuarien qui est lié à la morphologie de l'estuaire, à l'importance des marées et aux débits des rivières. Le temps de résidence des eaux est reconnu comme une propriété déterminant de manière importante le

mode de fonctionnement de ces estuaires. En effet, il détermine par exemple le temps qu'une particule de matière organique passe dans l'estuaire et donc, le degré de transformations que cette particule va pouvoir subir dans l'estuaire (Wollast, 1983; Etcheber et al., 2007).

Cette modification du fonctionnement d'un écosystème par les producteurs primaires est en grande partie liée au fait que les écosystèmes estuariens du plateau continental se distinguent par une forte diversité de producteurs primaires (Dubois, 2012). Cette diversité est liée à la faible profondeur de ces milieux, permettant l'existence de producteurs primaires benthiques infralittoraux et à l'influence des marées qui permet le développement de flores variées en fonction de l'étagement et du type de substrat. Par opposition avec les écosystèmes océaniques du large, la production primaire dans les écosystèmes estuariens ne se résume donc pas à la seule production primaire phytoplanctonique mais elle inclue aussi la production microphytobenthique, la production macroalgale, la production des angiospermes des prés salés et celle des herbiers inter- et subtidaux et de leurs épiphytes (voire des mangroves dans les systèmes tropicaux). A ces sources autochtones de matière organique s'ajoute une source de matière organique détritique d'origine continentale apportée par les rivières. La diversité de ces sources de matière organique complexifie de manière considérable notre compréhension du fonctionnement écologique des systèmes estuariens et côtiers et notamment le mode de fonctionnement des réseaux trophiques. En effet, la capacité des organismes à minéraliser la matière organique et à transmettre celle-ci aux échelons trophiques supérieurs est dépendante de la dégradabilité de celle-ci (Middelburg, 1989). La dégradabilité de la matière organique est elle-même dépendante (1) de la nature et de l'importance relative des sources dont elle dérive (débris de macrophytes, phytoplancton, effluents urbains, etc.) et (2) de son état de fraîcheur (McCallister et al., 2006). Le réseau trophique d'un écosystème côtier est donc très vraisemblablement contraint par l'importance relative des sources de matière organique, au même titre que la seule structure de taille de la communauté phytoplanctonique a un effet sur la structure du réseau trophique planctonique et sur les propriétés du système en termes de recyclage et d'export de matière organique (Legendre and Rassoulzadegan, 1995).

Le présent travail s'intéresse au fonctionnement de l'estuaire de la Gironde sous un angle principalement trophique. Cet estuaire représente en effet un cas d'étude non dépourvu d'intérêt pour investiguer les relations entre diversité des sources de matière organique et fonctionnement trophique. En effet, l'estuaire de la Gironde, qui sera décrit de manière plus précise au chapitre 2, se caractérise par une très forte turbidité de ses eaux. Ce niveau de turbidité élevé limite fortement la production primaire phytoplanctonique (Cloern et al., 1983; Grobbelaar, 1985; Cole et al., 1992; Kies, 1997) bien que les eaux de l'estuaire, en amont comme en aval ne soient pas dépourvues de chlorophylle a (Chla), selon les données du Service d'Observation du Milieu LITToral (SOMLIT). En conséquence, la concentration des matières en suspension en carbone organique est faible, en moyenne 1,5% (Veyssy, 1998;

Etcheber et al., 2007). De plus, cette matière organique en suspension dans les eaux de l'estuaire serait composée en très grande majorité (98%) par du matériel d'origine terrestre et de seulement 2% de phytoplancton avec un accroissement, vers l'aval, de la contribution relative du phytoplancton (jusqu'à 8,5%) Savoye et al., 2012). Cette matière organique est donc considérée comme en très grande majorité réfractaire et fortement diluée dans une matrice minérale et donc difficilement accessible aux consommateurs primaires. Ces conditions (relativement) extrêmes, particulières à l'estuaire de la Gironde, ont probablement des conséquences majeures sur les consommateurs primaires (herbivores et détritivores) et de manière plus large sur le fonctionnement du réseau trophique de l'estuaire et le rôle de cet estuaire à l'échelle de la zone côtière adjacente.

L'importance des différentes sources de production primaire reste très mal connue et certains auteurs ont résumé le fonctionnement global du milieu dans deux modèles théoriques : le modèle RCC et le modèle RPM. Le modèle RCC (River Continuum Concept) admet que la dynamique du milieu est contrôlée par les apports extérieurs en provenance des rivières par rapport à la production des estrans qui reste négligeable tandis que la production autochtone est limitée par la turbidité (Minshall et al., 1985). Le modèle RPM (Riverine Productivity Model) quant à lui considère que bien que la production locale soit faible, elle peut toutefois concurrencer la production allochtonne. Celle-ci serait majoritairement liée à une production du microphytobenthos par les estrans du milieu (Thorp and Cothran, 1984).

1.2 Objectif et organisation du manuscrit

Dans ce contexte, ce travail de thèse cherche à apporter des éléments de réponse à la question suivante : quelle est l'importance des producteurs primaires autochtones dans le fonctionnement du réseau trophique de l'estuaire de la Gironde ?

Cette question sera abordée à partir de trois études complémentaires ayant fait appel à des méthodologies diverses qui sont détaillées ci-dessous.

- Le premier axe s'intéresse à la production primaire phytoplanctonique dans l'estuaire de la Gironde. En effet, si la production primaire dans l'estuaire est fortement limitée en raison des conditions de forte turbidité, les concentrations en chlorophylle a dans les eaux ne sont pas nulles et présentent des variations intra- et interannuelles ; de plus, il n'existe très peu d'estimation quantitative de cette production ; ce qui permettrait pourtant de mieux contraindre le réseau trophique proposé par Lobry et al. (2008). Cependant, l'une des rares mesure de production disponible remonte aux travaux de Irigoien and Castel (1997b). Cette carence est liée à

de très fortes contraintes méthodologiques pour estimer directement cette production primaire. Dans le présent travail, le choix s'est porté sur un travail de modélisation permettant de manière indirecte d'obtenir une estimation de cette production primaire phytoplanctonique. Le modèle utilisé décrit la dynamique de la chlorophylle *a* au moyen d'un modèle de transport et réaction qui simule dans l'espace et le temps l'évolution de toute variable considérée comme dissoute dans le milieu (Soetaert and Herman, 1995a,b,c). De cette manière, la production potentiellement produite dans le système et la fraction consommée ou advectée par les courants peut être estimée. Ceci est possible en appliquant des méthodes d'ajustement non linéaire qui calculent les différences ou résidus entre le modèle et les données observées. Les conclusions de cette première approche sont vérifiées en utilisant un modèle biogéochimique simple. Ce travail a été réalisé en collaboration avec Karline Soetaert du Nederlands Instituut voor Ecologie (NIOO).

- Le second axe de ce travail a été consacré à la caractérisation et à une amorce de quantification de la production primaire microphytobenthique en domaine intertidal. En effet, dans l'hypothèse d'une production primaire phytoplanctonique faible, la production microphytobenthique peut potentiellement constituer une ressource trophique importante dans un tel milieu. Cette production microphytobenthique a été mesurée à l'aide de la technique des chambres benthiques qui permet d'obtenir une mesure *in situ* de la production primaire, de la respiration et du métabolisme des estrans. Ce travail a été réalisé grâce à une collaboration avec l'équipe du professeur Dominique Davoult, de la station biologique de Roscoff (Université Pierre et Marie Curie, Paris 6).
- Enfin, le troisième axe s'est intéressé à estimer l'importance relative de ces deux sources de matières organiques (phytoplancton et microphytobenthos) par rapport aux autres sources (apports des rivières et production des phanérogames des rives) pour les organismes benthiques et planctoniques de l'estuaire. Ce travail a été réalisé en utilisant les isotopes stables de l'azote et du carbone comme traceurs de l'origine et du devenir de la matière organique dans les réseaux trophiques benthiques. Ce travail a été réalisé en collaboration avec N. Savoye et V. David de l'UMR EPOC.

1.3 Description des méthodes

1.3.1 Utilisation d'un modèle de transport et réaction

1.3.1.1 Choix du modèle utilisé

Un des objectifs de ce travail de modélisation était d'expliquer la dynamique de la biomasse phytoplanctonique telle qu'elle est décrite par les fluctuations des concentrations en chlorophylle a dans la colonne d'eau. La dynamique temporelle de la chlorophylle a en un point fixe de l'estuaire est expliquée dans le modèle par (i) la dynamique de la chlorophylle a observée en amont et en aval, (ii) son advection plus ou moins rapide vers l'aval ou l'amont (elle-même dépendante de la résultante des courants et de la morphologie de l'estuaire au(x) point(s) considéré(s)) et (iii) de la résultante entre production primaire et consommation par les hétérotrophes. Ce travail a pu être réalisé par l'utilisation d'un modèle de transport et réaction appliqué à l'estuaire de la Gironde. Un tel modèle permet de faire la part entre le simple transport physique d'un composant considéré comme dissous (ici, la chlorophylle a) [partie « transport » du modèle] et l'éventuelle dynamique biologique du composant (ici, la résultante de la production primaire et de la consommation par les hétérotrophes) [partie « réaction » du modèle]. Après ajustement du modèle aux données d'observation, la différence entre les résultats du modèle de transport avec les réactions associées et le modèle de transport seul sans réaction permet d'estimer l'importance de la dynamique biologique dans les fluctuations de la chlorophylle a . Cette méthode étant très indirecte pour estimer quelle est la production primaire phytoplanctonique dans l'estuaire de la Gironde, les résultats obtenus sont confortés en ajoutant un modèle simple décrivant la dynamique biogéochimique de l'azote dans les eaux de l'estuaire sous l'hypothèse d'une production primaire nulle.

Les modèles de transport-réaction (ou RTMs) ont traditionnellement été développés et utilisés pour étudier entre autres l'altération des roches et la formation des sols (Thyne et al., 2001; Soler, 2003; De Windt et al., 2004), le devenir du zooplancton marin dans les estuaires (Soetaert and Herman, 1994a), la dynamique des nutriments dans un bassin de drainage et dans les estuaires (e.g., Soetaert and Herman, 1995d; Regnier and Steefel, 1999; Vanderborght et al., 2002), le transport réactif dans les eaux souterraines, comme les contaminations des aquifères (e.g., Murphy and Ginn, 2000; Barry et al., 2002; Brun and Engesgaard, 2002; Thullner et al., 2005; van Breukelen et al., 2004), les transformations diagénétiques précoces dans les sédiments (e.g., Soetaert et al., 1996; Boudreau, 1997; Berg et al., 2003; Jourabchi et al., 2005), le couplage benthos-pelagos dans les océans (e.g., Soetaert et al., 2000; Archer et al., 2002; Lee et al., 2002), la migration et la maturation dans les bassins sédimentaires (e.g., Person and Graven, 1994). Ainsi, en intégrant les connaissances expéri-

mentales, théoriques et observationnelles sur les processus géochimiques, biologiques et physiques (transport) dans des modèles mathématiques, les modèles de transport-réactions (RTMs) offrent des outils de prévisions tandis que la comparaison entre les simulations des prévisions du modèle et les mesures peuvent aider à identifier les lacunes (zones d'ombre) dans la compréhension conceptuelle d'un système spécifique ou des incertitudes dans le paramétrage correct des processus biogéochimiques (Jourabchi et al., 2005).

Le modèle de transport-réaction utilisé ici a déjà été appliqué à l'estuaire de l'Escaut (Soetaert and Herman, 1994a) et a été modifié pour être adapté à l'estuaire de la Gironde. En effet, l'équation d'advection-dispersion utilisée est bien adaptée pour décrire le transport et la réaction d'un composé dans le cas d'un estuaire ou d'un fleuve où les gradients verticaux et horizontaux peuvent être négligés au regard des forts débits des rivières (Soetaert and Herman, 1994a) comme c'est le cas pour l'estuaire de la Gironde où les débits d'eaux douces sont en moyenne de l'ordre de 700 à 1000 m³.s⁻¹ (contre environ 100 m³.s⁻¹ dans l'Escaut). Il s'agit d'un modèle 1D (unidimensionnel) qui cherche donc à modéliser le comportement de la chlorophylle *a* le long de l'axe amont-aval de l'estuaire de la Gironde. Ce choix simplificateur néglige le gradient transversal existant (des salinités légèrement plus faibles sont en effet observées sur la rive droite par rapport à la rive gauche (Allen et al., 1974; Cancino and Neves, 1999)) et le gradient vertical qui apparaît surtout dans la partie la plus aval de l'estuaire (Cancino and Neves, 1999). Le modèle considère ainsi que sur la zone étudiée, la colonne d'eau est bien mélangée. La prise en compte de ces variations nécessiterait l'utilisation d'un modèle 3D en trois dimensions (longueur, largeur et profondeur) nettement plus complexe.

Ce type de modélisation 3D a déjà été développé dans l'estuaire de la Gironde pour étudier la dynamique hydro-sédimentaire (Sottolichio and Castaing, 1999; Cancino and Neves, 1999). Ces modèles prennent donc en compte les gradients transversaux et verticaux et ont l'avantage de regarder la dynamique des particules dans toutes les dimensions et de proposer une vision large échelle des processus d'érosion, suspension et sédimentation. Ils permettent par exemple de simuler le bouchon vaseux de l'estuaire. Cependant les modèles dits 3D sont surtout appliqués en océan ouvert où les phénomènes physiques occupent pratiquement tous les niveaux de l'échelle spatio-temporelle (Nihoul, 1984; Nihoul et al., 1989; Nihoul, 1993). Leur mise en œuvre se révèle toutefois difficile à cause du très grand nombre de paramètres et du nombre important des données qui sont nécessaires pour leur calibration. Même si les résultats sont satisfaisants pour le cas des variables inertes, son application avec les variables biologiques ou biogéochimiques réactives n'a pas encore été envisagée jusqu'à présent dans l'estuaire de la Gironde.

1.3.1.2 Paramétrisation et Calibration

La mise en œuvre d'un modèle passe successivement par plusieurs étapes : la conceptualisation, la formulation mathématique des processus et la paramétrisation avant l'application du modèle et sa vérification. La paramétrisation du modèle est l'une des étapes clés de la modélisation. En effet, les équations utilisées reposent sur l'utilisation de paramètres dont la valeur est constante tout au long de la simulation. Ces paramètres sont obtenus soit (1) à partir de valeurs issues de la littérature ou sur la base de résultats de mesures antérieures (méthode « forward ») (Soetaert et al., 2010) ou bien (2) en utilisant une procédure de calibration à partir du modèle lui-même (méthode Inverse ou « backward ») (Soetaert et al., 2010).

Dans la première approche, les différents paramètres initialement connus sont utilisés pour produire un résultat permettant de tester les hypothèses de fonctionnement écologique et de réaliser des prédictions. Dans la seconde approche, les paramètres ne sont pas disponibles directement par l'expérimentation (Beven and Freer, 2001) et la première étape consiste à trouver un premier jeu de paramètres en forçant le modèle à produire les meilleurs paramètres possibles, c'est-à-dire ceux qui, lorsqu'ils sont utilisés dans le modèle, produisent le meilleur ajustement aux données d'observation. C'est ainsi que l'on procède généralement pour des applications en modélisation par analyse inverse en minimisant l'écart entre le modèle produit et les données réellement mesurées dans le système.

Dans notre cas, les paramètres du modèle ont été estimés par la méthode inverse. Les méthodes d'analyses inverses sont des méthodes mathématiques qui consistent à résoudre un système d'équations sous-déterminé (i.e. : où le nombre d'inconnues (ici, les valeurs des paramètres du modèle) est supérieur au nombre d'équations). Il s'agit d'une méthode de résolution « sous contrainte » au cours de laquelle, le système d'équations sera résolu sous une condition de minimisation ou de maximisation d'une relation. Il existe différentes méthodes inverses qui dépendent du domaine d'application et du type de contrainte appliqué (Niquil et al., 2012). Ces méthodes ont trouvé de nombreuses applications dans divers domaines scientifiques notamment en océanographie (e.g. Tarantola, 1987; Vezina and Platt, 1988; Benett, 1992; Niquil et al., 2012).

Le principe de la méthode inverse utilisée ici est de proposer un ensemble de paramètres issus de la littérature et qui vont être ajustés automatiquement à la relation décrite par le modèle. Cet ajustement automatique est réalisé de la manière suivante : au cours de d'une première étape, un seul paramètre à la fois est ajusté au modèle. Il s'agit en fait de simuler le modèle pour une certaine gamme de valeurs de ce paramètre et d'estimer l'écart moyen entre le modèle et les données. Ainsi, les paramètres les mieux ajustés sont ceux qui minimisent le coût du modèle (Klepper, 1995). Une fonction possible pour le calcul de ce coût (*modCost*) est similaire à celle qui permet de calculer l'écart-type (Jorgensen

and Bendoricchio, 2001).

$$modCost = \left[\sum_{i=1}^n \frac{(x_{cal} - x_{obs})^2}{\bar{x}.n} \right]^{\frac{1}{2}} \quad (1.1)$$

où x_{cal} est la valeur simulée de la variable d'état, x_{obs} la valeur observée, est la valeur moyenne mesurée. Pour tout point de la variable i , la fonction estime la valeur de l'écart moyen pondérée (résidus) tel que :

$$res_i = \frac{x_{cal} - x_{obs}}{\bar{x}.n} \quad (1.2)$$

Cette étape produit donc un unique jeu de paramètres qui minimise la relation présentée ci-dessus. L'étape suivante a consisté à produire une distribution de probabilité pour chacun de ces paramètres et à estimer *in fine*, les conséquences de ces valeurs probables des paramètres sur les sorties du modèle et sur la qualité de l'ajustement de celui-ci aux données d'observation. La méthode fait appel aux statistiques Bayésiennes, qui sont étroitement liées aux problèmes inverses (Dowd and Meyer, 2003). Les statistiques Bayésiennes permettent notamment d'obtenir la distribution de probabilité *a posteriori* de chaque paramètre et du modèle lui-même.

Une fois le meilleur ajustement trouvé et les paramètres obtenus, ces derniers vont servir pour initier une chaîne de Markov Monte-Carlo (MCMC) afin d'obtenir l'incertitude associée à chaque paramètre. Concrètement, l'incertitude de la prédiction des valeurs observées (y) provient de deux sources d'erreurs principales : une erreur liée à l'incertitude des paramètres θ du modèle et une autre provenant des mesures elles-mêmes ϵ tel que :

$$y = f(x, \theta) + \epsilon \quad (1.3)$$

L'incertitude due à θ est couverte par la distribution *a posteriori* des paramètres alors que la variabilité due au bruit est contenue dans la loi de distribution (gaussienne dans notre cas) et dans la distribution *a posteriori* de σ^2 (Laine, 2008). En d'autres termes, la variance totale dans y est partitionnée en une variance qui peut être expliquée par le modèle (somme des carré de la régression ou SRR) et la variance qui n'est pas expliquée par les variables indépendantes, c'est-à-dire la somme des carrés des erreurs ; SSE. L'effet de ces deux incertitudes sur les sorties du modèle est estimé et peut être visualisé comme des gammes de valeurs qui représentent la distribution *a posteriori* des paramètres.

1.3.1.3 Suivi écologique et données utilisées

Les données utilisées dans cette première partie de notre travail ont été extraites de plusieurs bases de données disponibles. En effet, la mise en place d'un réseau de surveillance écologique du Centre Nucléaire de Production Électrique (CNPE) de Blaye à partir de 1978 a permis, au travers de campagnes océanographiques récurrentes, un échantillonnage complet et un suivi régulier de nombreux paramètres le long du gradient de salinité des eaux de l'estuaire. Ce suivi complété par des approches « recherche » concernant la caractérisation du fonctionnement estuarien permet à l'heure actuelle d'avoir un ensemble assez complet de données sur cet environnement et son fonctionnement.

⊕ **Données SOMLIT (Service de l'observation du Milieu LITToral).**

Les campagnes ont été initiées à partir de 1997 en complément des suivis dits du Blayais, autour de la centrale nucléaire. Elles consistent en une démarche systématique d'observation des milieux littoraux par les stations marines françaises. Elles sont issues d'initiatives locales, fondées sur des opportunités et/ou des traditions scientifiques propres à chaque station. L'objectif visé est d'homogénéiser l'acquisition de paramètres communs hydroclimatiques, chimiques et biologiques via une observation systématique et coordonnée au niveau national afin de permettre une étude comparée de séries sur les trois façades du littoral français. Dans le modèle, les données utilisées sont entre autres : l'oxygène, les sels nutritifs (Ammonium, Nitrates) et la Chlorophylle *a* au point 2 (PK 86), le point K (PK 30), le point E (PK 52).

⊕ **Les campagnes SOGIR (Service d'Observation de l'estuaire de la Gironde)**

Elles complètent l'échantillonnage du SOMLIT au niveau du point F (PK 67) dans l'estuaire. Le suivi blayais a été mis en place depuis 1975 après l'implantation de la centrale et a permis de disposer de l'une des bases de données les plus vieilles et la plus régulière faisant de l'estuaire de la Gironde le site le mieux suivi avec une base de plus de 37 ans. Ces données ont été utilisées pour la comparaison du modèle avec les données au PK 67.

⊕ **Les campagnes RETROGIR (REseau TROphique de la Gironde).**

Ces données ont été acquises au cours des travaux de thèse de Valérie David en 2003 dans le but d'étudier d'une part la distribution spatio-temporelle des organismes planctoniques, principalement les communautés zooplanctoniques. D'autre part, d'analyser les relations trophiques existantes au sein de ce compartiment. Ces données nous ont permis de valider le modèle physique en confrontant nos sorties de modèle aux données de salinité à différents points fixes de l'estuaire.

⊕ **Les données libellules :**

Ces campagnes qui ont eu lieu entre 1982 et 1985, juste après la mise en place du suivi du

milieu dans le cadre du Blayais, ont permis d'étudier l'effet des rejets de la centrale sur les communautés biologiques du milieu. Elles ont été utiles pour calibrer le modèle physique et estimer le coefficient de dispersion.

1.3.2 Mesures de la production primaire et du métabolisme benthique

La production primaire est la quantité de matière accumulée au cours d'un ensemble de processus biologiques qui utilisent une énergie externe (lumière) pour produire des composés organiques. Il s'agit principalement des processus de photosynthèse (synthèse des matières organiques à partir du CO₂, de l'eau, d'ions minéraux et de lumière) et de chimioautotrophie. Les producteurs primaires sont, dans la majorité des écosystèmes marins des algues microscopiques en suspension dans la colonne d'eau (Phytoplancton) ou présents à la surface des sédiments (Microphytobenthos), d'une part mais aussi des bactéries photosynthétiques, d'autre part.

Le métabolisme net de l'écosystème NEP (Net ecosystem production), permet de définir le rôle et l'état d'un écosystème. Celui-ci se définit comme la somme de toutes les productions nettes des communautés (Compartiment planctonique, microphytobenthos, macrophytes) constituant un écosystème. C'est-à-dire la différence entre la production nette de carbone organique par les organismes autotrophes (production primaire nette : Pnette ou NPP en anglais) et la consommation de carbone par respiration des organismes hétérotrophes (Rh).

$$NEP = P_{nette} - Rh \quad (1.4)$$

De nombreuses techniques permettent de déterminer cette NEP et d'en déduire le statut trophique du système (autotrophie/hétérotrophie, Gattuso et al., 1998; Gazeau et al., 2004; Middelburg et al., 2005). L'une d'elle consiste à mesurer une production brute (Pbrute ou GPP en anglais) à la lumière et une respiration totale de la communauté (RC ou CR pour Community Respiration), par les organismes autotrophes (Ra) et hétérotrophes (Rh) à l'obscurité. La méthode la plus couramment employée consiste à incuber, en conditions contrôlées, des carottes de sédiment prélevées avec de l'eau surnageant. La production primaire est alors estimée en mesurant l'évolution de la concentration en oxygène dans l'eau surnageant par la méthode de Winkler ou en continu grâce à une électrode à oxygène (Davis and MacIntyre, 1983). La mesure des flux d'O₂ (méthode traditionnellement utilisée dans les études biogéochimiques des zones côtières) peut en effet conduire à sous-estimer la respiration si un temps de latence existe entre la production des composés réduits et leur réoxydation (Pinckney et al., 2003). C'est donc la technique mise en œuvre par Migné et al. (2002) qui a été employée pour estimer la production benthique des zones intertidales de la Gironde grâce à une collaboration avec

Dominique Davoult de la station marine de Roscoff. La production primaire est estimée en mesurant l'évolution de la concentration en CO₂ à l'interface air-sédiment. Une technique similaire a été utilisée en milieu subtidal (Boucher and Clavier, 1990; Clavier et al., 2011) pour mesurer la quantité d'oxygène produite à l'interface eau-sédiment. L'application en milieu intertidal offre un double avantage : (1) elle permet d'obtenir directement des mesures *in situ* de la quantité de carbone inorganique fixée pendant la photosynthèse et de s'affranchir de l'utilisation du quotient photosynthétique (rapport entre le volume d'oxygène produit et le volume de gaz carbonique consommé) qui est très variable selon les systèmes et (2) la mesure des flux de CO₂ permet de mesurer à la fois la respiration oxique et anoxique.

La méthode consiste à mesurer les flux de CO₂ *in situ* à l'interface air-sédiment à l'aide des chambres benthiques (Migné et al., 2002). Les mesures sont effectuées à la lumière, en condition de lumière saturante, vérifiées avec un capteur de lumière, puis à l'obscurité grâce à l'utilisation d'une cloche opaque (sans ôter l'embase du sédiment). Ce système permet de mesurer le métabolisme benthique et d'estimer respectivement la production primaire nette (PPN : bilan de la production brute et de la respiration, cloche transparente) et la respiration de la communauté benthique (RCB : cloche opaque) à l'interface air-sédiment. L'évolution de la concentration en CO₂ ($\mu \text{ molCO}_2.\text{mol}^{-1} \text{ air}$) est représentée en fonction du temps et la pente de la droite ($\mu \text{ mol de CO}_2 \text{ mol}^{-1} \text{ air}.\text{min}^{-1}$) est ramenée au volume du système, au m⁻², puis exprimée en mgC.m⁻².h⁻¹ représentant les flux de carbone.

1.3.3 Les isotopes stables comme marqueurs trophiques.

La dernière étape de ce travail de thèse a consisté à évaluer l'importance relative des producteurs primaires phytoplanctoniques, microphytobenthiques et les apports allochtones de matière organiques dans le fonctionnement de la base des réseaux trophiques planctoniques et benthiques dans l'estuaire de la Gironde. Ce travail s'est basé sur l'utilisation des isotopes stables du carbone (¹³C) et de l'azote (¹⁵N) comme marqueur trophique.

Un marqueur trophique en milieu naturel est un composé qui permet de déterminer l'origine de la matière organique assimilée par un organisme consommateur présent dans un milieu où les sources sont multiples (Peterson and Fry, 1987). Un marqueur est dit parfait lorsqu'il est facilement identifiable et d'origine unique et n'est pas transformé par les processus métaboliques d'intégration et d'assimilation, donc stable (Dalsgaard and John, 2004). Dans le milieu naturel, les marqueurs trophiques parfaits sont rares voire inexistant, on a donc recours à d'autres composés, moins parfaits, tels que les isotopes dont les modes de transferts et de dégradations sont connus et/ou quantifiables.

L'intérêt des marqueurs isotopiques réside dans la conservation de l'information sur l'origine de

la matière organique puisque sa composition dépend principalement de celle des éléments minéraux originels et de leurs disponibilités (O’Leary, 1984), ainsi que des voies de synthèse utilisées (Smith and Epstein, 1971; O’Leary, 1984). De ce fait, les différents groupes de producteurs primaires ont des compositions isotopiques caractéristiques (Peterson et al., 1985).

Les isotopes stables sont largement utilisés en sciences et en particulier en océanographie, par exemple pour identifier des sources de matière (e.g. des polluants, McClelland and Valiela (1998) ou des processus (e.g. la nitrification, la dénitrification ; (Carini et al.), pour estimer des taux (e.g. turnover du carbone dans les sols, Bernoux et al., 1998), pour déterminer des ressources trophiques (e.g. contributions relatives des proies au régime alimentaire d’un consommateur, Lemons et al., 2011), pour confirmer, rejeter ou contraindre des modèles dérivés d’autres techniques (e.g. la modélisation par analyse inverse, Eldridge et al., 2005), quantifier les contributions relatives des différents groupes de producteurs primaires à la matière organique particulaire en suspension et à la matière organique sédimentaire (e.g. Cifuentes et al., 1988; Jaschinski et al., 2008; Machas and Santos, 1999; Savoye et al., 2012), identifier dans les études de réseaux trophiques les transferts de matière d’un échelon à un autre, notamment dans les réseaux trophiques marins (Minagawa and Wada, 1984; Fry et al., 1984; Takai et al., 2004; Bode et al., 2006). Dans les systèmes côtiers, l’utilisation combinée du $\delta^{15}\text{N}$ et du $\delta^{13}\text{C}$ permet de mieux discriminer ces différents groupes (e.g. Machas and Santos, 1999), cette discrimination étant bien souvent spécifique au site d’étude.

Une des principales applications du $\delta^{13}\text{C}$, est l’identification des sources de matière organique particulaire (MOP) et de leur origine. Il existe une grande variabilité dans la composition isotopique en $\delta^{13}\text{C}$ des différents producteurs primaires rencontré dans les systèmes côtiers (Dubois, 2012) :

- plantes terrestres en C3 (-32 à -22 ‰)
- plantes terrestres en C4 (-16 à -9 ‰),
- phanérogames marines (-15 à -3 ‰),
- macroalgues (-28 à -8 ‰),
- plantes des marais salés en C3 (-26 à -23 ‰),
- plantes des marais salés en C4 (-14 à -12‰),
- microalgues benthiques (-24 à -10‰),
- phytoplancton marin (-24 à -17 ‰)
- phytoplancton d’eau douce (-31 à -24 ‰).

Ces différences de $\delta^{13}\text{C}$ sont principalement liées : (1) au mode de fixation du carbone inorganique par les différents types de producteurs primaires (O’Leary, 1984), (2) à la signature isotopique de leur

source de carbone inorganique dissous (e.g. Chanton and Lewis, 1999), et (3) à l'équilibre entre disponibilité et demande en carbone inorganique (Riebesell, 1993). Le fait que certaines sources possèdent des gammes de $\delta^{13}C$ qui se chevauchent rend difficile la discrimination totale par le $\delta^{13}C$ des différents groupes de producteurs primaires. L'utilisation d'autres outils en complément peut permettre de mieux discriminer les différents producteurs primaires.

Le $\delta^{15}N$ des producteurs primaires dépend, comme le $\delta^{13}C$, des voies de synthèse organiques mais également de la signature isotopique des nutriments utilisés et de leur disponibilité (Montoya, 2008). Cependant, contrairement au $\delta^{13}C$, il n'existe pas de valeurs de $\delta^{15}N$ réellement caractéristiques de certains groupes de producteurs primaires en raison de la forte variabilité des signatures isotopiques des nutriments (Peterson, 1999).

1.3.4 Le fractionnement isotopique

La signature isotopique des consommateurs intègre celle de la nourriture assimilée et non pas uniquement de la nourriture ingérée. Lors du transfert de matière organique d'un producteur primaire à un consommateur primaire ou d'une proie à un prédateur, un fractionnement isotopique a lieu, conduisant à un enrichissement en isotopes lourds dans l'échelon supérieur (DeNiro and Epstein, 1978). Pour le carbone, il existe un équilibre entre différents processus biologiques conduisant à cet enrichissement : (1) une perte préférentielle du ^{12}C pendant la respiration, (2) une consommation des composés enrichis en $\delta^{13}C$ pendant la digestion et/ou l'assimilation, (3) un fractionnement métabolique pendant la synthèse des différents tissus (DeNiro and Epstein, 1978; Tieszen et al., 1983; Fry et al., 1984). Le fractionnement isotopique en carbone est relativement faible et relativement constant. Il se situe autour de 1‰ (DeNiro and Epstein, 1978; Checkley and Entzeroth, 1985; Post, 2002; Vander Zanden and Rasmussen, 2001; Vanderklift and Ponsard, 2003). L'enrichissement en $\delta^{15}N$ est principalement dû à une excréption préférentielle de ^{14}N , en général sous forme d'urée et d'ammonium (Minagawa and Wada, 1984). Le fractionnement isotopique en azote classiquement retenu est de 3,5‰ (DeNiro and Epstein, 1981). Si ce fractionnement isotopique semble effectivement correct pour les niveaux trophiques supérieurs (i.e. les consommateurs secondaires ; Minagawa and Wada, 1984; schoeninger and DeNiro, 1984; Peterson and Fry, 1987; Post, 2002), il peut s'avérer très variable, notamment entre les producteurs primaires et les consommateurs primaires (Ruess et al., 2004; MacNeil et al., 2005). Vanderklift and Ponsard (2003) rapportent un enrichissement moyen en $\delta^{15}N$ de $2,54 \pm 0,11$ ‰, basé sur un grand nombre d'articles comprenant aussi bien des carnivores que des herbivores. Il semble donc pertinent d'utiliser ce fractionnement dans les études de transfert de matière lorsque les organismes étudiés sont des herbivores potentiels. Nous avons donc logiquement choisi d'utiliser ce

fractionnement de 2,54 en azote et 1 dans le cadre de notre travail.

1.3.5 Les modèles de mélange

Les modèles de mélange permettent d'estimer les contributions relatives des différentes sources de matière organique à la production d'un consommateur en tenant compte du fractionnement isotopique et de la variabilité des signatures isotopiques des sources. Ces modèles sont des systèmes d'équations de bilan de masse basés sur les rapports isotopiques et/ou élémentaires. Ils sont utilisés aussi bien pour déterminer la composition relative d'un mélange de matière organique particulière (e.g. Schaal et al., 2010) que pour déterminer la composition relative des ressources trophiques d'un consommateur (e.g. Leduc et al., 2006). Etant donné le nombre important de sources potentielles de matière organique en milieu côtier, le système d'équations du modèle de mélange est souvent sous-déterminé : il y a plus d'inconnues (contribution de chaque source) que d'équations (nombre de traceurs + 1). Plus le système d'équations est sous-déterminé, plus l'incertitude associée au résultat du calcul de mélange est grande. Afin de minimiser cette incertitude, il est donc nécessaire d'augmenter le nombre d'équations et/ou de réduire le nombre de sources. L'augmentation du nombre d'équations passe par l'augmentation du nombre de traceurs utilisés. Classiquement, les modèles de mélange utilisent le $\delta^{13}C$ et le $\delta^{15}N$ de façon combinée.

Différents logiciels ont été développés afin de résoudre les systèmes d'équations des modèles de mélange, tels qu'IsoSource (Phillips and Gregg, 2003), MixSir (Moore and Semmens, 2008) ou SIAR (Parnell et al., 2010). IsoSource calcule et fournit par exemple l'ensemble des solutions possibles en prenant en compte une incertitude générale (tolérance) sur l'ensemble des traceurs. Il a l'avantage de permettre la résolution de systèmes déterminés, aussi bien que de systèmes sur- et sous-déterminés. Par contre l'incertitude associée aux valeurs d'entrée ne peut qu'être la même pour toutes ces valeurs. Ceci contraint l'utilisateur à n'utiliser que des traceurs de grandeurs et d'incertitudes équivalentes. SIAR et MixSir sont quant à eux basés sur des statistiques bayésiennes et fournissent une probabilité de solutions.

Au contraire d'IsoSource, SIAR et MixSir permettent d'associer une incertitude spécifique à chaque valeur d'entrée. Ces deux modèles sont fortement similaires et nous avons fait le choix d'utiliser SIAR sous la plate-forme logicielle R 2.14.

CHAPITRE 2

PRÉSENTATION DU SITE : L'ESTUAIRE DE LA GIRONDE

2.1 Description physique et hydro-morphologique

2.1.1 Morphologie

Avec une superficie de 625 km² à marée haute, l'estuaire de la Gironde (Fig.2.1) est le plus grand estuaire d'Europe occidentale. Il est situé sur la côte atlantique au sud-ouest de la France. L'estuaire, tel qu'il est considéré dans ce travail, correspond à la partie comprise entre la pointe du Verdon au contact de l'Océan Atlantique et la zone de confluence des deux systèmes hydrologiques que sont la Dordogne et la Garonne au niveau du bec d'Ambès, soit une longueur d'environ 76 km. Ce système fluvio-estuarien présente une largeur maximale d'environ 12 km dans sa section aval et 2,5-3 km dans sa partie amont. Suivant la morphologie du milieu, le système peut être divisé en deux zones distinctes :

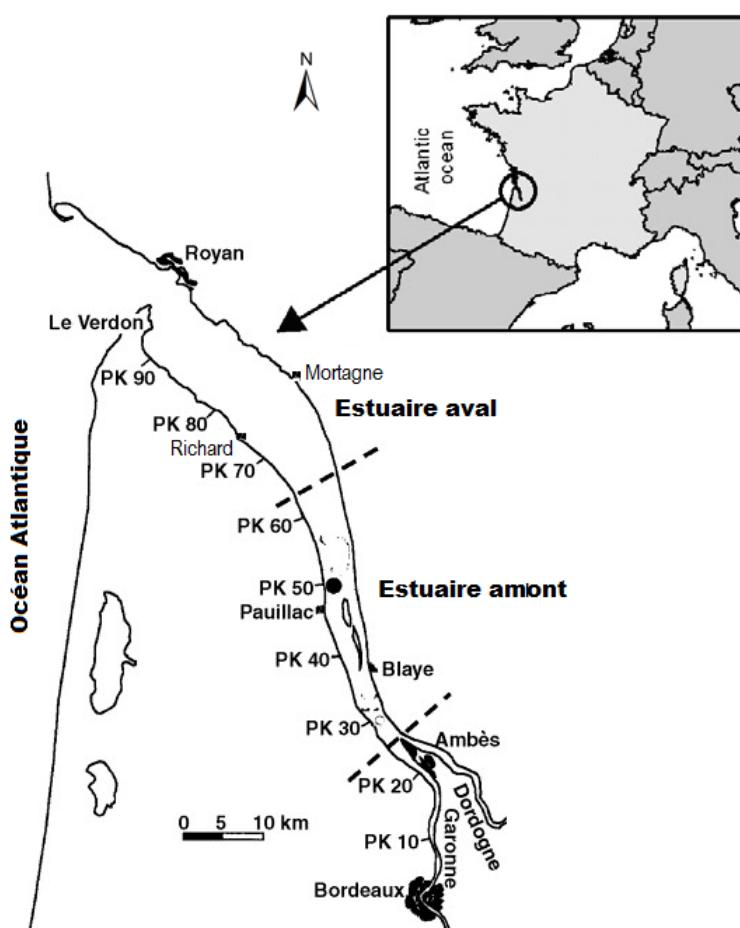


FIGURE 2.1 – Carte de la Gironde montrant la position de l'estuaire aval et de l'estuaire amont ainsi que les distances kilométriques à partir de Bordeaux (PK)

- L'estuaire amont, situé entre le bec d'Ambès et Pauillac (PK¹ 50) est caractérisé par un système de chenaux à méandres séparés par des barres de marée et des îles. La profondeur dans le chenal

1. Point kilométrique correspondant à la distance en kilomètre depuis la ville de Bordeaux prise comme point à 0 km

de navigation, situé le long de la rive gauche, varie entre 6 et 10 m.

- ④ L'estuaire aval, d'une morphologie plus simple est constitué par deux chenaux distincts séparés par des successions de barres de marée allongées. Le chenal principal suit la rive gauche. La profondeur moyenne, de l'ordre de 6 m(Cancino and Neves, 1999), est constante jusqu'à une rupture de pente localisée à 10 km en amont de l'embouchure (au niveau du PK 80). En aval de ce point, la profondeur augmente nettement pour atteindre 30 m à l'embouchure. C'est dans cette partie de l'estuaire que les zones intertidales atteignent leur largeur maximale avec plus de 3 km de largeur à marée basse près de Mortagne sur la rive droite et entre Le Verdon et le phare de Richard (PK 75) sur la rive gauche.

2.1.1.1 Conditions hydrologiques

Les conditions hydrodynamiques sont extrêmement variables du fait des interactions entre les flux d'origines marine et fluviale. Les apports d'eau douce sont très majoritairement liés aux débits fluviaux de la Garonne et de la Dordogne (Fig.2.2). La moyenne annuelle des débits fluviaux de l'ensemble Garonne + Dordogne se situe habituellement entre entre 500 et 1000 $m^3.s^{-1}$ mais des valeurs maximales de débit allant jusqu'à 7500 $m^3.s^{-1}$ peuvent être atteintes de manière très épisodiques (Cancino and Neves, 1999). Le débit moyen calculé sur la période comprise entre 1997 et 2009, correspondant à la période de notre étude était de 729 $m^3.s^{-1}$ (Données du Grand Port Maritime de Bordeaux, GPMB). Sur cette période les débits maximaux ont été atteints au mois de janvier 2001 avec une valeur de 6068 $m^3.s^{-1}$. Les minima ont été atteints au mois d'août 1998 avec un débit de 113 $m^3.s^{-1}$

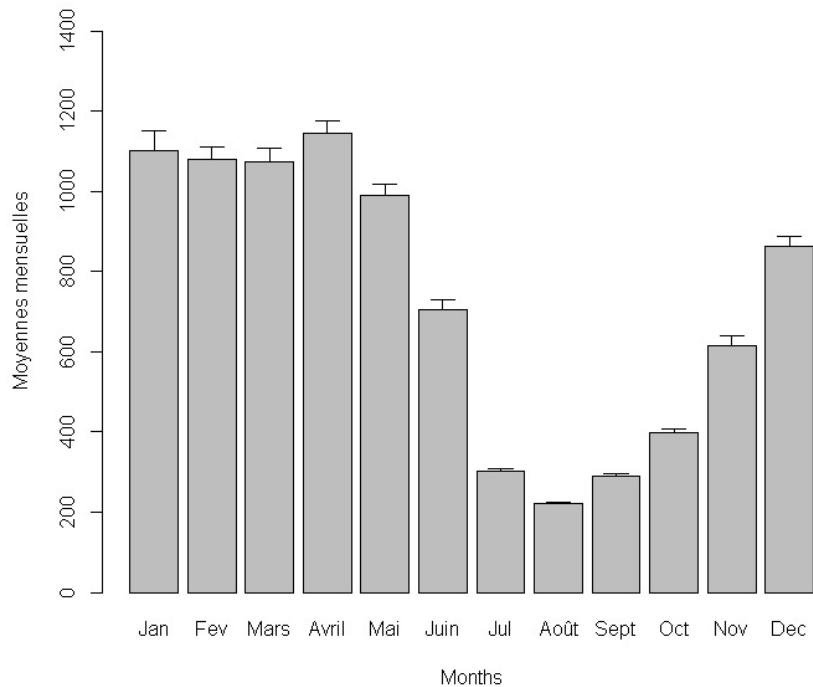


FIGURE 2.2 – Histogramme des débits liquides de la Gironde (Garonne + Dordogne). Moyennes mensuelles de 1997 à 2009 (Données fournies par Grand Port Maritime de Bordeaux, GPMB)

Le débit fluvial est fortement dépendant des précipitations et des conditions hydrologiques de l’ensemble du bassin versant. La région Aquitaine est sous l’influence d’un climat océanique tempéré. Les précipitations (Fig.2.3) fluctuent entre 50 mm en été et 100 mm d’eau en hiver (Tank et al., 2002) avec une moyenne journalière de 2,33 mm d’eau, calculée sur l’ensemble de la période comprise entre janvier 1999 et février 2009 (Données Météo France). Si on se réfère à cette valeur, l’ensemble de l’estuaire recevrait un apport journalier direct d’eau douce par précipitation équivalent à environ $24 \text{ m}^3.\text{s}^{-1}$. En revanche, les apports latéraux d’eau douce sont mal connus à l’heure actuelle. Toutefois, afin de mener notre étude, nous avons considéré ces flux latéraux d’eau comme négligeables au regard des débits de la Garonne et de la Dordogne.

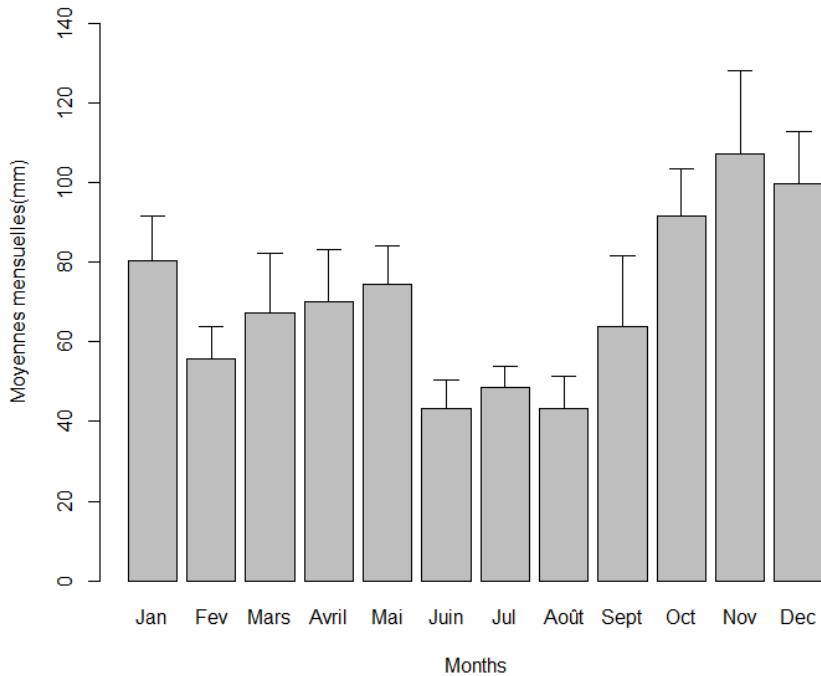


FIGURE 2.3 – Histogrammes représentant les moyennes mensuelles et les écarts-types des hauteurs des précipitations (mm d'eau) mesurées à la station de Royan de 1997 à 2009 (Données Météo France)

L'influence de la marée doit être considérée en distinguant la marée dynamique et la marée saline. La marée dynamique correspond à la pénétration de l'onde de marée dans l'estuaire et se traduit par une variation du niveau de l'eau. En raison des forts débits fluviaux, l'onde de marée subit un amortissement qui empêche la propagation de celle-ci beaucoup plus loin dans les eaux fluviales. La marée saline quant à elle ne concerne qu'une fraction plus limitée du système fluvio-estuarien de la Gironde, elle est limitée, en amont par la limite de l'intrusion saline (SIL). La limite amont de la position moyenne de l'intrusion saline est localisée au PK 35 pendant les faibles débits fluviaux et au PK 70 pendant les forts débits (Cancino and Neves, 1999). Durant les périodes de forts débits, une forte advection fluviale réduit l'impact de la marée dynamique dans la partie amont de l'estuaire et repousse la limite tidale beaucoup plus en aval.

L'estuaire de la Gironde se présente comme un estuaire macrotidal avec une amplitude de marée qui varie entre 1,5 m lors des marées de faible coefficients et 5,5 m lors des marées de forts coefficients. L'onde de marée atteint une hauteur de 6 m aux environ de Bordeaux (à 100 km de l'embouchure) avant de subir une atténuation 70 à 80 km en amont de Bordeaux pendant les périodes de faibles débits (Sottolichio and Castaing, 1999; Cancino and Neves, 1999). La courbe du marégraphe est symétrique à l'embouchure aux alentours du Verdon. Cependant une asymétrie assez marquée se développe en amont, prolongeant le jusant et réduisant la durée du flot. Dans le chenal de navigation, les vitesses de courant atteignent $3 \text{ m}^3.\text{s}^{-1}$ en surface et $1,5 \text{ m}^3.\text{s}^{-1}$ à proximité du fond au cours des

marées de vives eaux. La circulation résiduelle résulte de la confrontation de deux phénomènes : la marée en aval et le débit fluvial en amont, mettant en jeu deux masses d'eaux aux caractéristiques différentes. Les courants résiduels produits par les phénomènes d'advection liés aux gradients verticaux de densité sont orientés d'une façon générale vers l'amont au fond et vers l'aval en surface (Fig 2.4). Dans l'estuaire aval, le flux résiduel est dirigé vers l'amont dans sa partie sud et vers l'aval dans la partie nord. L'embouchure présente un schéma de circulation assez complexe (Fig 2.4 Cancino and Neves, 1999).

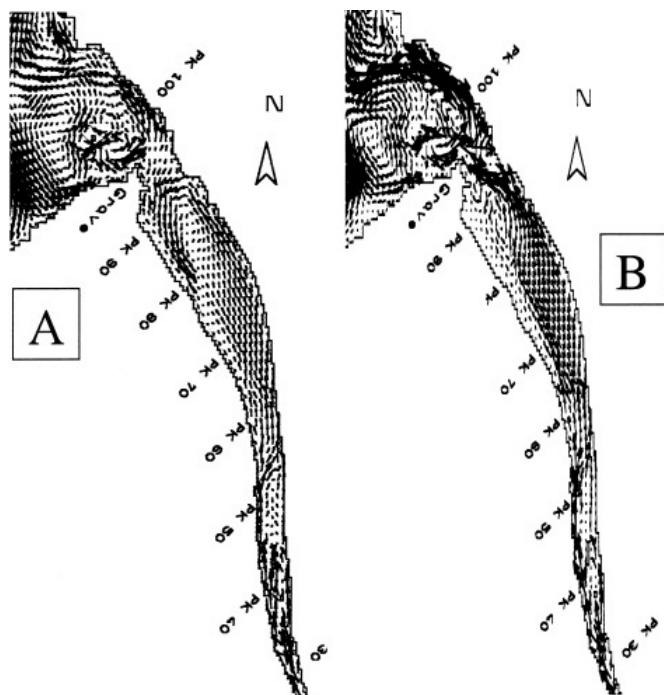


FIGURE 2.4 – Flux résiduel des courants dans l'estuaire de la Gironde. (A) Vitesse barométriques résiduels à la surface ; (B) Flux résiduels intégrés sur la profondeur d'après Cancino and Neves (1999).

Dans de telles conditions hydrodynamiques le temps nécessaire pour remplacer l'eau douce introduite dans l'estuaire peut varier de quelques jours à plusieurs mois tandis que les particules, elles, peuvent séjournner plusieurs années, notamment dans la zone de maximum de turbidité (Bouchon vaseux). Les valeurs de temps de résidence estimées à l'heure actuelle dans le milieu varient de 20 à 86 jours (soit 3 mois : Jouanneau and Latouche, 1981)

2.1.1.2 Températures

Les températures de l'eau et de l'air agissent sur les organismes benthiques et planctoniques. Les valeurs de température de l'eau dans l'estuaire de la Gironde varient entre 6 °C en hiver et 25 °C en été (Fig 2.5, Données issues de la base de donnée SOMLIT. Moyennes mensuelles depuis 1997)

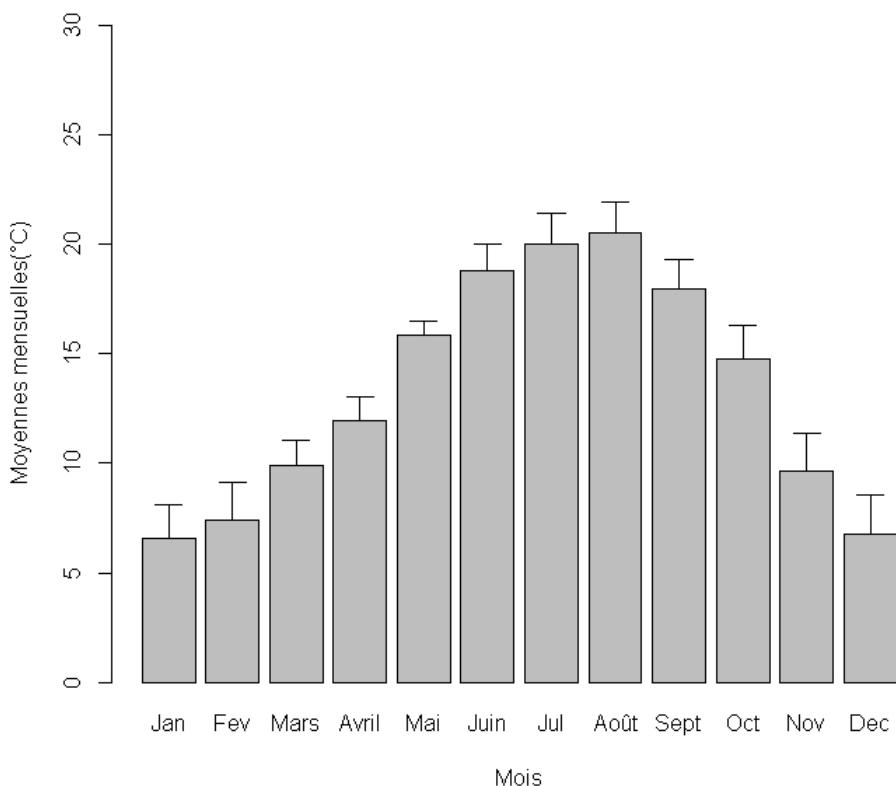


FIGURE 2.5 – Évolution saisonnière des températures de l'eau à quatre stations d'échantillonnage (PK 30, PK52, PK67, PK86) le long du gradient de salinité de l'estuaire de la Gironde. Données calculées à partir de la base de données Somlit/Blayais.

La différence de températures entre les eaux fluviales et les eaux marines peut être supérieure à 3°C. Un gradient longitudinal de température le long de l'axe amont aval est donc généralement observé. Le gradient vertical quant à lui est plus marqué en aval où une stratification entre les eaux néritiques de fond et les eaux estuariennes de surface s'effectue (système bi-couche, Castaing, 1981). L'évolution des températures de l'eau depuis les 30 dernières années a fait l'objet de nombreuses recherches du fait de son rôle primordial dans les processus biologiques. Il ressort que les eaux de l'estuaire ont subi un réchauffement d'environ +2°C au niveau du PK 52 (David et al., 2005)

2.1.2 Caractéristiques biogéochimiques

2.1.2.1 L'oxygène dissous

Le niveau d'oxygène est un bon indicateur de la capacité d'un milieu à supporter la vie. L'oxygène en milieu aqueux provient à la fois des échanges atmosphériques entre l'air et l'eau ainsi que de l'activité photosynthétique des plantes. Des chutes des niveaux d'oxygène peuvent cependant résulter du métabolisme des organismes aquatiques liés au processus de respiration, de la décomposition de la matière organique par les bactéries, ou encore de l'oxydation chimique de composés organiques et

inorganiques..

Alors que de nombreux estuaires font face à des déficits en oxygène dans leur zone de turbidité maximum (Parker et al., 1994; Mitchell et al., 1999; Uncles et al., 1998), l'estuaire de la Gironde présente des niveaux d'oxygénation relativement élevés (80 à 95 % de saturation : Etcheber et al., 2007). Il peut être considéré comme bien oxygéné sur presque toute la colonne d'eau, en dépit des conditions hypoxiques saisonnières dans la lentille de vase durant les conditions de faibles débits (Abril et al., 1999). Cependant des zones de faibles concentrations en oxygène sont également observables dans la Gironde, généralement dans sa partie amont (amont du PK 30) avec des valeurs pouvant descendre en deçà de 30% de saturation. Ces conditions exceptionnelles d'hypoxie sont observées en fin de marée basse aux alentours de Bordeaux en période estivale marquée par des conditions d'étiage.

2.1.2.2 Les sels nutritifs

Les nitrates sont à des concentrations souvent supérieures à $100 \mu\text{mol.L}^{-1}$ et représentent à eux seuls environ 90% de l'azote minéral. Les silicates dépassent largement $70 \mu\text{mol.L}^{-1}$. Quant aux phosphates, des valeurs comprises entre 2 et $4 \mu\text{mol.L}^{-1}$ ne sont pas rares dans les eaux de l'estuaire (Deborde et al., 2007). van Spaendonk et al. (1993) estiment que la comparaison des concentrations avec les constantes de demi-saturation (Ks) pour chaque élément permet de déterminer les seuils de limitation de la production primaire. Ainsi les concentrations en dessous des différents Ks proposés limitent la croissance des organismes photosynthétiques. Si l'on compare les valeurs de l'estuaire aux constantes de demi-saturation proposées par van Spaendonk et al. (1993), il apparaît que les concentrations en nutriments dans l'estuaire de la Gironde sont telles qu'elles ne peuvent pas être considérées comme des facteurs de limitation de la production primaire. Cependant, compte tenu de la forte turbidité des eaux estuariennes, la production primaire autochtone phytoplanctonique est probablement très faible voire inexistante (Irigoinen and Castel, 1997a).

TABLE 2.1 – Comparaison des valeurs de nutriments ($\mu\text{mol.L}^{-1}$) mesurées dans l'estuaire de la Gironde avec les valeurs de seuil de demi-saturation (Ks) susceptibles de limiter la production primaire selon van Spaendonk et al. (1993)

Nutriments	Estuaire de la Gironde	Concentration limites (Ks) proposées par Spaendoek (1993)
Nitrates + Ammonium	56-160	1-2
Silicates	63-121	1-5
Phosphates	0.7-1.3	0,1-0,5

2.1.2.3 Matières en suspension (MES)

L'estuaire de la Gironde est marqué par de très fortes concentrations en matières en suspensions (MES) de la colonne d'eau. Dans la zone concernée par cette étude (PK30 - PK90), les concentrations en MES varient entre 16 et 3554 mg.L⁻¹ avec une forte variabilité spatiale et temporelle. Cette forte concentration en matière en suspension est le fait, en partie, des mouvements résiduels du milieu. Il existe en effet, au niveau de la zone de l'intrusion saline de l'estuaire, une zone connue sous le nom de «point nodal» où les courants résiduels s'annulent, résultant en une sédimentation des particules en suspension. Il se forme alors une lentille de vase qui donnera lieu par la suite à une large zone dite bouchon vaseux. Les particules sont donc piégées dans cette zone qui, sous l'action des variations de courants de marée liées au cycle tidal et des courants liés aux débits fluviaux, va se déplacer vers l'aval ou vers l'amont de l'estuaire.

L'estuaire de la Gironde est donc marqué par cette zone de turbidité maximale avec des concentrations de matières en suspension > 1 g.L⁻¹ (Castaing, 1981). Pendant les périodes de bas débits et de mortes eaux, la sédimentation des matières en suspension est très prononcée et la vase fluide (en moyenne MES > 10 g.L⁻¹, jusqu'à 30 g.L⁻¹ apparaît dans le fond du chenal formant des tâches allongées de 10 à 15 km sur une épaisseur environ 2 m (Sottolichio and Castaing, 1999). La masse sédimentaire représentée par le bouchon vaseux dans l'estuaire de la Gironde représenterait entre 4.10⁶ et 5.10⁶ tonnes de sédiments.

2.1.3 Caractéristiques biologiques

2.1.3.1 Producteurs primaires

Les études réalisées jusque-là ont révélé que l'estuaire de la Gironde présente de très faibles biomasses phytoplanctoniques comparées à d'autres estuaires nord-Européens avec de faibles variations saisonnières de la chlorophylle-a (Lemaire et al., 2002). Ceci est à mettre en relation avec une production primaire phytoplanctonique très faible en raison de la forte turbidité mesurée dans les parties amont et médiane de l'estuaire (Irigoin and Castel, 1997a). Il existe toutefois en Gironde, comme dans bon nombre de systèmes, un gradient horizontal de productivité croissante en direction de la mer où la turbidité décroît et la pénétration de la lumière augmente (Cloern et al., 1985). Goosen et al. (1999) ont en effet montré que la production primaire du phytoplancton était extrêmement faible en amont (PK 30) et augmentait progressivement vers l'embouchure de l'estuaire (PK 100), en dépit de la faible concentration de chlorophylle (production primaire mesurée à l'aide de la méthode du carbone 14). Du fait des fortes turbidités, les blooms de phytoplancton sont limités aux aires et pé-

riodes de faibles concentrations en MES, généralement apparaissant pendant l'été et situé seulement dans la partie aval de l'estuaire (Irigoien and Castel, 1997a). Il semblerait donc que dans le bouchon vaseux, il n'y ait pas ou peu de production primaire planctonique possible et que la biomasse chlorophyllienne soit localement due en partie à la remise en suspension du microphytobenthos issues des vasières intertidales et/ou à des particules végétales détritiques (Irigoien and Castel, 1997a). Dans cette zone, les fortes valeurs de chlorophylle *a* ($20 \mu\text{g.L}^{-1}$) seraient d'avantage liées à la présence du bouchon vaseux, qui joue un rôle de piège à particules, et non à une production autochtone (Maurice and Romana, 1993). A l'échelle de l'estuaire, Irigoien and Castel (1997a) estiment que la production phytoplanctonique totale n'excède pas $5 \text{ gC.m}^{-2}.\text{an}^{-1}$.

2.1.3.2 Consommateurs

Faune planctonique

La composition faunistique des communautés du plancton estuarin est majoritairement dominée par l'holoplancton alors que le meroplancton principalement constitué par des larves d'annélides, de mollusques et de cirripèdes, est presque inexistant dans l'estuaire (Feral, 1994).

Dans l'estuaire de la Gironde comme dans la plupart des estuaires nord Européens, l'holoplancton se compose essentiellement de copépodes (Sautour and Castel, 1995) et des Mysidacées (David et al., 2005). Ces deux taxons (copépodes et mysidacées), se caractérisent par leur paucispécificité mais de fortes biomasses (David et al., 2006a). La distribution des différentes espèces présente une variabilité spatiale très marquée d'une espèce à l'autre (Fig 2.6) probablement liée à la disponibilité de proies dans le milieu mais également liée à leur préférendum halin et thermique (McLusky, 1981; Sautour and Castel, 1995). Ainsi, le copépode *Eurytemora .affinis* et le mysidacé *Neomysis integer* semblent inféodés à la zone amont de l'estuaire qui représente le centre de distribution pour ces espèces.

A contrario, les copépodes du genre *Acartia* et le mysidacé *Mesopodopsis slabberri* préfèrent des salinités plus importantes et colonisent donc préférentiellement la zone méso-polyhaline de l'estuaire (David et al., 2006a).

Sur un cycle annuel, le maximum d'abondance du copépode *Eurytémora affinis*, se situe entre avril et mai, et juin pour le mysidacé *N.integer* et entre août et septembre pour les deux autres groupes (David et al., 2005; Selleslagh et al., 2012) Fig.2.7.

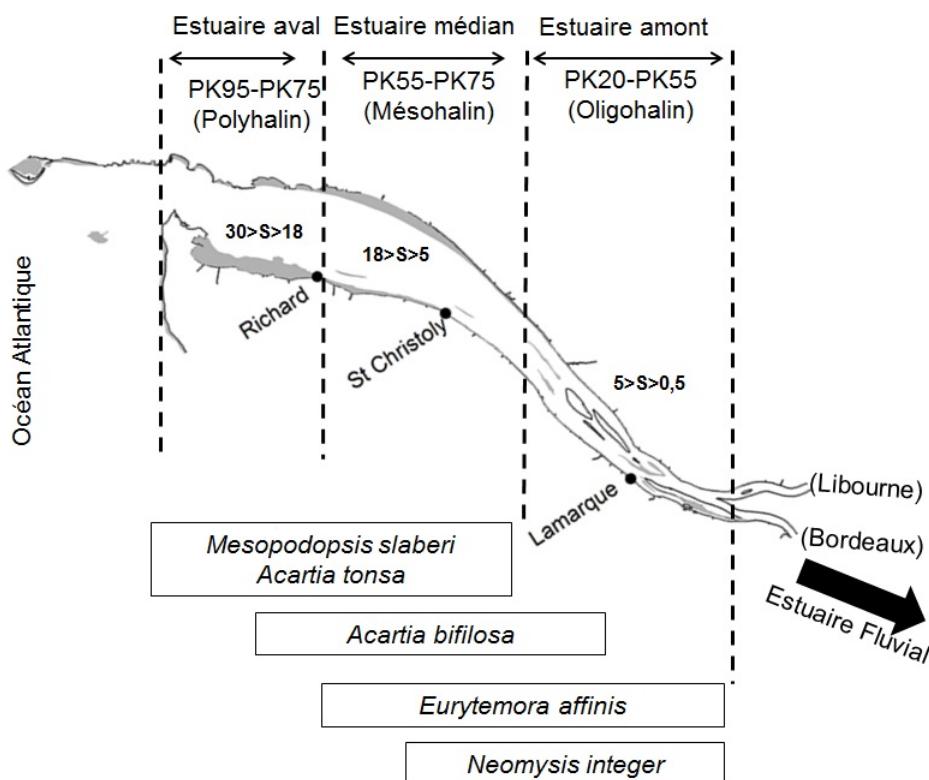


FIGURE 2.6 – Distribution longitudinale des principales espèces de zooplancton le long du gradient de salinité et rôle de la salinité dans la répartition des espèces (adapté de Mees et al. (1993)).

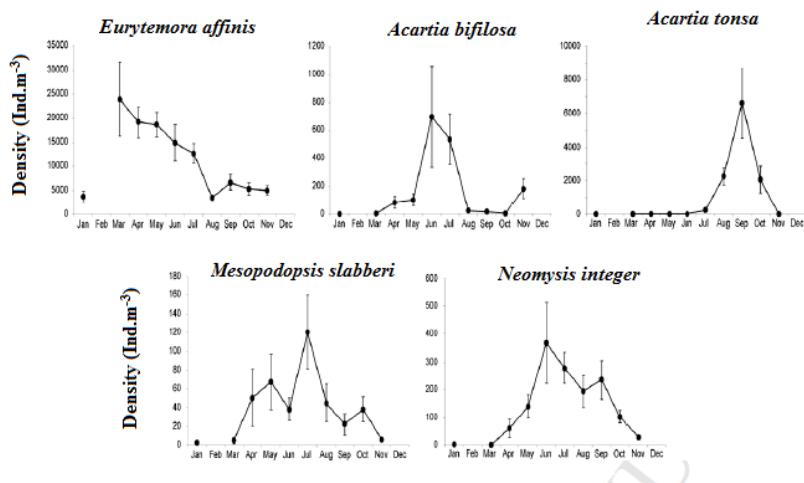


FIGURE 2.7 – Moyenne mensuelle (± écart-type) des abondances (Ind.m⁻³) des espèces du zooplancton entre 2004 et 2008 (Selleslagh et al., 2012)

Faune benthique

La macrofaune benthique de la zone étudiée se caractérise par un faible nombre d'espèces adaptées aux contraintes écologiques particulières de l'estuaire de la Gironde. Les peuplements de macrofaune présentent divers aspects de la communauté à *Macoma balthica* (Bachelet, 1979, 1980;

2.1 Description physique et hydro-morphologique

Borja et al., 2004). Ces peuplements montrent en effet un nombre d'espèces décroissant de l'aval vers l'amont de l'estuaire. Les organismes macrobenthiques présentent des abondances élevées (plusieurs milliers d'individus par m²), bien que très variables, dans les zones intertidales situées dans la partie aval de l'estuaire. Les zones subtidales, en revanche, se distinguent par des peuplements benthiques extrêmement clairsemés (Bachelet, 1979; Blanchet et al., 2004, Fig.2.8).

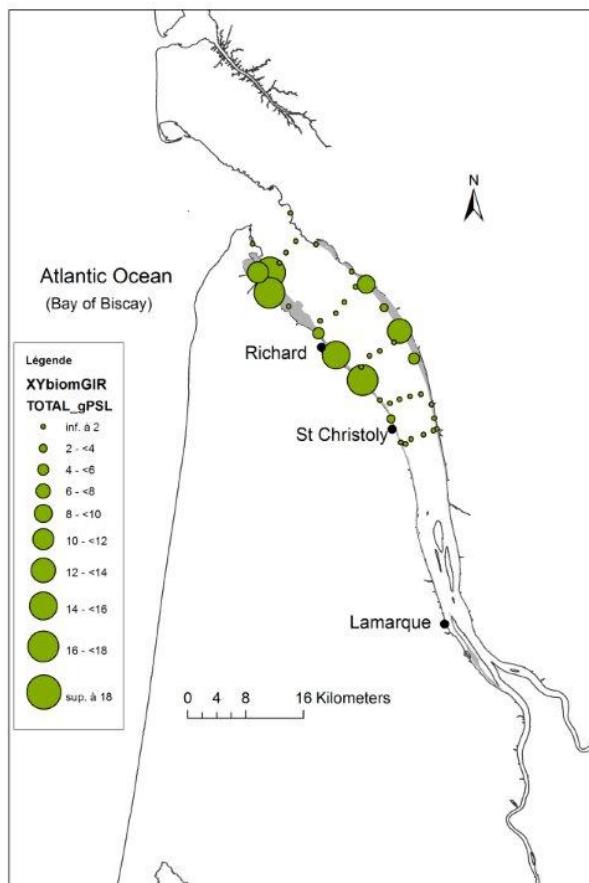


FIGURE 2.8 – Biomasses de la macrofaune benthique des zones subtidales et intertidales de l'estuaire de la Gironde. Données de l'Automne 2008 (Blanchet and Gouillioux, com. pers.)

La méiofaune est principalement composée de nématodes. Les densités sont, là encore nettement plus élevées sur les estrans où elles sont de l'ordre de 750 à 7500 ind.10cm⁻² que dans les chenaux (10 à 100 ind.10cm⁻², Castel et al., 1994).

2.1.3.3 Prédateurs

Ichtyofaune

L'ichtyofaune est riche et très diversifiée. Environ 75 espèces de poissons, appartenant à plusieurs guildes écologiques fréquentent régulièrement les eaux estuariennes (estuairegironde.net/est/ceg-409.html).

On note particulièrement la présence dans le milieu de 11 espèces de migrants amphihalins classiquement et historiquement recensées en Europe de l'Ouest (Lobry et al., 2003). Il apparaît donc que l'estuaire de la Gironde est un espace globalement préservé (Mauvais and Guillaud). L'estuaire est notamment identifié comme lieu de passage, de migration pour de nombreuses espèces en relation avec la fonction de nourricerie qu'on confère aux milieux estuariens. En effet, en analysant l'abondance des différentes guildes, Lobry (2004) a montré que seuls 8% d'espèces pouvaient accomplir leur cycle écologique entièrement dans l'estuaire, dont notamment le gobie buchotte (*Pomatoschistus minutus*), qui est le poisson autochtone le plus abondant. Le reste est composé d'espèces effectuant des migrations saisonnières tels que les migrants juvéniles (23%) ou apparaissant de façon périodique comme les poissons dulçaquicoles (20%) ou marins apparaissant irrégulièrement (23%). Les migrants amphihalins, quant à eux, représentent 15% des migrants alors que seuls 11% sont des espèces marines temporaires. Les assemblages de poissons se structurent selon un cycle saisonnier le long du gradient amont-aval avec une opposition surface-fond marquée. Les espèces pélagiques, généralement marines, sont plus présentes en été et les espèces benthiques et démersales, en majorité sédentaires en hiver (Lobry, 2004).

2.1.4 Pressions et impacts sur le milieu

L'estuaire de la Gironde est l'un des plus vastes de l'Europe de l'ouest par sa superficie. La population aux abords de l'estuaire est estimée à $1,2 \cdot 10^6$ habitants (Feral, 1994). Comme beaucoup d'autres systèmes, l'estuaire de la Gironde fait l'objet de diverses pressions anthropiques plus ou moins localisées dans le milieu : l'entretien du chenal de navigation, la construction de ports et l'artificialisation des berges, l'extraction de granulats, la pêche, des contaminations chimiques, et du pompage d'eau à grand débit (Mauvais and Guillaud).

2.1.4.1 Entretien du chenal de navigation

Pour des raisons économiques liées à la navigation des navires, l'activité de dragage dans l'estuaire de la Gironde est réalisée par le Grand Port Maritime de Bordeaux (GPMB). Celle-ci permet de maintenir une superficie d'environ 18 km^2 de chenal de navigation. Typiquement, chaque année, environ 8 850 000 tonnes de sédiments sont extraites (près de 24 000 tonnes par jour, Audry et al. (2007)). Après chaque opération de dragage, la vase est transportée à la sortie de l'estuaire où elle est claquée en dehors du chenal de navigation où les forts courants de marée favorisent sa dispersion. Cette activité contribue cependant à maintenir le degré élevé de turbidité dans l'estuaire.

2.1.4.2 Installations portuaires et construction de ports

Historiquement, le système fluvio-estuaire Gironde-Dordogne-Garonne a hébergé une activité portuaire importante avec, à l'heure actuelle, six principaux pôles portuaires : Bordeaux et Bassens, situés sur la Garonne et Ambès, Blaye, Pauillac et Le Verdon, situés dans l'estuaire de la Gironde. L'ensemble de ces terminaux sont gérés par Bordeaux Port Atlantique (Port Autonome de Bordeaux) et engendrent un trafic compris entre 8 et 9 millions de tonnes de marchandises (8 381 128 tonnes en 2011 (données Bordeaux Port Atlantique)). Ces différents centres portuaires sont chacun spécialisés :

- le port de bordeaux est dédié à l'accueil des navires de croisière
- le terminal de Bassens est dédié au trafic de céréales, de conteneurs, de produits forestiers et des colis lourds ;
- le terminal d'Ambès est un pôle pétrochimique ;
- le port de Blaye est dédié aux céréales et aux liquides ;
- le terminal portuaire de Pauillac est utilisé pour la logistique Airbus et les trafics d'hydrocarbures ;
- le port du Verdon L'avant-port pour les trafics conteneurs et les escales de croisières

Un septième terminal (Grattequina, sur la Garonne), dédié aux trafics de colis lourds et aux granulats, est en cours de développement. A ces structures s'ajoutent une quarantaine de petits ports dédiés à la plaisance et à l'activité de pêche. Le plus récent aménagement de port est la création du complexe Port Médoc, inauguré en 2004, situé sur la rive gauche, en face de Royan, sur le site de La Chambrette. L'installation de cet ensemble sur 15 Ha, a eu pour conséquence la disparition de la vasière préexistante avec des conséquences importantes sur la macrofaune benthique (Lucia, 2005).

2.1.4.3 Endiguement et Artificialisation des berges

L'artificialisation des berges de l'estuaire est évidente puisque l'estuaire inclurait environ 130 km de digues. Il s'agit d'un phénomène ancien avec une poldérisation très importante au cours des XVII^{ème} et XVIII^{ème} siècles au cours desquels les marais du bas Médoc ont été polderisés par des ingénieurs flamands et hollandais (Buffault, 1897). Ces aménagements ce sont traduits par d'importants changements de l'aspect de l'estuaire (Fig.2.9).

2.1.4.4 Pollutions chimiques

L'estuaire de la Gironde est considéré comme relativement peu pollué (Lobry, 2004) mais le système présente toutefois de nombreuses agressions liées aux activités humaines et par conséquent une augmentation de la pollution dans l'eau et les sédiments du fait des contaminations chimiques. Il



FIGURE 2.9 – Carte du Bas Médoc avant les travaux de poldérisation, issue de l'ouvrage de Buffault (1897)

est connu pour être affecté par une importante pollution chronique polymétallique (Cd, Zn, Cu, As et Hg) historique liée aux anciennes activités minières et de traitement du mineraï (Blanc et al., 1999; Boudou, 2002; Durrieu et al., 2005). L'origine de cette pollution se situe en amont de l'estuaire dans le bassin de Decazeville où les eaux de lessivage enrichies en MES chargées en cadmium (Cd) et en zinc atteignent l'estuaire après un passage par le Riou-Mort, le Lot puis la Garonne (Lapaquellerie et al., 1996). Les polluants organiques (HAP et PCB) sont également présents mais l'estuaire ne serait que peu marqué (Budzinski et al., 1997). Les teneurs en micropolluants organiques (PCB et HAP) sont parfois préoccupantes.

CHAPITRE 3

MISE EN ÉVIDENCE DE L'INFLUENCE DE
L'HYDRODYNAMISME SUR LA PRODUCTION PRIMAIRE AU
MOYEN D'UN MODÈLE DE TRANSPORT-RÉACTION

3.1 Introduction du chapitre 3

Ce chapitre est présenté sous la forme d'une publication scientifique en préparation. Il est le fruit d'une collaboration avec Karline Soetaert du NIOO aux Pays-Bas et a été présenté oralement au congrès international de modélisation en Italie (Ecological modelling, Riva del garda, Italy-2010).

Le précédent chapitre a présenté les principales caractéristiques de l'estuaire de la Gironde, notre site d'étude. Dans ce chapitre, il s'agit de faire le lien entre la production primaire du milieu et certaines de ces caractéristiques. La principale question que nous abordons dans le présent chapitre est celle de l'existence ou non de la production primaire phytoplanctonique dans l'estuaire de la Gironde, un milieu extrêmement turbide. Il s'agit donc d'expliquer les variations de la biomasse phytoplanctonique observées par les fluctuations des concentrations en chlorophylle *a* dans la colonne d'eau.

Du fait des multiples facteurs susceptibles d'influencer la dynamique spatiale et temporelle de la production phytoplanctonique en milieu estuaire, nous avons choisi d'aborder la question sous l'angle de la modélisation mathématique. Le modèle choisi pour la présente étude est un modèle de transport et réaction qui permet de faire la part entre le simple transport physique de la chlorophylle *a* et sa réaction en lien avec une dynamique biologique.

En calculant donc la résultante entre les résultats du modèle et les données disponibles, nous nous proposons de répondre à un certain nombre de questions qui renseignent sur le comportement du phytoplancton dans l'estuaire de la Gironde et donc de sa production dans la colonne d'eau. Les questions que nous nous posons reposent essentiellement sur la capacité du milieu à soutenir une activité de production locale de phytoplancton. Si tel est le cas, quelles sont les zones susceptibles de développer une telle activité ou sinon, quel est le moteur de la production primaire dans les eaux de la Gironde.

Evidence for the influence of Hydrodynamic as a driver for primary production in a highly turbid and macrotidal estuary (The Gironde, France) by means of a one dimensionnal Reactive and Transport model

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3.2 Abstract

In most macro tidal and turbid systems, both light limitation and flushing times are the two important drivers that can affect primary production. In this paper, we applied a tidally-averaged one-dimensional, transport and reaction model to examine chlorophyll and nutrients (NH_4^+ , NO_3^- and O_2) dynamics under hydrodynamics constraints in the Gironde estuary, one of the most turbid macrotidal estuary among the west European systems. This was done in two steps. We first used a transport model to simulate salinity data and used this to dynamically estimate both the estuarine residence times and constant dispersion coefficient. Next we fitted the transport model to observed chlorophyll *a* and dissolved nutrients in order to estimate algal production and biogeochemical processes rates. Finally, a mass budget calculation was realized to calculate the amount of outwelling of nitrogen from the estuary. The model was numerically solved in R considered as a simulating platform and model outputs were confronted with data available at two different stations in-between the boundaries. The model reasonably reproduced the observed longitudinal profiles of simulated variables. Nitrification was identified as the major process in the water column, consuming NH_4^+ and producing about 20% of nitrogen leaving the estuary. Estimates of different rates were considerably low and the estuarine production strongly depends on inputs with the advective transport.

Keywords : Estuary, Nutrients, Primary production, Residence time, 1D Reactive-transport model, Gironde estuary

3.3 Introduction

Estuaries receive high riverine amounts of allochthonous nutrients and organic matter characterized by its high refractory nature in comparison to marine particulate organic matter (Abril et al., 2002; Blair et al., 2004; Etcheber et al., 2007; Keil et al., 1997). Estuaries are well known to modify transfers from river to coastal sea of both dissolved (e.g. nitrogen (N) Billen et al. (1991)) and particulate compounds (e.g. cycles of deposition and resuspension and oxic/anoxic oscillation. Among the processes that affect the estuarine dynamics, primary production can have a strong effect since it increases dissolved oxygen and consumes dissolved inorganic nitrogen (N) and phosphorus (P) from water column. Two important drivers can affect primary production in macro tidal estuaries : *i*) The turbidity that strongly limits photosynthesis (Cole et al., 1992; Irigoien and Castel, 1997a) determines for a large part the auto-/heterotrophic status of the estuaries and *ii*) The residence times which determine the quantity and quality of constituents that reaches the sea (Wollast, 1983). Macrotidal estuaries are characterized by high turbidity, resulting from strong tidal currents and bottom re-suspension of fine particles that limit phytoplankton growth (Muylaert and Sabbe, 1999). Photosynthesis, the process through which phytoplankton biomass increases is hence strongly limited due to light availability. In such systems, respiration or consumption of organic matter largely exceeds production and the system is heterotrophic (Billen et al., 1995; Garnier et al., 2001; Gattuso et al., 1998; Goosen et al., 1999). However, locally, positive values of net production can be observed when conditions are more favourable to primary producers. For instance, in the seaward direction where suspended matter concentration decreases and light availability increases, an increased phytoplankton production exists in many estuaries (Cloern et al., 1985). This local production can be transported upstream and can explain the patterns of phytoplankton biomass variability in some estuaries. Primary production and biological processes in estuarine environments are affected by physical forcings at a variety of scales (Lewis and Platt, 1982). Because estuaries are major land-ocean interfaces, particles are transported through them before they can reach the coastal zone and the ocean. Local changes in nutrients and phytoplankton concentrations are affected by horizontal transport (Lucas et al., 1999). Tides, currents and river water discharge as well as complicated geomorphological structure of such systems have a major impact on the ecology and water quality. Factors such as water residence time (Ketchum and Institution, 1952; Lucas et al., 1999; Tett et al., 2003), salinity tolerance, light, nutrients and grazing control phytoplankton growth (Ferreira et al., 2005). The estuarine residence time is a master variable that determines the relative importance of biological and physical processes. The longer the quantity spends in the estuary, the more it will be altered by biological processes. With respect to algae, the residence time determines whether they stay long enough in the system to generate an algal bloom, such that

systems with short residence times are expected to have lower algal biomass. Residence times also affect other estuarine processes such as primary production. Residence times act on primary production and can thus be used to characterize an estuary (Braunschweig et al., 2003). In short-residence time estuaries, autochthonous processes are negligible and POM composition can easily be modelled as a conservative mixing between continental and marine end-members ; in contrast, in long residence time estuaries (e.g. macro tidal estuaries), autochthonous processes such as primary production and bacterial reworking of POM cannot be neglected (Middelburg and Herman, 2007). The relationship between nutrients, oxygen and primary production is widely acknowledged. Based on the precepts that phytoplankton biomass (as chlorophyll *a* concentration) is a meaningful indicator of ecosystem trophic status and is regulated by the nutrient resources (Cloern, 1999), several approaches have been used to describe algal biomass as a function of nutrient loading and oxygen levels. Because phytoplankton assimilates nutrients and the estuarine blooms can thus impact nutrients fluxes to coastal waters (Admiraal and van der Vlugt, 1990; Jordan et al., 1991). As a consequence, the change in both nutrients and oxygen levels can thus be used as a good indicator of the ability of a system to support life. Here, we hypothesized that primary production was mainly controlled by transport and mixing processes along the estuarine gradient of a highly turbid estuary. Consequently, dissolved compounds might exhibit conservative situation as they are not consumed or produced within the system. Models that combine physics and biological processes are good tools to evaluate the different processes that change the composition of biological quantities in natural systems. However, complete hydrodynamic models are difficult to develop, are not always available, and due to computational constraints, they may not be the best suited to answer specific biological questions. An alternative to complex 3-D hydrodynamic models for estuarine systems are tidally-averaged applications that describe the flow of matter across supposedly homogeneous compartments. Traditionally such models have been developed and used to investigate the fate and transport of a selected set of chemical constituents within a given compartment of the Earth system (Soetaert et al., 1996; Regnier and O’Kane, 2004; Thomann and Mueller, 1987). One advantage of the 1-D tidally averaged description is that it is relatively simple to estimate the estuarine residence time. This has been done for the Scheldt estuary by Soetaert et al. (1996) using a very simple box model comprising only 13 compartments that cover 100 km of length. The present paper use the same approach, based on data collected in the oligo-mesohaline part of the Gironde estuary, to investigate the hydrodynamic influence on the estuarine primary production. The Gironde estuary is considered as a model of a typical highly turbid (concentration of suspended matter up to 10 g.L^{-1} ,(Allen et al., 1974)) macrotidal system of western Europe. This maximum turbidity zone, due to an asymmetric tidal wave, is displaced along the estuary according to river flows and tidal cycles (Sottolichio and Castaing, 1999). Consequently, primary production is limited by light

availability (Irigoien and Castel, 1997a; Goosen et al., 1999) and physical constraints. The estimated and mostly used residence time values are classically described to range from 20 days to 86 days (Jouanneau and Latouche, 1981; Pham et al., 1997; Romana and Breton, 1982). We applied a simple one-dimensional reactive transport model in order to determine the effect of hydrodynamical transport on algal and nutrients dynamics. The model was first used as transport only to observed salinity data. Next, the obtained constant dispersion coefficient was used to fit a reaction and transport model to chlorophyll and dissolved nutrients data. Finally, residence times and nutrients inputs fluxes at the system boundaries are estimated by the transport model.

3.4 Material and Methods

The Gironde ($45^{\circ}20'N$, $0^{\circ}45'W$) is a macro tidal coastal plain-type estuary, located in the southwest of France, discharging into the Atlantic Ocean (Figure 3.1). The system is formed by the junction of Garonne and Dordogne rivers, which together drain a catchment area of $71\ 000\ km^2$ (Jouanneau and Latouche, 1981). It is the largest estuary in France and one of the biggest in Europe, covering approximately an area of $625\ km^2$ at high tide. It is about 12-km wide at the mouth and more than 2.5-km wide in the upstream part. The estuary is about 76-km long from the inlet near Le Verdon to Bec d'Ambès. The channel depth varies between 7 and 10 m on average (Cancino and Neves, 1999; Gaedke and Ebenhoh, 1991). All these characteristics are found in table 3.1.

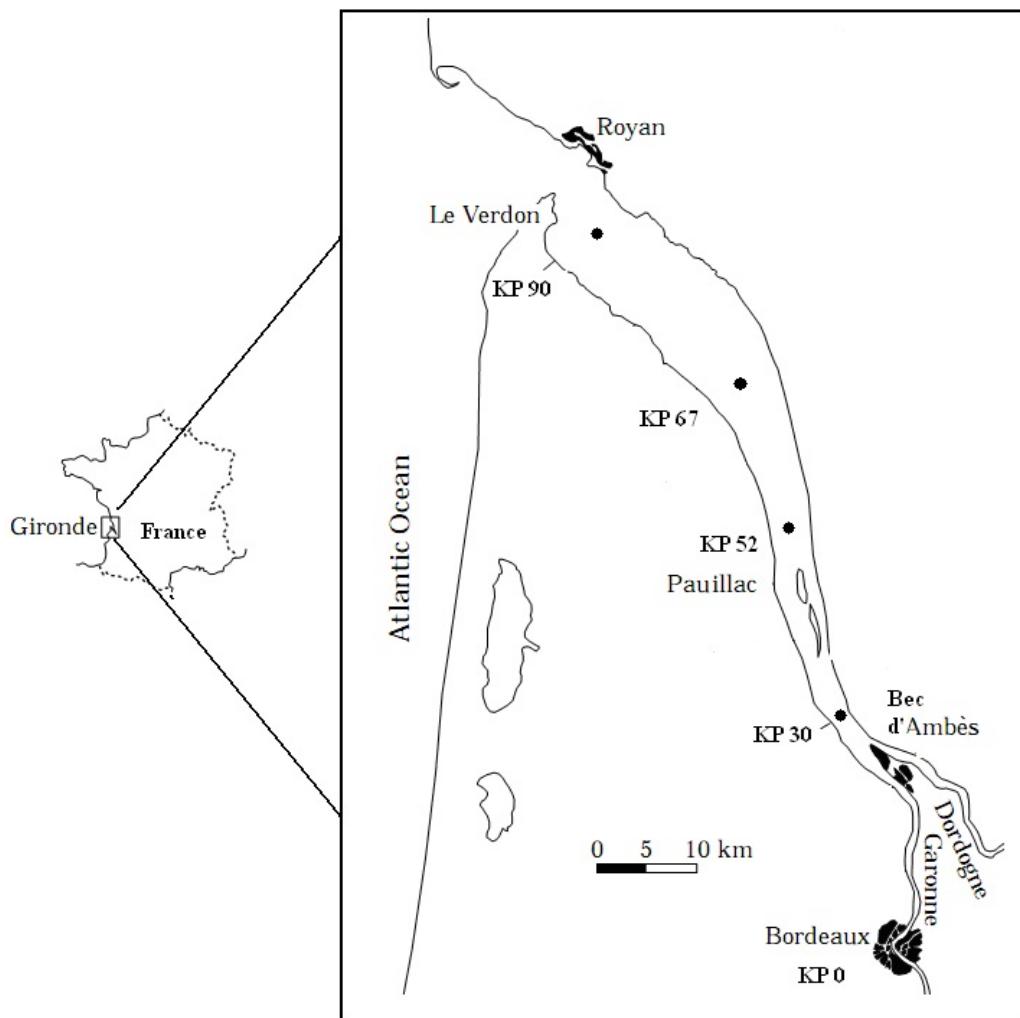


FIGURE 3.1 – Map of the Gironde estuary showing all sampling points. KP (Kilometric points) indicates the distance expressed in kilometres from the city of Bordeaux (KP0). In this paper, we consider the oligo-mesohaline part of the estuary comprised between 30 and 90 kilometers from the city of Bordeaux, (i.e. KP 30 at Bec d'Ambès and KP 90 at Mortage).

TABLE 3.1 – Basic information about the Gironde estuary

Properties	Values	Units
Surface Area	625	km ²
Length	70	km
Catchment area	71 (103)	km ²
Mean channel depth	7-10	m
Annual river flow	743	m ³ s ⁻¹
Tide amplitude	1.55 - 5.5	m

In this paper, we consider the oligo-mesohaline part of the estuary comprised between 30 and 90

kilometers from the city of Bordeaux, (i.e. KP 30 at Bec d’Ambes and KP 90 at Mortage).

3.4.1 Available data

Available salinity, nutrients and chlorophyll data were retrieved from two databases collected by the SOMLIT (Service d’Observation en Milieu LITToral ; <http://somlit.epoc.u-bordeaux1.fr/fr/>) and CPNE Blayais monitoring programs, sampling the Gironde in January and monthly inbetween March-November between 1997 and 2009. During each campaign, four stations were sampled in the upper, middle and lower part of the estuary according to the scope of the SOMLIT (for further information see Goberville et al. (2010)). Sampling was performed at 4 stations, the two stations located at the boundaries (KP30, KP90) and two intermediate stations (KP52 and KP 67). These stations are located 30 (KP 30), 52 (KP 52), 67 (KP 67) and 86 km (KP 86) downstream the city of Bordeaux (Fig.3.1). Sampling was performed at two water depths (1m below the surface and 1m above the bottom), and at four tidal moments. Salinity data from surface and deep water were averaged while only data from the upper layer were used for chlorophyll and nutrients assuming homogeneity of the water column but considering that the production only occurs in a thin layer at the surface.

3.4.2 Modelling procedure

Mass transport was simulated by means of a horizontal 1-Dimensional box model assuming that vertical and lateral gradients were negligible. The model is expressed as a finite difference equation (O’Kane, 1980; Thomann and Mueller, 1987). Such modelling approach is suitable for tidally influenced systems and has already been used in the Scheldt estuary to estimate the residence time, nitrogen budgets and carbon flows (Soetaert and Herman, 1995a,b,c). The governing equation underlying the model is thus the general 1D-advection-dispersion-reaction equation, which, expressed in terms of flows is.

$$\frac{\partial C}{\partial t} \Big|_{dispersion} = -\frac{1}{A_x} \cdot \frac{\partial(Q \cdot C)}{\partial x} + \frac{1}{A_x} \cdot \frac{\partial C}{\partial x} \left(A_x \cdot E \frac{\partial C}{\partial x} \right) + r \cdot C \quad (3.1)$$

The macroscopic formulation (3.1), combines two sub-models that first account for the mass transport with freshwater flow and tidal dispersion (first and second terms) as well as reaction (third term). C is the concentration of any compounds in the model, A_x (m^2) is the variable cross-sectional surface, x (m) the position along the length axis, Q the flow rate ($m^3.s^{-1}$) and r is the reaction rate. In the model, effects of tides are taken into account through the dispersion coefficient (D , $m^2.s^{-1}$) calibrated with salinity, a conservative constituent.

3.4.2.1 Transport sub-model

To approximate Equation 3.1, the spatial extent was subdivided into 70 discrete boxes extending from the upstream river boundary (KP 30), to the downstream boundary (KP 90) near the sea. The estuarine cross-sectional area A_x in Gironde was assumed to follow an exponential law (Eq.3.2).

$$A_x = A_0 e^{\beta x} \quad (3.2)$$

x is the distance in km from bec d'Ambe. A_0 is the cross section area at the upstream boundary and β is a shape factor. We fitted this equation to cross-sections calculated as a product of depth at 10 km intervals (Goosen et al., 1999) with estuarine width. Fluxes at the interfaces were numerically approximated using a finite difference approximation (Eq 3.3) that calculates the value of the function in a finite number of grid cells. The physical sub-model described here considers the estuary to be well mixed. Consequently, concentrations were calculated in the centre of supposedly homogeneous compartments. The rate of change of concentrations in box i is calculated by a finite difference approximation (Eq 3.4). This partial differential equation (PDE) is converted to a set of ordinary differential equations (ODEs) that calculate the value of the function in a finite number of grid cells or boxes.

$$\frac{dC_i}{dt} = -\frac{1}{A_i} \cdot \frac{\Delta_i(A \cdot J)}{\Delta x_i} \quad (3.3)$$

$$= -\frac{\Delta_i(A \cdot J)}{\Delta V_i} + r \cdot C_i \quad (3.4)$$

Where $\Delta V_i = \Delta x_i \cdot A_i$. In this equation, the local change in time of a state variable C (defined per unit of mass) within an elementary volume, V , of fluid results from a transport imbalance through the surface bounding V and the production and /or destruction (r) of C inside V

(Nihoul, 1993; Soetaert and Herman, 2009). Δ_i means that the mass flux gradient is to be taken around box i , i.e. as the difference of mass fluxes at the downstream ($i, i+1$) and upstream ($i-1, i$) interface. is to be taken around box i , i.e. as the difference of mass fluxes at the downstream ($i, i+1$) and upstream ($i-1, i$) interface.

$$\Delta_i(A \cdot J) = A_{i,i+1} \cdot J_{i,i+1} - A_{i-1,i} \cdot J_{i-1,i} \quad (3.5)$$

and $(A \cdot J)_{i_1,i} = Q \cdot C_{i-1} - E_{i-1,i} \cdot \Delta C_{i-1,i}$

Here we have defined the bulk dispersion coefficient ($m^3 \cdot d^{-1}$) at the interface between box $i-1$ and i as :

$$E_{i-1,i}^* = \frac{A_{i-1,i} \cdot E_{i-1,i}}{\Delta x_{i-1,i}} \quad (3.6)$$

And $\Delta x_{i-1,i}$ the "dispersion distance (m)" from the centre of box i-1 to the centre of box i. i=1..N and N denoting the most downstream compartment.

$$E_{i-1,i}^* = \frac{A_{i-1,i} \cdot D}{\Delta x} \quad (3.7)$$

3.4.2.2 Reaction sub-model

The second sub-model represents reactions terms accounting for net primary production and biogeochemical processes. These reactions are coupled with the transport sub-model to investigate the dynamics of simulated compounds.

Estimating net production/consumption of variables

Net production or consumption of any constituent in the estuary was assessed by comparing observed concentrations with the concentrations that occur under conditions of conservative behaviour. Data at boundaries for NO_3^- , NH_4^+ , Chlorophyll *a* and oxygen were simulated with the transport model assuming that variables are conservatively transported through the estuary. As oxygen dynamics also included physical processes always occurring within the system, we also considered re-aeration processes to account for oxygen water-atmosphere exchange. Next a simulation was run with a constant net production/consumption term included as first order reaction proportionally to the substance concentration in order to test the null hypothesis and compare the significance or non-significance between transport and reaction model. This gives the importance of going further in our analysis as we can know whether variables are only transported or also react in the estuary.

Biogeochemical model

Description The present model considers the biogeochemical dynamics of the estuary to be mainly controlled by four state variables : Nitrate (NO_3^-), ammonium (NH_4^+), Oxygen (O_2) connected by flows accounting for nitrification, mineralization (ammonification) and oxygen air-water exchange (Fig.3.2). Nitrates and Nitrites are not distinguished in the model and all data referring to the state variable NO_3^- are the summed values of $\text{NO}_3^- + \text{NO}_2^-$. Nitrification and mineralization are both regulated by oxygen saturation (Weiss, 1974) and temperature dependency functions modelled with a Q_{10} formulation using standard Q_{10} of 2. Primary production was considered to be negligible and was not

taken into account. The rates of changes of each modelled variable are presented in table 3.2.

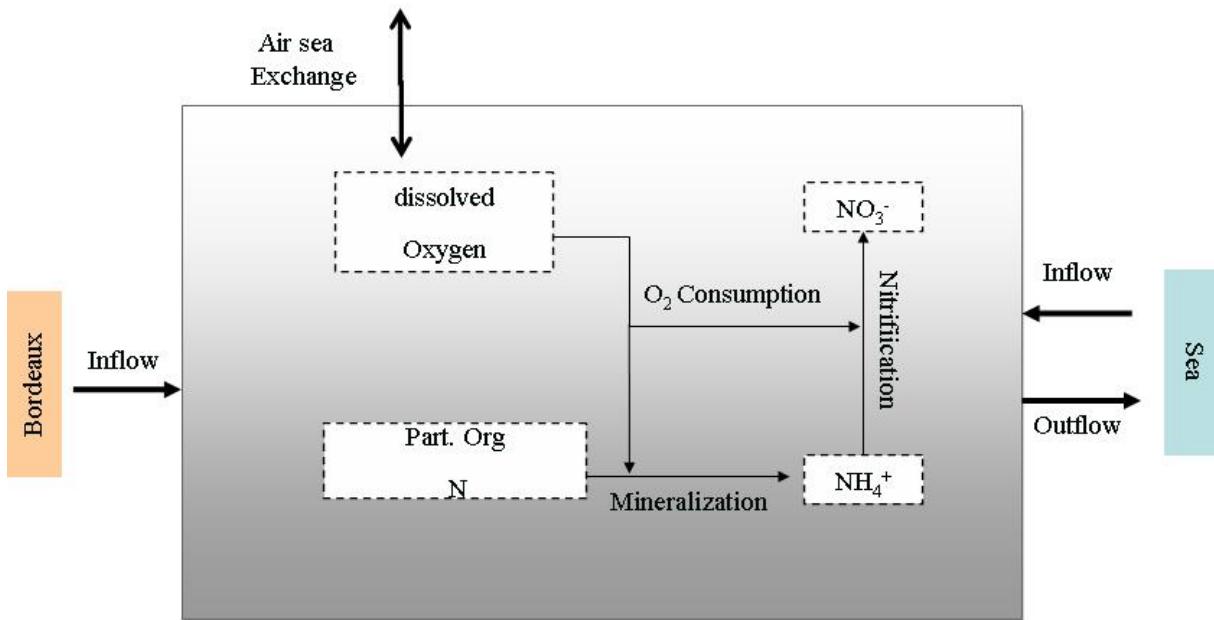


FIGURE 3.2 – Biogeochemical interactions of the model represented as flows between variables. Boxes are simulated variables and arrows between them represent the flows

TABLE 3.2 – Rates of changes in the model

$$\frac{dChla}{dt} = TranChla + Production \quad (3.8)$$

$$\frac{dNO_3^-}{dt} = TranNO_3^- + Nitrification \quad (3.9)$$

$$\frac{dNH_4^+}{dt} = TranNH_4^+ + Mineralization - Nitrification \quad (3.10)$$

$$\frac{dO_2}{dt} = TranO_2 + AirSeaFlux - 2.Nitrification - Mineralization \quad (3.11)$$

3.4.2.2.1 Modelled processes All processes simulated in the biogeochemical sub-model are described below.

Mineralization. In aquatic systems the major heterotrophic activity is due to bacteria that mineralize the particulate and dissolved organic matter consuming oxygen according to



3.4 Material and Methods

Oxic mineralization is thus considered to be the most important process of organic matter degradation. The amount of ammonium produced by means of mineralization (ammonification) relates to the amount of CO_2 production through the (fixed) Nitrogen to Carbon ration. (Eq.3.12, Table 3.4)

Nitrification. Nitrification is another bacterial activity controlling nitrogen speciation and oxygen levels (Soetaert and Herman, 1995c; Vanderborgh et al., 2007). As bacterial biomass is not modelled as such, the process is described as first order with respect to ammonium concentrations. It is an oxygen demanding process : the oxidation of ammonium (NH_4^+) to nitrate consumes 2 moles of oxygen per mole of ammonium according to Equation 3.13 :



Air-sea exchanges. The balance of oxygen in the model accounts for the nitrification and mineralisation but also includes the effect of re-aeration. Oxygen flows through air-water interface is the main source of oxygen into the Gironde estuarine water column, where primary production is strongly limited by light availability (Irigoinen and Castel, 1997a). Mixing processes and wind effects are supposed to play an important role in the transfer of O_2 from atmosphere to water. The so-called re-aeration process is modelled following O’Kane (1980) and expressed as a piston-velocity ($m.d^{-1}$) times the difference between in situ oxygen concentration and the saturation oxygen concentration. As wind, current, surface area and turbidity affects the piston velocity, the later was calculated using an explicit linear relation proposed in (Abril et al., 1999). In the Gironde, the water column is assumed to be well oxygenized and the re-aeration flux is supposed to be instantaneously homogenized over the water depth.

TABLE 3.3 – Formulations used for processes that affect nutrients dynamics in the model. List of variables can be found in table 3.3

Processes	Model equations
Production	$r_p \cdot Chla$
Nitrification	$r_{Nitri} \cdot \frac{O_2}{O_2 + ksO_2} \cdot NH_4^+ \cdot f(T)$
Mineralization	$r_{Mini} \cdot \frac{O_2}{O_2 + ksO_2} \cdot PON \cdot f(T)$
Aeration	$piston \cdot \frac{O_{2Sat} - O_2}{Depth}$
f(T)	$e^{kT - T_{opt}}$

TABLE 3.4 – Parameters values used in the model. Calibrated parameters are $rMin$ and $rNitri$ the others were mainly taken from the literature.

	Values	Units	Meaning
KsO_2	30	$\text{mmol}O_2 \cdot m^3$	Oxygen half-saturation constant
r_{Nitri}	0.42	d^{-1}	Nitrification rate
r_{Min}	0.0088	d^{-1}	Mineralization rate
r_p	- 0.019	d^{-1}	Net production rate
$CNratio$	8.5	mmoC/mmolN	C/N ratio
kt	- 0.069	—	Temperature effect
T_{opt}	18	$^{\circ}\text{C}$	Optimal temperature

3.4.3 Calibration and parameter estimation

The mathematical equation 3.1 depends on two unknown quantities, the dispersion coefficient (D) and the first-order consumption rate, r . An essential step in the modeling process is model calibration, during which these parameters are estimated, based on data. The data from the two intermediate stations (KP52 and KP 67) were used as observed values. In the first step, the model is used to simulate salinity. As the salinity distribution changes only due to transport, the consumption rate r equals zero in equation 3.1. Fitting the model to observed salinity values then provides an estimate of the dispersion coefficient E . In order to make the model as simple as possible, we tested whether it is possible to reproduce transport with only one coefficient E , i.e. Equation 3.6 becomes :

$$E^*_{i-1,i} = \frac{A_{i-1} \cdot E}{\delta_x} \quad (3.14)$$

where δ_x equals 1 km and constant. This way, the effect of mixing on constituents varies along the estuary only due to the changes in estuarine morphology (as represented in cross-section surface $A_{i-1,i}$). Next, we used the derived dispersion coefficient to transport Chlorophyll-a and nutrients, assuming that there is no effect of biological processes on this quantity in the estuary, i.e we fixed the production/consumption rate r , to zero. Finally, a first-order production/consumption rater was fitted, given a net growth rate of phytoplankton or net in the estuary.

The aim of calibration is to improve the values of parameters. During the two calibrations we ran, only one coefficient was fitted to data (E when fitting salinity and r when fitting chlorophyll and nutrients). A simple way to find the best-fitted parameter is to run the model for a sequence of values,

each time estimating the discrepancy of the model with the data (by means of a model cost function, see below). The best-fit parameter value is then the one where the model cost is minimal. Next, this best-fit value was used to initiate a Markov Chain Monte Carlo (MCMC) in order to estimate the parameter uncertainty. Finally the effect of the parameters uncertainty on the model output was estimated and can be visualized as ranges that represent the distribution of the model response as a function of the parameter values, generated by the MCMC.

3.4.4 Initial and boundary conditions

Initial conditions were obtained by first estimating the steady-state conditions of the model with respect to the forcing freshwater flow and boundary conditions at the initial point of the integration (first date). In the model, the two stations (KP 30, K P87, Fig.6.3) located upstream and downstream respectively provided the boundaries conditions and two other intermediate stations (KP 52 and KP 67), the observed values that were used to compare with the model output.

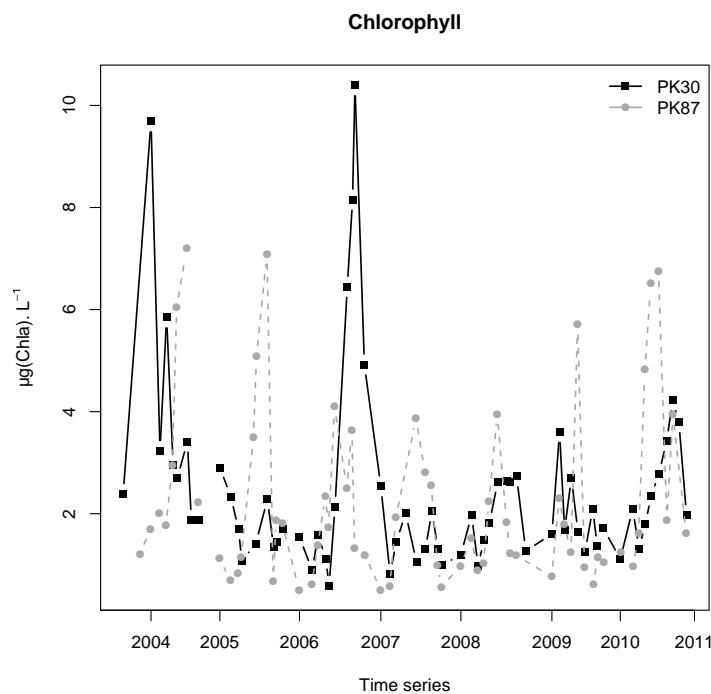


FIGURE 3.3 – Time series of chlorophylla ($\mu\text{g}(\text{chla}) \cdot \text{L}^{-1}$) representing boundary condition at KP 30 (black) and KP 90 (grey) respectively

3.4.5 Numerical estimate of average residence time

After finetuning the transport, the model is used to estimate the residence time in the Gironde. In the literature, the term residence time is used in different ways, and often refers to the average

freshwater transit time calculated as :

$$RT = \frac{V_{ED}}{Q} \quad (3.15)$$

Where V_{ED} is freshwater volume and Q is discharge. This freshwater transit time relates to residence time of freshwater, starting from the head of the estuary. However, a more general definition of residence time relates to the material and starting distribution Sheldon and Alber (2002). Li et al. (2010) defined the residence time of a water parcel as "The average time required for a water parcel at any given location of a system to leave through the system exit". Following Takeoka (1984) approach for an instantaneous material released in a reservoir, the transport model presented here, was able to numerically estimate the residence time of water parcels by means of the concentration of a conservative tracer in the centre of each compartments (i). The initial concentration of each compartment is fixed to 1 while the others are considered empty. Considering $\xi(i, t)$ the relative amount of released material remaining in the estuary at any given time t , that is :

$$\xi_{(i,t)} = \frac{1}{S_{(i,0)} \cdot V_i} \sum_{i=1}^N S_{(i,t)} \cdot V_i \quad (3.16)$$

The average residence time of this water parcel integrated by parts is shown to be equal to :

$$RT_i = \int_0^\infty \xi_{(i,t)} dt \quad (3.17)$$

In equation 3.16, N is the number of compartments considered in the model, $S(i,t)$, the concentration of the conservative tracer in compartment i at time t . $V(i)$, the corresponding volume. Keeping the concentration at the boundaries at 0, the total concentration is followed by simulating the model over time and space.

3.4.6 Implementation of the model

The reactive transport equation was implemented using R as a simulating platform (Soetaert and Herman, 1995a). The software is freely available (<http://www.r-project.org>) and contains useful packages directly downloadable from the website such as : ReacTran package (Soetaert and Meysman, 2011) contains routines that enable the development of reactive transport models in aquatic systems. We used function tran.volume.1D from this package to estimate the volumetric transport term in a one-dimensional domain. The R package deSolve (Soetaert et al., 2010) contains several numerical methods to solve differential equations and function ode.1D was used to integrate the model in time.

The steady-state conditions used to initialize the model were estimated using function steady.1D from the R-package rootSolve (Soetaert and Herman, 2009). We used the R-package FME (Soetaert et al., 2010) to confront our mathematical model with data. We used its algorithms to estimate the residuals, the variable and model costs ; sum of squared residuals (modCost), sensitivity (sensFun) and Monte Carlo analysis (modMCMC), parameter identifiability, model fitting and provides a Markov-chain based method to estimate parameter confidence intervals (sensRange).

3.5 Results

3.5.1 Transport Model

The physical model described here summarizes the transport of several dissolved or particulate components in the water mass. These types of models account for movement of water within which they are transported. The validity of our 1-D solute transport model can easily be checked by comparing the observed salinity with the calculated profiles. Fig.3.4 shows the comparison of observed (open circles) and simulated (full line) salinity for two points along the estuary (KP 52 and KP 67) located at 22 and 38 km downstream the upper boundary (Fig.3.4).

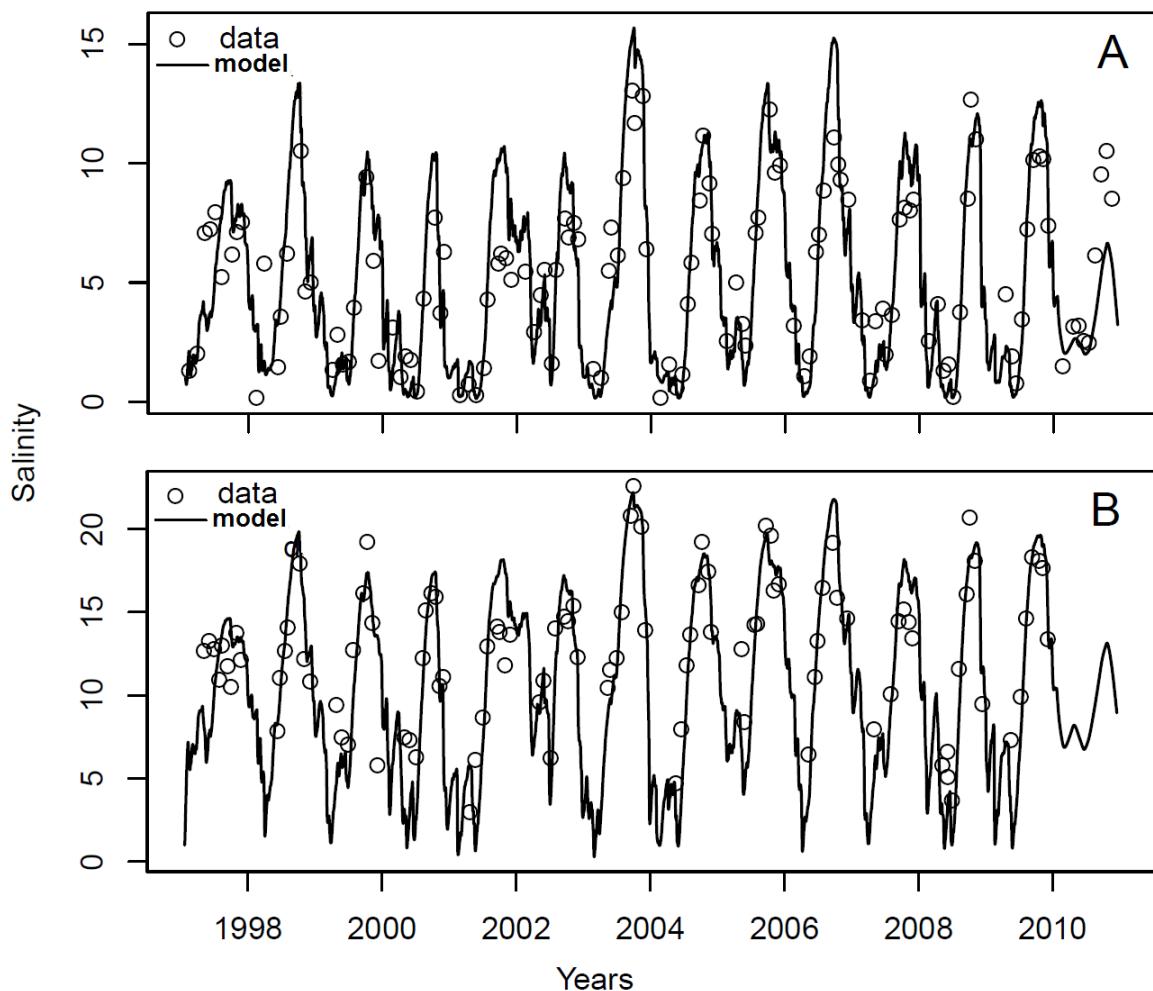


FIGURE 3.4 – Observed data (open circles) and model output of salinity (black lines) for KP 52 (A) and KP 67 (B). The conservative situation (only transport) is presented for all the simulated period (1997-2009)

Observed data (open circles) and model output of salinity (black lines) for KP 52 (A) and KP 67 (B). The conservative situation (only transport) is presented for all the simulated period (1997-2009). The model well reproduced the salinity at both stations (KP52 and KP67 ; Fig. 3.4) except in winter situation at KP 67 when the station Pk67 was not sampled from January to March.

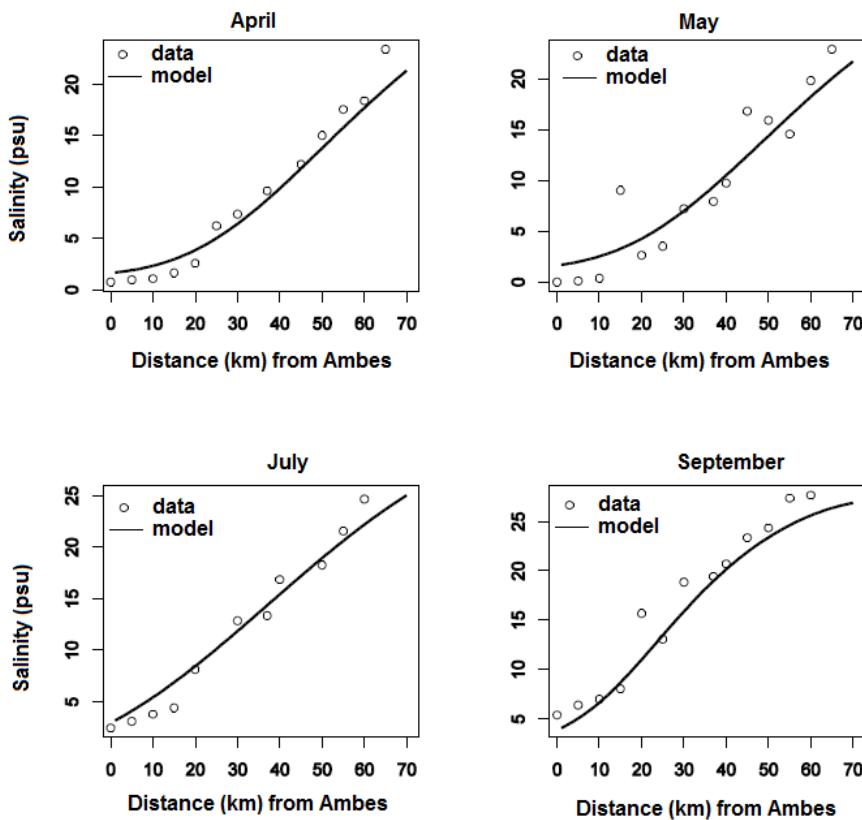


FIGURE 3.5 – Salinity distribution along the estuarine gradient during a validation procedure. Open circles are observed data collected in the year 2003 (retrogrir campaign, (David et al., 2005)). Full line is the model at a specific date

The model explained almost all the variability in salinity data and only a small fraction (22%) remained unexplained (Table 3.5) due to natural variability and missing data at KP 67. This consistency of physical model with observed salinity data allowed us to use the resulted physical model as support to assess the dynamics of nutrients and chlorophyll in the Gironde estuary.

TABLE 3.5 – Variance partitioning in the model

Parameters	data SSR	Model SSR	% not explained
KP 52	-	429.02	8.56
KP 67	-	677.41	13.52
Total	5009.22	1106.527	22.08

The relative good agreement between observations and model output demonstrates that estuary hydrodynamics and the dispersion/advection processes have been well simulated in the model. The constant dispersion coefficient seemed to be adapted to the system under study. The best calibrated value of the dispersion coefficient ($m^2.s^{-1}$) as normal distribution of prior parameters and the random

3.5 Results

walk obtained with Markov chain analysis (1000 runs and 74.52 % acceptance rate) give a best-fitted value of $332.25 \text{ m}^2\text{s}^{-1}$

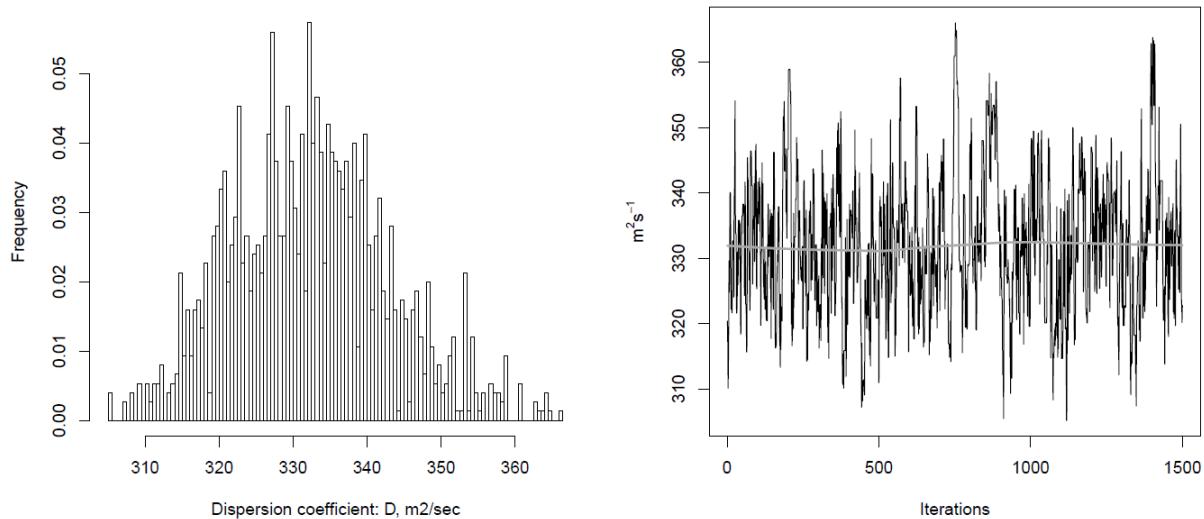


FIGURE 3.6 – Results of the MCMC random walk with 1500 iterations and a normal distribution with different prior of dispersion coefficients). Full line is the model at a specific date

3.5.1.1 Revisited residence times in the Gironde

Residence times were numerically calculated for both winter and summer situations 2005 (Figure 3.7). The residence time in all parts of the modelled system was less than 20 days. Upstream and downstream parts have the lowest residence time, as there is larger chance of being transported across the external boundaries due to advection and/or dispersion. differences between summer and winter conditions are especially apparent in the middle of the system.

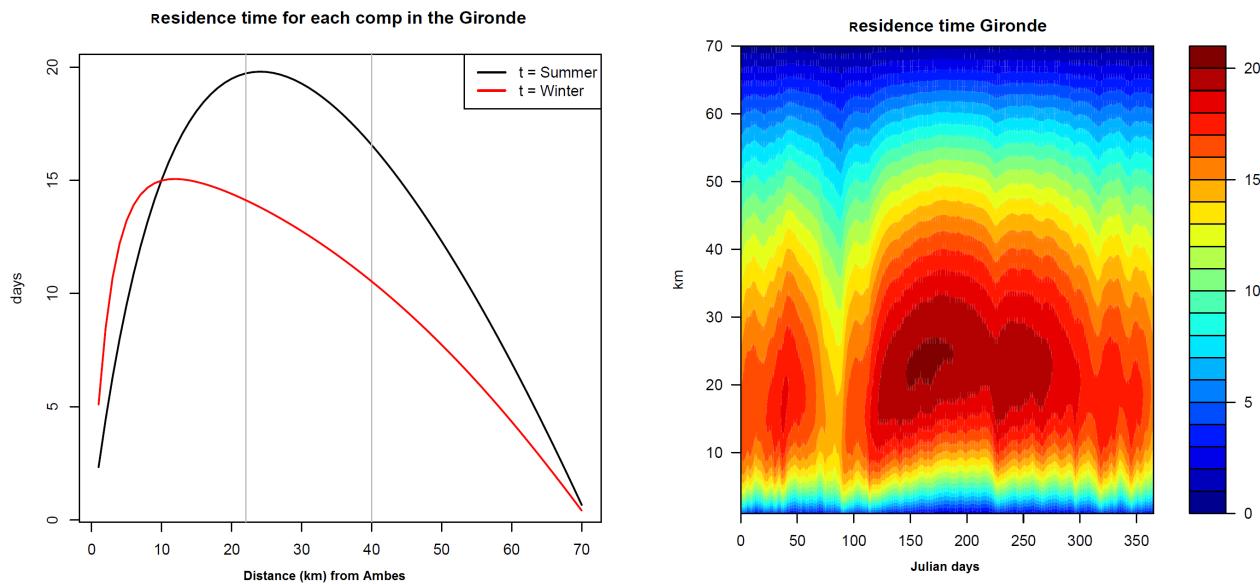


FIGURE 3.7 – Residence times in days of water parcels in the center of model boxes for winter and summer conditions. The grey vertical lines denote the position of the sampling stations, KP 52 and KP 67.

In the upstream part, residence times in winter increases up to a maximum value of 14 days observed at a distance of 10 km from the upstream boundary. The overall, residence time in the estuary is higher in summer, reaching a maximum of 17 days 20 to 30 km downstream from the upstream boundary. The residence time of the water masses at the sampling stations KP 52 and KP 67 varies from 10 to 17 days.

3.5.2 Reaction model

3.5.2.1 Coupling reactions terms with transport model

Results for the conservative and non-conservative behaviour of all variables are represented in table 3.6. SSR calculated with the transport model only assuming reaction term equal 0, as well as SSR estimated with a transport-reaction model a first order reaction term are also given. The reaction and transport model minimizes the SSR compare to the conservative model but the r value give a different situation with respect to data between the two models. Statistical p-values compare the significance or non-significance discrepancy between model output and in situ data as calculated by the cost function. The negative r value (-0.004) for chlorophyll and associated p-value of (0.527) shows that both reaction and conservative models are not significantly different. Ammonium concentrations ($r=-0.06957$, p-value =0.000218) and nitrates ($r=0.0113$, p-value = $3.58 \cdot 10^{-11}$) are consumed and produced respectively in the estuary. These results suggest that nutrients in the estuary are not only conservatively transported.

3.5 Results

TABLE 3.6 – Results of statistical analysis (t-test) between the conservative model (without reaction, $r=0$) and when a reaction term ($r \neq 0$). SSR are square sum residuals. P-value represents the statistical significance.

	SSR Transport only	SSR transport + Reaction	p-value	r
Chlorophyll-a	324.15	127.15	0.527	-0.02
Nitrates	70125.43	49165.55	3.58 10-11	0.0112
Ammonium	126	86	2.18 10-4	-0.0695

3.5.2.2 Reactive Chlorophyll-a model

Fine-tuning production rates

Primary production is not explicitly modelled in our model. As phytoplankton growth rates is somewhat complicated to estimate in natural system and particularly in the Gironde where chlorophyll is mostly diluted in a pool of suspended matter. Now we use Bayesian technics to improve our parameter estimation. The estimated production or consumption rate of chlorophyll-a using the automatic calibration and MCMC (3000 runs and 83 % acceptance rate) analysis are in Fig.3.9.

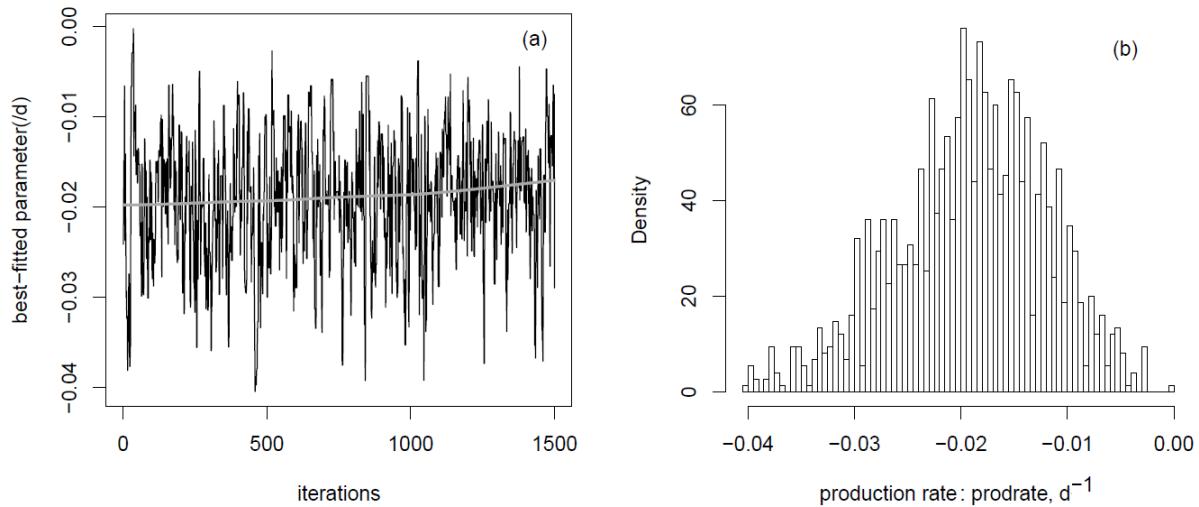


FIGURE 3.8 – Results of the MCMC random walk with 1500 iterations and a normal distribution with different prior production rates.

The best-fitted parameter converged to a value close to -0.019 and an estimated standard deviation of 0.007. This is confirmed by histogram of distributions using prior distribution in a range of previous values table 5. This value suggest globally an export of chlorophyll a from the estuary. The discrepancy between data and model outputs at station KP52 shows that reactive chlorophyll using the

estimated rate is slightly or even not different from the transport outputs and both are closely related to in-situ data (Fig.3.9a). This indicates the importance of transport in the dynamics of chlorophyll at this station where the dynamics is strongly controlled by the input from the upstream boundary conditions. This indicates the importance of transport in the dynamics of chlorophyll at this station where the dynamics is strongly controlled by the input from the upstream boundary conditions.

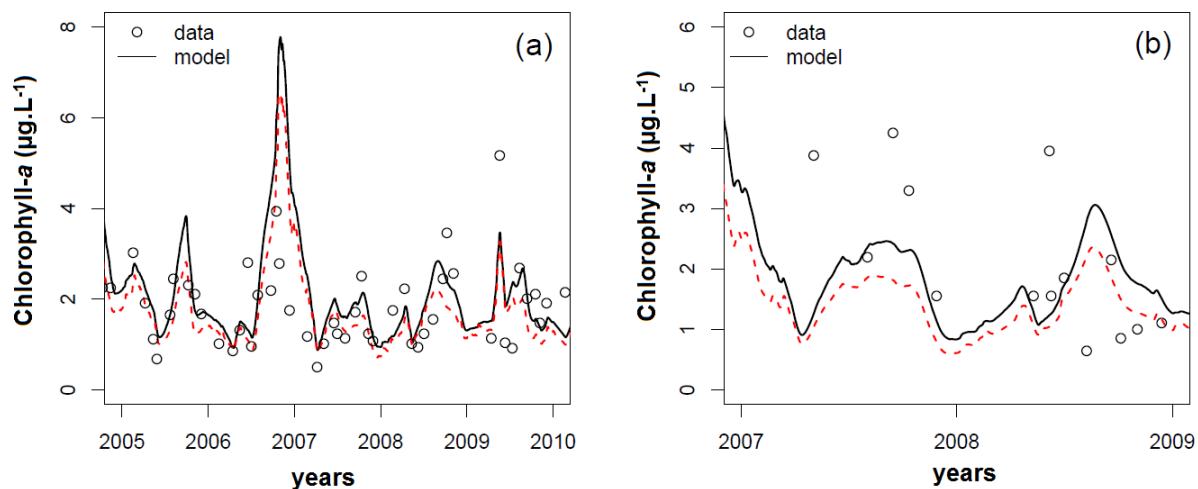


FIGURE 3.9 – Comparison of model outputs with data at two intermediate stations (KP 52 (a) and KP 67 (b)). Open circles represent in situ chlorophyll concentration in $\mu\text{g.L}^{-1}$, dotted lines, the dynamic simulation with reaction added and full black line is the simulation without any reaction (transport only)

At station 67 (Fig.3.9b), the discrepancy is more noticeable between both reactive and conservative chlorophyll models with data but remain within the same range of $1\text{-}4 \text{ mgChla.m}^{-3}$ and a average value around 2. The net production rate estimated with only data from KP 67 was positive and equal to 0.021 d^{-1} . However this value still remains very low and doesn't improve so much the model (Fig.3.9b) indicating that the chlorophyll dynamics at this station is still influenced by concentrations from the boundaries and evidences the role of transport in the dynamics of chlorophyll.

3.5.2.3 Dynamics of nutrient : Model versus data comparison

Ammonium

Observed data and model output for transport only and transport + reaction at KP 52 and KP 67 are plotted on Figure 3.10

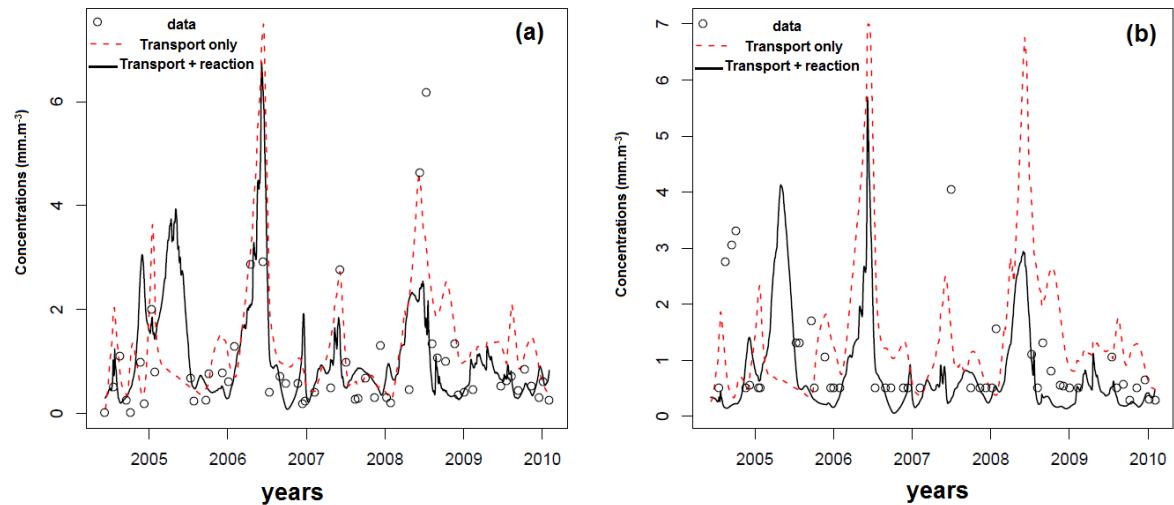


FIGURE 3.10 – Comparison between model outputs and data with and without reaction at two different stations. Open circles represent *in situ* ammonium concentration in mmol.m^{-3} ; dotted line represent the dynamic simulation without (transport only) and full black line is the simulation with reaction added.

The conservative model tends to over-estimate ammonium concentrations compared to observed data whereas the transport plus reaction model outputs are close enough and give a better adjustment. The comparison between the conservative behaviour and *in situ* data clearly shows that ammonium is not only passively transported through the system and reacts giving a consumption of ammonium in the estuary. In the model ammonium is produced by mineralization of organic matter and consumed by nitrification. The estimated mineralization rate by calibration using the automatic fitting method was equal 0.00887 d^{-1} . The relative good fit between data and model indicates that nitrification is by far the dominant process responsible for the rapid decrease of ammonium concentration in the estuary.

NO₃⁻ state variable (Nitrates+Nitrites)

Nitrification is the main process controlling the production of nitrate in the model. Comparison between model outputs from both conservative and reactive transport models with *in situ* data are plotted on Figure 3.11.

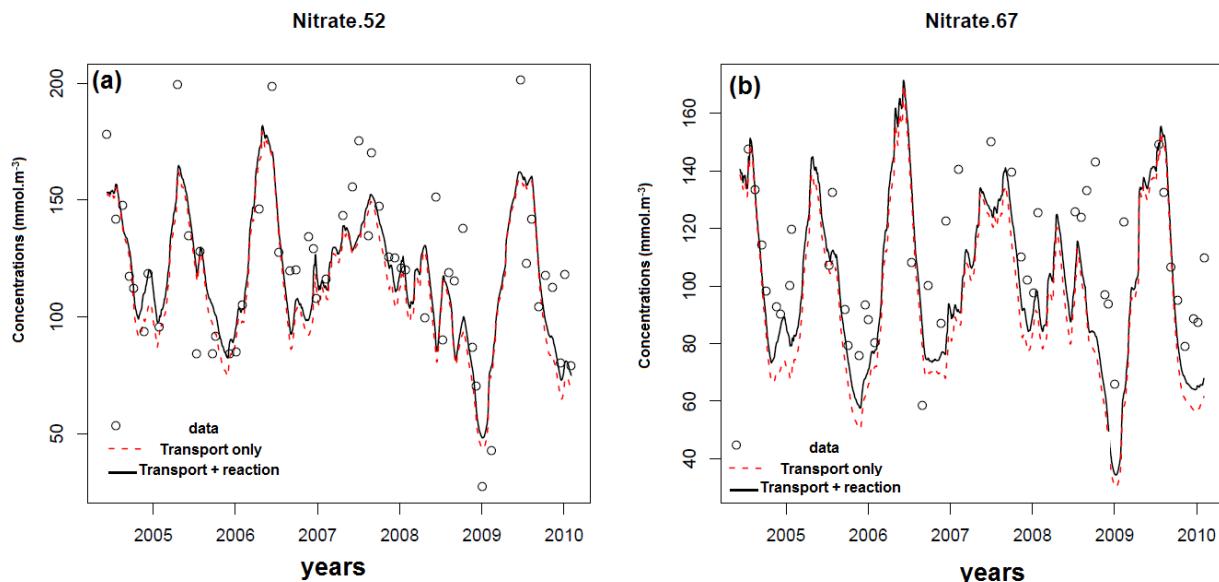


FIGURE 3.11 – Comparison between model outputs and data with and without reaction at two intermediate stations. Open circles represent in situ nitrates concentrations in mmol.m^{-3} ; dotted lines represent the dynamic simulation without reaction and full line is the reaction model.

During the simulation period, the concentrations of nitrates were sufficiently high and did not fall below 30 mmol.m^{-3} .

Globally in the estuary nitrates contributes to the increase of nitrogen concentration but the inclusion of nitrification process only marginally improved the fit between data and models, as compared to the transport model, probably due to the low value of $r\text{Nitri}$ (0.42 d^{-1} , Table 3.4) used. Low ammonium concentrations ($< 3 \text{ mmol.m}^{-3}$) likely limit the nitrification process.

Oxygen

The dynamics of nitrogen in the model is controlled by re-aeration, nitrification and mineralisation. As the later process requires oxic conditions it consumes oxygen. Evolution in time of oxygen concentrations with respect to the transport model outputs with and without reactions is presented in Figure 3.12. When oxygen was conservatively transported concentrations were overestimated with respect to observed data and showed that air-water exchange was balanced by oxygen consuming processes occurring within the estuary. Seasonality and peaks of oxygen concentrations at station 52 are well-reproduced and remain in the range of 200 to $350 \text{ mmolO}_2.\text{m}^{-3}$.

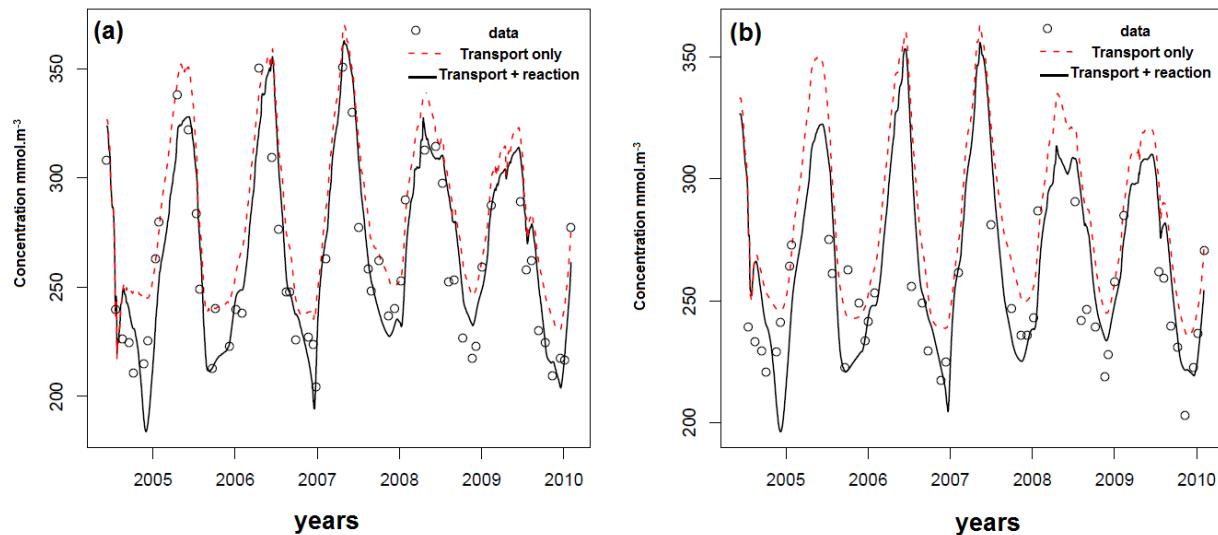


FIGURE 3.12 – Comparison between model outputs and observed data with and without reaction at two intermediate stations. Open circles represent in situ oxygen concentration in $\text{mmol} \cdot \text{m}^{-3}$, dotted lines, the dynamic simulation without reaction and full black line is the simulation with reaction added.

At station 67 observed data for oxygen were missing from January to March and the model was unable to reproduce peaks occurring in winter. Looking at the two stations, the oxygen concentrations values were not different enough and were in the same order of magnitude indicating that the estuary remains globally well-oxygenated and rapidly renewed in the water column due probably to strong mixing processes.

3.6 Discussion

3.6.1 Mixing processes and Salinity distributions

Mixing processes have a major impact on the biology, chemistry, ecology and water quality of estuarine environments (Vallino and Hopkinson Jr, 1998). The Gironde estuary is a transition zone of waters from the rivers Dordogne and Garonne to the Atlantic ocean and salinity distribution reflects both end members concentrations. Tidal currents mix the fresh and seawater and thus control the change of salinity concentration in the longitudinal axis of the estuary. We used a one-dimensional model to reproduce the variability in time and space of salinity. The assumption was to ignore the lateral and vertical gradients of salinity. In reality, the asymmetry of the tidal wave when propagating upstream, coupled to density residual circulation (Allen et al., 1974) induces a stratification of water column near the mouth. However, the observed and predicted salinity profiles (Fig.3.4) matched well such that the model can be considered as representative of dispersion in the overall system. Using a

dynamic model avoids problems associated with estimating D from a profile of salinity that have not attained steady-state distribution (Vallino and Hopkinson Jr, 1998). The value of $342.6 \text{ m}^2.\text{s}^{-1}$ found in the present study is in the same order of magnitude as for macroscopic turbulent diffusion (Regnier et al., 1997) and accords well with a previous estimate of $250\text{-}400 \text{ m}^2.\text{s}^{-1}$ in the Gironde (Pham et al., 1997). This parameter is highly dependent on many factors that are unique to individual estuaries. It varies over space and time in response to changes in channel shape, freshwater discharge, tidal currents and wind stress (Fischer, 1976). Soetaert and Herman (1994b), using the same approach, have estimated an approximate mean value of $350 \text{ m}^2.\text{s}^{-1}$ while Vanderborght et al. (2007) selected a value up to $1350 \text{ m}^2.\text{s}^{-1}$ for the same Scheldt estuary. Salinity distribution in estuaries is not just influenced by fresh water discharge and marine inputs, but also from other points of fresh water discharge and rainfall and evaporation (Zimmermann, 1976). The climate of the region is temperate and under oceanic influence. Monthly rainfall fluctuates between 50 mm in summer and 100 mm in winter (Tank et al., 2002) with daily average values of 2.33 mm between 01-01-1997 to 08-02-2009 (Data from Meteo France, at Pauillac station). Scaled to the whole area, this gives a supply of fresh water of the order of $23.87 \text{ m}^3.\text{s}^{-1}$; which is very low (3%) compared to the river discharges ($500\text{-}1000 \text{ m}^3.\text{s}^{-1}$). Fresh water inputs from surrounding land of the Gironde estuary are not available and their effect, if any, is probably weak. The effect of freshwater discharge is clear from the seasonal variation in salinity which is obviously related to freshwater discharges, which usually reach a maximum in January-February and a minimum in August-September david05.

3.6.2 Residence time

The distribution of the residence time (Fig.3.7) was estimated by calculating the average time in the Gironde estuary of a water volume originally present in one of the compartments j , assuming that the value obtained represents the residence time at a point located in the middle of a box. It is thus the time the parcel needs to cover the part of its path that remains after arriving for the first time at a certain position x in the estuary (as a parcel may pass through x more than once). Consequently, the time scale defined here differs from the time interval the parcel will need to pass through the entire system from inlet to outlet, the so-called transit time. Such a time scale is generally long as it depends on the ratio between freshwater input from the entrance and volume of the system. It can be called the residence time of freshwater (Hilton et al., 1998; Hagy et al., 2000). The "residence time" of water in the Gironde estuary was estimated between 16 to 86 days (Jouanneau and Latouche, 1981) and Pham et al. (1997) defines the time required to replace the fresh-water of the estuary being equal to 20 days in flood and 86 days during low water. In fact, these values are very simple to estimate

if we apply equation (7). Considering the volume of the Gironde ($2.8 \cdot 10^9 \text{ m}^3$ estimated by Taverny (1991) and the mean river flow (between 400 and $2000 \text{ m}^3 \cdot \text{s}^{-1}$) we easily calculate values of 16 and 81 days. However, this ignores tidal effects, which tend to reduce the real residence time. None of these estimates applies to particle dynamics in the Gironde. Due to tidal asymmetry in deposition and resuspension cycle, the Gironde behaves like a trap for particles and riverine particulate organic carbon (POC) (Ittekkot and Laane, 1991; Zhang et al., 1998; Abril et al., 1999). The consequence of this is an estuarine turbidity maximum (ETM) to be developed (Etcheber et al., 2007). The residence time as we estimated it is the time it takes for a dissolved(-like) substance such as chlorophyll to leave the estuary from any given location according the definition given by Li et al. (2010). Based on that our results showed that the residence time for fine particles particles like chlorophyll is very short, and they cannot stay more than 20 days in the Gironde. This is simply explained by the strong mixing coefficient and the strong fresh water discharges that simultaneously act to rapidly push particles out from the system. The zones where residence time are shorter (upstream and downstream) are the ones where the effects of dispersion and river flow are the most important while in the middle the residence times are larger. This can be related to the estuarine morphology and currents speed because around the sampling stations, where residence times are maximum, the estuary is at its widest. Particles can stay much longer compare to borders limits where effects of tide and fresh water are important.

3.6.3 Importance of estuarine primary production

The trophic status was analysed by estimating the production/consumption rates from chlorophyll data. The current work has a rate not noteworthy different from zero, suggesting conservative behaviour of chlorophyll in the Gironde estuary (Fig.3.9). This result was expected in the Gironde, due to the existence of a maximum turbidity zone, where photosynthesis is strongly limited by light availability (Cole et al., 1992; Irigoien and Castel, 1997a; Garnier et al., 2001) and production seems to be controlled by bacterial activity (Heip et al., 1995; Abril et al., 1999). This is generally observed in many macro tidal estuaries where heterotrophy exceeds autotrophy (Billen et al., 1995; Gattuso et al., 1998; Goosen et al., 1999; Garnier et al., 2001). It should be noted that our estimate provides the net effect only, and does not take into account local primary production or resuspension of microphytobenthos from intertidal areas (Irigoien and Castel, 1997a). If these processes take place, then they are balanced by consumption rates, e.g. linked to the grazing activity of calanoid copepods (Sautour and Castel, 1995) and mysids (Mees et al., 1993), whose productions are usually very high (Castel and Feurtet, 1989; Mees et al., 1993). This high secondary production allows the systems to support several vital functions for fishes or shrimps : nursery areas, migration routes, habitats, etc (Elliott and

Hemingway, 2002).

3.6.4 Effect on the estuarine biogeochemistry

Our model suggest that nutrient in the Gironde are not affected by primary production as this process was not considered. Biogeochemical processes were represented by nitrification, ammonification and oxygen consumption. These coupled processes together with transport maintain nutrient concentrations within the range of values measured in other macro tidal estuaries (van Spaendonk et al., 1993). Nitrification appears to be the most important process in the water column of the Gironde that drives both ammonium and nitrates concentrations. Previous studies have already identified nitrification and denitrification as a key processes affecting nutrients dynamics (Abril et al., 1999). Normally the normal site of denitrification is in the bottom, but in some estuaries, the processes can occur in the water column (Soetaert and Herman, 1995b). The fact that only nitrification can relatively well reproduce levels of nitrates suggests that denitrification is negligible in the pelagic system of Gironde. The amount of nitrogen to the sea accounts for about 20 % ($0.85 \text{ GmolN.yr}^{-1}$). Ammonium enters the estuary from both rivers and sea sides to supply ammonium concentration for nitrification. Hence the estuary is a net ammonium consumer (Figure 3.13).

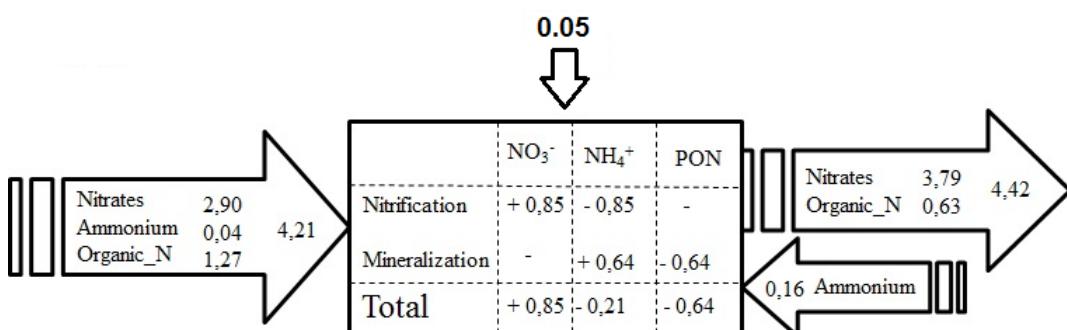


FIGURE 3.13 – Gironde estuarine budgets in GmoleN.yr^{-1} . Two processes : Nitrification and mineralization were assumed to significantly change the nutrients concentrations. The estuarine budget seems to be completed by small inputs. The main box indicates the budget inside the system. Arrows are nutrients fluxes in or out of the system.

As nitrification and ammonification are coupled processes, the small NH_4^+ concentrations cannot support the production of nitrates observed at the two stations. Production of nitrates seems to be limited by low ammonium although estimated nitrification rates seem to be very low compared to those in other estuaries (Rodrigues et al., 2007). In average, during the entire simulated period, nitrification rates range between $0.072 \text{ mmol.m}^{-3}.\text{d}^{-1}$ and $8.99 \text{ mmol.m}^{-3}.\text{d}^{-1}$ with an average value of $0.899 \text{ m}^{-3}.\text{d}^{-1}$ and tend to decrease towards the sea. Values of potential nitrification activity estimated by (Abril

et al., 1999) in experimental conditions reported a value of $300 \text{ mmol.m}^{-3}.\text{d}^{-1}$ ($10\text{-}14 \mu\text{mol.L}^{-1}$).

Our values remain extremely low and we can hypothesize that physical conditions coupled with low ammonium concentrations of the estuary probably limit nitrification. Nitrates resulting from nitrification are directly related to the longitudinal distribution of NH_4^+ . According to the model calculation, approximately 20 % of estuarine NO_3^- is derived from nitrification and the rest (80 %) is produced majoritarily in rivers and transported in the estuary. It is thus likely that most biogeochemical processes have been achieved before entering the estuary. As pointed out the largest part of organic matter coming from rivers is degraded before entering the middle of the estuary (Lin, 1988). However some estuaries such as Tyne estuary : $1.1 \text{ mmol}(\text{NH}_4^+).\text{m}^{-3}.\text{d}^{-1}$, (Rodrigues et al., 2007), Tamar Estuar : $0.9 \text{ mmol}(\text{NH}_4^+).\text{m}^{-3}.\text{d}^{-1}$, (Owens, 1986) experienced similar conditions. These two estuaries exhibit short residence times : between 5-20 days (Ahad et al., 2008) and less than 14 days (Uncles and Stephens, 1990), respectively. The budget also shows that a fraction of nutrients is supplied in the middle probably from the exchange with suspended matter. The maximum turbidity area has been already implied in the exchange of nutrient with water column and probably nitrates and ammonium can be added from sediment constantly re-suspended from the bottom by dredging activities. Typically, an average of about $8.85 \times 10^6 \text{ tons.yr}^{-1}$ of sediment are dredged annually i.e., $24,000 \text{ tons d}^{-1}$ (Audry et al., 2007). After each dredging operation, the dredged sediments are transported downstream and re-deposited outside the navigation channel, where intense estuarine currents favour dispersion. Sediment in the Gironde has already been implied in the exchange of nutrient with water column. At high suspended particles concentrations, some exchangeable phosphorus (P) remained linked to particles, until suspended particulate concentration decreased downstream of the estuary (Deborde et al., 2007).

3.7 Conclusion

Our model is a first attempt to couple a dynamic model to understand natural processes that determine the dynamics of a relatively complex system and investigate the effect of hydrological forces. The model allows to estimate physical and ecological parameters combining a dynamic simulation and an automatic calibration. It can be defined as an exploratory tool. The main conclusions of our work concern the hydrodynamical control of dissolved variable in the Gironde. We have shown that both chlorophyll and nutrients concentrations in some degree reflect the end-members concentrations imposed at the boundaries indicating a strong influence of hydrodynamic conditions. The calibration of the net primary production evidences that the system receives most of its biomass from external productive areas and cannot be considered as a productive system. This heterotrophic estuary is however dominated by biogeochemical processes that produce nitrates when oxic conditions are

3.7 Conclusion

guaranteed. However, to advance further in our understanding of the dynamics of the river-estuary continuum environment in a sens of complete modeling approach more data are needed.

CHAPITRE 4

PRODUCTION PRIMAIRE MICROPHYTOBENTIQUE ET MÉTABOLISME
BENTHIQUE EN MILIEU INTERTIDAL

Introduction du chapitre

Dans le précédent chapitre nous avons étudié la dynamique de la chlorophylle *a* et des sels nutritifs, considérés comme des proxys de la production primaire phytoplanctonique, au moyen d'un modèle unidimensionnel de transport et réaction. Les résultats indiquent que la production primaire dans l'estuaire de la Gironde est fortement dépendante des mouvements physiques de l'eau sous l'influence de la marée et des débits comme principaux facteurs de contrôle. Les résultats de cette première partie renforcent l'hypothèse d'une origine marine ou très en aval du phytoplancton et une quasi-absence de production primaire phytoplanctonique entre la confluence des deux rivières Garonne et Dordogne et le PK 52 voire 67.

Cependant, le phytoplancton n'est pas l'unique producteur primaire potentiel dans les milieux côtiers de faible profondeur. La production microphytobenthique des 50 km² de vasières intertidales de la Gironde peut jouer un rôle dans la dynamique biologique de cet écosystème. Ces microalgues sont susceptibles d'être remises en suspension dans la colonne d'eau et pourraient contribuer à alimenter les réseaux trophiques benthiques voire planctoniques. Cependant, à l'heure actuelle, nous ne disposons d'aucune mesure de cette production dans l'estuaire de la Gironde. Cette partie du travail de thèse a donc consisté à mesurer la production primaire microphytobenthique au moyen d'une technique particulièrement bien adaptée aux zones intertidales vaseuses. Cette technique permet en outre de réaliser des mesures du métabolisme de l'ensemble de la communauté benthique. Nous avons donc couplé ces mesures d'activités à des dénombrements de l'ensemble de la communauté benthique : des procaryotes à la méio- et macrofaune benthique.

Le présent chapitre se présente sous la forme d'une publication scientifique soumise à *Hydrobiologia*. Il vise à étudier la production primaire des vasières localisées le long du gradient amont-aval de la Gironde. L'objectif étant de montrer l'importance de ce compartiment dans la dynamique écologique du milieu et son rôle dans le statut trophique de l'estuaire.

Intertidal benthic primary production and community metabolism in a highly turbid estuary

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4.1 Abstract

A study of benthic community metabolism was performed at three intertidal locations along the salinity gradient of the Gironde estuary during the productive period. Indeed, in this highly turbid ecosystem, where phytoplanktonic primary production is very limited, microphytobenthic primary production on tidal mudflat may play a key role in the foodweb and biogeochemical functioning of this estuary. Primary production and respiration during emersion were estimated by means of benthic chambers measuring *in situ* fluxes of carbon dioxide using infra-red gas analyser. Measures were obtained at two seasons. Results are discussed in relation to biological parameters (Chlorophyll *a*, macrofauna, meiofauna and Prokaryotes). The rate of gross primary production (GPP) measured at saturated irradiance was highly correlated to sediment chlorophyll *a* (Chla) content and showed a strong spatial variability among stations. During early spring (March), GPP displayed a decreasing gradient from the downstream station toward the upstream station and values varied between 125 and 1.5 mgC.m⁻².h⁻¹ whereas no significant difference among the three sampling stations were observed in June (average value was 49 mgC.m⁻².h⁻¹). The benthic community respiration (CR) was much higher during the latter period (range 9-35 mgC.m⁻².h⁻¹) than during the early spring period (range 1-6 mgC.m⁻².h⁻¹). The trophic balance of the community estimated by the net primary production (NPP), evaluated from the difference between GPP and CR, showed that the studied benthic communities, during the studied periods, were most generally, autotrophic during spring and heterotrophic or poorly autotrophic during summer. The results obtained showed that intertidal mudflats of the Gironde estuary are probably as productive as most other intertidal mudflats. However this production

is probably not sufficient to sustain a high metazoan biomass as compared with other estuarine ecosystems.

Keywords : benthic chambers, primary production, benthic community, estuary, tidal flat, microphytobenthos

4.2 Introduction

Coastal ecosystems, despite their low relative area at the scale of the global oceans, are recognized as highly active on a biogeochemical point of view. They indeed represent 20% of the total ocean primary production (Gattuso et al., 1998; Duarte et al., 2005). Littoral zones are thus highly productive areas and are also responsible for a significant share of the cycling of carbon and nutrients in the ocean rendering them key sites of biogeochemical processes (mineralization in coastal sediments would represent half of the total mineralization taking place in the world ocean floors : (Middelburg et al., 2005)). The role of littoral area on biogeochemical fluxes is enhanced by the fact that it represents the interface between the land and the ocean, whereby most of the exchanges of materials between these major systems take place (Duarte, 2000). Among the different coastal ecosystems, estuaries play a major role in production, degradation and transfer of organic matter from rivers to ocean. They are often considered as particularly active in terms of biological production and exhibit the highest values of productivity in the world (Walker and Mossa, 1982). This high productivity is supported mainly by microalgal communities that colonize both the water column and the sediments (Admiraal, 1984; McLusky, 1989; Underwood and Kromkamp, 2000) as well as by seagrasses and macroalgae. Despite this high productivity, most estuaries are also characterized by an elevated global respiration rate and are considered to be net heterotrophic systems (Gattuso et al., 1998; Gazeau et al., 2004). This global characteristic is related to the high continental inputs enhancing turbidity in the water column that limits light penetration and as a consequence primary production (Irigoin and Castel, 1997a). Although phytoplankton is the major contributor to the marine primary production at a global scale, it is quantitatively the second source of particulate organic matter after continental inputs in estuarine systems (Veyssié, 1998). Primary production (PP) in estuaries is also characterised by a strong spatial variability due to turbidity : growth is generally low upstream where turbidity is important and higher downstream where turbidity decreases and light penetration increases (Colijn, 1978; Cloern et al., 1985; Lemaire et al., 2002).

A lot of studies recognize communities of microalgae that inhabit the intertidal flats of estuaries

and bays, (i.e. microphytobenthos) as highly important primary producers (Admiraal, 1984; Blanchard and Cariou-Le Gall, 1994; Guarini et al., 2000). Their production may provide as much as one third (Sullivan and Moncreiff, 1988) or two third (Asmus, 1982) of total primary production in some coastal and estuarine systems. Depending on environmental conditions it may equal or exceed that of phytoplankton by a factor of ten in some intertidal habitats (Cadée and Hegeman, 1974; Varela and Pena, 1985). Hence microphytobenthic production in macrotidal estuaries where turbidity is high may represent a key parameter for estuarine food web functioning..

However, despite the potential important role played by intertidal zones and microphytobenthic communities in estuarine production (Colijn and de Jonge, 1984; de Jonge, 1995), biomass (De Jonge and Colijn, 1994) and fluxes (de Jonge, 1995), their contribution to the estuarine carbon budget is rarely considered and generally leads to some under or-over estimation of the global estuarine budget (Cahoon et al., 1999). This is mainly due to the strong variability of intertidal habitat due to patchiness at all scales of time and space and to the lack of standardized methods. Indeed, such estimations require i) a good knowledge of both temporal and spatial variability of the studied system, ii) direct (*in situ* monitoring of changes in CO₂ or O₂ concentrations) or indirect (modelling or laboratory incubations under artificial irradiance conditions) measurements of gross primary production. Traditional, methods used for monitoring microphytobenthic primary production are destructive as, for example, core sampling (Blanchard and Guarini, 1996) or ¹⁴C incorporation (Blanchard and Guarini, 1996; Cadée and Hegeman, 1974; Miles and Sundback, 2000; Steele and Baird, 1968). Non-destructive *in situ* methods, such as oxygen microelectrodes (Brotas et al., 2003) and variable fluorescence measurements (Serodio et al., 1997; Kromkamp et al., 1998; Serodio and Catarino, 2000; Brotas et al., 2003) are also used. But, scaling up these measurements to larger areas is contentious, and the validity of estimation of carbon production rates from fluorescence measurements is still being fiercely debated (e.g. (Brotas et al., 2003; Perkins et al., 2003)). Moreover, despite the reasons for yielding better correlations when compared with fluorescence measurements, gross oxygen production is not as ecologically relevant as carbon fixation as a parameter for quantifying primary production (Migné et al., 2004).

In order to estimate whether estuaries are sinks or sources of CO₂, one needs to understand the processes that determine the balance between primary production and its consumption by respiration. For these reasons, the benthic metabolism has been estimated using benthic chambers (Migné et al., 2002), that seemed to be the method of choice to measure carbon (CO₂) fluxed at the air-sediment interface. The measured metabolism allows estimating both the photosynthetic activity of microphytobenthic algae as well as the community respiration within each benthic chamber.

The aim of this study was to estimate the potential importance of benthic microalgal production in

an estuarine environment characterized by its very high turbidity drastically reducing phytoplanktonic production (i.e. Gironde estuary). The specific goals were (1) to provide, using benthic chambers measurements of microphytobenthic primary production in such an environment (the first ones in the Gironde estuary mudflats) and (2) to analyse the relationships between benthic community structure and metabolism during the productive period.

4.3 Material and methods

4.3.1 Study area

The Gironde estuarine system, located in the south-western coast of France is one of the major estuaries of North-Western Europe. It is formed by the gathering of the Garonne and Dordogne rivers (Fig.4.1), which together drain a 71.000 km² catchment area. Downstream of the confluence between the two rivers, the studied system covers an area of 625 km² including 50 km² of intertidal flats (Santos et al., 1997).

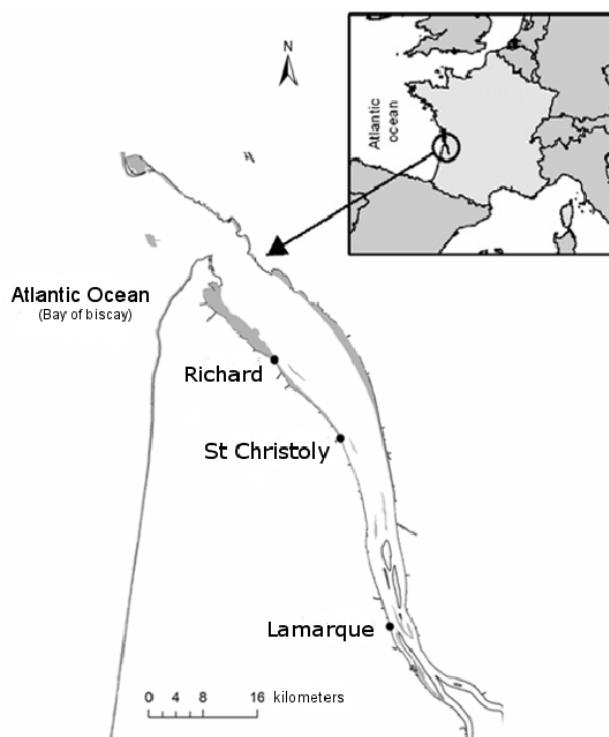


FIGURE 4.1 – Map of the Gironde estuary (France) showing the sampled stations from up to downstream (Lamarque, St Christoly and Richard).

The estimated tidally averaged volume is about 3.160 109 m³(Nzigou et al., prep). The tidal regime is semi-diurnal with mean neap and spring ranges of 1.55 m to 5.5 m respectively. Tidal amplitude increases progressively towards the upper estuary, reaching its maximum value at 180 km from the

mouth before decreasing in the fluvial narrower sections (Sottolichio and Castaing, 1999). Currents velocities can reach up to 2 m.s⁻¹. In the present study, three stations (Lamarque, St-Christoly, Richard) located along the Gironde estuary at distances of 35, 65 and 75 kilometers downstream the city of Bordeaux respectively, were sampled in March 2010 and June 2011. The different stations were selected to represent the salinity gradient occurring along the Gironde estuary. At all stations, sediments consisted in pure muds. (average grain size < 63 µm).

4.3.2 Benthic community metabolism

4.3.2.1 Incubation procedure

Under emerged conditions (low tide), benthic chambers systems functioning in closed-circuit were used in triplicate to estimate, at two different conditions, net community primary production (ambient light) and the community respiration rate (darkness). Each benthic chamber consisted in a dome (6.7 L and 30 cm in diameter) of transparent (For experiments in ambient light) or opaque (For those in darkness) Perspex fitted on a crown wheel of stainless steel. Each system was carefully pushed 10 cm into the substrate enclosing a volume of L and a surface area of 0.071m². Changes in CO₂ concentrations (ppm) were measured with an infrared gas analyser (LiCor Li 800) and PAR (Photosynthetically available radiations, 400 to 700 nm) reaching the chamber was quantified with a quantum sensor (LiCor Li-192SA). For more details on the design and use of chambers see (Migné et al., 2002). As measurements were carried out at low tide, we opted for short incubations (10-15 min). For each system, three incubations were performed at light (conditions of light saturation) and averaged to get one mean value per chamber

4.3.2.2 Estimates of community primary production and respiration

For each experiment, CO₂ data were recorded every 15 seconds and stored with a data-logger LiCor Li-1400. After one incubation, latency due to the stabilization of the system and / or the adaptation of organisms to new conditions of light was observed and then the response was linear. The obtained linear regression allowed the calculation of the slope which gives either a consumption (negative sign) or production (positive sign) of CO₂ (ppm). CO₂ fluxes were then calculated using the slope (SCO₂) of CO₂ concentrations ($\mu\text{molCO}_2.\text{molair}^{-1}$) against time (min⁻¹). Results at the community level were then expressed in carbon unit (mgC m⁻² h⁻¹) assuming a molar volume of 22.4 L.mol⁻¹ at standard temperature and pressure and a molar mass of 12 gC.mol⁻¹ CO₂. The following equation allowed calculating the amount of CO₂ produced or consumed in the system during one hour of incubation.

$$CO_2 Flow(\mu mol.m^{-2}.h^{-1}) = \frac{S_{CO_2}}{22.4A_s} \cdot 60 \cdot V_s \quad (4.1)$$

With Vs and As the volume and surface area of the system, respectively. CO₂ flow : benthic community Net Primary Production (NPP) and benthic Community Respiration (CR) were then estimated in mgC.m⁻².h⁻¹. Gross primary production (GPP) was calculated from NPP and CR as :

$$GPP = NPP + CR \quad (4.2)$$

Productivity (mgC.mgChla⁻¹.h⁻¹) was calculated as the ratio between production and chlorophylla biomass :

$$\frac{GPP}{Chla} \quad (4.3)$$

Benthic community description

Prokaryotes

Three sediment samples (one per benthic chamber) were collected with a 2.6 cm inner diameter (5cm depth) cut-off syringe. To avoid any air-contamination, plastic cores were immediately closed at both sides using plastic caps and carefully fixed in a cool box until return to laboratory. Samples were kept refrigerated and were processed within 6 hours from sampling. Triplicate 1mL sediment samples were taken from the core (1) from the top 5 mm of the core and (2) from the 30-50 mm fraction, and were mixed with 1mL of formalin (3.7 % final concentration) and stored at -80°C until analysis. From formalin preserved samples, Prokaryotes were desorbed from sediment particles using a protocol modified from (Duhamel and Jacquet, 2006). Tween 80 (0.5% final concentration) and sodium pyrophosphate (0.1% final concentration) were fixed with the sample by gentle shaking (30 min , 720 rpm). The suspension was then sonicated (ultrasonic bath, 20 min). Finally cellular fractions containing Prokaryotes were purified using a migration on Gentodenz density gradient (1.310 g.mL⁻¹) according to (Amalfitano and Fazi, 2008). Cellular fractions were preserved in formalin (3.7% final) at -80°C until flow cytometry analysis in the *Plateforme Cytométrie-Imagerie* (Observatoire Océanologique de Banyuls sur Mer, <http://www.obs-banyuls.fr/pci/>). The determination of the bacterial abundance was performed by flow cytometry (Marie et al., 2001). Cytogram analysis provided event numbers, identified as prokaryotic cell numbers, during the counting time (1 min).

4.3.3 Microphytobenthic biomass (chlorophyll a)

After each incubation, the top 1 cm of sediment were sampled in triplicate inside the benthic chamber area with a 2.4 cm inner diameter cut-off syringe. These three samples by chamber were pooled to reflect the average concentration of chlorophyll *a* within each chamber and were stored in a cool box until return to laboratory where they were maintained at -80°C until analysis. Sediments cores were then defrosted in the dark and Chl-*a* extraction was performed with 90% acetone (Strickland and Parsons, 1972). The amount of chlorophyll was determined by fluorimetry according to the method of (Yentsch and Menzel, 1963; Holm-Hansen et al., 1965), and Chl-*a* concentration was calculated according to Lorenzen (1966).

Meiofauna

Sediment samples were collected inside the benthic chamber area with a plastic (inner 3 cm diameter) cut-off syringe. The top 3 cm of sediment were sampled in triplicate per station and preserved in a 4% formalin solution. In the laboratory, sediment samples were passed through a 0.063 mm mesh sieve and stained with Rose Bengale. The extraction of meiofauna was performed according to the density separation technique (Jonge and Bouwman, 1977) using colloidal silica Ludox® HS 40 as a high solution to extract meiofauna organisms from sediment. The method is based on differences in specific weight between meiobenthos and sediment. Meiofauna organisms float at the surface, while sediment particles sink. According to (Fricke, 1979) and (Koop and Griffiths, 1982) a 10% increase of measured densities was applied to take into account loss during the extraction process.

Macrofauna

At each station, three 400 cm² replicate sediment samples (20 cm deep) were collected at close proximity (< 50 cm) of benthic chambers systems. Sediments were then sieved through 0.5 mm mesh size. The remaining fraction was fixed using 4% formalin solution and stained with Rose Bengale. In the laboratory, organisms were identified at the species level when possible and counted. Biomasses for each species of each sample were obtained as ash-free dry weight after 48 h drying at 60°C and subsequent calcination at 450°C during 4 h.

Data analysis

Two-way analysis of variance was used to compare sampling dates and stations. Prior to the analysis, homogeneity of variance was checked using Cochran-C test. When necessary, data were

Log₁₀(x+1)-transformed to achieve homogeneity of variances. Wherever such a transformation was insufficient to obtain homogeneity of variances, non-parametric Kruskal-Wallis test was used in order to perform the comparison. In case of statistical differences, suggesting that the null hypothesis was rejected, at least one variance in a site differs from the others, a post-hoc multiple comparison of treatments test was applied to identify the groups of data that differ from each other using R-function kruskal in the R-package : agricolae. The test provides both non-parametric ANOVA and post-hoc test to make pairwise comparisons between treatments mean of the ranks (Conover, 1999). Each time two or more samples were not significantly different, the average of both samples was taken.

4.4 Results

4.4.1 Benthic community description

4.4.1.1 Microphytobenthic biomass (chlorophyll a)

There was significant differences of chlorophyll-a concentrations between sampling periods (ANOVA, $p = 0.016$) and among sampling stations ($p < 0.001$) with no significant interactions between these two factors ($p = 0.223$). Chl-*a* concentrations were always higher in the downstream station (Richard) compared to the upstream station (Lamarque) with the intermediate station (St Christoly) displaying intermediate values (Fig. 4.2).

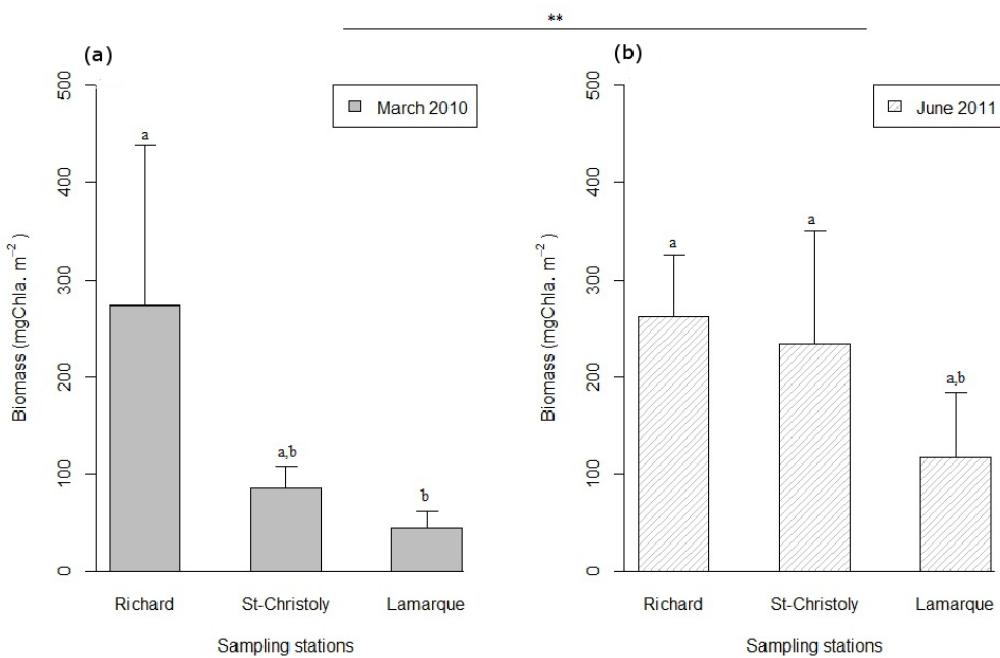


FIGURE 4.2 – Mean (\pm standard error) of chlorophyll-a biomass (mg Chl-a.m^{-2}) at the three sampled sites (Richard, St-christoly and Lamarque) for the two periods (March and June, capital letters A and B, respectively). Small letters a and b were used to show which values statistically differ from others.

In March 2010, average Chl-*a* concentrations ranged from 273 mgChl-*a*.m⁻² at the downstream station against 44 mgChl-*a*.m⁻² at the upstream station. In June 2011, Chl-*a* concentrations were in the same order of magnitude at the downstream station Richard and intermediate station with average value ranging between 233 and 262 mgChl-*a*.m⁻² whereas lower concentrations were measured at the upstream (116 mgChl-*a*.m⁻²) station.

Prokaryotes

Abundances of prokaryotes measured at the top five millimeters stratum of the sediments were not significantly different among stations nor between sampling periods (K-W test, $p > 0.05$) (Fig. 3) with an average value of $15 \pm 7 \ 10^6 \text{cells.g}^{-1}$ of sediment. In March, variation among stations was observed within the stratum 30-50 mm : the upstream station (Lamarque) displayed the highest values of abundances ($12 \pm 4 \ 10^6 \text{cells.g}^{-1}$ of sediment) compared to the downstream station (Richard, $6.8 \pm 1.7 \ 10^6 \text{cells.g}^{-1}$ of sediment) and, especially, to the intermediate station ($0.7 \pm 0.2 \ 10^6 \text{cells.g}^{-1}$ of sediment) ($p < 0.05$) (Fig. 3). In June, no significant difference was observed between the upstream station (Lamarque) and the downstream site (Richard) for the two strata ($p > 0.05$). As observed in March 2010 values of abundances were significantly lower at the intermediate station than in both other stations for the 30-50 mm fraction (1 vs 2 and $5 \pm 3 \ 10^6 \text{cells.g}^{-1}$ of sediment, for St Christoly vs Richard and Lamarque, respectively) (Fig. 4.3).

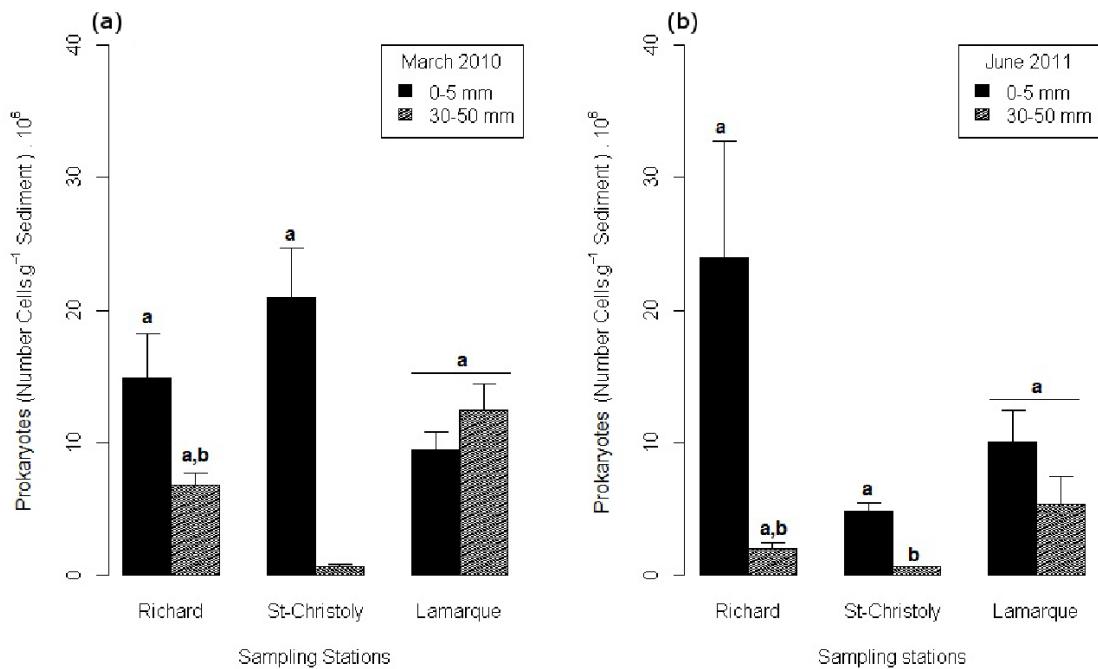


FIGURE 4.3 – Abundance of prokaryotes (number of cells per gram of sediment) by sites and strata (0-5 mm (Upper layer) and 30-50 mm (Deep layer)) for each of the two sampling periods : March 2010 and June 2011. Small *a* and *b* were used to show which values statistically differ from others.

Meiofauna

At all stations and during each sampling periods, nematods were, by far, the dominant taxa representing on average 90%(± 8) of total meiofauna abundance (Table 4.1). ANOVA showed that overall densities of meiofauna were higher in June 2011 (1 055(± 381) individuals. 10 cm^{-2} with no significant difference among stations, Fig.4.4) than in March 2010 ($p < 0.001$).

4.4 Results

TABLE 4.1 – Average density (\pm standard deviation) of meiofauna taxa at each station and periods (number of individuals. 10cm^{-2}) total abundance (total N)

	March 2010			June 2011		
	Richard (downstream)	St Christoly (intermediate)	Lamarque (upstream)	Richard (downstream)	St Christoly (intermediate)	Lamarque (upstream)
<i>Nematoda</i>	489 \pm 162	260 \pm 40	169 \pm 56	843 \pm 149	1293 \pm 157	809 \pm 254
<i>Copepoda</i>	27 \pm 10	14 \pm 1	7 \pm 2	46 \pm 6	60 \pm 11	19 \pm 3
<i>Cop. nauplii</i>	130 \pm 41	1 \pm 1		10 \pm 6	18 \pm 12	21 \pm 8
<i>Ostracoda</i>	1 \pm 1					
<i>Bivalvia</i>	1 \pm 1			2 \pm 1	1 \pm 1	
<i>Gasteropoda</i>				19 \pm 5	12 \pm 5	
<i>Rotifera</i>						3 \pm 3
<i>Acarina</i>				2		
<i>Turbellaria</i>	1 \pm 1					8 \pm 4
<i>Nemertea</i>					1 \pm 1	
Total N	649 \pm 214	276 \pm 42	176 \pm 58	922 \pm 166	1384 \pm 186	861 \pm 271

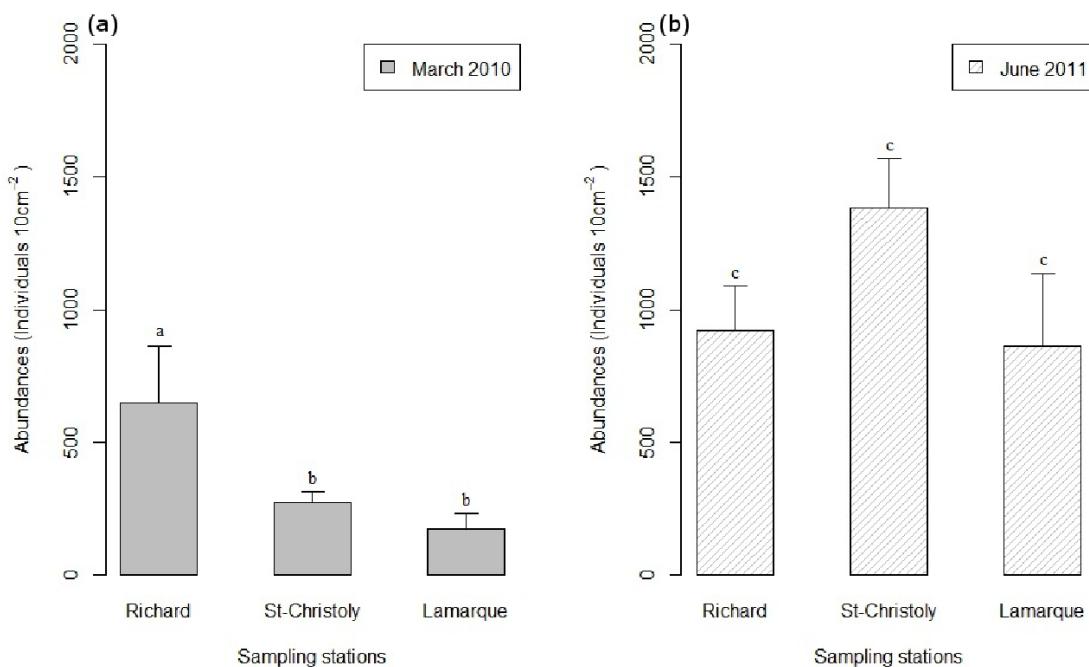


FIGURE 4.4 – Abundances (individuals per 10cm^2 , mean \pm standard error) of total meiofauna sampled at the three stations during the two periods (March 2010 and June 2011). Letters a, b and c show significant ($p<0.05$) differences among situations (dates and sites).

(ANOVA, $p = 0.028$ for the stations effect and $p = 0.003$ for the interaction term) ;, higher abundance of meiofauna were observed at the downstream station in March 2010 (653 \pm 356 indi-

viduals. 10cm^{-2}) compared to the intermediate and upstream stations (respectively 165 ± 59 individuals. 10 cm^{-2} on average for the two other stations).

Macrofauna

The benthic macrofauna composition was different according to the position of the stations along the upstream-downstream axis (Table 4.2). It displayed higher species density at the downstream and intermediate stations compared to the upstream station where the benthic macrofauna is highly dominated by oligochaetes (Table 4.2). In the intermediate and downstream stations, this taxa was absent and the fauna included polychaetes of the Nereidae and Spionidae families as well as the deposit-feeding bivalves *Scrobicularia plana* and *Macoma balthica* (Table 4.2).

Total abundance of macrofauna was only slightly different (K-W test, $p = 0.046$) with lower densities in the upstream station in June 2011 (841 ± 786 ind. m^{-2}) and higher densities in downstream and intermediate stations in March 2010 ($> 6\,000$ ind. m^{-2} , on average) (Table 2, Fig. 4.5a,b).

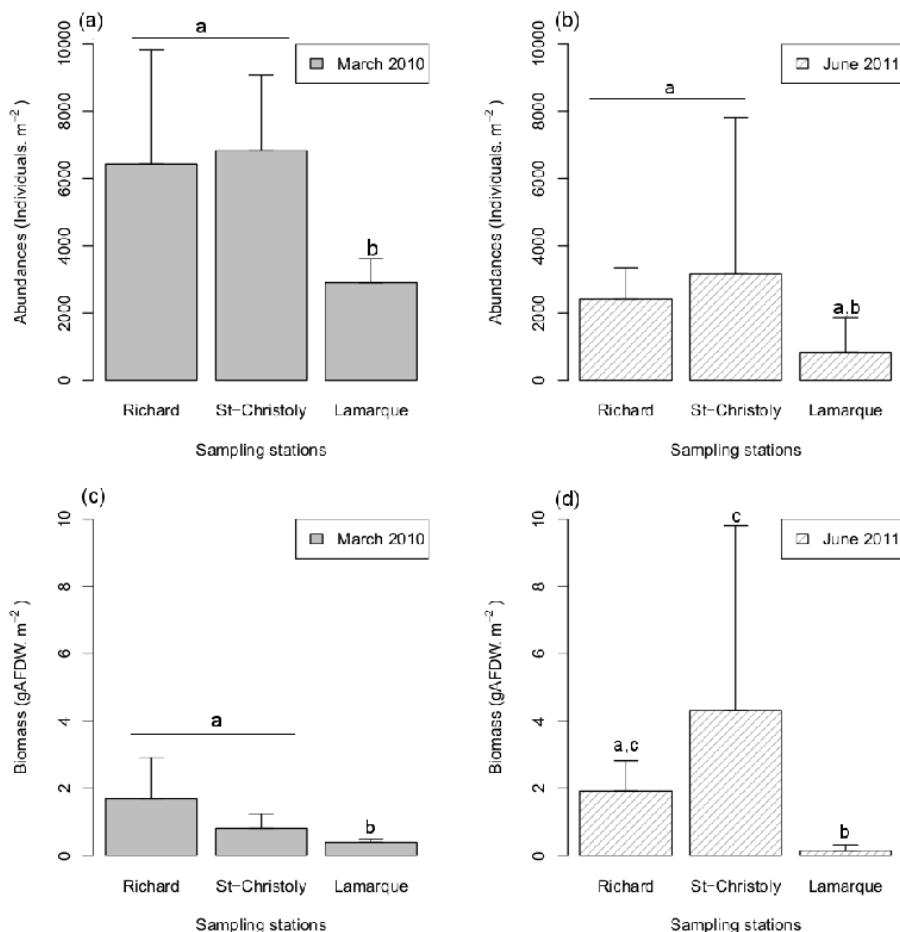


FIGURE 4.5 – (a,b) Abundance (individuals per m^2 , mean \pm standard error) and (C,D) biomass ($\text{gAFDW}\cdot\text{m}^{-2}$, means \pm standard errors) of total macrofauna sampled at three stations during the two periods (March 2010 and June 2011). Small letters *a*, *b* and *c* were used to show which sample statistically differed from others.

TABLE 4.2 – Average density (\pm standard deviation) of macrofauna taxa at each station and periods (number of individuals.m $^{-2}$) together with average number of taxa per sample (S), total abundance (total N), total biomass and mean individual biomass (calculated as the ratio between total biomass (in mg) and total number of individual, expressed in mg.individual $^{-1}$

	March 2010				June 2011			
	Richard (downstream)	St Christoly (intermediate)	Lamarque (upstream)	Richard (downstream)	St Christoly (intermediate)	Lamarque (upstream)		
<i>Abra tenuis</i>	8 ± 14							
<i>Corophium volutator</i>	908 ± 992	2633 ± 430		2200 ± 757	2816 ± 4229	166 ± 160		
<i>Cyathura carinata</i>	8 ± 14				50 ± 66			
<i>Heteromastus filiformis</i>	125 ± 132							
<i>Hydrobia ulvae</i>	266 ± 142	33 ± 57	16 ± 14	8 ± 14	33 ± 28			
Dolichopodidae						83 ± 144		
<i>Macoma balthica</i>	8 ± 14							
<i>Neanthes succinea</i>	225 ± 156	150 ± 108		208 ± 137	16 ± 28			
<i>Nereis diversicolor</i>					208 ± 200			
Oligochaeta						591 ± 713		
Polydora sp.	8 ± 14							
<i>Scrobicularia plana</i>						25 ± 43		
<i>Streblospio shrubsolidii</i>	4875 ± 1915	4016 ± 1645	8 ± 14			16 ± 28		
S (per sample)	6 to 7	3 to 4	2	2 to 3	4 to 5	2 to 3		
total N (ind.m $^{-2}$)	6433 ± 701	6833 ± 1835	2908 ± 678	2425 ± 746	3175 ± 4114	841 ± 786		
total biomass (g.m $^{-2}$)	1.68 ± 0.397	0.813 ± 0.351	0.385 ± 0.1	1.913 ± 0.269	4.316 ± 3.669	0.143 ± 0.098		
individual biomass (mg.ind $^{-1}$)	0.261 ± 0.052	0.119 ± 0.04	0.132 ± 0.00001	0.821 ± 0.184	4.577 ± 4.804	0.205 ± 0.124		

In March 2010, total biomass of macrofauna was not significantly different among stations with an average value of 0.4 gAFDW.m^{-2} . Higher biomasses were however measured in the downstream and intermediate stations in June 2011 with values reaching more than 3 gAFDW.m^{-2} , on average vs $0.14 \text{ gAFDW.m}^{-2}$ in the upstream station (Fig. 4.5c,d). Average individual biomass of macrofauna was higher in the downstream and intermediate stations in June 2011 compared to the upstream station and the March 2010 period (K-W test, $p = 0.027$) (Table 4.2).

4.4.2 Benthic community metabolism

In March 2010, a decreasing significant gradient (K-W test, $p = 0.018$) of gross primary production (GPP) was measured under saturating irradiance from down-to-upstream. Higher values of GPP at the downstream station (Richard : $125 \text{ mgC.m}^{-2.h}^{-1}$ decreased to $38 \text{ mgC.m}^{-2.h}^{-1}$ at the intermediate station and reached $1.5 \text{ mgC.m}^{-2.h}^{-1}$ at Lamarque, the upstream station (Fig. 3). In contrast, in June 2011, there was no significant difference (K-W test, $p = 0.193$) in GPP among the three sampling stations, with an average value of $49(\pm 17) \text{ mgC.m}^{-2.h}^{-1}$ (Fig.4.6).

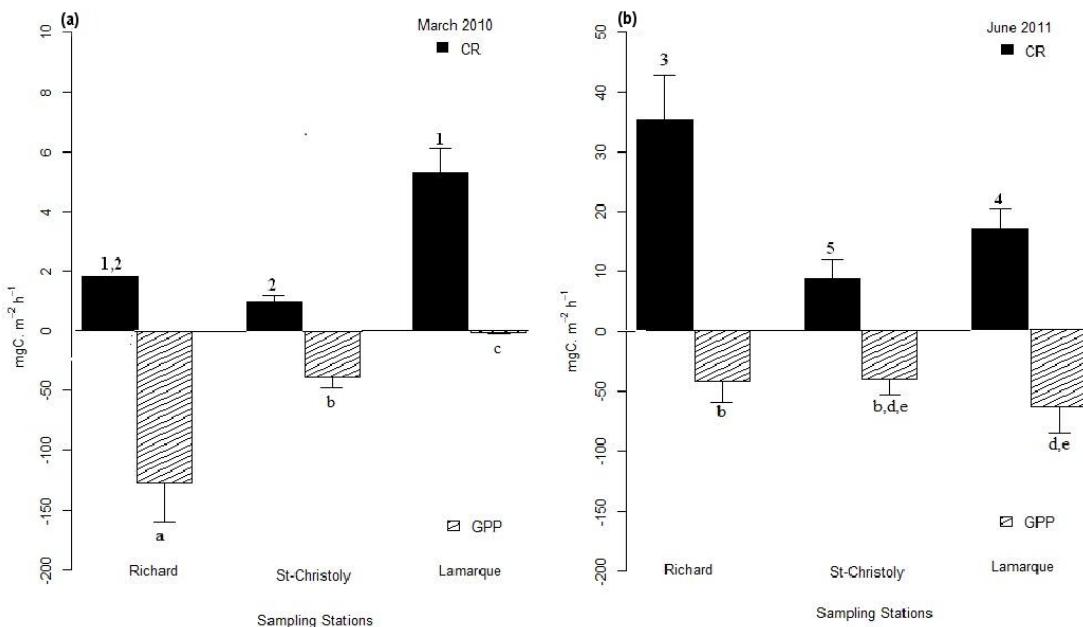


FIGURE 4.6 – Gross primary production (GPP, $\text{mgC.m}^{-2.h}^{-1}$, negative values, mean±standard error) and community respiration (CR, $\text{mgC.m}^{-2.h}^{-1}$, positive values, mean±standard error) measured within benthic chambers at three sampling sites in March 2010 (A) and June 2011 (B). Digits 1 to 5 were used to show which values of RC differed from others.

Benthic community respirations (CR) measures were significantly higher in June 2011 ($20.3 \pm 4.7 \text{ mgC.m}^{-2.h}^{-1}$, on average) than in March 2010 ($2.7 \text{ mgC.m}^{-2.h}^{-1}$, on average) (ANOVA, $p < 0.001$) (Fig. 4.6). In March 2010, slightly higher CR was measured at the upstream station (5.3

4.4 Results

$\text{mgC.m}^{-2}.\text{h}^{-1}$) compared to the downstream and intermediate stations ($1.4 \text{ mgC.m}^{-2}.\text{h}^{-1}$, on average). In June 2011, the lowest CR values were measured at the intermediate station (St-christoly) with a value of CR similar to the highest value measured during the March 2010 period ($8.7 \text{ mgC.m}^{-2}.\text{h}^{-1}$ (Tukey HSD test, $p = 0.169$)). The highest value of CR was measured at the downstream station (Richard $35.5 \text{ mgC.m}^{-2}.\text{h}^{-1}$) whereas the intermediate CR value (but significantly different (Tukey HSD test, $p=0.011$)) was recorded in the upstream station (Lamarque) (Fig.4.6).

The trophic balance of the community, as evaluated from the NPP values, showed that the benthic communities, during the studied periods, were most generally, autotrophic or slightly heterotrophic (Fig. 4.7). Slight heterotrophy ($3.84 \text{ mgC.m}^{-2}.\text{h}^{-1}$) was indeed recorded at the upstream station in March 2010 (Fig. 4.7).

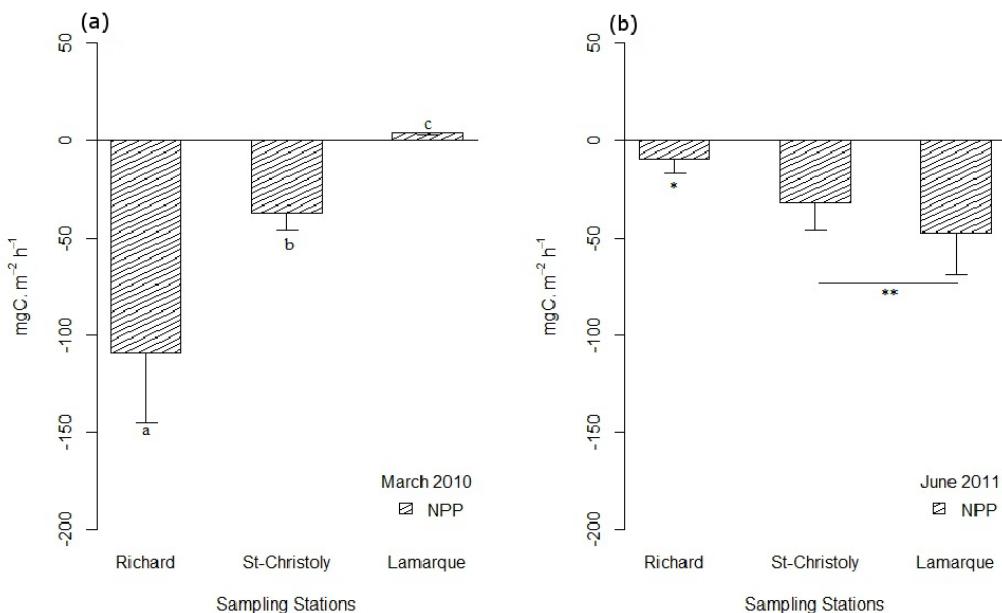


FIGURE 4.7 – Net primary production (NPP, $\text{mgC.m}^{-2}.\text{h}^{-1}$) measured within benthic chambers at three sampling sites in March 2010 (A) and June 2011 (B). Negative fluxes represent the consumption of CO_2 (autotrophy) and positive fluxes represent the production of CO_2 (heterotrophy). Small letters and stars were used to show which values differ from others.

Productivity, as estimated by the GPP :Chl-a ratio, was not significantly different across stations and dates (ANOVA, $p > 0.8$ for both factors) with the noticeable exception of the upstream station of Lamarque in March 2010 which displayed very low GPP :Chl-a ratio ($0.05 \text{ mgC.m}^{-2}.\text{h}^{-1}$) causing significant interaction between sampling period and stations (ANOVA, $p = 0.002$) (Fig. 8). Excepting this particular case, the average GPP :Chl-a ratio was $0.35 \text{ mgC.mgChl-}\alpha^{-1}.\text{h}^{-1}$ (Fig. 4.8).

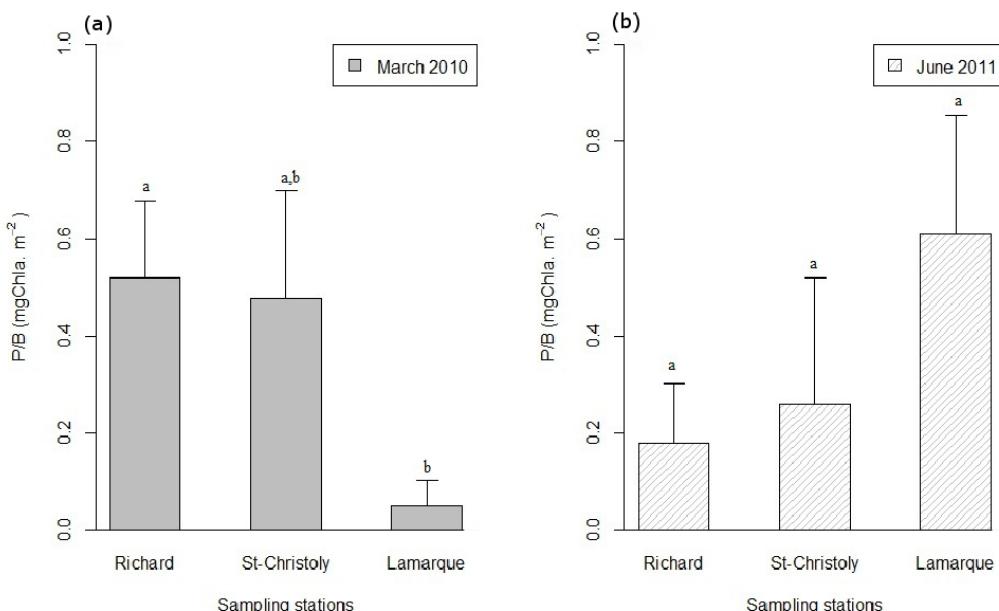


FIGURE 4.8 – Productivity (P/B ratio, mgC.mgChla⁻¹.h⁻¹, mean ±standard deviation) measured at the three sampling stations for each period. Small letters *a* and *b* were used to show which sample statistically differ from others.

4.5 Discussion

4.5.1 Seasonal variations of benthic community structure in the Gironde estuary mudflats

Comparison between the two different periods showed that microphytobenthos biomass (chlorophyll-a concentration) was both more important and evenly distributed along the estuarine gradient in June than in March. Gross Primary Production (GPP) displayed a similar pattern with high GPP located downstream in March and moderate but evenly located GPP in June.

Meiofaunal abundances closely matched the pattern of microphytobenthos abundance with overall higher densities in June than in March, together with a homogeneous spatial distribution of abundance in June. In contrast, the highest densities were concentrated in the downstream station in early Spring (March).

Macrofaunal biomasses were in the same order of magnitude during the two periods, but globally significantly higher in March than in June. Concomitantly, the average individual body mass of macrozoobenthic organisms was higher in June than in March indicating that larger organisms were sampled in June. These patterns indicate two contrasting situations with an early Spring situation corresponding to the onset of the microphytobenthic production period (mainly located downstream)

taking advantage of higher temperatures downstream (<http://somlit.epoc.u-bordeaux1.fr/fr/>) and seasonal light increases. During this period, high GPP level was rapidly reached in response to favorable environmental conditions. A similar pattern of early spring onset of microphytobenthic production period in the Gironde estuary mudflats has been revealed by increased biomass of microphytobenthos by Santos et al. (Santos et al., 1997). These authors pointed out the importance of light availability and temperature (and salinity) as the main factors explaining microphytobenthic biomass variations. Because microphytobenthos corresponds to photoautotrophic cells, a direct effect of the irradiance annual cycle on microphytobenthos is expected. In addition, temperature is known to have a significant effect on primary production and growth rates of microphytobenthos both at a seasonal scale (Cadée and Hegeman, 1974) and at an hourly scale (Admiraal, 1976; Colijn and Buurt, 1975) during the emersion periods on intertidal mudflats (Rasmussen et al., 1983). As a result, both factors are generally reported in the literature as having a combined positive relationship on microphytobenthos production, explaining the different temporal variations of the observed patterns of this production (Cibic et al., 2007; Colijn and de Jonge, 1984). Hence microphytobenthic cells probably react more quickly than metazoans (meio- and macrofauna) to the changes of environmental conditions during this early spring period. However high productive meiofaunal organisms characterized by short life cycles, showed a similar temporal pattern : densities were low in the stations where microphytobenthos biomass was limited (upstream) whereas higher densities were observed downstream where high microphytobenthic production occurred. Observed levels of density were in accordance to those measured in winter in the oligo-mesohaline region of the Gironde estuary by Santos et al. (1996). Abundance of macrofauna was high and composed by rather small individuals. Temperatures during this period begin to increase and vary on a daily basis. Hence the heterotrophic activity, as measured through the Community Respiration (CR), was still very low ($2.94 \pm 2.27 \text{ mgC.m}^{-2}.\text{h}^{-1}$). This was probably due to low temperatures measured at this period (Table 4.3). In their paper, (Santos et al., 1997) indeed published values of temperatures in the sediment and it appeared that temperature followed a clear seasonal pattern between 5.8 °C in February and 23.8 °C in July. From these results the steep increase of temperatures begins during spring in the study area. Temperature is a key factor controlling the biological activities, and especially respiration of poikilotherms benthic organisms.

Based on our observations, early spring in the Gironde estuary mudflats would thus correspond to a strong reduced activity of heterotrophic organisms, still under the influence of low temperatures. In contrast, the samples collected in June represented a late spring/summer situation where high microphytobenthic biomasses occurred along the whole estuary mudflats. One reason could be the reduction of river flows that usually takes place from March until September (Selleslagh et al., 2012). We can argue that favorable conditions to MBP growth occurred more downstream and can progressively

extend to the upstream estuary with the reduction of fresh water influence after March (Fig. 4.9).

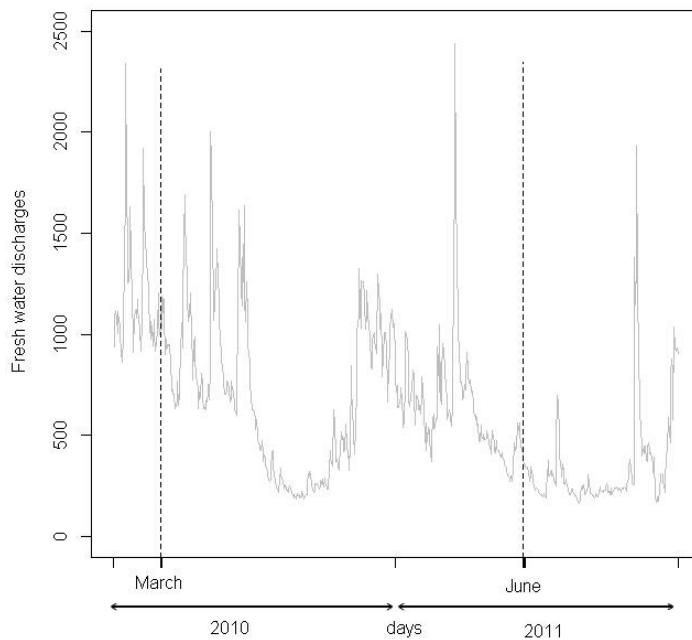


FIGURE 4.9 – River flow ($\text{m}^3.\text{s}^{-1}$) in March 2010 and June 2010 for the Gironde estuary. Dotted vertical lines represent the values of river runoff at the two period of study during the years 2010 and 2011.

Meiofauna densities increased in response to higher available microphytobenthic biomass and reached levels ($> 1\,000 \text{ ind.}10 \text{ cm}^{-2}330$) in accordance to summer values reported by Santos et al. (1996). Macrofauna densities were lower than in early spring situation with a tendency toward larger organisms. The spring period, from the onset of microphytobenthic primary production corresponds to the main period of growth for macrobenthic organisms in the Gironde estuary (Bachelet, 1979). In the Gironde estuary tidal flats, the main recruitment period usually occurs during late summer and autumn as shown by Bachelet (1979, 1980); Bachelet et al. (1980) and, more recently by (Selleslagh et al., 2012). In terms of benthic metabolism, the benthic community respiration (CR) was much higher during this period (range $9\text{--}35 \text{ gC.m}^{-2}.\text{h}^{-1}$) than during the early Spring period (range $1\text{--}6 \text{ gC.m}^{-2}.\text{h}^{-1}$) revealing stronger heterotrophic activity during late spring-summer period in relation to higher temperature in summer. As a consequence, at the scale of the benthic community the balance between autotrophy and heterotrophy may shift toward heterotrophy or reduced autotrophy in summer in opposition to overall autotrophy in early spring. Indeed high respiration rate measured in summer may probably exceed or almost equal primary production when considering the relatively short duration available (on a 24H-basis) for microphytobenthic production (i.e. low tide during day).

4.5.2 Comparison with other estuaries and ecosystems

The abundances of the macrobenthic community estimated in the present paper are in the same order of magnitude than those sampled in the nearby ecosystems such as the Tagus(França et al., 2009) and Duoro(Mucha et al., 2005) estuaries. The seasonal dynamics did not differ from the usual seasonal pattern of temperate estuarine macrobenthic community with an increase of density during late summer and autumn and a decrease in abundances during winter and spring when the minimum values are reached (França et al., 2009; Marques et al., 1993; Selleslagh et al., 2012; Ysebaert et al., 2003). Indeed, our results indicate the highest values of density in March while the highest biomass values are in June. In their paper, Mucha et al. (2005) found similar results in terms of abundances even though no general pattern could be identified due to strong variability occurred at different stations. This seasonal pattern of densities and biomass reflects the recruitment patterns of the most abundant species, which usually takes place during late summer and autumn in the Gironde estuary (Selleslagh et al., 2012). Most macrobenthic species show faster growth rates during spring and summer months, when temperatures values increase (Beukema, 1974; Ysebaert et al., 2003).

Microphytobenthic biomass recorded in the current study, as estimated by Chl-a concentrations, were in the range of high values classically measured during Spring and Summer in intertidal mudflat in temperate areas (i.e. $> 100 \text{ mgChlo-a.m}^{-2}$) (Pinckney and Zingmark, 1993; Underwood et al., 1999). Microphytobenthic productivity (P/B ratio, in $\text{mgC.mgChl-a-1.h}^{-1}$) estimations generally ranged between 0.11 and 0.88 $\text{mgC.mgChl-a-1.h}^{-1}$ (excluding particular low values recorded at the upstream station in March). These values are in the range of other values measured on microphytobenthos of sheltered tidal flats using the same methodology (i.e. from 0.1 to $< 1.0 \text{ mgC.mgChl-a-1.h}^{-1}$ (Davoult et al., 2009; Hubas and Davoult, 2006; Migné et al., 2004; Spilmont et al., 2006) and much lower than those reported for exposed sandy beaches measured by Spilmont et al. (2005). The particular low value found at the upstream station in March is probably due to the stress conditions caused by an exceptional spring flooding that occurred in the system two days prior to the sampling (Fig. 4.9). This comforts our hypothesis on the effect of freshwater in the intertidal mudflats and in the estuarine production. Because river flows are highly variable in the Gironde and more perceptible in the upstream part, the situation in March with strong freshwater discharges compared to June (Fig. 8b) describes the sensitivity of microphytobenthic to rapid salinity decrease events.

Our results tend to show that the increase of microphytobenthos biomass reduces the productivity of the sediment during high microalgal production. This is in accordance with (Blanchard et al., 2001) who found in Marennes-Oléron Bay that microalgal biomass followed a logistic growth curve, converging towards a maximum value at which primary productivity tends to zero, when grazing and/or

resuspension are low. The same observations have been recently shown along the English Channel by Davoult et al. (2004) and Spilmont et al. (2006). Consequently, the first estimates of Gross Primary Production (GPP) for the Gironde estuary mudflats provided by the current study are in the range of GPP measured in other temperate mudflats 378 during spring and summer periods (Davoult et al., 2009). Our study did not provide enough data to calculate an accurate estimation of the yearly microphytobenthic primary production on the Gironde mudflats, but these first measures however suggest that these mudflats are as productive as most estuarine mudflats (i.e. $> 100 \text{ gC.m}^{-2}.\text{yr}^{-1}$ (Brotas et al., 1995; McIntyre and Amspoker, 1986; Spilmont et al., 2006; van). Nevertheless, the very high turbidity of the Gironde estuarine waters most probably stops the microphytobenthic primary production as soon as the tide rises and consequently limits this primary production at a daily (and yearly) scale (Barranguet et al., 1998; van). This limitation has been already hypothesized in most estimates in estuarine or coastal embayments (Migné et al., 2009; Spilmont et al., 2006). However the primary production of the subtidal microphytobenthic community in temperate coastal ecosystems can reach 57 mg C m⁻² day⁻¹ in winter and 111 mg C m⁻² day⁻¹ in late summer in coastal ecosystems where turbidity is limited (Ni Longphuirt et al., 2007). When comparing benthic metazoans densities and biomass, one the most striking feature of the Gironde estuarine mudflats is the very low biomass of macrofauna. Biomasses measured during our study indeed provided estimated values of biomass up to gAFDW.m⁻² and usually lower than 2 gAFDW.m⁻². These biomass values are particularly low compared to other estuarine mudflats (Fujii, 2007; Ricciardi and Bourget, 1999; Ysebaert et al., 1998) and most sheltered and semi-sheltered tidal flats (Ricciardi and Bourget, 1999) but in accordance with the observations reported by (Heip and Herman, 1995). Most macrozoobenthic organisms sampled consisted of primarily deposit-feeding organisms without any suspension feeders, although suspension feeders, such as the common cockle *Cerastoderma edule*, are usually conspicuous suspension feeders of the estuarine (downstream) macrozoobenthic assemblages(Borja et al., 2004; Ysebaert et al., 1998). In addition, meiofauna hardly reached a maximum density over ca. 1 000 ind.cm⁻² during our study periods, in accordance with values provided by (Santos et al., 1997). Though these values are not outside of recorded densities of meiofauna in other estuarine flats, the level of densities was at most, moderate (Heip et al., 1990; Smol et al., 1994). Prokaryotes densities measured in this study can hardly be compared to existing values since the different authors used very different methodologies to estimate Prokaryote densities in sediments (Amalfitano and Fazi, 2008; Caron, 2005; Donovaro et al., 2006; Duhamel and Jacquet, 2006). Community Respiration : is in the same order of magnitude than those recorded in sheltered tidal flats in the same period using the same methodology (Davoult et al., 2004; Hubas and Davoult, 2006; Migné et al., 2009; Spilmont et al., 2006) and higher than those reported on exposed sandy beach (Spilmont et al., 2005)

Based on these comparisons we hypothesize that the metazoan activity on the Gironde mudflats is food-limited in relation to (1) the characteristics of the water column : very high SPM concentrations combined with low organic carbon content which is probably mostly refractory (Savoye et al., 2012) and (2) strong competition among benthic organisms for the main available food resource : micro-phytobenthos. However, unpublished observations showed that both densities and biomass are higher on the Gironde intertidal flats than in the subtidal area (also see Brosse et al. (2000). Intertidal flat probably still play a key-role for the foodweb functioning of the Gironde estuary.

4.6 Acknowledgements

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CHAPITRE 5

APPORT DE L'OUTIL ISOTOPE À LA COMPRÉHENSION DU
FONCTIONNEMENT DU RÉSEAU TROPHIQUE DE L'ESTUAIRE DE LA

GIRONDE

Introduction du chapitre

Au cours des deux études précédentes, nos résultats ont montré (1) le faible niveau de production primaire phytoplanctonique dans les eaux turbides de l'estuaire de la Gironde et (2) l'existence d'une production microphytobenthique non négligeable sur les estrans vaseux de l'estuaire. Ce chapitre présente les résultats d'une étude que nous avons réalisée afin d'estimer le rôle de ces deux sources de matière organique dans le réseau trophique benthique et planctonique de l'estuaire. L'objectif était de mettre en évidence l'importance relative de ces deux sources au regard des apports des rivières et de la production primaire des macrophytes des rives de l'estuaire.

L'outil que nous avons privilégié pour réaliser ces estimations est l'utilisation des isotopes stables de l'azote et du carbone comme traceurs trophiques permettant de déterminer les principales sources utilisées par les consommateurs primaires dans l'estuaire de la Gironde. Cette étude a consisté à acquérir des données concernant la faune et la flore benthique et à synthétiser un ensemble de données acquises sur le compartiment planctonique au cours d'études précédentes (David et al., 2005). Les résultats obtenus sont présentés sous la forme d'une publication scientifique qui sera soumise dans un journal international.

Apport de l'outil isotope à la compréhension du réseau trophique

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5.1 abstract

The littoral zone contains ecosystems featuring high and diverse primary productions which constitute the base of complex food webs. At the crossroad between ocean and continents, coastal ecosystems appear the most geochemically and biologically active areas of the biosphere. The biological activity of coastal ecosystems is fueled by organic matter fluxes from a variety of local and imported sources such as it remains difficult to know exactly which source(s) are important at the base of food webs that support high levels of secondary productivity. In this study, the Gironde estuary, a macrotidal estuary, located in the South-Western France was investigated in order to determine food web structure and estimate the diet composition of primary consumers. Our objectives were first to synthesize available data on benthic and planktonic primary consumers isotope signature in order to analyze their trophic behavior in such an extreme condition. Then we compared stable isotope ratios between consumers and food resources for better understanding their ecological importance to the coastal environment. It appeared that benthic organisms proved to be highly selective in their food source since alternative deposit/suspension feeders were able to selectively collect and assimilate phytoplankton from the water column despite its low availability. Alternative deposit/suspension feeders reach their upstream limit at KP 52 and are not found in upstream stations (PK 30). Planktonic species, in contrast relied on a less specialized, omnivorous feeding strategy. However, downstream phytoplanktonic production plays a key-role for most species with a decreasing importance from downstream to upstream regions. Microphytobenthic production is poorly used by most planktonic taxa with the exception of mysids that are known to display benthopelagic behavior.

Keywords : Stable isotopes, Gironde estuary, Organic matter, Planktonic organisms, Benthic consumers, primary producers.

5.2 Introduction

Coastal ecosystems, at the crossroad between ocean and continents, are characterized by a great diversity of primary producers that makes them the most geochemically and biologically active areas of the biosphere (Gattuso et al., 1998) despite their relatively small areal extent : 6% of earth and 8.5% of marine biomes (Costanza et al., 1998). In comparison with open oceans ecosystems where primary production is dominated by phytoplankton, coastal systems display both a high level of primary production and a much higher diversity of primary producers. Indeed, the biological activity of coastal ecosystems is fueled by organic matter fluxes from a variety of local and imported sources ranging from local primary production by phytoplankton, benthic microalgae, by macrophytes systems such as seagrass beds (Duarte, 1991), macroalgal beds, mangroves (Kathiresan and Bingham, 2001) and salt marshes (Adam, 1990; Bouillon and Boschker, 2006) together with terrestrial inputs through river discharges. Hence, pool of organic matter available for primary consumers is therefore mostly derived from a mixture and heterogeneous food sources of different nutritive values. Many studies have focused on estuaries where organic matter sources are well discriminated, mostly continental vs. oceanic end-members (e.g. Cifuentes et al. 1988; Papadimitriou et al. 2005; Liu et al. 2006; Zhou et al. 2006; Ramaswamy et al. 2008). All micro and macroscopic primary producers contribute to the pool of particulate organic matter (POM) together with continental inputs that drive the estuarine food web functioning (Sintes et al., 2004; Lobry et al., 2008; Savoye et al., 2012). POM plays a key role in ecosystem functioning and especially in trophic transfers because different primary producers and corresponding detritus are not available to the same extent to primary consumers, depending on their biochemical composition (Tenore and Dunstan, 1973; Grémare et al., 1997). Finally, the spatial complexity of estuaries, variations in water and organic matter exchange, and multiple potential organic matter sources all complicate the determination of the relative importance of organic matter sources that support estuarine consumers. Consequently, it remains difficult to know exactly which source(s) are important at the base of food webs that support high levels of secondary productivity in estuaries such as many fishes and birds of commercial and/or patrimonial importance (Degaan and Garritt, 1997; Moreira, 1997; Brosse et al., 2000; Vinagre et al., 2008). The importance of phytoplankton and benthic microalgae, for instance, are indicated by their high variability and the short, efficient nature of algae-based food webs leading to fish (Ryther, 1969; Keller et al., 1990; Mallin and Pearl, 1994) challenging the historical thought of saltmarsh plant as primarily fueling estuarine food web (Teal, 1962; Galvan et al., 2008). It thus appears that identifying the contribution of different sources of organic matter is essential for better understanding their ecological importance to coastal environment.

Different tools such as elemental ratios and isotopic composition of organic matter have been widely used to investigate the origin of primary producers in riverine, estuarine, coastal and shelf systems (Michener and Kaufmann, 2007; Dubois, 2012; Savoye et al., 2012). Because of their physiology and of the origin of their nutrient resources, different primary producers usually exhibit different isotopic and/or elemental signatures. As a result stable isotopes of different elements (carbon, nitrogen and sulphur) have proven useful as tracers of organic matter and can help to understanding the food web structure in a variety of aquatic ecosystem (Degaan and Garritt, 1997). The use of stable isotopes to determine food web structure involves the comparison of stable isotope ratios between consumers and food resources and requires distinct differences in isotopic values among food resources. The Gironde estuary is an interesting case study because of its very high level of turbidity which prevents phytoplankton production along most of its length (Irigoin and Castel, 1997a; Goosen et al., 1999; Nzigou et al., prep.). In such an extreme condition our objectives were to synthesize available data on benthic and planktonic primary consumers isotope signature in order to analyze their trophic behavior in such an extreme condition. Until now, the food web structure of the Gironde estuary has been constructed without taking into account microphytobenthos contribution in spite of the important role it can play to supply primary production in water column especially in this turbid systems where phytoplankton production is scarce.

5.3 Material and methods

5.3.1 Study area

The present study was carried out in the Gironde estuary ($45^{\circ} 20' N$, $0^{\circ} 45' W$), a macrotidal (tidal range 1.7-5.3 m) estuary, located in the South-Western France (Fig.5.1). It is the largest French estuary (625 km^2 at flood tide) and one of the biggest in Europe resulting from the gathering of two large rivers, the Garonne and Dordogne rivers. Their drainage basins amount for $71,000 \text{ km}^2$ and the mean annual combined river flow is nowadays around 500 m.s^{-1} (average values from 2007 to 2009, Savoye et al. 2012). One of the main characteristics of the system is the high turbidity (up to few g L^{-1}) of surface waters (Etcheber et al., 2007; Abril et al., 2002). The total mass of particles in the system, due to the existence a maximum turbidity zone (MTZ), can reach 4-5 millions tons of particles (Allen et al., 1974). As river flow increases, the MTZ moves seaward, splits into two, and part is temporally trapped in the lower estuary and/or exported to the ocean (Doxaran et al., 2009; Sottolichio and Castaing, 1999; Etcheber et al., 2007; Jouanneau and Latouche, 1981).

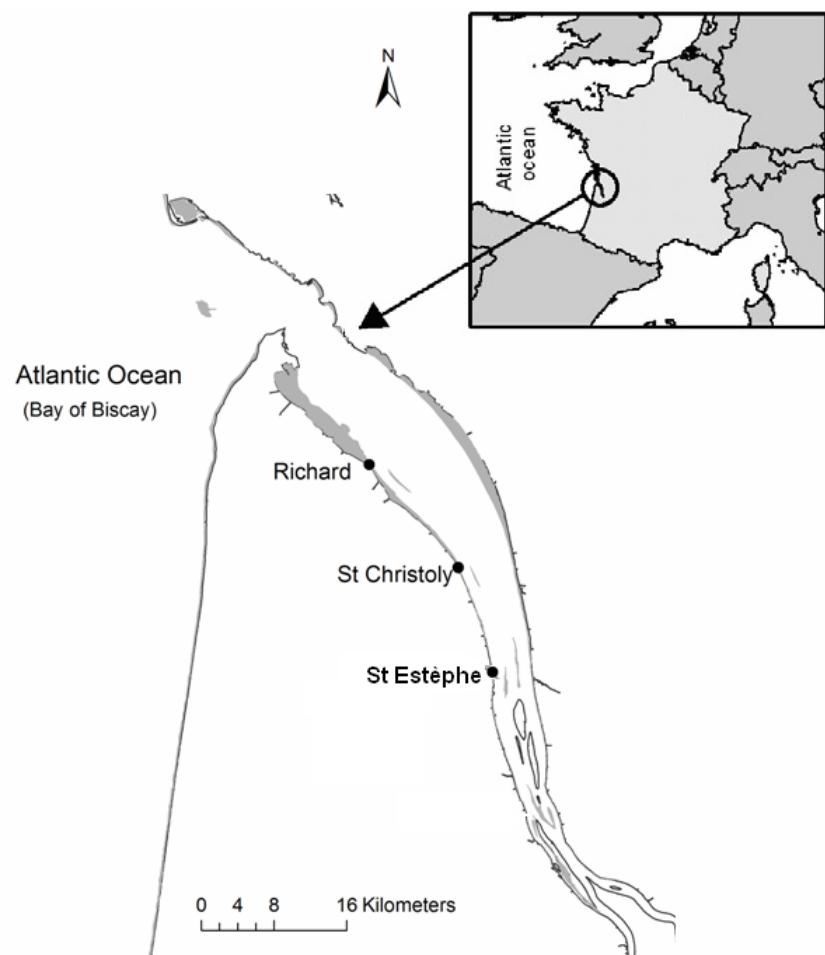


FIGURE 5.1 – Map of the Gironde estuary (France) showing the sampled stations from up to downstream (Lamarque, St Christoly and Richard).

5.3.2 Available data

5.3.2.1 Benthic organisms and organic matter sources

In order to integrate potential temporal variations benthic organisms were collected on three occasions : Autumn 2009 and 2010, and Summer 2010. In order to take into account spatial variations along the estuarine salinity gradient, three sites were sampled at low tide on the intertidal mud flats of the Gironde, namely Richard (KP 78 ; 45°44' N, 0° 87' W), St-Christoly (KP 67 ; 45°36' N, 0° 78' W) and St-Estèphe (KP 55 ; 45°27' N, 0° 72' W) (Fig.5.1). Each station was considered as representing a different part of the estuary as described in Jouanneau and Latouche, 1981 : the upstream, median and downstream parts of the estuary were represented by stations St-Estèphe, St-Christoly and Richard, respectively (Fig.5.1).

Macrophytes were collected by hand for organic carbon and nitrogen elemental and isotopic compositions. At each site the main different species of macrophytes were collected. Several groups of macrophytes were obtained, namely green macroalgae of ulvaceae group, brown macroalgae Fucus

5.3 Material and methods

vesiculosus as well as angiosperms from adjacent wetlands namely rushes (*Juncus* sp.) and reeds. In the laboratory, plants were identified by group or at genus levels. Samples were carefully cleaned with filtered seawater, drained and cut before being stored at -20° C in aluminum foil until analysis.

Microphytobenthos was collected at each occasion during low tide where it formed dense and highly productive diatom-dominated layers at the surface of the finegrained sediments (Serodio et al., 2001). However, in sandy-silty sediments substrate containing a large part of mud, the collection of a pure fraction of microalgal cells, devoided of detrital material and meiofauna is difficult to obtain. In our study, we used a method from Riera et al. (1999) modified by Herlory et al. (2005) and recently applied in Arcachon Dubois (2012) or Marenne Oleron Lebreton (2009) bays. The method is based on the light-induced vertical migration of the cells (Kromkamp et al., 1998; Serodio et al., 2001; Underwood et al., 2002) Hence, the top first centimetre was collected within a 400-cm² area. Back in the laboratory, sediment containing microalgae was sieved through a 500-100-m mesh and put into flat trays to form a 1-cm thick layer. At the time of low tide, the top of sediment layer was covered with 3 nylon screens (100-m mesh). The trays were disposed close to the windows such as, in daylight, microalgae could continue their migration, according to their endogenous rhythm through sediments and nets. The collection of microphytobenthos was performed the day after and during the time of the corresponding low tide in real conditions. This was performed by rinsing the upper nylon screen (or the second one when there was enough material) with filtered seawater. Therefore we can assume that the material sampled using this method contains pure and fresh material. The collected material was fixed by successive centrifugations of 5 min at 1000 rpm and stored at -80 ° C until analysis. Sediment samples were taken by hand by scraping the upper first centimetre of mud over a total surface of 280 cm². In the laboratory, sediment was then freeze-dried until analysis.

Benthic macrofauna was collected over a total surface area of approximately 800 cm² (20 cm deep). Back in the laboratory, sediment samples were sieved through 500-m mesh sieve. Organisms collected were identified alive to the species level whenever possible. Identified individuals were cleaned and incubated overnight in filtered seawater to allow evacuation of gut content. Organisms with calcareous shells (bivalves, gastropods etc.) were carefully dissected so that any piece of shell was removed from the whole soft-body used for isotopes analysis. Samples were stored at -20 °C into pre-combusted (4H) and HCl-cleaned glass vials (10%) until the analysis.

Planktonic organisms

In order to integrate both spatial and temporal variations, zooplankton samples were collected in spring and summer 2002, 2003 and 2004 at three sites located along the estuarine gradient (KPs 65,

50 and 30) (Fig.5.1). Copepods were collected using a WP2-type net whereas mysids and gammarids were collected using an IOSN mesh with a 500 – mmesh. Samples were sorted alive and identified to species level. Only organisms displaying empty guts were collected in filtered seawater for analysis. Samples were rinsed in distilled water, dried at 60°C for 48H and grounded to powder until analysis.

Phytoplankton isotope signatures

Phytoplankton isotope signatures were estimated based on the work of Savoye et al. (2012) in the Gironde estuary. Based on a review of water column organic matter data collected from 2007 to 2009 in the Gironde estuary, these authors proposed a relationship that allows calculating the $\delta^{13}C$ signature of phytoplankton as a function of salinity in the Gironde estuary :

$$\delta^{13}C_{phytoplakton} = -7.43 \cdot 10^3 \text{ Salinity}^2 + 0.648 \text{ Salinity} - 34.5 \quad (5.1)$$

Using this relation, marine (=downstream estuarine) phytoplankton signature was calculated using the highest salinity value observed at KP 86 using the SOMLIT database (Service d'Observation en Milieu LITToral ; <http://somlit.epoc.u-bordeaux1.fr/fr/>). As well, the average signature of estuarine phytoplankton and its variability was calculated at each sampled stations (Richard, St Christoly and St Estèphe) integrating the SOMLIT salinity data measured each month during years 2009 and 2010 at KPs 86, 67 and 56, respectively. Finally, river phytoplankton signature was obtained using the above relation.

5.3.2.2 Stable isotopes $\delta^{13}C$ and $\delta^{15}N$ analysis

All collected samples were stored at -80°C until the analysis. Before stable isotope analysis, samples were freeze-dried, and then grounded into a fine and homogeneous powder using a ball mill. Powders were weighed (0.4 mg to 1.5 mg) into tin cups for the determination of N isotopic composition, and in silver cups for the determination of C isotopic composition. Except for zooplankton, the latter powder was decarbonated using 1.2N HCl to remove any carbonate debris (Riera et al., 1999; Kennedy et al., 2005). All Samples were analysed for C or N elemental and isotopic composition using an elemental analyser (EA ; NC2500, CarloErba®) coupled to an isotope ratio mass spectrometer (IRMS ; Isoprime, GV Instruments®). IRMS daily drift was monitored using home-made standards (caseine, glycine) and data were corrected consequently whenever necessary. Isotopic composition was calibrated against home-made standards and reference material (IAEA-N2). Stable isotope data were expressed in part per thousand (‰) deviations from international standards using the following equation : All isotopic data were expressed in the conventional delta notation

$$\delta^{13}X = (R_{sample}/R_{standard} - 1).1000 \quad (5.2)$$

Where X = ^{13}C or ^{15}N , and R = ratio of heavy/light isotope content ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$). Analysis uncertainty was less than 0.02 % (Dubois, 2012)

5.3.2.3 Data analysis

Isotopes signatures of on a one hand, organic matter sources and primary producers and, consumers, on the other hand were analyzed separately using cluster analysis. Cluster analysis was used to put in evidence the existence of homogeneous groups of organic matter source, primary producers or consumers, based on their isotopes signatures. Distance matrix was build using euclidean distance between samples. Cluster analysis was then performed using the group average method. The distance matrix can be used to statistically analyze the effect of factors such as (e.g.) life position (benthic/pelagic) using PERMANOVA method (Anderson et al., 2008). All analyses were performed using PRIMER v6 (Clarke and Gorley, 2006).

5.3.2.4 Mixing models

IsoSource mixing models (Phillips and Gregg, 2003) and SIAR (Parnell et al., 2008, 2010) or MixSIR (Moore and Semmens, 2008) provide estimates of the proportion of each source in a mixture isotope. These models are generally grouped into two categories : Bayesian models (e.g. SIAR and MixSIR) and non-Bayesian (e.g. IsoSource). Mixing models including Bayesian approaches are particularly useful when working with n isotopes in systems where the number of sources exceeds the number of isotopes analyzed +1 (n +1). They offer several advantages, including the incorporation of uncertainty to the sources, the consumers and the trophic enrichment factor (Parnell et al., 2010). The possibility to interpret *a posteriori* distributions as probability densities or the incorporation of error terms for specific discrimination factors are other advantages proposed by such models. In our study, we used the SIAR approach (Stable Isotope Analysis in R, Parnell et al., 2010) as the method of choice to quantify the relative contribution of organic matter source to the diet of sampled consumers. Indeed, besides the advantage of being run with an open source and freely distributed software, R, SIAR model allows to take into account the concentration of carbon and nitrogen in the samples (Phillips and Koch, 2002). In the SIAR program (siar package, R.2.14.1), we ran 10 000 iterations using a specific function for single data point, as only one data point was provided into the data file for each consumer. Then, outputs of the proportion of different sources in the diet of each consumer were produced as boxplots representations ; while a biplot showing the isotope composition of each

element (source or consumer) was plotted.

5.4 Results

5.4.1 Organic matter sources

Five different primary producers were retrieved and analyzed during the study (Fig. 5.2). Among them, angiosperms (reeds and rushes) displayed the lowest $\delta^{13}\text{C}$ with an average value of -26.7‰(± 1.2) and low $\delta^{15}\text{N}$ values 5.5‰(± 0.8). Two groups of macroalgae were also distinguishable thanks to their isotopes signatures : *Fucus vesiculosus* was only present at the downstream station in low abundance and restricted to rocks located near the dykes. This species displayed higher $\delta^{15}\text{N}$ values than angiosperms (8.3‰(± 0.7) together with much higher $\delta^{13}\text{C}$ values (-18.5‰(± 0.3)). Ulvaceae displayed a highly variable isotope signature at the downstream station with very high values of $\delta^{13}\text{C}$ (-10.7‰(± 2.7) and high $\delta^{15}\text{N}$ (9.1‰(± 2.7)). At the intermediate station, ulvaceae displayed much less variable isotopes signatures with a high average $\delta^{13}\text{C}$ (-16.6‰(± 0.4) and low $\delta^{15}\text{N}$ (6.0‰(± 0.3)). As for *Fucus vesiculosus*, these green macroalgae were retrieved from dykes but were never observed on sediment surface. Microphytobenthos ^{13}C signature could only be obtained on two samples retrieved from the upstream station ; the average $\delta^{13}\text{C}$ was -16.7‰(± 0.2)). Three values of microphytobenthos $\delta^{15}\text{N}$ were obtained from the intermediate and upstream stations. On average, the $\delta^{15}\text{N}$ value was 3.0‰(± 0.4) (Fig.5.2)

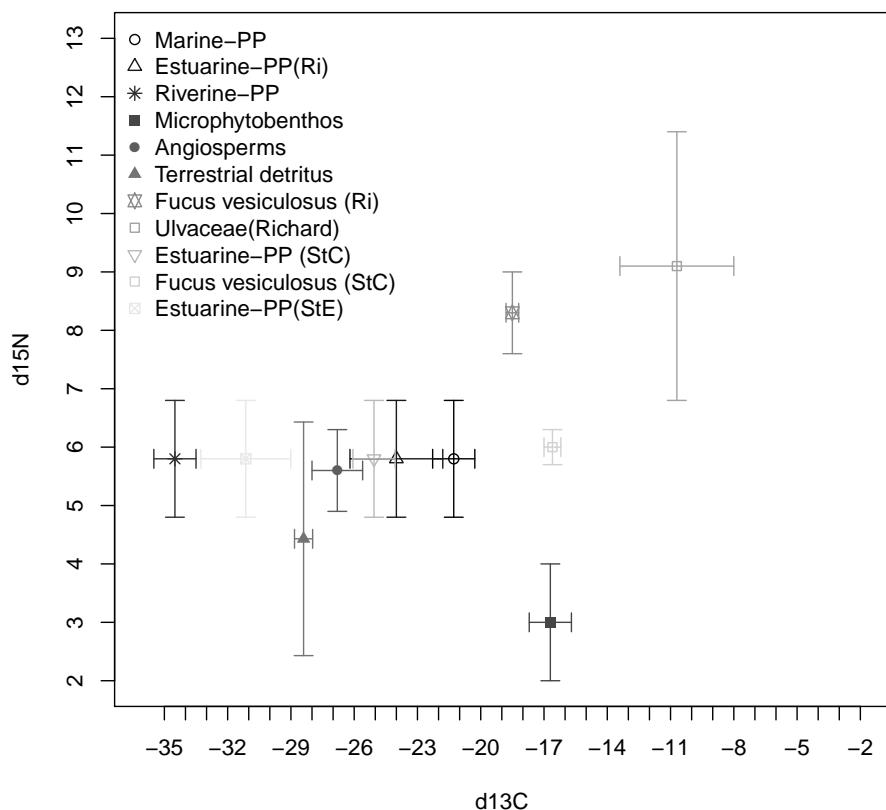


FIGURE 5.2 – Dual plot of primary consumers and organic matter sources average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($\pm\text{SD}$). When necessary, the name of the station was indicated between brackets ; Ri : Richard (downstream) ; StC : St Christoly (intermediate station) and StE : St Estèphe (upstream station).

Sediments organic matter signatures were similar and stable across stations with an average $\delta^{13}\text{C}$ value of $-25.0\text{\textperthousand} (\pm 0.2)$ and $5.5 (\pm 0.1)$ for $\delta^{15}\text{N}$. According to the relationship proposed by Savoye et al. (2012) using data collected from 2007 to 2009 in the Gironde estuary the signature of the marine (downstream estuarine waters) phytoplankton is $-21.3\text{\textperthousand} (\pm 1)$ and $5.8\text{\textperthousand} (\pm 1)$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Using the same relation, river phytoplankton signature was $-34.5\text{\textperthousand} (\pm 1)$ for $\delta^{13}\text{C}$ and $5.8\text{\textperthousand} (\pm 1)$ for $\delta^{15}\text{N}$. At each sampling station, we were also able to estimate the estuarine phytoplankton signature (Table 5.1, Fig. 5.2). Estuarine phytoplankton $\delta^{15}\text{C}$ decreased from the downstream station ($-24.0\text{\textperthousand} (\pm 2.2)$) to the upstream station ($-31.1\text{\textperthousand} (\pm 2.2)$) (Table 5.1).

TABLE 5.1 – . : Mean and standard deviation of organic matter sources and primary producers isotope signatures within the Gironde estuary. Only organic matter sources and primary producers indicated in bold were considered in the primary consumers diet evaluation. Macroalgae were not considered because of their very low biomass at the scale of the ecosystem and mixed organic pools (water column POM and sediments OM) were not included. regarding the low number of samples, the SD included in the mixing model was increased.

Sources/Primary producers	$\delta^{13}\text{C}$ (‰(±SD))	$\delta^{15}\text{N}$ (‰(±SD))	Sources
Marine phytoplankton	21.3(±1)	5.8(±1)	Savoye et al. (2012)
Estuarine phytoplankton			
downstream (Richard)	-24.0(±2.2)	5.8(±1)	Savoye et al. (2012)
- intermediate (St Christoly)	-25.1(±1.4)	5.8(±1)	Savoye et al. (2012)
- upstream (St Estèphe)	-31.1(±2.2)	5.8(±1)	Savoye et al. (2012)
Microphytobenthos	-16.7(±1)*	3.0(±1)*	this study
Angiosperms (reeds and rushes)	-26.8(±1.2)	5.6	this study
<i>Fucus vesiculosus</i>	-18.5(±0.3)	8.3(±0.7)	this study
Ulvaceae			
upstream (Richard)	-10.7(±2.7)	9.1(±2.3)	this study
intermediate (St Christoly)	-16.6(±0.4)	6.0(±0.3)	this study
Terrestrial detritus	28.4(±0.4)	4.4(±2)	Savoye et al. (2012)

5.4.2 Consumers

According to their isotopes signatures, benthic consumers were clearly separated from planktonic consumers (PERMANOVA, $p<0.001$). Benthic consumers indeed displayed higher $\delta^{13}\text{C}$ than most planctonic consumers whereas there were few differences in $\delta^{15}\text{N}$ (Fig.5.3). Among benthic consumers, cluster analysis put in evidence three different groups of consumers according to their isotopes signatures. Firstly, omnivorous and carnivorous species such as the isopod *Cyathura carinata*, polychaetes of the Nereidae family and Dolichopodidae larvae were distinguished from other benthic consumers by their higher $\delta^{15}\text{N}$ values (Fig.5.3). A second group of consumer consisted in the grazing/deposit feeding gastropod *Hydrobia ulvae*. The latter organisms were characterized by the highest $\delta^{13}\text{C}$ value among benthic primary consumers. Finally, the last group gathered the alternative suspension/deposit feeders species consisting in the two bivalve species *Macoma balthica* and *Scrobicularia plana* as well as the amphipod *Corophium volutator* (Fig.5.3). These species were distinguished from other macrofauna species by low $\delta^{13}\text{C}$ and, to a lesser extent, low $\delta^{15}\text{N}$ values (Fig.5.3, Table 5.2).

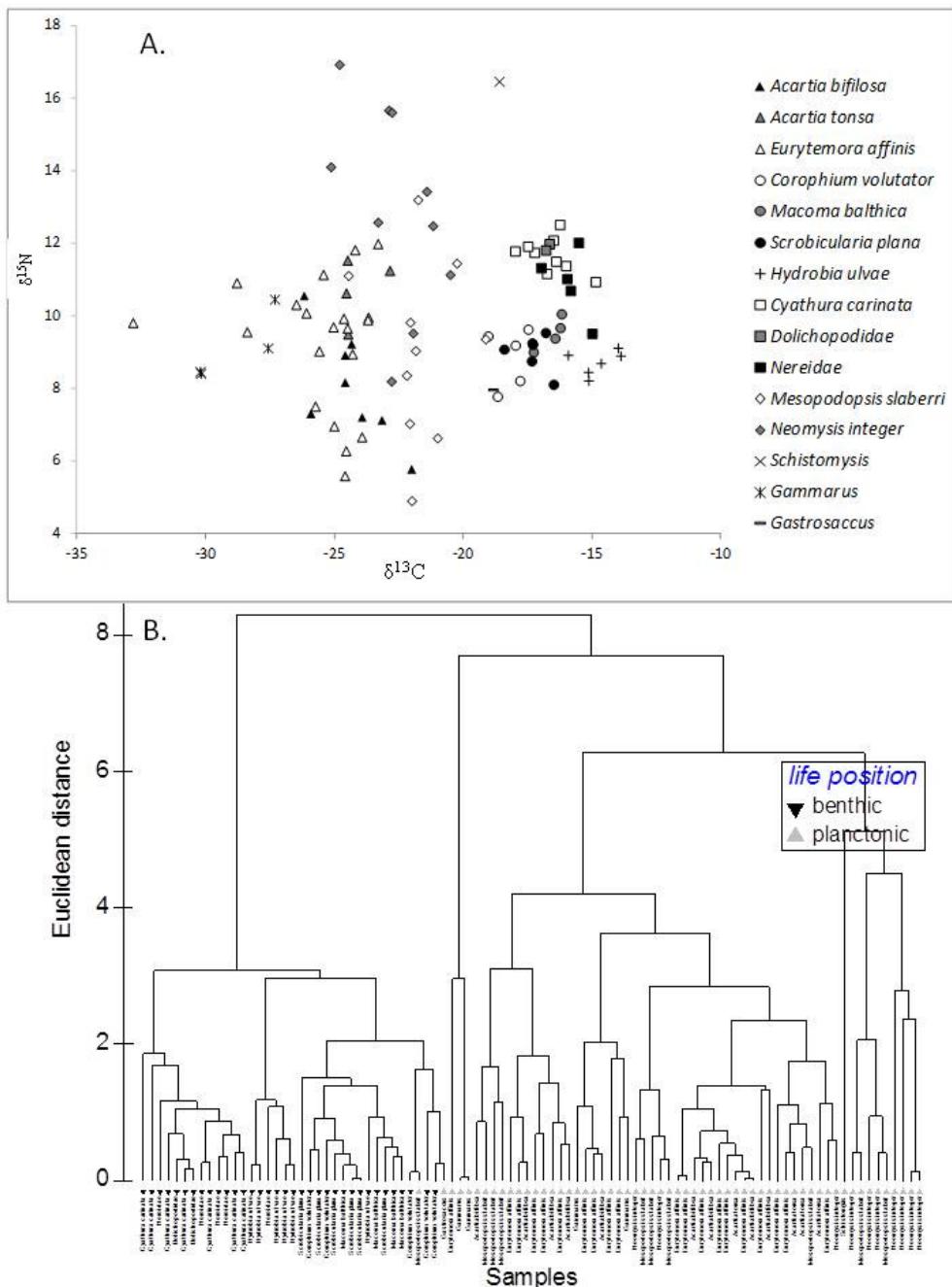


FIGURE 5.3 – (A) Dual plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of planktonic and benthic consumers and (B.) cluster analysis performed on the matrix of euclidean distances among samples.

Zooplanktonic species displayed a much higher variability of their $\delta^{15}\text{N}$ signatures than benthic species (Fig.5.2). As a consequence, few planktonic species clustered in a given group according to cluster analysis. Nevertheless, the mysids *Neomysis integer* generally displayed very high $\delta^{15}\text{N}$ values together with *Schistomysis* sp. however only one sample was retrieved for the latter species. *Mesopodopsis slabberi* signature was also highly variable regarding $\delta^{15}\text{N}$ but the average value of $\delta^{15}\text{N}$ was clearly lower than the previous species. The numerically dominant copepod *Eurytemora affinis*

5.4 Results

TABLE 5.2 – Mean and standard deviation of benthic consumers isotope signatures within the Gironde estuary.

Consumers	$\delta^{13}\text{C}$ (‰(±SD))	$\delta^{15}\text{N}$ (‰(±SD))	Sources
Benthic species			
<i>Corophium volutator</i>			
downstream (Richard)	–17.5	9.6	this study
intermediate (St Christoly)	–18.3(±0.5)	8.5(±1.0)	this study
upstream (St Estèphe)	–18.4(±0.9)	8.8(±0.9)	this study
<i>Macoma balthica</i>			
downstream (Richard)	–16.3(±0.7)	9.7(±0.3)	this study
intermediate (St Christoly)	–17.3	9.0	this study
<i>Scrobicularia plana</i>			
downstream (Richard)	–17.1(±0.7)	9.1(±0.5)	this study
intermediate (St Christoly)	–17.4(±1.0)	8.8(±0.6)	this study
<i>Hydrobia ulvae</i>			
downstream (Richard)	–14.3(±0.6)	8.8(±0.3)	this study
intermediate (St Christoly)	–15.2(±0.6)	8.6(±0.3)	this study
Nereidae			
downstream (Richard)	–16.6(±0.7)	11.4(±0.5)	this study
intermediate (St Christoly)	–15.4(±0.6)	10.1(±0.8)	this study
<i>Cyathura carinata</i>			
downstream (Richard)	–16.3(±0.2)	12.0(±0.6)	this study
intermediate (St Christoly)	–16.0(±1.0)	11.2(±0.3)	this study
upstream (St Estèphe)	–17.6(±0.4)	11.8(±0.1)	this study
Dolichopodidae larvae			
upstream (St Estèphe)	–16.7(±0.1)	11.9(±0.1)	this study

displayed lower $\delta^{13}\text{C}$ values than the mysids with extremely low values (Fig.5.2, Table 5.3). Its $\delta^{15}\text{N}$ values was also variable but in the same or lower than benthic species. Among Acartia species, *A. tonsa* displayed higher $\delta^{15}\text{N}$ than *A. bifilosa*. Both species $\delta^{13}\text{C}$ were in the same range than *E. affinis* without the extremely low values recorded in the latter species. Gammarus species displayed low $\delta^{13}\text{C}$ values (Fig.5.2, Table 5.3).

TABLE 5.3 – Mean and standard deviation of planktonic isotope signatures within the Gironde estuary.

Consumers	$\delta^{13}\text{C}$ ‰($\pm\text{SD}$)	$\delta^{15}\text{N}$ ‰($\pm\text{SD}$)	Sources
Planktonic species			
<i>Eurytemora affinis</i>	-25.5(± 2.2)	9.3(± 1.8)	this study
<i>Acartia tonsa</i>	-24.1(± 0.8)	10.7(± 0.9)	this study
<i>Acartia bifilosa</i>	-24.4(± 1.3)	8.2(± 1.5)	this study
<i>Mesopodopsis slabberi</i>	-21.7(± 1.4)	9.1(± 2.5)	this study
<i>Neomysis integer</i>	-22.7(± 1.5)	13.0(± 2.8)	this study
<i>Gammarus</i> spp.	-28.8(± 1.6)	9.1(± 1)	this study
<i>Gastrosaccus</i> sp.	-18.8	8.0	this study
<i>Schistomysis</i> sp.	-18.6	16.5	this study

5.4.3 Estimation of the diet composition of primary consumers

Before running the SIAR mixing model, a selection of sources of organic matter was applied : only fresh primary producers were retained, excluding sediments and water column organic matter as the later represent a mixture of sources. Moreover, macroalgae (*Fucus vesiculosus* and ulvaceae) were not used in the mixing model because the abundance of both organisms was very scarce and restricted to the few available hard substrates (dykes). In particular, no drifting macroalgae were observed on the sediment during the sampling campaign and during the other monthly monitoring campaign that are conducted on these sites (Bachelet, pers. com.). The sources used for the mixing model are indicated in Table 5.1 (in bold) and were proposed to each primary consumers except for *Hydrobia ulvae* for which only benthic sources were considered available. *Corophium volutator* was the only species that was retrieved at the three sampling sites however it was only collected in autumn at the upstream station. According to the mixing model outputs, this species use almost equally both microphytobenthos and marine or estuarine phytoplankton (Fig. 5.4). Few spatial variations of $\delta^{13}\text{C}$ were observed for this species along the estuarine gradient. Both alternative suspension/deposit feeders bivalves *Scrobicularia plana* and *Macoma balthica* would mostly rely (ca. 60-70 %) on estuarine phytoplankton at downstream station and, in a lesser proportion, on microphytobenthos (ca. 10-20 %). In contrast, both species relied mainly on microphytobenthos which would account for approximately 70% of their diet in intermediate station, whereas estuarine phytoplankton would only account for about 20 %. Finally *Hydrobia ulvae* would almost only feed on microphytobenthos (Fig. 5.4).

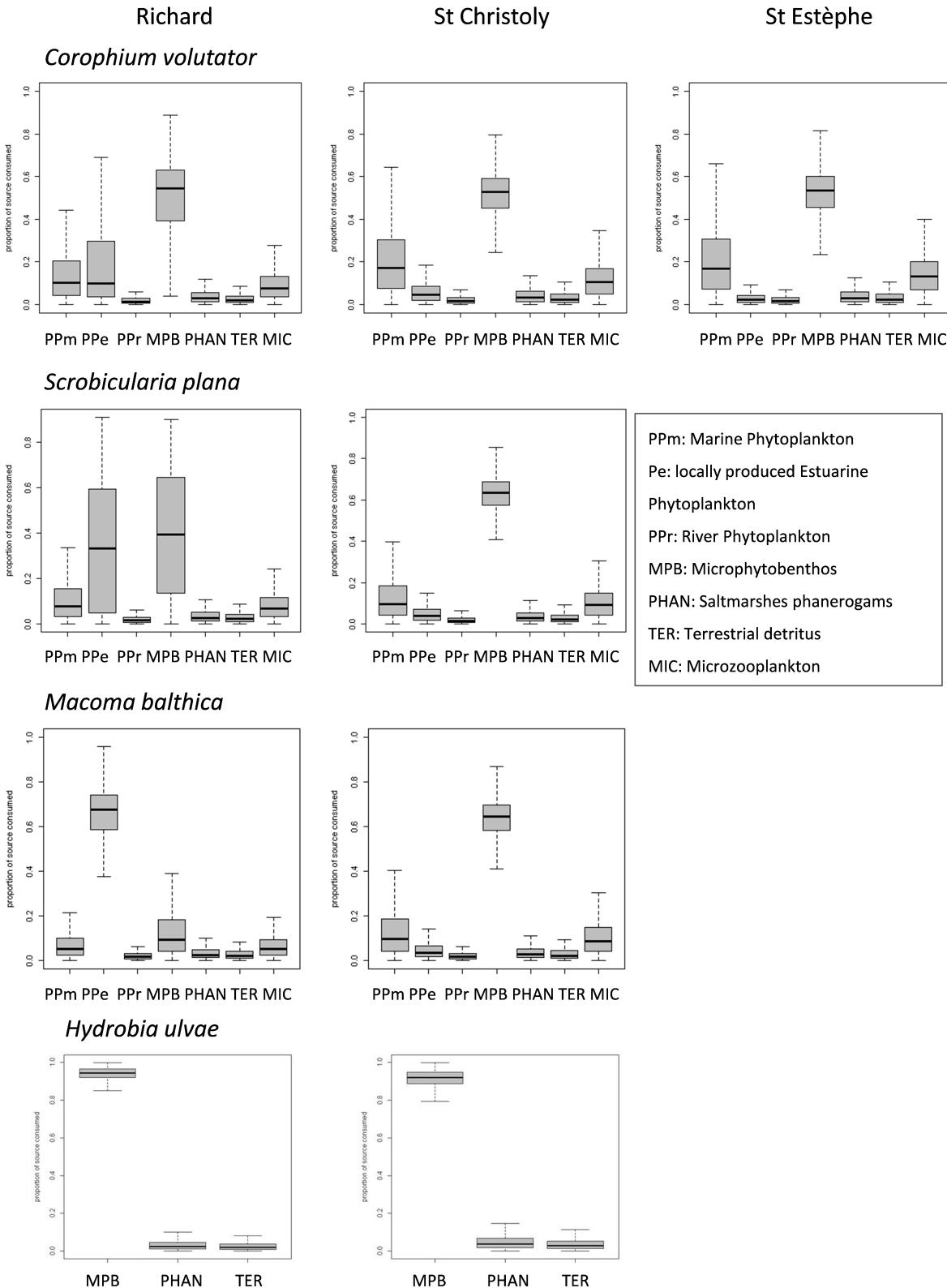


FIGURE 5.4 – Results from the mixing model showing relative contribution of each food source to each benthic primary consumer species within the salinity gradient of the Gironde estuary (downstream : Richard, intermediate : St Christoly ; upstream : St Estèphe)

Among copepods, *Acartia bifilosa* displayed an omnivorous feeding behavior using all available

5.4 Results

food sources in similar proportions (Fig. 5.5). *Eurytemora affinis*, which only occurs in the upstream part of the estuary also displayed an omnivorous feeding behavior however, in contrast to the previous species, *E. affinis* appeared more carnivorous with microzooplankton as its main food source (>20%, on average) and with a negligible contribution of microphytobenthos (<10%) (Fig. 5.5). *Acartia tonsa* clearly displayed a dominance of microzooplanktonic preys in its food resource (>40%) and a significant use of terrigenous detritus (median value of relative contribution 20%).

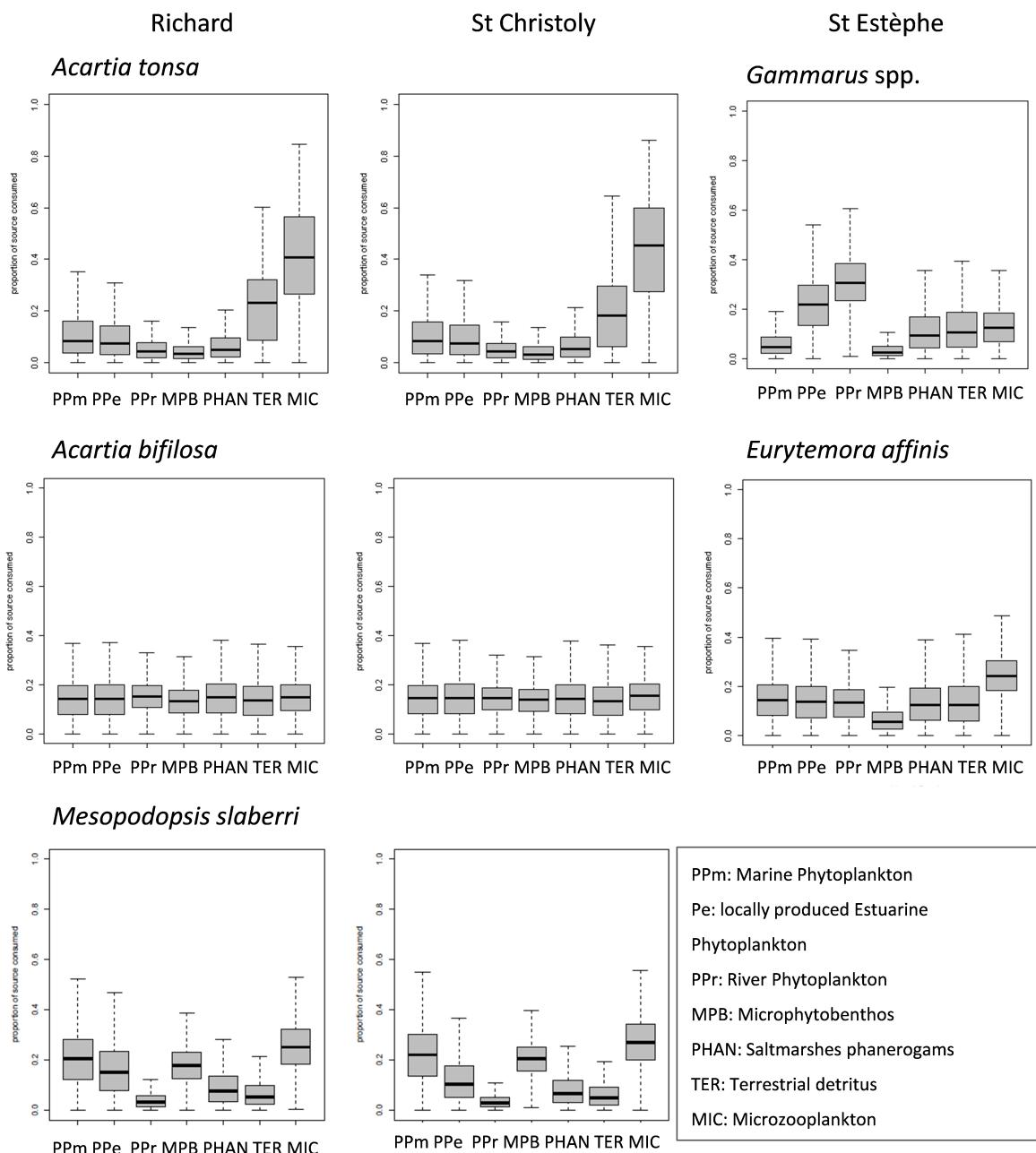


FIGURE 5.5 – Results from the mixing model showing relative contribution of each food source to each planktonic primary consumer species within the salinity gradient of the Gironde estuary (downstream : Richard, intermediate : St Christoly ; upstream : St Estèphe

According to the mixing model results, *Mesopodopsis slabberri* would primarily feed on marine

and estuarine phytoplankton as well as from microphytobenthos but also included zooplanktonic metazoan in its diet (Fig. 5.5). Finally, *Gammarus* spp. appeared as one of the few taxa that mainly relied on river phytoplankton and, to a lesser extent on terrigenous and phanerogams detritus as well as microzooplankton (Fig. 5.5).

5.5 Discussion

5.5.1 Organic matter sources isotopic signatures

According to Savoye et al. (2012), water column POM isotope signature is usually comprised within a very narrow range for $\delta^{13}C$ (from 25.0 ‰ to 25.5 ‰) and display $\delta^{15}N$ comprised between 4 ‰ and 6 ‰. These values are very similar to the signature of sediments POM measured in this study suggesting that the composition of sediments and water column POM is not different and that tidal currents result in a strong mixing of sediments and water column organic matter. Hence, according to these authors, sediment organic matter would mainly consist in organic matter of terrestrial origin (98%) and only 2% of phytoplankton (Savoye et al., 2012).

Microphytobenthos $\delta^{13}C$ isotopic signature could only be obtained on one occasion which may limit our conclusions regarding the role of these primary producers on the functioning of the food web. However, the measured value (-16.7‰) is in the range of reported epipelagic microphytobenthos signatures from mudflats (Riera et al., 1996, 1999; Machas et al., 2003). Phanerogams δ^{13} isotopic signatures reported in Table 5.1 were typical of *C₃*-plants from saltmarshes (e.g. Cifuentes et al., 1988; Finlay and Kendall, 2007; Galvan et al., 2008). Despite the large variability of *Ulvaceae* $\delta^{15}N$ isotopic signatures at the downstream stations, its isotopic values were in the range of other coastal ecosystems (Riera et al., 1996; Machas and Santos, 1999; Machas et al., 2003; Dubois et al., 2007). Due to the absence of macroalgae on sediments surface, they were not included in the mixing model.

5.5.2 Feeding mode and food sources of benthic macrofauna

Benthic intertidal primary consumers displayed little spatial and temporal variations in their food sources use in the investigated region. The most common feeding mode across the studied region was alternative suspension/deposit feeding which occurred in *Macoma balthica*, *Scrobicularia plana* and *Corophium volutator*. Isotope signatures and mixing model estimates suggested that these species mainly relied on microphytobenthic production and on phytoplanktonic production inputs from marine or downstream production. Though they acquire their food through different feeding apparatus (Meadows and Reid, 1966; Cadée, 2001), the importance of both microphytobenthos and phytoplank-

ton for these species in estuarine and bays tidal flats has been demonstrated in many different systems such as in the Schelde estuary (Herman et al., 2000; Hagerthey et al., 2002; Rossi et al., 2004), Marennes-Oléron bay (Leguerrier et al., 2003), Aiguillon cove (Riera et al., 1999) or Wadden sea flats (Reise, 1992; Kamermans, 1994). Grazing was the other well represented feeding mode in the Gironde estuary mudflats. Grazers consisted in the gastropod *Hydrobia ulvae* which did not reach the upstream station (Bachelet, 1979, this study). The latter species appeared to rely almost exclusively on microphytobenthic production according to the mixing model results. The importance of microphytobenthos to micrograzer such as *H. ulvae* has been put in evidence in many studies on tidal flats (e.g. Morrisey, 1988; Haubois et al., 2005; Hagerthey et al., 2002). However, this species displays trophic plasticity depending on the locally available food sources in its habitat (Riera, 2010), it can feed on various food sources from saltmarsh plant to detritic organic matter and associated bacteria. In the case of the Gironde, sediments organic matter seemed to be an improbable food source for this species, according to its isotopic signature however this species is reputed as a deposit feeder (Fenchel et al., 1975). Benthic omnivores and predators were mainly represented by nereid worms *Hediste diversicolor* and *Alitta succinea*, the isopod *Cyathura carinata* and dolichopodiae larvae. Among these taxa, nereids displayed the most variable isotopic signature in accordance with their omnivorous behavior which has been documented in both nereid species (Cammen, 1980; Ronn et al., 1988; Riisgard, 1991; Vedel and Riisgard, 1993; Nielsen et al., 1995; Kristensen and Mikkelsen, 2003). Predatory behavior of *Cyathura carinata* is also known from the literature (Wagele et al., 1981). According to their isotopic signatures these omnivores and carnivores rely exclusively on benthic preys including meiofauna which was not sampled in this study (Fig.5.6). No suspension feeders were collected during this study, in accordance with previous observation showing that this feeding mode is extremely rare in the Gironde mudflats (pers. obs.).

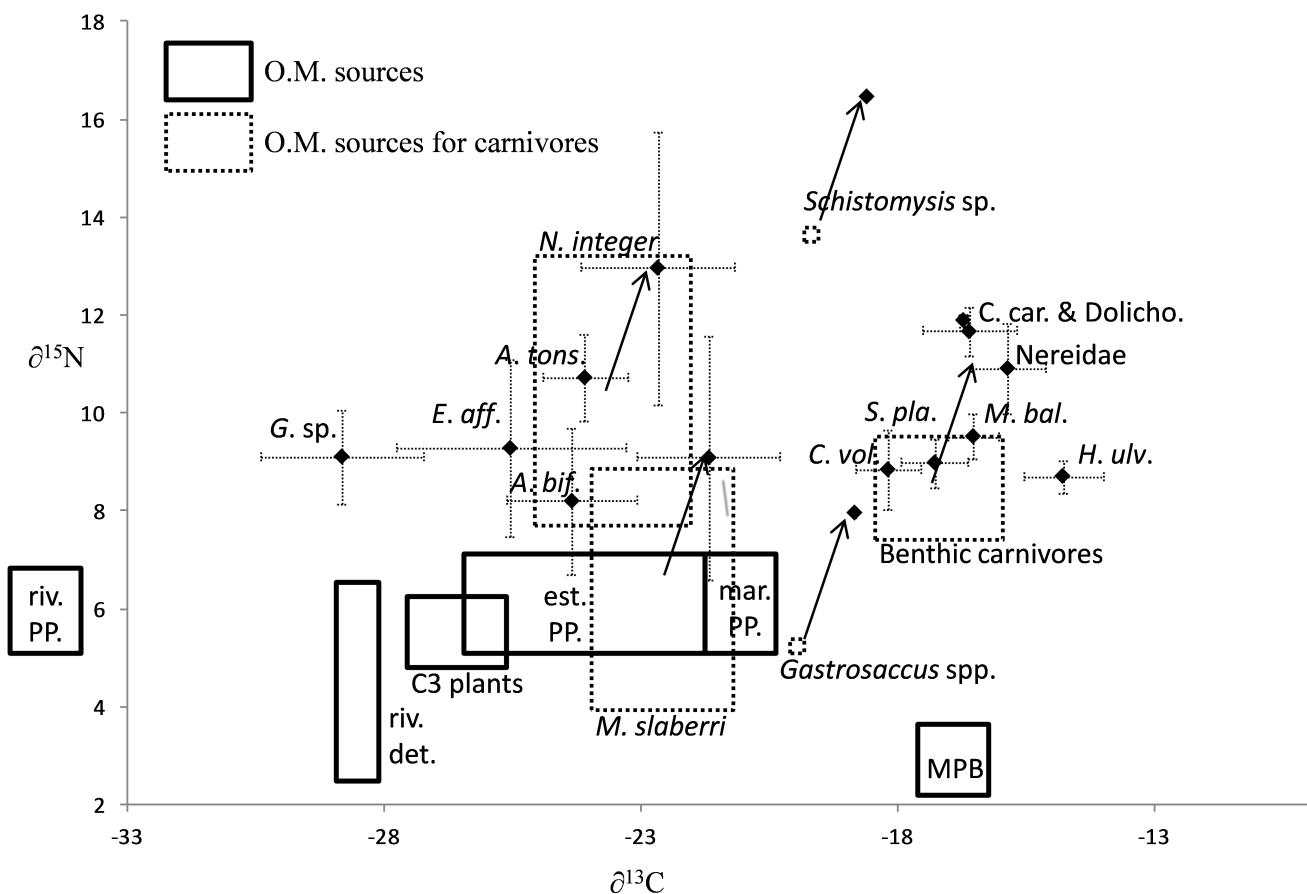


FIGURE 5.6 – Dual plot of the average isotopic signature ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of each species ($\pm\text{SD}$) together with the main organic matter sources signatures. Dotted boxes indicate the theoretical food sources of the omnivorous and carnivorous species according to an average 2.5 ‰ enrichment from prey to consumer for $\delta^{15}\text{N}$ and 1 ‰ in $\delta^{13}\text{C}$

5.5.3 Food sources for planktonic food web

In contrast to benthic macrofauna, zooplanktonic species displayed much larger range of isotopic signatures and use of food sources. This variability of isotopic signature compared to benthic species may be due to shorter population turn-over of small zooplankton. This may explain the variability of isotopic signature since this signature reflects the local food that was assimilated during a much lower duration than for benthic macrofauna which display lower P/B ratio. As a consequence isotopic signature of zooplankton would only integrate short-time feeding conditions. However, at the species and ecosystem -scales, zooplanktonic species displayed larger food spectra than benthic species. In particular, most zooplanktonic species included carnivorous behavior.

As a species, the copepod *Eurytemora affinis* was able to feed on almost all type of food sources including marine and riverine phytoplankton, terrestrial inputs, saltmarshes plant debris and microzooplankton but only few resuspended microphytobenthos. The changing diet of this species as a

function of organic matter sources availability is well documented (Heinle et al., 1977; Gasparini et al., 1999). Despite its preference for phytoplankton (Tackx et al., 2003), *E. affinis* is also able to feed on detritus (Heinle et al., 1977) and on nano- and microzooplankton (White and Roman, 1992). Given the low phytoplanktonic production due to high level of turbidity in the Gironde estuary, this species is able to adapt its feeding behavior as a function of available resources that very according to season and location.

Acartia bifilosa, which populations are located in the downstream part of the estuary displayed lower isotopic signature variation than *E. affinis* (Fig.5.3 ; Table 5.2) reflecting its more restricted spatial distribution. The food plasticity *a priori* for this species is less than *E. affinis* more dependant of phytoplankton (Gasparini et al., 1999) As a consequence this species relied less on terrestrial detritus than *E. affinis* and its diet could include a (small) fraction of microphytobenthos.

Acartia tonsa populations are located in the same region than *A. bifilosa*. However, its trophic behavior was clearly more carnivorous than the latter species. These observations are in good accordance with literature data stating that this species feed on copepods nauplii when phytoplankton biomass is low (Lonsdale et al., 1979; Paffenhofer and Stearns, 1988).

The mysid *Neomysis integer* is known for its carnivorous diet, especially on the copepod *E. affinis* (Aaser et al., 1995; Irvine et al., 1995; Fockedey and Mees, 1999; David et al., 2006b,a). *Mesopodopsis slabberri* is a marine species which lives in the coastal zone and uses estuaries in summer during juvenile development

5.5.4 Conclusions : food sources and lower food web functioning in a highly turbid estuary

Benthic and planktonic organisms in the Gironde estuary live in a condition where detritic organic matter in both sediments and water column is of poor feeding quality (Savoye et al., 2012) and highly diluted in a large amount of inorganic material with an average POC concentration in SPM of 1.5% (Veyssi, 1998; Etcheber et al., 2007). Phytoplankton production is highly limited and can be considered as only occurring in the downstream part of the estuary. In such conditions, the main contributors to the intertidal benthic food web were phytoplankton and microphytobenthos with little to no use of terrestrial inputs nor of C3- saltmarshes plants production. The role of saltmarshes plant in the benthic food web of estuarine systems has been long debated (see Galvan et al. (2008)). An increasing number of studies based on isotope signatures have shown as well that saltmarshes plants were poorly exploited by benthic organisms in many estuarine or littoral systems (e.g. Riera et al., 1999; Herman et al., 2000; Hugues et al., 2000; Carman and Brian, 2002; van Oevelen et al., 2006;

Galvan et al., 2008. In the Gironde estuary, saltmarshes are scarcely represented with, only 11 km² out of 625 km². The scarcity of saltmarshes in this ecosystem is probably directly or indirectly due to the presence of dykes on a large portion of the estuary that both limit the available space for saltmarshes development and increase current velocity which prevent saltmarshes development. In these conditions, benthic organisms proved to be highly selective in their food source since alternative deposit/suspension feeders were able to selectively collect and assimilate phytoplankton from the water column despite its low availability. As a consequence, alternative deposit/suspension feeders reach their upstream limit at KP 52 and are not found in upstream stations (Bachelet and Cornet, 1981) (this study). Further upstream, the lack of phytoplankton production (Goosen et al., 1999; Nzigou et al., prep) would prevent these species from meeting their trophic requirements. Planktonic species, in contrast to benthic organisms relied on a less specialized, omnivorous feeding strategy. However, downstream phytoplanktonic production still plays a key-role for most species with a decreasing importance from downstream to upstream regions. Microphytobenthic production is poorly used by most planktonic taxa with the exception of mysids that are known to display benthopelagic behavior.

The fact that, even in a situation of strongly limited phytoplanktonic situation, phytoplanktonic primary production is still one of the major organic matter source that sustain secondary production probably implies severe food limitation on species living in the estuary. This is evidenced when considering the very low biomass of benthic organisms within the Gironde estuary compared to other estuarine systems (Heip et al., 1995; Nzigou et al., prep). In contrast there is no clear evidence of reduced abundance of zooplankton in the Gironde compared to (e.g.) the Charente estuary which is also a highly turbid estuary but with higher POC concentrations in SPM (2 to 9 % vs 1.5 % in the Gironde estuary, according to Moderan et al. (2010). The possible trophic plasticity of most zooplanktonic species probably made them more suitable for such an environment.

This study aimed at giving a grossly average image of both planktonic and benthic food web within the Gironde estuary. However, given the importance seasonality of all trophic compartments in the Gironde (Selleslagh et al., 2012) and the spatial heterogeneity of this system a full understanding of the functioning of this system and of how species feed and adapt their overall life strategies to the constraint of a highly turbid estuary must include both seasonal and spatial dimensions.

CHAPITRE 6

SYNTHÈSES ET CONCLUSIONS

6.1 Synthèse des données acquises

6.1.1 La production primaire dans l'estuaire de la Gironde

Une quasi-absence de production primaire phytoplanctonique dans la partie médiane et amont de l'estuaire ?

Le travail de modélisation qui a été développé dans la première partie du manuscrit (Chapitre III) a montré que, dans la zone étudiée, c'est-à-dire en aval du PK 30 et jusqu'au PK 67, la chlorophylle a se comporte essentiellement comme une substance dissoute dont les variations de concentrations au cours du temps sont dépendantes des fluctuations observées en amont (PK 30) ou en aval (PK 87). En effet, le bon ajustement du modèle physique de transport aux salinités mesurées montre que le modèle de transport reproduit de façon satisfaisante la dynamique des composés dissous à comportement conservatifs. De plus afin d'obtenir un bon ajustement du modèle aux données d'observation, le meilleur taux r , qui traduit la différence instantanée entre production primaire et consommation, vaut $-0,02 \text{ j}^{-1}$ et n'est pas significativement différent de 0. Cela indique que la meilleure façon de reproduire les fluctuations des concentrations en chlorophyllea est de considérer ce composé comme dissous et non réactif (conservatif) ou bien que tout ce qui est produit serait instantanément consommé. L'ajout d'un modèle de dynamique des nutriments azotés dans l'estuaire permet de montrer que la dynamique de ces éléments est bien décrite au moyen de réactions biogéochimiques simples qui ne tiennent pas compte d'une éventuelle production primaire dans la colonne d'eau. Ce travail présente donc un faisceau de présomption vers une absence de production primaire phytoplanctonique dans cette région de l'estuaire. Ainsi, la chlorophyllea serait transportée dans l'estuaire sous l'action des débits fluviaux et

6.1 Synthèse des données acquises

des courants de marée, représentés dans le modèle par le coefficient de dispersion D , la marée n'étant pas décrite explicitement dans le modèle. Cette hypothèse d'une absence de production phytoplanctonique va dans le sens des travaux de Goosen et al. (1999) et sont confirmées par les observations de Savoye et al. (2012). En effet, ces auteurs ont tenté de déterminer la composition et l'origine de la matière organique dans l'estuaire de la Gironde et notamment d'identifier la signature isotopique du phytoplancton. D'après leurs résultats, basés sur la période 2007 à 2009, la signature isotopique ($\delta^{13}\text{C}$) du phytoplancton a pu être calculée en fonction de la salinité. L'observation des données utilisées (reproduite sur la figure 6.1) montre qu'il n'existe aucune valeur disponible pour calculer cette signature pour des salinités supérieures à 0 et inférieures à 15 (Fig. 6.1). Ces résultats vont dans le sens d'une absence de phytoplancton sur cette gamme de salinité. Cette gamme de salinité inférieure à 15 correspond aux conditions écologiques du PK 52 et, dans une moindre mesure, à celles du PK 67 où des salinités supérieures à 15 sont limitées aux périodes estivales et automnales de faibles débits (Fig. 3.4, page 53). Les fortes concentrations en MES mesurées dans cette partie de l'estuaire dans laquelle oscille la majorité du temps, le bouchon vaseux, empêchent la pénétration de la lumière et la production phytoplanctonique.

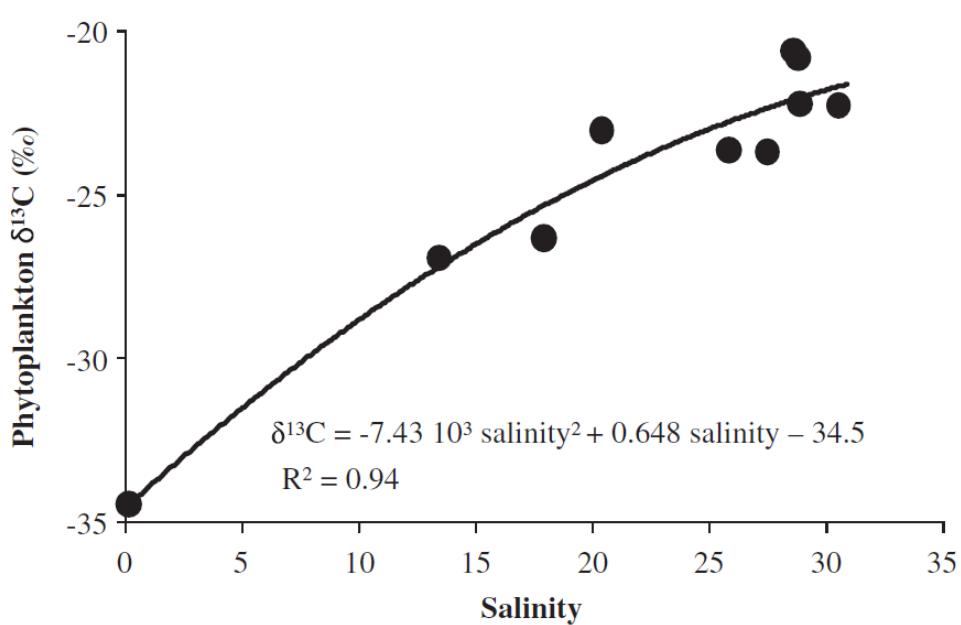


FIGURE 6.1 – $\delta^{13}\text{C}$ du phytoplancton en fonction de la salinité dans l'estuaire de la Gironde. L'équation de la relation entre ces deux variables est indiquée. (reproduit de Savoye et al. (2012)). Les données utilisées pour la caractérisation de la signature isotopique du phytoplancton n'existent pas sur la tranche de salinité comprise entre 0 et 15

Une production phytoplanctonique localisée dans la partie aval de l'estuaire

Si les fluctuations observées de concentration en chlorophylle *a* au niveau des PK 52 et 67 sont essentiellement liées aux variations observées en aval et/ou en amont, la question de l'origine du phytoplancton dans l'estuaire de la Gironde reste posée. En effet, en moyenne les concentrations en chlorophylle *a* aux PK 30 et au PK 87 sont sensiblement égales, avec des pics de concentrations plus élevées mais plus rares au PK 30 qu'au PK 87 (Fig. 6.3, reproduite ci-dessous, par commodité).

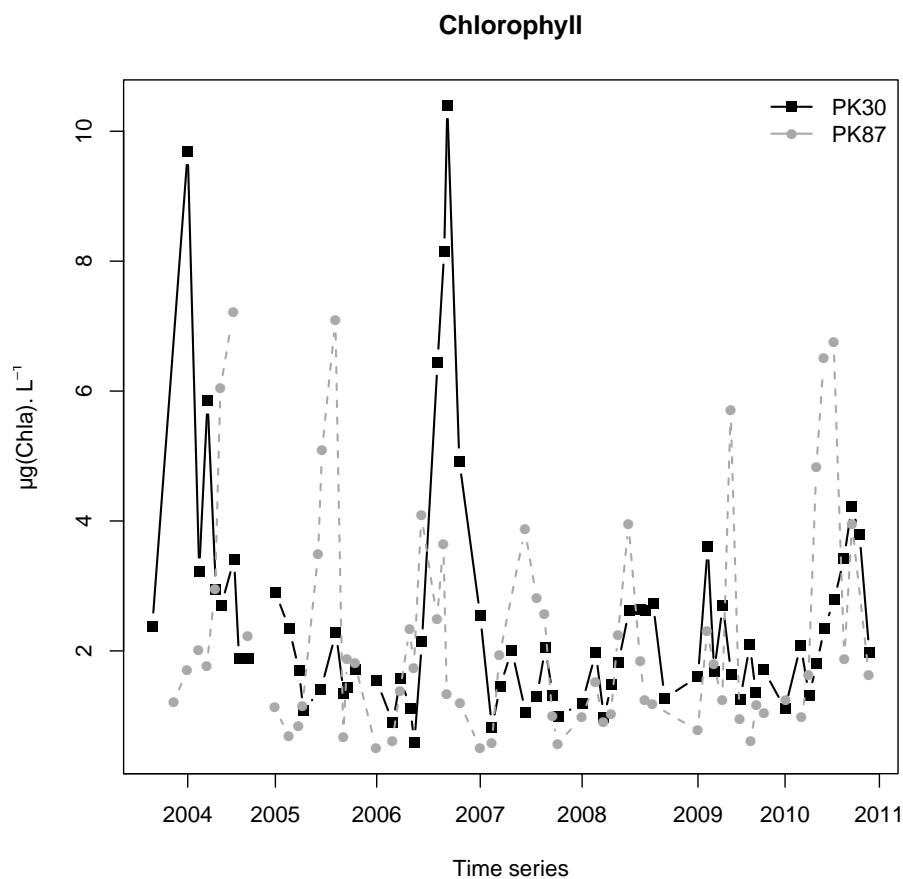


FIGURE 6.2 – Fluctuations temporelles des concentrations en chlorophylle *a* aux PK 30 et 87 dans l'estuaire de la Gironde entre 2003 et 2011.

Cependant, dans l'estuaire amont, les valeurs de MES descendent rarement en dessous de 200 mg.L⁻¹ et la profondeur euphotique¹ est très faible et inférieure à 20 cm, en théorie, d'après les travaux de Irigoien and Castel (1997b). En effet, selon l'estimation faite par Irigoien and Castel (1997b) sur la profondeur euphotique du milieu, le coefficient d'atténuation par les matières en suspension KE vaut : 0.13 + 0.049 MES. Celui-ci est très variable le long du gradient de salinité. La profondeur euphotique ZEu associée, diminue avec une augmentation du coefficient d'extinction KE. En considérant par

1. la profondeur à partir de laquelle l'éclairement photo synthétiquement actif (ou PAR) atteint 1% de sa valeur en surface. Elle est exprimée en mètres

6.1 Synthèse des données acquises

exemple les valeurs de MES suivantes : 50, 100, 200, 500, 1000 mg.L⁻¹ dans l'estuaire, les valeurs de coefficient d'extinction (KE) seraient de l'ordre de 2,58 ; 9,93 ; 24,63 ; 49,13 respectivement (valeurs en m⁻¹) correspondant à des valeurs de profondeur euphotique très faibles autour de 1,78 m, 0,46 m, 0,18 m et 0,09 m. Il paraît donc évident que cette partie amont de l'estuaire ne peut supporter une production de phytoplancton. La présence de chlorophylle *a* au niveau du PK 30 serait soit issue des débris végétaux d'origine terrestre ou liés à des artefacts comme la fluorescence de certaines matières organiques (e.g. Huguet et al. (2009)). L'hypothèse d'un phytoplanton fluvial paraît peu vraisemblable étant donné que de fortes turbidités sont rencontrée encore très en amont dans la Garonne et dans la Dordogne. Au niveau de Bordeaux (Garonne) et de Libourne (Dordogne), la turbidité demeure élevée dans les eaux de surface avec une valeur minimum de 1.2g.L⁻¹ (Etcheber et al., 2011).

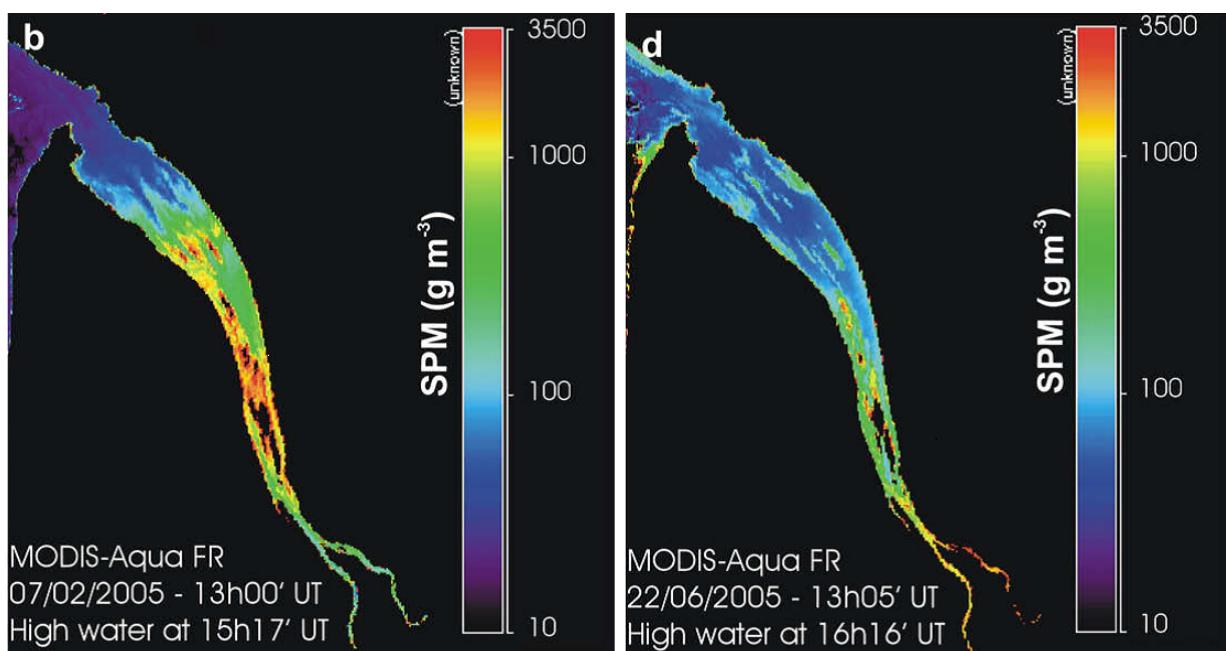


FIGURE 6.3 – Exemple des cartes de concentrations des MES de surface établies dans la Gironde par Doxaran et al. (2009) au cours d'une période de fort débit et de débit moyen, respectivement

En revanche, la zone aval de l'estuaire enregistre des valeurs de MES qui peuvent être inférieures à 100 mg.L⁻¹ et parfois même inférieures à 50 mg.L⁻¹ (Doxaran et al., 2009)(Fig 6.3.). Ces valeurs de MES sont largement en dessous de celles prédictes par Irigoien and Castel (1997b) pour permettre une production primaire. Il semble donc que la zone aval de l'estuaire reste potentiellement productive au cours des périodes où les concentrations en MES sont suffisamment faibles soit principalement en été et au début de l'automne. Cette période estivo-automnale étant caractérisée par de faibles débits fluviaux.

La production primaire microphytobenthique

La production microphytobenthique n'avait jamais été directement mesurée sur les vasières de l'estuaire de la Gironde alors qu'elle l'a été dans d'autres écosystèmes du littoral français (Baie du Mont Saint Michel : Davoult et al. (2009), Baie de Somme : Michel et al. (1998); Macdonald et al. (2003); Migné et al. (2004); Spilmont et al. (2007), Estuaire de la Seine : Spilmont et al. (2006), Littoral sableux en Manche orientale : Davoult et al. (2004)). L'ensemble des mesures prévues à l'origine n'a pas pu être réalisé, néanmoins cette étude a permis d'obtenir des mesures pendant la période productive de début de printemps et d'été (Chapitre 5). Les résultats acquis montrent que la production des vasières de l'estuaire est probablement du même ordre que celle rapportée pour d'autres systèmes intertidaux vaseux comme en estuaire de Seine. Nous ne disposons pas de suffisamment de mesures pour réaliser un modèle de production pour les estrans de la Gironde. Néanmoins, si, tel que le suggère nos résultats, on considère que la production microphytobenthique sur ces vasières est du même ordre que celles mesurées dans des systèmes proches, c'est-à-dire des valeurs comprises de l'ordre de 70 à 160 gC.m⁻².an⁻¹ (Cahoon et al., 1999; Kristensen, 1993; Migné et al., 2004; Serodio and Catarino, 2000; Spilmont et al., 2006), la production primaire microphytobenthique sur les 50 km² de vasières de l'estuaire de la Gironde représenterait entre 6 et 13 gC.m⁻².an⁻¹ à l'échelle des 625 km² de l'estuaire. A cette échelle, la production microphytobenthique se localiserait en très grande majorité dans la partie aval où se situe la plus large vasière (Fig.4.1.). De plus, il semblerait que cette production primaire puisse être perturbée par les phénomènes de crues de courtes durées comme cela a été observé au niveau de notre station amont, durant la période printanière. Si tel est le cas, la production microphytobenthique pourrait être limitée en période de forts débits amont.

6.1.2 Utilisation des différentes productions primaires dans l'estuaire de la Gironde : conséquences sur le fonctionnement de l'écosystème

Une synthèse des données isotopiques, incluant notamment celles acquises par Pasquaud (2006) sur l'ichtyofaune et quelques organismes benthiques subtidiaux de l'estuaire de la Gironde montre que la signature isotopique du benthos intertidal serait différente de celle du benthos subtidal (Fig. 6.4) bien que peu d'échantillons aient été analysés en raison de la rareté du benthos dans le domaine subtidal de l'estuaire de la Gironde. En particulier, la signature isotopique des organismes benthiques subtidiaux apparaît plus allégée en ¹³C que celle du benthos intertidal, probablement en liaison avec l'utilisation du microphytobenthos en domaine intertidal et son absence en tant que source trophique pour les organismes subtidiaux (Fig. 6.4). D'après cette synthèse, certains groupes de poissons apparaissent assez clairement tirer, de manière directe ou indirecte, une partie majeure de leur nourriture

du benthos intertidal. C'est le cas de certains groupes de flets *Platichthys flesus* et de soles *Solea solea* mais aussi les bars *Dicentrarchus spp.* à travers de la prédation qu'ils exercent sur les crevettes, les mysidacés, les juvéniles de poissons plats et les gobies (Pasquaud et al., 2008) (Fig. 6.4). D'autres espèces semblent également dépendantes des zones intertidales comme le mullet *Liza ramada* dont la signature isotopique suggère l'exploitation d'une ressource benthique intertidale, consistant probablement en organismes de la méiofaune. Enfin certains *Argyrosomus regius* sembleraient se nourrir exclusivement d'organismes benthiques intertidaux. Néanmoins, Pasquaud et al. 2008, 2010 ont montré, sur la base des contenus stomacaux, que cette espèce se nourrissait principalement de mysidacés et de crevettes avec une faible contribution des organismes benthiques. Enfin, les crevettes grises *Crangon crangon* semblent principalement exploiter le stock benthique intertidal alors que *Palaemon longirostris* inclurait probablement une plus grande part de zooplancton dans son régime trophique.

Le benthos subtidal, malgré sa rareté, semblerait participer de manière importante dans le régime trophique d'un autre groupe de soles (Fig. 6.4). De même, *Liza aurata* semble se nourrir d'une ressource benthique subtidale, par opposition à *Liza. ramada* qui exploiterait le domaine intertidal. Le plancton et les mysidacés de la zone aval semblent être exploités par un groupe d'*Argyrosomus regius*, et par les sprats (*Sprattus sprattus*), l'aloise et indirectement, par un groupe d'anguilles (Fig. 6.4). Un autre poisson planctivore d'origine marine *Engraulis encrasiculus* semblerait se nourrir d'une source plus marine que le sprat. *Mesopodopsis slabberri* semble jouer un rôle prépondérant dans le régime alimentaire de la plupart de ces espèces (Pasquaud et al., 2008). Le plancton de la zone amont et les gammarides semblent peu exploités par la plupart des espèces de poissons étudiés ici, à l'exception de deux groupes d'anguilles et d'un groupe de flets, qui se nourrissent probablement d'une ressource benthique amont non échantillonnée dans notre étude. Les gobies, qui représentent l'une des rares espèces réellement résidentes dans l'estuaire de la Gironde (Lobry, 2004), présenteraient un régime trophique mixte basé sur des proies planctoniques de la zone aval et des proies benthiques intertidales (Fig. 6.4), en accord avec les observations sur les contenus stomacaux réalisés par Pasquaud et al. (2008, 2010). La détermination des proies de l'ichtyofaune et de leur origine à partir des seules signatures isotopiques est un exercice complexe en raison de la diversité des ressources et des mélanges possibles, l'analyse des contenus stomacaux complète de manière satisfaisante l'approche isotopique chez ces espèces. D'après le premier essai de synthèse réalisé ici, il ressort que :

- la très grande majorité des espèces étudiées ici exploitent directement ou indirectement la production primaire intertidale, qui est surtout localisée dans la partie aval de l'estuaire et/ou la production primaire phytoplanctonique également située en aval ;
- le benthos intertidal mais aussi subtidal jouent un rôle dans le régime trophique des poissons

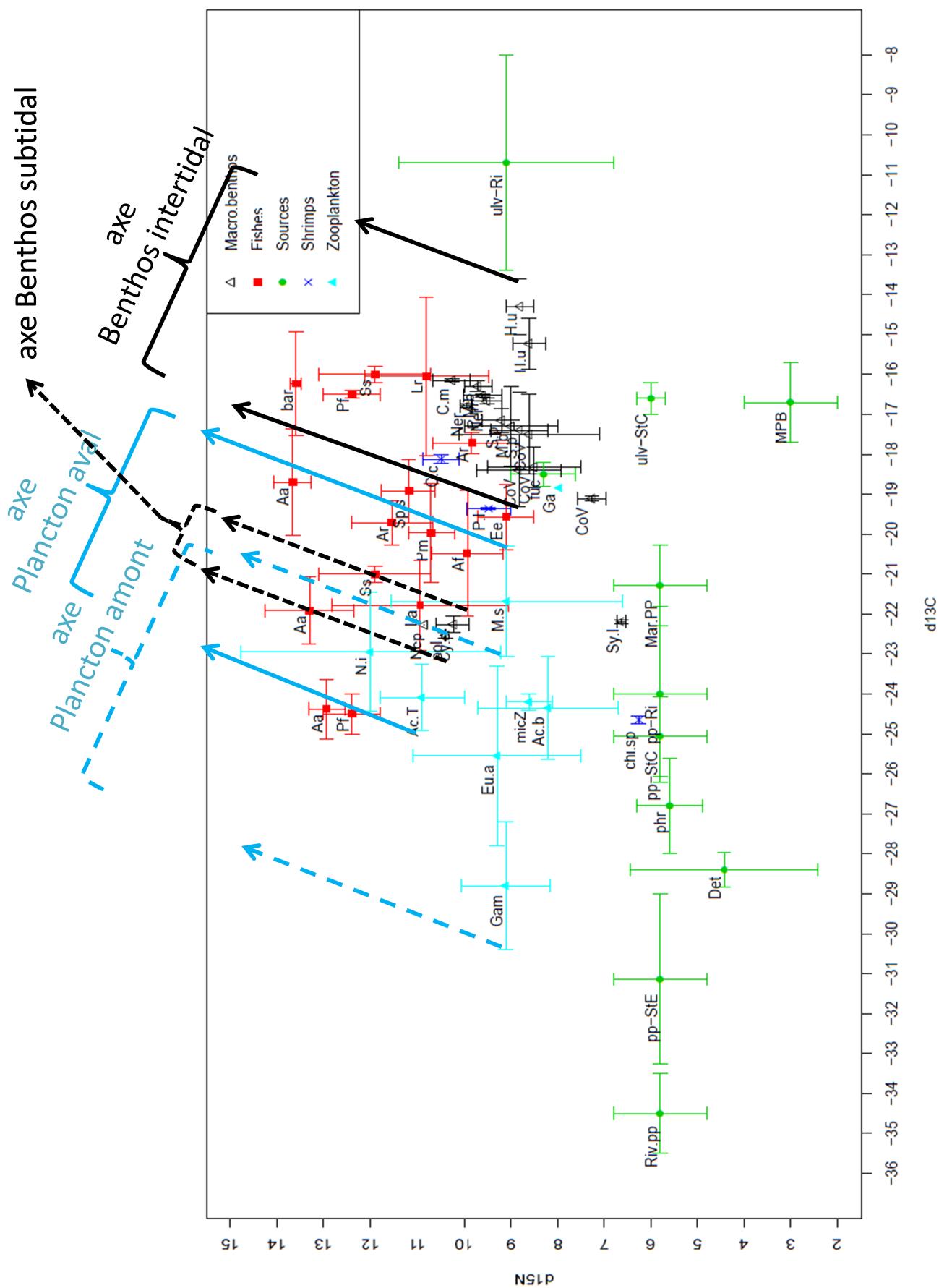


FIGURE 6.4 – Synthèse des données isotopiques acquises sur l'estuaire de la Gironde. Les noms d'espèces sont indiqués dans la Table 6.1

TABLE 6.1 – Tableau récapitulatif représentant les codes et les espèces correspondantes

Codes	Espèces	Codes	Espèces
bar	<i>Dicentrarchus labrax</i>	chi.sp	Chironomus spp.
Aa	<i>Anguilla anguilla</i>	micZ	microzooplancton
Ar	<i>Argyrosomus regius</i>	Eu.a	<i>Eurytemora affinis</i>
Sp.s	<i>Sprattus sprattus</i>	Ac.b	<i>Acartia bifilosa</i>
Ss	<i>Solea solea</i>	Ac.T	<i>Acartia tonsa</i>
Pf	<i>Platichthys flesus</i>	N.i	<i>Neomysis integer</i>
La	<i>Liza sp</i>	M.s	<i>Mesopodopsis slaberi</i>
Lr	<i>Liza ramada</i>	Ga	<i>Gastrosaccus spp.</i>
Pm	<i>Pomatoschistus minutus</i>	Sch	<i>Schistomysis spp.</i>
Af	<i>Alosa fallax</i>	Gam	<i>Gammarus spp.</i>
Ee	<i>Engraulis encrasiculus</i>	M.b	<i>Macoma balthica</i>
Mar.PP	phytoplancton marin	H.u	<i>Hydrobia ulvae</i>
pp-Ri	phytoplancton estuaire -Richard	S.p	<i>Scrobicularia plana</i>
Riv.pp	phytoplancton rivière	CoV	<i>Corophium volutator</i>
pp-StE	phytoplancton estuaire -StE	pol	Polychaeta indéterminé
pp-StC	phytoplancton estuaire-StC	Nep	<i>Nephtys spp.</i>
fuc	<i>Fucus vesiculosus</i>	Ner	<i>Nereis spp.</i>
ulv-Ri	ulvaceae-Richard	C.m	<i>Carcinus maenas</i>
ulv-StC	ulvaceae-StChristoly	P.m	<i>Pachygrapsus marmoratus</i>
phr	angiospermes (phragmite)	Cy.c	<i>Cyathura carinata</i>
MPB	microphytobenthos	Sy.l	<i>Synidotea laticauda</i>
Det	detritus terrestres	C.c	<i>Crangon crangon</i>
		P.l	<i>Palaemon longirostris</i>

plats ;

- Ⓐ le zooplancton de la partie amont de l'estuaire, malgré son abondance, ne semble pas être exploité par les espèces considérées ;
- Ⓑ Le gobie, espèce résidente de l'estuaire, exploite le zooplancton de la partie aval ainsi que le benthos intertidal.

Dans un système hautement turbide comme l'estuaire de la Gironde, le réseau trophique est alimenté par la production primaire localisée principalement dans la zone aval où se situent la plus large vasière et où la production phytoplanctonique peut avoir lieu en période de faibles concentrations en MES. La partie amont, zone de turbidité maximum semble peu exploitée par les principales espèces de poissons qui constituent, pour la très grande majorité, des espèces ne fréquentant l'estuaire que de manière saisonnière, durant la période estivale et automnale (Selleslagh et al., 2012). Les écosystèmes estuariens ont la réputation de zone de très forte production biologique (Costanza et al., 1998; Day, 1981) qui jouent un rôle fondamental de nourricerie pour les juvéniles de certains poissons marins (Elliott et al., 2007; Franco et al., 2008; McLusky and Elliott, 2004). Selon les résultats de notre étude, l'estuaire de la Gironde ne peut pas, à notre avis, être considéré comme un système fortement productif, au moins dans sa partie aval en raison (1) des contraintes exercées sur les productions primaire microalgales, la faiblesse de la production macroalgale, la faible surface occupée par les prés salés et (2) de la difficulté d'accès au carbone organique détritique en raison de sa forte dilution dans une matrice inorganique et de son caractère réfractaire. Des travaux récents, réalisés dans le cadre de la Directive Cadre européenne sur l'Eau (DCE), sur la mise au point d'un indicateur poissons en eaux de transition estuarienne (Courrat et al., 2009; Delpech et al., 2010) classent l'estuaire de la Gironde comme l'estuaire le plus dégradé parmi les 13 estuaires français pris en compte dans l'étude. Cet indice est basé sur une combinaison de 4 métriques incluant la densité totale des poissons, la densité des poissons diadromes, la densité des juvéniles de poissons marins migrateurs et la densité des espèces démersales (Delpech et al., 2010). Si cet indice est apparu bien corrélé à un indice de pression incluant notamment les polluants chimiques (Courrat et al., 2009; Delpech et al., 2010), les résultats de ces travaux semblent aller également dans le sens d'un estuaire de la Gironde peu productif, notamment pour les juvéniles de poissons marins.

6.2 Limites des approches utilisées et perspectives

L'une des principales limites de cette étude est le manque de prise en compte explicite de la dimension temporelle du fonctionnement de l'estuaire de la Gironde. Par exemple, les mesures de la production primaire microphytobenthique n'ont été réalisées qu'en deux occasions : au printemps et

6.2 Limites des approches utilisées et perspectives

en début d'été. Ces données ne sont pas suffisantes pour permettre d'estimer de manière satisfaisante la production primaire microphytobenthique et les principaux facteurs qui la contrôlent, notamment l'impact des crues sur cette production. Etant donné l'importance de cette production dans le fonctionnement de cet écosystème, il s'avèrerait pertinent de mener des campagnes supplémentaires au minimum en période automnale et hivernale. Ces données supplémentaires permettraient d'ajuster un modèle (type modèle de Webb) permettant, en fonction des données d'irradiance, d'estimer via ce modèle la production primaire annuelle du microphytobenthos dans l'estuaire. Concernant ce même compartiment biologique, le fait de ne disposer que d'une unique mesure fiable de la signature isotopique représente une sévère limitation de la portée de nos conclusions. De même la signature isotopique de la macrofaune benthique subtidal devra être confirmée. Ce dernier travail est en cours dans le cadre du programme de recherche CAPALEST.

A terme, il serait utile d'utiliser les données isotopiques comme contrainte pour améliorer le modèle de réseau trophique existant pour l'estuaire de la Gironde (Lobry et al., 2008). Cette approche a été déjà utilisée dans l'escaut (Van den Meershe, 2009; Van den Meersche et al., 2011; van Oevelen et al., 2006). La zone aval est d'après nos résultats une zone d'intérêt majeur pour le fonctionnement du réseau trophique. Il serait donc nécessaire de renforcer les données sur cette zone. Cela permettrait de mieux ajuster les paramètres du modèle dont la dispersion et les différents taux estimés dans la présente étude. Ainsi, étant donné l'importance de l'hydrodynamisme dans les flux de composés dans la colonne d'eau, l'utilisation de notre approche par modélisation 1D pourrait être utilisée à partir de données collectées en aval du PK 86, à l'entrée de l'estuaire. Du fait que cette zone avale est connue pour être stratifiée (Allen et al., 1974), il sera probablement nécessaire de passer à une modélisation 2D prenant en compte cette stratification.

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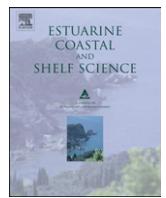
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Appendices

ANNEXE A

PUBLICATIONS SCIENTIFIQUES



Seasonal succession of estuarine fish, shrimps, macrozoobenthos and plankton: Physico-chemical and trophic influence. The Gironde estuary as a case study

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ABSTRACT

Characterization of the structure and seasonal variability of biotic communities is essential for a better understanding of estuarine ecosystem functioning and in order to manage these highly fluctuating and naturally stressed systems. Numerous studies have investigated the role of environmental factors in controlling temporal variations in biotic communities. However, most have concluded that the explanatory power of physico-chemical variables was significant but not sufficient to explain ecological dynamics. The present study aimed to propose the importance of trophic interactions as an additional structuring factor of species seasonal variability by examining simultaneous dynamics of all estuarine biotic communities, using the oligo-mesohaline area of the Gironde estuary (SW France) as a case study. Data on the main biological groups (fish, shrimps, macrozoobenthos and plankton) sampled during a five-year period (2004–2008) at monthly intervals using a well standardized protocol, as well as data on environmental variables, were compiled here for the first time. According to species composition, the Gironde estuary is used as a nursery, feeding, resident and migratory habitat. For almost all species, strong seasonal fluctuations occurred with a succession of species, indicating an optimization of the use of the available resources over a typical year by estuarine biological communities. Multivariate analyses discriminated four seasonal groups of species with two distinctive ecological seasons. A clear shift in July indicated a biomass transfer from a “planktonic phase” to a “benthic–demersal phase”, corresponding to spring and summer–autumn periods, respectively. With regard to the temporal fluctuations of dominant species of all biological groups, this study highlighted the possible influence of trophic relationships, predation in particular, on seasonal variations in species abundance, in addition to the physico-chemical influence. This study enabled us to collate important seasonal data and to discuss their integration into seasonal models of estuarine functioning and/or specific prey–predator models. In a global change context, prey abundance variations could generate changes in the temporal dynamics of their predators (and conversely), and potentially in the functioning of the whole estuarine system.

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1. Introduction

Estuarine and coastal areas are widely considered to be among the most productive and valuable aquatic areas in the world (Day et al., 1981; Costanza et al., 1997). They are associated with important ecological functions such as primary and secondary production and nutrient cycling and provide permanent or transitory habitats for reproduction, migration, feeding and nursery for many animal species (Beck et al., 2001; Elliott and Hemingway,

2002; Gili, 2002). Due to these ecological properties, estuaries and coasts are also associated with highly valuable goods and services for human society (Costanza et al., 1997) and are consequently subjected to high human pressures such as fishing, harbour activities, dredging or industrial pumping (Post and Lundin, 1996). Estuaries are transition zones between seas and freshwater and are therefore also characterized by large fluctuations in the physico-chemical conditions of the environment. As a consequence, species that inhabit such ecosystems must be able to tolerate a wide range of environmental conditions. It is now fully recognized that human activities have an increasing effect on the quality of fresh and marine waters (Vanderborght et al., 2007). In this context, the need to protect these essential habitats is becoming clear to

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authorities who have implemented directives during these last decades, such as the European Water Framework Directive or the European Marine Strategy. Implementing these directives implies, first and foremost, a better understanding of the functional aspects of ecosystem dynamics (De Jonge et al., 2006). Knowledge of the simultaneous structure and variability of the dominant biological compartments is essential for comprehending ecosystem functioning but such information is very scarce for European aquatic ecosystems, and for French estuaries in particular.

In fluctuating habitats such as temperate estuaries, biotic communities are characterized by a strong seasonal, and spatial, heterogeneity and variability (McLusky and Elliott, 2004). Such temporal variations have been attributed to fluctuations in physico-chemical variables (both short- and long-term physico-chemical water conditions: e.g. wind speed and direction, turbidity, wave height, salinity, state of the tide, time of day and temperature) (Baird et al., 1991; Thiel et al., 1995; Beyst et al., 2001; McLusky and Elliott, 2004; Selleslagh and Amara, 2007, 2008a), combined with biological variables, including the timing of spawning seasons and hence the influx and efflux of individuals to and from populations (Gibson et al., 1993), food availability (Pasquaud et al., 2008), and predation pressure (Van der Veer and Bergman, 1987). However, there is still much confusion over which factor influences or controls biotic temporal variations (Beyst et al., 2001) since numerous studies dealing with this topic were based on only a limited part of the year, range of the system and specific species or assemblages. Papers dealing with the seasonal variability of fauna almost exclusively integrated physico-chemical factors, leading to poorly explained relationships ($\pm 20\%$, see Selleslagh and Amara, 2008b for example) and suggested other predictors, such as predation or competition (e.g. Marshall and Elliott, 1998). Understanding species variability requires a study at a large temporal scale and, above all, knowledge of the dynamics of other species because of interannual variations (Henderson and Bird, 2010) and biological interactions (Monaco and Ulanowicz, 1997). With increased attention to the collection of multi-year data sets, ecologists have better opportunities to test functional hypotheses driving temporal dynamics. Studying interactions between the biological compartments of an ecosystem provides a good picture of the biological community structure and is an essential step to understanding how an aquatic system functions (Thrush et al., 1999; Pasquaud et al., 2010), which is in turn essential for integrated estuarine management. It also provides a better understanding for the dynamics of ecological networks (David et al., 2006).

The Gironde estuary, in south-west France, is the largest French estuary. It is known to support a large number of fish, macrocrustacean (Lobry et al., 2006) and benthic (Bachelet, 1985) species. It is an important nursery area, a residence habitat for permanent species, as well as a migration route for amphihaline species (e.g. Rochard et al., 2001) and is also of important economic interest (G. Castelnau, personal communication). As a consequence of many studies, the Gironde estuary is one of the most surveyed estuarine systems in France. Previous studies emphasized possible trophic implications of seasonal successions in biological assemblages (e.g. David et al., 2005, 2006; Lobry et al., 2006; Pasquaud et al., 2010). Lobry et al. (2008) first proposed an integrated picture of the whole Gironde estuarine food web using an Ecopath modelling approach at the annual level. David et al. (2006) identified predator-prey processes in the zooplankton food web and Pasquaud et al. (2010) described fish food webs at various periods of the year. However, to date no studies have combined the seasonal dynamics of all ecological compartments, particularly since macrozoobenthos sampling is recent. The aims of this study were: (1) to describe the simultaneous seasonal dynamics of fish, macrozoobenthos,

shrimps and phyto- and zooplankton, considering dominant species; (2) to relate their fluctuations to environmental variables, and (3) to discuss trophic interactions structuring the seasonal dynamics of species. This work is the first analysis providing a comprehensive overview of the recent seasonal succession of biological assemblages (fish, macrozoobenthos, shrimps and plankton) in the Gironde estuary in the course of a year. The temporal changes in the main biological components of the oligomesohaline area of the Gironde were analysed to test the hypothesis that trophic interactions have the important and additional influence of physico-chemistry on the seasonal variability of estuarine communities.

2. Materials and methods

2.1. Study area

The Gironde estuary ($45^{\circ}20'N$, $0^{\circ}45'W$; Fig. 1) is located in SW France and opens onto the Atlantic Ocean. This is the largest estuary in France (Lobry et al., 2003), covering an area of 625 km^2 at high tide. It is 12 km wide at the mouth and 76 km long to the upstream salinity limit, where the Garonne and Dordogne rivers meet. The catchment covers $81,000 \text{ km}^2$ and the mean annual rate of freshwater flow is ca. $1000 \text{ m}^3 \text{ s}^{-1}$ (Sottolichio and Castaing, 1999). The Gironde is a macrotidal estuary with a tidal range of 4.5 m at the mouth and over 5 m at Bordeaux. The hydrodynamic conditions are highly variable due to the interaction of marine and fluvial flows,

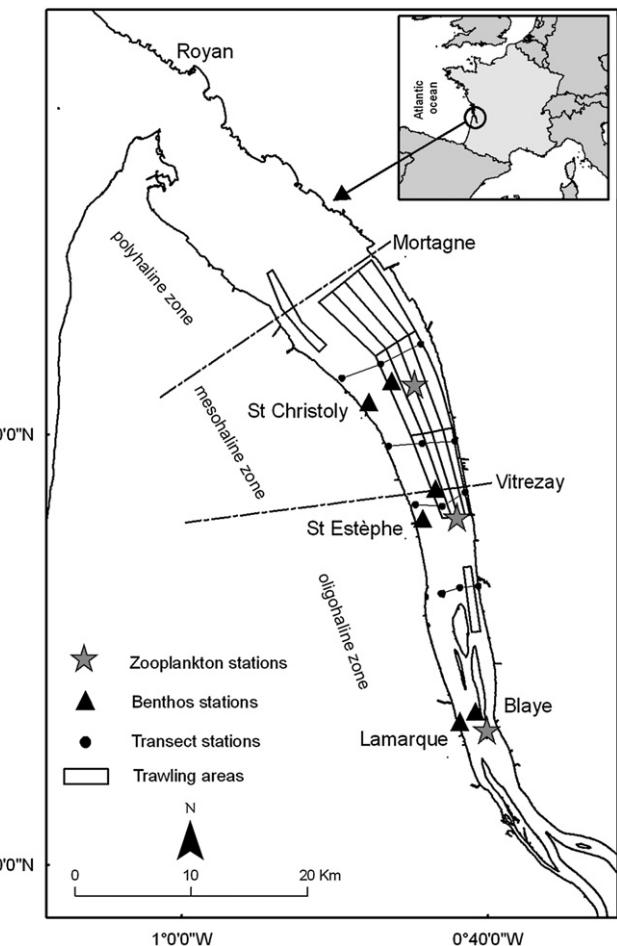


Fig. 1. Map of the Gironde estuary and location of the sampling stations and areas.

leading to strong temperature and salinity gradients. The Gironde is one of the most turbid estuaries in Europe ($\text{SPM} > 500 \text{ mg l}^{-1}$, Sautour and Castel, 1995). Particulate matter is tidally resuspended and concentrations may exceed 1 g l^{-1} at the upstream limit of salinity intrusion (Allen et al., 1974). This zone of maximum turbidity, which is due to an asymmetric tidal wave, migrates seasonally according to river flow and tidal cycles (Sottolichio and Castaing, 1999). As a consequence of the high turbidity, primary production is limited mainly to the upstream zone. However, there is a large zooplanktonic biomass (Castel, 1993) and the food web seems to be based on the detritus pool (Irigoin and Castel, 1995; Lobry et al., 2008). The Gironde estuary is notable amongst other French or European estuaries in having a long-term (30 years) biological database. In this paper, the study area is the zone between Blaye and Mortagne, covering the oligo-mesohaline area (Fig. 1).

2.2. Sampling surveys

As part of various ecological monitoring programmes (e.g. impact of a nuclear power plant, monitoring of European sturgeon *Acipenser sturio*, European Water Framework Directive WFD, Service d'Observation en Milieu LITToral SOMLIT), the main biological compartments (fish, macrozoobenthos, shrimps and plankton) of the Gironde have been surveyed and the environmental conditions measured regularly for several decades, except for macrozoobenthos.

2.2.1. Fish and shrimp samplings

Fish and shrimps were collected using two types of sampling methods that use different gears:

A 'Transsect' survey was set up by the French Institute for Research in Environmental Science and Technologies (Irstea) in 1979 to monitor small fish species or juvenile stages of larger species and shrimps, around the Blayais nuclear power plant, and this survey is still ongoing. Since 1991, it has been standardized (see for instance Pronier and Rochard, 1998 and Lobry et al., 2003). The sampling sites are located within four transects which cross the estuary in the mesohaline and oligohaline sectors (Fig. 1). Each transect consists of three sites, one close to each bank and one on the middle axis of the estuary (Fig. 1). Simultaneously at each site, one fishing sample is taken near the surface and one near the bottom. Surface samples are collected using two $4.0 \times 1.0 \text{ m}$ rectangular frame nets, equipped with a flowmeter, fitted on both sides of the boat. The subconical nets have a stretched mesh size of 18 mm in the main section and 2.8 mm in the cod end. For the benthic samples, a dragnet with a $2.0 \times 1.2 \text{ m}$ frame is used. Runners keep the frame 0.2 m above the bed. The net meshes are identical to those used for surface sampling. Sampling lasts between 5 and 7 min and is performed in daytime at high tide $\pm 3 \text{ h}$, with the gear being towed against the current. The sampled fauna consists mainly of small pelagic and juveniles fish species, as well as shrimps. The catch was preserved in 5% seawater buffered formalin. At the laboratory, individuals were identified to species level (except for *Pomatoschistus* and *Palaemon* genus) and counted. In order to standardize captures between samples, abundances were expressed as number of individuals and biomass per 1000 m^3 of filtered water. Total biomass (fresh weight W , g) was measured by species at each station.

A second fish survey (so-called 'Sturat' survey) was set up by Irstea in 1994 in the context of monitoring the European sturgeon *Acipenser sturio* in the Gironde estuary (Rochard et al., 2001). Trawl surveys were performed once a month almost every year from 1994 to 2000. The sampling sites were located within fourteen zones in the oligohaline and mesohaline sectors of the estuary (Fig. 1).

Sampling was carried out during daylight hours on the flood or ebb tide, using a wide-mouth bottom trawl (vertical opening 3.5 m and horizontal opening 13 m and with a mesh size of 70 mm in the cod end). Trawl tows lasted 30 min on average. Fish were identified, counted and measured to the nearest millimetre (FL) before being returned to the water. The fish samples consisted mainly of large benthic-demersal species. For each sample, species abundance was expressed as the number of individuals and biomass per $100,000 \text{ m}^2$. In this study, biomass (fresh weight W , g) was determined for each species using the equation $W = a \text{ TL}^b$ (www.fishbase.org), where TL is the total length.

2.2.2. Macrozoobenthos sampling

Macrozoobenthic fauna has been sampled from 2004 at three sites (Lamarque, St-Estèphe and St-Christoly) in the oligohaline and mesohaline sectors (Fig. 1). Samples were collected every year at monthly intervals between April and November, and also in February in the intertidal. Two stations were selected at each site: one at mid-tide level and one at a depth of approximately 8 m (Fig. 1). Macrozoobenthos was sampled with a Smith-McIntyre grab (0.1 m^2 , 5 replicates) at subtidal stations and with a hand corer (0.0066 m^2 , 10 replicates) at intertidal stations. Samples were washed and sieved through a 0.5 mm mesh; the remaining fraction was fixed in 4% buffered formalin and stained with Rose Bengal. In the laboratory, macrozoobenthic fauna was sorted, identified to species level (except oligochaetes) and counted using a binocular microscope. As intertidal and subtidal areas are not equal in the estuarine zone considered (10 and 90%, respectively), abundances were balanced by the relative percentage of intertidal and subtidal areas and expressed as number of individuals per m^2 .

2.2.3. Zooplankton sampling

As the copepods *Eurytemora affinis*, *Acartia bifilosa*, and *Acartia tonsa* and the mysids *Neomysis integer* and *Mesopodopsis slabberi* accounted for the majority of zooplanktonic abundance (>90%) in the oligo-mesohaline zone of the Gironde estuary, they were selected as target species (David et al., 2005). Samples were collected during monthly cruises at different locations along the estuary (Fig. 1). During each survey, three stations were regularly sampled ten months per year (January and March to November): station K (off Lamarque), station E (off St-Estèphe) and station F (off St-Christoly) (Fig. 1). Sampling was carried out at 3 h intervals during the tidal cycle and at two levels (1 m below the surface and 1 m above the bottom). From each depth, zooplankton was collected with a standard WP-2 net equipped with a $200 \mu\text{m}$ mesh. The catch was preserved and fixed in buffered 5% seawater-formaldehyde solution until identification and analyses. Abundances were expressed as numbers of individuals per m^3 based on average value of the surface and bottom samples over the tidal cycle of the three stations.

2.3. Environmental data

Environmental factors (temperature, salinity, suspended particle matter [SPM] concentration and chlorophyll *a* [Chl *a*] concentration) were measured at each tidal state and each depth 10 months a year (January and March–November during the SOMLIT surveys) from 1979. Water temperature and salinity were measured with a Valeport MK 108. SPM concentrations (mg l^{-1}) were analysed gravimetrically according to conventional oceanographic techniques: estuarine water samples were collected using Niskin bottles and 50–500 ml were filtered through GF/F Whatman filters. After filtration, filters were immediately dried at 60°C and stored until analysis. SPM concentrations were determined as weight differences before and after filtration. Chlorophyll *a* content

($\mu\text{g l}^{-1}$) was measured by spectrometry and was used as a proxy for phytoplankton biomass. In addition, flow data from the Bordeaux Harbour Authorities were used.

2.4. Data selection and analysis

The main goal of this study was to provide a comprehensive overview of the present seasonal dynamics of the main biological compartments of the estuarine food web of the Gironde. We thus focussed on data collected in the oligo-mesohaline area between 2004 and 2008, corresponding to the location and period with the most recent available data for each component. Large fish were the exception and for them we took data from January 1998 to December 2000 since the 'Sturat' surveys stopped in 2000. During these periods, sampling protocols were standardized and we assumed that time intervals were sufficiently short for no major changes in biological dynamics to have occurred (David et al., 2005; Henderson and Bird, 2010; Henderson et al., 2011).

As we focussed on main dynamics, we selected only the most representative species for each compartment. Concerning 'Transect' data, we only took into account dominant small fish and shrimp species that occurred in more than 50% of the samples and with an abundance $>2 \text{ ind. } 1000 \text{ m}^{-3}$. In the same way, only species with an occurrence $>50\%$ and a mean abundance $>1 \text{ ind. } 100,000 \text{ m}^{-2}$ were considered in the 'Sturat' data. For macrozoobenthos, only species with an occurrence $>50\%$ and a mean abundance $>5 \text{ ind. m}^{-2}$ were considered. Thus, only 9 macrozoobenthic species (of the 47 species represented in the database) remained and were included in the analyses. Due to their low abundance, crabs were not considered. A preliminary procedure was carried out in order to group sympatric fish and macrozoobenthos species with the same temporal pattern (*Alosa alosa* and *Alosa fallax* called *Alosa* spp.; *Bathyporeia pilosa*, *Gammarus salinus* and *Gammarus zaddachi* called *Bathyporeia + Gammarus*). Finally, we considered the 5 main zooplankton species (*Eurytemora affinis*, *Acartia bifilosa*, *Acartia tonsa*, *Neomysis integer*, *Mesopodopsis slabberi*; Castel, 1993) in our analyses.

The database analysed was composed of monthly values of environmental factors (temperature, salinity, river flow, SPM) and biological factors (phytoplankton biomass (Chl *a* concentrations), abundance and/or biomass of zooplankton, macrozoobenthos, shrimp and fish species). Canonical correspondence analysis (CCA) was performed in order to assess environmental influences on biological components. Square-root transformation was applied to species abundances and Monte Carlo permutations were used to test the significance of analysis. Ascendant Hierarchical Clustering analysis (AHC) was performed to group species according to their temporal dynamics. The aggregation criterion used was Ward's criterion. Multivariate analyses were performed with R software (R Development Core Team, 2005).

3. Results

3.1. Environmental conditions

All selected environmental variables showed classical seasonal variations (Fig. 2). Highest water temperature was observed in summer months (from June to September) with a maximum of $22.3 \pm 0.2^\circ\text{C}$ in July and the lowest values during winter with a minimum of $7.7 \pm 0.2^\circ\text{C}$ in January. Salinity and river flow showed inverse variations. Low salinities were observed between January and May (minimum average value = 5.4 ± 0.9 in May) when river flow was highest ($>1000 \text{ m}^3 \text{ s}^{-1}$) while high salinities were observed in summer and autumn when river flows were low. SPM showed a seasonal pattern with lowest concentrations

between January and July (around 500 mg l^{-1}) and high concentrations from August to November (around 1200 mg l^{-1}).

3.2. Seasonal dynamics of biological components

3.2.1. Phytoplankton biomass

Chlorophyll *a* concentrations ranged from $1.5 \pm 0.2 \text{ }\mu\text{g l}^{-1}$ in January to $6.0 \pm 1.5 \text{ }\mu\text{g l}^{-1}$ in August with two peaks, one in spring ($5.3 \pm 0.9 \text{ }\mu\text{g l}^{-1}$) and another in summer ($6.0 \pm 1.5 \text{ }\mu\text{g l}^{-1}$).

3.2.2. Zooplankton

Zooplankton abundance showed strong intra-annual changes (Fig. 3). *Eurytemora affinis* was the most abundant zooplanktonic species throughout the year with a minimum average abundance $>3400 \text{ ind. m}^{-3}$ in January. Very high abundances of *E. affinis* occurred in spring (24,005 ind. m^{-3} in March) with decreasing values until summer and autumn. *Acartia* showed a clear successional pattern, with *Acartia bifilosa* occurring essentially during June and July with a peak of abundance in June (699 ind. m^{-3}) and *Acartia tonsa* being more abundant from August to October with a peak of abundance in September (6631 ind. m^{-3}). Mysids *Mesopodopsis slabberi* and *Neomysis integer* were mainly present from April to October, with a maximum abundance in summer (120 ind. m^{-3} in July for *M. slabberi* and 367 ind. m^{-3} in June for *N. integer*).

3.2.3. Macrozoobenthos

Oligochaetes were by far the most abundant benthic taxa in the Gironde estuary throughout the year with abundance $>400 \text{ ind. m}^{-2}$ (Fig. 4). Abundances of the amphipod *Corophium volutator* (intertidal), the polychaete *Streblospio shrubslii* and the gastropod *Hydrobia ulvae* (intertidal) showed marked seasonal changes with a peak in September ($>5000 \text{ ind. m}^{-2}$, $>300 \text{ ind. m}^{-2}$ and $>80 \text{ ind. m}^{-2}$ respectively, Fig. 4). The polychaete *Heteromastus filiformis* and the amphipods *Bathyporeia pilosa + Gammarus* spp. were more abundant in spring and/or early summer (April–July) with mean densities of 139 and 21 ind. m^{-2} , respectively, whereas the polychaete *Hediste diversicolor* was more abundant in summer and autumn (August–November). In contrast, the isopod *Cyathura carinata* and the bivalve *Scrobicularia plana* were abundant only during winter months (October–February, Fig. 4) with a peak in density of 178 ind. m^{-2} and 147 ind. m^{-2} respectively in October.

3.2.4. Shrimps

White shrimps *Palaemon* spp. were more abundant from August to December while the brown shrimp *Crangon crangon* showed marked seasonal changes with peak densities ($>45 \text{ ind. } 1000 \text{ m}^{-3}$) occurring in warm months (July and August). For both shrimp species biomass fluctuations paralleled those of abundance, with a biomass peak of $27.2 \text{ g } 1000 \text{ m}^{-3}$ and $7.8 \text{ g } 1000 \text{ m}^{-3}$ for *Palaemon* spp. and *C. crangon*, respectively (Fig. 5).

3.2.5. Fishes

Although 65 fish species were collected during the study period, only 12 were considered in the analysis. Small pelagic fish species showed marked seasonal variations in abundances with different dates of abundance peaks (Fig. 6). While *Sprattus sprattus* occurred essentially during late spring–early summer (May–June) with densities of ca. 10 ind. 1000 m^{-3} , the abundance peak of anchovy *Engraulis encrasicolus* occurred later, in August–September ($>40 \text{ ind. } 1000 \text{ m}^{-3}$). Regarding other small fish, abundances of *Syngnathus acus* and *Pomatoschistus* spp. showed clear intra-annual changes, with peaks in August (71.7 and 193.3 ind. m^{-3} , respectively; Fig. 6). Variability in fish biomass paralleled that of

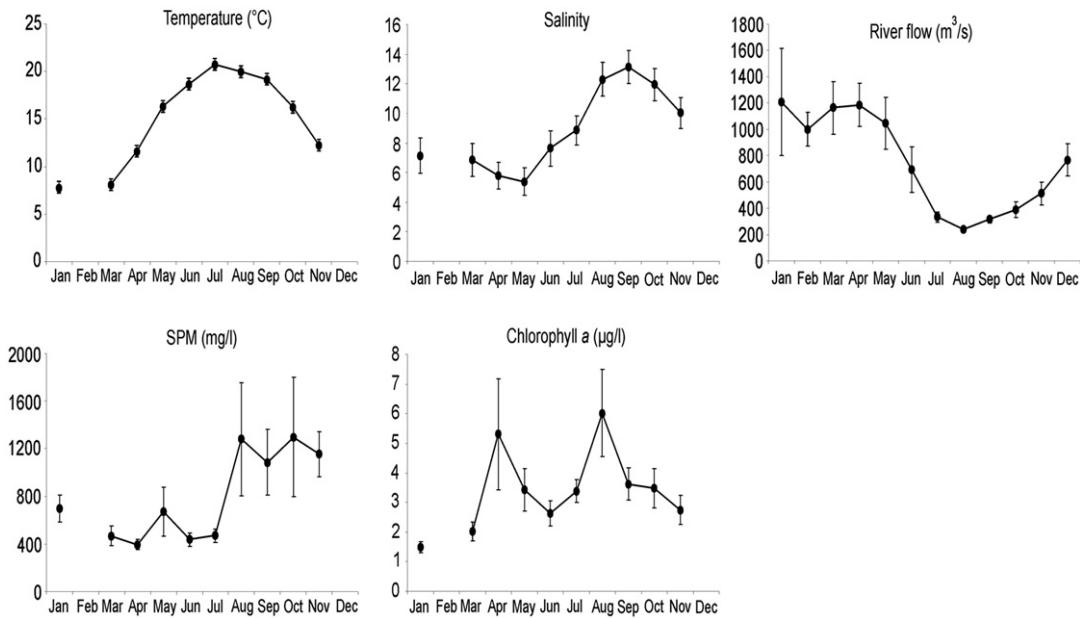


Fig. 2. Mean monthly variations of environmental variables in the Gironde estuary averaged for 2004–2008. Vertical bars indicate standard errors of the means.

abundance for most species, with however a delay of one month in the peak of biomass for *E. encrasicolus* (15.8 g 1000 m⁻³) and *S. acus* (16.2 g 1000 m⁻³) (Fig. 6), reflecting individual growth. *S. sprattus* showed a second peak of biomass which was not observed for abundance.

Concerning larger fish (Fig. 7), *Alosa* spp. showed important seasonal changes and were more abundant during winter months (December–February) with ca. 10 ind. 100,000 m⁻². There was a considerable difference in the timing between the biomass and density peaks for *Alosa* spp. with biomass peaks in May (276.1 g 100,000 m⁻²) and September (363.6 g 100,000 m⁻²; Fig. 6). The most abundant fish species on an annual scale, *Liza ramada*, also showed higher densities between December and February (>200–300 ind. 100,000 m⁻²) and also in April (Fig. 7). Cooler months were also marked by the presence of *Merlangius merlangus* with a peak of density occurring in February (Fig. 7). Abundances of

Argyrosomus regius showed clear intra-annual changes with peaks occurring in August (86.0 ind. 100,000 m⁻²), whereas densities of *Dicentrarchus labrax* decreased steadily until August, followed by a peak (10.2 ind. 100,000 m⁻²) in September (Fig. 7). The biomass of *D. labrax* paralleled abundance, although with a delay of one month (2778.1 g 100,000 m⁻² in October) (Fig. 7), and peaked again in July which was not the case for abundance. On the other hand, *Solea solea* was present throughout the year with abundances ranging from 0.3 ind. 100,000 m⁻² in December to 39.6 ind. 100,000 m⁻² in September. These flatfishes displayed higher (but variable) abundances and biomass during the summer and autumn months. *Anguilla anguilla* and the flatfish *Platichthys flesus*, however, showed no clear temporal pattern, with considerable variability in their abundances from month to month. Both species occurred throughout the year with abundances ranging from 15.1 ind. 100,000 m⁻² in August to 64.9 ind. 100,000 m⁻² in

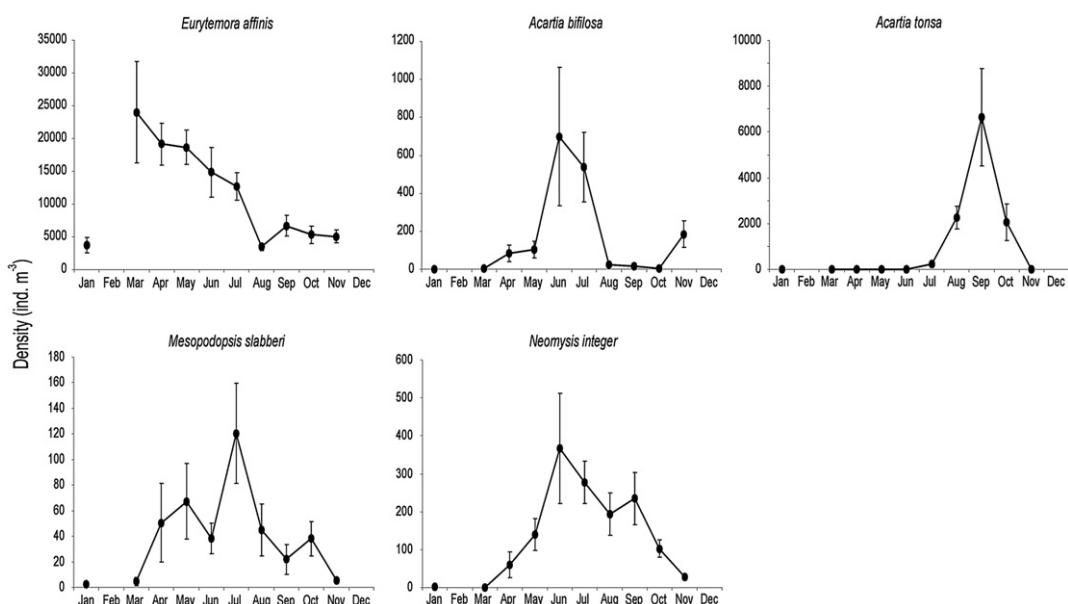


Fig. 3. Mean (\pm SE) monthly abundance (ind. m⁻³) of zooplanktonic species averaged for 2004–2008.

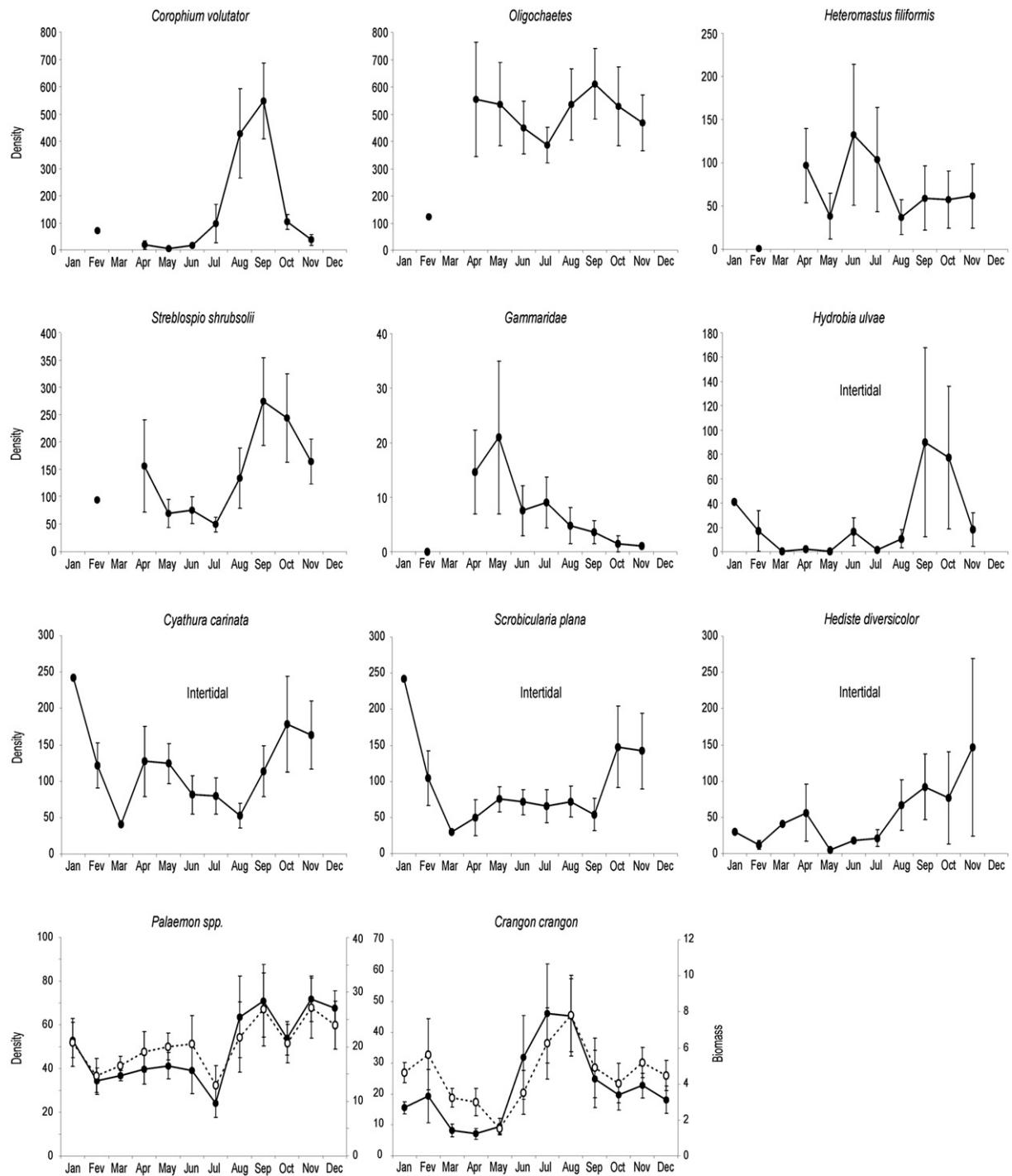


Fig. 4. Mean (\pm SE) monthly abundance (ind. m^{-2}) of macrozoobenthic species averaged for 2004–2008. For species exclusively collected and abundant in the intertidal zone, mean abundance was calculated only with intertidal samples. For other species mean was calculated with both subtidal and intertidal samples, taking into account a ratio subtidal:intertidal area 9:1.

May for *P. flesus* and from 0.4 ind. $100,000\ m^{-2}$ in August to 6.9 ind. $100,000\ m^{-2}$ in July for *A. anguilla* (Fig. 7).

3.3. Species associations and relation with environmental variables

The seasonal changes in the abundance of phyto- and zooplanktonic, macrozoobenthic, shrimps and fish species and their relationships with environmental variables were analysed using multivariate analyses. The ascendant hierarchical clustering (AHC) showed a division into four distinct groups of species

according to their seasonal abundance. Cluster 1 was associated with spring months and was composed of phytoplankton, *Eurytemora affinis*, *Acartia bifilosa*, *Mesopodopsis slabberi*, *Bathyporeia + Gammarus*, *Heteromastus filiformis*, *Sprattus sprattus*, *Platichthys flesus* and *Anguilla anguilla*. Cluster 2, associated with summer months, was composed of *Neomysis integer*, *Corophium volutator*, *Crangon crangon*, *Argyrosomus regius*, *Syngnathus acus*, *Pomatoschistus* spp., *Engraulis encrasicolus* and *Solea solea*. Cluster 3, associated with late autumn, was composed of *Cyathura carinata*, *Scrobicularia plana* and *Merlangius merlangus*. Cluster 4, associated

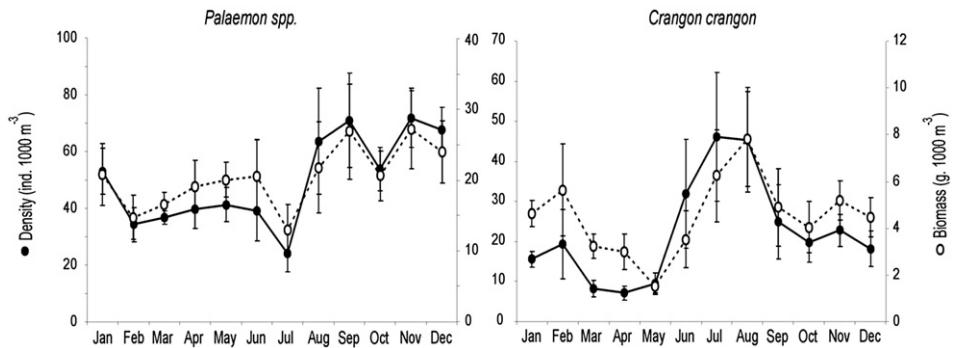


Fig. 5. Mean (\pm SE) monthly abundance (full line, ind. m^{-3}) and biomass (hatched line, g $1000 m^{-3}$) of shrimps averaged for 2004–2008.

with autumn months, was composed of *Acartia tonsa*, *Hydrobia ulvae*, *Streblospio shrubsolii*, *Hediste diversicolor*, *Palaemon* spp., *Dicentrarchus labrax* and *Alosa* spp. (reported in Fig. 8).

The CCA analysis indicated that the environmental variables measured (temperature, salinity, SPM and flow) significantly explained 25.5% of the species abundance variations in the Gironde estuary. Axes 1 and 2 accounted for 71.8% of the variability explained (Fig. 8). Considering their vector length and correlation with axes, salinity (best correlated with axis 1, $r = 0.97$) and temperature (best correlated with axis 2, $r = -0.81$) are the most important environmental variables influencing the species seasonal variations (Fig. 8). Group 1 species are more abundant during months of low salinity and high flow, Groups 3 and 4 species are more abundant during months of low temperature and either intermediate or high salinity, respectively, whereas both temperature and salinity have a positive effect on Group 2 species (Fig. 8).

4. Discussion

4.1. Relevance of biological data

In the Gironde estuary, numerous studies have described the structure and spatio-temporal variability of biotic compartments considered separately (e.g. Santos et al., 1996 for meiofauna; David et al., 2005 for zooplankton; Lobry et al., 2003, 2006 for fish; Béguer

et al., 2010 for white shrimp), as well as the trophic interactions between a small number of trophic levels (e.g. David et al., 2006; Lobry et al., 2008; Pasquaud et al., 2010). However, studies on the biological groups considered here have never been conducted until now, partly because of the lack of any recent long-term survey of the macrozoobenthic communities. Therefore, using the present analysis, based on a five-year period (2004–2008, except for large fishes) and monthly sampling, it is possible for the first time to characterize and synthesize the comparative dynamics of representative biological components of the Gironde estuary: plankton (both zooplankton and phytoplankton, described by Chl a), macrozoobenthos, shrimps and fish. In addition, environmental data for this study were gathered simultaneously.

From available data on these biological groups, the present paper also identifies data gaps and emphasizes the need to improve knowledge about specific groups or parts of the estuary. Sampling of the main biotic groups in the Gironde estuary is restricted to the oligo-mesohaline area. Whereas investigations are conducted on large fish throughout the estuary (from Blaye to Royan) during 'Sturat' surveys, very few data exist on small fish and shrimps ('Transect' surveys), or on zooplankton and benthos in the polyhaline sector; these were therefore not considered in the present study. Thus our conclusions cannot be extrapolated to the entire estuary or must be given careful consideration even if ongoing studies indicate that polyhaline communities do not differ strongly

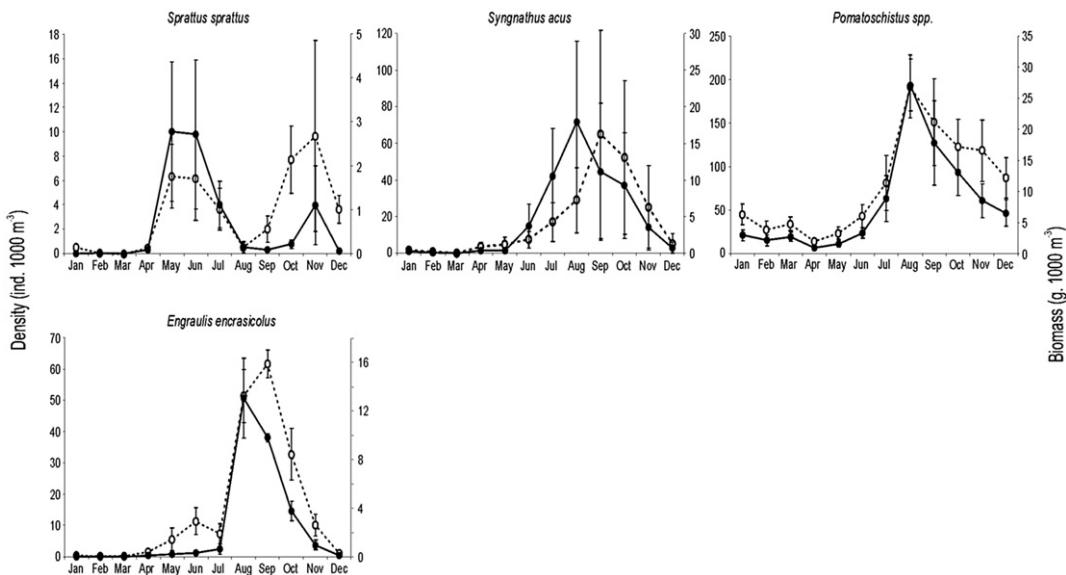


Fig. 6. Mean (\pm SE) monthly abundance (full line, ind. $1000 m^{-3}$) and biomass (hatched line, g $1000 m^{-3}$) of small fish species averaged for 2004–2008.

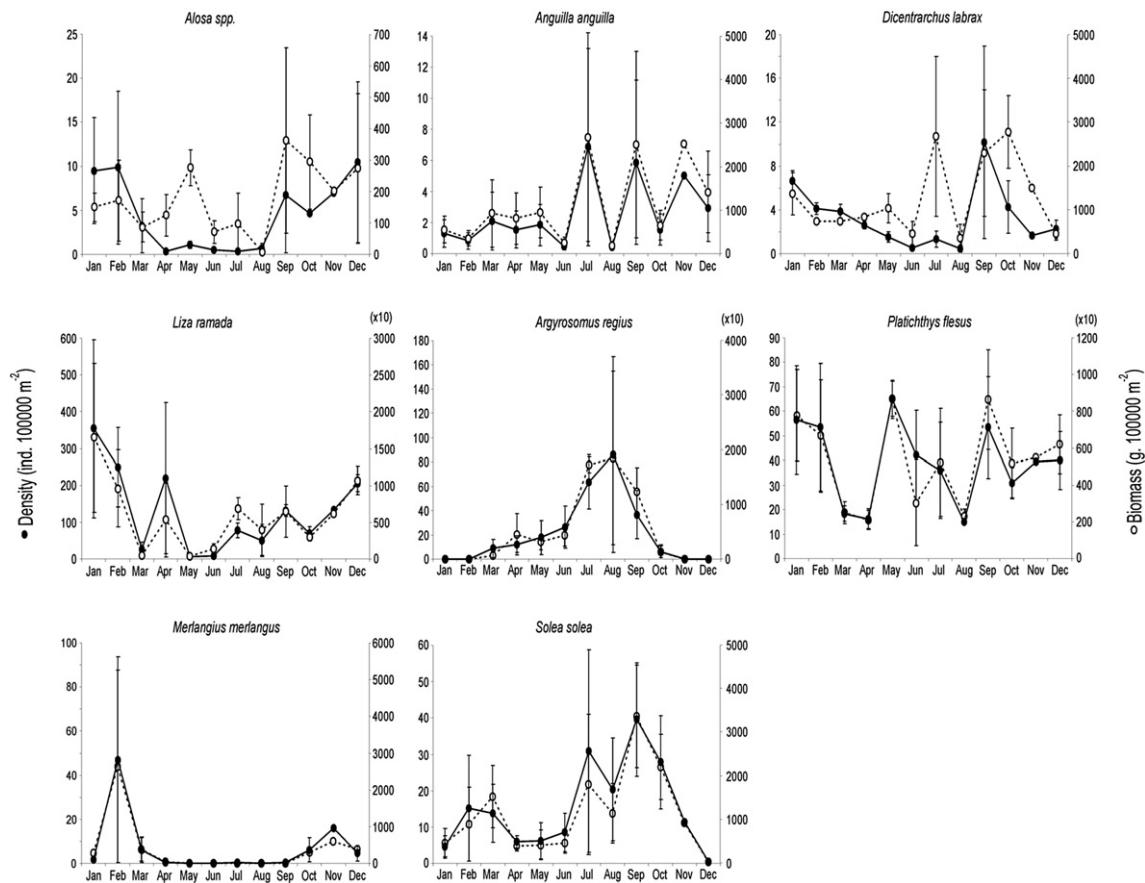


Fig. 7. Mean (\pm SE) monthly abundance (full line, ind. $100,000\text{ m}^{-2}$) and biomass (hatched line, g $100,000\text{ m}^{-2}$) of large fish species averaged for 1998–2000.

from those in the oligo-mesohaline area; this is the case at least for fish and shrimps (Ifremer, unpublished data). Regarding zooplankton and macrozoobenthos, winter data are lacking because long-term monitoring is usually from April to November. Four months (December–March) were therefore deleted from the database since, values were missing for at least one of the species considered, resulting in a lack of information (see for example Selleslagh and Amara, 2008b) in the global multivariate analysis. Nevertheless, the seasonal pattern highlighted by the analysis is ecologically significant as the period considered in the analysis represents the most productive period in the Gironde estuary (Sautour and Castel, 1995). Furthermore, results are consistent with previous results (e.g. Lobry et al., 2006 for fish and David et al., 2005 for zooplankton). Investigations on large fishes were conducted throughout the estuary during 'Sturat' surveys, including the polynhaline sector, until 2000; we therefore used the three most recent years (1998–2000) to estimate and analyse the temporal dynamics of large fish in the oligo-mesohaline area of the Gironde estuary.

While the selectivity of the sampling gears used in this study is perhaps not well adapted to all fish species (for instance, the selectivity of otter trawl for benthic/epibenthic species such as *Anguilla anguilla*, *Platichthys flesus* and *Solea solea* is sometimes questioned; Lobry, 2004), the use of different sampling methods (trawling and transect) that overlap in terms of selectivity allows for a good description of the fish composition and abundance, as recommended by several authors (e.g. Whitfield and Marais, 1999; Selleslagh and Amara, 2008b). The present study is based on the largest biological database available for the Gironde estuary, including investigation of the most important biological groups at

monthly intervals, data which are rather scarce in other French and European estuaries. Furthermore, it focussed on a period for which the different protocols (gears, number of stations, sampling frequency, etc.) were well standardized.

4.2. Composition, temporal dynamics and relation with environment

The small number of abundant species occupying the Gironde estuary (i.e. twelve fish and 9 macrozoobenthos dominant species against a total of 65 and 47 species, respectively) was attributed to the wide variation in annual water temperature (about 15°C), as reported by Lazzari et al. (1999) in temperate regions. The composition and dynamics of fish, as well as of their potential prey, emphasized the feeding, residence, migratory and nursery functions of the Gironde estuary (Rochard et al., 2001; Lobry et al., 2006; Pasquaud et al., 2010). In the present study, most species use the estuary during the spring and summer, providing evidence that many marine species use it as a transitory key habitat (Gili, 2002) and in particular as a nursery habitat for fish. This is true in other shallow water systems for Clupeidae, flatfish and bass (Beyst et al., 2001; Selleslagh and Amara, 2008b; Henderson and Bird, 2010) or mysids (Hamerlynck and Mees, 1991). During the settlement period, which has been related to the timing of spawning and the planktonic phase (DeMartini, 1999) a sharp decrease in abundances was observed for many species. This may be the result of a variety of factors, including response to declining temperature (Clark et al., 1996; Beyst et al., 2001), movements

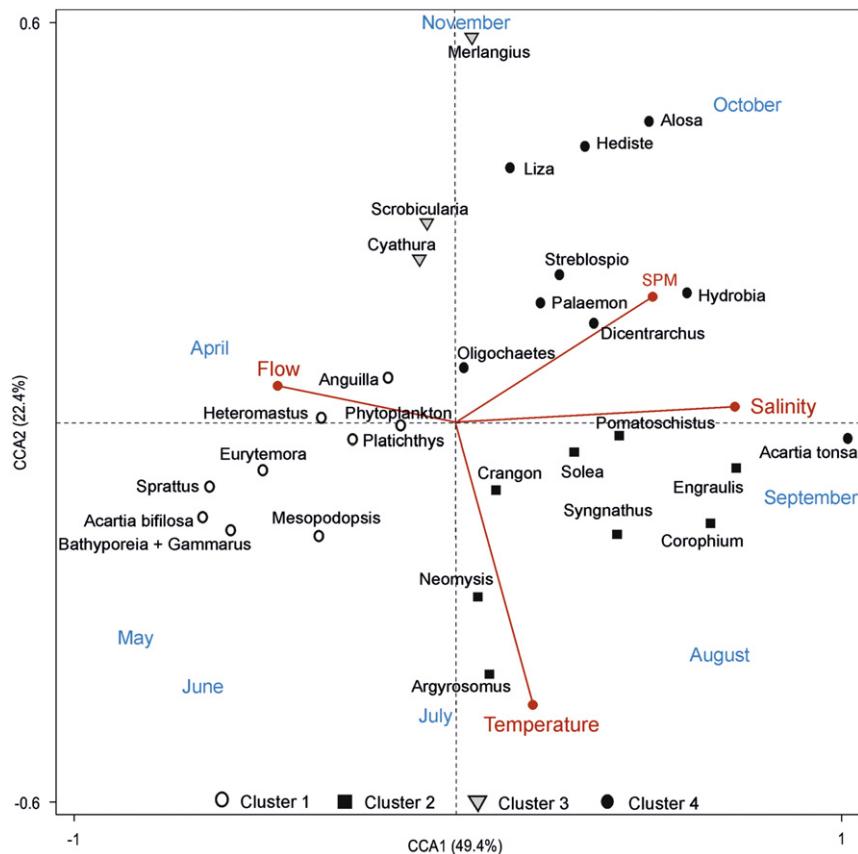


Fig. 8. CCA ordination diagram based on species abundances, with environmental parameters represented by vectors.

between feeding grounds, the need to leave the estuary to breed or predation (Henderson and Bird, 2010).

Temporal fluctuations in biological communities were particularly marked and show a discrimination of species into four seasonal groups. This seasonal pattern is characteristic of estuarine or coastal species and has been observed in many other temperate systems for different biological compartments (e.g. Ross et al., 1987; Clark et al., 1996; Maes et al., 1998; Ramos et al., 2006; Modérán et al., 2010). From an ecological point of view, two distinctive ecological seasons can be discriminated. Results show a clear shift occurring in July, indicating a biomass transfer from a "planktonic phase" to a "benthic-demersal phase" with the former distinguished by very high densities of plankton, in particular the copepod *Eurytemora affinis*. This planktonic phase is characterized by the arrival of sprat *Sprattus sprattus* juveniles, the growth of *Alosa* spp. and the development of mysid populations, and corresponds overall to low densities of macrozoobenthos and fish. After July, corresponding to maximal temperature, the transition to high salinities and the beginning of a period of maximum turbidity, plankton decreases sharply while benthic and demersal species grow, particularly in September–October. This second phase is characterized by the recruitment and development of numerous macrozoobenthic species, the growth of *Palaemon* spp. and higher densities of *Crangon crangon*. This period also corresponds to an increase in *Pomatoschistus* spp., *Syngnathus acus*, *Dicentrarchus labrax*, *Solea solea*, *Engraulis encrasicolus* and *Argyrosomus regius* abundances. Between the two phases, a transition period may be identified, characterized by the absence or low density of the main species and a noticeable abundance of species such as *Merlangius merlangus* or *Liza ramada*; corresponding to the poorly documented

"winter period" from November to March. Shrimps, *Platichthys flesus*, *L. ramada* and, to a lesser extent, *D. labrax* are still abundant in this transition period. This is consistent with previous studies which suggested a benthic pattern of trophic interactions in winter (Lobry et al., 2006; Pasquaud et al., 2010). The hypothesis of two different trophic flow structures during the year needs to be explored more deeply by constructing and comparing seasonal food web models, as suggested by Lobry et al. (2008). In this way, by providing important elements on biological dynamics, the present study not only provides a better understanding of the functioning of the Gironde estuary but also lays the foundations for seasonal trophic modelling of this kind.

In shallow habitats, temperature and salinity are often considered to control the seasonal patterns of species occurrence (e.g. Thiel et al., 1995; David et al., 2005, among others). Results from the present study indicated these two parameters as the most structuring variables of temporal distribution of phytoplankton, zooplankton, macrozoobenthos, shrimps and fish species. According to CCA, *Eurytemora affinis* was positively correlated with river flow and negatively with salinity. This is in accordance with David et al. (2005) who explained that it results from its seasonal cycle and ecological requirements, with maxima occurring in winter–early spring, corresponding to periods of high river flow. In agreement with other authors, mysids *Mesopodopsis slabberi* and *Neomysis integer* showed positive correlations with temperature (Sorbe, 1981; David et al., 2005). The same trend was observed for other species, i.e. *Crangon crangon*, *Argyrosomus regius* and *Syngnathus acus*, in other marine or estuarine ecosystems (e.g. Quéro and Vayne, 1987; Beyst et al., 2001; Selleslagh and Amara, 2007, 2008a). Phytoplankton, *E. affinis* and *M. slabberi* were clustered

together; this agrees with the common view that chlorophyll *a* influences the use of estuaries by copepods and mysids (Gasparini and Castel, 1997; David et al., 2005). SPM has been identified as a structuring variable for species seasonal variations, in particular for zooplankton (David et al., 2005). In the present study, *Acartia tonsa* was correlated with SPM, as reported by David et al. (2005). High turbidities (high SPM) affect its survival by limiting selective feeding (Gasparini and Castel, 1997). Regarding macrozoobenthos, species variations and abundances are indicative of main recruitment periods, which accords with previous works on benthic population dynamics (Bachelet, 1981; Bachelet and Yacine-Kassab, 1987).

Results indicated that the main temporal changes in the structure and density of fish, macrozoobenthos, shrimps and phyto- and zooplankton reflect the different times of recruitment of species and their relations with physico-chemical variables, but also to other variables with regard to the high unexplained variability. The CCA analysis indicated that measured environmental variables (temperature, salinity, SPM and river flow) explained 25.5% of the species abundance variations in the Gironde estuary. The great majority of papers dealing with the seasonal variability of fauna almost exclusively integrated physico-chemical factors, leading to poorly explained relationships ($\pm 20\%$ as in the present case) and they suggested other predictors, such as predation or competition (e.g. Marshall and Elliott, 1998). David et al. (2005) showed that the summer decrease in the copepod *Eurytemora affinis* is controlled by a combined effect of temperature and predation. Similarly, Selleslagh and Amara (2008b) showed that biotic variables (potential predators or preys for fish) have an additional influence to abiotic variables on fish abundances in the Canche estuary. In addition, studies dealing with seasonal variability of fauna were based on specific species or assemblages, yet understanding species variability requires knowledge of the dynamics of other species because of biological interactions (Monaco and Ulanowicz, 1997).

4.3. Influence of trophic interactions

Describing seasonal dynamics from primary producers to top predators gives a better understanding of estuarine functioning and a first overview of the dynamics of trophic interactions between species in the estuary. Sharp decreases following abundance peaks, seasonal successions of species with trophic similarities, coincidence between the increase of one species and the decline of another or parallel patterns observed between species suggest trophic implications such as mortality due to predation or competition.

In the Gironde estuary, high secondary production explains the occurrence during the same period of many fish species, especially those using estuaries as a nursery area (Lobry et al., 2006, 2008). Copepods, in particular *Eurytemora affinis*, play a significant role in estuarine food webs as an important food supply for many fishes, shrimps and mysids (Sorbe, 1983; Fockedey and Mees, 1999; Lobry et al., 2008; Pasquaud et al., 2008). In the present study, *E. affinis* showed maximum densities from March to May and then decreased in summer. Probably in relation to this, *Neomysis integer* also showed maximum densities during June, one month later, suggesting predation by *N. integer* on copepods, with a possible food limitation (David et al., 2006). *N. integer* is known to control the copepod biomass in some estuarine ecosystems (Roff et al., 1988; Irvine et al., 1995) and *E. affinis* is known to be the main prey in the diet of *N. integer*, as shown by stomach content analysis (Fockedey and Mees, 1999) or laboratory experiments (Winkler and Greve, 2004). Recently, David et al. (2005) related the seasonal variation of *N. integer* to the temporal distribution of copepods in the Gironde, which was verified thereafter by David et al. (2006)

using a prey–predator model. In addition, the mysid *N. integer* can constitute an important prey for fish, demersal fishes in particular. *Argyrosomus regius*, the largest demersal fish in the Gironde estuary, feeds on hyperbenthic species: *Crangon crangon* and *Pomatoschistus* spp. and a large proportion of mysids (Pasquaud et al., 2008, 2010). These trophic interactions are observed in multivariate analysis where *N. integer*, *C. crangon* and *A. regius* showed a similar trend and were grouped together. The seasonal dynamics of the meagre could thus explain the decrease in density of both *N. integer* and *C. crangon* in summer due to predation. It is also likely that the migration of *A. regius* to marine waters in late summer explains the peak in abundance of *Pomatoschistus* spp. one month later because of limited predation. In the same way, the seasonal pattern of *Sprattus sprattus* in relation to *E. affinis* and *Acartia bifilosa*, *Dicentrarchus labrax* in relation to *Palaemon* spp., and *Engraulis encrasicolus*, in relation to *Acartia tonsa*, can be partially explained.

Flatfishes are known to prey upon epibenthic species, especially polychaetes, which influence their distribution and migration behaviour in shallow water areas (Gibson, 1994; Vinagre et al., 2006; Nicolas et al., 2007). In the Vilaine estuary, Nicolas et al. (2007) reported that the density of juvenile sole was positively affected by the benthic invertebrate biomass. Although *Solea solea* and *Platichthys flesus* consume polychaetes, benthic isopods and shrimps in the Gironde estuary (Pasquaud et al., 2008), such interactions were not suggested by the present study. Conversely, although a high correlation was observed between *S. solea* and the benthic amphipod *Corophium volutator*, a common prey of *S. solea* (Nicolas et al., 2007; Vinagre et al., 2008), few individuals were retrieved from fish stomachs by Pasquaud et al. (2008).

Competition seems possible for species which exhibit a specialist feeding strategy in the case of food limitation (Pasquaud et al., 2010) and it can play a determining role in temporal partitioning in estuarine fish (Henderson and Holmes, 1991; Ogburn-Matthews and Allen, 1993). The present results presume such a trophic partitioning for the small pelagic fish *Sprattus sprattus* and *Engraulis encrasicolus*, which are both known to be zooplanktivores (Pasquaud et al., 2008, 2010). These findings agree with Henderson and Holmes (1991), who reported that the differing occupancy of flatfishes in the lower Severn estuary reduced potential inter-specific competition. Due to different assemblages of prey consumed by fish (Pasquaud et al., 2008) and a recognized degree of plasticity in prey item choice, inter-specific competition for food appears relatively limited in the Gironde. Pasquaud et al. (2008) suggested a considerable sharing of resources which would limit inter-specific competition for access to food resources. Several studies have shown that prey are generally not a limiting resource in estuaries (Lobry et al., 2008; Selleslagh et al., 2012a, 2012b), discarding the trophic competition hypothesis. The life cycle of *S. sprattus* and *E. encrasicolus*, which have different spawning periods, is probably the reason for the time-lag observed between these two species rather than a competitive partitioning of resources, considering the very high abundance of copepods in the Gironde estuary. Furthermore, *S. sprattus* and *E. encrasicolus* display different feeding strategies, which could narrow diet overlap, minimize inter-specific competition and allow the co-occurrence of species (Pasquaud et al., 2010). Although trophic competition seems relatively low regarding these concerns, this process needs to be explored further since the 'seasonal trophic bottleneck' seems to be a non negligible phenomenon controlling estuarine dynamic patterns.

Taking all these considerations into account, the present study shows that the temporal variability of estuarine species is predominantly influenced by physico-chemical variables and trophic interactions, most notably predation. In future, it will be

interesting to carry out further analysis of dependence of the species seasonal dynamic on prey (or conversely on predators) fitting predator–prey models, especially between mysids and the meagre *Argyrosomus regius*.

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